

THE FOSSIL HIPPOPOTAMIDAE OF ASIA, WITH NOTES ON THE RECENT SPECIES

by

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with pls. I-XXII and 5 figs.

Quant aux naturalistes qui reconnaissent que les variétés sont restreintes dans certaines limites fixées par la nature, il faut, pour leur répondre, examiner jusqu'où s'étendent ces limites, recherche curieuse, fort intéressante...

CUVIER, G., Discours sur les révolutions de la surface du globe, 3rd ed., Paris, 1825, p. 118.

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INTRODUCTION

The study of extinct animals requires the knowledge of the anatomy of more or less closely comparable recent species of which sufficient material is available to check the individual variation. For the fossil Hippopotamidae of Asia we have in *Hippopotamus amphibius* L. a species in which the variation has been studied since the days of Cuvier. Various specific names have been given to the forms now or formerly inhabiting different regions in Africa, but in the opinion of modern authors they represent only geographical subspecies. The study of the literature and that of a series of 34 skulls convinced me that the supposed differential characters do not occur constantly in skulls from a special region in Africa. These characters are found in every combination, without preference to a special locality. And this is not to be wondered at, since the "races" have been created mostly on single specimens and not on series. Be this as it may, the material examined gave me a good idea of the amount of variation to be found within a species of *Hippopotamus*, the fossil Asiatic representatives of which form the main subject of the present paper.

The following is a brief survey of the literature.

In 1820 the Muséum National d'Histoire Naturelle at Paris received an adult male skeleton of *Hippopotamus amphibius* L., from an animal shot by Delalande at the lower Berg river, forty miles from Cape Town. It was the first complete skeleton of this species that arrived in Europe. Cuvier had been in want for this material for a long time. In 1804 (Cuvier, 1804 b) he had published on fossil remains of hippopotamuses, a large form from the Val d'Arno in Italy¹), and a pigmy species of which the origin was unknown to him²). For comparison Cuvier had at his disposal only the skeleton of a foetus described and figured earlier in that year (Cuvier, 1804 a). The adult Cape skeleton was adequately described and figured in the "Ossemens fossiles" (Cuvier, 1821).

Two years afterwards a second skeleton of *H. amphibius*, from Senegal, was acquired by the Paris Museum. It was fully adult as shown by the well worn M³; in the Cape specimen only the anterior cusps of M³ were worn. The differences between the two specimens induced Desmoulins (1825 a, p. 222) to refer them to two distinct species which were named *H. capensis*

1) *Hippopotamus amphibius antiquus* Desmarest (= *H. major* Cuvier auct.). See Hooijer, 1942 a; the remains did not originate from Montpellier too, as I stated in that paper, but were only supposed to come from that locality.

2) This form turned out to be the pigmy species from the Pleistocene of Cyprus, *Hippopotamus minor* Desmarest (= *H. minutus* Cuvier auct.). See Hooijer, 1946, p. 303/304.

and *H. senegalensis* respectively. In the opinion of Desmoulins the hippopotamus from the typical locality, the Nile, might represent a third species. Lesson proposed the name *Hippopotamus abyssinicus* for the Abyssinian form in 1842, but this is a nomen nudum (fide Lydekker, 1915, p. 387).

In 1846 Duvernoy compared Delalande's Cape skeleton with two skeletons from Senegal and one from Abyssinia. It is certain that Desmoulins' Senegal specimen was not re-examined by Duvernoy, for in the Senegal specimens seen by the latter author M³ was worn only at the anterior cusps. In the Abyssinian skull M³ was not yet fully in place. Duvernoy agreed with Desmoulins that the Cape form is distinct from that of Senegal. The former was distinguished by Duvernoy as *H. australis*, whilst the Senegal specimens and that from Abyssinia received the name *Hippopotamus typus*, „la même, sans doute, observée par Zerenghi dans le Nil égyptien, au commencement du XVIIe siècle" (Duvernoy, 1846 a, p. 650). Three years afterwards a skull from Natal is referred to *H. australis* by Duvernoy, who again insists on the differences between the S. African form and that from Senegal and Abyssinia.

Miller (1910) compared a hippopotamus skull from Angola, in which M³ is not fully in place, with another skull originating from the Zambesi river and with M³ worn. Since the amount of variation observed in a series of eight skulls from British East Africa was not unusually great, and the Zambesi skull agreed with the latter in all important features, the Zambesi and British East African specimens were together "assumed to represent true *H. amphibius* from the upper-Nile". The Angola skull became the type of a new species, *H. constrictus*.

According to Heller (1914), however, the British East African material is distinctive. This author is the first to use subspecific names; the E. African hippopotamus is named *Hippopotamus amphibius kiboko* (type is an adult male skull from Lake Naivasha, Kenya). The Zambesi form is referred to *H. a. capensis*, while subspecific rank is also given to *constrictus* and to the Egyptian *amphibius*.

A fifth subspecies, *Hippopotamus amphibius tschadensis*, is founded by Schwarz (1914) on an old female skull from Bornu, Nigeria. An old male skull, from the lower Schari, is referred to the latter race too (Schwarz, 1920).

To sum up, five races of *Hippopotamus amphibius* L. have been distinguished: the northern or typical race *H. a. amphibius* L., the Cape hippopotamus *H. a. capensis* Desmoulins (syn. *H. a. australis* Duvernoy), the Angola hippopotamus *H. a. constrictus* Miller, the East African hippopotamus *H. a. kiboko* Heller, and the Nigerian hippopotamus *H. a. tschadensis*

Schwarz. These names are listed in all conscience by, e.g., Lydekker (1915, pp. 389-392), Allen (1939, pp. 457-458), and Harper (1945, pp. 414-415).

A critical examination of Miller's 1910 paper brought Van der Maarel (1932, pp. 96-100) to the conclusion that *constrictus* has no right to specific distinction. Some of the cranial characters of "*australis*" (*capensis*) are dealt with too, and these are also shown to be of no value as species characters. Van der Maarel, however, not being acquainted with the literature on the East African and the Nigerian hippopotamus (Heller, 1914; Schwarz, 1914, 1920), was unaware of the fact that these names had already long been used in a subspecific sense only, and he overlooked a few papers in the older literature (Desmoulins, 1825 a, Duvernoy, 1846 a, 1849 a-c). More recently Shortridge (1934, p. 643) and Hill and Carter (1941, p. 150) stated *H. a. constrictus* to be indistinguishable from *H. a. capensis*.

In the following account it will be shown that the distinguishing characters mentioned by the above cited authors are invalid even for racial distinction. I have also checked the individual variation in characters that are much relied upon in the literature on the fossil hippopotamuses from Asia, which proved to be of great help in determining the systematic significance of these characters as affording means of distinction between the various fossil forms.

ON THE VARIATION OF HIPPOPOTAMUS AMPHIBIUS L.

The recent material listed below belongs to the collections of the Leiden Museum (fifteen skulls and a skeleton), the Zoological Museum at Amsterdam (eleven skulls and a skeleton), the Zoological Laboratory at Utrecht (two skulls and a mandible), the "Museum van het Onderwijs" at The Hague (two skulls), the "Museum van den Arbeid" at Amsterdam (one skull), and the Natural History Museum at Rotterdam (one skull). I am indebted to Prof. Dr. L. F. de Beaufort (Amsterdam), Prof. Dr. Chr. P. Raven (Utrecht), Dr. W. E. van Wijk (The Hague), Mr. H. Heyenbrock (Amsterdam) and Mr. L. P. Pouderoen (Rotterdam) for the permission to examine the material in the musea under their charge.

Skulls, sex unknown, M² erupting

1. Leiden Museum, cat. ost. k. Congo, from the Rotterdam Zoo, 1889.
2. Leiden Museum, cat. ost. l. Congo, from the Rotterdam Zoo, 1889.
3. Amsterdam Museum, labelled G. Leopoldsville, Congo, C. de Haan don., 1900.

Male skulls, M² worn

4. Leiden Museum, cat. ost. i. Zanzibar, captain Van Duin don., 1888.
5. Leiden Museum, cat. ost. o. Zambesi, A. de Haas don., 1889.
6. Complete skeleton. Leiden Museum, cat. ost. a. Nile, coll. E. Rüppell, 1827.
7. Zoological Laboratory, Utrecht, no. 1. No data.
8. Mandible. Zoological Laboratory, Utrecht, no. 3. No data.
9. "Museum van het Onderwijs", The Hague, no. 51.895. Premaxillaries lost.
10. Leiden Museum, cat. ost. b. Cabinet d'Anatomie, 1861.

Male skulls, M³ erupting

11. Leiden Museum, cat. ost. m. Inhamissengo, Mozambique, H. P. N. Muller don., 1893.
12. Leiden Museum, cat. ost. p. Caia, Portuguese East Africa, 1930.
13. Amsterdam Museum, no. 518. No data.
14. Amsterdam Museum, no. 517. Premaxillaries lost.
15. "Museum van het Onderwijs", The Hague, no. 3608. Premaxillaries lost.

Male skulls, M³ worn

16. Amsterdam Museum, no. 519. No data.
17. Amsterdam Museum, labelled Congo.
18. Leiden Museum, cat. ost. n. Inhamissengo, Mozambique, H.P.N. Muller don., 1893.
19. Leiden Museum, cat. ost. e. Cabinet d'Anatomie, 1861.
20. Right half of skull. Leiden Museum, cat. ost. j. Congo, J. G. A. Goethart don., 1889.
21. Amsterdam Museum. South Africa, of an individual named Cyrus, that lived for about 24 years in the Amsterdam Zoo.
22. Complete skeleton. Amsterdam Museum, no. 183. The individual to which the skeleton belonged lived in the Amsterdam Zoo from 1860 to 1884.
23. Amsterdam Museum, no data.
24. "Museum van den Arbeid", Amsterdam. Premaxillaries lost.
25. Natural History Museum, Rotterdam. No data.

Female skulls, M² worn

26. Leiden Museum, cat. ost. f. Cape.
27. Amsterdam Museum, from the Carp collection. Pongwe, British East Africa.

Female skulls, M³ worn

28. Leiden Museum, cat. ost. q. South Africa, H. P. N. Muller don., 1941.
29. Amsterdam Museum, no data.
30. Leiden Museum, cat. ost. d. South Africa.
31. Leiden Museum, cat. ost. h. Zanzibar, captain Van Duin don., 1888.
32. Amsterdam Museum, no. 649. Premaxillaries lost.
33. Amsterdam Museum. East Africa, of an individual that died in the Amsterdam Zoo in January 1940.
34. Zoological Laboratory, Utrecht, no. 2. No data.
35. Leiden Museum, cat. ost. c. Cabinet d'Anatomie, 1861.

The locality is recorded for 18 out of the 35 specimens. The skeleton from the Nile (no. 6) is stated by Jentink (1887, p. 166) to be the type of

Geoffroy, but I did not succeed in detecting the origin of this statement.

Skulls nos. 4 and 31 are from Zanzibar. Van der Maarel (1932, p. 97) has strong doubt as to the correctness of this record for the locality, because hippopotamuses would not occur in this island, "these being surely bound to large rivers". Van der Decken (vide Kersten, 1869, p. 70), however, states that hippopotamuses have repeatedly been observed in Zanzibar, and we find the same statement in Brehm's "Tierleben" (Strassen, 1916, p. 37) and in Joleaud (1920, p. 23).

As is true of so many Mammals, the males have bigger canines than the females. The greater diameter of the lower C varies from 38 to 49 mm in the females, and from 62 to 78 mm in the males. The males also grow to a larger size than the females. Is it more than a coincidence that the biggest skulls (nos. 21 and 22, with condylo-basal lengths of 760 and 770 mm respectively) are from individuals that lived over twenty years in a Zoo?

INCISORS. — Both in the upper and in the lower jaw of *Hippopotamus amphibius* L. normally two incisors develop on each side. The cylindrical I_1 is the largest, and its alveolus extends almost throughout the whole length of the symphysis. The I_2 is always smaller than the central lower incisor; as is evident from the measurements 1 to 6 recorded in table I the diameter of I_2 varies from 0.51 to 0.73, or from one-half to three-fourths of that of I_1 , while the depth of the alveolus of I_2 is even more variable, ranging from 0.40 to 0.75 of that of the alveolus of I_1 . The upper incisors, which are often lost in the Museum skulls, are subequal in size, more or less curved, and usually possess a longitudinal strip of enamel along the outer curve.

Desmoulins (1825 a, pp. 219-220) remarked that in *capensis* the I_2 are more curved, and the I_1 are more procumbent than in *senegalensis*. Duvernoy (1849 a, p. 684) mentions that *capensis* is characterized by its upper I being curved and deeply grooved. The latter author also remarks that the I_1 in *capensis* is bigger than that in "typus", and that in the Cape hippopotamus I_2 is shed in the adult stage, whilst it should persist in the typical form.

In the Paris Museum I have examined the type skull of *Hippopotamus amphibius capensis* Desmoulins, and also the Natal skull which was referred to the southern form by Duvernoy in 1849. In both skulls the right I_2 is missing, and there is no trace of their alveoli. The Cape skull also lacks the left lower premolars, and the right pd^1 , but the alveoli of these teeth are not closed and point to the teeth having been in place until the death of the individual. In the figures of this skull given by Cuvier (1821, Hippopotame

vivant, pls. I-II) the complete dentition is represented. Blainville (1847, Atlas, pls. I-II), however, gives other figures of the same skull in which the left I_2 is not indicated, while the alveoli of the central lower incisors, the right lower premolars, and the left pd^1 are empty. Blainville, though his figures are reversed, is evidently right in not figuring the I_1 , for the incisors that are placed in the Cape mandible are much too small for their alveoli and must have belonged to another individual. This makes it even more difficult to account for Duvernoy's statement as to the large I_1 in *capensis*. The measurements recorded in table I do not point to the South African hippopotamus having especially large I_1 , and I am unable to find distinguishing characters in the shape of the upper incisors either.

Among the specimens examined by me there are some instances of missing lower lateral incisors. Skull no. 32 lacks the left I_2 , while in skulls nos. 9 and 35 both I_2 are missing without any trace of their alveoli left. Friedlowsky (1869, p. 338 fig. IV) and Stehlin (1900, p. 434) refer to similar cases. Unfortunately there is no record for the exact locality of these anomalous specimens, but the skulls nos. 21, 26, 28 and 30 that are from S. Africa possess the I_2 on either side. The latter specimen even is an instance of unilateral hexaprotodontism, having an alveolus for the I_3 on the left side (Hooijer, 1942 b, p. 194, fig. 2).

I do not agree with Duvernoy that I_2 , if absent, was shed only in the adult stage. Skull no. 9 is not yet fully adult, and the two adult mandibles nos. 32 and 35 that lack one or both I_2 are distinctly narrower (width between the canines 198 and 205 mm against 228 to 265 mm) than the other mandibles of the same sex. It is far more probable that in these cases the I_2 has never developed as is typical of *H. liberiensis*. In the latter species two incisors occasionally develop on one side (Flower, 1887) while the Leiden Museum possesses a specimen which has three incisors on one side in the mandible (Hooijer, 1942 b, p. 194). The pigmy Liberian hippopotamus thus displays the same variation in number of its lower incisors as does *H. amphibius*, and the process of reducing the number of these elements is only more advanced in *H. liberiensis* than it is in *H. amphibius*.

There is another case of abnormal incisor development in my collection of skulls of *H. amphibius*, but this is definitely pathological. In specimen no. 18 the central lower incisors are placed considerably behind the level of the outer incisors which are comparatively large. The alveolus of the right I_1 is only 70 mm deep whilst the symphysis measures 165 mm. At the left side the alveolus of id_1 is still present, and the atrophied germ of the left I_1 is buried in the bone of the jaw. This remarkable anomaly has been fully discussed elsewhere (Hooijer, 1941).

Which is the incisor that has been eliminated in the normal dentition of *H. amphibius*? Some authors (Blainville, Joleaud, and Reynolds) claim to have found an id_3 in the milk dentition, but I was able to show (Hooijer, 1942 b) that the germ supposed to be that of the missing incisor in reality is that of the permanent canine. In order to find out which incisors are the missing ones I examined the front parts of upper and lower jaw of two foetuses of *H. amphibius* in serial sections. One of the specimens (Leiden Museum, reg. no. 4053) measures 18 cm from nose to root of tail; the other (Leiden Museum, reg. no. 1481) is about twice that long (32 cm). The specimens appeared to be already too old to settle the question definitely. In the younger stage the lower cd had already developed enamel, and both incisor germs were in the bell-shaped stage. Lingually of these germs the dental lamina shows a deep ingrowth, while between the germs the dental lamina is rudimentary. There is not even the slightest indication of a germ that might be taken for that of a third incisor. In the second stage the two incisors also had developed enamel, and the dental lamina lingually of the germ of the cd has given off the germ of the C, the first permanent element to develop, that was almost in the cap-shaped stage. As a whole the dental lamina is more reduced than that in the first specimen.

In the upper jaw matters are slightly different. The dental lamina in the first stage is seen to extend a good deal in advance of the germ of the central incisor without, however, showing any differentiated outgrowth that might be regarded as evidence of a tooth germ. In the older stage this anterior portion of the dental lamina appeared to be more reduced than that between the germs. These facts seem to point to the presence of a vestigial tooth germ in advance of the central incisor in stages younger than those which I have seen. Consequently the two developing incisors in the upper jaw may be id^2 and id^3 . As in the lower jaw the comparison of the degree of reduction of the dental lamina in the two stages gives no indication as to the position of the missing incisor, the reduction must have taken place earlier in the lower jaw than in the upper. This is well in accord with the facts observed in the permanent dentition.

Extra incisors in the lower permanent dentition do not only develop between I_2 and C (Hooijer, 1942 b, fig. 2); Harger (1932) has recorded an instance of an extra lower incisor that is behind and between the two that normally develop. The homology of the incisors of *H. amphibius* can perhaps be determined upon examination of foetuses younger than those I was able to study.

CANINES. — The adult lower C of *H. amphibius* are of an even thickness over their entire length, and circularly curved. Upon wear against the

antagonist in the upper jaw an almost vertical abrasion surface is formed on the concave posterior surface, whereby the upper C usually is worn away to a few mm in advance of the anterior border of its alveolus. The upper C, which is curved and grows from persistent pulp too, has the abrasion surface on its convex anterior surface. Anomalies, rather frequent among menagerie specimens, result from an originally perhaps only slight misdirection of one of the antagonists. Most often the lower canine is pushed outward by the growing upper canine, the growth of the teeth is no more compensated by wear, and it is even known that lower canines which grow freely finally pierce the body of the mandible and grow into their own pulp cavity so as to form a complete ring (Matthes, 1939).

It was Desmoulins (1825 a, p. 220) who has tried to base specific differences on minor variations in the length of the lower canines. In the *capensis* skull the tip of the lower C reaches 27 mm (one "pouce") above the lateral protuberance of the maxillary, while in *senegalensis* the lower canine extends upward only to 27 mm below the alveolar border of the upper C. The measurements of these teeth are given in a subsequent paper (Desmoulins, 1825 b, p. 357). In *capensis* the length of the lower C, measured as a chord of the concave side, is 218 mm. I found the length of the lower C in the Cape skull to be 270 mm when measured along the convex outer surface (measurement 7 in table I). In skull no. 11 the length of the lower C measured in this way even is 285 mm, and indeed the tip of this canine extends to about 25 mm above the lateral protuberance of the maxillary. The latter specimen is still younger than the Cape specimen in Paris, M³ being erupting and unworn. In skulls nos. 14 and 16, in which the length of the lower C along the outer curve is 195 and 240 mm respectively, the lower C protrudes ca. 15 mm above the lateral protuberance of the maxillary. But the canine may also reach a greater height than that in the *capensis* skull. In skull no. 17 the tip of the left lower C (length along anterior surface 270 mm) extends to about 31 mm above the lateral protuberance of the maxillary, while the right lower C in skull no. 23 (length ca. 300 mm) rises to the same height. The left lower canine of the latter skull, however, measures only 280 mm, and its tip is 19 mm above the protuberance. In skull no. 25 the canines are equally long (295 mm) but the maxillary protuberances have unequally developed, and at one side the canine is higher above the protuberance than at the other. The extra-alveolar lengths of these canini is not especially great, however; Matthes (1939, p. 199) gives 34 cm as maximum length for normal lower C.

In the type skull of *capensis* as well as in skulls nos. 11, 14, 16, 17, and 23 the mode of wear of the upper C is normal; the tooth is worn off almost

along the anterior upper border of its alveolus (the upper C are lost in skull no. 25). According to Desmoulins (1825 b, p. 357) *senegalensis* had upper C that were worn away only to 45 mm in front of the anterior upper border of the alveolus; the length of the canine is 135 mm when measured along the concave posterior surface. In keeping with the long upper C, the lower canine is more worn than usual, and the tip of the latter, as stated already above, remained 27 mm below the alveolar border of the upper C. As a result of this unusual mode of wear the abrasion surface is 25° more oblique than that in the Cape skull. I have found similar anomalies in my collection. In skull no. 29 the anterior length of the upper C is 16 mm; in skull no. 6 it is 30 mm at the right side but only 6 mm at the left. The posterior length of the upper C may differ considerably in one and the same skull too: in skull no. 21 the length of the upper C measured along the concave posterior surface is about 140 mm at the right side against only about 70 mm at the left. The extra-alveolar length thus varies in the upper as well as in the lower C of one and the same specimen, and it needs no further comment that the differences recorded by Desmoulins are only individual and have no systematic value.

Duvernoy (1846 a, p. 649) observed that the canini in the Abyssinia skull are bigger than those in the others; this character does apparently not apply to the Senegal skulls and thus is not typical of "*typus*". Heller (1914) mentions that *kiboko* has smaller C than has *amphibius*, and Schwarz (1914) states *tschadensis* to differ from *amphibius* by the same character. Schwarz's statement may be accounted for by a difference in sex, the type of *tschadensis* being a female. Measurements are given only by Heller, and his observations are recorded in table I (measurements 7 and 8). It will be seen that the *kiboko* lower canine is well within the variation limits of the lower C in adult male skulls (nos. 16-25), and that canines of a similar or even smaller size occur in specimens from South Africa (the type of *capensis*), the Congo (skull no. 17), and Mozambique (skull no. 18).

Leidy (1854, p. 211) states that in *capensis* the upper C are characterized by having a longitudinal strip not covered by enamel on the posterior surface. This strip is stated to be 7 mm wide, both in males and females. In true *amphibius* the upper C would have a complete enamel coating posteriorly. In table I (measurement no. 11) the width of the strip on the posterior surface of the upper C is seen to vary from 1 to 17 mm; it is absent in the Nile specimen (no. 6) as well as in some E. African skulls (nos. 4, 5, 11, and 18), while in the S. African skull no. 26 the strip is only 1 mm wide.

A peculiar variation in shape found in one of my specimens may be recorded here. In skull no. 31 the upper C are twisted for about 90° . The

curvature and mode of wear of this tooth is normal, but the shallow longitudinal groove that is normally found on the inner curve gradually shifts to the medial side when passing along the tooth from the pulp cavity to the extremity. At the alveolar border the groove is found at the medial instead of at the posterior surface of the canine. A left upper C of *amphibius* that is twisted to a lesser degree has been figured by Falconer and Cautley (1847, pl. 62 fig. 14).

P₂ — C DIASTEMA. — Duvernoy (1846 a, p. 649) remarks that the diastema between P₂ and C is longer in *capensis* ("australis") than in *amphibius* ("typus"). I have taken this measurement (table I measurement no. 12), which proves to vary between 97 and 135 mm in the S. African skulls (type of *capensis*, and nos. 21, 26, 28, and 30) which is almost equal to the total amount of variation (from 95 to 140 mm).

PREMOLARS. — Duvernoy (1846 a, p. 649) observed the upper premolars to be larger, and the P⁴ especially to be more complicated in structure in *amphibius* ("typus") than in *capensis*. When studying the variability in shape of the upper P I was struck by the differences in pattern displayed by these teeth, apparently without any geographical base. The P⁴ varies from a two-cusped to a five-cusped tooth, an account of which is given below.

The first premolar in *H. amphibius* is a milk element that rarely has a successor in the second dentition. Reynolds (1922, pl. V fig. 3) figures a (fossil) P¹, and I have found a large alveolus in skull no. 13 that must have contained a P¹, its dimensions being far too large for a milk tooth (Hooijer, 1942 b, p. 190 footnote). As we follow the lower premolars backward we observe the accessory cusp to the lingual side of the main cusp to become stronger, and the posterior cingulum to become more raised; the upper premolars likewise become more complicated passing from the anterior to the posterior. As a rule in Mammals the fourth milk premolar is molariform, and the tooth which replaces it has a less complex pattern. In *H. amphibius* the pd₄ has three pairs of cusps behind one another and is, therefore, long enough for the P₄ to have sufficient room to erupt. The P₄ is much less frequently rotated than the P⁴ of which the milk predecessor is relatively smaller. The upper last milk premolar is shed later than the lower; in skull no. 11 the former is still present and the tip of its successor is seen at its lingual side while the P₄ is already in place. In skull no. 18 the right P₄ is erupting but the left pd₄ is not yet shed. There is no trace of a P⁴ at the left side; an X-ray photograph showed that this element has not devel-

oped at all. This is the only instance of complete reduction of a premolar met with in my material. Premolars are rather frequently missing in *amphibius* skulls, but in many cases it is evident that they were lost during life. The cases of missing teeth recorded below refer only to those of which the alveoli are closed or closing. One of the oldest skulls (no. 34) has lost all upper premolars as well as both M¹. P₂ is lost on either side in skulls nos. 32 and 34, the left in skulls 17 and 28, the right in skull no. 31. P₂ is missing in skull no. 25 (both sides), the right in skulls 3 and 30. P₃ is lost in skull no. 21 on either side, and in skull no. 15 on the right side only. The right P₄ is missing in skull no. 5.

As will appear from the following account on the cusp addition in the upper premolars the Osbornian system of nomenclature has been adopted; it is not convenient to use Scott's system for the upper premolar cusps since it is now agreed upon (references in Gregory, 1916) that the primary cusp in the upper molar as well as in the upper premolar is the antero-external (paracone) rather than the antero-internal (protocone). "What does it matter except to minds spoiled by a too literal use of words if the protocone was not the "apex of the original reptilian crown"?" (Gregory, l.c., p. 250).

P₂ possesses but one cusp, the paracone, surrounded by a cingulum that is broadest postero-lingually. The tooth is provided with two roots which are subequal in size. In P₃ the posterior moiety of the crown is distinctly wider than the anterior and is supported by a broad root which is constricted in its middle. In skull no. 19 the P₃ has a small extra postero-internal root. Two cusps may have developed posteriorly to the paracone of P₃, the metacone labially and the metaconule lingually, as shown by the specimens figured on pl. I (figs. 1 and 2). Occasionally only the metaconule is present (skull no. 5), or only the metacone (skull no. 10). These latter cusps are hardly more than elevations of the posterior cingulum in skulls nos. 30 and 31 (pl. I figs. 3-4). In P₄, which often resembles P₃ in the relative development of the posterior cusps, a new element is added, viz., the antero-internal cusp or protocone, which has always more developed than the posterior elements.

In skull no. 30 the P₄ (pl. I fig. 5) has incipient posterior cusps as in the associated P₃ (pl. I fig. 3); the protocone has already become confluent with the paracone. The cingulum has well developed posteriorly and runs obliquely down along the sides of the crown.

In skull no. 20 (pl. I fig. 6) P₄ has a distinct protocone which is much smaller than the paracone; both cusps have a separate root, and the crown is wider anteriorly than posteriorly. The metacone is merely an outgrowth at the base of the paracone and has less developed than the corresponding

element in the associated P³ (pl. I fig. 7). The metaconule, damaged in P³, is incipient in P⁴. The cingulum is absent along the labial surface.

The P⁴ in skull no. 31 (pl. I fig. 8) has a protocone which has only a little less developed than the paracone. The two posterior cusps are small but distinct. The cingulum has well developed anteriorly and posteriorly, and is almost absent along the labial and lingual surfaces. The paracone has a separate root. The posterior root tends to be divided into a small labial and a large lingual portion, which latter extends to the antero-internal angle of the crown to support the protocone.

The left P⁴ in skull no. 28 (pl. I fig. 9; this specimen is from S. Africa, as is also skull no. 30) presents not less than five cusps, two anteriorly and three posteriorly. The cusps are connected almost up to their summits. The paracone is the largest, and there are weak grooves anteriorly and posteriorly like in the cusps of a true molar. The protocone is but slightly smaller than the paracone. The posterior cusps, which represent (passing from the labial to the lingual) metacone, metaconule, and hypocone, are almost equal in size and have less developed than the anterior cusps. The right P⁴ of the same skull (pl. I fig. 10) is much smaller than the left and is more simply built; there are but two posterior cusps, hardly more than elevations of the cingulum, which correspond in position to the metaconule and the hypocone. The anterior cingulum is highest at the protocone and descends obliquely along the paracone. It has also developed along the lingual surface of the crown except at the base of the protocone. Like in the foregoing specimen the protocone has no root of its own but is supported by the large posterior root which extends also along the lingual surface. The paracone has a separate root.

The right P⁴ in skull no. 25 (pl. I fig. 11) has five cusps too, but these are not so crowded as in the specimen presented in pl. I fig. 9. The hypocone is the smallest and arises from the cingulum; in the left P⁴ of the same skull (pl. I fig. 12) the hypocone is absent. Not only the paracone but also the protocone (especially in the left P⁴) and the metacone (especially in the right P⁴) possess a vertical groove anteriorly and one posteriorly; the worn surface consequently presents a trefoil pattern like that of the cusps of the true molars. The paracone has a small internal lobe. The metaconule presents a more simple structure, this cusp not being pinched in anteriorly and posteriorly. The cingulum is high at the anterior lobe of the protocone, while along the paracone it runs steeply down. At the labial surface it forms a low and smooth ledge, but the cingulum rises again steeply along the posterior surface of the metacone. The lingual cingulum has well developed along the metaconule, especially so in the right P⁴ in which it supports the

hypocone. There are two external roots, one below the paracone and the other below the metacone. The third root is placed internally, mainly below the metaconule.

The left P⁴ of skull no. 25 (pl. I fig. 12) is the most molariform specimen of P⁴ I have ever seen. This tooth is distinguished from a true molar only by its less elongated shape; in a molar the anterior and the posterior pair of cusps are more widely spaced. From the comparison with the corresponding tooth on the right side in the same skull (pl. I fig. 11) it is evident that the postero-internal cusp is the metaconule, as it is in the upper molar of many Artiodactyls (Gregory, 1916, p. 249).

MOLARS. — According to Schwarz (1914) *tschadensis* is characterized by M₃ being larger than M₂; in *amphibius* these lower molars would have about the same size. Now in hippopotamuses the last lower molar is typically distinctly larger than the other molars, and we must accept that Schwarz referred to the upper molars when stating the third to be larger than the second in *tschadensis*. Miller (1910) states that *constrictus* has narrower molar crowns than has *amphibius*. The measurements of the upper and lower molars given in table I (measurements 13-24) illustrate the rather great amount of variation. M³ is larger than M² in all male skulls with M³ worn (nos. 16-25), and the same character is also found in the oldest three female skulls (nos. 33-35). On the basis of this character it is only possible to refer skulls nos. 30 and 31, and probably also nos. 29 and 32, to *amphibius*. Molars narrower than those of the *constrictus* skull are found in a Congo skull (no. 20) as well as in skulls from E. Africa (nos. 27 and 31) and S. Africa (no. 30); the variation in molar dimensions in skulls from the same region shows that this character is not a satisfactory one on which to base a subspecies either.

UPPER TOOTHROW (P²-M³). — Duvernoy (1846a, p. 649) found the upper tooththrow to be shorter in *capensis* than in the Abyssinia skull, but does not refer to the Senegal skulls in this connection. Miller (1910) mentions that in *constrictus*, in contradistinction to *amphibius*, the upper tooththrows are divergent posteriorly. Schwarz (1914) states the tooth series to be shorter, as a whole, in *tschadensis* than in *amphibius*. The lengths of the lower tooth series recorded by Schwarz (1920, p. 874) as being 51.4 and 56.6 mm respectively, have not been taken into account; the length P₂-M₃ varies from 232 to 298 mm in my series of skulls (table I measurement 25) and the data provided by Schwarz evidently refer to a single tooth only. The lengths of whole tooth series are not rather satisfactory as offering means of distinc-

tion because of the gaps that occasionally separate the premolars. The interval between P_2 and P_3 is 18 mm in skull no. 13, and even 40 mm in skull no. 28. In skull no. 14 the interval between P^2 and P^3 is 22 mm, and we find the same diastema in skull no. 16.

Duvernoy apparently referred to a difference in total length, and did not compute ratios. P^2 - M^3 measures 275 mm in the Abyssinia skull, which is only 28 mm more than the length P^2 - M^3 in the *capensis* skull. Leidy (1854, p. 212) gives the following measurements, from which it is evident that

	Cape ♂	Cape ♀	Guinea
a. Length P^2 - M^3	267	228	210
b. Condylo-basal length	686	660	572
c. Ratio a : b	0.39	0.35	0.37

S. African skulls are not characterized by a short toothrow. The difference in relative length does not constitute a sexual difference either, for both the male and the female skulls (table I measurements 26-28) vary more widely than those of Leidy in this respect.

From the figures given by Miller (1910, pl. II) it would appear that the divergence of the molar series in the *constrictus* skull is more apparent than real. In the latter skull M^3 has not yet fully protruded and consequently its alveolus has not yet attained its full width.

The relative length of P^2 - M^3 in the type skull of *tschadensis* (0.41) exceeds that in any of the skulls measured by me, in which the ratio of P^2 - M^3 length to the condylo-basal length varies from 0.31 to 0.40. Few skulls have a shorter toothrow than the *tschadensis* specimens, and among these (nos. 20, 24, 29, 30, 32 and 35) are Congo as well as S. African specimens. It is thus impossible to account for Schwarz's statement that the Nigerian hippopotamus is characterized by the shortness of its toothrow.

RAMUS HORIZONTALIS. — The height of the ramus of the mandible is comprised five times in its length in *capensis*, against four times in the Senegal skulls and three two-thirds in the Abyssinia skull (Duvernoy, 1846 a, p. 646). From table I (measurements 30, 34 and 35) it will be seen that the S. African skulls nos. 21, 28 and 30 are nearer to "*typus*" (Senegal 0.25, Abyssinia 0.27) than to *capensis* (0.20). Other measurements (29 and 32) and ratios (31 and 33) have been taken in order to check the individual variation, since these characters serve to distinguish between the fossil Asiatic forms.

SYMPHYSIS. — According to Miller (1910) the symphysis in *constrictus* is shorter relative to the length of the mandible than that in *amphibius*. Much

attention has been paid to the relative length of the symphysis in the study of the fossil Asiatic forms of hippopotamus, and, as I shall show further on, there is a progressive shortening of the symphysis in the Asiatic series and this character is of great systematic significance. In the African hippopotamus, however, no reliance can be placed on the relative length of the symphysis; the S. African skulls (nos. 21, 26, 28 and 30) vary in the ratio of the length of the symphysis to the length of the mandible from 0.29 to 0.34 so as to include both *constrictus* (0.32) and typical *amphibius* (our Nile skull no. 6: 0.34). In one of the E. African skulls (no. 12) the symphysis is relatively longer (0.39) than in Miller's *amphibius* skull (0.36). I have also computed the ratio of the symphysis length to the width across the lower C (table I ratio 39) in which the difference between *constrictus* (0.48) and Miller's *amphibius* (0.56) is more pronounced, but in which the S. African material varies from 0.45 to 0.57. While in relation to the mandibular length the symphysis in skulls nos. 15 and 26 is as long as, or shorter than that in *constrictus*, in relation to the width across the lower C the symphysis in these skulls is even longer than that in Miller's *amphibius* skull.

THE OBLIQUENESS OF THE RAMUS ASCENDENS. — Desmoulins (1825 a, p. 221) found the ascending ramus of the mandible to be 15° more oblique in *senegalensis* than in *capensis*. I have measured the angle between the line connecting the processus angularis and the deepest point of the notch between the processus coronoideus and the processus condyloideus, and the horizontal plane (table I measurement 44) and found a variation from 65° to 82° or 17° ; in the S. African material the amount of variation is 11° .

HEIGHT OF PROCESSUS CORONOIDEUS. — Miller (1910) states that in *constrictus* the height of the coronoid process is smaller relative to the length of the mandible than that in *amphibius*. See table I ratio 46. It will be seen that skulls from the Congo as well as from S. Africa may have the coronoid process either higher than that in *amphibius* (nos. 1, 2, 26 and 28) or even lower than that in *constrictus* (skulls nos. 3, 20, 21, and the Cape skull in the Paris Museum).

THE CRISTA SAGITTALIS. — The sagittal crest is relatively shorter in *senegalensis* than it is in *capensis* (Desmoulins, 1825 a, p. 219); in the former it is at the most one-sixth, in the latter at the least one-fifth of the length from the nuchal crest to the tip of the nasals. Duvernoy (1846 a, p. 647) gives the following measurements:

	Cape	Senegal I	Senegal II
a. Length of crista sagittalis	100	60	70
b. Length from nuchal crest to tip of nasals	570	560	565
c. Ratio a : b	0.18	0.11	0.10

The measurements recorded in table I show the sagittal crest to be of the same relative length as, or even longer than that in *capensis* in skulls nos. 1, 9, 12, 15, 19, 20, 21, and 34 which are in part from the Congo or E. Africa, while in the S. African skulls nos. 26 and 30 the sagittal crest is as short as that in the Senegal specimens.

MEDIAN LENGTH OF THE MAXILLARY. — According to Duvernoy (1849 a, p. 685) the maxillary is proportionally longer in the Natal skull (referred to *capensis*) than in that from Abyssinia (referred to “*typus*” = *amphibius*). The greatest length of the maxillary relative to the length from the palatine to the premaxillaries (table I, measurements and ratio 50-52), however, is found in some of the E. African skulls (nos. 4 and 27), while the shortest maxillary occurs in a S. African skull (no. 21).

PREMAXILLARIES. — Duvernoy (1846 a, p. 646) states that the premaxillaries in the Senegal and Abyssinia skulls are broader and more prominent than those in the Cape skull, and gives the following measurements:

	Cape	Abyssinia	Senegal I	Senegal II
Width of premaxillaries	233	236	255	258

The Abyssinia skull differs as much from those of Senegal as does that from the Cape, and measurement 53 in table I shows that a Mozambique and a Congo skull (nos. 18 and 20) have narrower premaxillaries even than the Cape skull in the Paris Museum, whilst my skull no. 21 from S. Africa exceeds the Senegal specimens in the width of the premaxillaries.

THE ANTERIOR NARIAL ORIFICE. — Duvernoy (1849 a, p. 684) states that the anterior narial orifice is wider than high in “*typus*”, and higher than wide in *capensis*. There are but six skulls in the series examined by me (nos. 1, 21, 22, 31, 33, and 34) in which the vertical diameter of the anterior nares is less than the horizontal, and among these there is one skull from S. Africa. The other skulls all have the anterior nares higher than wide as was supposed to be typical of *capensis*.

THE ANTERIOR WIDTH OF THE MAXILLARY. — Miller (1910) states that in *constrictus* the anterior width of the maxillary relative to the zygomatic width is less than that in *amphibius*. Schwarz (1914) writes that *tschadensis*

is characterized by its broad rostrum. There are only few skulls (table I ratio 56) in which the maxillary is nearly as wide anteriorly as that in the *amphibius* skull of Miller and the *tschadensis* skulls; one of them is from the Congo (no. 17) and another from Zanzibar (no. 31). They differ considerably in this respect from other skulls, showing that this variation, again, is only individual.

THE RATIO OF ZYGOMATIC WIDTH TO CALVARIUM LENGTH. — Duvernoy (1846 a, p. 645) mentions that in *capensis* the calvarium is longer in proportion to its width than that in "*typus*". Schwarz (1914) observed that in *tschadensis* the zygomatic arches are slightly narrower than those in *amphibius*, but distinctly less expanded behind than those in *capensis*. As is evident from table I (ratio 57) the two *tschadensis* skulls differ considerably in this ratio (0.55 and 0.72 respectively), and all of my skulls are intermediate between these extremes in this respect. In not less than 19 skulls I found the calvarium to be proportionally longer than that of *capensis*.

THE ROSTRAL CONSTRICTION. — The Natal skull is stated to be narrow in its middle portion by Duvernoy (1849 a, p. 685). *H. a. constrictus* is characterized by having a deep pre-orbital constriction (Miller, 1910), while in *kiboko* this constriction is less well marked (Heller, 1914). Schwarz (1914) states the rostrum of *tschadensis* to be broad, tubular, and not constricted. In table I the rostral constriction (measurement 58, taken over the ventral border of the infraorbital foramen) is divided by the condylo-basal length (ratio 59) as well as by the zygomatic width (ratio 60). The former ratio varies from 0.14 to 0.23, the latter from 0.23 to 0.36. It will be observed that in *constrictus* the rostrum is more constricted than that in the other type skulls, but that two S. African skulls (nos. 28 and 30) are very near to the former in proportions, while the Cape skull of the Paris Museum and skull no. 21 (also from S. Africa) present nearly the opposite extreme. The relative width of the rostral constriction does not afford characters to distinguish between *amphibius*, *kiboko* and *tschadensis* either.

THE POSITION OF THE FORAMEN INFRAORBITALE. — Desmoulins (1825 b, p. 359) states that the posterior border of the infraorbital foramen is placed above the middle of the "cinquième molaire" in the Senegal skull, and above the front of the "quatrième molaire" in *capensis*. The Cape skull in the Paris Museum has the posterior border of the infraorbital foramen placed above the back part of P³ (Blainville (1847, Atlas, pls. I and II) gives more accurate figures than Cuvier (1821, Hippopotame vivant, pl. I fig. 1, pl. II

fig. 1)). The posterior border of the infraorbital foramen varies in position from above the front part of P³ (skulls nos. 21 and 26) to above the middle of P⁴ (skull no. 25); the former skulls originate from S. Africa but have the infraorbital foramen even more advanced in position than that in the Senegal skull of Desmoulins.

THE ZYGOMATIC ARCH. — Desmoulins (1825 a, p. 220) mentions that the suture between the jugal and the squamosal is straight in "*senegalensis*"; the jugal bone extends backward to half a "pouce" above the lower border of the glenoid fossa. In *capensis*, on the other hand, the jugal bone is less elongated posteriorly and remains one "pouce" in advance of the glenoid fossa. Duvernoy (1849 a, p. 685) states that in the Natal skull (referred to *capensis*) the jugal is closer to the glenoid fossa than is the case in other skulls. A careful comparison showed me that either of the two variations are found in the S. African material, skull no. 26 presents the *capensis* character, the others (nos. 21, 28 and 30) the *senegalensis* character. The E. African skulls vary in the same way. Duvernoy (1846 a, p. 645) adds that in "*typus*" the point of intersection of the tangents of the zygomatic arches is situated on the tip of the nasals, while in *capensis* the tangents intersect at a point 10 cm in front of the nasals. In most of the S. African skulls (nos. 21, 28 and 30) the point of intersection of the tangents is more than 10 cm in front of the nasals, but this character also holds for the E. African skulls nos. 12 and 33, and for the Congo skulls nos. 1 and 2 in contradistinction to skulls nos. 3 and 17 from the Congo which present the "*typus*" character.

THE ORBIT. — Variations in the shape of the orbit and its degree of elevation above the level of the frontals received much attention by various authors. In the fossil Hippopotamidae of Asia the elevation of the orbit offers a very good character for discrimination, but the points of difference stressed by Duvernoy, Miller, Heller, and Schwarz do not appear to be well taken. Duvernoy (1846 a, p. 645) found that in *capensis* the orbit is wider than high in contradistinction to that in "*typus*". Miller (1910) states that in *constrictus* the vertical diameter of the orbit is not conspicuously greater than the horizontal diameter, and that the orbit is less elevated above the median portion of the frontals than is the case in *amphibius*. Heller (1914) mentions that in *kiboko* the orbit is much elevated, and more circular than that in *capensis*. Schwarz (1914) states *tschadensis* to be characterized by its strongly projecting orbits which are "decidedly laid forward"; "when seen from in front their lateral margin is seen to be placed almost vertically". The figures given by Schwarz in a subsequent paper (Schwarz, 1920,

pl. 33) show these statements to be exaggerated. On my request Prof. R. Mertens of Frankfurt kindly sent me some measurements of the type skull of *tschadensis* which were omitted by Schwarz. Contrary to Duvernoy, Schwarz (1920, p. 873) states the orbit in *capensis* to be higher than wide.

The measurements provided by Leidy (1854, p. 212):

	Cape	Cape	Guinea	Gambia
	♂	♀		
a. Vertical diameter of orbit	76	76	57	76
b. Horizontal diameter or orbit	64	64	51	64
c. Difference a-b	+12	+12	+6	+12
d. Elevation of orbit above level of frontals	51	25	25	19

show that in S. African skulls the height of the orbit may exceed its horizontal diameter. It will be seen, too, that there is no correlation between the shape of the orbit and its degree of elevation; though the vertical diameter of the orbit distinctly exceeds the horizontal diameter the degree of elevation above the frontals is rather different, ranging from 19 to 51 mm. While in skulls nos. 26, 11, 17, 19, 32, 13, the *kiboko* skull, skull no. 25, and Miller's *amphibius* skull the difference between the vertical and the horizontal diameters of the orbit steadily increases from +2 to +25 mm, the elevation above the frontals remains almost the same (38-42 mm). In skulls in which the orbit is even more elevated (skull 35, and the ♀ *tschadensis* skull: 44 mm), the orbit is even wider than high.

The measurements discussed above are given in table I (measurements 61-64). I have also taken the height of the calvarium from the palatine to the middle of the frontals (measurement 65), and the ratio of the latter to the condylo-basal length and to the elevation of the orbit (table I ratio 66 and 67). The variation in the ratio of the height of the calvarium to its length (0.23-0.28) is very much smaller than that of the ratio of the elevation of the orbit to the calvarium height (0.10-0.32) as might be expected. The latter ratio provides a measure for the relative degree of elevation of the orbit which proves to be very useful in distinguishing between the fossil Asiatic forms. The ♀ *tschadensis* skull indeed has a much elevated orbit (ratio 67 is 0.29), but the orbit is more elevated in skulls nos. 14, 35, and 31, the latter originating from Zanzibar. The orbital angle (table I measurement 68, measured between the line connecting the middle of the upper and the middle of the lower border of the orbit, and the horizontal plane) is not more than 63° in the type of *tschadensis*; in 25 of my 34 specimens the orbital angle is greater than 63°, and *tschadensis* consequently is not peculiar in this character either.

THE OCCIPUT. — Miller (1910) states that in *constrictus* the occipital region is much less elevated than that in *amphibius*. Heller (1914) mentions that *kiboko* is characterized by the great elevation of the lambdoidal crest, while Schwarz (1914) writes that in *tschadensis* the lambdoidal crest is much lower than the upper margin of the orbit. The height of the occiput from the lower border of the foramen magnum (table I measurement 69), however, is but one mm less than the height from the palatine to the upper margin of the orbit (table I measurements 64+65) in the example of *tschadensis*, and in 21 of my 34 skulls the orbit is higher. In *constrictus* the occiput is more elevated above the interorbital region than that in *amphibius* instead of the reverse as would follow from Miller's text, but the difference is so small (+15 and +6 against a variation of +4 to +43) as to be negligible.

THE NASALS. — Heller (1914) states that *kiboko* is characterized by its wide nasal bones. The nasals in eight skulls from Lake Naivasha (Br. E. Africa) vary in least width from 40 to 49 mm, the Nile skulls vary in nasal width from 27 to 38 mm, and the Zambesi material from 29 to 32 mm. The total range of variation in least nasal width I found is from 16 to 55 mm, the lowest figure occurring in a Mozambique skull (no. 11). Other skulls from Portuguese East Africa (nos. 12 and 18), however, have the nasal about twice as broad (27 and 33 mm respectively), while in another E. African skull (no. 33) the nasal is not less than 50 mm in least width.

THE LACRIMAL.—In *Hippopotamus amphibius* the lacrimal normally is interposed between the frontal and the maxillary. It borders at the nasal and has a postero-external prolongation that forms part of the orbital margin. In the skull of the fossil Hippopotamidae of Asia as well as in the recent pigmy hippopotamus from Liberia, *H. liberiensis* Morton, and *H. protamphibius* Arambourg from the Pleistocene of E. Africa the frontal joins the maxillary and consequently the lacrimal does not come into a contact with the nasal. The latter development occasionally occurs in *H. amphibius* too (Grandidier and Filhol, 1894, p. 161 fig. 1; Major, 1896, p. 978; Stehlin, 1900, p. 434; Dietrich, 1928, p. 8), but I did not meet with this peculiarity in my collection of 34 skulls. Another variation recorded by Dietrich (1928, p. 8), Colbert (1935, p. 282), and Arambourg (1944 b) consists in the lacrimal having no contact with the orbital margin, but this condition is not represented in my collection either. Variations in shape and size of the lacrimal are shown in figs. 1-5, representing the left lacrimal of skulls nos. 11, 12, 6, 10, and 18 respectively. In the above order the

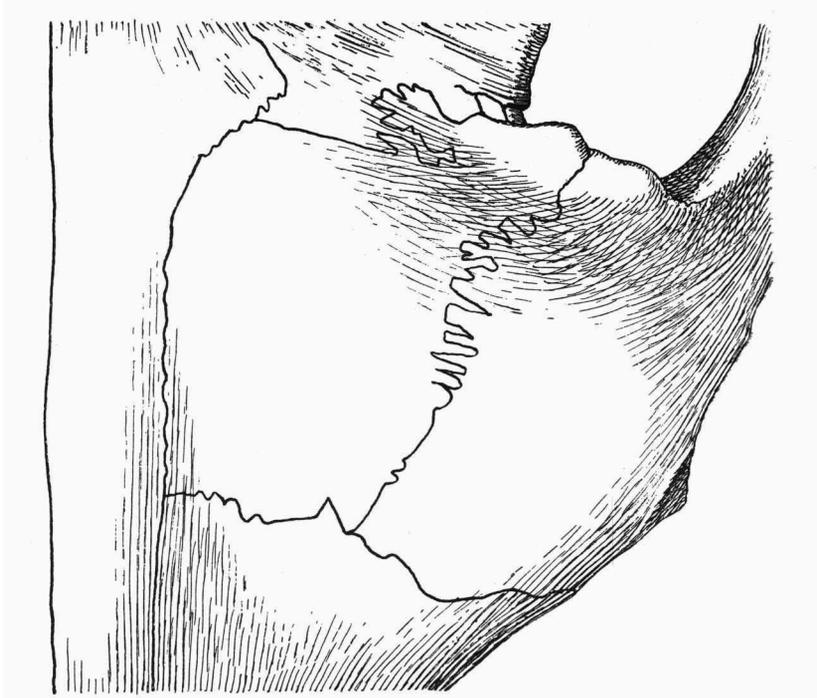


Fig. 1. *Hippopotamus amphibius* L. Left lacrimal of skull
no. 11. $\times 2/3$.

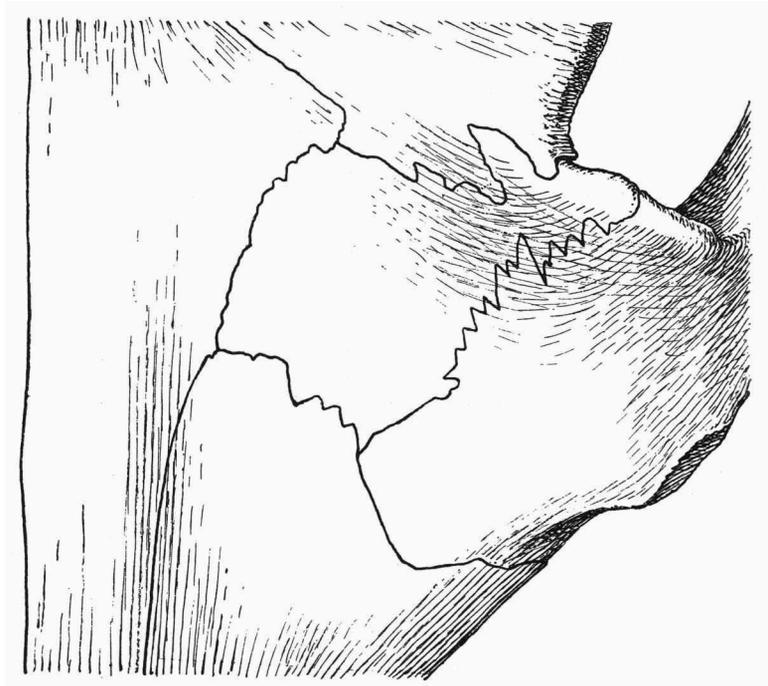


Fig. 2. *Hippopotamus amphibius* L. Left lacrimal of skull
no. 12. $\times 2/3$.

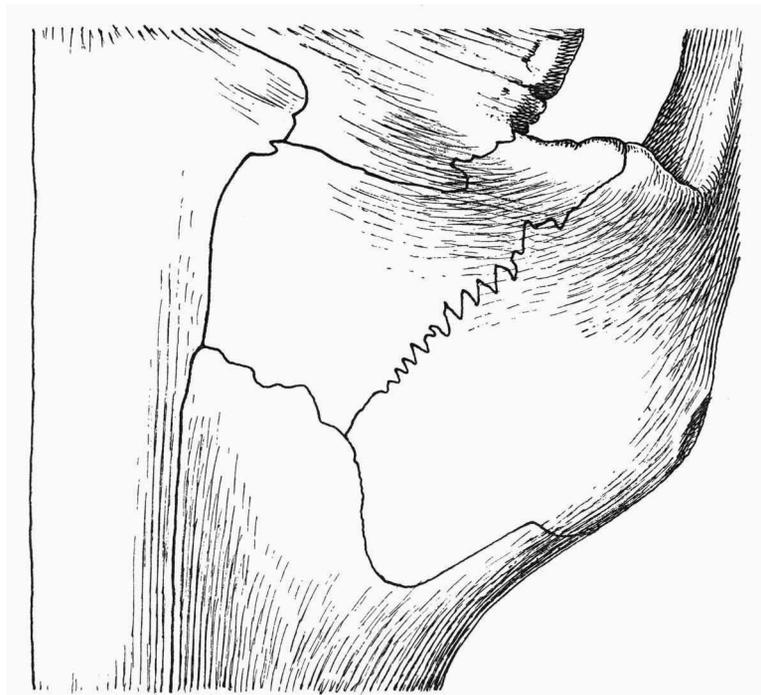


Fig. 3. *Hippopotamus amphibius* L. Left lacrimal of skull
no. 6. $\times 2/3$.

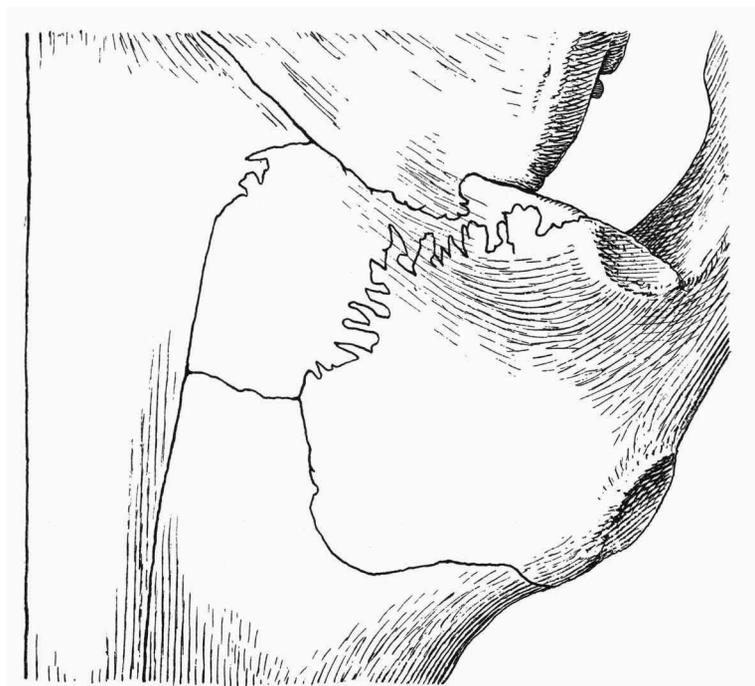


Fig. 4. *Hippopotamus amphibius* L. Left lacrimal of skull
no. 10. $\times 2/3$.

orbital angle is 59° , 61° , 70° , 72° , and 78° respectively, and it will be observed that in keeping with the increasing orbital angle there is a tendency toward elimination of the postero-lateral tongue of the lacrimal on the upper surface of the skull that extends to the orbit. This coincidence, however, I believe to be only casual, for the other skulls do not fit into this scheme. I agree with Dietrich (1928, p. 8) that the elevation of the orbit bears no relation to the shape of the lacrimal.



Fig. 5. *Hippopotamus amphibius* L. Left lacrimal of skull
no. 18. $\times 2/3$.

SCAPULA. — Desmoulins (1825 a, p. 220) states: "L'échancrure de l'angle costal de l'omoplate, si prononcée dans l'*H. Capensis* (V. Cuvier, loc. cit. [Cuvier, 1821, Hippopotame vivant], pl. 1 et pl. 2, fig. 6), est à peine sensible dans l'*H. Senegalensis* [où ce n'est qu'une section droite qui unit les deux bords postérieurs de l'os (Desmoulins, 1825 b, p. 360)] dont la proportion de taille est pourtant au moins d'un neuvième plus forte. L'échancrure que l'on voit aussi sur le *Capensis* (fig. cit.) entre l'apophyse coracoïde et la cavité glénoïde n'existe pas dans le *Senegalensis*". The scapula of *capensis* has been figured by Cuvier (1821, Hippopotame vivant, pl. I A,

pl. II fig. 6) and by Blainville (1847, Atlas, pl. I); the latter author also figures the Senegal scapula (l.c., pl. V, upper side at the right). The difference in shape of the notch at the posterior angle as well as that of the notch between the glenoid cavity and the tuber scapulae (coracoid) that struck Desmoulins is so small as to be accounted for by individual variation. There is no considerable size difference either: as judged by Blainville's figures the height of the *capensis* scapula is 469 mm against 450 mm in the Senegal specimen; the maximum antero-posterior diameter is 315 mm both in the former and in the latter.

HUMERUS. — Desmoulins (1825 a, p. 220): "La ligne âpre qui prolonge le bord externe de la poulie rotulienne du fémur, figure 10 [Cuvier, 1821, Hippopotame vivant, pl. II fig. 10] est fortement échancrée sur le condyle externe dans le *Capensis*, cette échancrure manque dans le *Senegalensis*". In Desmoulins' subsequent paper (1825 b) no words are bestowed on this supposedly specific character. The figure of Cuvier referred to represents no femur but the distal part of the humerus. Neither this figure nor that of the distal part of the femur (Cuvier, l.c., fig. 17) present reliable differences from the figures of the corresponding parts of the Senegal skeleton (Blainville, 1847, Atlas, pl. V).

PELVIS. — Desmoulins (1825 a, p. 220) finally remarks that "le bord pubien du détroit supérieur du bassin, échancré au milieu par deux éminences iléopectinées si prononcées, comme montre la fig. 14, pl. 2, de Cuvier, est droit dans le *Senegalensis*, où il n'y a de même pas de traces de ces éminences ni de la saillie de la symphyse pubienne qui divise l'échancrure". The ilio-pectineal eminence, however strong in the figure of Cuvier referred to by Desmoulins, is also shown in the right os coxae of the Senegal skeleton figured by Blainville (1847, Atlas, pl. V).

NUMBER OF VERTEBRAE. — Duvernoy (1849 a, p. 685) states that the Cape skeleton has fifteen thoracic and four lumbar vertebrae, while the Senegal skeletons have sixteen thoracic and four lumbar vertebrae. Blainville (1847, p. 26) states to have examined the skeletons mentioned "sans trouver d'autres différences que celles que l'on doit évidemment considérer comme individuelles; différences qui cependant, réduites en mesures millimétriques, pourraient paraître quelque chose aux personnes qui étudient l'ostéologie sans considérations physiologiques, mais qui au fond ne sont en aucune manière spécifiques".

In concluding the present chapter it can be stated that the characters relied upon by the above cited authors are subject to too strong an individual variation to be reliable. There is no skull in my collection that does not combine characters supposedly typical of at least three, and mostly even of four of the subspecies.

Pleistocene remains referable to the recent species often present dimensions pointing to individuals of larger size than the recent. They have been described under various names from many Villafranchian and younger localities in Africa as well as in Southern and Western Europe. Cuvier (1824, p. 527) designated the large fossil hippopotamus as *H. major*, which name is antedated by *H. antiquus* Desmarest (1822, p. 388). Except for the authors previously cited (Hooijer, 1942 a, p. 280) the name *H. antiquus* has been used by Von Meyer (1832, p. 73) and Murray (1866, p. 166) too. Since size is the only criterion by which to distinguish the fossil from the recent form, the former is worthy of subspecific distinction from the latter only, as recognized already by Boule (1910, p. 193). The correct name consequently would read *Hippopotamus amphibius antiquus* Desmarest. Stehlin (1900, p. 467 footnote) records an I_1 with a diameter of 60 mm; the largest I_1 in my collection of recent skulls (no. 22) measures 59 mm in cross section. Lorenzo and Erasmo (1936, p. 16) figure a left lower C (l.c., pl. II fig. 1) with a greater diameter of ca. 80 mm, and Tuccimei (1891, p. 132) even records a specimen 91 by 62 mm in diameters. The largest lower C seen by me (an isolated specimen from Natal presented to the Leiden Museum in 1896 by Mr. A. Maassen) measures 78 by 49 mm in cross section. The fossil molars figured by Capellini (1879), viz., an M_2 (l.c., pl. I figs. 1-2, length 65 mm, width 41 mm) and an M^2 (l.c., pl. III figs. 3-4, length 62 mm, width 56 mm), and the M^3 recorded by Houghton (1922, p. 15, length 58 mm, width 50 mm) agree in size with the largest among the corresponding recent molars.

Fossil remains representing varieties or at the most races of the living *H. amphibius* have been described under the following names:

- a. *H. annectens* Falconer (1849, p. 236; cf. Stromer, 1905, p. 115) from the Nile above the cataracts.
- b. *H. sirensis* Pomel (1890, p. 1114) and *H. icosiensis* Pomel (1896, p. 28) from the Pleistocene of Algeria (cf. Boule, 1910, p. 195; Arambourg, 1948, p. 329).
- c. *H. ponderosus* Scott (1907, p. 254) from the Pleistocene of Zululand (cf. Arambourg, 1948, p. 329).
- d. *H. amphibius* var. *robustus* Fraas (1907, p. 238) from the Pleistocene Vaal River Gravels (cf. Arambourg, 1948, p. 329; Cooke, 1949).

- e. *H. amphibius kaisensis* Hopwood (1926) from the Pleistocene Kaiso Bone Beds (cf. Arambourg, 1948, p. 328).
- f. *H. gorgops* Dietrich (1926, 1928, recently (Deraniyagala, 1947) even raised to distinct generic rank) from the Pleistocene of Oldoway, E. Africa (cf. Arambourg, 1948, p. 329).
- g. *H. westphali* Lyle (Pniel, Barkley West district), *H. helmei* Lyle and *H. venteri* Lyle (Florisbad, Hagenstadt, 30 miles N.N.W. of Bloemfontein) from S. Africa (Lyle, in Dreyer and Lyle, 1931, pp. 13-20). Cooke (1949) is also of the opinion that these species are nothing but *H. amphibius* L.

The forms enumerated below for the sake of completeness are certainly distinct from *H. amphibius* L. The relationships between these species is still obscure; references will be found in Hooijer (1946) and Arambourg (1948), and some of them will be referred to in the sequel.

- a. *Hippopotamus sicalus* Hooijer (= *H. sivalensis* Seguenza, 1902, nec Falconer et Cautley, 1836) from the Pontian of Sicily.
- b. *H. pantanellii* Joleaud (= *H. hipponensis* Pantanelli, 1879, nec Gaudry, 1876) from the Plaisancian of Casino near Siena in Italy.
- c. *H. protamphibius andrewsi* Arambourg (= *H. hipponensis* Andrews, 1902, nec Gaudry, 1876) from the Astian of Wadi Natrun in Egypt.
- d. *H. hipponensis* Gaudry from the Villafranchian of Algeria.
- e. *H. imaguncula* Hopwood from the lower Pleistocene of Kaiso, Lake Albert, E. Africa.
- f. *H. protamphibius* Arambourg from the lower Pleistocene of Omo, Lake Rudolph, E. Africa.
- g. *H. minor* Desmarest (syn. *H. minutus* Cuvier) from the Pleistocene of Cyprus.
- h. *H. pentlandi* Von Meyer from the Pleistocene of Sicily, Malta and Crete.
- i. *H. melitensis* Major from the Pleistocene of Malta and Crete.
- j. *H. lemerlei* Grandidier (syn. *H. madagascariensis* Guldberg), sub-fossil from Madagascar.

The recent pigmy species of *Hippopotamus* from Liberia, *H. liberiensis* Morton, differs from all other species of *Hippopotamus* of which the skull is known in the combination of progressive characters (reduction of the incisors to two on each side in the upper and one on each side in the lower jaw) as well as generalized features (orbits not elevated above level of frontals). This species presents some remarkable resemblances to the fossil Asiatic hippopotamuses in certain skull and postcranial characters as noticed in the next chapter, and is supposed to have split off from the primitive

African stock at least since the beginning of the Pliocene (Arambourg, 1948, p. 335, see also Stehlin, 1900, p. 488). Quite recently Deraniyagala (1949, p. 22) described another new genus of hippopotamuses, one that is transitional in characters between "*Hexaprotodon*" and *Choeropsis*, viz., *Prechoeropsis*. It is, however, not altogether convincing, on the evidence of this single imperfect mandible from the middle Nile delta, that it represents a form in which I_2 and I_3 should be shed in the adult, and its relation to the recent pigmy hippopotamus is open to severe doubts. This specimen gives no conclusive proof as to the vestigial nature of the smaller lower incisors. It is to be hoped that further finds will throw more light on the status of this fossil specimen; for the present the systematic position of "*Prechoeropsis*" is uncertain.

THE FOSSIL HIPPOPOTAMIDAE OF ASIA

The fossil remains of *Hippopotamus* from Java to be described in the following pages are the first to have been collected in this island. They form part of the Dubois collection (referred to below as Coll. Dub.), now in the Leiden Museum, which was brought together by Eug. Dubois in the years 1890 to 1900¹). The Dubois collection contains also *Hippopotamus* remains from the Siwaliks of the Punjab, collected in 1895 in the vicinity of Hari-poor on the Somb Nuddy, Sirmur State. The completion of the present monograph was considerably delayed until, recently, I had the opportunity to study the Siwalik and Narbada material of *Hippopotamus* in the British Museum (Natural History) at London. I am indebted to Dr. A. T. Hopwood who kindly placed the specimens at my disposal. My thanks are due to Prof. Dr. B. G. Escher and Prof. Dr. I. M. van der Vlerk who permitted me to study the material of the Cosijn collection from the Lower Pleistocene of Java preserved in the Geological Museum at Leiden.

The first record of fossil hippopotamuses in Asia is that by Clift (1828) who figures some jaw fragments collected in 1826 by Crawford in Burma, 250 miles below Ava on the left bank of the Irrawaddy river. The only statement given by Clift concerning these remains is that they indicate an animal that is smaller than the living *H. amphibius*.

1) Martin (1883, p. 12, pl. I fig. 2) has described and figured a tooth fragment from a boring at Ngembak, res. Semarang, Java, as *Hippopotamus* spec., but this fragment belongs to *Bubalus* (Dubois, 1908, p. 1265). The specimen is in the Geological Museum at Leiden (no. 42386).

In 1836 Falconer and Cautley published a description of the skull of a fossil hippopotamus from the Siwalik Hills in India, which received the name *Hippopotamus (Hexaprotodon) sivalensis*, the subgenus being established on the presence of six incisors. The recent *H. amphibius*, normally having four incisors, is placed in the subgenus *Tetraprotodon*. The authors also point to certain cranial differences between the fossil Asiatic and the recent African species. Numerous figures of the skull, teeth, and parts of the skeleton were published in Falconer and Cautley's "Fauna Antiqua Sivalensis" (1845-1849, cited below as F.A.S.). Figures of three more species of *Hippopotamus*, viz., *H. (Hexaprotodon) iravaticus*, *H. (Hexaprotodon) namadicus*, and *H. (Tetraprotodon) palaeindicus*, appear for the first time in the latter work too. The description of the plates was not published until 1868, in the Paleontological Memoirs of Falconer (1868).

A discussion of the four species distinguished by Falconer and Cautley was presented by Lydekker (1884 a). *H. palaeindicus* is shown to have been hexaprotodont as well as the other Asiatic forms. In the sequence *H. iravaticus* (from Burma), *H. sivalensis* (Siwaliks), *H. namadicus* and *H. palaeindicus* (both from the Narbada (Nerbudda) Beds in Central India) the species exhibit a gradual reduction in size of I_2 in keeping with increase in size of I_1 and I_3 , and a shortening of the symphysis. "It is highly probable that these four species represent the actual line of descent in which these modifications have been accomplished" (Lydekker, l.c., p. 47/48). Lydekker also observed the general shortening of mandible and calvarium in this series; *H. sivalensis* and *H. palaeindicus* were the only species, however, of which the calvarium was known to Lydekker. The calvarium of the former species is stated to differ from that of the latter in its less elevated orbits as well as in other characters to be dealt with below. The calvarium of *H. iravaticus* remained unknown until, in 1938, Colbert described an incomplete calvarium from the Upper Irrawaddy fauna of Burma.

The fossil species of *Hippopotamus* found in Java by Dubois could not be identified with any of the forms described before, but, because of its exhibiting the greatest resemblance to *H. sivalensis*, Dubois (1908, p. 1265) proposed to name the Javan form *Hexaprotodon sivajavanicus*. Von Koenigswald (1933, 1934 a and b) distinguishes three species of *Hippopotamus* from Java, viz., *H. simplex* (Upper Pliocene), *H. antiquus* (Upper Pliocene and Lower Pleistocene), and *H. namadicus* (Middle and Upper Pleistocene). The latter species, therefore, would occur both in the Narbada Beds and in Java, and *H. sivajavanicus* is regarded as a synonym. In the opinion of Von Koenigswald the three Javan species represent an evolutionary line parallel to that already established by Lydekker on the evidence

of the Burmese and Indian material, and, in the absence of intermediate forms between *H. sivalensis* and *H. namadicus*, the latter species is supposed to have migrated from Java to India (Von Koenigswald, 1935 a, p. 198).

Fossil remains of *Hippopotamus* have been recorded from Ceylon by Deraniyagala (1936-1948) as *H. sinhaleyus*.

In the present paper the various forms of *Hippopotamus* from the Siwaliks, the Narbada Beds, Burma, Ceylon, and Java, to all of which full specific rank was given, are treated as subspecies of *H. sivalensis*, the oldest and best known of the extinct Asiatic forms. An exception is made only for *H. iravaticus* which, apart from its definitely smaller size, differs in certain cranial and dental characters from the other Asiatic forms which would seem to justify a specific distinction. But I cannot imagine that full species would show so much intergradation as *H. sivalensis*, *H. namadicus*, *H. palaeindicus*, and the Javan forms do. With the enormous amount of variation of *H. amphibius* in mind the differences between these forms must be regarded as of subspecific significance only. The subspecies of *H. sivalensis* as defined in the present work are the following:

H. sivalensis sivalensis Falconer et Cautley (Siwaliks),

H. sivalensis namadicus Falconer et Cautley (Narbada Beds),

H. sivalensis palaeindicus Falconer et Cautley (Narbada Beds; as yet inseparable forms from Burma and Ceylon),

H. sivalensis duboisi nov. subsp. (Siwaliks of the Punjab),

H. sivalensis sivajavanicus (Dubois) (= *H. simplex* Von Koenigswald) (Java),

H. sivalensis koenigswaldi Hooijer (= *H. antiquus* Von Koenigswald, 1934, nec Desmarest, 1822) (Java), and

H. sivalensis soloensis nov. subsp. (= *H. namadicus* Von Koenigswald, 1934, nec Falconer et Cautley, 1847) (Java).

Under the head of each of the subspecies is given (a) a synonymy, (b) a diagnosis, (c) a survey of the literature pertaining to the subspecies in question, and (d) a description of new material, if any. The measurements are recorded in tables II and III at the end of the present paper. The system of dental nomenclature adopted, in accord with Osborn (1907, pp. 171-173), runs as follow:

Upper molars:	paracone	antero-external cusp
	protocone	antero-internal cusp
	metacone	postero-external cusp
	metaconule	postero-internal cusp

Lower molars:	protoconid	antero-external cusp
	metaconid	antero-internal cusp
	hypoconid	postero-external cusp
	entoconid	postero-internal cusp
	hypoconulid	"talon" of M ₃

The extinct hippopotamuses from Asia are distinguished from the living species *H. amphibius* L. by a number of characters which permit of a separation of these forms from the recent species which is regarded by most modern authors as of generic value (*Hexaprotodon*). This is, of course, only a matter of taste. I prefer not to split the genus *Hippopotamus* because this would leave us a certain number of as yet unsatisfactorily identifiable forms from Europe and Africa which certainly do not belong to *Hippopotamus* sensu stricto with *H. amphibius* as the genotype and for which the creation of new generic names then would be inevitable. I cannot see, e.g., how the "about twelve extinct ones [species] from the Pleistocene of Europa, Africa and Madagascar" fit into the genus *Hippopotamus* in the restricted sense as recently defined by Deraniyagala (1947, p. 228).

The following characters, typical of the Asiatic forms, apply to certain non-Asiatic forms as well:

The presence of six incisors instead of four constitutes a character also found in *H. pantanellii* Joleaud from the Plaisancian of Italy (references in Hooijer, 1946, p. 302) and *H. hipponensis* Gaudry from the Villafranchian of Algeria (Arambourg, 1944 a). A deep instead of merely a shallow longitudinal groove posteriorly in the upper C occurs in not less than three non-Asiatic forms too, viz., in *H. siculus* Hooijer from the Pontian of Sicily (Hooijer, 1946), in *H. protamphibius* Arambourg from the Lower Pleistocene of Abyssinia (Anthony, 1946), and in *H. liberiensis* Morton. The lacrimal is separated from the nasal by an anterior prolongation of the frontal in *H. protamphibius* Arambourg (1944 b, 1948, p. 316/17) and in *H. liberiensis* Morton too.

The skull of the Asiatic hippopotamuses is furthermore characterized by the premaxillaries being in contact with each other along their entire length (in *H. amphibius* the premaxillaries are separate for a portion of their length), by the constricted part of the calvarium being less elongated and the maxillaries expanding more rapidly anteriorly than is the case in *H. amphibius*, by the nasals being hardly instead of greatly broadened behind, and by the angular process of the mandible not being pointed forwards. All of these characters are shared by the skull of *H. liberiensis*. The resemblance of the Asiatic forms to *H. liberiensis* is also displayed throughout the postcranial skeleton.

In contradistinction to the fossil European and African forms of *Hippopotamus* enumerated on p. 29 the Asiatic forms are evidently very closely related. Within the species *H. sivalensis* it is possible to follow certain trends in the evolution of the skull and teeth which will be set forth in the concluding chapter. I shall begin, however, with the discussion of *H. iravaticus* which is placed at the starting point of the Asiatic series by Lydekker.

Hippopotamus iravaticus Falconer et Cautley

? *Hippopotamus*, Clift, Trans. Geol. Soc. London, ser. 2, vol. 2, 1828, p. 373, pl. 40 figs. 3-4, pl. 41 figs. 19-20.

Hippopotamus (Hexaprotodon) iravaticus Falconer et Cautley, Fauna Antiqua Sivalensis, London, 1847, pl. 57 figs. 10-11, Ibid., 1849, pl. 83 fig. 12 (description: Falconer, 1868 I, p. 498, 529), Falconer, Journ. Acad. Nat. Sci. Philad., ser. 2, vol. 1, 1849, p. 237, Pal. Mem. I, London, 1868, p. 142.

Hippopotamus iravaticus, Lydekker, Rec. Geol. Surv. Ind., vol. 15, 1882, p. 31, *ibid.*, vol. 16, 1883, pp. 83 and 91, Mem. Geol. Surv. Ind., ser. 10, vol. 3, 1884, pp. 42 and 131, Cat. Foss. Mamm. Br. Mus., part 2, London, 1885, p. 309, Cat. Siw. Vert. Indian Mus., part 1, Calcutta, 1885, p. 53, Rec. Geol. Surv. Ind., vol. 20, 1887, p. 76; Schlosser, Abh. k. bayer. Akad. Wiss., Math.-Phys. Kl., vol. 22, part 1, 1903, p. 207; Pilgrim, Rec. Geol. Surv. Ind., vol. 40, 1910, pp. 196 and 203; Haug, Traité de Géologie, part 2, Paris, 1911, p. 1724; Pilgrim, Rec. Geol. Surv. Ind., vol. 43, 1913, p. 285; Matthew, Bull. Amer. Mus. Nat. Hist., vol. 56, 1929, p. 449; Van der Maarel, Wet. Med. Dienst Mijnb. Ned. Ind., no. 15, 1932, p. 91.

H[ippopotamus] iravaticus, Falconer, Pal. Mem. I, London, 1868, p. 21; Woodward, Geol. Mag., n.s., dec. 3, vol. 3, 1886, p. 117; Nicholson and Lydekker, A Manual of Palaeontology, 3rd ed., vol. 2, Edinburgh and London, 1889, p. 1317; Woodward, Outlines of Vertebrate Palaeontology, Cambridge, 1898, p. 346; Pilgrim, Rec. Geol. Surv. Ind., vol. 43, 1913, p. 300; Arambourg, Mission Scientifique de l'Omo 1932-33, vol. 1, fasc. 3, 1948, p. 333.

Hexaprotodon iravaticus, Falconer, Pal. Mem. II, London, 1868, p. 407; Trouessart, Catalogus Mamm., Quinquennale Suppl., Berlin, 1905, p. 664; Matthew, Bull. Amer. Mus. Nat. Hist., vol. 56, 1929, p. 557; Colbert, Trans. Amer. Phil. Soc. Philad., n.s., vol. 26, 1935, p. 280, Bull. Amer. Mus. Nat. Hist., vol. 74, 1938, p. 419, fig. 61 and fig. 62 right fig., Trans. Amer. Phil. Soc. Philad., n.s., vol. 32, 1943, p. 408, fig. 83.

[*Hexaprotodon*] *iravaticus*, Leche, Lunds Univ. Arsskr., N.F., Avd. 2, vol. 16, no. 10, 1921, p. 42.

H[ippopotamus] iravaticus Blainville, Ostéographie Hippopotamus, Paris, 1847, p. 241.

H[ippopotamus] iravadicus Blainville, *Ibid.*, p. 241; Major, Proc. Zool. Soc. London, 1896, p. 976; Osborn, The Age of Mammals, New York, 1910, p. 329.

Hippopotamus (Hexaprotodon) iravadicus, Medlicott and Blanford, Manual Geology India, Calcutta, 1879, p. 574.

Hippopotamus iravadicus, Lydekker, Journ. As. Soc. Beng., vol. 49, part 2, 1880, pp. 27 and 35.

H[ippopotamus] iravadicus Giebel, Die Säugethiere, Leipzig, 1855, p. 220, Odontographie, Leipzig, 1855, p. 78.

Hexaprotodon iravadicum Lydekker, Rec. Geol. Surv. Ind., vol. 9, 1876, p. 91, Mem. Geol. Surv. Ind., ser. 10, vol. 1, 1876, p. 78.

Hippopotamus (Hexaprotodon) iravaddicus Roger, Corr. Blatt zool. min. Ver. Regensburg, vol. 35, 1881, p. 169, Ber. Naturw. Ver. Schwaben u. Neuburg, vol. 29, 1887, p. 93, *Ibid.*, vol. 32, 1896, p. 211.

Hippopotamus irawaddicus, Trouessart, Catalogus Mamm., nov. ed., vol. 2, Berlin, 1898, p. 830.

[*Hippopotamus*] *irawaddicus*, Zittel, Handbuch der Palaeontologie, part 1, vol. 4, Vertebrata (Mammalia), Munich and Leipzig, 1893, p. 346.

non *Hippopotamus iravadicus* Noetling, Rec. Geol. Surv. Ind., vol. 30, 1897, p. 242, pl. XIX and pl. XX fig. 1.

Hippopotamus iravaticus Wadia, Geology of India, London, 1919, p. 239; Depéret, Bull. Soc. Géol. France, ser. 4, vol. 21, 1921, p. 163; Stamp, Geol. Mag., vol. 59, 1922, p. 498; Chhibber, Geology of Burma, London, 1934, pp. 254 and 257; Wadia, Geology of India, London, 1939, p. 273.

Hippopotamus *iravaticus* Chhibber, Geology of Burma, London, 1934, p. 254.

Diagnosis: The smallest of the Asiatic species, closely comparable to *Hippopotamus lemerlei* Grandidier from Madagascar as to size. Six incisors in the lower jaw; I_2 slightly above, and I_3 below the level of I_1 , and both not much smaller than I_1 . Mandibular symphysis very long relative to its width. A deep longitudinal groove posteriorly in the upper C. Upper molars of a simple structure, differing from those of *Hippopotamus sivalensis* Falconer et Cautley in the lesser expansion of the lobes of the cusps, and in the lesser development of the cingula. Lacrimal separated from nasal by an anterior prolongation of the frontal. Orbit apparently hardly elevated, and rather central in position.

Holotype: A mandibular symphysis figured in "Fauna Antiqua Sivalensis", pl. 57 fig. 10, and preserved in the British Museum (no. 14771).

Horizon: Upper Irrawaddy Beds, Lower Pleistocene.

Locality: Irrawaddy River valley, Burma.

The present species, of which I have seen no material, is based upon two specimens of the symphysis from Ava (Burma) figured in F.A.S. (pl. 57 figs. 10 and 11). The distal part of a small radius subsequently figured in F.A.S. (pl. 83 fig. 12) is also referred to the present species. The distal parts of a radius and of a femur in the Indian Museum at Calcutta, supposed to originate from Ava, were ascribed to this form by Falconer (1868 I, p. 142). The species was recorded from Sub-Himalaya and Burma by Lydekker (1883, p. 91), who presented a description of the type mandible (Lydekker, 1884 a, pp. 42-43). It is a subadult specimen with P_2 half protruded, irregularly arranged incisors and a very long symphysis as recorded above in the diagnosis. Lydekker also emphasizes the fact that I_3 is laterally compressed, but a later specimen has disproven this view. Several specimens of the symphysis of small hippopotamuses from Burma in the Indian Museum are stated to belong very probably to the present form; this may hold for the jaw fragments from the left bank of the Irrawaddy river collected in 1826 by Crawford and figured by Clift (1828, p. 373, pl. 40 figs. 3-4, pl. 41 figs. 19-20) too. An occiput from Burma in the Indian Museum

provisionally referred to the present species (Lydekker, 1885 b, p. 53), unfortunately, has never been described or figured.

A worn femur from Burma was identified with the present species by Noetling (1897). Since the bone possesses a third trochanter it does not belong to the genus *Hippopotamus* at all, and may be a perissodactyle femur.

Pilgrim (1910, p. 203) records *iravaticus* from the Middle Siwaliks of Yenangyaung (Burma) and Asnot, though the latter locality is uncertain (Pilgrim, 1913, p. 300), and afterwards from the Dhok Pathan zone (l.c.). Stamp (1922, p. 498) found *iravaticus* only in the upper fauna from the Irrawaddy sediments, in a conglomerate zone some 4500 feet above the base of the Irrawaddies at Yenangyaung. This horizon agrees faunally with the Tatrot zone (Upper Siwaliks) of Lower Pleistocene age (Colbert, 1938, p. 278), and yielded a partial calvarium and a left upper C well described and figured by Colbert (1938, pp. 419-423). From his descriptions I take that the teeth are of a simpler build than those in *H. sivalensis*, and the cranial characters mentioned above in the diagnosis. The upper C, a cross section of which was kindly sent to me on my request by Dr. Colbert, has a relatively unexpanded internal lobe, but the posterior groove is as well defined as that in *H. sivalensis*. The partial symphysis described by Colbert in 1943 (Colbert, 1943, p. 409 fig. 83) from the Upper Irrawaddy Beds has somewhat larger incisors, which are compressed in a different way as compared to those in the holotype, but similar differences are found in various races of *H. sivalensis* too and are of no importance.

Mainly on the ground of its extremely long symphysis the present species is regarded as more primitive than any other Asiatic hippopotamus by Lydekker, a conclusion that is corroborated by Colbert's description of the calvarium. We know, however, as yet practically nothing of the amount of variation within this species, and I still may quote Lydekker (1885 a, p. 309): "Other specimens are required to indicate its full affinities".

The measurements of the calvarium and the mandibles will be found in tables II and III at the end of the present work. Specimen no. 1 in table III is Lydekker's specimen, no. 2 is that described by Colbert.

Hippopotamus sivalensis Falconer et Cautley

Diagnosis: Size variable; larger in the continental than in the Javan subspecies. Six incisors both in the upper and in the lower jaw. The upper C has a deep longitudinal groove on its posterior surface. The anterior premolars diverge from each other on the opposite sides of the calvarium and the mandible. The premaxillaries are in contact with each other along

their entire length. The constricted part of the calvarium is less elongated and the maxillaries expand anteriorly more rapidly than in *H. amphibius* L. The nasals are hardly expanded posteriorly, and the lacrimal is separated from the nasal by an anterior prolongation of the frontal. The angular process of the mandible is not pointed forwards.

Holotype: A calvarium from the Siwaliks described by Falconer and Cautley (1836).

Horizon: The species ranges from the Lower Pleistocene ¹⁾ to the Upper Pleistocene.

Locality: The various subspecies occur in India, Burma, Ceylon, and Java.

The subspecies of the present species are distinguished by their size as well as by the degree of elevation of the orbits above the level of the frontals, the shape of the occiput, the relative length of the postdental part of the calvarium, the structure of the upper molars, the relative length and height of the mandibular symphysis, the relative height of the horizontal ramus, and the relative size of the lower incisors, as will be fully set forth in the following pages.

This is the appropriate place to explain the terms large, small, low, high, long, and short as used in the diagnoses of the subspecies with respect to size and shape of the skull and its parts, and which would be meaningless without the definition of some standard. Most of the terms refer to indices and are, therefore, independent of gross size. Size in the gross of a subspecies would be judged most reliably by the total length of the calvarium or of the mandible, which, unfortunately, is not known for all of the subspecies. Some of the subspecies are based on teeth exclusively. According to the size of the teeth, particularly the widths of the upper and lower molars, the Javan subspecies are definitely smaller than the Indian. The largest of the continental subspecies is *H. sivalensis palaeindicus*, the dimensions of the skull of which are equal to those of a medium-sized *H. amphibius* skull (a large female or a small male). Two of the Javan

1) The Tji Djoelang and the Kali Glagah faunae of Java which yield the oldest remains of *Hippopotamus* in this island have been determined as Middle and Upper Pliocene in age by Von Koenigswald (1935 a), but are placed in the Lower Pleistocene by Colbert (1942, p. 1454, 1943, p. 426) and Movius (1944, p. 84). This difference of opinion depends upon the age of the Tatrot zone of the Siwaliks with which the above mentioned Javan faunae are correlated. The Tatrot zone has a strong Villafranchian aspect, and the Villafranchian marks the beginning of the Pleistocene as unanimously agreed upon at the International Geological Congress at London in 1948. In the present paper the Tji Djoelang and Kali Glagah faunae as well as the Tatrot zone are taken as of Lower Pleistocene age.

subspecies, viz., *H. sivalensis sivalensis* and *H. sivalensis koenigswaldi*, may be characterized as being small since their skull dimensions are markedly smaller than those of the smallest adult female skull of *H. amphibius* which I have seen. The most progressive Javan subspecies, which is described in the present paper as *H. sivalensis soloensis* nov. subsp., is of larger dimensions than the other subspecies from Java mentioned above, and partly falls within the variation limits of *H. sivalensis sivalensis*; its size, therefore, is indicated as "moderate".

The orbit is elevated above the frontals to a degree different for the various subspecies, and offers one of the most valuable characters for discrimination. The orbito-cephalic index, which is the elevation of the orbit above the frontals as a percentage of the height of the calvarium from the palatine, varies from 9 in a specimen of *H. sivalensis sivalensis* with a low orbit to 41 in a peculiar specimen from the Siwaliks of the Punjab in the Dubois collection. The orbit is also very high in *H. sivalensis soloensis* (orbito-cephalic index 34-39); the range of variation of this index in *H. amphibius* is 10 to 32.

The occiput also varies markedly in its relative height. The occiput index, which is the height (from basion) as a percentage of the width, varies from 78 in a specimen of *H. sivalensis sivalensis* with a high occiput to 60 in a specimen of *H. sivalensis soloensis*; the range of variation in *H. amphibius* is practically the same, the occiput index varying from 77 to 60.

The postdental part of the calvarium is variable in length, as expressed in the P⁴-M³-condyle index which is the length P⁴-M³ as a percentage of the length from the posterior border of M³ to the posterior border of the occipital condyles. This index is 63 in a specimen of *H. sivalensis sivalensis* in which the postdental portion is long, against 84 in *H. sivalensis palaeindicus* with a short postdental portion. In *H. amphibius* the postdental portion of the calvarium is typically shorter than that in *H. sivalensis* but the range of variation of the index is equally wide (from 74 to 96).

The mandibular symphysis is markedly longer in some of the subspecies than in others. The symphysis length-width index, which is the length of the symphysis as a percentage of the interval between the lower C, is 96 in a specimen of *H. sivalensis sivalensis* with a very long symphysis, and only 57 to 64 in *H. sivalensis namadicus* which is characterized by its very short symphysis. In *H. amphibius* the symphysis length-width index varies from 64 to 87, the latter value is within the variation limits of *H. sivalensis sivalensis*. The symphysis height-length index, which is the height of the symphysis as a percentage of its length, likewise affords a good subspecific

character, being very low (37-50) in *H. sivalensis sivalensis* against high to very high (60-ca. 77) in *H. sivalensis palaeindicus*. The range of variation of the symphysis height-width index in *H. amphibius* (49-64) is again transitional between the two extremes.

In keeping with the progressive shortening and increase in height of the symphysis the horizontal ramus of the mandible becomes higher too. The ramus length-height index, which is the length of the ramus from front to M_3 as a percentage of its height at M_2 , decreases from 298 in a specimen of *H. sivalensis sivalensis* with a low ramus to 214-232 in *H. sivalensis soloensis* in which the ramus is very high. In *H. amphibius* the horizontal ramus of the mandible is typically lower than that in *H. sivalensis* but the range of variation of the index is equally wide (from 268 to 350).

Though Lydekker (1882 a, p. 32, 1884 a, p. 39) and Van der Maarel (1932, p. 105) state that no sufficient distinction can be drawn between the different species of *Hippopotamus* from the structure of the molars, Von Koenigswald (1934 a, 1940, p. 62) remarks that in progressive forms the enamel pattern of the molars is more complicated than that in primitive forms. It is indeed possible to distinguish between two types of upper molars, which I shall refer to below as the *sivalensis* type and the *palaeindicus* type respectively. The upper molars of *H. sivalensis sivalensis* (F.A.S., pl. 62 fig. 1; Lydekker, 1884 a, p. 38 fig. 1 b, 1885 a, p. 298 fig. 38 b) as well as those of *H. sivalensis sivajavanicus* (Van der Maarel, 1932, pl. VI fig. 3) have the posterior lobe of the paracone never directed outward and never extending labially beyond the anterior lobe of the metacone to the degree typical of that in the upper molars of *H. sivalensis palaeindicus* (F. A. S., pl. 57 figs. 1b and 2 a, pl. 58 fig. 4 b, pl. 62 fig. 11) and in those of *H. sivalensis soloensis* (Stremme, 1911 b, pl. XVI fig. 7). Though this is practically the only character by which the two types can be distinguished, the development of the cingula and of the "trefoil pattern" of the cusps being too variable to be reliable, I have no doubt that the two types are really distinct. Some of the upper molars of *sivajavanicus* show an initial development of the *palaeindicus* character, and there are upper molars from Java that cannot be referred with certainty to either of the two types, but this could be expected since there is intergradation in all of the characters serving to distinguish between the subspecies. It is very probable that there is also a difference in the degree of hypsodonty between the *sivalensis* and the *palaeindicus* type, but this could not be established because of the lack of sufficiently well preserved upper molars.

Hippopotamus sivalensis sivalensis Falconer et Cautley

Hippopotamus, Durand, Asiatic Researches, vol. 19, 1836, pl. IV figs. 1, 2, and 4, pl. V fig. 1, pl. VI figs. 1 and 2.

Hippopotamus (Hexaprotodon) sivalensis Falconer et Cautley, Asiatic Researches, vol. 19, 1836, p. 51, Fauna Antiqua Sivalensis, London, 1847, pls. 59-61, pl. 62 figs. 1-10, pls. 63-66, pl. 68 figs. 19-21 (description: Falconer, 1868 I, pp. 449-505, 508), Falconer, Journ. Acad. Nat. Sci. Philad., ser. 2, vol. 1, 1849, p. 237, Pal. Mem. I, London, 1868, p. 130, pls. XI-XII, p. 142; Medlicott and Blanford, Manual Geology India, Calcutta, 1879, p. 574, pl. XVIII figs. 6 and 8.

non *Hippopotamus (Hexaprotodon) sivalensis* Seguenza, Boll. Soc. Geol. Ital., vol. 21, 1902, p. 162, pl. VII.

Hippopotamus sivalensis Falconer et Cautley, Journ. As. Soc. Beng., vol. 4, 1835, p. 706 (nomen nudum), Falconer, Ibid., vol. 6, 1837, p. 233; Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 589; Lydekker, Journ. As. Soc. Beng., vol. 49, part 2, 1880, pp. 27 and 35, Rec. Geol. Surv. Ind., vol. 15, 1882, p. 32, Ibid., vol. 16, 1883, pp. 83 and 91, Mem. Geol. Surv. Ind., ser. 10, vol. 3, 1884, p. 37, pl. VI fig. 1, p. 131, Trans. Roy. Dublin Soc., ser. 2, vol. 3, 1884, p. 77, Cat. Foss. Mamm. Br. Mus., part 2, London, 1885, p. 297, Cat. Siw. Vert. Indian Mus., part 1, Calcutta, 1885, p. 51, Rec. Geol. Surv. Ind., vol. 20, 1887, p. 76; Trouessart, Catalogus Mamm., nov. ed., vol. 2, Berlin, 1898, p. 830; Major, Geol. Mag., n.s., dec. 4, vol. 9, 1902, p. 194, fig. 1; Schlosser, Abh. k. bayer. Akad. Wiss., Math.-Phys. Kl., vol. 22, part 1, 1903, p. 95; Pilgrim, Rec. Geol. Surv. Ind., vol. 40, 1910, pp. 202 and 203; Haug, Traité de Géologie, part 2, Paris, 1911, p. 1724; Terra, Vergl. Anat. menschl. Gebisses, Jena, 1911, p. 318; Pilgrim, Rec. Geol. Surv. Ind., vol. 43, 1913, p. 324; Van der Maarel, Wet. Med. Dienst Mijnb. Ned. Ind., no. 15, 1932, p. 89.

non *Hippopotamus sivalensis* Seguenza, Boll. Soc. Geol. Ital., vol. 26, 1907, p. 106, pl. V figs. 49-54, pls. VI and VII.

H[ippopotamus] sivalensis, Blainville, Ostéographie Hippopotamus, Paris, 1847, pp. 71 and 240, Atlas, pls. III, V, VII and VIII; Giebel, Die Säugethiere, Leipzig, 1855, pp. 219 and 220, Odontographie, Leipzig, 1855, p. 77, pl. XXXIII fig. 4; Murray, The geogr. distr. Mamm., London, 1866, p. 166; Falconer, Pal. Mem. I, London, 1868, p. 21; Lydekker, Rec. Geol. Surv. Ind., vol. 15, 1882, p. 103; Woodward, Geol. Mag., n.s., dec. 3, vol. 3, 1886, p. 117, pl. III figs. 3-5; Nicholson and Lydekker, A Manual of Palaeontology, 3rd ed., vol. 2, Edinburgh and London, 1889, p. 1317, fig. 1190; Dubois, Natuurk. Tijdschr. Ned. Ind., vol. 51, 1891, p. 97; Zittel, Handbuch der Palaeontologie, part 1, vol. 4, Vertebrata (Mammalia), Munich and Leipzig, 1893, p. 346; Major, Proc. Zool. Soc. London, 1896, p. 976; Woodward, Outlines of Vertebrate Pal., Cambridge, 1898, p. 346; Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1265; Stromer, Zeitschr. deut. geol. Ges., vol. 66, 1914, p. 32, Monnier and Lamberton, Bull. Acad. Malgache Tanarive, n.s., vol. 3, 1922, p. 211, pl. VII left fig., Arambourg, Compt. Rendus Acad. Sci. Paris, vol. 218, 1944, p. 602 fig. I; Hooijer, Arch. Néerl. d. Zool., vol. 7, 1946, p. 309 fig. 1 a-b; Arambourg, Mission Scientifique de l'Omo 1932-33, vol. 1, fasc. 3, 1948, p. 317, fig. 30 B.

Hexaprotodon sivalensis, McClelland, Journ. As. Soc. Beng., vol. 7, 1838, p. 1042, pl. LIX fig. 4; Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 587; Falconer, Pal. Mem. II, London, 1868, p. 407; Lydekker, Rec. Geol. Surv. Ind., vol. 9, 1876, p. 90; Flower and Lydekker, Cat. Mus. Roy. Coll. Surg., part 2, London, 1884, p. 337; Trouessart, Catalogus Mamm., Quinquennale Suppl., Berlin, 1905, p. 664; Leche, Lunds Univ. Årsskr., N. F., Avd. 2, vol. 16, no. 10, 1921, p. 42; Matthew, Bull. Amer. Mus. Nat. Hist., vol. 56, 1929, p. 444; Colbert, Trans. Amer. Phil. Soc. Philad., n.s., vol. 26, 1935, p. 278, figs. 122-126, 127 A, A¹, 128 A; De Terra and Teilhard de Chardin, Bull. Amer. Phil. Soc. Philad., vol. 76, 1936, p. 808.

- Hexaprotodon*, Owen, Odontography, London, 1840-45, vol. 1, p. 566, vol. 2, pl. 143 fig. 1.
- Hippopotamus silvalensis* Bronn, Index Pal., part 2 B, Stuttgart, 1849, p. 704.
- H[ippopotamus] silvalensis*, Van der Maarel, Wet. Med. Dienst Mijnb. Ned. Ind., no. 15, 1932, p. 106.
- Hippopotamus hexaprotodon* L[aurillard], Dict. univ. d'Hist. nat., 2nd ed., vol. 7, Paris, 1868, p. 212.
- Hexaprotodon sivalense* Lydekker, Mem. Geol. Surv. Ind., ser. 10, vol. 1, 1876, p. 78; Matthew, Bull. Amer. Mus. Nat. Hist., vol. 56, 1929, p. 557.
- Hexaprotodon anisiperus* McClelland, Journ. As. Soc. Beng., vol. 7, 1838, p. 1045, pl. LIX fig. 5.
- H[ippopotamus] anisoperus* Blainville, Ostéographie Hippopotamus, Paris, 1847, p. 76.
- H[ippopotamus] anisoporus* Blainville, Ostéographie Hippopotamus, Paris, 1847, p. 241.
- Hexaprotodon anisoperus*, Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 587.
- Hippopotamus anisoperus*, Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 589, *Ibid.*, part 2 B, Stuttgart, 1849, p. 704.
- [Hippopotamus] anisoperas* Giebel, Die Säugethiere, Leipzig, 1855, p. 220.
- Hexaprotodon megagnathus* McClelland, Journ. As. Soc. Beng., vol. 7, 1838, p. 1045, pl. LIX fig. 6; Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 587.
- Hippopotamus megagnathus*, Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 589, *Ibid.*, part 2 B, Stuttgart, 1849, p. 704.
- H[ippopotamus] megagnathus*, Blainville, Ostéographie Hippopotamus, Paris, 1847, p. 76; Giebel, Die Säugethiere, Leipzig, 1855, p. 220.
- Hexaprotodon platyrhynchus* McClelland, Journ. As. Soc. Beng., vol. 7, 1838, p. 1045, pl. LIX fig. 7; Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 587.
- Hippopotamus platyrhynchus*, Bronn, Index Pal., part 1 A, Stuttgart, 1848, p. 589, *Ibid.*, part 2 B, 1849, p. 704.
- H[ippopotamus] platyrhynchus*, Blainville, Ostéographie Hippopotamus, Paris, 1847, p. 76; Giebel, Die Säugethiere, Leipzig, 1855, p. 220.

Diagnosis: Size moderate to large, orbit low to moderate, occiput high to moderate, postdental part of calvarium long to moderate. Upper molars large with the lobes of the anterior cusps in the transverse valley opposed to those of the posterior cusps, and the posterior lobe of paracone never markedly extending labially beyond the anterior lobe of metacone, cingulum variable in development. Mandibular symphysis very long to long relative to its width, and very low relative to its length. Ramus horizontalis low to moderately low at M_2 relative to its length, and height at M_2 equal to or less than length M_1-M_3 . I_2 two-thirds to about equal in size to I_1 , and I_3 slightly smaller than I_1 .

Holotype: A calvarium from the Siwaliks described by Falconer and Cautley (1836).

Horizon: Upper Siwaliks, Lower Pleistocene.

Locality: Siwalik Hills, N. India.

The present subspecies is founded on the description of a well preserved calvarium from the Siwalik Hills by Falconer and Cautley (1836). A wealth of material, not only of the calvarium and mandible but also of

the postcranial skeleton subsequently was figured in F.A.S. In 1838 McClelland named three more species, *H. anisiperus*, *H. megagnathus* and *H. platyrhynchus*, which are founded on certain mandible fragments the dimensions of which would be distinctive. The height of the mandible at pd_1 is 152 mm in a specimen referred to *H. megagnathus* (McClelland, 1838, p. 1043) which is one-half larger than that in the series of mandibles of *H. sivalensis sivalensis* measured by me in the British Museum, but the anterior width of the same specimen is 305 mm, which is not larger than that in the latter series. The dimensions of the mandible of *H. platyrhynchus* are smaller than those in the above mentioned series, but McClelland's specimen may be not yet adult. Lydekker (1884 a, p. 37) states that *H. sivalensis* was subdivided by McClelland apparently on insufficient grounds, and does not even cite McClelland's names. On the other hand, Lydekker distinguished between two varieties of the present form, the variety "*latidens*" having wider molars with better developed inner cingulum than that called "*angustidens*" (Lydekker, 1884 a, p. 39). To the latter variety he refers a small left mandibular ramus from the Siwaliks of the Punjab previously (Lydekker, 1882 a, p. 32) identified as *H. iravaticus*. Lydekker also places emphasis on the position of M^3 relative to the posterior border of the palate and to the anterior zygomatic root (processus zygomaticus maxillae) as means of distinction between the two varieties. A gradual gradation in these characters exists in the collection, however, and in a subsequent paper (Lydekker, 1885 a, p. 297) the two varieties are only cursorily referred to.

In his discussion of the cranial variations in the present form Lydekker (1884 a, p. 39/40) remarks upon certain calvariums which in their more prominent orbits and shorter postorbital portion as compared to the other specimens exhibit a marked step from the type in the direction of the Narbada hippopotamuses. I have been unable to find differences in the relative length of the postorbital portion of the calvarium in the various subspecies of *H. sivalensis*. The ratio of the postorbital to the preorbital length varies from 0.74 to 0.83 in *H. sivalensis sivalensis* (Colbert, 1935, p. 287), whilst in the most progressive Javan subspecies *H. sivalensis soloensis* this ratio varies from ca. 0.77 to 0.81. There is, however, an evolutionary trend in the species which affords an important character for discrimination between the primitive and the progressive races, viz., the tendency for the upper molar series to shift backward. The postdental portion of the calvarium in *H. sivalensis sivalensis* is definitely longer relative to the length P^4-M^3 than that in *H. sivalensis palaeindicus*; the P^4-M^3 -condyle index is 63-77 in the former against 82-84 in the latter

subspecies. While in *H. sivalensis sivalensis* the posterior border of M^3 mostly is in advance of the posterior border of the palate, it does sometimes (British Museum, no. 17068, figured in F.A.S., pl. 59 fig. 3, vide Lydekker, 1884 a, p. 39, and American Museum of Natural History, no. 19784, vide Colbert, 1935, p. 283) reach as far backward as the posterior border of the palate. In *H. sivalensis palaeindicus*, on the other hand, the posterior border of M^3 is slightly behind that of the palate (Lydekker, 1884 a, p. 46).

Lydekker's statement as to the prominence of the orbits in the present subspecies is correct; as will be shown below there is one calvarium in the Dubois collection in which the orbit is as much elevated as that in one specimen of *H. sivalensis palaeindicus*.

The present form has been recorded from the Pontian of Sicily by Seguenza (1902, p. 162; 1907, p. 106); from the figures given by this author, however, I have been able to show (Hooijer, 1946) that part of the supposed *Hippopotamus* remains in reality belong to *Diceros* aff. *pachygnathus* (Wagner) and to *Parabos* (?) spec. The true *Hippopotamus* remains from Sicily proved to belong to a new species which I described as *Hippopotamus siculus*.

Pilgrim (1910, p. 202) records *sivalensis* from the Upper Siwaliks of the Siwalik Hills; the variety *angustidens* is stated to occur in the Middle and Upper Siwaliks of Asnot and Dhok Pathan (l.c., p. 203). Afterwards *sivalensis* was restricted to the Boulder Conglomerate Zone (Pilgrim, 1913, p. 324). Colbert (1935, p. 35) states the present form to occur in the Tatrot and Pinjor Zones (Upper Siwaliks) and (l.c., pp. 281-285) gives a list of the distinguishing cranial characters.

In the British Museum (Natural History) at London I have measured some thirty specimens and fragments of the calvarium and of the mandible of the present subspecies. These specimens as well as those recorded by Falconer and Cautley (1836), Lydekker (1884 a), and Colbert (1935 and 1938), and the specimens in the Dubois collection are listed below, and the numbers given to the specimens refer to those given in tables II and III at the end of the present work.

Calvariums

No. of specimen	reference or Museum no. ¹⁾
1 and 2	Falconer and Cautley, 1836, p. 42; molars of B.M. nos. 10379 and 16381 respectively.
3	B.M. no. 2269, figured in F.A.S., pl. 59 fig. 1.

1) B.M. = British Museum (Natural History) at London; A.M. = American Museum of Natural History at New York.

No. of specimen	reference or Museum no.
4	B.M. no. 16175, figured in F.A.S., pl. 59 fig. 2; molars of B.M. no. 17068, figured in F.A.S., pl. 59 fig. 3.
5	B.M. no. 17084, figured in F.A.S., pl. 60 fig. 1; molars of B.M. no. M. 489.
6	B.M. no. 17081, figured in F.A.S., pl. 60 fig. 2; molars of B.M. no. M. 491.
7	B.M. no. 15929, figured in F.A.S., pl. 60 fig. 3.
8	B.M. no. 16377; molars of B.M. no. 17469.
9	B.M. no. 16382; molars of B.M. no. 15935.
10	B.M. no. 16378; orbit of B.M. no. 40889.
11	B.M. no. 16380; canine of B.M. no. 17827.
12	B.M. no. 15931; canine of B.M. no. 17469.
13	A.M. no. 19781, Colbert, 1935, p. 287.
14	A.M. no. 19776, Colbert, l.c. (P ⁴ -M ³ -condyle index from Colbert, l.c., p. 284 fig. 124).
15	A.M. no. 19794, Colbert, 1935, p. 287; canine of A.M. no. 19972, Colbert, 1938, p. 422.
16	A.M. no. 19817, Colbert, 1935, p. 287; molars of the same specimen in Colbert, 1938, p. 422.
17	A.M. no. 19775, Colbert, 1935, p. 287.
18	A.M. no. 19784, Colbert, l.c.
19	Coll. Dub. no. 3148.
20	Coll. Dub. no. 3101.
21	Coll. Dub. no. 3138.

Mandibles

1	Lydekker, 1884 a, p. 41 (var. <i>angustidens</i>).
2	Lydekker, l.c. (typical form).
3	B.M. no. 16316.
4	B.M. no. 16355.
5	B.M. no. 16359.
6	B.M. no. 36722.
7	B.M. no. 17085, figured in F.A.S., pl. 61 fig. 5.
8	B.M. no. 48454.
9	B.M. no. ? (matrix preserved between rami).
10	B.M. no. 16358 (not listed by Lydekker, 1885 a, pp. 297-302).
11	B.M. no. 32541.
12	A.M. no. 19776, Colbert, 1935, p. 288; molars of Mining Dept. Delft, no. K.A. 10412.
13	A.M. no. 19784, Colbert, l.c.
14	A.M. no. 19918, Colbert, l.c.
15	Coll. Dub. no. 3147.

Coll. Dub. no. 3148, Kodawala, 2 miles N.E. of Haripoor on the Somb Nuddy, Sirmur State, Punjab (pl. V fig. 5).

Slightly deformed calvarium, broken off slightly in advance of the infra-orbital foramen. The zygomatic arches are almost completely lost. On either side of the dorsal surface the sutures of the lacrimal are well seen: the lacrimal reaches the anterior border of the orbit and is separated from the nasal by a rostral prolongation of the frontal. It extends as far anteriorly

as the jugal. The dorsal surface is flattened in the middle, the frontal crests are sharp, the sagittal crest and the temporal crests are strongly damaged. The orbits, though broken off to a considerable extent, seem to have been elevated to a little extent only. There is a rather deep pit in the maxillary beneath the anterior zygomatic root. The infra-orbital foramen is not large and is situated above P_3 .

The occipital condyles are entire, but the paroccipital processes have partly broken off. Between the rounded bullae, provided with a medio-rostral point, the basilar tubercles on the basioccipital are visible. The V-shaped posterior border of the palate extends a good deal behind the molar series; there is a median ridge on the palate.

The left P^4 is the only premolar that is preserved; it is much worn and shows an antero-internal enamel infolding. The M^1 is much damaged and worn, and the infolding of the enamel border at the lingual side of the left specimen as well as a small enamel islet are the last traces of the transverse valley. M^2 has a well developed cingulum as well as M^3 , of which latter the left specimen still shows an enamel islet between the metacone and the metaconule as the last trace of the longitudinal valley. The length of all molars is much reduced by interproximal wear.

As a consequence of the old age of the individual to which this calvarium has belonged the P^4 - M^3 -condyle index presents a rather low figure; that is to say, the tooth-series is rather short relative to the length of the post-dental portion. In the British Museum material the above index varies from 68 to 77, but from one of Colbert's figures of a rather well preserved calvarium in the American Museum collection (Colbert, 1935, p. 284 fig. 124) I take this index to be only 64; in our specimen it is 63. The structure of the molars does not furnish a key as to the identity of the present specimen since the lingual cingulum is always very variable in development. The shape of the occiput is hardly characteristic either. Size and the elongated postdental portion, however, leave no doubt as to the subspecific position. The fact that there is a deep pit under the anterior part of the zygomatic arch in the present form is stressed by Colbert (l.c., p. 282) who states that this probably served as an attachment for the buccinator muscle. I found this pit to be very variable in *H. amphibiis* as well as in the present species, and do not consider its presence to be a matter of great moment as a diagnostic character. The measurements of the present specimen will be found under no. 19 in table II.

Coll. Dub. no. 3101, Samalka, 2 miles N.W. of Haripoor on the Somb Nuddy, Sirmur State, Punjab.

Incomplete calvarium, broken off in front of the orbits, the right of

which had to be filled with plaster. The left orbit could be cleared off the matrix; the elevation above the frontals is moderate. The right zygomatic arch is for the greater part missing; the left, apart from a small portion restored with plaster, is complete. The occiput is slightly elevated, and the occipital condyles have broken off. The postglenoid processus as well as the basioccipital and the pterygoids are lost; the bullae are preserved. What is left of the palate extends behind the molar series.

The teeth are badly damaged with the exception of the right M^3 which latter, however, is much worn down. The anterior cusps have become confluent on the worn surface and so have the posterior. There are remains of a strong lingual cingulum, especially on M^2 .

The elevation of the orbit in the present specimen is slightly more stressed than that in the British Museum series in which the orbito-cephalic index varies from 9 to 16. In our specimen this index is 18, which is also the value found in one of the *sivalensis palaeindicus* specimens. The measurements are given under no. 20 in table II.

Coll. Dub. no. 3138, Samalka, 2 miles N.W. of Haripoor on the Somb Nuddy, Sirmur State, Punjab (pl. IV fig. 2).

Fragment of right maxillary with pd^4-M^3 . The specimen has broken off along the median ridge on the palate, and a few cm in advance of M^1 . The anterior part of the jugal is preserved but much damaged below.

Of the posterior milk premolar only the very much worn posterior moiety is left. M^1 is entire except for the lingual surface of the protocone. Fortunately the longitudinal valley between the posterior cusps, as well as the whole of the transverse valley, are well shown. The posterior lobe of the paracone is opposed directly to the anterior lobe of the metacone, and the posterior lobe of the protocone, which is only small, is opposed directly to the anterior lobe of the metaconule. The cingulum is high and wide at the anterior surface, continues along the labial and the lingual surfaces, and rises again posteriorly. Some small accessory cusplets are formed at the entrances to the transverse valley. The "trefoil pattern" is well shown on the posterior cusps; each cusp is pinched in anteriorly and at the posterior side and consequently is formed of three lobes. In the metacone we observe the enamel figure to be even more complicated as a result of the presence of a fourth lobe, a small one, that has developed on the lingual surface and projects into the longitudinal valley. The metaconule has a corresponding depression. A structure like that of the metacone in this specimen we might conveniently designate as "four-leaved clover pattern" to use a botanical comparison again.

M^2 has crumbled away to the level of the cingulum which is strong;

apart from its posterior portion the cingulum itself is undamaged. Of the original wearing surface the main and the anterior lobe of the protocone are preserved only. The tooth appears to have been not fully in place for the cingulum is on a lower level than that of M^1 , at any rate the M^2 has not been long in use. It is much larger than the preceding molar but has essentially the same structure; the lobes of the cusps in the transverse valley have the same mutual position which is so markedly characteristic of the present form. Not much seen of the fourth lobe to the metacone, showing that this structure disappears with proceeding wear. Of M^3 only the apices of the cusps are visible; evidently this tooth had not yet cut the gums.

The present molars display the structural type that I have designated above as the *sivalensis* type. The teeth are in no way inferior in structural complexity to those of *H. amphibius*. As Colbert (1935, p. 281) correctly observes, any differences between *H. amphibius* and *H. sivalensis* in the molar teeth are very slight, in fact, so slight as to be practically non-existent. It must be borne in mind, however, that the molars are comparable only when the specimens are in the same stage of wear. As the molar becomes more worn down the main lobes of the cusps become relatively larger; the anterior lobes of the protocone and the paracone soon become confluent with each other and with the anterior cingulum, making the pattern less complicated. The "four-leaved clover pattern" of the metacone is shown only in a certain stage of wear, viz., while the posterior lobes of the metacone and of the metaconule are becoming confluent with each other and with the posterior cingulum. In more advanced stages of wear the lingual lobe to the metacone diminishes again, leaving only a slight tumefaction on the lingual surface of the metacone and a corresponding indentation on the labial surface of the metaconule. The lobes in the transverse valley of the upper molars do not change appreciably during the process of wear and consequently offer the most reliable distinguishing characters. The present molars agree with those of *H. sivalensis sivalensis* (F.A.S., pl. 62 fig. 1) in having the posterior lobe of the paracone directly opposed to the anterior lobe of the metacone, while in *H. sivalensis palaeindicus* (F.A.S., pl. 57 figs. 1 b and 2 a, pl. 58 fig. 4 b, pl. 62 fig. 11) the posterior lobe of the paracone is more or less directed outward and extends labially beyond the anterior lobe of the metacone. Both types occur in the Javan subspecies of *H. sivalensis* too, and while the *sivalensis* type of upper molar is found in a subspecies (*H. sivalensis siva javanicus*) that has the greatest craniometrical similarity to *H. sivalensis sivalensis*, the *palaeindicus* type is very clearly shown in a subspecies (*H. sivalensis soloensis*) that has the greatest resemblance in cranial characters to *H. sivalensis palaeindicus*. The difference in

the structure of the molars goes hand in hand with definite cranial differences, and therefore I believe that the difference between the two types, however small, is fundamental. If it is ignored we are destroying the only character available for the distinction of the upper molars. The measurements of the molar teeth of the present specimen are given under no. 21 of table II.

Coll. Dub. no. 3137, Samalka, 2 miles N.W. of Haripoor on the Somb Nuddy, Sirmur State, Punjab.

Fragment of right maxillary with very badly damaged teeth. The premolars have completely broken off; the series, however, is seen to curve outward anteriorly as is typical of the species *H. sivalensis*. The subspecific position is rendered certain by the structure of the M^2 and M^3 in which the posterior lobe of the paracone is opposed directly to the anterior lobe of the metacone. M^3 is well in advance of the posterior border of the palate. Measurements cannot be given.

Coll. Dub. no. 3147, Baro, $4\frac{3}{4}$ miles W.N.W. of Haripoor on the Somb Nuddy, Sirmur State, Punjab (pl. X fig. 2).

Right horizontal ramus of the mandible, broken off a few cm behind M_3 . The alveoli of I_3 and I_2 are exposed over their entire length; of that of I_1 the proximal portion is preserved only, it extends to the posterior border of the symphysis. The diameter of the latter alveolus cannot be measured exactly but does not seem to differ much from that of I_3 . This interesting specimen clearly shows that the alveoli of three incisors do not run parallel to each other; that of I_2 , the smaller of the three, becomes higher relative to that of I_3 when passing from front to back. At the alveolar margin these incisors were approximately on the same level. Only a small part of the canine is preserved, its enamel cover is striated longitudinally.

The single alveolus of the pd_1 is placed half-way between the C and the P_2 , of which latter, as well as of P_3 and P_4 , only the roots are present. Of M_1 even the roots have got lost. M_2 is very much worn down, and the cingulum is lost. M_3 is the best preserved tooth but also much worn; the transverse valley is indicated by infoldings of the labial and of the lingual enamel borders. The hypoconulid is triangular in shape, and a cingulum is perceivable along the entoconid and the hypoconid.

In the original description of the present form it was stated that the three lower incisors are of subequal size, but the series of mandibles in the British Museum measured by me show the greater diameter of I_2 to vary from two-thirds to about nine-tenth of that of I_1 , while I_3 is always slightly smaller than I_1 . The transverse section of the symphysis, depicted in F.A.S., pl. 62 fig. 4 a, shows I_2 to be definitely smaller than the other incisors and

also shows that this incisor is higher in position than I_1 and I_3 , a condition that reminds of that in *H. sivalensis namadicus* (see F.A.S., pl. 57 fig. 12). Measurements of the symphysis cannot be given, but the relative height of the horizontal ramus renders the subspecific position of the present specimen certain. The length of the three molars is equal to the height of the ramus at M_2 , making a molar length-ramus height index of 100, while the ramus length-height index is 250; the latter index varies from 259 to 298 in the British Museum material seen by me. Our specimen falls a little outside the variation ranges shown by the British Museum series which is, however, not very large.

In the Mining Department of the Technical College at Delft there is a fragment of the right horizontal ramus with P_4-M_3 from the Siwaliks (exact locality unknown) that belongs to the present subspecies too. I am indebted to Prof. Dr. J. H. F. Umbgrove for the permission to examine this specimen. The measurements of the molars are recorded under no. 12 in table III. M_3 is of the same size as that in the foregoing specimen (Coll. Dub. no. 3147, recorded under no. 15 in table III) and is the best preserved tooth, P_4-M_2 being too much worn to show any detail of their structure. The M_3 is in a stage of wear comparable to that represented in F.A.S., pl. 61 fig. 4. Protoconid and metaconid have become confluent, and so have the posterior cusps, hypoconid and entoconid. The protoconid extends more posteriorly than the metaconid; the posterior lobe of the latter is large and extends lingually beyond the anterior lobe of the hypoconid as it does in the specimen figured in F.A.S., pl. 61 fig. 5. The entoconid is simply built, as usual, and must have had a very small anterior lobe, if any. The hypoconulid is subtriangular in shape.

I have been unable to find subspecific differences in the structure of the lower molars, but the relative height of the present ramus points to its belonging to the present subspecies. The measurements cannot be taken exactly due to the specimen being somewhat crushed.

Hippopotamus sivalensis namadicus Falconer et Cautley

Hippopotamus (Hexaprotodon) namadicus Falconer et Cautley, Fauna Antiqua Sivalensis, London, 1847, pl. 57 fig. 12, pl. 58 figs. 1-3 (description: Falconer, 1868 I, p. 498), Falconer, Journ. Acad. Nat. Sci. Philad., ser. 2, vol. 1, 1849, p. 237; Medlicott and Blanford, Manual Geology India, Calcutta, 1879, pp. 385 and 574, pl. XX fig. 2.

Hippopotamus namadicus, Falconer, Pal. Mem. II, London, 1868, p. 644; Lydekker, Journ. As. Soc. Beng., vol. 49, part 2, 1880, pp. 32 and 34, Rec. Geol. Surv. Ind., vol. 16, 1883, p. 78, Mem. Geol. Surv. Ind., ser. 10, vol. 3, 1884, pp. 43 and 131, Cat. Foss. Mamm. Br. Mus., part 2, London, 1885, p. 294, Rec. Geol. Surv. Ind., vol. 20, 1887, p. 73; Trouessart, Catalogue Mamm., nov. ed., vol. 2, Berlin, 1898, p. 830; Schlosser, Abh.

k. bayer. Akad. Wiss., Math.-Phys. Kl., vol. 22, part 1, 1903, p. 195; Van der Maarel, Wet. Med. Dienst Mijnb. Ned. Ind., no. 15, 1932, p. 92; De Terra, Early Man, Philadelphia, 1937, p. 267; Colbert, in Osborn, Proboscidea, vol. 2, New York, 1942, p. 1449.

H[ippopotamus] namadicus, Blainville, Ostéographie Hippopotamus, Paris, 1847, p. 241; Giebel, Die Säugethiere, Leipzig, 1855, p. 220, Odontographie, Leipzig, 1855, p. 78; Falconer, Pal. Mem. I, London, 1868, p. 21; Lydekker, Rec. Geol. Surv. Ind., vol. 15, 1882, pp. 102 and 103, Cat. Foss. Mamm. Br. Mus., part 2, London, 1885, p. 295 (partim); Woodward, Geol. Mag., n.s., dec. 3, vol. 3, 1886, p. 117; Nicholson and Lydekker, A Manual of Palaeontology, 3rd ed., vol. 2, Edinburgh and London, 1889, p. 1317; Dubois, Natuurk. Tijdschr. Ned. Ind., vol. 51, 1891, p. 97; Zittel, Handbuch der Palaeontologie, part 1, vol. 4, Vertebrata (Mammalia), Munich and Leipzig, 1893, p. 346; Arambourg, Mission Scientifique de l'Omo 1932-33, vol. 1, fasc. 3, 1948, p. 333.

[Hippopotamus] namadicus, Haug, Traité de Géologie, part 2, Paris, 1911, p. 1883.

Hexaprotodon namadicus, Falconer, Pal. Mem. I, London, 1868, p. 21, Ibid. II, London, 1868, p. 407; Lydekker, Rec. Geol. Surv. Ind., vol. 9, 1876, p. 88; Koken, Pal. Abh., vol. 3, part 2, 1885, p. 83; Trouessart, Catalogus Mamm., Quinquennale Suppl., Berlin, 1905, p. 664; Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1264; Matthew, Bull. Amer. Mus. Nat. Hist., vol. 56, 1929, p. 557.

Hex[aprotodon] namadicus, Leche, Lunds Univ. Årsskr., N.F., Avd. 2, vol. 16, no. 10, 1921, p. 43.

Hexaprotodon namadicum Lydekker, Mem. Geol. Surv. Ind., ser. 10, vol. 1, 1876, p. 78.

Diagnosis: Size large, mandibular symphysis very short relative to its width, and very high relative to its length. I_2 two-thirds to four-fifths the size of I_1 , I_3 equal to or larger than I_1 in size.

Holotype: A mandibular symphysis figured in "Fauna Antiqua Sivalensis", pl. 57 fig. 12.

Horizon: Middle or Upper Pleistocene.

Locality: Narbada Valley, Central India.

Four specimens of the mandible figured in F.A.S. (pl. 57 fig. 12, pl. 58 figs. 1-3) constitute the material on which this subspecies is based. One of the specimens (F.A.S., pl. 58 fig. 2) is markedly smaller than the others, but may not this be attributable to a sexual difference? The specimens were described by Lydekker (1884 a, pp. 43-44), who gives also the measurements which permit of the diagnosis presented above. In the British Museum I have measured one of the specimens (B.M. no. 36838, figured in F.A.S., pl. 58 fig. 3), the others still being inaccessible. From a note book of the late Prof. Dubois I took the measurements of an Indian Museum specimen (no. F. 147) also remarked upon by Lydekker (l.c., p. 43) because of its having I_2 placed above the level of the other incisors, a character that is much less marked in the other specimens. The present subspecies is at once distinguished from the foregoing by its very short and very high symphysis, and by its relatively larger I_3 the greater diameter of which is equal to, or longer than, that of I_1 . There is no difference in the ratio between the

greater diameters of I_1 and I_2 between *H. sivalensis sivalensis* and *H. sivalensis namadicus*, however, though in the latter subspecies the incisors are slightly the larger. The following subspecies, *H. sivalensis palaeindicus*, differs from the present form in the paramount development of I_1 and I_3 and the relatively much reduced I_2 which is higher in position than the other incisors, thereby marking it as a more progressive form than the present. Since both *namadicus* and *palaeindicus* originate from the Narbada Beds but undoubtedly represent different subspecies the question arises as to whether the two forms occur in different geological horizons. It would seem probable that *palaeindicus* is somewhat younger in geological age than *namadicus*. The sedimentary characters of the Narbada Beds, which indicate that these beds were formed at different times (there are two zones of the Narbada alluvium, a lower zone of Middle Pleistocene age, and an upper zone of Upper Pleistocene age, separated by an erosion interval: Colbert, 1942, p. 1449), would seem to strengthen this supposition. The exact stratigraphical position of the specimens within the series of alluvia being unknown, it is impossible to make out whether or not the two Narbada subspecies are contemporaneous. The measurements of the specimens are given in table III nos. 1-4, and the reference to the specimens is as follows:

Mandibles

No. of specimen	reference or Museum no.
1	Indian Museum, no. F. 147, measured by Dubois.
2	B.M. no. 36840, figured in F.A.S., pl. 58 fig. 2, measurements in Lydekker, 1884 a, p. 44.
3	B.M. no. 36838, figured in F.A.S., pl. 58 fig. 3, measured by the present author.
4	B.M. no. 36839, figured in F.A.S., pl. 58 fig. 1, measurements in Lydekker, 1884 a, p. 44.

Hippopotamus sivalensis palaeindicus Falconer et Cautley

Hippopotamus (Tetraprotodon) palaeindicus Falconer et Cautley, Fauna Antiqua Sivalensis, London, 1847, pl. 57 figs. 1-9, pl. 58 figs. 4-10, pl. 62 figs. 11-12 (description: Falconer, 1868 I, pp. 497-499 and 502), Falconer, Journ. Acad. Nat. Sci. Philad., ser. 2, vol. 1, 1849, p. 236, Pal. Mem. I, London, 1868, p. 146; Medlicott and Blanford, Manual Geology India, Calcutta, 1879, pp. 385, 574, pl. XX fig. 7.

Hippopotamus palaeindicus, Lydekker, Journ. As. Soc. Beng., vol. 49, part 2, 1880, pp. 32 and 34, Rec. Geol. Surv. Ind., vol. 15, 1882, pp. 33 and 102, Ibid., vol. 16, 1883, pp. 79 and 91, Mem. Geol. Surv. Ind., ser. 10, vol. 3, 1884, p. 44, pl. VI fig. 2, p. 131; Koken, Pal. Abh., vol. 3, part 2, 1885, p. 83; Lydekker, Cat. Foss. Mamm. Br. Mus., part 2, London, 1885, p. 293, Rec. Geol. Surv. Ind., vol. 20, 1887, p. 73; Trouessart, Catalogus Mamm., nov. ed., vol. 2, Berlin, 1898, p. 831; Schlosser, Abh. k. bayer. Akad. Wiss., Math.-Phys. Kl., vol. 22, part 1, 1903, p. 195; Trouessart, Catalogus Mamm.,

Quinquennale Suppl., Berlin, 1905, p. 665; Haug, *Traité de Géologie*, part 2, Paris, 1911, p. 1883; Stremme, in Selenka and Blanckenhorn, *Die Pithecanthropus-Schichten auf Java*, Leipzig, 1911, p. 104; Van der Maarel, *Wet. Med. Dienst Mijnb. Ned. Ind.*, no. 15, 1932, p. 93; Colbert, in Osborn, *Proboscidea*, vol. 2, New York, 1942, p. 1449; Hooijer, *Arch. Néerl. d. Zool.*, vol. 7, 1946, p. 302.

H[ippopotamus] palaeindicus, Blainville, *Ostéographie Hippopotamus*, Paris, 1847, p. 240; Giebel, *Die Säugethiere*, Leipzig, 1855, p. 219, *Odontographie*, Leipzig, 1855, p. 77; Falconer, *Pal. Mem. I*, London, 1868, p. 21; Lydekker, *Cat. Foss. Mamm. Br. Mus.*, part 2, London, 1885, p. 295 (partim); Woodward, *Geol. Mag.*, n.s., dec. 3, vol. 3, 1886, p. 117; Nicholson and Lydekker, *A Manual of Palaeontology*, 3rd ed., vol. 2, Edinburgh and London, 1889, p. 1318; Zittel, *Handbuch der Palaeontologie*, part 1, vol. 4, *Vertebrata (Mammalia)*, Munich and Leipzig, 1893, p. 346; Major, *Proc. Zool. Soc. London*, 1896, p. 976; Woodward, *Outlines of Vertebrate Palaeontology*, Cambridge, 1898, p. 346; Dubois, *Tijdschr. Kon. Ned. Aardr. Gen.*, ser. 2, vol. 25, 1908, p. 1264; Monnier and Lamberton, *Bull. Acad. Malgache Tanarive*, n. s., vol. 3, 1922, p. 211, pl. VII right fig.; Matthew, *Bull. Amer. Mus. Nat. Hist.*, vol. 56, 1929, p. 556; Arambourg, *Mission Scientifique de l'Omo 1932-33*, vol. 1, fasc. 3, 1948, p. 333.

Tetraprotodon palaeindicus, Falconer, *Pal. Mem. II*, London, 1868, p. 406; Lydekker, *Rec. Geol. Surv. Ind.*, vol. 9, 1876, p. 87.

Hex[aprotodon] palaeindicus, Leche, *Lunds Univ. Årsskr.*, N.F., Avd. 2, vol. 16, no. 10, 1921, p. 43.

Tetraprotodon palaeindicum Lydekker, *Mem. Geol. Surv. Ind.*, ser. 10, vol. 1, 1876, p. 78

Tetraprotodon namadicus (misprint), Lydekker, *Rec. Geol. Surv. Ind.*, vol. 9, 1876, p. 88.

Hipp[opotamus] (Tetraprotodon) palaeindicus, Roger, *Corr. Blatt zool. min. Ver. Regensburg*, vol. 35, 1881, p. 169.

Hipp[opotamus] palaeindicus, Roger, *Ber. Naturw. Ver. Schwaben u. Neuburg*, vol. 32, 1896, p. 211.

H[ippopotamus] palaeindicus Prato, *Rivista Ital. di Paleont.*, vol. 18, 1912, p. 23.

Diagnosis: Size large, orbit moderately elevated, occiput moderate to low, postdental part of calvarium short. Upper molars large, the posterior lobe of the paracone extends labially beyond the anterior lobe of the metacone. The upper molar series extends more backward than the posterior border of the palate. Mandibular symphysis short to very short relative to its width, and high to very high relative to its length. Ramus horizontalis very high at M_2 relative to its length. I_1 and I_3 much enlarged; I_2 one-third to one-half the diameter of I_1 , and I_3 equal to or larger than I_1 in size.

Holotype: A fragmentary mandibular symphysis figured in "Fauna Antiqua Sivalensis", pl. 57 fig. 5.

Horizon: Middle or Upper Pleistocene.

Locality: Narbada Valley, Central India.

The present subspecies is founded on a fragmentary symphysis, two incomplete calvariums, fragments of calvarium and mandible and some vertebrae and limb bones figured in F.A.S. The distinction of the mandible of the present form from that of the foregoing subspecies has been indicated

above (p. 51). The type mandible was erroneously reconstructed as tetraprotodont by Falconer since no traces were left of the very small I_2 , but subsequent specimens described by Lydekker showed this form to be hexaprotodont as well as the other Asiatic forms. The first hexaprotodont mandible found by Lydekker (1882 b, p. 103) has a small I_2 wedged in between the upper triangular spaces between I_1 and I_3 . I_3 in this specimen, however, was only slightly larger than I_1 while in an Indian Museum specimen recorded by Falconer (1868 I, p. 147) the diameter of the alveolus of I_3 was one-fourth longer than that of the alveolus of I_1 . There are two mandibles in the British Museum similar to that recorded by Lydekker in 1882 (which latter has been figured by Lydekker, 1884 a, pl. VI fig. 2) which have been referred to in Lydekker's 1884 paper (Lydekker, 1884 a, p. 45/46) and which I have examined. The symphysis length-width index of one of the specimens (B.M. no. 41663) shows the symphysis to be not so very short as that in *H. sivalensis namadicus*; in the second specimen (B.M. no. 40893) the symphysis is as short relative to its width as that in the foregoing subspecies. The latter specimen is so complete as to enable me to compute the ramus length-height index, which shows the ramus to be as high relative to its length as that in a specimen of *H. sivalensis soloensis*, the terminal form of the Javan series, decidedly higher than that in *H. sivalensis sivalensis*.

The calvariums listed under the present subspecies in F.A.S. (pl. 57 fig. 1 and pl. 58 fig. 4) are in the British Museum and were described by Lydekker (1884 a, p. 46) who gives, however, no measurements. I have examined the two specimens, and their distinctive characters are mentioned in the above diagnosis. The orbit is not very much elevated above the frontals, though the elevation is more marked than that in *H. sivalensis sivalensis*; in one of the calvariums (B.M. no. 36825) the orbit is as much elevated as that in one of the calvariums of *H. sivalensis sivalensis* in the Dubois collection (no. 3101), but in the second specimen of the present form (B.M. no. 36824) the orbit is higher than that in the Siwalik form. The upper molar series extends behind the posterior border of the palate, which is not the case in the other subspecies. In this character as well as in the marked shortness of the postdental portion of the calvarium the present subspecies is more advanced than any other of the subspecies of *H. sivalensis*. The mandibles, as remarked above, likewise present a rather progressive form; in the paramount development of I_1 and I_3 and in the reduction in size of I_2 they are unsurpassed by any other subspecies. There is, therefore, every reason to believe that the calvariums and the mandibles are correctly associated, and this has been adopted in the present paper, but it must be kept in mind that

the future find of calvariums in the Narbada Beds with more progressive characters than those mentioned above will force us to refer the latter to the less advanced form, *H. sivalensis namadicus*, the calvarium of which I accept to be unknown for the present.

The specimens recorded by Falconer (1868) and Lydekker (1884 a) as well as those measured by the present author are listed below, and the numbers given to the specimens refer to those given in tables II and III of this work.

Calvariums

No. of specimen	reference or Museum no.
1	B.M. no. 36824, figured in F.A.S., pl. 57 fig. 1.
2	B.M. no. 36825, figured in F.A.S., pl. 58 fig. 4.

Mandibles

1	Falconer, 1868 I, p. 147.
2	Indian Museum, no. F. 149, Lydekker, 1884 a, p. 46.
3	B.M. no. 40893, measured by the present author.
4	B.M. no. 41663, measured by the present author.

Hippopotamus sivalensis duboisi nov. subsp.

Diagnosis: Size moderate, orbit very high, occiput moderate. Upper molars small and of the *palaeindicus* type.

Holotype: A partial calvarium in the Dubois collection (no. 3146) described and figured in the present paper (pl. V fig. 3).

Horizon: Pleistocene.

Locality: Naliwala on the Somb Nuddy opposite Haripoor, Sirmur State, Punjab.

There is a specimen of the calvarium in the Dubois collection from the Punjab which is remarkable in several respects. It has broken off four cm in front of the orbits, the right of which is wholly intact; of the left a large part is missing. The elevation of the orbit above the median level of the frontals is more marked than in any specimen of the present species I have ever seen. The lacrimal sutures are well shown, the bone is separated from the nasal by an anterior prolongation of the frontal as is typical of the present species. The zygomatic arches are for the greater part lost, and beneath their anterior portion there is a deep pit. The frontal crests are sharply defined and unite with each other in a well-marked sagittal crest which is partly injured. The left occipital condyle is incomplete, and so are the paroccipital processes. The basicranial surface is superficially damaged;

the posterior border of the palate extends well behind the posterior border of M^3 .

M^2 and M^3 , and at the left side also the posterior portion of M^1 , are preserved. These teeth are decidedly smaller than those of any continental subspecies of *H. sivalensis*. The state of preservation is not splendid; the left M^2 , however, has a damaged metaconule only and is best suitable for a description. The tooth is moderately worn; the anterior cusps have become confluent with the anterior cingulum and there is but a small enamel islet as a remnant of the antero-posterior valley. The metacone and metaconule are separated by a larger enamel islet and have become confluent with the posterior cingulum. Both labially and lingually the cingulum forms a distinct ledge. The lobes of the cusps in the transverse valley of the molar are well shown, and the posterior lobe of the paracone, which is larger than that of the protocone, is directed slightly outward and extends labially beyond the anterior lobe of the metacone. The same structure is seen in the right M^2 of the posterior moiety of which only the anterior lobes of the metacone and the metaconule are preserved. The mutual position of the lobes is exactly the same, again, in the M^3 on either side; these molars have for the greater part crumbled away.

The upper molars of the present specimen have the characteristic *palaeindicus* pattern, but the specimen differs markedly from *H. sivalensis palaeindicus* in having smaller teeth, in being much lower (at the infraorbital foramen, from the palatine, and from alveolus of M^3 to top of orbit), and in having a more elevated orbit. The M^3 does not extend behind the posterior border of the palate either. *H. sivalensis soloensis* from Java which has molars of the same small size and of the same structural type as those of our present Punjab specimen and of which the orbit is only slightly less elevated, differs from the latter again in the greater height of the calvarium. The calvarium of *H. sivalensis koenigswaldi* from Java is as low as the present specimen, but the Javan subspecies is distinguished at once by its less elevated orbit, shorter postdental portion, and shorter postorbital length. The subspecies of *H. sivalensis* from Burma and Ceylon to be discussed below have upper molars which are of the *palaeindicus* type too, but differ from *H. sivalensis duboisi* nov. subsp. by their large size.

It is certainly surprising to find in the Siwaliks of the Punjab a form like the present which differs from *H. sivalensis sivalensis* in the orbit being much more elevated and in the structure of the upper molars which are of the small size of those in the Javan subspecies. I have named this new subspecies in honour to its discover, the late Prof. E. Dubois. The measurements will be found in table II.

Hippopotamus sivalensis cf. palaeindicus Falconer et Cautley

Hippopotamus, sp. Lydekker, Cat. Foss. Mamm. Br. Mus., part 2, London, 1885, p. 310.

Hexaprotodon (?) sp. Colbert, Bull. Amer. Mus. Nat. Hist., vol. 74, 1938, p. 424, fig. 62 left fig.

Hexaprotodon sp., cf. *sivalensis* Colbert, Trans. Amer. Phil. Soc. Philad., n.s., vol. 32, 1943, p. 409.

Next to *Hippopotamus iravaticus*, remains of a large form of *Hippopotamus* have been recorded from Burma. Lydekker (1885 a, p. 310) listed, without a specific name, fragments of lower incisors from the Siwaliks of Burma which agree with *H. sivalensis palaeindicus* as to their very large size. Colbert (1938, p. 424), likewise without a specific name, figures a well-preserved right M³ from the Lower Pleistocene Upper Irrawaddy fauna of Burma (l.c., fig. 62) which is exactly of the size (length 53 mm, width 45 mm) of that of *H. sivalensis palaeindicus* and in which the *palaeindicus* pattern is most excellently shown. The posterior lobe of the paracone extends labially beyond the anterior lobe of the metacone, and the metaconule is completely separated from the paracone. The cingulum has distinctly developed both labially and lingually. More recently Colbert (1943, p. 409) recorded a fragment of a lower C, again from the Upper Irrawaddy Beds, indicative of a large type of *Hippopotamus*. Because of their size and contemporaneousness with and their contiguity to the Siwalik species, Colbert regards the remains recorded by him as probably referable to *H. sivalensis sivalensis*. The structure of the upper molar, however, is different from that of the Siwalik form but agrees with that of the Narbada forms which are, however, somewhat younger in geological age. If the large lower incisors recorded by Lydekker originate from the Upper Irrawaddy fauna (and this is most probably the case since in the Lower Irrawaddy fauna no *Hippopotamus* would occur: Colbert, 1938, p. 276) these specimens give evidence of the existence of a form of *Hippopotamus* in the Lower Pleistocene of Burma which is as much specialized in its incisor dentition as is the Middle or Upper Pleistocene *H. sivalensis palaeindicus*. The upper molar figured by Colbert does not permit of a distinction between the large Burmese form and the Narbada form either. For the present it seems best to indicate the large form from Burma as *Hippopotamus sivalensis cf. palaeindicus*; the probability is great that the Burmese form is distinct from the Narbada form but the remains at hand do not justify the creation of a new sub-specific name.

Hippopotamus sivalensis sinhaleyus Deraniyagala

Hippopotamus (*Hexaprotodon*) ? *sivalensis* Deraniyagala, Geol. Mag., vol. 73, 1936, p. 318, figs. 1-3.

Hippopotamus ? *sinhaleyus* Deraniyagala, Journ. Royal As. Soc. (Ceylon Branch), vol. 33, 1936, pp. 166 and 167.

Hexaprotodon sivalensis Deraniyagala, Ceylon Journ. Sci., sect. B, vol. 20, 1937, p. 196, pl. V fig. 3, textfig. 4.

Hippopotamus sivalensis sinhaleyus Deraniyagala, Journ. Royal As. Soc. (Ceylon Branch), vol. 34, 1939, pp. 232, 233, fig. 1, pp. 383, 384, figs. 3-4.

Hexaprotodon sinhaleyus Deraniyagala, Spolia Zeylanica, vol. 24, 1944, p. 37, pl. VI, textfigs. 7-9, 10 b and c, and 11, Ibid., vol. 24, 1946, p. 168, pls. XXII and XXIII, text fig. 3, Journ. Royal As. Soc. (Ceylon Branch), vol. 37, 1947, p. 230, pl. I figs. 3-5, Ceylon Administration Reports, part 4, July, 1948, p. F 8.

Diagnosis: Size large, upper molars large and of the *palaeindicus* type. Lower incisors (I_1 and I_3 ?) much enlarged.

Holotype: The unworn left M_3 figured by Deraniyagala (1936, figs. 1-3).

Horizon: Ratnapura, equivalent to Upper Siwaliks, Lower Pleistocene.

Locality: Ratnapura district, Ceylon.

The present form has already been given a special name, which is most probably justified, but it cannot as yet be separated structurally from *H. sivalensis palaeindicus*. Of special importance are the big lower incisors (an I_1 (?) 49 mm in diameter, and an I_3 (?) 37 mm in diameter), and the structure of the upper molar (Deraniyagala, 1944, pl. VI fig. t) which is of the *palaeindicus* type, the posterior lobe of the paracone extending labially beyond the anterior lobe of the metacone. The lower canines vary widely in dimensions, evidently due to male or female sex, and the largest specimens even exceed those of *H. sivalensis palaeindicus* as to size (greater diameter 67 mm). The remains of humerus and femur are indicative of individuals of the size of *H. sivalensis sivalensis* and exceeding the Javan forms in size. Unfortunately no remains of the calvarium or of the mandible have been recorded. Since the Ratnapura Beds, besides Upper Siwalik forms, contain *Elephas maximus* L. subsp., Deraniyagala (l.c., p. 53) supposes that there was redeposition in the Ratnapura Beds during late Pleistocene times.

***Hippopotamus sivalensis sivajavanicus* (Dubois)**

Hippopotamus, Dubois, Natuurk. Tijdschr. Ned. Ind., vol. 51, 1891, pp. 95 and 97, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 24, 1907, p. 454.

Hexaprotodon sivajavanicus Dubois, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 25, 1908, p. 1265; Stromer, Zeitschr. deut. geol. Ges., vol. 66, 1914, p. 31; Leche, Lunds Univ. Årsskr., N.F., Avd. 2, vol. 16, no. 10, 1921, p. 47; Van der Maarel, Leidsche Geol. Med., vol. 5, 1931, p. 474.

Hippopotamus sivajavanicus, Martin, Unsere palaeozoologische Kenntnis von Java, Leiden, 1919, p. 108; Van Es, The age of Pithecanthropus, The Hague, 1931, p. 31; Van der Maarel, Wet. Med. Dienst Mijnb. Ned. Ind., no. 15, 1932, p. 95; Raven, Bull.

Amer. Mus. Nat. Hist., vol. 68, 1935, p. 263; Hooijer, Zool. Med. Museum Leiden, vol. 29, 1948, p. 178.

? *Hippopotamus sivajavanicus*, Soergel, Palaeontographica, suppl. 4, part 3, 1913, p. 2, non *Hippopotamus (Hexaprotodon) sivajavanicus* Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Ind., no. 23, 1933, pp. 31 and 90.

H[ippopotamus] sinajavanicus Weber, Die Säugetiere, 2nd ed., Jena, 1928, vol. 2, p. 547.

H[ippopotamus] sivajanicus Von Koenigswald, Proc. Kon. Akad. Wet. Amst., vol. 37, 1934, p. 656.

Hippopotamus, Anonymus, Jaarboek Mijnwezen, vol. 58, Alg. Ged., 1929, p. 50.

Hippopotamus sp. Van der Maarel, Wet. Med. Dienst Mijnb. Ned. Ind., no. 15, 1932, p. 82, pl. V fig. 5, pl. VI figs. 1-4, pl. VII figs. 1-2, pl. XVIII fig. 3, pl. XIX figs. 1-2, pl. XX fig. 2.

Hippopotamus (Hexaprotodon) simplex Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Ind., no. 23, 1933, p. 33, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 52, 1935, p. 539, upper fig. opposing p. 540; Ter Haar, Geol. Kaart van Java, Toel. blad 58 (Boemijoe), 1935, p. 37; Hetzel, Ibid., blad 54 (Madjenang), 1935, p. 33.

Hippopotamus simplex Von Koenigswald, Proc. Kon. Akad. Wet. Amst., vol. 37, 1934, p. 654, figs. 1-2, Ibid., vol. 38, 1935, pp. 194 and 195, Wet. Med. Dienst Mijnb. Ned. Ind., no. 28, 1940, p. 62.

Hexaprotodon simplex Von Koenigswald, Quartär, vol. 2, 1939, p. 31.

"primitive hippopotamus" Callenfels, Ill. London News, vol. 188, no. 5060, 1936, pp. 624 and 625, fig. 5 skeleton.

Diagnosis: Size small, orbit moderately elevated, postdental part of calvarium long. Upper molars small and of the *sivalensis* type. Mandibular symphysis short to very short relative to its width. I_2 about equal in size to I_1 , and I_3 decidedly smaller than I_1 .

Holotype: A calvarium in the Dubois collection (no. 2908) described and figured in the present paper (pl. II fig. 4, pl. III fig. 2).

Horizon: Lower Pleistocene 1).

Locality: Western and Central Java.

Some short references were given by Dubois (1891, 1907), who in 1908 presented the following diagnosis (translated into English from Dubois, 1908, p. 1264/65):

It is a *Hexaprotodon*, like the fossil hippopotamuses of India. It is widely separated, however, from the two Nerbada species: *Hexaprotodon namadicus* and *H. palaeindicus*, by the length of the mandibular symphysis and by the proportional size of the incisors. In the latter points as well as in the shape of the skull it is very close to *H. sivalensis*, from which latter it differs, apart from its slightly smaller size, in the greater height between the palate and the nasals relative to the length, in the relatively broader upper jaw, and especially in the lower incisors not being placed on a straight line.

1) The correlations by Colbert (1942, p. 1454, 1943, p. 426) have been adopted in the present paper. See note on p. 37.

It is distinctly very close to the Siwalik form, and, while the Narbada forms in the paramount development of the lateral incisor show themselves to be the final branch of the *Hexaprotodon*-tribe, *Hexaprotodon sivajavanicus* Dub., even surpassing *H. sivalensis* in the relatively larger medial incisor, certainly was nearer to the stock of the African hippopotamus.

Soergel (1913, p. 2) identifies as *H. sivajavanicus* the *Hippopotamus* remains collected by Elbert in the Kendeng Beds of Java, but gives neither descriptions nor figures. A description of the material secured by the Selenka expedition to Trinil in Java was presented by Stremme (1911 b) who does not venture to identify the specimens as to the species. Van der Maarel (1932) describes material from Boemiajoe and Watoelang in Java as *Hippopotamus* spec. too. In the opinion of Von Koenigswald (1933, p. 31) the material recorded by Stremme and Soergel as well as the Watoelang specimen of Van der Maarel are referable to *sivajavanicus*; it is supposed (l.c., p. 32) that the latter species is identical to *palaeindicus*. In a subsequent paper (Von Koenigswald, 1934 b, p. 656) the supposed *sivajavanicus* remains are referred to *namadicus*. In my opinion the Javanese *namadicus* is a subspecies distinct from the Narbada form; in the sequel, therefore, I shall refer to the Java form as *soloensis*.

The material from Boemiajoe described and figured by Van der Maarel is supposed by Von Koenigswald (1933, p. 33) to belong to a new species, which he named *H. simplex*. As will appear from the description of the type specimen of *H. sivalensis sivajavanicus*, the two names are synonyms.

According to Von Koenigswald the present form is the geologically oldest hippopotamus in the island of Java, occurring in the Upper Pliocene of Boemiajoe (Kali Glagah fauna: Von Koenigswald, 1935 a, p. 194) and in the Middle Pliocene Tji Djoelang fauna (l.c., p. 195). These two faunae are referred to the Lower Pleistocene by Colbert (1942, p. 1454, 1943, p. 426). Evidently the reason why Von Koenigswald does not accept Dubois's name *sivajavanicus* for the "Pliocene" hippopotamus of Java is that he considers *H. simplex* to be geologically older than the material in the Dubois collection. Dubois has definitely stated that *sivajavanicus* is very close to the Siwalik form *sivalensis* in its skull characters, and this statement alone militates against its reference to the Narbada *palaeindicus* or *namadicus* with which the Middle and Upper Pleistocene Javan material was classed by Von Koenigswald. The suppression of the name *sivajavanicus* in favour of that of *namadicus* (Von Koenigswald, 1934 b, p. 656), therefore, is entirely unjustified.

Von Koenigswald particularly paid attention to the characters of the mandible. Both in *sivalensis* and in "*simplex*" the incisor dentition does

not yet exhibit any specialized features (Von Koenigswald, 1934 b, p. 657). The lower incisors, which are almost equal in size (l.c., p. 654), are placed on a straight line; occasionally I_2 is somewhat higher in position than the other incisors, but this is not stressed (l.c., p. 657). Unlike *namadicus* and *palaeindicus*, "*simplex*" may have I_3 as the smallest incisor; this is the case in the mandible described by Van der Maarel (1932, p. 83). In a mandible referred to the present form by Von Koenigswald (1934 b, p. 654 fig. 1) I_3 is somewhat larger, and I_2 somewhat smaller than I_1 . The mandibular symphysis is relatively shorter than that in *sivalensis* (Von Koenigswald, 1933, p. 33) and agrees with that of the Narbada *namadicus* (l.c., p. 34), from which latter, however, it differs in not having the steep anterior surface characteristic of the Narbada forms (Von Koenigswald, 1934 b, p. 657). The horizontal ramus of the mandible is slender and low (Von Koenigswald, 1933, p. 33) in comparison to that of *soloensis*; the molars have the simple pattern of those of the Siwalik form but are smaller.

The Museum of the Geological Survey at Bandoeng (Java) possesses a mounted skeleton of the present form, which has been figured by Von Koenigswald (1935 d). It is composed of different finds, and the ribs and tarsal bones have been modelled after those of the recent African species. The height of the skeleton is given as 1.20 m, the length (from anterior border of mandible to pelvis) as 2.40 m. Unfortunately an adequate description of the calvarium has never been published by Von Koenigswald, who only remarks upon the slight degree of elevation of the orbits (l.c., p. 540). The *sivajavanicus* skeleton has subsequently been figured by Callenfels (1936, p. 625 fig. 5), who gives on the same photograph a calvarium of the progressive Javan subspecies *soloensis* as well as a female *amphibius* skull. The marked difference in the degree of elevation of the orbit that exists between the calvarium of *sivajavanicus* and that of *soloensis* (in which latter, as I shall show below, the orbit is even more elevated than that in *amphibius*) can be seen at a glance.

The specimens belonging to the present subspecies are listed below, and the numbers given to the specimens refer to those given in tables II and III.

Calvariums

No. of specimen	reference or Coll. Dub. no.
1	Coll. Dub. no. 2908 (holotype).
2	Coll. Dub. no. 2079 and no. 2318 d and e.
3	Van der Maarel, 1932, p. 105, pl. VI figs. 3-4.

Mandibles

1	Van der Maarel, 1932, p. 84, pl. VII.
2	Van der Maarel, 1932, p. 82, pl. VI figs. 1-2.

- 3 Van der Maarel, 1932, p. 86, pl. XX fig. 2, and p. 88, pl. V fig. 6.
Interval between C recorded by Von Koenigswald, 1934 b, p. 654.

Coll. Dub. no. 2908, Kedoeng Broeboes (pl. II fig. 4, pl. III fig. 2).

Calvarium. Part of the premaxillaries between the alveoli of I¹ is lost, and the rostral expansion of the maxillaries incomplete. The left orbit is well preserved in contradistinction to the right; the left zygomatic arch has broken off behind the orbit. The occiput is damaged except for the condyles.

The most conspicuous character of the present calvarium is the flatness of the dorsal surface. The orbit is not much elevated; the orbitocephalic index is not more than 17 which falls within the variation limits of this index in *H. sivalensis sivalensis* (9-18). The postdental part of the calvarium agrees in its great relative length with that of the latter subspecies too, the P⁴-M³-condyle index being 66 against 63-77 in *H. sivalensis sivalensis*. In the more progressive Javan subspecies the orbit is more distinctly elevated, and the postdental part is relatively shorter. Unfortunately the occiput index cannot be given.

Of the incisors only the left I³ is present but broken off at the alveolar border. It is rounded in cross-section and 14 mm in diameter. The alveoli of the other incisors are filled with matrix. I¹ and I² are laterally compressed, the alveolus of I² measures 20 by 15 mm; I¹ is certainly not much different in size. Thus I³ is the smallest of the series. This is the case in *H. sivalensis sivalensis* (F.A.S., pl. 62 fig. 3) too. The canine is preserved at the right side only; it shows clearly the deep posterior groove which is typical of the species. The anterior divergence of the premolar series and the short and marked rostral constriction likewise constitute specific characters. The premolars are considerably worn, and so are the anterior molars. Nothing definite can be said as to the structure of the M¹ and M² except that the lingual cingulum is well developed; on the inner side of M² it is seen to obstruct the entrance to the transverse valley. The left M³ has broken off, but the right is complete. Between the anterior pair of cusps the longitudinal valley has already disappeared by wear, and the anterior cingulum is confluent with the main lobes. The lingual cingulum has given off an accessory cusplet in the entrance to the transverse valley. The posterior lobes of the anterior cusps are placed slightly labially of the anterior lobes of the posterior cusps, and the posterior lobe of the protocone is opposed to the longitudinal valley between the posterior cusps. The posterior lobe of the paracone is larger than that of the protocone and extends beyond the anterior lobe of the metacone. This character, however, is not so marked as that in typical *palaeindicus* molars (cf. F.A.S., pl. 62 fig. 11, M²) though the present molar undoubtedly marks a step in the direction of the *palaeindicus*

type. The M^3 of the specimen figured by Van der Maarel (1932, pl. VI fig. 3) also shows an initial development of the *palaeindicus* character, while the associated M^2 agrees with the *sivalensis* molars in the lobes of the anterior cusps being opposed to those of the posterior cusps in the transverse valley. The cingulum is more distinctly developed in the present molars than in those figured by Van der Maarel, but the cingulum is variable in the *sivalensis* molars too.

Dubois has stated that the present form, though smaller, is very close to *H. sivalensis sivalensis* in the shape of its calvarium, and this is correct: the orbito-cephalic index as well as the P^4 - M^3 -condyle index of the present calvarium are the same as those in the Siwalik form. Dubois has moreover remarked that the height between palate and nasals, and the width of the maxillary are relatively greater in the Javan form. From the inspection of table II it is seen that most of the dimensions of the holotype of *H. sivalensis sivajavanicus* are smaller than the corresponding in the series of *H. sivalensis sivalensis*, and some of them (height from top of orbit, vertical diameter of orbit, and interorbital height) fall within the variation limits of the observations in the Siwalik series. The height of the present type-calvarium at the infraorbital foramen (145 mm), however, is equal to the maximum found in the *sivalensis sivalensis* series (no. 8), the width over the border of the maxillary at the infraorbital foramen (114 mm) is greater than all but one (no. 11) of the observations in the Siwalik series. The width of the palate at M^1 (63 against 43-62 mm) and that at pd^1 (132 against 104-125 mm) exceed the corresponding values in *H. sivalensis sivalensis*, and the present calvarium consequently is fully in accord with the diagnosis given by Dubois. There can be no doubt that this is the specimen on which Dubois founded his name *sivajavanicus*. Von Koenigswald (1933, p. 32) has admitted that he had no sufficient material of the calvarium to check Dubois's statements, and he only takes into account the characters of the mandible given by Dubois which has led him to the conclusion (Von Koenigswald, 1933, p. 32) that *sivajavanicus* would very probably be identical to *palaeindicus*. From Dubois's remarks concerning the skull it is clear that Dubois possessed a complete calvarium, and if this specimen would have corresponded to *palaeindicus* Dubois would not have written that it is very close to *H. sivalensis* but slightly smaller.

The present calvarium does not belong to the most progressive form of *Hippopotamus* from Java but on the contrary to the most primitive of the subspecies, named *H. simplex* by Von Koenigswald, and the latter name consequently has to be placed in the synonymy of *H. sivalensis sivajavanicus*.

Coll. Dub. no. 2079, Soember Waroe (pl. V fig. 4).

Palate, broken off in front of P⁴. The posterior border of the palate is damaged, and the anterior zygomatic roots are preserved. P⁴ is rather worn and is rotated for about 90°. The main cusp and the lingual accessory cusp have become confluent, and an enamel strip indicates the valley between the former and the posterior (now lingual) cingulum. M¹, incomplete on the right side, is so very much worn down that the mutual position of the lobes in the transverse valley is no longer visible.

M² is much worn but the shape of the central ends of the labial and lingual entrances to the transverse valley leaves no doubt as to the structural type of the molar; the posterior lobes of the anterior cusps were directly opposed to the anterior lobes of the posterior cusps as is typical of the *H. sivalensis sivalensis* upper molar. The lingual cingulum is already worn and fills the lingual entrance to the transverse valley; that of the labial side, however, is still complete along the metacone and has unequally developed on both sides, the height from the base of the enamel being 4 mm in the left against 6 mm in the right molar.

M³ shows a similar asymmetrical development of the labial cingulum, that is absent along the paracone of the left specimen but is developed as a 6 mm high ledge at the antero-labial side of the paracone of the right molar, while in the latter the metacone cingulum is stronger than that in the left molar too. The most conspicuous difference between the right and the left M³ is found in the position of the lobes of the cusps in the transverse valley. The left M³ is of the *sivalensis* type; in the right the groove separating the posterior lobes of protocone and paracone is not placed in the same antero-posterior line as the longitudinal groove between the posterior cusps but distinctly to the lingual side of the latter. The posterior lobe of the paracone is neither directly opposed to the anterior lobe of the metacone (as in the *sivalensis* type) nor does it extend labially beyond the latter lobe (as in the *palaeindicus* type); on the contrary the posterior paracone lobe is opposed to the longitudinal valley between the posterior cusps. I have never seen another upper molar of *H. amphibius* or of *H. sivalensis* in which the antero-posterior valley between the anterior cusps is situated lingually of that between the posterior cusps, most often the groove separating the anterior cusps is placed to the labial side of that between metacone and metaconule. The lingual cingulum in either of the two M³ is strongly developed, forming a ledge about 12 mm in height along the protocone and the entrance to the transverse valley. The sinuous course of the longitudinal enamel islet between the posterior cusps indicates that there is a fourth lobe to the metacone; this four-leaved clover pattern is more distinctly shown in the left M³ than in the right.

I have two isolated upper molars in the Dubois collection which may be referred to the present form. A worn right M¹, found between Dekes and Wadegan, shows the *sivalensis* type very clearly (pl. VIII fig. 16), and the labial cingulum is only 7 mm high at the paracone. In a left M² with the posterior cusps just touched by wear (Coll. Dub. no. 2318 d, from Kedoeng Broeboes, pl. VIII fig. 15) the lobes of the cusps in the transverse valley likewise are directly opposed to each other; the labial cingulum is as high as that in the M¹ but the lingual cingulum, absent in the M¹, forms a ledge 10 mm in height along the protocone. Both labially and lingually an accessory cusplet is formed at the entrance to the transverse valley. The measurements of the present specimens as well as those of the M² and M³ of the Soember Waroe palate are given under no. 2 in table II.

The characters of the mandible given by Dubois in his diagnosis of *H. sivalensis sivalensis* are not very definite, and it does not quite appear from his text which of the specimens of the mandible in his collection served as the type specimen. Dubois states the mandible of *sivajavanicus* to be widely different from that of *namadicus* and *palaeindicus* in the length of the symphysis; the symphysis length-width index varies in the Narbada forms from 57 to 67, in the Javan material from 62 to 79 approximately, and thus the symphysis only averages longer in the Javan than in the Narbada material. Dubois states furthermore that, while in the Narbada forms I₃ shows the maximum development, *sivajavanicus* on the contrary surpasses even *H. sivalensis sivalensis* in the larger medial incisor. Van der Maarel (1932, p. 106) thought that Dubois meant I₂ when writing about the medial incisor, and observes that in the Boemiajoe mandible described by himself I₂ is stronger relative to I₁ than is often the case in *H. sivalensis sivalensis*. The ratio I₂:I₁ is 0.67-0.91 in the Siwalik form; in the Javan material this ratio varies from 0.67 to ca. 0.89, and in the specimen described by Van der Maarel the ratio is ca. 0.93. There is no difference in the relative size of the I₂ between the Javan and the Siwalik material. Consequently it is more probable that Dubois meant I₁ when he wrote medial incisor, and this makes his observation, vague as it may be, correct. For in *H. sivalensis sivalensis* the ratio I₃:I₁ varies from 0.90 to 0.95, while in the Javan material in the Dubois collection this ratio varies from 0.75 to 0.96; the Javan material thus has a relatively stronger I₁, in the average, than has the Siwalik material. Dubois has also mentioned that the lower incisors are not placed on a straight line, but this is the case in every mandible in his collection, and even holds for the mandibles described by Van der Maarel (1932, pl. VI fig. 2 and pl. XIX fig. 2).

Of the calvariums of *Hippopotamus* in the Dubois collection no. 2908

exclusively corresponds full well with the diagnosis given by Dubois, and this specimen belongs to the most generalized of the Javan subspecies which later received the name *simplex*. There is no mandible in the Dubois collection, however, which agrees exactly with the mandibles from Boemiajoe described by Van der Maarel and which have been referred to "*H. simplex*" by Von Koenigswald. In none of the mandibles collected by Dubois the height at pd_1 is so small as that in the specimen figured by Van der Maarel (1932, pl. VI figs. 1-2; height at pd_1 74 mm, equal to that in the mandible of *H. iravaticus* and about one-fourth smaller than that in other Javan mandibles by the same width between the lower C), and the specimen figured by Von Koenigswald (1934 b, p. 654 fig. 1) seems to differ from the mandibles from Java available to me by the same character. It is very unfortunate that the height of the symphysis has not been recorded for these specimens, for the symphysis height-length index is of great value as a diagnostic character (above, p. 39). This index varies in the Javan material from 49 (which is within the variation range of *H. sivalensis sivalensis*: 37-50) to 71 (*H. sivalensis palaeindicus*: 60-ca. 77). The symphysis has the tendency to become higher relative to its length, and the lesser height of the symphysis seems to be a character by which the *sivajavanicus* mandibles are distinguishable from those of *koenigswaldi*. As long as we do not have more data on the mandibles figured by Van der Maarel and by Von Koenigswald it is impossible to make out whether these mandibles are really lower at the symphysis than those which I have in the Dubois collection. Of the latter, four specimens undoubtedly belong to the most progressive form *H. sivalensis soloensis*, and the other mandibles have been listed by me under the head of the following subspecies, *H. sivalensis koenigswaldi*. The diagnosis of the present subspecies, which refers to Van der Maarel's specimens exclusively as far as the mandible is concerned, will have to be extended if new material is added.

Hippopotamus sivalensis koenigswaldi Hooijer

Hippopotamus spec., Cosijn, Verh. Geol. Mijnb. Gen. Ned. Kol., Geol. Ser., vol. 9, 1931, p. 119.

Hippopotamus (Hexaprotodon) antiquus Von Koenigswald, De Ing. in Ned. Indië, vol. 1, part 11, sect. 4, 1934, p. 192, pl. IV fig. 4; Proc. Kon. Akad. Wet. Amst., vol. 38, 1935, p. 193, De Ing. in Ned. Indië, vol. 2, part 10, sect. 4, 1935, p. 86 figs. 3-4; Ter Haar, Geol. Kaart van Java, Toel. blad 58 (Boemiajoe), 1935, p. 37; Duyfjes, Ibid., blad 110 (Modjokerto), 1938, p. 40; Von Koenigswald, Quartär, vol. 2, 1939, p. 35; Hooijer, Arch. Néerl. d. Zool., vol. 6, 1942, p. 280.

Hippopotamus antiquus Von Koenigswald, Proc. Kon. Akad. Wet. Amst., vol. 37, 1934, p. 655 figs. 3-4; Ibid., vol. 38, 1935, p. 194, Ibid., vol. 39, 1936, p. 1000; Callenfels, Man, vol. 36, 1936, p. 210; Anonymus, Nature, vol. 139, February 13, 1937, p. 294; Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Ind., no. 28, 1940, p. 60, pl. II fig. 12.

H[ippopotamus] antiquus Von Koenigswald, Tijdschr. Kon. Ned. Aardr. Gen., ser. 2, vol. 52, 1935, p. 540; Arambourg, Mission Scientifique de l'Omo 1932-33, vol. 1, fasc. 3, 1948, p. 333.

Hippopotamus koenigswaldi Hooijer, Arch. Néerl. d. Zool., vol. 6, 1942, p. 281, Zool. Med. Museum Leiden, vol. 29, 1948, p. 178.

Diagnosis: Size small, orbit high, occiput moderate, postdental part of calvarium moderate. Upper molars small and either of the *sivalensis* type or transitional between the latter and the *palaeindicus* type. Mandibular symphysis moderate to short relative to its width, and low relative to its length. Ramus horizontalis moderately low at M_2 relative to its length, and height at M_2 less than length M_1-M_3 . I_2 two-thirds to about equal in size to I_1 , and I_3 three-fourths to about equal in size to I_1 .

Cotypes: An unfigured mandible from Goenoeng Boetak referred to by Von Koenigswald (1934a, p. 192), and a lower molar figured by Von Koenigswald (l.c., pl. IV fig. 4), originating from the Djetis deposits of Sangiran.

Horizon: Lower Pleistocene.

Locality: Java.

Remains of a hippopotamus from the Poetjangan layers N. of Modjokerto in Eastern Java have been recorded first by Cosijn (1931, p. 119). The fauna from these deposits has been named the Djetis fauna by Von Koenigswald who placed it in the Lower Pleistocene. The name *Hippopotamus antiquus* bestowed upon this form by Von Koenigswald (1934a, p. 192) is a homonym of *Hippopotamus antiquus* Desmarest, 1822, and consequently I have replaced Von Koenigswald's name by *H. koenigswaldi* (Hooijer, 1942a, p. 281). The type material briefly described or figured by Von Koenigswald is not accessible to me, but fortunately I was able to study the first found *Hippopotamus* remains originating from the type locality of the Djetis fauna, viz., the material contained in the Cosijn collection and preserved in the Geological Museum at Leiden. There is also material referable to the present form in the Dubois collection. The scattered notes on the present form as given by Von Koenigswald are assembled below.

H. sivalensis koenigswaldi is smaller than *H. s. sivajavanicus*; the lower incisors are about equal in size but I_2 is placed more distinctly above the level of the other incisors. The height of the horizontal ramus of the mandible is smaller than the length M_1-M_3 (Von Koenigswald, 1934 a, p. 192), a character that applies to *H. s. sivajavanicus* too (l.c., 1933, p. 34), but the present form is closely related to *H. s. soloensis* with which it agrees in

having a steep anterior surface of the mandible (l.c., 1934 b, p. 657) like the Narbada forms. In the upper jaw the I^3 is much reduced in size (l.c., p. 655) like in *soloensis* but the upper molars do not possess a high cingulum, the molars are of a simple structure (l.c. 1934 a, p. 192), and the protuberance of the maxillary above the C is less developed than that in *soloensis* (l.c., 1935 c, p. 87). According to Von Koenigswald the present form is the only hippopotamus to occur with the Djetis fauna, but it is said to occur in the Kali Glagah fauna too (Von Koenigswald, 1934 b, p. 657, 1935 a, p. 194, 1939 a, p. 30) in which latter it is associated with *H. s. siva-javanicus*.

The following specimens have been assigned by me to the present subspecies; the numbers given to the specimens refer to those given in the tables II and III at the end of the present paper.

Calvariums

No. of specimen	reference or Coll. Dub. no.
1	Coll. Dub. no. 2919.
2	Coll. Dub. no. 2907.
3	Coll. Dub. nos. 2188, 2008 b (M^2) and 314 (M^3).

Mandibles

1	Geol. Mus. Leiden no. 27934 and nos. 28138 and 28124 (M_2 - M_3).
2	Coll. Dub. no. 2916.
3	Coll. Dub. no. 2910.
4	Coll. Dub. no. 99.
5	Coll. Dub. no. 2918.
6	Coll. Dub. no. 513.
7	Coll. Dub. no. 2932.
8	Coll. Dub. no. 2931.
9	Coll. Dub. no. 2934.

Coll. Dub. no. 2919, Padas Malang (pl. II fig. 3, pl. IV fig. 1).

Calvarium broken off in front of P^3 , just in advance of the rostral constriction. The upper surface is severely damaged in front of the orbits, which are well elevated above the frontals. The zygomatic arches are complete and slenderly built; the postorbital processes have got lost. The occiput is well preserved and is only slightly elevated above the level of the frontals. There is no pit beneath the anterior portion of the zygomatic arch.

The dentition as a whole is badly preserved; the premolars have crumbled away. The left M^1 is complete but so much worn down that nothing is preserved of the lobes in the transverse valley. In M^2 the posterior lobes of protocone and paracone are equally large, and the latter extends more posteriorly than the former. The posterior groove of the protocone is placed

more labially than the anterior groove of the metaconule. The anterior lobes of metacone and metaconule are not clearly shown, the metacone has a small lingual lobe. M^3 is not much worn, the right has broken off. The cingulum is only weakly developed; there is only a small ridge at the antero-external side of the paracone, and none lingually as far as can be judged from the damaged specimen. The posterior lobe of the protocone is in contact with the anterior lobe of the metacone, thereby excluding the paracone from contact with the metaconule.

The molars of the present specimen are not of the *palaeindicus* type but rather of the *sivalensis* type; unfortunately it cannot be ascertained whether the lingual cingulum is low as is stated to be typical of the present form. Von Koenigswald writes the molars to be a simple structure but figures only a lower molar (Von Koenigswald, 1934 a, pl. IV fig. 4; 1940, pl. II fig. 12) which does not yield subspecific characters. Though the occiput index (ca. 72) is within the variation limits of *H. sivalensis sivalensis* (71-78), the orbito-cephalic index (32) shows the orbit to be even higher than that in *H. sivalensis palaeindicus* (18-26). In the latter index as well as in the P^4 - M^3 -condyle index (79) the present calvarium is widely different from that of *H. sivalensis siva javanicus* from which latter it differs in its smaller size too.

Coll. Dub. no. 2907, Nonko (N.W. of Trinil).

Partial calvarium; only the lower and the right surface (without the orbit) are preserved. The specimen has broken off behind the last molar. The alveoli of the right I^2 and I^3 are preserved, the former measures 12 by 17 mm, the latter is rounded and has a diameter of 12 mm. Above the right canine the maxillary forms a protuberance about 55 mm high and wide. The C possesses the deep U-shaped longitudinal posterior groove typical of the species; the abrasion surface is vertical and the inner surface has no coating of enamel. The premolar series diverges in front on either side; the right have broken off and of the left only parts of the alveoli are seen. Of the molars the left M^3 and the right M^2 and M^3 are present; M^2 has the posterior lobes of the anterior cusps directly opposed to the anterior lobes of the posterior cusps while the metacone has the four-leaved clover pattern. There is a lingual cingulum that forms merely a thickening of the bases of protocone and metaconule. It forms an accessory cusp in the transverse valley. In M^3 , which is but slightly worn, the *sivalensis* type of structure is also shown, and the lingual cingulum forms no distinct ledge either. It consists of a band of enamel that rises along the protocone to a height of 17 mm but is not so distinctly marked off as that in the *soloensis* molars; at the entrance to the transverse valley it falls steeply off and makes

a point again at the lingual surface of the metaconule. The metacone has but a small posterior lobe, and the posterior cingulum is decidedly narrower than the anterior, as is characteristic of a last molar. At the labial surface the cingulum has so weakly developed as to be practically absent.

Coll. Dub. no. 2188, Kedoeng Loemboe (pl. VIII fig. 10).

Left half of palate and a right M^1 belonging to the same individual. The median crest is preserved for a length of ca. 10 cm. Of the C only the posterior surface is present; it shows a deep longitudinal median groove. The pd^1 has broken off and is separated from the P^2 by an interval of 15 mm. P^2 is a narrow, two-rooted tooth with a main cusp and a small posterior cusplet. A very weak and crenulated cingulum is present anteriorly and posteriorly and reaches its maximum development at the anterior moiety of the inner surface. The tooth measures 28 by 17 mm. P^3 is slightly larger (length 29 mm, width 18 mm) and has the accessory posterior cusp as well as the cingulum more strongly developed. The last permanent premolar has not yet erupted; pd^4 is considerably worn. M^1 has a distinct but low (7 mm) lingual cingulum which is not yet worn. The posterior lobes of protocone and paracone are rather small; the latter is somewhat larger than the former but is directly opposed to the anterior lobe of the metacone. Part of the posterior cingulum is lost by interproximal wear with M^2 which latter is unfortunately missing. Of the M^3 the two anterior cusps are present only, and unworn; the tooth is not yet fully in place. The posterior lobe of the paracone extends more posteriorly than that of the protocone. The anterior lobe of the protocone passes gradually into the anterior cingulum; the inner surface of the molar does not show any trace of a cingulum.

A pair of M^2 , little worn, one of which is shown in pl. VIII figs. 11-12 (Coll. Dub. no. 2008 b) has the longitudinal groove between the anterior cusps placed distinctly labially of that between the posterior cusps. The posterior lobe of the paracone is distinctly larger than that of the protocone but does not extend labially beyond the anterior metacone lobe. The molar is intermediate between the *sivalensis* and the *palaeindicus* type and the cingulum is limited at the lingual side to a serrate ridge at the most 8 mm in height that fades away along the metaconule. Labially the cingulum forms an indistinct low band. A pair of M^3 from Kedoeng Loemboe (pl. VIII figs. 13-14) (Coll. Dub. no. 314) totally without labial or lingual cingula and, like the foregoing specimens, of an intermediate structural type, may be referred to the present subspecies too.

Geol. Mus. Leiden, no. 27934, between Djetis and Gondang (pl. V fig. 1).

Mandible, the right ramus broken off behind M_1 , the left at the posterior

half of M_3 . The anterior surface of the symphysis, below the overhanging part containing the incisors, is vertical, it is almost perpendicular to the lower surface. The incisors are lost but the alveoli are well shown, at least those of the right side. I_1 is the largest, I_2 the smallest and placed above the level of the other incisors. I_3 is slightly laterally compressed. The mutual position of the incisors is clearly shown in the photograph (pl. V fig. 1) which has been taken parallel to the upper surface of the symphysis.

The right C has broken off in its alveolus, that of the left is filled with matrix. In the right ramus all teeth have broken off, the alveolus of the pd_1 is faintly indicated. The left P_2 , monocuspid with faint cingulum, is damaged at the base only. P_3 is damaged posteriorly, P_4 has a weak cingulum and a posterior cusplet. M_1 has broken off below the level of the longitudinal valley and the enamel is not preserved. M_2 and M_3 have broken off at the alveolar border.

According to Von Koenigswald "*Hippopotamus antiquus*" (= *H. sivalensis koenigswaldi*) is the only hippopotamus to occur in the Djetis deposits from which the present specimen is derived. Does the present specimen differ from the mandibles of *H. sivalensis sivajavanicus* in the same points as Von Koenigswald states the mandible of *H. sivalensis koenigswaldi* does? It is true that the anterior border of the jaw is steep, which should be characteristic of the Djetis hippopotamus (Von Koenigswald, 1934 b, p. 657), but the I_2 is not placed more distinctly above the level of the other incisors in the present specimen than in that figured by Van der Maarel (1932, pl. VI fig. 2). In the mandible referred to *sivajavanicus* by Von Koenigswald (1934 b, p. 654 fig. 1), however, the displacement of I_2 is less marked than that in Van der Maarel's specimen. The present mandible also is not smaller in all dimensions than those of *sivajavanicus*: the interval between the C (200 mm) is smaller indeed than that in *sivajavanicus* (ca. 215 mm to 245 mm) but the height at pd_1 (95 mm) is greater than that in a specimen recorded by Van der Maarel (no. 2 in table III, 74 mm). Hence it follows with little doubt that the symphysis height-length index is higher in *koenigswaldi* than it must be in *sivajavanicus*. As stated above (p. 65) this is probably the only character by which the mandibles of the two subspecies can be distinguished; the right half of the symphysis of *sivajavanicus* figured by Van der Maarel (1932, pl. XIX fig. 2) seems to have the steep anterior surface supposedly characteristic of *koenigswaldi*, and thus this distinguishing character would seem to fall in too.

In the Cosijn collection from the Djetis deposits N. of Modjokerto in Eastern Java¹) there are also two partial rami of the mandible which supplement the description given above, the molars being preserved.

Geol. Mus. Leiden, nos. 28138 and 28124, N. of Modjokerto (pl. IV fig. 4).

Part of left horizontal ramus with M_1 - M_3 , and part of right ramus with P_4 - M_3 . The fragments agree so closely that they must have belonged to one and the same individual. The height of the ramus at M_2 (ca. 120 mm) is less than the length M_1 - M_3 (ca. 130 mm) which is characteristic of the present subspecies as well as of *H. sivalensis sivajavanicus*. The molar length-ramus height index, which is the length of the three lower molars as a percentage of the height of the ramus at M_2 , is ca. 108 in the present specimen; in *H. sivalensis sivalensis* this index varies from 100 to ca. 141, and in *H. sivalensis soloensis* in which the height of the ramus exceeds the molar length the index is less than 100 (94 in one specimen). Von Koenigswald (1934 a, p. 192) records a mandible from Goenoeng Boetak in which the length M_1 - M_3 is 115 mm and the height of the ramus 98 mm, making an index of 117.

The P_4 is slightly rotated; there is a well-developed accessory cusp lingually of the main cusp, and the lingual cingulum is weak. M_1 is much worn and damaged. In M_2 the longitudinal valley is worn off, and the posterior cingulum has become confluent with entoconid and hypoconid from side to side. The anterior cingulum is still marked off by enamel infoldings at the outer and inner anterior angles of the crown. The protoconid extends more posteriorly than the metaconid and has a much deeper posterior groove than the latter. The same characters are seen in M_3 , of which the hypoconulid is incomplete. The united posterior lobes of the anterior cusps are opposed to the anterior lobes of the posterior cusps which have become confluent too. The infolding of the enamel behind the anterior cingulum is much deeper at the outer than at the inner side. The hypoconulid has a labial pillar.

The M_2 of *H. sivalensis koenigswaldi* figured by Von Koenigswald (1934 a, pl. IV fig. 4; 1940, pl. II fig. 12) agrees with that of *H. sivalensis sivajavanicus* (Van der Maarel, 1932, pl. VI fig. 1, pl. VII fig. 2, pl. XX fig. 2) in the posterior protoconid groove being deeper than that of the metaconid, in the protoconid extending more posteriorly than the metaconid, and in the anterior groove of the entoconid being less sharp than that of the hypoconid. Less worn molars to be described below show certain details more clearly. Apart from their lesser width, the molars in the mandibles to

1) Though Cosijn (1932) has given a map of the region surveyed by him and has marked each locality where fossils were collected with a number, the vertebrate remains are catalogued in the Geological Museum without a reference to the exact locality. Some of them even are labelled "Java" only.

be dealt with below do not differ from those in the present specimen. The amount of variation in the width of M_2 and M_3 (from 31 to 35 mm), however, is even less than that recorded by Van der Maarel (30-36 mm) in *H. sivalensis sivajavanicus*. There is apparently not a single character by which to distinguish the present and following mandibles from those of *H. sivalensis sivajavanicus* described by Van der Maarel unless it be the lesser height of the symphysis in the latter subspecies. The classing of the following specimens with *H. sivalensis koenigswaldi*, therefore, is only provisional.

Coll. Dub. no. 2916, Kedoeng Broeboes (pl. V fig. 2).

Mandible, broken off behind M_3 . The anterior border, below the projecting upper part with the incisors, is almost vertical. I_1 on both sides, as well as the left I_2 , have broken off at the alveolar border which is injured, the right I_2 and I_3 are lost, and the left I_3 has broken off 3 cm inside its alveolus. I_2 is placed slightly above the level of I_1 , and I_3 below the latter, though not so markedly as is the case in the mandibles of *H. sivalensis sivajavanicus* (Van der Maarel, 1932, pl. VI fig. 2 and pl. XIX fig. 2). Both I_2 and I_3 are smaller relative to I_1 than in the foregoing mandible, but I_2 is decidedly the smallest of the series. A great part of the lateral walls of the canine alveoli is lost, and only the right C is partly preserved. Of the premolars only fragments of the roots are present. The symphysis is decidedly lower than that in the foregoing specimen, the symphysis height-length index being 49 against ca. 56 in the latter. The length of the three molars exceeds the ramus height at M_2 .

The right M_1 is partly preserved and shows the posterior protoconid groove to be very deep. M_2 is not damaged. Protoconid and metaconid are confluent as well as the posterior cusps. The protoconid, with a posterior groove much more marked than that in the metaconid, extends more posteriorly than the latter. The anterior hypoconid groove is more distinct than that of the entoconid. M_3 is less worn and has the same characters as M_2 ; the entoconid, however, not being confluent with the cusp beside it, is now shown to be very simply built: the entoconid has only a very small anterior, and no posterior lobe. The hypoconulid joins the posterior lobe of the hypoconid and has a basal accessory pillar on either side.

The simply built entoconid, perceivable only in comparatively little worn lower molars, is shown in the molars of *H. sivalensis sivajavanicus* (Van der Maarel, 1932, pp. 85 and 87) as well as in those of *H. sivalensis soloensis* (Von Koenigswald, 1934 a, pl. IV fig. 5). It is shown in *H. sivalensis sivalensis* too (F.A.S., pl. 61 fig. 5 and pl. 62 fig. 2). It is im-

possible to distinguish between the lower molars of the various subspecies on the ground of the structure of the lower molars.

Coll. Dub. no. 2910, Tritic.

Mandible, the right ramus broken off at M_3 and the left some cm behind the last molar. It has a steep anterior surface, like the foregoing specimens, and three incisors are completely preserved. The two central incisors possess an abrasion surface that is placed at the outer side of their tips, as is usual in *H. amphibius* too. The left I_2 is placed at a higher level than the central I_1 at the alveolus but is more procumbent to the effect that, at its tip, which is obliquely worn off at the outer side, it is not higher than I_1 . The central incisors have an extra-alveolar length of about 105 mm, I_2 projects only one-half as far. The right I_3 has broken off in its alveolus, the left is missing. The alveoli of I_3 are placed on a level with the central incisors, they are smaller than I_1 but larger than I_2 , as usual. The canines have broken off as well as the premolars and molars. The ramus is as slender as that of the foregoing specimen (ramus length-height index 277 and 273 against 232 at the most in *H. sivalensis soloensis* and *H. sivalensis palaeindicus*).

Coll. Dub. no. 99, Tritic (pl. X figs. 1 and 3).

Mandible, the symphysis and the left postdental portion partly restored with plaster. The right ramus has broken off behind the mandibular foramen. Since the symphysis is so very incomplete indices cannot be given, but the antero-inferior edge is less abrupt than that in the other mandibles seen by me and the height at pd_1 (80 mm) is only slightly greater than that in a *sivajavanicus* mandible (74 mm). The present specimen is evidently nearer to the Boemiajoe mandibles described by Van der Maarel than the other specimens examined by me, but in its molar length-ramus height index (118 against ca. 108-125) and in its ramus length-height index (272 against 273-277) it agrees well with the other mandibles here listed under *H. s. koenigswaldi*. The two central incisors are preserved and have an abrasion surface at the outer side of their tips. The left I_1 has a deep vertical groove in the abrasion surface, and the tip of the right I_1 has broken off at a similar groove. Vertical grooves in the abrasion surfaces of the lower incisors exceptionally occur in *H. amphibius* too and are caused by the enamel strip on the upper I . This enamel strip normally does not partake in the formation of an abrasion surface on the antagonist, and the present specimen must have had an anomaly in the position of the upper I . I_2 is placed distinctly above the level of the other incisors and is about one-fourth smaller in diameter than I_1 . A horizontal line along the lower surface of I_2 passes through the centers of I_1 and I_3 . The right I_2 is lost and only the lower part of its alveolus is preserved. The right I_3 as well as the right

C are missing, the left I_3 has broken off in its alveolus, and the alveolus of the left C only is present.

The alveolus of pd_1 is indicated by a rugosity, the other premolars have broken off except the right P_4 . The latter possesses strong accessory lingual and posterior cusps in addition to the main cusp. M_1 , preserved on the left side only, is too much worn for comparison purposes, but M_2 is entire. The posterior protoconid groove is rather deep; the entoconid is still separate in the left (confluent with the hypoconid in the right) and has the simple structure already noticed above: there is only a very small anterior and hardly a posterior lobe. A small accessory cusp occurs at the labial entrance to the transverse valley in the right M_2 which is absent in the left. M_3 is only very slightly worn, and not only the entoconid but also the metaconid is seen to be very simply built. This is, however, more marked in the right than in the left M_3 . While in the right M_3 the metaconid has no posterior lobe, and the posterior protoconid lobe is in contact with the anterior lobe of the hypoconid, in the left M_3 the metaconid has a posterior lobe which extends even more posteriorly than that of the protoconid, and makes a contact with the anterior hypoconid lobe. The hypoconulid, which forms a big heel to the crown larger even than any of the main cusps, is separated from entoconid and hypoconid by a wide cleft partly filled by the posterior hypoconid lobe.

The present specimen illustrates again the amount of individual variation in the molar pattern; the posterior metaconid lobe, absent in the right M_3 , is wedged in between the two outer cusps in the left. This difference in structure would have disappeared as soon as the longitudinal valley between protoconid and metaconid is worn away.

The left ramus ascendens is for the greater part preserved; the coronoid process has broken off but the condyloid process is entire. It differs in shape from that of *H. amphibius*: the rounded lateral part of the condyle is less prominent than that in *H. amphibius* and in the latter species the articulation surface passes more gradually into the condylo-coronoid notch. The ascending ramus is incomplete posteriorly, but the angular process is tolerably well preserved and is seen to form no point anteriorly as it does in *H. amphibius*.

The five following specimens of the mandible consist of the symphysis only. They vary slightly in the steepness of the anterior surface and the I and C have broken off; in all of them the lower border of I_2 is slightly below the line connecting the centers of I_1 and I_3 , as shown in the specimen figured on pl. IX fig. 3.

Coll. Dub. no. 2918, Papan Djaran (pl. IX fig. 3). I_2 dext. is lost.

- Coll. Dub. no. 513, Nonko, N.W. of Trinil. The C is rather narrow.
 Coll. Dub. no. 2932, Nonko, N.W. of Trinil. Anterior border damaged.
 Coll. Dub. no. 2931, Kedoeng Broeboes. Much damaged anteriorly and at the right side.
 Coll. Dub. no. 2934, Kedoeng Broeboes. Upper and posterior surfaces incomplete.

***Hippopotamus sivalensis soloensis* nov. subsp.**

Hippopotamus sp. Stremme, N. Jahrb. f. Min., 1911, p. 57, Selenka and Blanckenhorn. Die Pithecanthropus-Schichten auf Java, Leipzig, 1911, p. 104, pl. XVI figs. 6-7, pl. XIX fig. 6; Van der Maarel, Wet Med. Dienst Mijnb. Ned. Ind., no. 15, 1932, p. 89, pl. XVIII figs. 1-2, pl. XIX fig. 3.

Hippopotamus (Hexaprotodon) sivajavanicus Von Koenigswald, Wet. Med. Dienst Mijnb. Ned. Ind., no. 23, 1933, pp. 31 and 90.

Hippopotamus (Hexaprotodon) namadicus Von Koenigswald, De Ing. in Ned. Indië, vol. 1, part 11, sect. 4, 1934, p. 194, pl. IV figs. 5-6, Proc. Kon. Akad. Wet. Amst., vol. 38, 1935, p. 190.

Hippopotamus namadicus Von Koenigswald, Proc. Kon. Akad. Wet. Amst., vol. 37, 1934, p. 655, figs. 5-7, Ibid., vol. 39, 1936, p. 1000; Callenfels, Man, vol. 36, 1936, p. 210; Anonymus, Nature, vol. 139, February 13, 1937, p. 294; Von Koenigswald, Quartär, vol. 2, 1939, pp. 38 and 45, Wet. Med. Dienst Mijnb. Ned. Ind., no. 28, 1940, p. 60, pl. III fig. 6; Hooijer, Zool. Med. Museum Leiden, vol. 29, 1948, p. 178.

H[ippopotamus] namadicus Arambourg, Mission Scientifique de l'Omo 1932-33, vol. 1, fasc. 3, 1948, p. 333.

Hippopotamus nomadicus Callenfels, Ill. London News, vol. 188, no. 5060, 1936, p. 624, p. 625 fig. 5 (middle skull).

Diagnosis: Size moderate, orbit very high, occiput moderate to low, postdental part of calvarium moderate. Upper molars small and of the *palaeindicus* type. Mandibular symphysis short relative to its width, and very high relative to its length. Ramus horizontalis very high at M_2 relative to its length, and height at M_2 exceeding length M_1-M_3 . I_2 three-fourths to about equal in size to I_1 , and I_3 slightly smaller, or even larger than I_1 .

Holotype: A calvarium in the Dubois collection (no. 2914) described and figured in the present paper (pl. II fig. 1, pl. III fig. 1, pl. VI fig. 1).

Horizon: Middle and Upper Pleistocene.

Locality: Central and Eastern Java.

As stated already under the head *Hippopotamus sivalensis sivajavanicus* (Dubois) the material which Von Koenigswald in 1933 referred to Dubois's species is assigned to *H. s. namadicus* in 1934. The latter subspecies is based on four partial mandibles from the Narbada Beds in central India, and their characters have already been dealt with above. In the opinion of Von Koenigswald the "*Hippopotamus namadicus*" occurring in the Middle Pleistocene Trinil fauna and (more frequently) in the Upper Pleistocene Ngan-

dong fauna of Java is doubtless the descendant of the Lower Pleistocene "*H. antiquus*" (= *H. sivalensis koenigswaldi*) of Java, and thence it is supposed to have migrated to India (Von Koenigswald, 1935 a, p. 198). I have come to the conclusion that the supposed Javanese *namadicus* is not identical to the Narbada form, but represents a collateral subspecies differing in primitive as well as in progressive characters. *Hippopotamus sivalensis soloensis* nov. subsp. differs from *H. sivalensis namadicus* in the mandibular symphysis being longer relative to its width, and in its smaller incisors of which I_3 is not usually larger than I_1 . The calvariums from Java differ from those assigned to *H. sivalensis palaeindicus* in their higher orbits, longer postdental part, smaller molars, and in the molar series not extending behind the posterior border of the palate. If the Narbada calvariums are correctly assigned to the most progressive of the two Narbada subspecies, the calvarium of *H. sivalensis namadicus* will have a less elevated orbit than those at present known, which would distinguish them at once from the Java calvariums to be described below.

Stremme (1911 b, pl. XVI figs. 6-7) figures two upper molars from the Middle Pleistocene of Trinil the less worn of which shows the *palaeindicus* type of structure very clearly¹). The posterior lobe of the paracone extends more posteriorly than that of the protocone, and is placed labially of the anterior metacone lobe. Van der Maarel (1932, p. 89, pl. XVIII figs. 1-2, pl. XIX fig. 1) records an occiput from Watoealang of which the height-width index is 60. Van der Maarel (l.c., p. 106) correctly stated that the Watoealang specimen has more affinity to the Narbada forms than to the Siwalik form, and this specimen has subsequently been referred to *H. siva-javanicus* (Von Koenigswald, 1933, pp. 31 and 33) and one year afterwards to *H. namadicus* (Von Koenigswald, 1934 b, p. 656). A beautiful complete calvarium of the present form has been figured, on a very small scale, by Callenfels (1936, p. 625 fig. 5 middle skull). It shows the very high orbit so markedly characteristic of *H. sivalensis soloensis*, and it is very unfortunate that this specimen was never described by Von Koenigswald nor even figured in a more satisfactory way. As far as the calvarium of the present form is concerned, Von Koenigswald (1934 b, p. 656/57) only mentions that the I^3 is reduced in size, like it is in *H. sivalensis koenigswaldi*. The mandible is stated to have a steep anterior surface like that of *koenigswaldi* (l.c., p. 657) but the height of the horizontal ramus exceeds the length M_1 - M_3 , I_2 is smaller and higher in position and the molars have a more complicated

¹) And so does the left upper molar figured by Von Koenigswald (1940, pl. III fig. 6).

pattern than is the case in *H. sivalensis koenigswaldi* (Von Koenigswald, 1934 a, p. 194).

The specimens belonging to the present subspecies are listed below, and the numbers given to the specimens refer to those given in tables II and III at the end of the present work.

Calvariums

No. of specimen	reference or Coll. Dub. no.
1	Coll. Dub. no. 2914 (holotype).
2	Coll. Dub. no. 2911.
3	Coll. Dub. no. 2909, and no. 2205 (M ³).
4	Coll. Dub. no. 2902, and no. 2318 a (M ²).
5	Coll. Dub. no. 1702, and Van der Maarel, 1932, p. 106 (occiput).

Mandibles

1	Coll. Dub. no. 2915.
2	Coll. Dub. no. 2929.
3	Coll. Dub. no. 2903.
4	Coll. Dub. no. 4908.

Coll. Dub. no. 2914, Tinggang (Solo Valley) (pl. II fig. 1, pl. III fig. 1, pl. VI fig. 1).

Calvarium with M²⁻³ dext. Apart from the dentition the specimen is rather well preserved, the major defects being the lack of part of the right anterior expansion of the maxillary and the loss of the greater part of the right orbit. The premaxillaries are united along their entire length and the foramen incisivum is rather small. On either side of the anterior narial orifice a crest is developed on the premaxillaries. The maxillaries expand rapidly anteriorly, and the left, which is complete, forms a protuberance about 65 mm high and wide above the canine. The nasals do not expand very much posteriorly; the sutures of the lacrimal are obliterated. The infraorbital foramen is placed above the P⁴; the border of the maxillary is much expanded below the rostral constriction. Beneath the anterior portion of the zygomatic arch there is only a shallow depression, the arches are entire and rather massively built. While the dorsal surface of the calvarium is very flat antero-posteriorly in front of the orbit (the nasals are only depressed anteriorly in the median line), the interorbital region is somewhat convex antero-posteriorly, and the occiput is well raised. The orbit has a considerable elevation, the postorbital process is missing. The occiput has a rather strong median vertical crest, and the foramen magnum tapers above into a median point. The condyles are complete but the paroccipital processes as well as the left postglenoid process damaged. The bullae appear to be

more rounded than those in *H. amphibius*. The pterygoid bones are injured but the posterior border of the palate is well preserved; it possesses a median point like that often seen in *H. amphibius* too.

The incisors are lost, but the alveoli, except that of the right I^1 , are well shown. That of I^1 measures 19 by 14 mm, that of I^2 23 by 14 mm, while that of I^3 is about 16 by 12 mm. The canines, broken off in their alveoli, possess the usual well-developed posterior longitudinal groove. The alveolus of the left pd^1 is preserved, it is a small and shallow pit much like that often seen in *H. amphibius*. P^2 is shown by its alveolus to have had two medially constricted roots. The posterior premolars have broken off, the premolar series distinctly converge posteriorly.

Of the molars parts of the right M^2 and M^3 only are available for study. The paracone of M^2 is for the greater part lost, its posterior lobe is directed labially and is much larger than the posterior protocone lobe. The metacone has a distinct lingual lobe. The lingual cingulum is much developed and has become confluent with the protocone; its exact height cannot be determined. It fills the lingual entrance to the transverse valley completely. The anterior groove of the metaconule is weak, its anterior lobe, therefore, is not so distinctly marked off as that of the metacone which is even constricted and in contact with the posterior paracone lobe without the latter extending labially beyond it. Of M^3 the posterior moiety is lost. The anterior lobe of the paracone is separated from the anterior lobe of the protocone, and either of them is confluent with the anterior cingulum; a small rectangular enamel islet has remained between. The posterior lobe of the paracone is large and directed labially, the anterior metacone lobe is wedged in between the former and the posterior protocone lobe which is the smallest. The paracone has a lingual lobe and thus shows the four-leaved clover pattern like the metacone in M^2 . The lingual cingulum forms a distinct strong ledge along the protocone, about 17 mm high and not less than 3 mm thick. At the entrance to the transverse valley it falls off distinctly. The posterior part of M^3 has broken off, but its posterior alveolar border is seen to be in advance of the posterior border of the palate.

The most characteristic features of the present specimen are the elevation of the orbit above the frontals to a degree exceeding that in *H. sivalensis palaeindicus* (orbito-cephalic index 36 against 18-26 in the Narbada form) while the postdental portion is relatively longer than that in the latter subspecies (P^4 - M^3 -condyle index 75 against 82-84 in *H. sivalensis palaeindicus*), thereby combining a progressive and a primitive character as compared to the calvarium of the Narbada form. In size the present specimen is decidedly inferior to the Narbada calvariums, but on the other hand it is

larger than the calvarium of *H. sivalensis koenigswaldi*. From the latter the present specimen differs too in the presence of a thick and high lingual cingulum on the upper molars which, however variable in *H. sivalensis sivalensis*, seems to be characteristic of the molars of *H. sivalensis soloensis* and of *H. sivalensis palaeindicus*. The *palaeindicus* type of structure is shown in M³ of the present specimen only; in M² the posterior paracone lobe does not extend labially beyond the anterior metacone lobe though it is distinctly directed outward like in the M¹ and M² of the specimen of *H. sivalensis palaeindicus* figured in F.A.S., pl. 57 fig. 2.

Coll. Dub. no. 2911, Tinggang (Solo Valley) (pl. VII fig. 1).

Calvarium, less well preserved than the foregoing specimen but with the dentition far better preserved. The specimen agrees with the holotype rather closely in the shape and size of its parts. The premaxillaries are incomplete medially; the maxillary protuberance above the C has broken off at the left side and is damaged at the right. The infraorbital foramen has the same position and the rostral constriction is as pronounced as that in the foregoing specimen; the swelling of the alveolar border of the maxillary in its middle portion is perhaps slightly more pronounced. The pit under the anterior portion of the zygomatic arch is somewhat deeper too. Both orbits have broken off, the zygomatic arches are, however, entire. The anterior part of the nasals is missing and the nasals are not depressed in the median line, they widen only slightly backward. The lacrimal sutures are invisible. The occiput is again well raised and has a strong median vertical crest; the right occipital condyle and the paroccipital processes are missing. The pterygoids and the right bulla are damaged; the posterior border of the palate is undamaged, extends behind M³ and has no median posterior projection.

The incisors are missing and their alveoli are not well shown except that of the right I¹ the greater diameter of which is about 22 mm, and that of I², filled with matrix, and 27 by 21 mm in diameters. Both incisors are larger than their homologues in the foregoing calvarium; there is no trace of an I³. The canines are not preserved, the premolars have broken off except the left P⁴. P⁴ is rotated for 90°, with its posterior surface facing inward. It is a small tooth (length 24 mm, width 20 mm) with a strong posterior, labial, and lingual cingulum, and a lingual accessory cusp confluent with the paracone.

M¹ is too much worn; in the right some small enamel islets represent the transverse valley, which have disappeared in the left. M² is more suitable for a description; the left lacks part of the metaconule, the right almost the whole of the metacone. Between the anterior lobes of protocone and paracone which have become confluent with the anterior cingulum, an

enamel islet is formed. The posterior lobe of the paracone is more than two times longer than that of the metacone and extends distinctly labially beyond the anterior metacone lobe. Added to that the lingual cingulum is very distinctly developed and makes a 3 mm wide and at least 15 mm high ledge both along protocone and metaconule which stamps this tooth as a very characteristic *palaeindicus* type. Labially there is a cingulum only at the base of the metacone, low but well raised from the surface. M^3 is almost complete at the left side, the metaconule only is for the greater part lost. The right M^3 has crumbled away except for its lingual cingulum that forms a wall varying from 5 to 7 mm in thickness and with a height of 16 mm along the anterior two-thirds of the lingual surface of the molar. It falls steeply off behind, and rises again (along the metaconule) into the posterior cingulum that is but partly preserved. The left M^3 shows the posterior paracone lobe to be situated labially of the anterior metacone lobe; the latter makes a contact with the posterior protocone lobe. The paracone is of the four-leaved clover pattern like that in the foregoing calvarium. There is no cingulum on the labial surface.

Coll. Dub. no. 2909, Tinggang (Solo Valley) (pl. VI fig. 2).

Right half of calvarium, with part of the left maxillary and of the left half of the occiput. The nasal is badly damaged, the premaxillary is incomplete anteriorly and has a crest on its upper surface like that in the holotype. The maxillary protuberance above the C is particularly well developed; it reaches not less than 70 mm above the alveolus of the canine and measures 72 mm antero-posteriorly. The orbit, too, is more elevated than that in the holotype, the orbito-cephalic index being 39 against 36 in the latter. The pit under the anterior part of the zygomatic arch is very distinctly developed. The zygomatic arch is complete, and the greater part of the postorbital process is present. The occipital condyle and the basicranial surface are lost.

The alveoli of the right I^1 and I^2 are well shown, the former measures 21 by 16 mm, the latter 26 by 20 mm. There is no trace of I^3 nor of its alveolus. Part of the canine is lost, the alveolus shows the tooth to possess the usual U-shaped and deep posterior longitudinal groove. P^4 is the only premolar preserved, slightly rotated, and of the same structure as that in the foregoing specimen but a little longer (26 by 20 mm).

M^1 is damaged; the posterior paracone lobe is still seen to be larger than the posterior protocone lobe. M^2 is well preserved except for some damage at the main lobe of the metacone. It is almost an exact image of the corresponding molar in the foregoing specimen and needs not to be described. M^3 has crumbled off.

Coll. Dub. no. 2902, Trinil.

Calvarium, broken into two parts that do not fit. The anterior fragment consists of the right premaxillary and anterior portion of the maxillary, the other comprises the posterior part of the maxillary with M^2-3 , the upper surface of the calvarium from 13 cm in front of the orbit backward with the left orbit broken off. The left zygomatic arch is missing, of the occiput the right part is preserved only but the condyle and basicranial surface are lost.

The incisor alveoli in the premaxillary show these elements to be smaller than those in the foregoing calvariums: I^1 measures 13 mm in diameter and appears to be rounded, I^2 is 21 by 14 mm, while I^3 is very small (the diameter of its indistinct alveolus would seem to be only ca. 11 mm). The canine, broken off in its alveolus, has a distinct posterior longitudinal groove nearer to the medial than to the lateral side. The maxillary protuberance is missing.

The posterior portion of the palate has a slightly convex interorbital surface with a concavity behind, and a well raised occiput like the foregoing specimens. The orbit is very high; the orbito-cephalic index ($34\frac{1}{2}$) is but slightly smaller than that in Coll. Dub. nos. 2914 and 2909 (36-39).

M^2 has broken off slightly in advance of the transverse valley and presents a very close similarity to its homologue in the preceding calvariums which is also the case with the M^3 ; a description is superfluous.

Coll. Dub. no. 1702, Kedoeng Loemboe (pl. VII fig. 2).

Palate with premolars and molars. The top of a calvarium, with the frontal, sagittal and nuchal crests and an occiput width of ca. 256 mm may have belonged to the same individual. The palate has broken off in front of P^2 at the right side; at the left side a small part of the premaxillary is preserved. In front of the left P^2 there is a rather large alveolus, 19 mm in diameter, that may have contained a P^1 . In the foregoing specimens the alveolus for the anterior premolar, if any, is so small as to represent undoubtedly that of pd^1 , a persistent milktooth, like in *H. amphibius*. P^2 is well-developed, moncuspid with a crenulated cingulum widest posterolingually. The paracone is slightly bent inward, the length is 28 mm, the width 23 mm. P^3 , preserved on the right side only, is slightly shorter (26 mm) by the same width, and has a better developed cingulum. While the tip of P^2 is just touched by wear, that of P^3 is almost half worn down. The pd^4 is still present but of course much worn; it is interesting to see that this milk element, too, shows the *palaeindicus* type of structure very clearly. The left pd^4 is already shed, but its successor is not buried in the bone below the former; it would seem that P^4 is completely suppressed

as is stated to occur occasionally in the Javan hippopotamus by Von Koenigswald (1935 d, p. 540). M¹, preserved at the right side only, is worn down below the level of the longitudinal valley. The posterior lobe of the paracone is larger than that of the protocone and is duplicated; there is a small lobe between the posterior and the main paracone lobe, exactly like in the left M¹ figured by Stremme (1911 b, pl. XVI fig. 6, not a right M¹ as stated in the explanation to the plate). The lingual cingulum is strong but worn and its height cannot be determined. At the labial side a cingulum is present too, which attains a thickness of 5 mm along the metacone.

The M² is entire on both sides. There is a very strong cingulum, 3-4 mm thick and about 18 mm high, along the whole of the lingual surface, and as thick as, but lower (at the most 12 mm) than the lingual also at the labial surface. The posterior paracone lobe extends labially beyond the anterior metacone lobe. This tooth is a very characteristic specimen like that figured by Stremme (1911 b, pl. XVI fig. 7) which, incidentally, shows the four-leaved clover pattern of the metacone as clear as our specimen. M³ has a lingual cingulum but slightly less developed than that of M²; the posterior paracone lobe is longer than that of the protocone but does extend labially beyond the anterior metacone lobe only in the left specimen; in the right M³ it is opposed to the anterior lobe of the metacone. The two molars differ in other points too: the protocone extends more anteriorly relative to the paracone in the left than in the right M³, and there are irregularly elevated patches of enamel in the transverse valley in front of the metaconule in the right M³ (decalcification?) that are absent in the left. The metaconule, as usual, is of a simple structure, it has neither an anterior nor a posterior lobe.

There is still a small collection of upper molars from various localities the structure of which shows them to belong to the present subspecies. Coll. Dub. nos. 2318 a (a left M² from Bangle) and 2205 (right and left M³ from Kedoeng Broeboes) show the *palaeindicus* type of structure very clearly (pl. VIII figs. 6 and 9); the lingual cingulum is 16-18 mm high and 2-4 mm thick in the M³; in M² it is partly lost but its development is not inferior to that in the last molar. An identical development of the lingual cingulum is seen in a right M² and M³ in a maxillary fragment from Bogo (Coll. Dub. no. 2084 b, pl. VIII fig. 5). In the M² the united anterior lobes of metacone and metaconule are wedged in between the posterior lobe of the paracone and the (smaller) posterior protocone lobe, like in the M² of *H. sivalensis palaeindicus* (F.A.S., pl. 57 fig. 1 b). The M³ has the posterior paracone lobe not extending labially beyond the an-

terior metacone lobe but nevertheless it is decidedly larger than the posterior protocone lobe. Hence it does not reveal the *palaeindicus* pattern, and neither does the right M³ in the palate from Kedoeng Loembœ (Coll. Dub. no. 1702). It is evident that the mutual position of the lobes of the cusps in the transverse valley of the upper molars does not always furnish a clue as to the subspecific position of the specimen, but, as said above, I would not like to ignore this point even though it is not a hard and fast rule; it is still the best character I could find for discrimination between the upper molars of the primitive and those of the progressive races of *H. sivalensis*. Both in Coll. Dub. no. 1702 and in no. 2084 b the M² is definitely of the *palaeindicus* type, and it is not unusual to find the last molar to be less constant in its characters than the other elements.

A right and left M² and M³ from Kedoeng Loembœ (Coll. Dub. no. 2077) are easy to identify; in either of them the posterior paracone lobe is labially of the anterior metacone lobe. Since the left M² and the right M³ are incomplete, the right M² (pl. VIII figs. 3-4) and the left M³ (pl. VIII figs. 1-2) have been figured, both in crown and in lingual view to show the heavily developed lingual cingulum. In the M² it has a crenated edge, in M³ it is lowest at the metaconule. An isolated right M³ (Coll. Dub. no. 153, pl. VIII fig. 8) shows the same development of the lingual cingulum as its homologue in Coll. Dub. nos. 2914, 2911 and 2902: there is a sudden fall of the cingulum at the level of the lingual entrance to the transverse valley; along the protocone it is at the most 15 mm high, and along the metaconule it gradually rises posteriorly from 5 mm to about 12 mm and is much less distinctly marked off. Incidentally, the same development of the lingual cingulum of M³ is found in *H. sivalensis palaeindicus* (F.A.S., pl. 57 fig. 2 a). The longitudinal groove between the anterior cusps is placed to the labial side of that between the posterior cusps and the posterior paracone lobe reaches to the main lobe of the metacone at the base. We have finally a right and a left series M¹-M³ from Soember Waroe (Coll. Dub. no. 2195, pl. II fig. 2, pl. X fig. 4) and a right M² and M³ of the *palaeindicus* type with heavy cingula (Coll. Dub. no. 2203, Kedoeng Broeboes). The measurements of the upper molars, as far as not recorded in table II, are given here.

Coll. Dub. no.	2084 b	2077	163	2195	2203
Length of M ²	46	44	—	—	41
Width of id.	42	39	—	35	38
Length of M ³	44	42	44	39	40
Width of id.	44	38	39	35	35

Coll. Dub. no. 2915, Solo Valley (pl. IV fig. 3, pl. VI fig. 4, pl. IX fig. 2).

Mandible, the left ramus broken off behind M_3 , the right ascending ramus and angular process partly preserved. The specimen is rather heavily built, with a thick symphysis and broad rami which increase steadily in height from the front backward. The anterior surface is vertical below the projecting portion containing the incisors. The angular process is not pointed forward as it does in *H. amphibius*. The symphysis length-width index in the present specimen is 69 which is a value found in *H. sivalensis koenigswaldi* (ca. 62-ca. 79) too, though in *H. sivalensis namadicus* (57-64) and in *H. sivalensis palaeindicus* (ca. 61-67) the symphysis is still shorter relative to its width. The symphysis height-length index is much more convenient as a subspecific character: in the present specimen this index is 71, a figure very much different from that in *H. sivalensis sivalensis* (37-50) or in *H. sivalensis koenigswaldi* (49-ca. 56) and which shows the present mandible to have the very high symphysis of the Narbada subspecies (60-ca. 77). The ramus is higher at M_2 than the length M_1 - M_3 and the molar length-ramus height index consequently is less than 100 (namely, 94) which it is not in the more primitive Javan races. A very significant index too is the ramus length-height index, which is 215 in the present jaw against 250-298 in *H. sivalensis sivalensis* and 272-277 in *H. sivalensis koenigswaldi*. The ramus is even higher than that in *H. sivalensis palaeindicus* (232), and the partially reconstructed ramus of *H. sivalensis namadicus* figured in F.A.S. (pl. 58 fig. 1 a) gives about the same figure.

The incisors have all broken off; I_2 is the smallest of the series but is not much elevated above the level of I_1 and I_3 . The size relations of the incisors are not different from those in *H. sivalensis koenigswaldi*. From the mandibles of *H. sivalensis namadicus* the present specimen differs in the smaller size of its incisors as well as in the fact that I_3 is smaller than I_1 , while in the Narbada forms I_3 is equal to, or larger than I_1 in its greater diameter.

Of the canines the alveoli only are present, and their dimensions indicate canines of the size of those in *H. sivalensis namadicus* and larger than those in *H. sivalensis koenigswaldi*. Of the premolars and molars only the right M_3 is preserved. The longitudinal valley is indicated by enamel islets only. The grooves in the lingual cusps are weaker than those in the labial cusps, and the lingual entrance to the transverse valley is the wider of the two. The hypoconulid is relatively large. The molar unfortunately does not show so many characters as it would have done in a less worn state but does not

seem to present differences from its homologue in *H. sivalensis koenigswaldi*. Added to that it is not larger. The M_3 of *H. sivalensis palaeindicus* is very distinctly larger than that of the Javan forms but does not differ in structure either. Von Koenigswald (1934 a, pl. IV figs. 4-5) figures two lower molars as belonging to *H. sivalensis koenigswaldi* and *H. sivalensis soloensis* respectively and states that the enamel pattern in the latter form is more complicated than that in the former. The differences in complexity between the two specimens figured, however, are due to the different stage of wear: the *soloensis* molar is much less worn than that of *koenigswaldi* and still shows the longitudinal valley, which is worn away in the latter specimen. The cingula are taken into use in the *koenigswaldi* molar which makes the tooth shorter than it would have been in a less worn state. As a point of difference it can be observed that the posterior metaconid lobe is longer in the *soloensis* specimen (l.c., fig. 5) than in that of *koenigswaldi* (l.c., fig. 4), but with a view to the variability shown in Coll. Dub. no. 99 this difference is of no importance.

Coll. Dub. no. 2929, Kedoeng Madoh (pl. IX fig. 1).

Mandibular symphysis. At the left side the medial border of the canine alveolus only is preserved, and the lower parts of the incisor alveoli. At the right side the upper surface of the symphysis is preserved only above the proximal parts of the alveoli of the incisors. The symphysis indices do not differ much from those of the preceding specimen, but the elevation of I_2 above the level of the other incisors is very much more marked; a line through the centers of I_1 and I_3 passes below the lower margin of I_2 . The alveolus of I_1 extends almost throughout the whole length of the symphysis, the alveolus of I_3 is about 70 mm deep and that of I_2 is 15 mm longer. I_3 is slightly smaller than I_1 , as usual in the Javan forms.

Coll. Dub. no. 2903, Trinil.

Right horizontal ramus of the mandible, broken off behind M_3 . The ramus length-height index (232) is exactly the same as that in *H. sivalensis palaeindicus*. The symphysis is damaged anteriorly and has broken off along the medial surface of the left canine. The alveoli of the left I_2 and I_3 are incomplete; the left I_1 as well as the right I_2 have broken off in their alveoli, and those of the right I_1 and I_3 are preserved. I_2 is well above the level of the other incisors and is the smallest incisor, a line connecting the centers of I_1 and I_3 forms a tangent to its lower border. The right canine has broken off in its alveolus and is again larger than that in *H. sivalensis koenigswaldi*. The premolars are lost except the M_3 which is not yet fully in place.

Coll. Dub. no. 4908, Kedoeng Broeboes.

Right symphyseal portion of mandible, broken off in the median line and behind P₄. The upper surface of the symphysis is lost except above the proximal parts of the incisor alveoli. I₂ is elevated above I₁ and I₃ to the same degree as that in the foregoing specimen, the alveolus of I₃ is slightly deeper than that of I₂. The steepness of the anterior surface of the symphysis is less marked than that in the foregoing specimens. The premolars are missing.

The present four lower jaws differ from those of *H. sivalensis namadicus* in the incisors being smaller, whilst I₃ is slightly smaller than I₁ instead of the reverse as is true in the Narbada forms. An identical development is occasionally shown in the Javan form too, however. Von Koenigswald (1933, p. 32) records a mandible from Ngandong in which I₃ would be about twice as large as I₁ but of which the incisor diameters stand in the relation of 2 : 1 : 3 approximately (l.c., p. 91). This specimen is regarded as an individual variation; usually I₁ and I₃ are about equal in size. A figure of the specimen was presented in a later paper (Von Koenigswald, 1934 b, p. 656 fig. 5; in the explanation of this figure read I₁ for I₃ vice versa) but neither of this nor of the other specimens Von Koenigswald gave the measurements. Of our specimens the measurements are recorded in table III.

We have, thus far, evidence of the presence of three forms of *Hippopotamus* in the Pleistocene of Java. The three "species" recorded by Von Koenigswald (*H. simplex*, *H. antiquus*, and *H. namadicus*) are represented in the Dubois collection and are dealt with under the heads *H. sivalensis siva-javanicus*, *H. sivalensis koenigswaldi*, and *H. sivalensis soloensis* respectively. There is a possibility of the existence of a fourth subspecies of *H. sivalensis* in Java that would seem to exceed the other Javan forms in size:

***Hippopotamus sivalensis* Falconer et Cautley subsp.**

Hippopotamus sp. Von Koenigswald, De Ing. in Ned. Indië, vol. 1, part 11, sect. 4, 1934, p. 192.

A fragment of upper jaw with M² from the Lower Pleistocene of Sangiran in Java is mentioned but not identified as to the species by Von Koenigswald (1934 a, p. 192). The molar is stated to be strikingly broad and thereby presenting a primitive structure. The length is given as 40 mm, the width as 48 mm. Though the tooth is stated to represent probably a new species no words are bestowed upon it in any subsequent paper by Von Koenigswald. The M² in the Kodawala calvarium of *H. sivalensis sivalen-*

sis (Coll. Dub. no. 3148) has nearly the same dimensions (the length much reduced by interproximal wear) which exceed those of the upper molars of the contemporaneous Javan forms *sivajavanicus* and *koenigswaldi* (width of upper molars 42 mm at the most). I guess the present Sangiran specimen to be an upper molar of *Hippopotamus sivalensis* comparable to *H. sivalensis sivalensis* and *H. sivalensis palaeindicus* as to size and with its antero-posterior diameter much reduced as a result of interproximal wear, but a definite conclusion can be arrived at only upon examination of the specimen itself.

POSTCRANIAL REMAINS OF HIPPOPOTAMUS FROM THE PLEISTOCENE OF JAVA

The attribution of postcranial remains to species or subspecies which until now are distinguished by cranial and dental characters only is a difficult task unless there is a marked difference in size or a stratigraphical separation between the species or subspecies from a special region to distinguish between. I have a number of vertebrae and limb bones from the Lower Pleistocene N. of Modjokerto in Eastern Java collected by Dr. J. Cosijn and preserved in the Geological Museum at Leiden, and also limb bones and pelvic remains from various localities in Java belonging to the Dubois collection. In general, the bones in the Cosijn collection are smaller than those in the Dubois collection, which would be in accord with Von Koenigswald's statement that *H. sivalensis koenigswaldi*, the only hippopotamus to occur in the Djetis deposits from which the Cosijn collection originates, is smaller than either *H. sivalensis sivajavanicus* or *H. sivalensis soloensis* which latter form was identified with *H. sivalensis namadicus* by Von Koenigswald. However, some of the bones in the Cosijn collection (parts of a radius and a caput of a femur) belong to the larger bones, and some astragali in the Dubois collection to the smaller. In the absence of other, more positive, evidence I would not like to infer from the presence of some comparatively large bones in the Cosijn collection the existence of either *H. s. sivajavanicus* or *H. s. soloensis* in the Lower Pleistocene Djetis fauna, and I prefer to leave all postcranial remains subspecifically unidentified for the present.

Geol. Museum Leiden, no. 18489, between Djokja and Oenarang, Central Java (pl. XI, middle figs.).

Epistropheus. The arcus vertebrae has broken off slightly in advance

of the incisura vertebralis cranialis. The right and left processus transversus are incomplete; the foramen transversarium, however, is entire. There are injuries at the fossa vertebrae, at the ventral spine, at the highest part of the processus spinosus, and at the left articulation surface for the atlas.

The processus spinosus is elongated backward to a slightly greater degree than that in the specimens of the epistropheus assigned to *H. sivalensis sivalensis* figured in F.A.S. (pl. 63 figs. 5-7), but in *H. amphibius* and in *H. liberiensis* this feature is much more marked. The articulation surfaces for the atlas are rather low and elongated transversely in our fossil as well as in *H. sivalensis sivalensis*; the height of these facets are about equal to the height of the foramen vertebrale, while in both recent species the former height is decidedly greater than the latter (table below). In *H. liberiensis* the articulation surfaces for the atlas are relatively broader than those in *H. amphibius*, and in this respect the former species is nearer to the Javan fossil than the latter.

When viewed from below (pl. XI, lower figs.) there is seen to be a great difference between the fossil and the recent forms. The strong transverse crest at the base of the processus spinosus passes gradually into the lower borders of the right and left atlas facets and forms an even arch, while in *H. amphibius* as well as in *H. liberiensis* the atlas facets are saddle-shaped, making the dens more prominent than it is in the fossil specimen. In *H. sivalensis sivalensis* (F.A.S., pl. 63 figs. 5-9) we find exactly the same evenly curved crest from side to side as that in the Javan fossil.

The facies articulares caudales in our fossil face more ventrally than laterocaudally, while in *H. sivalensis sivalensis* (F.A.S., pl. 63 figs. 5 a and 5 b) these facets face rather laterocaudally and only slightly ventrally. In *H. liberiensis* the posterior articular surfaces face more laterally and caudally than those in *H. amphibius*; the former species, therefore, agrees better with *sivalensis* than the latter does. The measurements are given here ¹⁾.

¹⁾ In this table as well as in the following the measurements given for *H. amphibius* are taken from the skeletons nos. 6 and 22 respectively.

Measurements of epistropheus

	<i>H. sivalensis</i>		<i>H. amphibius</i>	<i>H. liberiensis</i>	
	subsp. <i>sivalensis</i>	<i>sivalensis</i>			
	Geol. Mus. Leiden, 18489	F.A.S., pl. 63, div. figs.			
Length from dens to posterior border of processus spinosus	147	ca. 160	—	—	108
Length from dens to fossa vertebrae	100	ca. 105	—	—	72
Length from incisura vertebralis cranialis to incisura vertebralis caudalis	32	ca. 40	—	—	24
Width over facies articulares craniales	ca. 126	ca. 135	183	208	90
Width over constriction behind the latter	91	ca. 96	127	138	57
Width of fossa vertebrae	ca. 65	—	86	91	36
Width over processus articulares caudales	ca. 87	—	101	108	47
Anterior width of foramen vertebrae	35	ca. 40	42	44	22
Posterior width of the latter	43	—	ca. 54	ca. 57	26
Anterior height of the latter	29	—	ca. 33	ca. 32	19
Posterior height of the latter	30	—	ca. 36	ca. 31	17
Height of facies articularis cranialis	ca. 30	ca. 40	51	68	24
Height of processus spinosus from lower border of foramen vertebrae	75	ca. 78	102	108	47

Geol. Museum Leiden, no. 28019, Res. Soerabaja, Eastern Java (pl. XII, middle fig.).

Third vertebra cervicalis. The transverse processes have for the greater part broken off; the lateral and ventral plate-like parts of the latter are missing. The processus spinosus has also gone; the left processus articularis caudalis has completely, and the left processus articularis cranialis only for the lateral part, broken off. At the right side these processes are hardly damaged.

The present fossil agrees with the third of the cervical vertebrae of *H. liberiensis* in the presence of a strong and forked ventral spine, in the deep incisura intervertebralis cranialis, in the processus articularis caudalis extending for the greater part behind the fossa vertebrae, and in the shape of the dorsal boundary of the foramen transversarium which, in side view, stands about dorsoventrally. In *H. liberiensis* the corpus is relatively thicker antero-posteriorly only. *H. sivalensis sivalensis* (F.A.S., pl. 63 figs. 12, 12a between 12 and 12b (not the upper fig. 12a which represents the sixth cervical vertebra, see Hooijer, 1946, p. 315 footnote 1) and both figs. 12b) agrees with our Javan form in all of these characters except that the median spine is not forked. Both in *H. liberiensis* and in *H. sivalensis sivalensis* (F.A.S., pl. 63 fig. 1a) a ventral spine as well developed as that in the present fossil occurs on the third cervical vertebra only, in the more

posteriorly placed vertebrae the spine becomes less prominent; in *H. amphibius* the spines on the cervical vertebrae are weaker. In the shape of the caput vertebrae no marked differences can be found, but the foramen vertebrale in *H. amphibius* is broader and lower than that in the fossil as well as in *H. liberiensis*. As far as the general size is concerned the present fossil vertebra fits well to the epistropheus described above. The measurements are as follows:

Measurements of third vertebra cervicalis

	<i>H. sivalensis</i>		<i>H. amphibius</i>	<i>H. liberiensis</i>	
	subsp. <i>sivalensis</i>	F.A.S., pl.			
	Geol. Mus. Leiden,	63 fig. 12			
	28019				
Length of corpus vertebrae	50	ca. 48	59	68	33
Length from facies articularis cranialis to facies articularis caudalis	ca. 75	—	90	112	ca. 53
Width of caput vertebrae	ca. 62	ca. 68	76	75	30
Width of fossa vertebrae	73	ca. 72	91	95	ca. 35
Width over processus articulares craniales	ca. 90	—	108	120	52
Width over processus articulares caudales	ca. 100	—	110	153	54
Anterior width of foramen vertebrale	30	ca. 36	44	44	19
Height of caput vertebrae	48	ca. 53	58	70	ca. 30
Height of fossa vertebrae	55	ca. 62	65	70	32
Anterior height of foramen vertebrale	ca. 27	ca. 24	31	28	15
Greater diameter of foramen transversarium	12	ca. 13	17	18	6
Smaller diameter of the latter	10	ca. 9	14	13	5

Geol. Museum Leiden, no. 28234, Java.

Fifth or sixth vertebra thoracalis. As far as the slope of the processus spinosus is concerned the present specimens agrees best with the fourth thoracic vertebra of either of the two recent species. However, in the latter the processus transversus is not curved upward at its lateral end to the extent as that in the fossil; in this respect the fossil specimen has the greatest resemblance to the sixth thoracic vertebra of the recent species. The present specimen has belonged to an immature individual, for the epiphyses were not ankylosed to the corpus and are lost. The processus spinosus and the left processus transversus are for the greater part lost. The right transverse process is almost complete, the ventral spine has almost completely broken off.

The foveae costales craniales et caudales are equal in size, the latter are placed slightly higher than the former and face laterocaudally, the former

face craniolaterally. In F.A.S. (pl. 64 figs. 3-10) the vertebrae thoracales I, II, IV, V, VII, and VIII are figured; from front to back the processus spinosus becomes more inclined; the fovea costalis caudalis gradually shifts upward and comes nearer to the fovea costalis cranialis, the processus transversus becomes shorter, the facies articularis caudalis becomes smaller and shifts nearer to the median line. In all these characters the present fossil is intermediate between the second and the eighth vertebra thoracalis. The fovea costalis caudalis is placed as high as that in the eighth thoracic vertebra of *H. sivalensis sivalensis*, but is not so close to the fovea costalis cranialis. In the relative height of the processus transversus and in the slope of the spinous process the fossil specimen agrees closely with the fifth vertebra thoracalis presented in F.A.S., pl. 64 fig. 7a.

Geol. Museum Leiden, no. 27991, Java.

Proximal part of right scapula. The glenoid cavity is slightly damaged medially, the spina scapulae with the acromion has broken off; the tuber scapulae is complete. The maximum height of the fragment is 93 mm. The cavitas glenoidalis is strongly concave antero-posteriorly and decidedly longer than wide. About in a line with the spina scapulae a weak ridge is seen which gradually widens and extends to the glenoid cavity. Cranially and caudally of the latter ridge the lateral surface of the scapula is concave. The tuber scapulae is curved inwards, as is the case in *H. liberiensis* too; its lower border is slightly concave and its extremity is not curved upwards. In *H. sivalensis sivalensis* (F.A.S., pl. 65 figs. 1-5) we observe a great amount of variation, but the Javan fossil is somewhat smaller. Measurements are recorded below.

Measurements of scapula

	<i>H. sivalensis</i> subsp. Geol. Mus. Leiden, 27991	<i>H. amphibius</i>	<i>H. liberiensis</i>
Length from posterior border of cavitas glenoidalis to tuber scapulae	106	182	181
Length of cavitas glenoidalis	66	101 ca.	100
Width of the latter	46	76	88
Length from anterior border of cavitas glenoidalis to tuber scapulae	64	115	123
			47

Coll. Dub. no. 2094, Tinggang (Solo Valley) (pl. XIII, middle fig.).

Right humerus, almost completely preserved. The proximal part only shows injuries, viz., at the posterior and medial surface of the caput. The medial tuberosity (tuberculum minus) and a great anterior part of the lateral tuberosity (tuberculum majus) have broken off.

In its proximal part the fossil bone is very close to that of *H. liberiensis*; the shape of the fossa between the caput and the anterior parts of the medial and the lateral tuberosity, as well as the lateral tuberosity are exactly alike. In *H. amphibius* the anterior part of the lateral tuberosity is more elongated at its base and the posterior part is less prominent than in *H. liberiensis*. The fossa bicipitalis, as far as preserved in our fossil, is relatively narrower than that in *H. amphibius* and agrees better with that in *H. liberiensis*.

In F.A.S. (pl. 65 figs. 6-8) three proximal views of right humeri are represented which correspond well to our specimen except that in one of them (l.c., fig. 6 b) the posterior part of the lateral tuberosity is less prominent. In our fossil the crista deltoidea forms a rough tuberosity above the middle of the height of the bone, more prominent relative to the musculo-spiral groove than is the case in the recent species. Proximally of the tuberositas deltoidea the spiral of the crista deltoidea is continued at the posterior surface by a crest which extends to the collum humeri; this crest is seen in *H. sivalensis sivalensis* (l.c., fig. 7) and in *H. liberiensis* too. Slightly below the level of the deltoid tuberosity but at the medial surface of the shaft a teres tuberosity occurs, which, if present at all, is much weaker developed in the recent species. There is also a nutrient foramen, that is placed in the lower third of the anterior surface as it is in the recent forms too.

Our fossil possesses a distinct crista supinatoria; as shown in the plate a similar crest is not present in the recent species¹). This ridge is placed above the epicondylus lateralis and is about 35 mm long. It makes the anterior surface laterally of the fossa coronoidea and above the lateral epicondyle broader than and concave instead of flat as is the case in the recent species. The posterior surface laterally of the fossa olecrani is flattened and is as wide as the ridge of the bone above the medial epicondyle; in the recent specimens the posterior surface medially of the olecranon fossa is almost twice as wide as that to the lateral side of the fossa olecrani. In the figures of the humerus of *H. sivalensis sivalensis* representing the distal part (F.A.S., pl. 65 figs. 10-13) no supinator ridge is shown except, perhaps, in fig. 10 a. The measurements of the present and those of the following specimen are given in the table on p. 93.

1) Neither Cuvier (1821) nor Blainville (1847) mention a supinator ridge in their osteology of *H. amphibius*, and Edwards (1868) makes no mention of this ridge in his description of the humerus of *H. liberiensis* either. Reynolds (1822, p. 25) states in a description of a fossil *H. amphibius* humerus that there is no conspicuous supinator ridge. Dietrich (1928, p. 35 figs. 1-2) describes humeri from the Middle Pleistocene of East Africa which are identical with those of *H. amphibius* and states a true crista supinatoria to be absent (l.c., p. 36).

Geol. Museum Leiden, no. 27984, Res. Soerabaja.

Distal part of left humerus. It consists of the trochlea and the medial and lateral condyle. There are traces of a thin bony plate separating the coronoid and the olecranon fossa. At the middle of the anterior surface of the trochlea we find an indentation about 15 mm in diameter, which is flanked by two similar but weaker indentations. These three pits are separated by intervals of about 1 cm and were in all probability caused by crocodile teeth.

The present fragment is less massive than the corresponding part of the Tinggang humerus described above, and differs from the latter in the smaller width of the trochlea relative to the antero-posterior diameter of the medial epicondyle.

Measurements of humerus

	<i>H. sivalensis</i> subsp.		<i>H. amphibius</i>	<i>H. liberiensis</i>	
	Geol. Mus. Leiden 27984	Coll. Dub. no. 2094			
1. Length from caput to epicondylus medialis	—	317	370 ⁺	467	212
2. Proximal width over bases of lateral and medial tuberosities	—	128	147	153	75
3. Greater diameter over tuberositas deltoidea	—	88	92	98	51
4. Greatest distal width	109	114	153	144	64
5. Width of trochlea	72	83	105	106	46
6. Antero-posterior diameter of epicondylus medialis	98	99	136	142	59
7. Smallest width of shaft	—	46	54	59	29
8. Ratio 5 : 6	0.73	0.84	0.77	0.75	0.78
9. Ratio 2 : 1	—	0.40	0.40	0.33	0.35
10. Ratio 4 : 1	—	0.36	0.41	0.31	0.30

Geol. Museum Leiden, no. 28036, N. of Modjokerto (pl. XIV middle figs.).

Left radius and ulna, complete except for the part of the ulna proximally of the head of the radius. The bones fit exactly to the foregoing humerus fragment. The radius is ankylosed to the ulna, but there is an interosseous space. The anterior surface of the radius is convex from side to side, while the medial and the posterior surfaces are flattened. The only differences from the radius of *H. liberiensis* consist in the medio-posterior part of the facies articularis humeralis being more rounded and the saddle-shaped articulation surface for the scaphoid being relatively broader in its central part. As shown in the distal views the crest separating the facets for the scaphoid and the lunar has a different course, making the scaphoid facet

smaller relative to the lunar facet in *H. amphibius* than it is in *H. liberiensis* and in the fossil specimen. In *H. amphibius* the proximal and distal parts of the radius are relatively wider too.

The ulna possesses a longitudinal anterior ridge which is also found in *H. liberiensis* but not in *H. amphibius*. The lateral surface of the fossil ulna is not so narrow as that in *H. liberiensis*, and the posterior surface is concave throughout its length, while in *H. liberiensis* it is convex on a level with the head of the radius. The various figures of the radius of *H. sivalensis sivalensis* (F.A.S., pl. 65 figs. 9, 14-20, and 33) indicate specimens rather different in size; that of fig. 16 agrees in size with our Javan specimen but that of fig. 9 is decidedly larger. The radius ascribed to *H. sivalensis palaeindicus* (F.A.S., pl. 58 fig. 10) is also larger than our specimen; that of *H. iravaticus* (l.c., pl. 83 fig. 12) is slightly smaller. Stehlin (1925, p. 3) records a radio-ulna from Limbangan in Java the distal width of which is 85 mm, which is smaller than our present fossil. The dimensions of the present and the following specimens occur in the table on p. 95.

Geol. Museum Leiden, no. 28205, Java.

Distal fragment of right radius, length 13.5 cm. It differs from the preceding specimen in the scaphoid and lunar facets being less prominent posteriorly.

Geol. Museum Leiden, no. 28033, Java.

Proximal part of right radio-ulna. The fragment is 13.8 cm long; the proximal part of the radius (6.5 cm high) is complete, but the ulna has split longitudinally and its lateral part is missing. The olecranon ulnae is likewise lost. The bone is larger than the two foregoing specimens and fits well to the humerus from Tinggang (Coll. Dub. no. 2094). It agrees with the corresponding bone in *H. liberiensis* in the presence of a deep synovial fossa in the part of the incisura semilunaris for the medial condyle of the humerus. The medio-posterior part of the fovea capituli radii passes gradually into the adjoining surface of the ulna, and is less prominent than that in the above mentioned specimens.

Geol. Museum Leiden, no. 28221, locality unknown.

Proximal part of left radius, 13 cm long. The anterior border of the fovea capituli radii is incomplete. In shape and size it is very close to the preceding specimen.

Geol. Museum Leiden, no. 28021, locality unknown.

Distal part of right radius. The fragment, 15 cm in length, is somewhat rolled. It is larger than the first two specimens of the radius recorded above, and differs in the posterior surface being convex rather than flattened.

Measurements of radius and ulna

	<i>H. sivalensis</i> subsp. Geol. Mus. Leiden				
	28036	28205	28033	28221	28021
Total length of radius	224	—	—	—	—
Proximal width	ca. 67	—	74	73	—
Proximal antero-posterior diameter	50	—	58	—	—
Width at narrowest part of shaft	34	34	—	36	ca. 34
Distal width	75	78	—	—	85
Distal antero-posterior diameter	50	51	—	—	52
Distal width of ulna	45	—	—	—	—
Antero-posterior diameter at middle of shaft of ulna	24	—	—	—	—
Distal width of radio-ulna	96	—	—	—	—

	<i>H.s. sivalensis</i> (Lydekker, 1884 a, p. 43)	<i>H. iravaticus</i> (Falconer, 1868 I, p. 529)	<i>H. amphibi-</i> <i>bius</i>	<i>H. libe-</i> <i>riensis</i>	
Total length of radius	—	—	297	311	170
Proximal width	—	—	109	102	46
Proximal antero-posterior diameter	—	—	76	68	ca. 31
Width at narrowest part of shaft	—	—	45	46	ca. 25
Distal width	102	71	107	117	48
Distal antero-posterior diameter	55	43	78	78	37
Distal width of ulna	—	—	54	55	28
Antero-posterior diameter at middle of shaft of ulna	—	—	30	39	11
Distal width of radio-ulna	—	—	128	166	59

Coll. Dub. no. 9165, Kedoeng Broeboes (pl. XV, middle figs.).

Right second metacarpal. At the proximal extremity there is a slightly concave and antero-posteriorly elongated trapezoid facet that is narrower than in both recent species (proximal views, upper figs. in pl. XV) and decidedly less oblique than it is in *H. amphibi-*
bius. The lateral surface of the proximal extremity has two facets separated by a fossa, one anterior and one posterior, for articulation with the third metacarpal. The magnum facet, which is placed proximally of the anterior metacarpal III facet, is marked off from the latter by an edge in both recent species, while in the fossil specimen the two facets gradually pass into each other. The fossil metacarpal differs from the recent also in its more slender corpus and in the tuberosity surmounting the lateral distal indentation being very large. The distal articular surface is relatively narrow too, and, like in *H. libe-*
riensis, is more obliquely placed than that in *H. amphibi-*
bius. The dimensions are given here.

Measurements of second metacarpal

	<i>H. sivalensis</i> subsp. Coll. Dub. no. 9165	<i>H. amphibius</i>		<i>H. liberiensis</i>
Length	145	ca. 130	130	60
Proximal width	29	35	38	ca. 17
Proximal antero-posterior diameter	43	43	46	17
Middle width	31	36	39	17
Middle antero-posterior diameter	25	24	28	11
Distal width	38	38	41	20
Distal antero-posterior diameter	37	37	41	18

Coll. Dub. no. 8621, locality unknown.

Proximal portion of left fourth metacarpal. The proximal facets on the medial and the lateral side, for the third and the fifth metacarpal respectively, are injured, and the posterior prolongation has for the greater part broken off.

The large proximal facet for the unciform is subtriangular in shape and convex from before backward. It is widest and concave transversely in front; the medial side is the highest. Laterally it forms an overhanging edge above a deep fossa which latter is found in the corresponding bone of the recent species too and is placed behind the fifth metacarpal facet. The transverse concavity of the unciform facet is somewhat more stressed than that in *H. amphibius*; in *H. liberiensis* this facet is still more flattened. What is preserved of the proximal medial facet for the third metacarpal indicates that this facet had the same position as that in *H. amphibius*; in *H. liberiensis* the third metacarpal facet stands more vertically. The corpus is flattened antero-posteriorly and the medial (axial) surface is wider than the lateral which latter is more rounded. The posterior surface of the bone is slightly concave in the middle, like it is in the recent forms too. Few measurements can be given only:

Measurements of fourth metacarpal

	<i>H. sivalensis</i> subsp. Coll. Dub. no. 8621	<i>H. amphibius</i>		<i>H. liberiensis</i>
Least width of corpus	35	47	51	22
Least antero-posterior diameter	18	23	27	11

Coll. Dub. no. 8934, Kedoeng Broeboes.

Distal portion of third or fourth metacarpal. The distal articular surface is damaged but on its posterior surface the vertical ridge separating the facets for the two sesamoid bones is preserved; this ridge is closer to the

right than to the left side. Above the latter there is a deep pit posteriorly, to the right of the axis of the bone. This, together with the fact that the right surface of the bone is thicker, especially below, and more flattened than the left, indicates that the right surface of the present specimen is the axial surface. The distal indentation at the axial surface seems to be shallower than that on the abaxial surface, like it is in the recent bones too. I consider the present fossil bone fragment to belong either to a third metacarpal of the left, or a fourth metacarpal of the right side. The measurements of the corpus (least width 30 mm, antero-posterior 15 mm) show the present specimen to be slightly smaller than the preceding.

Geol. Museum Leiden, no. 27911, N. of Modjokerto (pl. XVI, middle figs.).

First phalanx of third or fourth digit. The concave proximal surface presents two glenoid cavities separated by a very low ridge. The right glenoid cavity is a little the larger. The right proximal tuberosity is closer to the border of the glenoid cavity and is more prominent than the left. The middle of the anterior surface is raised in its upper part, mostly so towards the left side. A deep proximal depression occurs at the posterior surface, somewhat nearer to the left than to the right side. The distal articulation surface is trochlear, consisting of a shallow sagittal groove separating two condyles the left of which is the larger. At the anterior surface the distal articulation surface encroaches more towards the left side. On either side the distal extremity presents a depression, the left of which is the deeper and is surmounted by a tubercle.

The present fossil phalanx has the most distinct affinities to the first phalanx of the third and the fourth digit of the manus in both recent species. It resembles *H. liberiensis* in its slender shape. The sagittal groove in the distal surface, however, is shallower in *H. liberiensis*, and the trochlea is relatively less enlarged antero-posteriorly than it is in the fossil bone. In *H. amphibius* the phalanges are thicker than the fossil specimen. Both in *H. amphibius* and in *H. liberiensis* the shape of the proximal articulation surface is different from that in our fossil, which latter has an indentation in the middle of its anterior border not visible in the recent bones.

While in *H. amphibius* the axial surfaces of the first phalanges of the third and fourth digit possess weaker distal depressions than the abaxial surfaces, the distal articulation surfaces encroach upon the anterior surface mostly toward the abaxial side, the posterior proximal depressions are nearest to the abaxial side, and the abaxial moiety of the phalanges has a longer antero-posterior diameter than the axial, in *H. liberiensis* the reverse conditions are found. Which of the surfaces of the fossil phalanx is the

axial consequently is impossible to determine. The differences between the first phalanges of the third and of the fourth digit are too slight to be of use in the present case, and added to that they are not constant.

It can only be stated that the present fossil is a first phalanx of the third or of the fourth digit. It has the greatest resemblance to that of left third digit of the manus in *H. amphibius* and to that of the left fourth digit of the manus in *H. liberiensis*, which bones are figured on either side of the fossil in pl. XVI. The measurements are as follows:

Measurements of phalanx I digitorum III or IV

	<i>H. sivalensis</i> subsp. Geol. Mus. Leiden 27911	<i>H. amphibius</i>	<i>H. liberiensis</i>
Greatest length	62	67	43
Proximal width	40	51	27
Proximal antero-posterior diameter	30	41	19
Distal width	33	45	23
Distal antero-posterior diameter	21	26	14
Least width of corpus	31	39	21
Least antero-posterior diameter	14	22	11

Coll. Dub. no. 9044/45, Trinil (pl. XVII figs. 1, 2, 4).

Pelvis, complete except for part of the right ala ossis ilium, and the ramus symphyseos of pubis and ischium. The medial boundary of the foramen obturatum is consequently lost, but in the symphysis behind this foramen the right and left ischium fortunately come into a contact. Less important injuries occur at the tuber sacrale, the left tuber coxae, the border of the acetabulum, the lateral part of the right tuber ischii and at the arcus ischiadicus.

The crista iliaca is sharp and slightly concave in the middle, like it is in *H. liberiensis* too; in *H. amphibius* the anterior border of the ilium is thickened and rough, and straight in the middle. The right and left tuber sacrale, although damaged, seem to have been more approximated and more elevated than those in *H. amphibius*; *H. liberiensis* differs from the former species in the same character again. The corpus ossis ilium is much more elongated than is the case in *H. amphibius*, the facies lunata of the acetabulum is directed more sideways and posteriorly, the ramus acetabularis ossis ischium is less slender and shorter than that in *H. amphibius*. In all these points the fossil specimen has the greatest resemblance to *H. liberiensis*. Our fossil agrees with *H. liberiensis* also in possessing a distinct ridge on the ventral surface of the ischium which ends in the lateral spine of the tuber ischiadicum.

The present fossil specimen differs in many more points from the male pelvises of *H. amphibius* and *H. liberiensis*, but only the above mentioned characters must be taken as of specific significance; the other characters are doubtless sexual. It is a remarkable fact that, of the recent hippopotamus, male pelvises exclusively are described or figured. The Cape skeleton of *H. amphibius* figured by Cuvier (1821, *Hippopotame vivant*; pelvis on pl. II fig. 14) is a male as well as the Senegal specimen figured by Blainville (1847, *Atlas*, pl. V: right os coxae presented in 5th and 6th figure) and the *liberiensis* skeleton figured by Edwards (1868, *Atlas*, pl. II). Our present fossil pelvis, being much more roomy than the male specimens available for comparison, must have belonged to an individual of the other sex. An account of the sexual characters in the *Hippopotamus* pelvis is given below.

The symmetrical parts in the female pelvis are more separated from each other than is the case in a male specimen. The ventral border of the apertura pelvis cranialis is wider in the female than in the male, and the pecten ossis pubis in the former is placed more ventrally and caudally than it is in the latter. The male also has a well-developed crest on the symphysis pubis.

The right and left corpus ossis ilium are more parallel in the female than in the male. In the latter the corpus ossis ilium is in the same plane as the central part of the ala ossis ilium, and the right and left corpus ossis ilium are inclined towards each other to the effect that their medial borders are much closer to each other than their lateral borders. In the female pelvis the width over the medial border of the corpus ossis ischium is not so small relative to the width over the lateral border as it is in the male. The fossil pelvis from Barrington figured by Reynolds (1922, p. 28 figs. 12 A, 12 B) must have belonged to a male individual.

The flat gluteal surfaces of the right and left corpus ossis ilium face much more laterally in the female than in the male, and as a consequence the width between the right and left incisura ischiadica major is much less different from the minimum width over the ilium above the acetabulum in the female than in the male (cf. measurements 6 and 8 in the table on p. 101/102). The right and left spina ischiadica are more parallel in the female pelvis too; in that of the male these are higher and somewhat inclined inwards.

The most striking sexual characters, however, are found in the post-acetabular part of the pelvis. In the male the right and left corpus ossis ischium form a narrow ventral wall of the pelvic cavity; they meet at an acute angle and each of them is more concave than they are in the female pelvis, in which latter they meet at an obtuse angle (cf. table on p. 102,

measurements 14 and 15). In the male *H. liberiensis* pelvis the right and left tuber ischiadicum even are almost vertically placed.

In lateral view the ischial part is highest in the male, and the incisura ischiadica minor consequently is deeper than it is in the female. The pelvis of the mounted skeleton of *Hippopotamus sivalensis sivajavanicus* (Dubois) figured by Von Koenigswald (1935 d) and Callenfels (1936) must have formed part of a male individual.

A sex determination is possible too for an isolated os coxae, or even for a part of it. The female os coxae is more twisted than that of a male. In the latter the ala ossis ilium and the corpus ossis ilium are in the same plane, the plane of the corpus ossis ischium intersects the ala ossis ilium about in its middle and is about perpendicular to the latter. The right os coxae of fossil *H. amphibius* figured by Cuvier (1821, Hippopotame fossile, pl. VI figs. 1-2) is that of a male individual. In the female the corpus ossis ilium is twisted relative to the ala ossis ilium and is nearer to the plane of the ramus acetabularis ossis ischium. The corpus ossis ischium is much twisted again relative to the latter; they form an angle of about 60° with each other. The plane of the corpus ossis ischium does not intersect the ala ossis ilium about in its middle, as is the case in a male specimen, but it intersects the plane of the ala ossis ilium in a line which runs more than one-half of the width of the ala ossis ilium laterally of the latter.

In an isolated ilium the sexual differences are the following: The facies glutaea of the ilium, apart from the tuber sacrale and the tuber coxae, is almost flat in the male, while in the female the lateral half of the facies glutaea is distinctly convex and the medial concave. On the opposite surface (the facies pelvina) the roughened medial pars articularis is much larger in the female than it is in the male, and consequently the smooth lateral pars iliaca is much smaller.

Since in the female Trinil pelvis the sacrum is lost it is impossible to check sexual differences in the conjugata anatomica and in the inclinatio pelvis.

The central part of the os coxae (between the ala ossis ilium and the corpus ossis ischium) presents marked sexual characters too. In the female the corpus ossis ilium is situated more nearly in a plane with the ramus acetabularis ossis ischium than is the case in the male, and the spina ischiadica is less high. The ramus acetabularis ossis pubis is much more nearly perpendicular to the corpus ossis ilium and to the ramus acetabularis ossis ischium in the female than it is in the male, in which latter the ramus acetabularis ossis pubis is directed distinctly caudally and ventrally.

Since in the fossil pelvis the medial boundary of the foramen obturatum

is lost it cannot be ascertained whether in the female the foramen obturatum is smaller than it is in the male, though it would seem that it is.

A female ischium is characterized by the corpus being twisted with regard to the ramus acetabularis; a separate corpus ossis ischium of a male is more curved than that of a female. The facies pelvina in either of the two sexes is concave, but in the male specimens this is most stressed. The facies ventralis is saddle-shaped in the male; the surface between the ventral spine of the symphysis pelvis and the lateral spine of the tuber ischiadicum, which is concave in the female, is convex in the male. The surface between the ventral spine of the tuber ischiadicum and the ramus acetabularis ossis ischium, almost flat in the female, is concave in the male.

Coll. Dub. no. 9957, Solo valley.

Right and left corpus ossis ischium in connection. That this specimen, like the foregoing Trinil pelvis, has formed part of a female individual, is at once evident from the obtuse angle between the right and the left part. The symphysis pelvis and the ramus acetabularis ossis ischium have broken off in front of the caudal border of the foramen obturatum. Part of the left border of the arcus ischiadicus is lost; the dorsal spine of the left tuber ischiadicum is slightly damaged. The facies pelvina is smooth and concave. The facies ventralis is almost flat between the ventral spine of the tuber ischiadicum and the ramus acetabularis ossis ischium, while it is concave between the ventral spine of the symphysis pelvis and the lateral spine of the tuber ischiadicum. The measurements are recorded in the table below.

Measurements of pelvis

	<i>H. sivalensis</i>		<i>H. amphibius</i>	<i>H. liberiensis</i>	
	subsp. 9044/45	Coll. Dub. 9957			
	♀	♀	♂	♂	♂
1. Length from crista iliaca to ventral spine of tuber ischiadicum	512	—	ca. 600	812	345
2. Length from crista iliaca to anterior border of acetabulum	310	—	ca. 310	416	185
3. Length from anterior border of acetabulum to ventral spine of tuber ischiadicum	304	—	ca. 330	445	184
4. Length of foramen obturatum	102	—	148	183	68
5. Length of ischium from caudal border of foramen obturatum to ventral spine of tuber ischiadicum	142	152	ca. 100	194	90
6. Width between right and left incisura ischiadica major	222	—	226	280	118
7. Width over lateral spine of tuber ischiadicum	ca. 298	316	222	352	114
8. Minimum width over ilium above acetabulum	298	—	372	435	182

	<i>H. sivalensis</i>		<i>H. amphibius</i>		<i>H. liberiensis</i>
	subsp. 9044/45 ♀	Coll. Dub. 9957 ♀	♂	♂	♂
9. Width over lateral border of acetabulum	322	—	397	494	194
10. Width between right and left spina ischiadica	202	—	167	228	90
11. Width between dorsal spines of tuber ischiadicum	198	ca. 208	160	246	86
12. Width between ventral spines of tuber ischiadicum	90	100	ca. 90	150	74
13. Width between right and left incisura ischiadica minor	210	211	174	270	58
14. Angle between right and left corpus ossis ischium ¹⁾	114°	106°	80°	82°	69°
15. Angle between right and left tuber ischiadicum ²⁾	105°	100°	ca. 40°	41°	16°
16. Greater diameter of narrowest part of corpus ossis ilium	68	—	98	108	46
17. Greater diameter of narrowest part of ramus acetabularis ossis ischium	58	—	46	59	28
18. Antero-posterior diameter of acetabulum	75	—	98	87	40
19. Height of spina ischiadica from lateral border of acetabulum	84	—	121	143	64

Geol. Museum Leiden, no. 28017, Res. Soerabaja (pl. XVII fig. 3).

Acetabular part of right os coxae which must have belonged to a male individual. A rather large part of the corpus ossis ilium is preserved, and the ramus acetabularis ossis pubis is preserved up to the eminentia iliopectinea. There is a very distinct tuberculum psoadicum. The facies lunata of the acetabulum is rather small, and the incisura acetabula is converted into a foramen by a transverse rod of bone. The spina ischiadica is partly damaged.

All characters of the present fragment point to its having belonged to a male. The angle between the ramus acetabularis ossis pubis and the corpus ossis ilium is less great than that in the female Trinil pelvis and agrees with that in the male pelvises of *H. amphibius* and *H. liberiensis*. This is apparent from the position of the eminentia iliopectinea (which is more developed in the female too) in respect to the facies lunata of the acetabulum. In the present specimen the ramus acetabularis ossis pubis must have occupied a less ventral and caudal position than that in the female pelvis;

1) Measured between the lines drawn from the caudal end of the symphysis pelvis to the right and to the left incisura ischiadica minor.

2) Measured between the lines drawn from the ventral spine to midway between the lateral and the dorsal spine of the tuber ischiadicum.

the apertura pelvis cranialis, therefore, was smaller. The preserved part of the ramus acetabularis ossis pubis is thicker than it is in the female specimens (measured over the eminentia iliopectinea 58 mm against 45-47 mm mm respectively). In the female pelvis a tuberculum psoadicum is hardly indicated while in the present fragment it is very distinct and even more developed than that in the male pelvis of the recent species. The acetabulum is distinctly smaller than that in the female Trinil pelvis (antero-posterior diameters 63 and 75 mm respectively), and the spina ischiadica, on the other hand, is higher in the present specimen than it is in the Trinil pelvis (height from lateral border of acetabulum 95 against 84 mm).

In F.A.S. two acetabular portions of the os coxae are represented, and both are ascribed to *H. sivalensis sivalensis*. In my opinion that of the left side (l.c., pl. 64 figs. 17 and 17 a) belongs to a male, and that of the right side (l.c., pl. 64 figs. 18 and 18a) to a female individual. In the first mentioned specimen the ramus acetabularis ossis pubis is about at right angles to the corpus ossis ilium, and a tuberculum psoadicum is developed, which latter is absent in the right specimen. In the latter, too, the ramus acetabularis ossis pubis is directed medio-cranially.

In the left specimen, however, the thickness of the ramus acetabularis ossis pubis and the height of the spina ischiadica are less than those in the right. The former difference is smaller than that between our female and male pelvises, but the latter probably is greater (the spina ischiadica of the right specimen is certainly injured at the level of the acetabulum, but that of the left probably too). The facies lunata of the acetabulum (and the fossa acetabuli) in the right specimen are larger than those in the left, and this difference is even more pronounced than that between our female and male specimens. It would hence seem evident that the left fragment (l.c., fig. 17) belongs to a male specimen smaller in size than the female to which the fragment of fig. 18 belongs.

Geol. Museum Leiden, no. 28143, N. of Modjokerto (pl. XVIII, middle fig.).

Proximal part of right femur, damaged only at the posterior and medial surface of the collum and the caput. The collum femoris, most distinctly marked off in front; bears a relatively small caput which is somewhat lower than the trochanter major. The anterior part of the latter rises to a greater height than its posterior part. In the relatively small size of its caput and in the prominence of the great trochanter the present fossil differs from the recent specimens but agrees well with the femora ascribed to *H. sivalensis sivalensis* (F.A.S., pl. 66 figs. 1-3) and to *H. sivalensis palaeindicus* (l.c., pl. 58 fig. 6) respectively. The posterior surface of the

fossil femur is more flattened than that in the recent femora. The caput of the present specimen fits well to the acetabulum (Geol. Museum Leiden, no. 28017) recorded above.

Geol. Museum Leiden, no. 27943, between Djetis and Gondang.

The present fragment, 12.5 cm long, belongs to a left femur and shows the lower part of the crista trochanterica, that of the fossa trochanterica, and also the trochanter minor. It is almost as large as the preceding specimen.

Geol. Museum Leiden, no. 28022, locality unknown.

The present specimen is part of a caput femoris, of larger size than the foregoing specimens and fitting well to the Trinil pelvis (Coll. Dub. no. 9044/45). The measurements are given below; in the table I also record measurements of a femur of *H. sivalensis sinhaleyus* from Ceylon sent to me by Dr. Deraniyagala and showing that the latter form exceeds the Javan subspecies in size (cf. Deraniyagala, 1948, p. F 8).

Measurements of femur

	<i>H. sivalensis</i>		<i>H. amphibius</i>	<i>H. liberiensis</i>
	subsp. <i>sinhaleyus</i>	Geol. Mus. Leiden, 28143		
Proximal width over caput and trochanter major	140	—	174	84
Antero-posterior diameter of caput	—	68	89	37
Transverse diameter of the latter	59	64	88	36
Antero-posterior diameter of trochanter major	73	—	94	44
Antero-posterior diameter at middle of shaft	50	—	60	31
Transverse diameter at same level	54	—	63	32

Coll. Dub. no. 6712, locality unknown (pl. XIX, middle fig.).

Left tibia. The medial and lateral condyles as well as the distal extremity are slightly injured. The lateral surface is more concave proximally from side to side than is the case in *H. amphibius*; *H. liberiensis* presents, however, a similar concavity. The crista tibiae in the fossil specimen is more obliquely placed than that in the recent forms. The lateral surface winds to the front downward and widens distally. The distal extremity is relatively less broad than that in *H. amphibius* but wider than that in *H. liberiensis*. Neither the condyles nor the distal articulation surface offer points of difference from the recent bones worth while recording.

Coll. Dub. no. 9143, locality unknown.

Right tibia. Of the proximal extremity the tuberositas tibiae only is preserved. The crista tibiae flattens out more abruptly in the middle of the

height than is the case in the preceding specimen. It is of the same size as the latter bone; the length measured from the tuberositas tibiae to the median ridge of the distal articulation surface is 256 mm in both specimens.

Coll. Dub. no. 9971, locality unknown.

Left tibia. The proximal extremity is lost, the crista projects less, and the posterior surface is more concave from side to side above. Very slightly larger than the preceding bones.

Geol. Museum Leiden, no. 27975, Res. Soerabaja.

Left tibia, without proximal extremity and malleolus medialis. This specimen is indistinguishable from the preceding.

Coll. Dub. no. 6716, Solo valley.

Left tibia. Proximally the lateral part of the condylus lateralis is damaged as well as the upper margin of the medial surface. The distal moiety is badly damaged: of the articulation surface the medial part is lost. In this specimen, again, the lateral surface is more concave above than it is in *H. amphibius*. The posterior surface below the condylus lateralis is even more concave from side to side. The present bone is longer than those mentioned above; the length from the tuberositas to the median distal ridge is ca. 295 mm against 256 in the latter. Measurements are recorded below.

Measurements of tibia

	<i>H. sivalensis</i> subsp.				Coll. Dub. no. 6716
	Coll. Dub. nos. 6712	9143	9971	Geol. Mus. Leiden, 27957	
Length from eminentia intercondyloidea to median distal ridge	262	—	—	—	305
Proximal antero-posterior diameter	ca. 100	—	—	—	—
Least width of shaft	43	42	41	41	45
Least antero-posterior diameter of idem	36	34	37	36	35
Distal width	64	64	70	ca. 70	—
Distal antero-posterior diameter	—	59	—	—	—
	<i>H. amphibius</i>			<i>H. liberiensis</i>	
Length from eminentia intercondyloidea to median distal ridge	360	382	202		
Proximal antero-posterior diameter	144	163	66		
Least width of shaft	64	61	29		
Least antero-posterior diameter of idem	52	53	22		
Distal width	98	103	43		
Distal antero-posterior diameter	78	87	38		

Coll. Dub. no. 10988, Bangle (pl. XX, middle figs.).

Left astragalus, slightly injured at the lower calcaneum facet only.

The fossil astragalus differs from that of *H. amphibius* in the same points as that of *H. liberiensis* does, viz., in the much more marked dif-

ference in level between the facies articularis cuboidea and the facies articularis navicularis, in the crest separating the latter facets running more in antero-posterior direction and in the former being smaller relative to the latter than is the case in *H. amphibius*. In the astragalus of *H. liberiensis*, like in that of the Pleistocene of Java, there is a tuberosity on the medial side immediately below the medial ridge of the trochlea not shown in the *H. amphibius* specimen. The fossil astragalus from Kedoeng Broeboes in Java figured by Stremme (1911 b, pl. XIX fig. 6) presents the same characters as does the present fossil, and the astragali of *H. sivalensis sivalensis* figured in F.A.S. (pl. 66 figs. 20-24, pl. 68 figs. 20-21) are much nearer to that of *H. liberiensis* than to that of *H. amphibius* too. The measurements of the present and the following specimens are given below.

Coll. Dub. no. 8671, Bangle.

Right astragalus, damaged at the medial side of the navicular facet. It differs from the preceding specimen in unimportant details, such as the extension of non-articular fossae, only.

Coll. Dub. no. 10362, locality unknown.

Right astragalus, injured posteriorly and at the lower calcaneum facet but corresponding well in size to the above mentioned specimens.

Coll. Dub. no. 8396, Tegoean (?).

Right astragalus, agreeing with the other specimens in structure but somewhat larger. The present specimen is of the same size as that figured by Stremme (l.c.). The Selenka expedition secured two specimens of the astragalus at Kedoeng Broeboes, and one of the specimens is preserved in the Berlin Museum while the other forms part of the Munich Museum collection (Stremme, 1911b, p. 105). The Berlin Museum specimen is that figured by Stremme; that in the Museum at Munich is mentioned by Stromer (1914, p. 31) who gives also the measurements (l.c., p. 24) which show the latter bone to be smaller than that of Stremme's figure. As shown in the table below the smaller of the two Selenka expedition specimens of the astragalus is of the size of the first three Dubois collection specimens.

Measurements of astragalus

	<i>H. sivalensis</i> subsp.					<i>H. amphibius</i>		<i>H. liberiensis</i>	
	Coll. 10988	Dub. 8671	nos. 10362	Stromer, 1914	Stremme, 1911 b	Coll. Dub. no. 8396			
Middle length	69	72	ca. 74	72	82	ca. 80	95	102	50
Lateral length	77	78	77	—	85	ca. 84	105	106	53
Distal width	63	63	—	60+	ca. 64	ca. 64	91	98	40
Lateral antero-posterior diameter	40	41	38	—	—	ca. 44	59	60	26

Geol. Museum Leiden, no. 28146, Java (pl. XXI fig. 1).

Right cuboid, the lateral part of the distal surface damaged. Some substance is lost of the ectocuneiform facet and at the postero-medial edge, while the tuberosity on the lower surface is missing.

In comparison with the cuboids of *H. amphibius* and *H. liberiensis* (two of the former and one of the latter species are represented in medial view on pl. XXI) the tuberosity on the upper or proximal surface is seen to be less developed than that in the recent specimens, while the articulation surface for the astragalus is less concave antero-posteriorly. In the fossil specimen the ectocuneiform facet is not separated from the facets for the metatarsals IV and V by a deep fossa, as it is in the recent species.

The fossil and the *H. liberiensis* cuboid differ much in the relative height of the anterior surface, but the two specimens of *H. amphibius* differ in the same character; the left cuboid of the Leiden Museum skeleton presented on fig. 3 of pl. XXI is higher anteriorly than the right cuboid of the Amsterdam Museum skeleton presented on fig. 4. The specimens differ in the configuration of the medial facets too. There are three facets for the navicular, a posterior (d), and anterior (b) facing inward and more or less upward and separated from the astragalus articular surface (a) by an edge, and a third facet (c) above and parallel to the facet for the ectocuneiform (e) and facing inward and upward too. Of these navicular facets the posterior only is shown in the fossil specimen, and in the cuboid of *H. liberiensis* we find the anterior and the lower facet for the navicular to be much smaller relative to the posterior than is the case in the *H. amphibius* specimens. In the cuboid of fig. 4 we find another facet for the ectocuneiform, below the posterior navicular facet, that is not shown in the specimen of fig. 3.

The lower navicular facet is smaller in the cuboid of fig. 4 than it is in that of fig. 3. Apparently this facet is occasionally even absent in *H. amphibius*, as may be taken from Stromer's account of the cuboid of *H. hipponensis* Gaudry (Stromer, 1914, p. 20). Stromer states the *H. hipponensis* cuboid to differ from that of *H. amphibius* in having an elongated facet for the navicular above and parallel to that for the ectocuneiform, and separated from the latter by an edge. The facet in question (c) is, however, present in both specimens of *H. amphibius* available to me. In *H. hipponensis*, like in the present Javan fossil, the posterior navicular facet is lower in position than that in *H. amphibius*. The measurements are given below. A left cuboid of *H. sivalensis sivalensis* is figured in F.A.S. (pl. 66 fig. 25); it seems to be larger and relatively narrower than our fossil but is figured on too small a scale for measurement.

Measurements of cuboid

	<i>H. sivalensis</i> subsp. Geol. Mus. Leiden, 28146	<i>H. amphibius</i>	<i>H. liberiensis</i>
Lateral length	30	44	41
Anterior length	31	52	43
Posterior length	41	64	70
Antero-posterior diameter	55	77	78
Transverse diameter	57	76	78

Coll. Dub. no. 6366, Kedoeng Broeboes (pl. XXII, middle figs.).

Right second metatarsal, slightly injured at and above the lateral part of the distal articular surface.

At the lateral surface of the proximal extremity we find two antero-posteriorly elongated facets separated by an edge; the lower is that for the third metatarsal and the upper is for the ectocuneiform. A larger and likewise antero-posteriorly elongated facet forms the proximal surface; it is relatively narrower than its homologue in the recent specimens and articulates with the mesocuneiform. At the medial surface of the proximal extremity we find a facet for the entocuneiform, facing rather backward.

The corpus of the fossil bone is much more slender than that in the recent species, and the distal articulation surface is more obliquely placed than that in *H. amphibius*, but less so than that in *H. liberiensis*. The measurements are as follows:

Measurements of second metatarsal

	<i>H. sivalensis</i> subsp. Coll. Dub. no. 6366	<i>H. amphibius</i>	<i>H. liberiensis</i>
Total length	86	ca. 93	107
Proximal width	19	27	31
Proximal antero-posterior diameter	25	30	33
Middle width	20	31	30
Middle antero-posterior diameter	18	30	35
Distal width	27	33	35
Distal antero-posterior diameter	26	35	39

INCERTAE SEDIS

In the Dubois collection there remain fragmentary incisors, canines, premolars, molars, and jaw fragments that do not give any clue as to their subspecific position. The specimens originate from the following localities:

- Bangle: Coll. Dub. nos. 272 b, 1718, 2193, and 11464.
 Bogo: Coll. Dub. nos. 272 a, and 2003 a.
 Dekes-Wadegan: Coll. Dub. nos. 285 and 2318 b.
 Kali Gedeh: Coll. Dub. no. 87.
 Karang Nonko: Coll. Dub. no. 516.
 Kebon Doeren: Coll. Dub. nos. 308 b, 311, 2201, 2207 b, 2904, and 2933.
 Kedoeng Broeboes: Coll. Dub. nos. 308 c, 310, 313, 323 a and b, 2013, 2019 a and c, 2084 c and d, 2174, 2190 a, 2204 a and b, 2207 a, 2318 c, 2528, 5527, 8243, and 11466.
 Kedoeng Loemboe: Coll. Dub. nos. 2000, 2189, 2196, and 2917.
 Ngawi: Coll. Dub. no. 1483.
 Padas Malang: Coll. Dub. no. 4857.
 Papan Djaran: Coll. Dub. nos. 2019 b, and 2905.
 Pati Ajam: Coll. Dub. no. 94.
 Redjoeno: Coll. Dub. no. 1804.
 Soember Waroe: Coll. Dub. nos. 308 a, and 2078.
 Tegoean: Coll. Dub. nos. 105, 2003 b, and 2082.
 Trinil: Coll. Dub. nos. 6964, 7058, and 11092.
 Tritik: Coll. Dub. nos. 95, 2921, 4475, 6927, and 6954.
 The following unidentifiable specimens are without a record for the exact locality: Coll. Dub. nos. 98, 100, 284, 308 d, 323 c, 324 a, 325 d and f, 425 a, 548, 1731, 2006, 2008 a, 2017, 2023, 2076, 2080, 2182, 2191, 2192, 2194, 2198, 2202, 2206, 2319, 2460 a, 2462 a, 2492 a, 2906, 2912, 2920, 2923-2926, 2935, 4234, 4483, 4606, 5760, 5803, 6391, 6490, 6491, 6654, 8473, and 11463.

SUBSPECIATION IN HIPPOPOTAMUS SIVALENSIS FALCONER ET CAUTLEY

Hardly any of the various subspecies of *H. sivalensis* as defined in the present paper is based on a series of calvariums and mandibles large enough to establish its variation limits with a tolerable degree of certainty. With the material at present known there is already much intergradation, which will only increase upon the examination of more specimens. Lydekker had in mind an evolutionary line leading from *H. sivalensis sivalensis* through *H. sivalensis namadicus* to *H. sivalensis palaeindicus* and Von Koenigswald has recorded three fossil forms of *Hippopotamus* from Java which form a similar evolutionary line; these forms are *H. sivalensis sivajavanicus*, *H. sivalensis koenigswaldi*, and *H. sivalensis soloensis* respectively. In either

of the two series the first member is Lower Pleistocene in age, and the last member belongs to the Middle and/or Upper Pleistocene.

The three Indian as well as the three Javan subspecies of *H. sivalensis* just mentioned exhibit certain gradual changes in the structure of their calvarium and mandible, and the most remarkable thing is that the transformations in both series are the same, though some characters are most advanced in one, and other characters are so in the other of the two series. I shall review these morphological changes in the following pages.

One of the most conspicuous trends observed is that for the orbit to become more elevated above the level of the frontals. This is most markedly so in the Javan series:

Orbito-cephalic index

<i>palaeindicus</i>	18—26	<i>soloensis</i>	34—39
<i>namadicus</i>	—	<i>koenigswaldi</i>	32
<i>sivalensis</i>	9—18	<i>sivajavanicus</i>	17

The occiput becomes lower relative to its width:

Occiput index

<i>palaeindicus</i>	61—ca. 70	<i>soloensis</i>	60—67
<i>namadicus</i>	—	<i>koenigswaldi</i>	ca. 72
<i>sivalensis</i>	71—78	<i>sivajavanicus</i>	—

The postdental part of the calvarium becomes more shortened, but this tendency is most marked in the Indian series:

P⁴-M³-condyle index

<i>palaeindicus</i>	82—84	<i>soloensis</i>	73—75
<i>namadicus</i>	—	<i>koenigswaldi</i>	79
<i>sivalensis</i>	63—77	<i>sivajavanicus</i>	66

There is also a tendency for the upper molar series to shift backward. While the posterior border of M³ is in advance of that of the palate in all subspecies described from Java, in *H. sivalensis sivalensis* the posterior border of M³ occasionally reaches as far backward as that of the palate. In *H. sivalensis palaeindicus*, however, the upper molar series extends backward beyond the posterior border of the palate.

In the absence of complete calvariums of the Narbada subspecies it is impossible to determine whether in the Indian series there is a difference between the subspecies in the relation of the postorbital to the preorbital length. In the Javan series there is no such difference: the calvarium of *H. sivalensis sivajavanicus* has a postorbital/preorbital length ratio of 0.80 and is not different in this respect from that of *H. sivalensis soloensis* in

which this ratio varies from ca. 0.77 to 0.81. The zygomatic index does not seem to offer subspecific characters either; it is 60-ca. 68 in *H. sivalensis sivalensis*, ca. 65 in *H. sivalensis sivajavanicus*, and 64-ca. 65 in *H. sivalensis soloensis*.

The mandible offers some data of interest too. The symphysis becomes shorter relative to the interval between the canines, but this tendency is hardly evident in the Javan series:

Symphysis length-width index

<i>palaeindicus</i>	ca. 61—67	<i>soloensis</i>	ca. 67—69
<i>namadicus</i>	57—64	<i>koenigswaldi</i>	ca. 62—ca. 79
<i>sivalensis</i>	ca. 83—96	<i>sivajavanicus</i>	60—ca. 67

The mandibular symphysis has the tendency to become higher relative to its length:

Symphysis height-length index

<i>palaeindicus</i>	60—ca. 77	<i>soloensis</i>	ca. 66—71
<i>namadicus</i>	68	<i>koenigswaldi</i>	49—ca. 56
<i>sivalensis</i>	37—50	<i>sivajavanicus</i>	—

The ramus horizontalis becomes higher relative to its length:

Ramus length-height index

<i>palaeindicus</i>	232	<i>soloensis</i>	214—232
<i>namadicus</i>	—	<i>koenigswaldi</i>	272—277
<i>sivalensis</i>	250—298	<i>sivajavanicus</i>	—

The ramus becomes higher relative to the length M_1 - M_3 too:

Molar length-ramus height index

<i>palaeindicus</i>	—	<i>soloensis</i>	94
<i>namadicus</i>	—	<i>koenigswaldi</i>	ca. 108—125
<i>sivalensis</i>	100—ca. 141	<i>sivajavanicus</i>	—

I_2 becomes smaller relative to I_1 , especially so in the Indian series:

Ratio $I_2 : I_1$

<i>palaeindicus</i>	0.30—0.49	<i>soloensis</i>	ca. 0.74—0.85
<i>namadicus</i>	0.70—0.81	<i>koenigswaldi</i>	0.67—ca. 0.89
<i>sivalensis</i>	0.67—0.91	<i>sivajavanicus</i>	ca. 0.93

I_3 becomes larger relative to I_1 , most markedly so again in the Indian series:

Ratio $I_3 : I_1$

<i>palaeindicus</i>	1.00—1.24	<i>soloensis</i>	0.88—ca. 0.96
<i>namadicus</i>	1.00—1.15	<i>koenigswaldi</i>	0.75—0.96
<i>sivalensis</i>	0.90—ca. 0.96	<i>sivajavanicus</i>	ca. 0.70

Von Koenigswald (1934 b) has emphasized that in the Javan series there is seen a gradual reduction of I^3 : in a specimen of *H. sivalensis sivajavanicus* the upper I are stated to differ hardly in size, while in the more progressive forms I^3 is reduced in size relative to the other upper incisors. The holotype

of *H. sivalensis sivajavanicus* has I³ only about three-fourths as large as I¹ and I²; in *H. sivalensis sivalensis* (F.A.S., pl. 62 fig. 3), however, the same is true. In *H. sivalensis soloensis* the upper incisors are rather variable; I² is always the largest, I¹ is smaller to a greater or lesser degree, while I³ even seems to be completely suppressed in some cases (Coll. Dub. nos. 2911 and 2909). The rostrum of *H. sivalensis namadicus* and that of *H. sivalensis palaeindicus* being unknown it cannot be ascertained whether I³ in the Indian series is progressively reduced too, though from the condition in *H. sivalensis sivalensis* it seems evident that it is.

In either of the two series the first subspecies has upper molars of the *sivalensis* type, and the upper molars of the last are of the *palaeindicus* type.

The above mentioned Indian and Javan subspecies form a sequence of morphological types, but I do not believe that either of these series represents a phylogenetical sequence. The contemporaneousness of *H. sivalensis sivalensis* and of a Burmese form as much specialized in its incisor dentition and with the same molar structure as *H. sivalensis palaeindicus* in the Lower Pleistocene would seem to point to the collateral development of the first and of the last member of the Indian series, and the fact that *H. sivalensis koenigswaldi* is admittedly the smallest of the Javan forms militates against its having an intermediate position between *H. sivalensis sivajavanicus* and *H. sivalensis soloensis* in the same line of descent.

H. sivalensis sivajavanicus is very close to *H. sivalensis sivalensis*, differing mainly in its smaller size. Similar size differences are often met with between insular and continental races of one and the same species. In *H. sivalensis koenigswaldi* the decrease in size is even more stressed. In the Indian series there is rather an increase in size, the specimens of *H. sivalensis palaeindicus* being the largest (equalling, as said above (p. 37) a medium-sized *H. amphibiis* skull as to size). The discovery of a small-sized calvarium in the Punjab Siwaliks (*H. sivalensis duboisi*) with the orbit higher than that of *H. sivalensis palaeindicus* and with upper molars of the same structure as that in the latter shows that a relatively small progressive form like *H. sivalensis soloensis* has lived on the continent too. And the lower Pleistocene molar from Java referred to above (p. 86) is probably indicative of the presence of a large-sized form in this island. These two finds greatly complicate the picture of the intraspecific evolution of *H. sivalensis*.

There are at least seven different forms of *H. sivalensis*, ranging from the Lower to the Upper Pleistocene and from India to Java, but with the material at hand it seems premature to express views as to the genetic interrelationships of the various subspecies. It has been demonstrated that the

TABLE I B.
Skull measurements of *Hippopotamus amphibius* L. subsp.

	ca- pen- sis	con- stric- tus	am- phi- bius	ki- boko	tschaden- sis	♀	♂	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
41. Ratio 36 : 40	0.70	—	—	—	—	—	—	0.75	0.69	0.80	0.82	0.77	0.78	0.78	0.66	0.81	0.80	0.64	0.82	0.76	0.72	0.76	0.69	0.71	0.69	0.87	0.78	0.70	0.71	0.77	0.73	0.69	0.78	0.78	0.68	0.66	0.65	0.68	0.86	0.71	0.68	0.79	
42. Height of symphysis	—	—	—	—	—	—	—	71	68	82	83	92	86	104	96	78	89	98	114	115	106	82	103	107	101	110	102	101	122	—	95	105	—	82	91	78	81	98	88	90	88	83	
43. Ratio 42 : 36	—	—	—	—	—	—	—	0.53	0.48	0.55	0.48	0.55	0.48	0.56	0.65	0.53	0.51	0.57	0.54	0.64	0.60	0.51	0.57	0.59	0.61	0.59	0.59	0.49	0.59	—	0.56	0.55	—	—	0.52	0.52	0.51	0.54	0.51	0.52	0.49	0.51	
44. Obliqueness of ramus ascendens	—	—	—	—	—	—	—	77°	75°	71°	78°	82°	73°	71°	67°	68°	77°	71°	80°	73°	73°	67°	74°	75°	70°	65°	—	66°	72°	—	68°	73°	74°	—	77°	69°	70°	75°	72°	74°	65°	72°	
45. Height of processus coronoideus	334	355	410	380	—	—	—	275	275	245	320	365	335	310	—	275	320	365	375	345	340	310	340	360	340	320	305	360	400	330	330	390	320	—	390	305	335	360	340	340	340	300	
46. Ratio 45 : 34	0.57	0.60	0.66	—	—	—	—	0.69	0.68	0.54	0.67	0.78	0.64	0.60	—	0.59	0.63	0.62	0.69	0.64	0.66	0.60	0.60	0.66	0.62	0.61	0.58	0.59	0.66	0.59	0.65	0.63	0.66	—	0.66	0.66	0.61	0.67	0.68	0.69	0.61	0.59	
47. Length of crista sagittalis	100	—	—	—	—	—	—	75	52	67	70	78	77	90	—	81	88	77	102	83	77	85	72	72	86	97	102	133	85	—	68	100	57	85	100	63	60	95	80	83	100	—	
48. Length from nuchal crest to tip of nasals	570	—	—	—	—	—	—	430	380	450	515	475	510	525	—	461	—	567	560	540	560	498	570	550	525	540	515	575	600	—	458	595	510	495	580	470	560	560	510	515	530	—	
49. Ratio 47 : 48	0.18	—	—	—	—	—	—	0.18	0.14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
50. Length from palatine to premaxillaries	405	—	—	—	—	—	—	336	326	0.15	0.14	0.16	0.15	0.17	—	0.18	—	0.14	0.18	0.15	0.14	0.18	0.13	0.13	0.16	0.18	0.20	0.23	0.14	—	0.15	0.17	0.11	0.17	0.17	0.17	0.13	0.11	0.17	0.16	0.16	0.19	—
51. Median length of maxillary	—	—	—	—	—	—	—	130	125	374	404	402	448	460	—	—	413	499	481	454	482	—	510	500	453	440	465	567	575	481	—	530	418	413	485	405	454	458	—	443	473	423	
52. Ratio 51 : 50	—	—	—	—	—	—	—	0.38	0.38	168	195	169	185	205	—	173	176	213	212	182	200	215	224	235	200	188	202	205	230	196	186	250	186	197	213	172	178	—	176	195	—	175	
53. Anterior width of premaxillaries	233	—	—	—	—	—	—	163	162	174	206	197	202	223	—	—	210	220	221	—	214	—	217	270	221	236	214	259	263	230	—	263	187	205	222	193	218	234	—	222	235	208	
54. Anterior width of maxillary	350	332	370	—	277	385	218	231	244	286	272	292	301	—	254	287	323	324	305	309	287	322	344	321	306	336	382	388	325	319	370	259	259	315	266	300	336	299	316	341	291		
55. Zygomatic width	440	435	435	442	327	458	338	351	331	372	361	403	381	—	368	389	404	411	414	416	368	436	415	397	402	414	471	483	419	403	452	365	358	411	389	396	403	359	404	408	392		
56. Ratio 54 : 55	0.80	0.76	0.85	—	0.85	0.84	0.65	0.66	0.74	0.77	0.75	0.72	0.79	—	0.69	0.74	0.80	0.79	0.74	0.74	0.78	0.74	0.83	0.81	0.76	0.81	0.81	0.80	0.78	0.79	0.82	0.71	0.72	0.77	0.68	0.76	0.83	0.83	0.78	0.84	0.74		
57. Ratio 55 : 27	0.65	0.63	0.60	0.61	0.55	0.72	0.66	0.71	0.61	0.62	—	0.62	0.59	—	—	0.64	0.57	0.61	0.65	0.62	—	0.62	—	0.62	—	0.62	0.63	0.64	0.62	0.63	0.62	—	0.60	—	—	0.59	0.67	0.61	0.62	—	0.65	—	
58. Rostral constriction	153	110	144	138	115	132	97	102	89	106	92	123	97	—	110	117	115	106	101	113	94	99	101	116	118	110	163	174	107	115	130	115	96	113	114	107	117	126	142	126	96		
59. Ratio 58 : 27	0.23	0.16	0.20	0.19	0.19	0.21	0.19	0.21	0.16	0.18	—	0.20	0.15	—	—	0.19	0.16	0.16	0.16	0.17	—	0.14	—	0.18	0.19	0.17	0.21	0.23	0.16	—	0.17	—	—	0.16	0.20	0.16	0.18	—	0.23	—			
60. Ratio 58 : 55	0.35	0.25	0.33	0.31	0.35	0.29	0.29	0.29	0.27	0.28	0.25	0.31	0.25	—	0.30	0.30	0.28	0.26	0.24	0.27	0.26	0.23	0.24	0.29	0.29	0.27	0.35	0.36	0.26	0.29	0.29	0.32	0.27	0.27	0.29	0.27	0.29	0.35	0.35	0.31	0.24		
61. Vertical diameter of orbit	71	75	90	80	70	—	66	69	70	74	74	73	72	—	72	69	81	83	78	84	75	82	80	74	77	70	88	79	72	73	92	66	73	86	78	70	75	79	73	79	63		
62. Horizontal diameter of orbit	81	70	65	60	72	—	59	56	62	63	59	61	53	—	63	61	71	75	60	65	60	68	67	62	62	67	73	67	—	63	71	64	70	70	58	67	63	63	59	—	67		
63. Difference 61-62	-10	+5	+25	+20	-2	—	+7	13	+8	+11	+15	+12	+19	—	+0	+8	+10	+8	+18	+19	+15	+14	+13	+12	+15	+3	+15	+12	—	+10	+21	+2	+3	+16	+20	+3	+12	+16	+14	—	-4		
64. Elevation of orbit above level of frontals	—	24	40	42	44	—	16	25	18	37	28	34	40	—	28	35	38	29	42	50	23	45	39	34	39	28	44	20	38	25	40	38	27	35	29	37	55	40	28	32	44		
65. Height of calvarium from palatine	—	181	208	—	150	—	135	135	140	157	146	158	151	—	148	153	182	188	156	166	160	176	165	167	174	173	179	204	160	166	195	144	160	171	155	163	173	156	149	177	145		
66. Ratio 65 : 27	—	0.26	0.28	—	0.25	—	0.26	0.27	0.26	0.26	—	0.24	0.23	—	—	0.25	0.25	0.28	0.24	0.25	—	0.25	—	0.26	0.27	0.27	0.24	0.27	0.24	—	0.26	—	—	0.25	0.27	0.25	0.26	—	0.24	—			
67. Ratio 64 : 65	—	0.13	0.19	—	0.29	—	0.12	0.19	0.13	0.24	0.19	0.22	0.26	—	0.19	0.23	0.21	0.15	0.27	0.30	0.14	0.26	0.24	0.20	0.22	0.16	0.25	0.10	0.24	0.15	0.21	0.26	0.17	0.20	0.19	0.23	0.32	0.26	0.19	0.18	0.30		
68. Orbital angle	—	—	—	—	63°	—	52°	57°	63°	65°	69°	70°	67°	—	66°	72°	59°	61°	68°	74°	77°	67°	68°	78°	61°	61°	67°	69°	78°	63°	65°	68°	69°	66°	63°	73°	70°	68°	68°	74°	70°		
69. Height of occiput from basion	193	196	214	—	193	—	163	171	168	195	170	193	170	—	180	192	186	205	198	186	174	200	192	186	192	194	222	221	—	185	209	—	—	198	182	172	197	167	187	202	—		
70. Difference 69-65	—	+15	+6	—	+43	—	+28	+36	+28	+38	+24	+35	+19	—	32	+39	+4	+17	+42	+20	+14	+24	+27	+19	+18	+21	+43	+17	—	+19	+14	—	—	+27	+27	+9	+24	+11	+38	+25	—		
71. Width of occiput	292	278	332	—	293	330	223	257	226	271	253	291	284	—	241	278	296	268	299	282	272	293	280	272	268	278	315	341	285	264	313	—	267	298	274	288	276	257	284	295	—		
72. Ratio																																											

TABLE II.
Measurements of the calvarium of *Hippopotamus iravaticus* Falconer et Cautley and of *Hippopotamus sivalensis* Falconer et Cautley

	<i>H. iravaticus</i>	<i>H. sivalensis sivalensis</i>																				<i>H.s. duboisi</i>	<i>H.s. palaeindicus</i>		<i>H.s. sivajavanicus</i>			<i>H.s. koenigswaldi</i>			<i>H.s. soloensis</i>						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		21	1	2	1	2	3	1	2	3	1	2	3	4	5	
No. of specimen	—	—	—	164	185	175	166	181	186	—	—	—	183	188	165	185	ca. 170	—	ca. 166	—	—	166	1	2	1	2	3	1	2	3	1	2	3	4	5		
Height of occiput from basion	—	—	—	164	185	175	166	181	186	—	—	—	183	188	165	185	ca. 170	—	ca. 166	—	—	166	176	ca. 195	—	—	—	ca. 146	—	—	162	164	—	—	142		
Width of occiput	—	224	246	—	—	—	232	250	—	—	—	—	245	263	220	235	ca. 240	—	ca. 234	—	—	247	200	280	—	—	—	204	—	—	241	248	—	ca. 250	236		
Occiput index	—	—	—	—	—	—	72	72	—	—	—	—	75	71	75	78	—	—	ca. 71	—	—	67	61	ca. 70	—	—	—	ca. 72	—	—	67	66	—	—	60		
Condylar-basal length	ca. 450	—	566	ca. 570	—	—	—	—	—	—	—	—	610	605	—	600	—	—	—	—	—	—	—	—	507	—	—	—	—	—	522	ca. 535	—	—	—		
Zygomatic width	—	—	366	386	—	ca. 350	ca. 325	361	—	345	—	—	ca. 390	390	332	360	—	—	—	ca. 368	—	—	400	377	ca. 328	—	—	310	—	—	332	347	—	ca. 345	—		
Zygomatic index	—	—	65	ca. 68	—	—	—	—	—	—	—	—	64	64	—	60	—	—	—	—	—	—	—	—	ca. 65	—	—	—	—	—	64	ca. 65	—	—	—		
Width of cranium at parietals	—	93	112	115	110	—	125	127	105	104	—	—	90	95	95	100	90	—	—	—	—	90	115	ca. 130	—	—	—	98	—	—	94	93	—	94	—		
Length pd ¹ -P ⁴	—	—	—	147	148	—	—	—	—	—	—	—	129	149	—	137	—	153	—	—	—	—	—	—	—	—	—	—	—	117	107	110	—	—	ca. 103		
Length M ¹ -M ³	102	—	—	111	124	—	—	—	—	—	—	—	126	130	113	108	132	128	145	109	ca. 120	—	—	143	135	108	109	—	111	110	108	115	123	ca. 123	—	114	
pd ¹ -C diastema	—	—	—	35	22	—	—	—	—	—	—	—	35	32	—	40	—	28	—	—	—	—	—	—	—	—	—	—	—	—	—	35	—	—	—	—	
Preorbital length	—	—	314	324	—	—	—	—	—	—	—	—	335	340	—	ca. 345	—	—	—	—	—	—	—	—	—	—	—	—	282	—	—	288	ca. 300	—	—	—	
Postorbital length	—	228	250	260	270	—	240	257	242	—	—	—	275	270	280	ca. 260	—	—	—	—	—	—	240	265	260	225	—	—	ca. 200	—	—	234	ca. 235	—	—	—	
Height, top of orbit to M ³ alveolus	—	—	—	170	—	167	177	160	—	131	—	—	160	150	140	ca. 160	—	—	—	ca. 145	—	—	163	205	190	157	—	—	165	—	—	188	—	190	188	—	
Width of condyles	—	—	—	147	—	—	122	129	—	—	—	—	129	130	140	120	130	—	128	—	—	—	—	142	144	118	—	—	119	—	—	129	ca. 130	—	—	—	
Width of palate at M ¹	44	—	—	ca. 55	57	—	—	—	62	—	—	—	47	48	53	45	60	60	43	ca. 53	—	—	—	62	58	63	54	—	46	—	ca. 40	ca. 60	ca. 60	—	—	ca. 58	
Width of palate at pd ¹	—	—	—	115	110	—	—	—	—	—	—	—	104	111	—	115	—	125	—	—	—	—	—	—	—	132	—	—	—	—	ca. 110	ca. 116	ca. 123	—	—	—	
Transverse diameter of C	38	—	—	—	—	—	—	—	—	—	—	—	ca. 50	45	52	ca. 50	—	60	—	—	—	—	—	—	—	—	—	—	—	—	40	—	—	—	—	—	
Antero-posterior diameter of id.	33	—	—	—	—	—	—	—	—	—	—	—	—	—	44	—	—	—	—	—	—	—	—	—	—	—	—	—	36	—	—	—	—	—	38	—	
Width over ventral border of infra-orbital foramen	—	95	110	96	103	—	—	—	97	—	—	—	—	—	—	—	—	—	—	94	—	—	—	103	—	93	—	—	—	—	—	98	96	—	—	—	
Width over border of maxillary, same level	—	—	—	112	110	—	—	—	106	—	—	—	—	—	—	—	—	—	—	99	—	—	—	114	101	114	—	—	98	—	ca. 96	115	118	—	—	—	
Height from alveolar border, same level	—	114	134	140	142	—	—	—	145	—	—	—	—	—	—	—	—	—	—	137	—	—	113	160	—	145	—	—	—	—	—	132	130	134	—	—	
Antero-posterior diameter of orbit	—	58	67	73	—	—	67	61	—	55	—	—	—	—	—	—	—	—	—	—	—	—	—	57	61	53	—	—	ca. 59	—	—	56	—	55	—	—	
Vertical diameter of orbit	—	61	58	60	—	61	63	65	—	62	—	—	—	—	—	—	—	—	—	—	57	—	—	—	66	68	61	—	—	64	—	—	70	—	75	65	—
Greatest interval between inner side of zygomatic arch and cranium	—	—	96	103	—	—	—	105	—	ca. 110	—	—	—	—	—	—	—	—	—	—	ca. 100	—	—	98	101	—	—	—	83	—	—	ca. 84	88	—	85	—	
Length P ⁴ -M ³	—	—	—	144	148	—	—	—	151	—	156	162	148	—	—	—	—	—	—	132	142	—	—	165	150	125	ca. 127	—	132	ca. 135	ca. 134	138	137	ca. 140	—	139	
Length from posterior border of M ³ to posterior border of occipital condyles	—	—	—	206	219	217	—	192	195	—	—	—	ca. 200	—	—	—	—	—	209	—	—	—	185	197	195	188	—	—	167	—	—	183	188	—	—	—	
P ⁴ -M ³ -condyle index	—	—	—	70	68	—	—	—	77	—	—	—	ca. 75	—	64	—	—	—	—	63	—	—	—	84	82	66	—	—	79	—	—	75	73	—	—	—	
Elevation of orbit above level of frontals	—	—	—	19	—	23	24	18	19	12	20	—	—	—	—	—	—	—	—	—	—	—	45	42	28	23	—	—	38	—	—	51	—	54	48	—	
Height of calvarium from palatine	—	—	—	146	143	142	151	134	148	127	126	—	—	—	—	—	—	—	—	144	130	—	110	160	158	137	—	—	120	—	—	140	141	140	140	—	
Orbito-cephalic index	—	—	—	13	—	16	16	13	13	9	16	—	—	—	—	—	—	—	—	—	18	—	41	26	18	17	—	—	32	—	—	36	—	39	34	—	
Length of M ¹	28	—	46	—	46	44	40	—	45	—	—	(35)	—	—	—	41	—	—	31	—	42	—	—	41	40	—	37	35	ca. 34	—	ca. 36	—	ca. 35	ca. 35	—	34	
Width of id.	29	—	37	—	38	36	39	—	41	—	—	41	40	—	—	40	—	—	40	—	37	—	—	36	39	35	36	35	34	—	32	—	32	—	—	31	
Length of M ²	36	53	—	(37 ¹)	53	50	51	—	54	53	48	48	(43)	—	—	53	—	—	39	—	48	—	42	54	54	38	42	40	42	40	42	43	45	46	ca. 50	44	
Width of id.	34	48	—	54	44	48	49	—	47	46	45	51	50	—	—	47	—	—	47	ca. 48	46	—	37	44	47	42	38	41	36	36	37	ca. 39	39	38	42	38	
Length of M ³	39	—	—	46	—	—	—	51	—	—	—	50	48	—	—	—	—	—	40	ca. 48	—	—	ca. 43	54	51	41	40	41	ca. 41	41	38	ca. 43	ca. 45	48	43	41	
Width of id.	37	—	—	52	—	—	—	45	—	—	—	52	49	—	—	—	—	—	44	ca. 47	—	—	ca. 38	—	46	40	39	42	ca. 38	36	37	39	38	39	40	39	

Lydekker (1884 a, p. 39) gives 47 mm, but the length of M² is not more than 37 mm, very much reduced by interproximal wear.

skull of *H. sivalensis* has evolved in the course of the Pleistocene, and we know also how it has evolved. There is a Lower Pleistocene stage with low orbits, elongated postdental portion, long and low symphysis, and low horizontal ramus, and a stage with high orbits, shortened postdental portion, and a short and high symphysis and horizontal ramus that appears higher up in the geological time scale and that prevails toward the close of the Pleistocene. The transformation has certainly been accomplished in several collateral lines, but the data contained in the present paper do not permit to identify these lines precisely.

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EXPLANATION OF THE PLATES

Plate I

Figs. 1-12, upper premolars of *Hippopotamus amphibius* L. (the numbers given refer to the list of skulls on p. 6/7); fig. 1, P³ dext. no. 25; fig. 2, P³ sin. no. 28; fig. 3, P³ sin. no. 30; fig. 4, P³ sin. no. 31; fig. 5, P⁴ sin. no. 30; fig. 6, P⁴ dext. no. 20; fig. 7, P³ dext. no. 20; fig. 8, P⁴ sin. no. 31; fig. 9, P⁴ sin. no. 28; fig. 10, P⁴ dext. no. 28; fig. 11, P⁴ dext. no. 25; fig. 12, P⁴ sin. no. 25. pa = paracone, pr = protocone, me = metacone, ml = metaconule, hy = hypocone. All figures natural size.

Plate II

Figs. 1-2, *Hippopotamus sivalensis soloensis* nov. subsp.; fig. 1, calvarium, Coll. Dub. no. 2914, Tinggang (Solo valley), left view (holotype); fig. 2, M¹-M³ dext., Coll. Dub. no. 2195, Soember Waroe, crown view.
 Fig. 3, *Hippopotamus sivalensis koenigswaldi* Hooijer, calvarium, Coll. Dub. no. 2919, Padas Malang, left view.
 Fig. 4, *Hippopotamus sivalensis sivajavanicus* (Dubois), calvarium, Coll. Dub. no. 2908, Kedoeng Broeboes, left view (holotype).
 Figs. 1, 3, and 4, one-fourth natural size; fig. 2, one-half natural size.

Plate III

Fig. 1, *Hippopotamus sivalensis soloensis* nov. subsp., calvarium, Coll. Dub. no. 2914, Tinggang (Solo valley), lower view (holotype)
 Fig. 2, *Hippopotamus sivalensis sivajavanicus* (Dubois), calvarium, Coll. Dub. no. 2908, Kedoeng Broeboes, lower view (holotype).
 Both figures one-fourth natural size.

Plate IV

Fig. 1, *Hippopotamus sivalensis koenigswaldi* Hooijer, calvarium, Coll. Dub. no. 2919, Padas Malang, lower view.
 Fig. 2, *Hippopotamus sivalensis sivalensis* Falconer et Cautley, fragment of right maxillary with pd⁴-M³, coll. Dub. no. 3138, Samalka, Punjab, lower view.
 Fig. 3, *Hippopotamus sivalensis soloensis* nov. subsp., mandible, Coll. Dub. no. 2915, Solo valley, upper view.
 Fig. 4, *Hippopotamus sivalensis koenigswaldi* Hooijer, right ramus with

P₄-M₃, Geol. Museum Leiden, no. 28124, N. of Modjokerto, upper view. Figs. 1 and 3, one-fourth natural size; fig. 2, one-half natural size; fig. 4, three-fifths natural size.

Plate V

- Figs. 1-2, *Hippopotamus sivalensis koenigswaldi* Hooijer; fig. 1, mandible, Geol. Museum Leiden, no. 27934, between Djetis and Gondang, anterior view; fig. 2, right half of mandible, Coll. Dub. no. 2916, Kedoeng Broeboes, upper view.
- Fig. 3, *Hippopotamus sivalensis duboisi* nov. subsp., calvarium, Coll. Dub. no. 3146, Naliwala, Punjab, right view (holotype).
- Fig. 4, *Hippopotamus sivalensis sivajavanicus* (Dubois), palate, Coll. Dub. no. 2079, Soember Waroe, lower view.
- Fig. 5, *Hippopotamus sivalensis sivalensis* Falconer et Cautley, calvarium, Coll. Dub. no. 3148, Kodawala, Punjab, lower view.
- Figs. 1 and 4, one-third natural size; figs. 2 and 3, one-fourth natural size; fig. 5, two-ninths natural size.

Plate VI

- Figs. 1-3, *Hippopotamus sivalensis soloensis* nov. subsp.; fig. 1, calvarium, Coll. Dub. no. 2914, Tinggang (Solo valley), upper view (holotype); fig. 2, calvarium, Coll. Dub. no. 2909, Tinggang (Solo valley), right view; fig. 3, mandible, Coll. Dub. no. 2915, Solo valley, right view.
- Figs. 1 and 2, one-fifth natural size; fig. 3, three-tenths natural size.

Plate VII

- Figs. 1-2, *Hippopotamus sivalensis soloensis* nov. subsp.; fig. 1, calvarium, Coll. Dub. no. 2911, Tinggang (Solo valley), lower view; fig. 2, palate, Coll. Dub. no. 1702, Kedoeng Loemboe, lower view.
- Fig. 1, one-fourth natural size; fig. 2, two-sevenths natural size.

Plate VIII

- Figs. 1-9, *Hippopotamus sivalensis soloensis* nov. subsp.; figs. 1-2, M³ sin., Coll. Dub. no. 2077 b, Kedoeng Loemboe; fig. 1, crown view; fig. 2, lingual view; figs. 3-4, M² dext., Coll. Dub. no. 2077 a, Kedoeng Loemboe; fig. 3, crown view; fig. 4, lingual view; fig. 5, M² and M³ dext., Coll. Dub. no. 2084 b, Bogu, crown view; figs. 6-7, M² sin., Coll. Dub.

no. 2205, Kedoeng Broeboes; fig. 6, crown view; fig. 7, lingual view; fig. 8, M³ dext., Coll. Dub. no. 163, Pati Ajam, lingual view; fig. 9, M² sin., Coll. Dub. no. 2318 a, Bangle, crown view.

Figs. 10-14, *Hippopotamus sivalensis koenigswaldi* Hooijer; fig. 10, M¹ dext., Coll. Dub. no. 2188, Kedoeng Loemboe, crown view; figs. 11-12, M² dext., Coll. Dub. no. 2008 b, Kedoeng Broeboes; fig. 11, crown view; fig. 12, lingual view; figs. 13-14, M³ sin., Coll. Dub. no. 314, Kedoeng Loemboe; fig. 13, crown view; fig. 14, lingual view.

Figs. 15-16, *Hippopotamus sivalensis sivajavanicus* (Dubois); fig. 15, M² sin., Coll. Dub. no. 2318 d, Kedoeng Broeboes, crown view; fig. 16, M¹ dext., Coll. Dub. no. 2318 e, between Dekes and Wadegan, crown view. All figures three-fourths natural size.

Plate IX

Figs. 1-2, *Hippopotamus sivalensis soloensis* nov. subsp.; fig. 1, mandibular symphysis, Coll. Dub. no. 2929, Kedoeng Madoh, anterior view; fig. 2, mandible, Coll. Dub. no. 2915, Solo valley, anterior view.

Fig. 3, *Hippopotamus sivalensis koenigswaldi* Hooijer, mandibular symphysis, Coll. Dub. no. 2918, Papan Djaran, anterior view.

All figures three-eighths natural size.

Plate X

Figs. 1 and 3, *Hippopotamus sivalensis koenigswaldi* Hooijer, mandible, Coll. Dub. no. 99, Tritik; fig. 1, upper view; fig. 3, left view.

Fig. 2, *Hippopotamus sivalensis sivalensis* Falconer et Cautley, right ramus horizontalis, Coll. Dub. no. 3147, Baro, Punjab, inner view.

Fig. 4, *Hippopotamus sivalensis soloensis* nov. subsp., M¹-M³ sin., Coll. Dub. no. 2195, Soember Waroe, crown view.

Fig. 1, two-ninths natural size; fig. 2, one-third natural size; fig. 3, one-fourth natural size; fig. 4, four-ninths natural size.

Plate XI

Figs. 1-6, epistropheus; figs. 1-2, *Hippopotamus amphibius* L., Leiden Museum, cat. a; figs. 3-4, *Hippopotamus sivalensis* Falconer et Cautley subsp., Geol. Museum Leiden, no. 18489, between Djokja and Oenarang; figs. 5-6, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1, 3, and 5, anterior views; figs. 2, 4, and 6, lower views. Figures not to scale but reduced to same size.

Plate XII

Figs. 1-3, third vertebra cervicalis; fig. 1, *Hippopotamus amphibius* L., Leiden Museum, cat. a; fig. 2, *Hippopotamus sivalensis* Falconer et Cautley subsp., Geol. Museum Leiden, no. 28019, Res. Soerabaja; fig. 3, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1-3 present lower views, all reduced to the same size.

Plate XIII

Figs. 1-3, humerus dext.; fig. 1, *Hippopotamus amphibius* L., Leiden Museum, cat. a; fig. 2, *Hippopotamus sivalensis* Falconer et Cautley subsp., Coll. Dub. no. 2094, Tinggang (Solo valley); fig. 3, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1-3 present posterior views, reduced to same size.

Plate XIV

Figs. 1-6, radius and ulna sin.; figs. 1-2, *Hippopotamus amphibius* L., Leiden Museum, cat. a; figs. 3-4, *Hippopotamus sivalensis* Falconer et Cautley subsp., Geol. Museum Leiden, no. 28036, N. of Modjokerto; figs. 5-6, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1, 3, and 5, anterior views; figs. 2, 4, and 6, distal views. All figures reduced to same size.

Plate XV

Figs. 1-6, metacarpal II dext.; figs. 1-2, *Hippopotamus amphibius* L., Leiden Museum, cat. a; figs. 3-4, *Hippopotamus sivalensis* Falconer et Cautley subsp., Coll. Dub. no. 9165, Kedoeng Broeboes; figs. 5-6, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1, 3, and 5, proximal views; figs. 2, 4, and 6, anterior views. All figures reduced to same size.

Plate XVI

Figs. 1-6, phalanx I digitorum manus; figs. 1-2, *Hippopotamus amphibius* L., Leiden Museum, cat. a; figs. 3-4, *Hippopotamus sivalensis* Falconer et Cautley subsp., Geol. Museum Leiden, no. 27911, N. of Modjokerto; figs. 5-6, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1, 3, and 5, proximal views; figs. 2, 4, and 6, anterior views. All figures reduced to same size.

Plate XVII

Figs. 1-4, *Hippopotamus sivalensis* Falconer et Cautley subsp.; figs. 1-2, pelvis of female individual, Coll. Dub. no. 9044/45, Trinil; fig. 1, upper view; fig. 2, left view; fig. 3, acetabular part of right os coxae of male individual, Geol. Museum Leiden, no. 28017, Res. Soerabaja, lower view; fig. 4, same portion of the female pelvis from Trinil represented on figs. 1-2 of the present plate to show the differences in the thickness of the ramus acetabularis ossis pubis (above in the figures), in the angle between the latter and the corpus ossis ilium (to the left in the figures), and in the size of the acetabulum.

Figs. 1-2, one-fifth natural size; figs. 3-4, three-tenths natural size.

Plate XVIII

Figs. 1-3, proximal part of femur dext.; fig. 1, *Hippopotamus amphibius* L., Leiden Museum, cat. a; fig. 2, *Hippopotamus sivalensis* Falconer et Cautley subsp., Geol. Museum Leiden, no. 28143, N. of Modjokerto; fig. 3, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1-3 present posterior views, all reduced to same size.

Plate XIX

Figs. 1-3, tibia sin.; fig. 1, *Hippopotamus amphibius* L., Leiden Museum, cat. a; fig. 2, *Hippopotamus sivalensis* Falconer et Cautley subsp., Coll. Dub. no. 6712, locality unknown; fig. 3, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1-3 present anterior views, all reduced to same size.

Plate XX

Figs. 1-6, astragalus sin.; figs. 1-2, *Hippopotamus amphibius* L., Leiden Museum, cat. a; figs. 3-4, *Hippopotamus sivalensis* Falconer et Cautley subsp., Coll. Dub. no. 10988, Bangle; figs. 5-6, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1, 3, and 5 anterior views; figs. 2, 4, and 6, distal views. All figures reduced to same size.

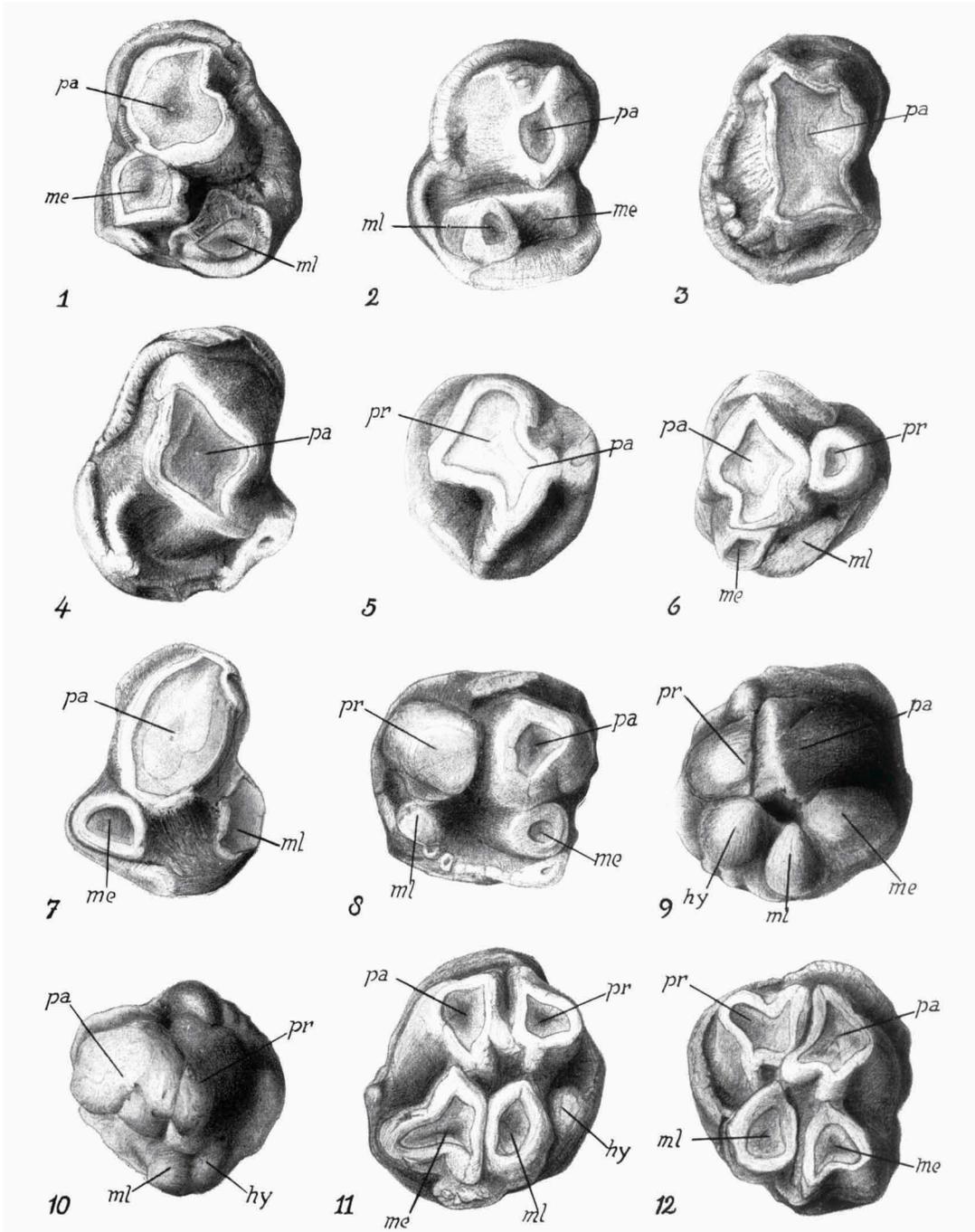
Plate XXI

Fig. 1, *Hippopotamus sivalensis* Falconer et Cautley subsp., cuboid dext., Geol. Museum Leiden, no. 28146, Java; fig. 2, *Hippopotamus liberiensis* Morton, cuboid dext., Leiden Museum, cat. a; figs. 3-4, *Hippopotamus*

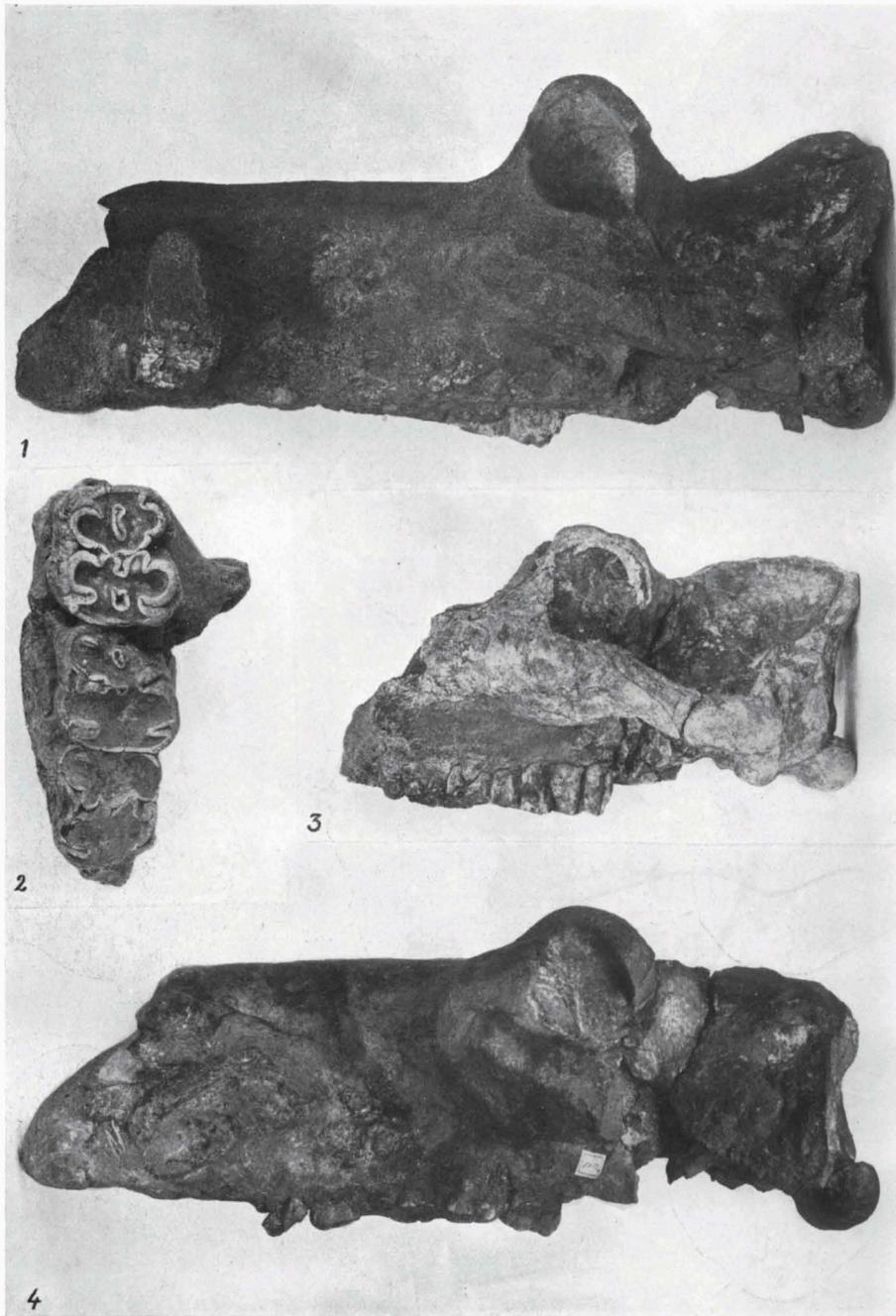
amphibius L.; fig. 3, cuboid sin., Leiden Museum, cat. a; fig. 4, cuboid dext., Amsterdam Museum, no. 183. Articular surfaces for (a) astragalus, (b-d) navicular, and (e-f) ectocuneiform. All figures present medial views, reduced to same size.

Plate XXII

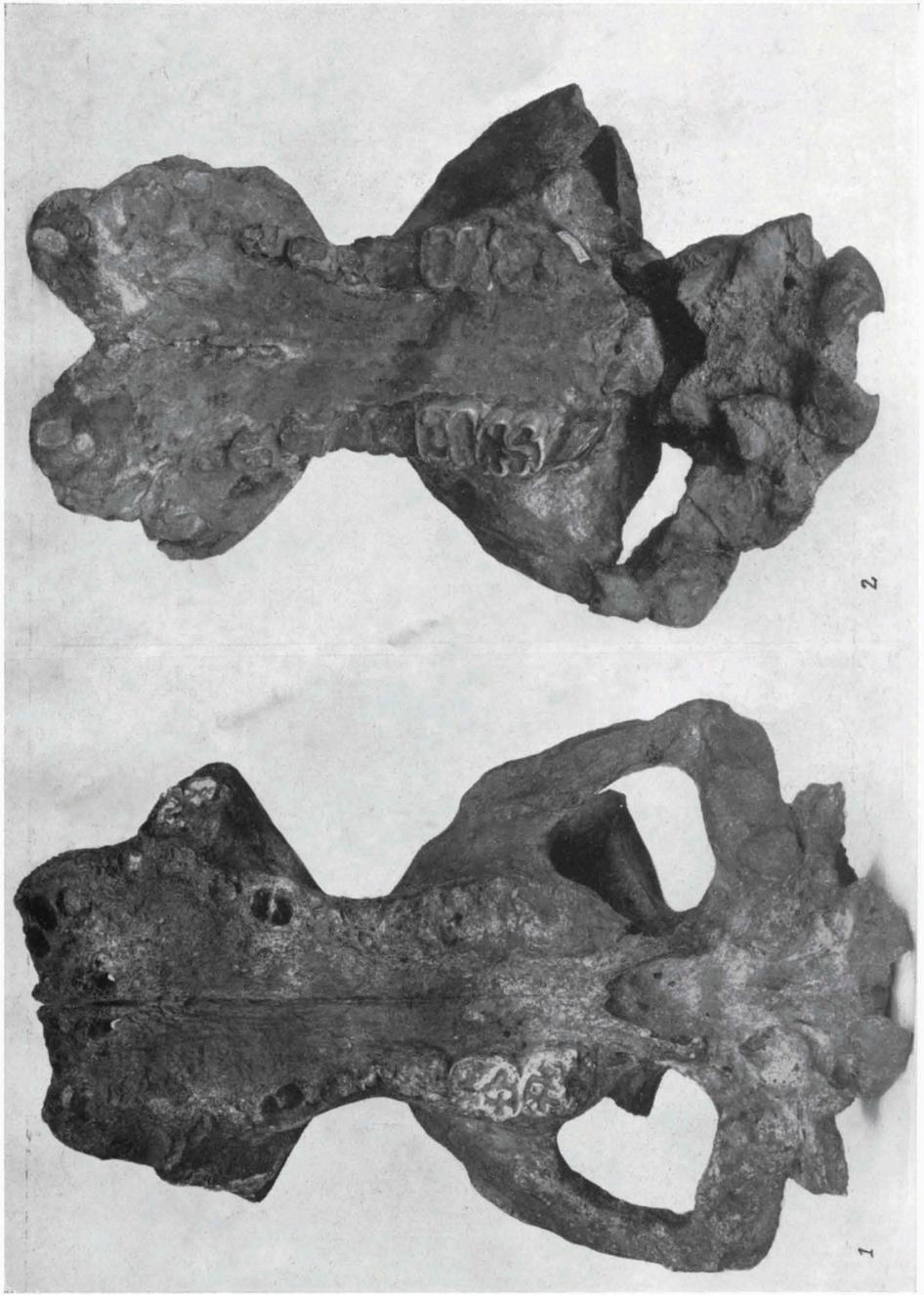
Figs. 1-6, metatarsal II dext.; figs. 1-2, *Hippopotamus amphibius* L., Leiden Museum, cat. a; figs. 3-4, *Hippopotamus sivalensis* Falconer et Cautley subsp., Coll. Dub. no. 6366, Kedoeng Broeboes; figs. 5-6, *Hippopotamus liberiensis* Morton, Leiden Museum, cat. a. Figs. 1, 3, and 5 proximal views; figs. 2, 4, and 6, anterior views. All figures reduced to same size.

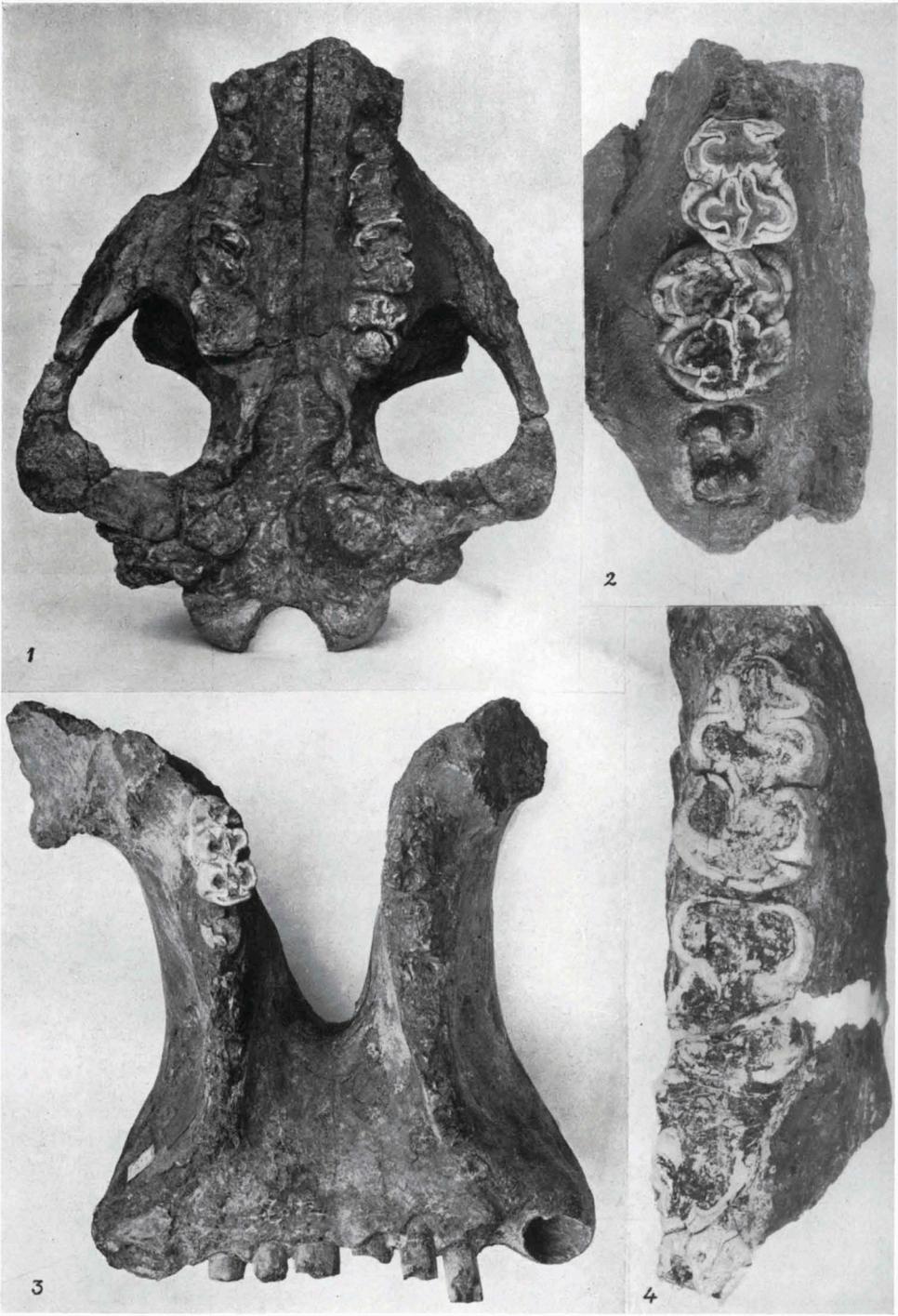


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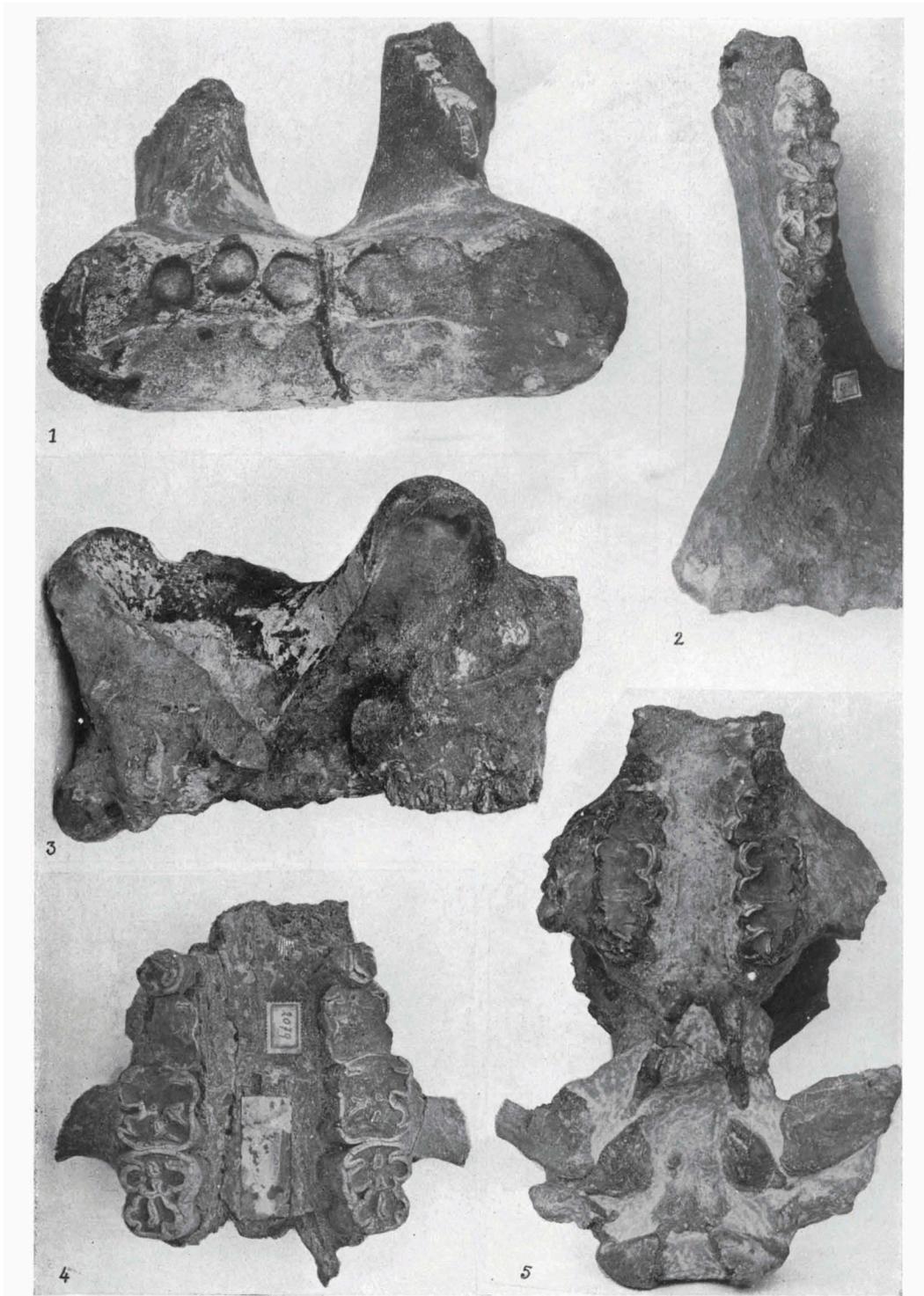


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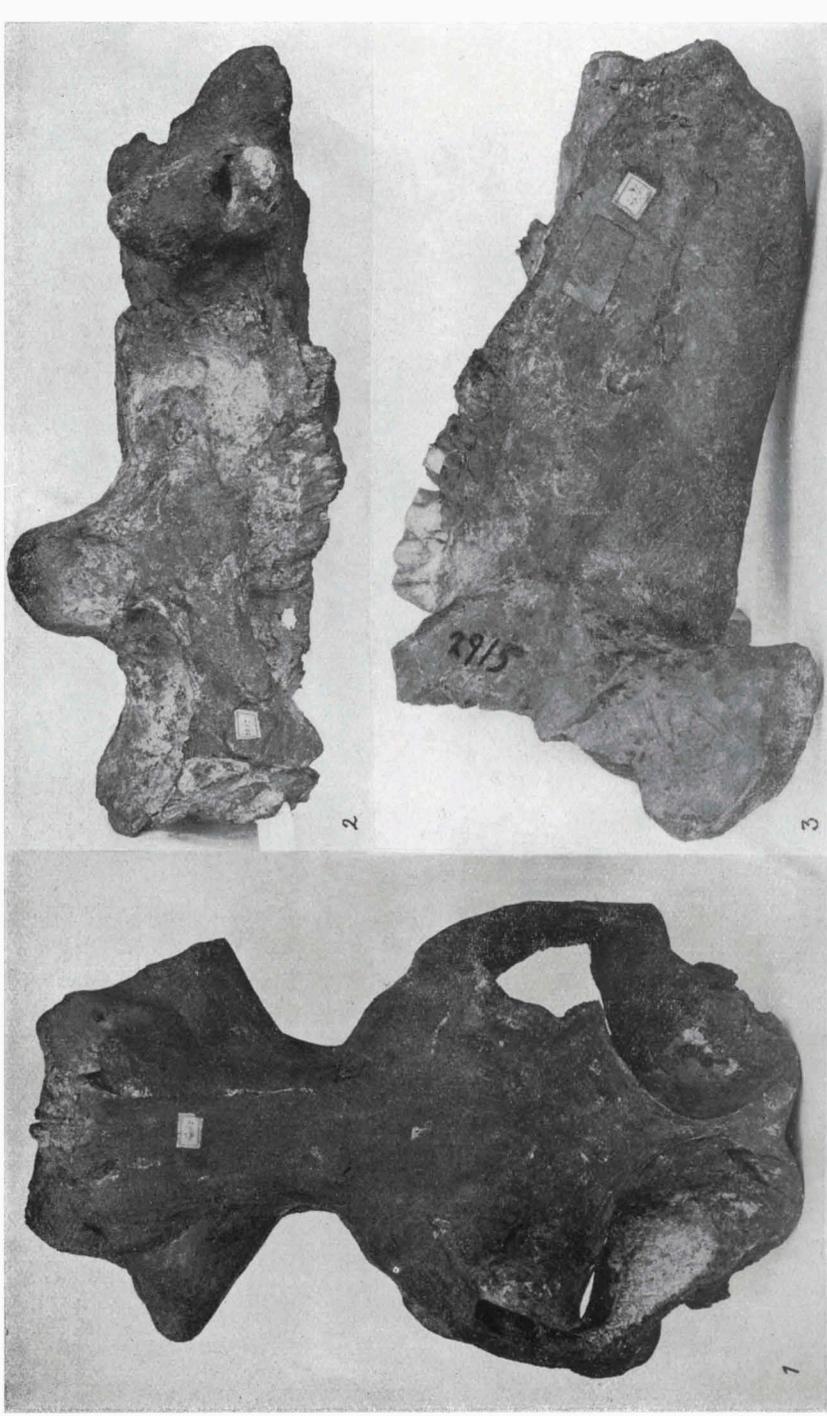




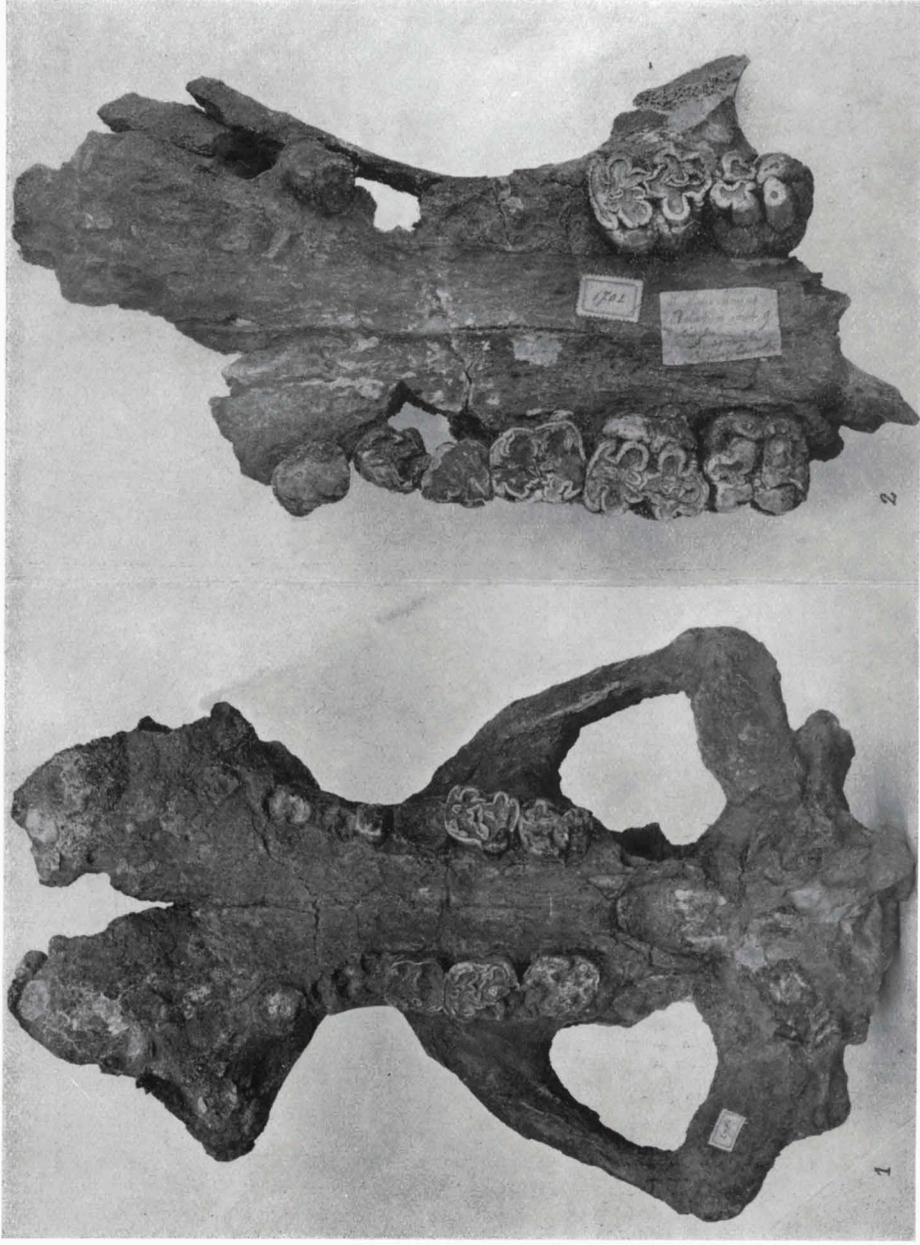
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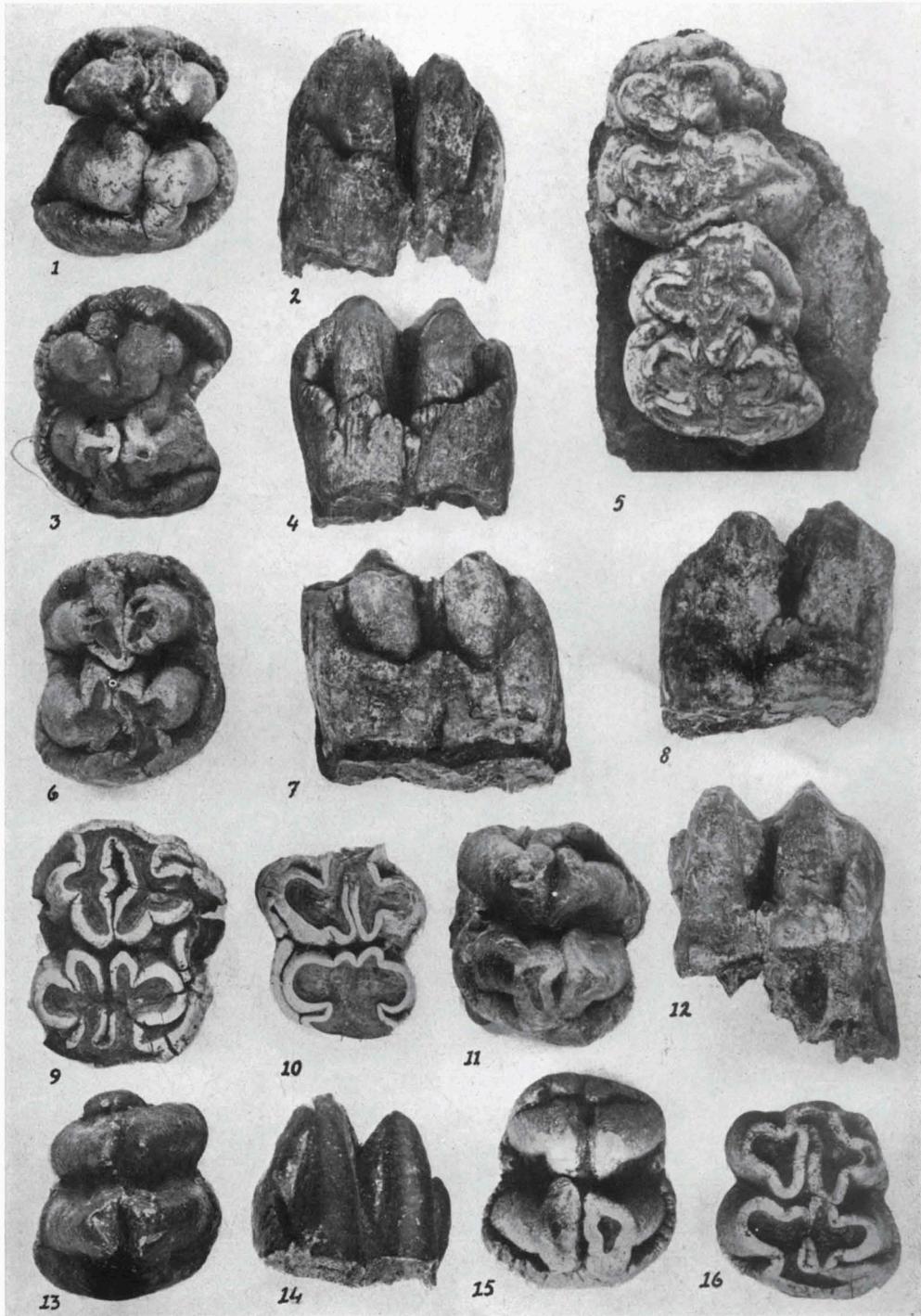
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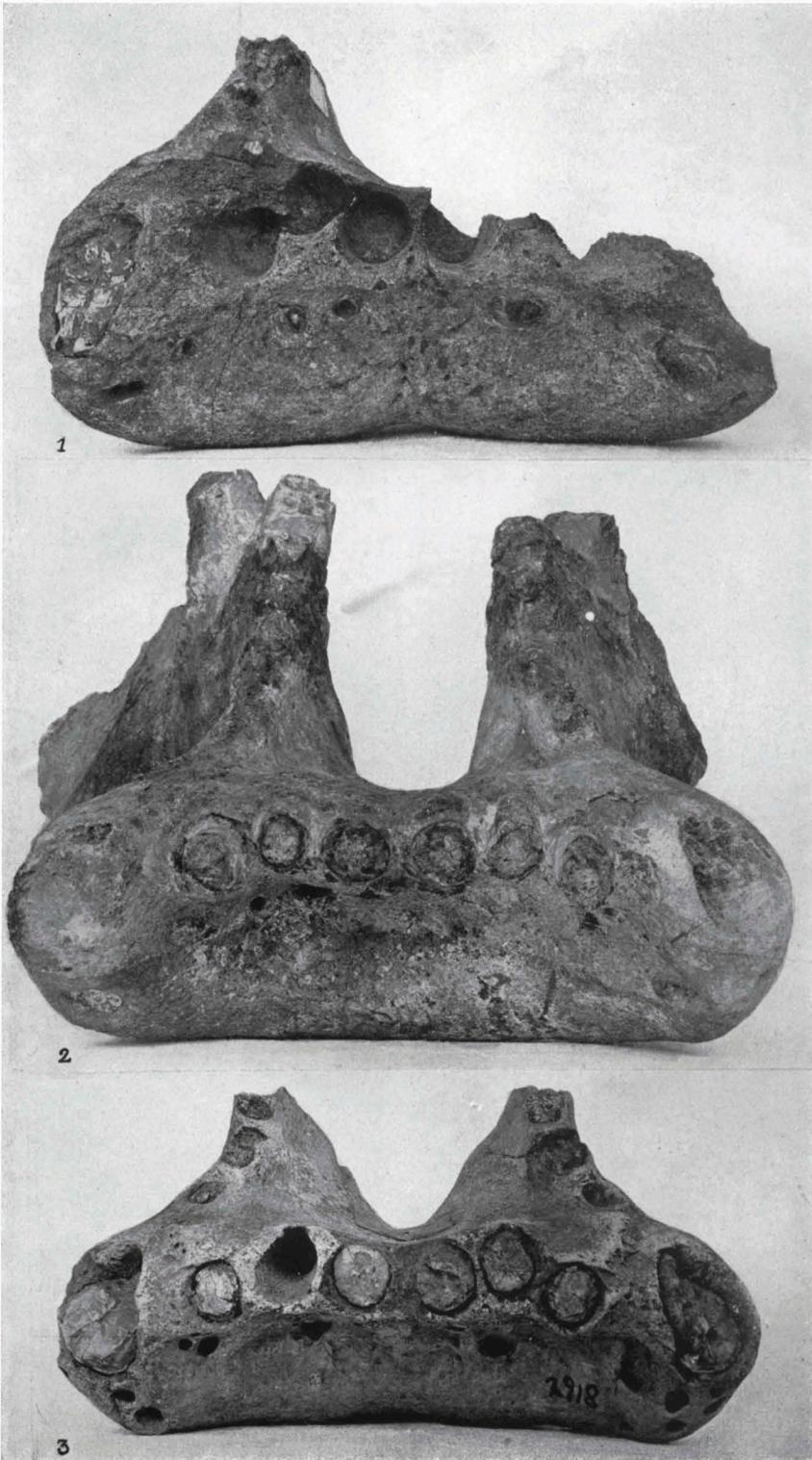
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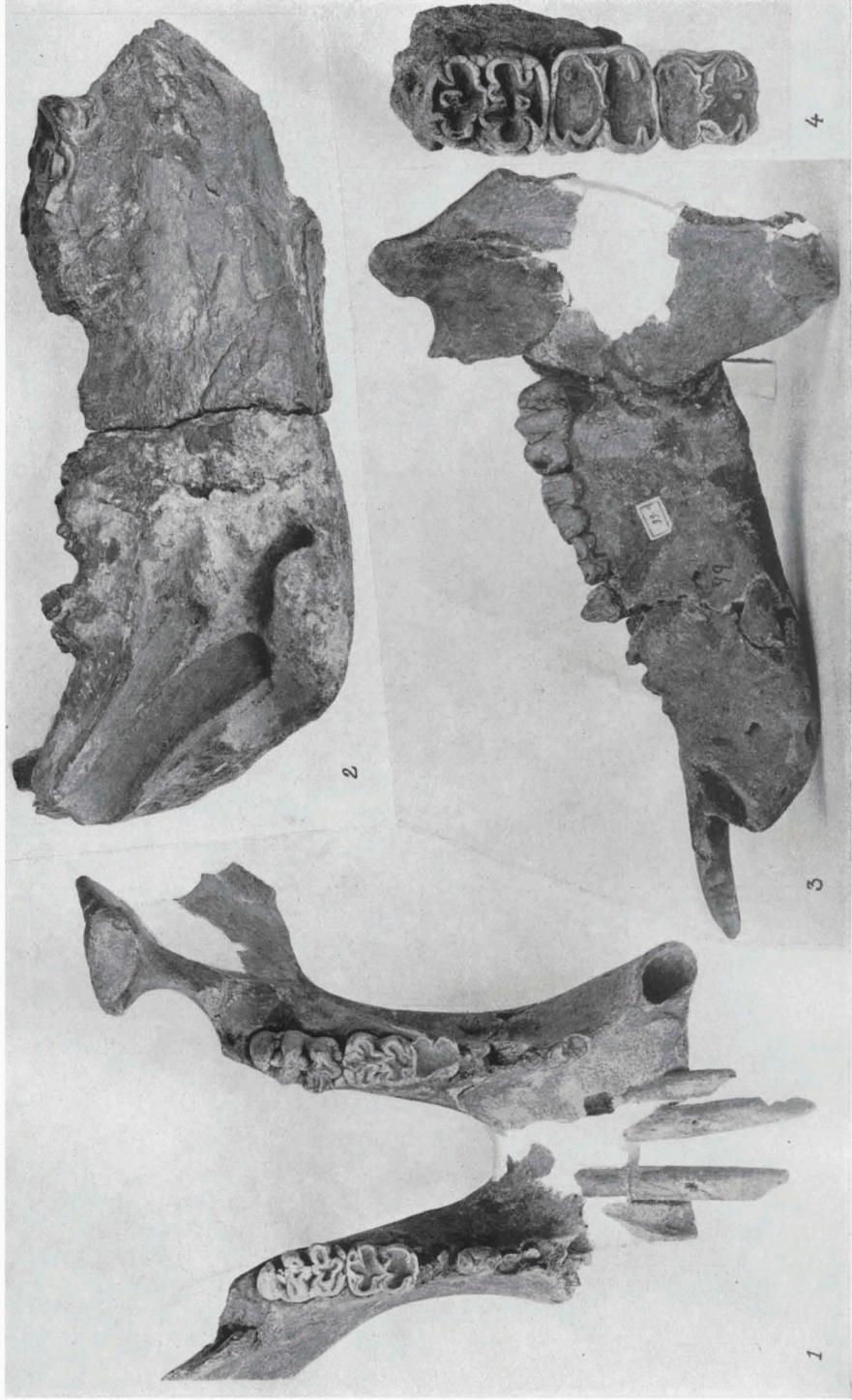
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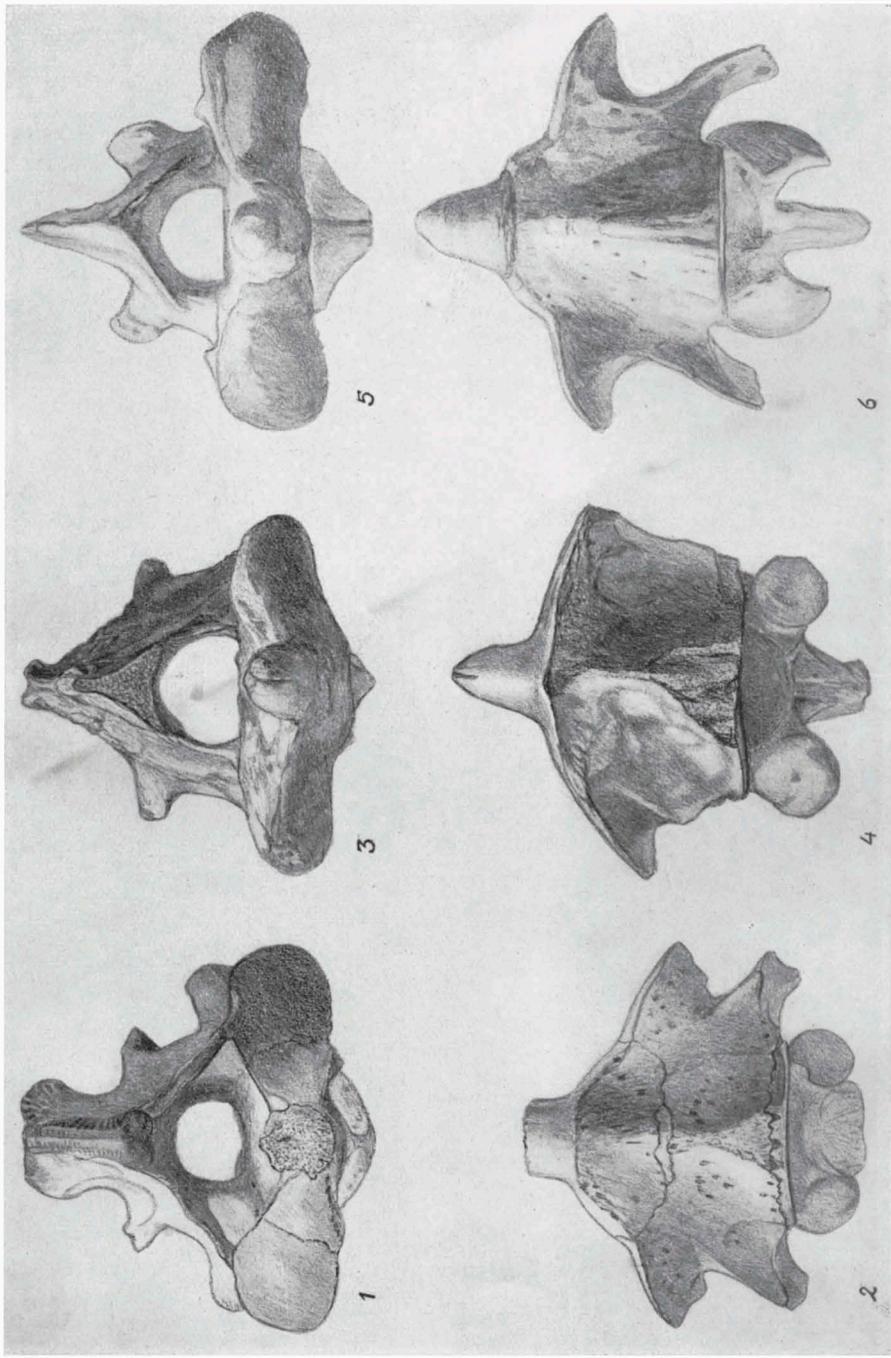
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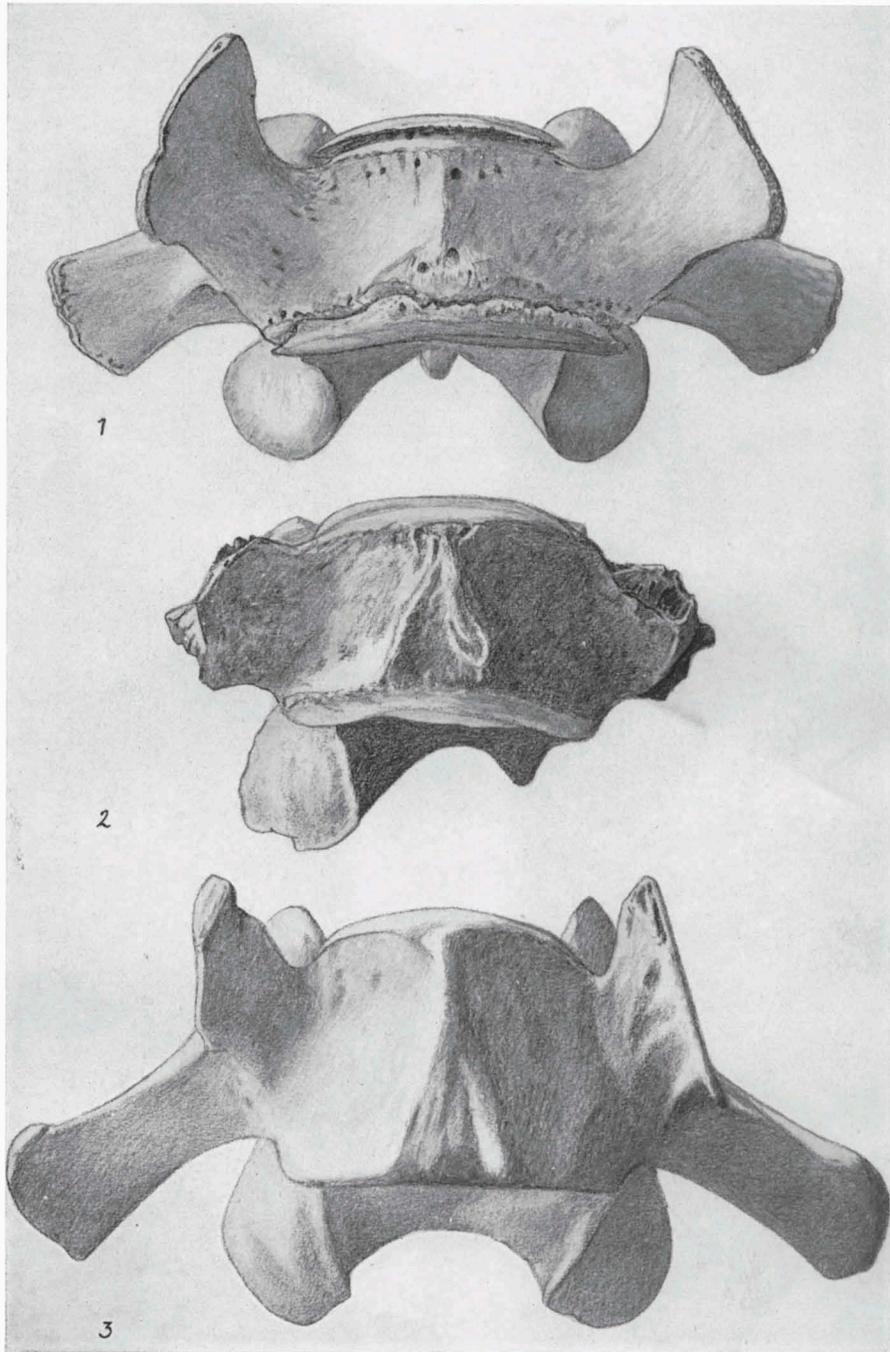


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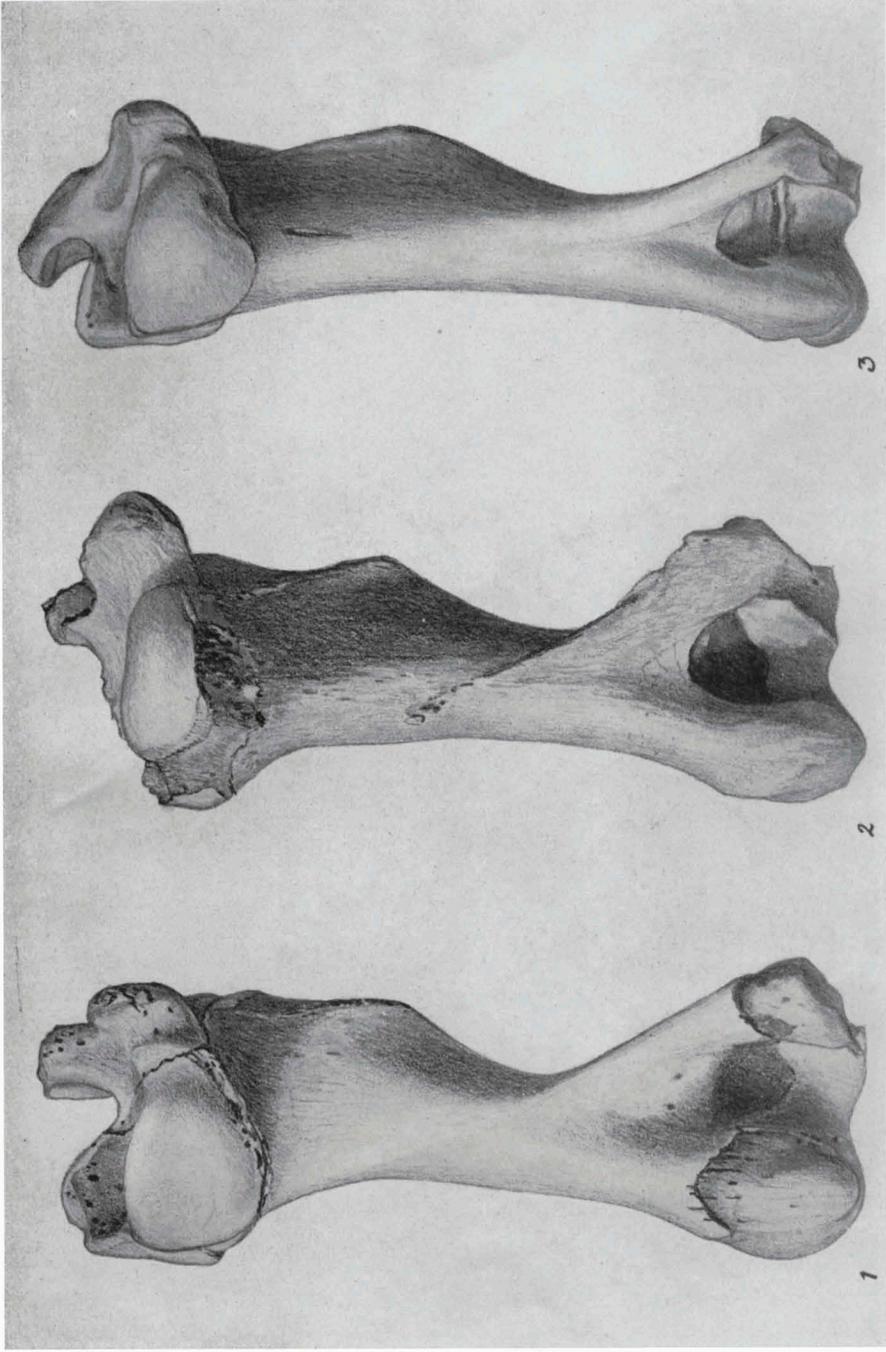


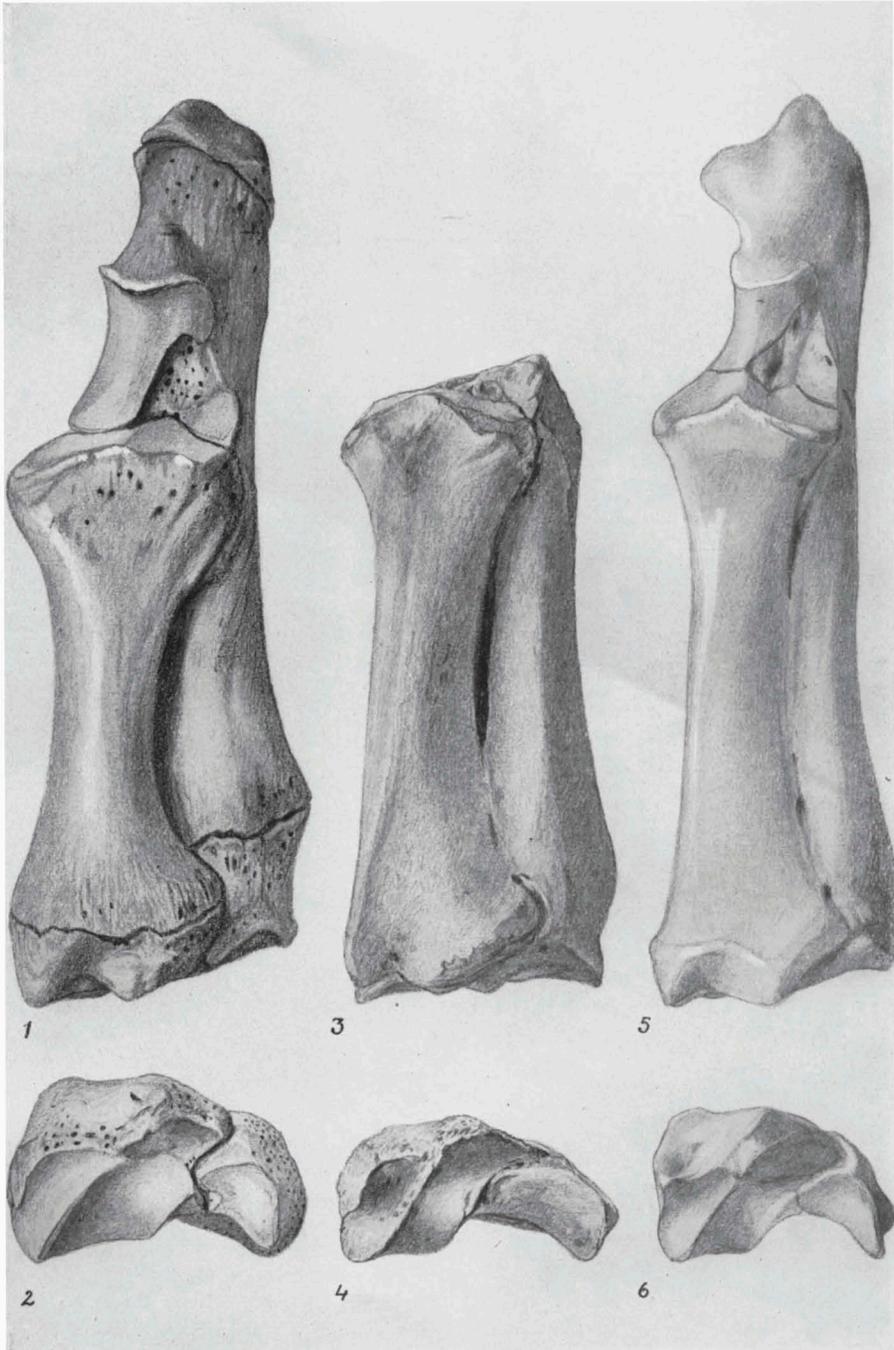
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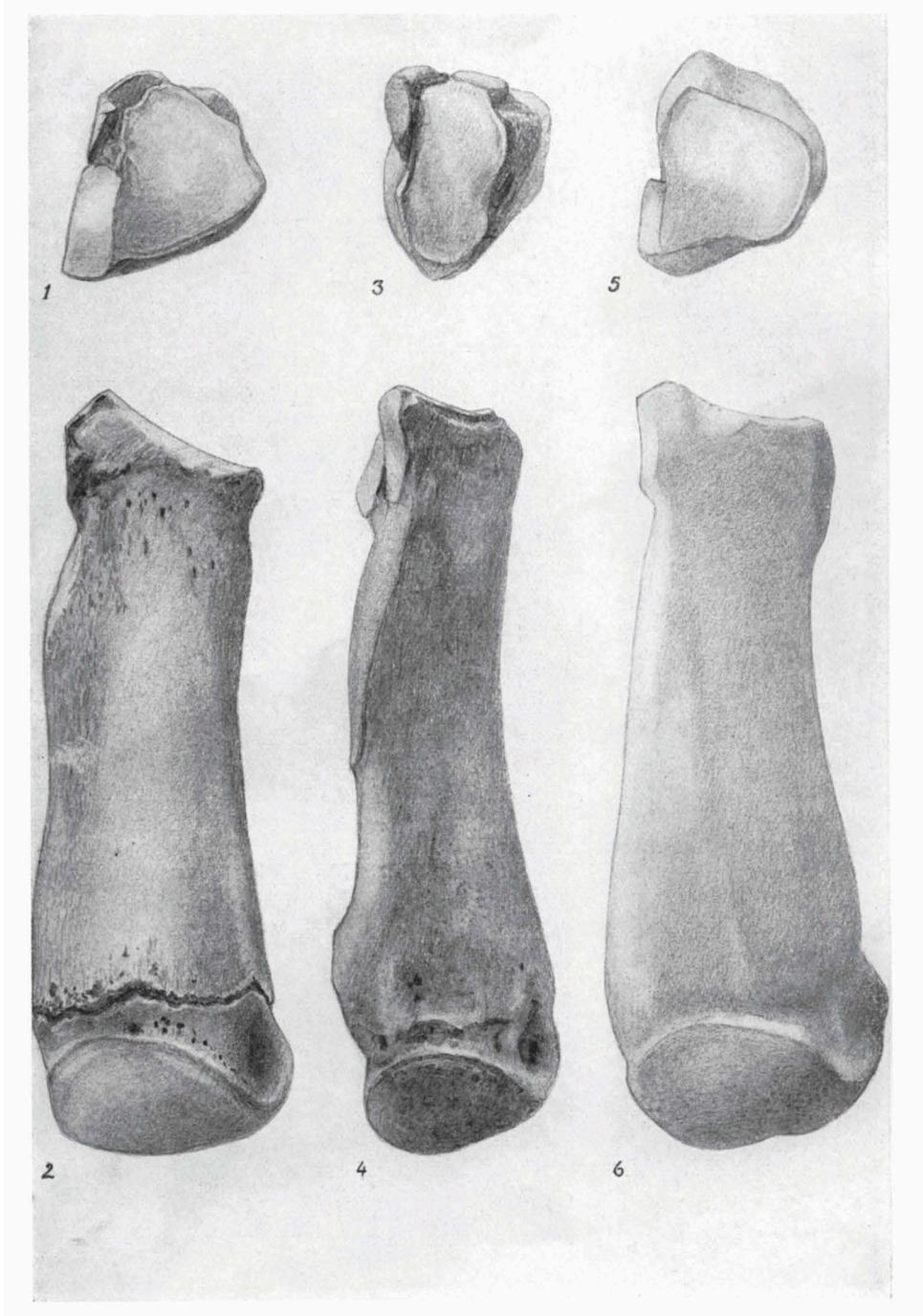


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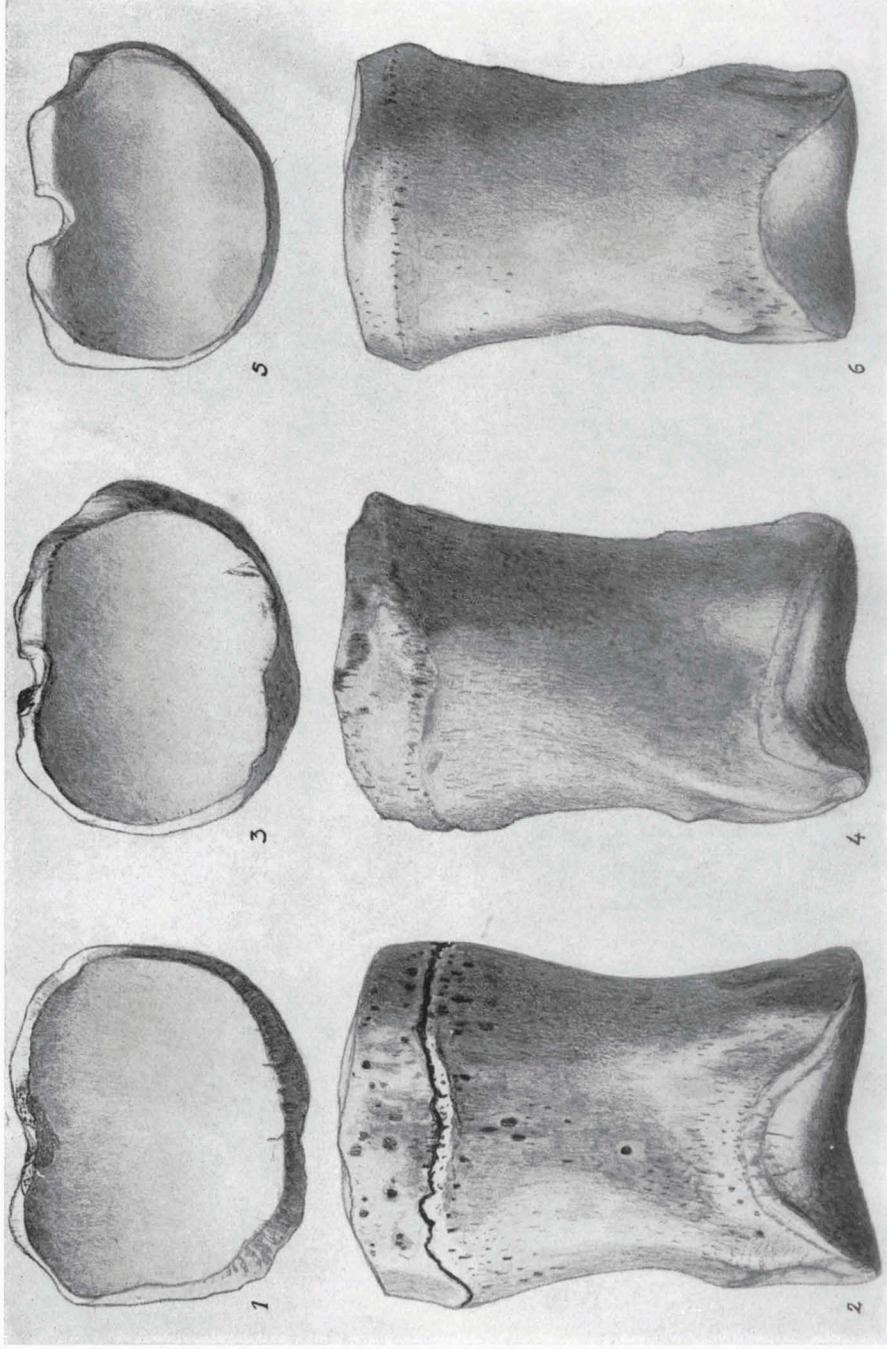


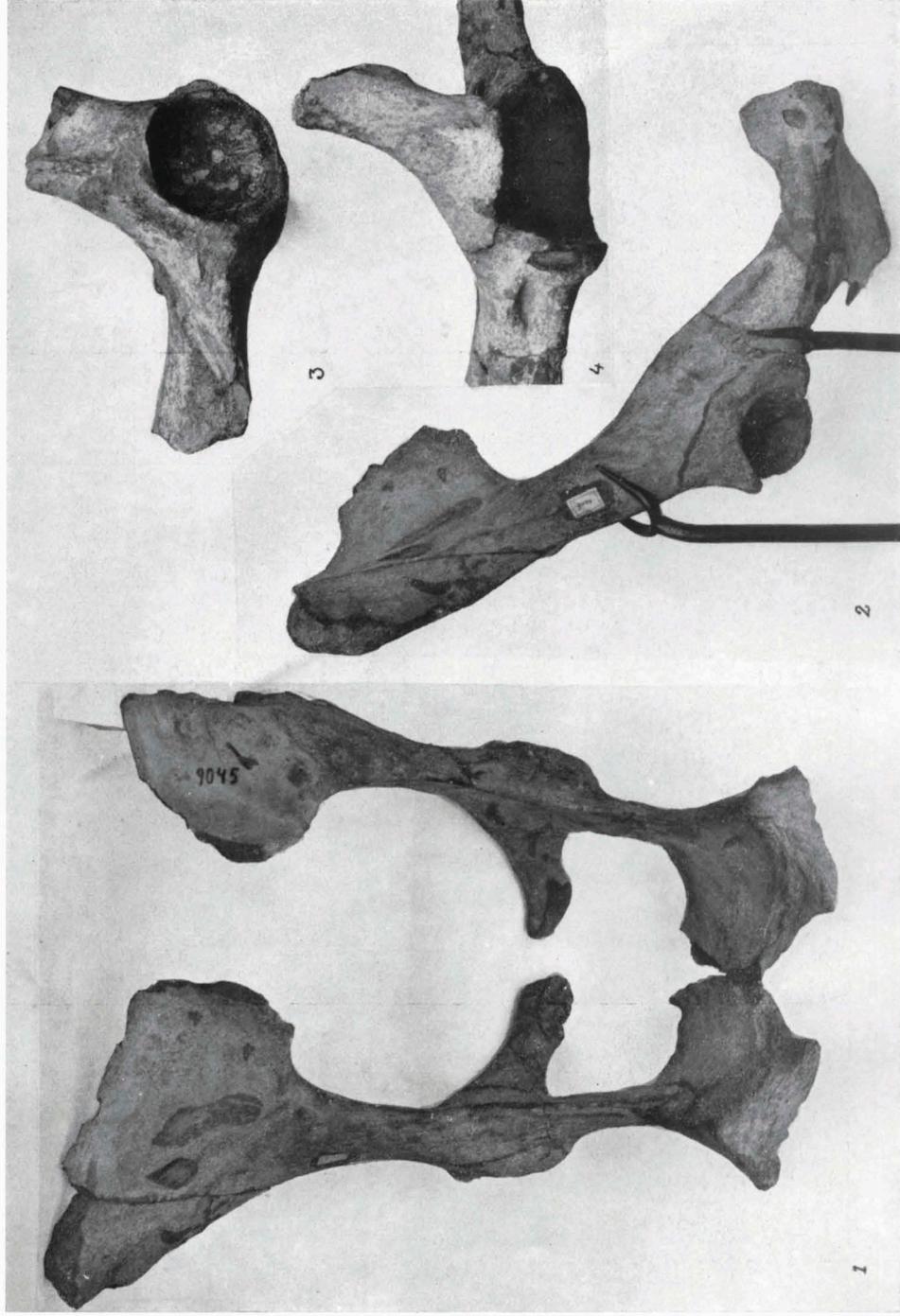


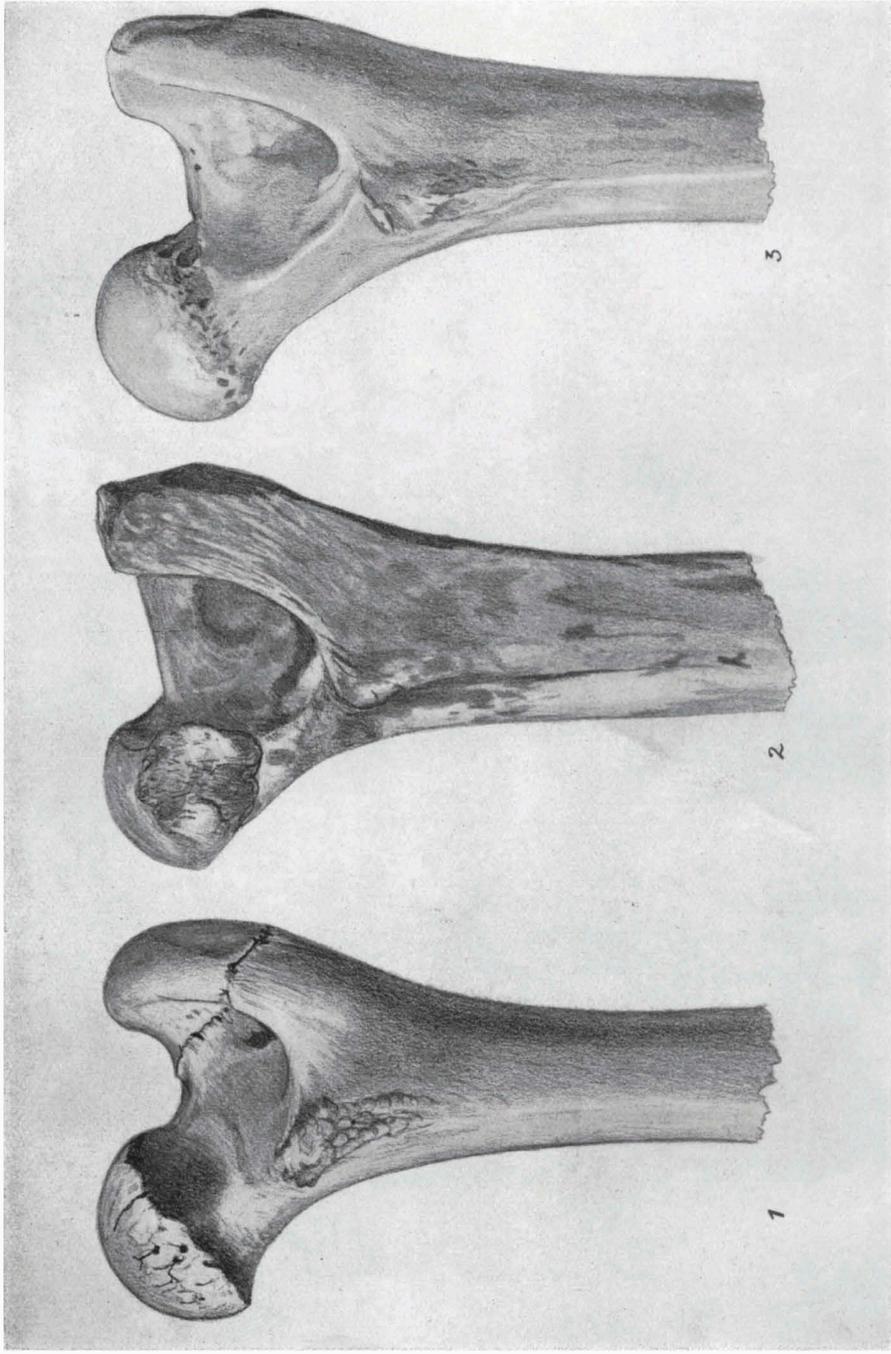
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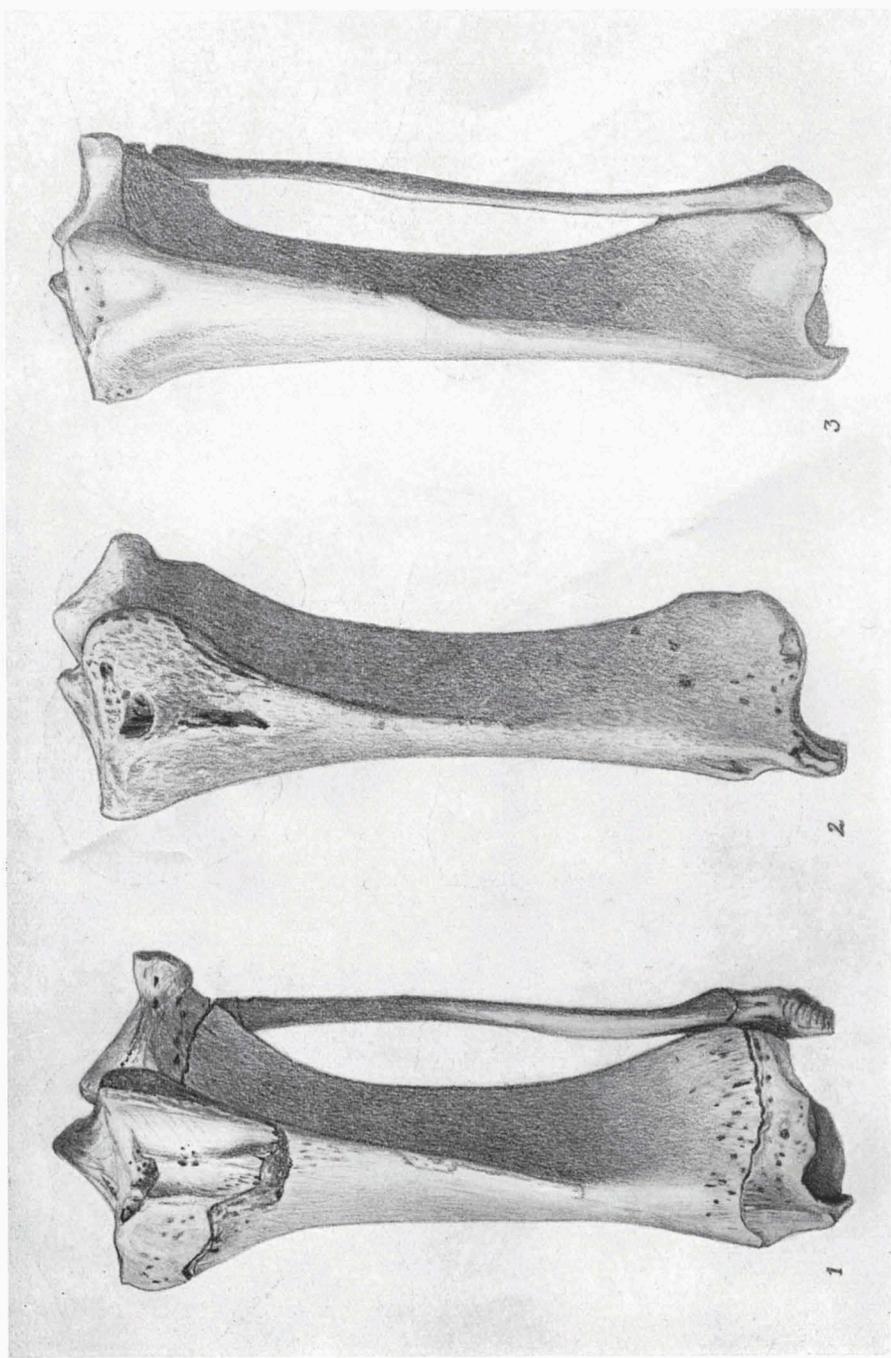


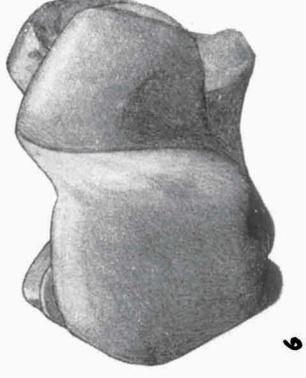
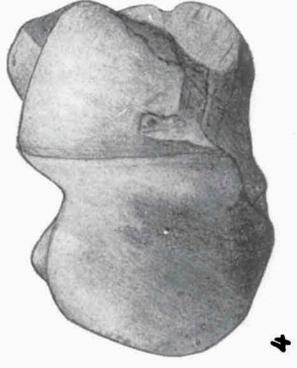
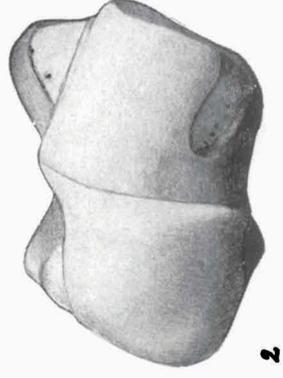
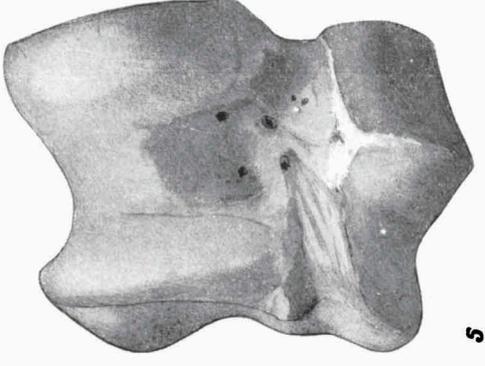
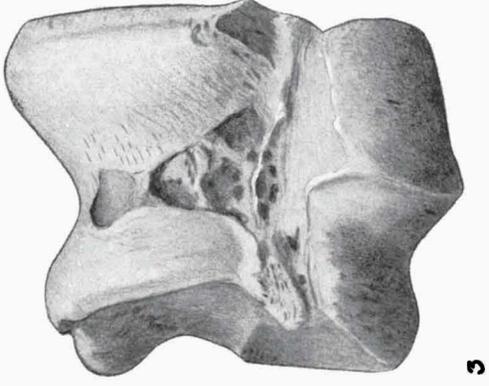
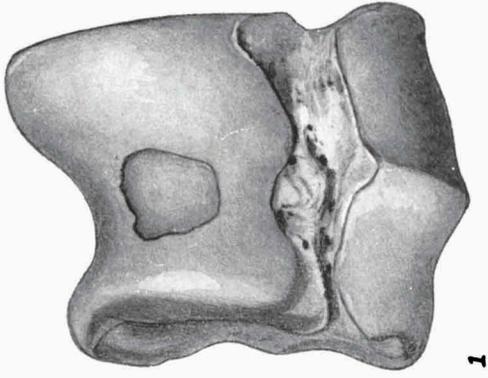
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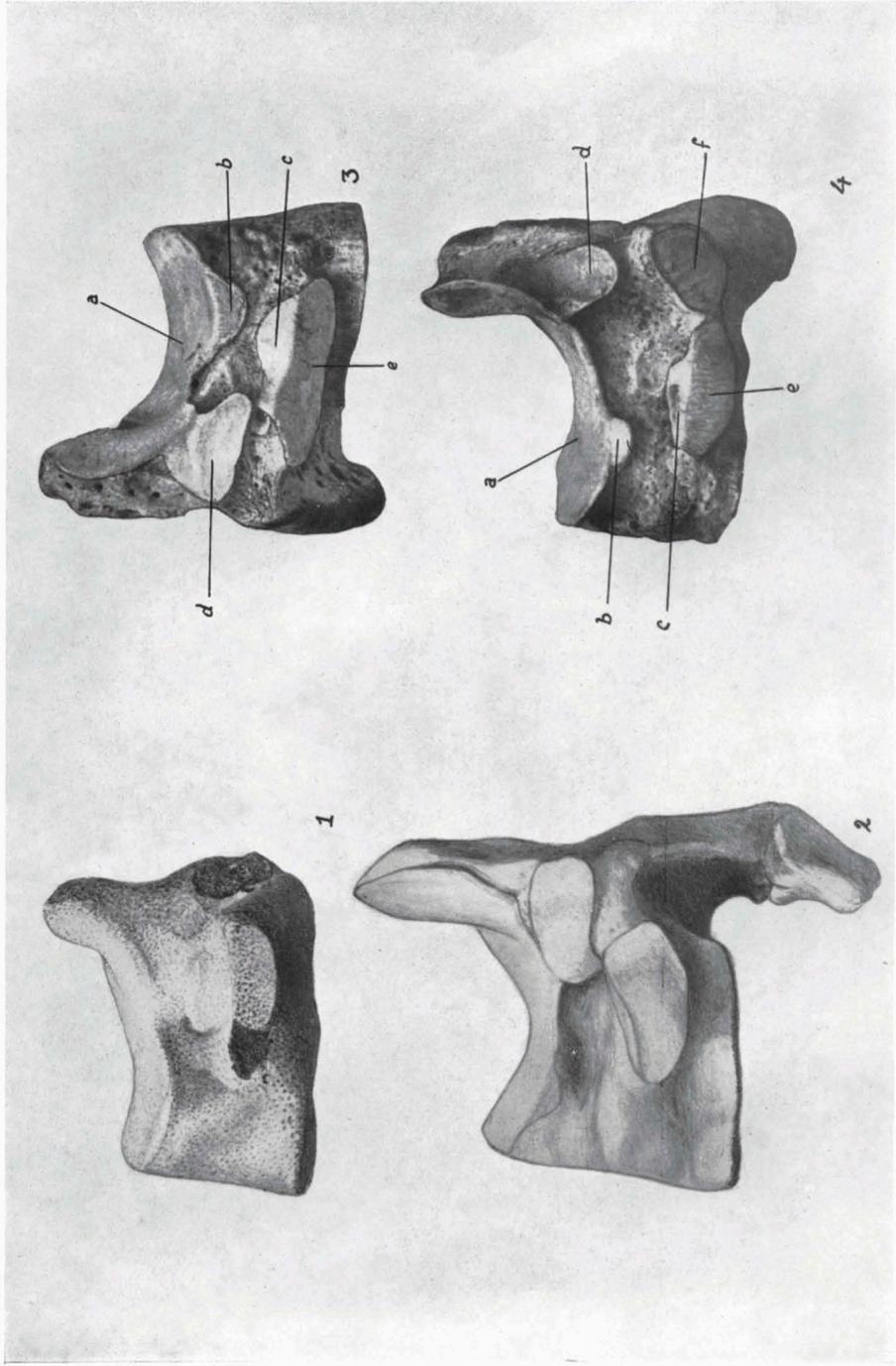


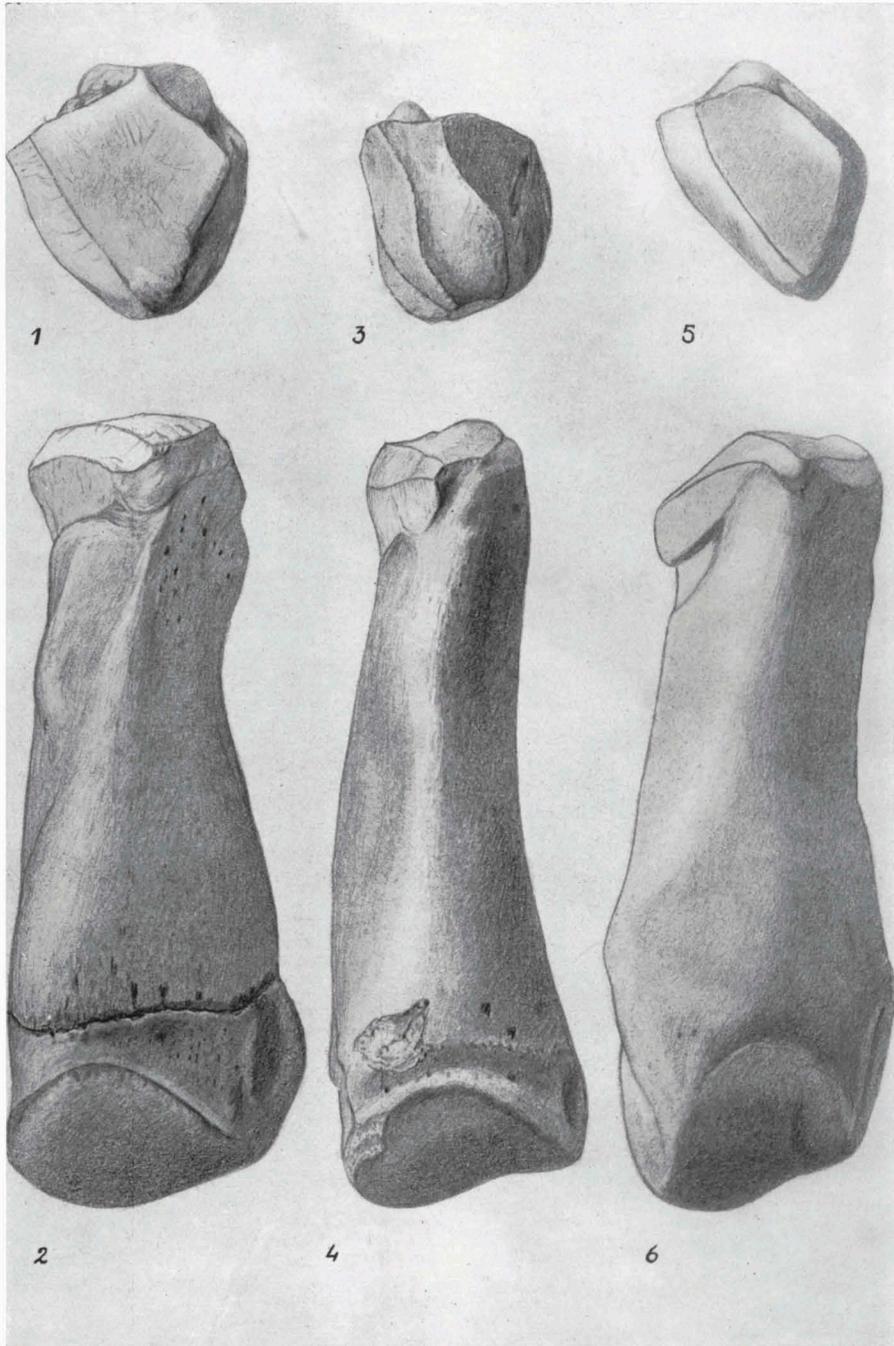






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