

ON THE SUPPOSED HEXAPROTODONT MILK DENTITION IN HIPPOPOTAMUS AMPHIBIUS L.

by

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With Plates VII—X and 2 textfigures

While studying the literature on recent and fossil Hippopotami it became evident to me that a number of authors ascribe a third milk incisor to *Hippopotamus amphibius* L. Consequently this species, as regards the milk dentition, should be "hexaprotodont" like the Pliocene and Pleistocene species of *Hippopotamus* from the Siwaliks of India, Burma and Java; and like *H. pantanellii* Joleaud (1920, p. 18) from Casino near Siena in Italy (vide Pantanelli, 1879, p. 318, pl. IV fig. 5). According to Major (1896, p. 978) young specimens of *H. lemerlei* Grandidier from Madagascar occasionally are hexaprotodont too.

When dealing with *Hippopotamus amphibius* L. Blainville (1847, p. 32) made the following remarks: "Dans le très-jeune âge, il est certain qu'il y a trois paires d'incisives en haut comme en bas, et que ces incisives sont beaucoup plus subégales, dont une paire excessivement petite n'est pas remplacée, la première supérieurement, la troisième inférieurement". But in a note he adds: "Je n'ai réellement vu que celle d'en bas, formant une petite calotte convexe en dedans et en dehors de la seconde; mais je suppose, par analogie, que la première d'en haut était gingivale et n'est pas restée dans la préparation." In the explanation of a figure, showing a very young lower jaw he states: "*H. amphibius* très-jeune; d'origine inconnue montrant les trois incisives." (l.c., p. 103). The figure (l.c., Atlas, pl. VIII lower side at the right) shows the right half of the jaw, in which id_1 , id_2 and cd can be distinctly seen! In the lower jaw with milk dentition, figured by Owen (1840-45, part II, pl. 143 fig. 2) also no third milk incisor is present.

Joleaud (1921, p. 20) remarks: "Sur les mâchoires d'un Hippopotame de 20 jours mort à la ménagerie du Jardin des plantes, I_1 et C pointent net-

tement sous la muqueuse qui recouvre les maxillaires, tandis que I_2 est à peine indiquée. Chez un individu un peu plus âgé, I_1 fait saillie de 5 mm et C de 10 mm; il est nettement indiqué et I_3 apparaît à l'état de trace". Of course with I and C he meant the milk teeth.

Reynolds (1922, p. 11) described a very young mandible in the Museum of the Royal College of Surgeons (no. 1873) and states to have found "an alveolus in which the germ of $\overline{d.i.3}$ can be distinctly seen". The lower jaw is figured (l.c., pl. V fig. 17), the small germ is situated on the medio-posterior side of cd. Previously Flower and Garson (1884, p. 368) stated about this specimen: "The milk-teeth are only appearing above the alveolar margin. The germs of the permanent incisors, canines and first molars have begun to calcify". Reynolds's statement has been copied by Weber (1928, p. 529, p. 546, fig. 368¹) and Van der Maarel (1932, p. 91 footnote²).

Dietrich (1928, p. 22) also mentions small cap-shaped tooth germs in alveoli between id_2 and cd, close to the latter. In his opinion they represent nothing else but the germs of the C, but he gives no proof whatever for this statement.

In order to settle the true nature of these tooth germs I examined a number of foetuses, neonati and young skulls of *Hippopotamus amphibius* L., partially or wholly in possession of the milk dentition. The specimens are in the collections of the Rijksmuseum van Natuurlijke Historie at Leiden, the Zoological Museum at Amsterdam and the Zoological Museum at Utrecht. I am indebted to Prof. Dr. L. F. de Beaufort and Prof. Dr. Chr. P. Raven for the loan of specimens. Röntgenograms of all specimens were kindly taken by Miss Dr. P. Zieren, Leiden. My thanks are due to Dr. L. D. Brongersma, Leiden, for his aid with the preparation of some lower jaws. Some informations I owe to Mr. C. N. van Rijswijk, D. D. S., the Hague. The plates were made by Mr. J. F. Obbes, the text-figures by Mr. M. A. Koekkoek, to both of whom I express my thanks.

The specimens are described according to their age. Some of them show peculiarities which, though not bearing on the question referred to in the title of this paper, are important enough to be mentioned here also.

1. In the lower jaw of a foetus (Leiden Museum, cat. syst. e, reg. no. 1481), length along back line from nose to root of tail 32 cm, the tips of the germs of cd have calcified. The length of the calcified enamel cap is

1) This figure is on ca. $\frac{1}{2}$ nat. size and not "Nat. Gr." as mentioned in the explanation.

2) Their statement, however, that an upper id_3 should occur in *amphibius* too, is not correct. Reynolds (l.c.) is not certain about this; in one specimen only he found "what is apparently the alveolus of d.i.3...".

about 3 mm, of that of the germ of id_1 about 1 mm; id_2 is practically invisible in the röntgenogram.

2. A foetus (Leiden Museum, cat. syst. a, Cape, Van Lidth de Jeude 1886), length along back line 50 cm, shows interesting features (pl. VII fig. 1). The germ of the lower cd has already well developed and measures about 12 mm ¹⁾, the dentine also has begun to calcify. The germs of id_1 and id_2 measure about 7 and 4 mm respectively. Behind them on each side the röntgenogram shows two very small enamel caps, the anterior close to the proximal end of the germ of cd , and the other a few mm behind it. Again 7 mm behind the latter another calcified enamel cap is to be seen, of slightly larger size. When the germs were exposed, it appeared that the two small ones, of which the anterior is slightly more developed than the posterior, are situated on a distinctly higher level than that of the incisors and canini and occur in the dental furrow in the position of pd_1 .

From back to front first the apices of the cusps of the developing pd_4 are visible in the ramus, easily to be identified from their typical arrangement in three pairs behind each other (pl. VII fig. 1). It is interesting to note that from the six but imperfectly calcified cusps of this tooth the antero-external ²⁾ (the protoconid) is much more prominent than the other cusps. According to Osborn (1907, p. 67) this is the oldest cusp. I examined too the germ of the upper pd_4 in this specimen and found the antero-external cusp (the paracone) to be far more calcified and more prominent than the other cusps. This agrees well with the embryological facts observed by Röse, Taeker, Leche and Woodward (vide Gregory, 1916, p. 246). In Gregory's view the paracone (and not the protocone as stated by Osborn) represents the summit of the reptilian upper molar.

The next tooth germ can be identified as representing pd_3 , it possesses one main cusp and a pair of smaller cusps behind the former. Thus it forms a transition between pd_4 and pd_2 , which has only one cusp. In front of the germ of this pd_2 the two small enamel caps occur, referred to above. As appears from the particulars in older jaws the anterior cap cannot be identified as the germ of the C, and therefore we must conclude that a double pd_1 occurs here.

A case of a double pd_1 in *Hippopotamus amphibius* L. has not been described previously. The same anomaly I found again in specimen 9

1) When giving measurements of tooth germs I mean the height of the enamel cap so far calcified and therefore visible in a röntgenogram.

2) In this particular tooth the labial cusp of the second pair. The two cusps in front, though, when fully developed, but little less prominent than the others, have got no special names and arise from the cingulum.

(see pl. X). (In a skull of the recent pigmy hippo, *Hippopotamus liberiensis* Morton (Leiden Museum, cat. ost. b, Büttikofer and Stämpfli 1887) I found a double pd_1 to occur in the right maxillary). The pd_1 , which has no successional tooth in the permanent dentition¹⁾, is very variable in the dentition of recent Hippopotami. Usually it has one root, somewhat constricted in the middle, but two roots may occur, e.g., in the upper jaw of specimens 7, 8 and 9. The variability of this tooth indicates that it is about to disappear. Specimen 5 will illustrate this (see pl. VII fig. 2).

As regards the incisors of specimen 2, in the dental furrow no tooth germ could be traced between id_2 and cd .

3. Next I examined the skull of a ♀ neonatus (Amsterdam Museum, no. 308), born in the Zoological Garden at Amsterdam July 24th 1862. The calvarium has been figured by Weber (1904, p. 57 fig. 45, p. 58 fig. 46; 1927, p. 76 fig. 55, p. 77 fig. 56). In the lower jaw id_2 is just appearing above the alveolar margin; cd projects about 12 mm and id_1 9 mm. A small alveolus occurs at the medio-posterior side of cd . This in all probability contained a tooth germ which has been lost in the dried skull. The premolars have not yet erupted; the enamel cappings of the cusps of pd_3 and pd_4 have almost wholly calcified and are united at their base. The four main cusps of pd_4 do not differ greatly in size.

4. Another dried neonatus-skull in the Zoological Museum at Utrecht agrees in all important features with the preceding Amsterdam specimen.

5. The lower jaw prepared from a ♀ neonatus that lived in the Amsterdam Zoological Garden August 18th-22nd 1920 shows an alveolus at the medio-posterior side of cd , containing a tooth germ (pl. VII fig. 2). Only the capping of 0.2 mm thickness has calcified. In the left ramus there is no pd_1 , neither as calcified structure nor simply as enamel organ. Of the right pd_1 the enamel cap has almost entirely calcified; it is impossible to overlook this tooth, which moreover has not yet erupted. In this specimen

1) This was Cuvier's opinion as early as 1821, and many later authors have adopted the same view. The pd_1 often is still present when M_2 has already erupted; in the upper jaw this tooth subsists longer than in the lower. Its alveolus gradually becomes shallower and directed anteriorly instead of vertically. Dietrich (1928, p. 23) believes that the development of the huge C obstructs that of P_1 in the lower jaw, and the same should be true as to the upper jaw. In lower jaws of *Hippopotamus amphibius* L. indeed I never found an alveolus or a tooth in the position of the anterior premolar with dimensions not fitting into the milk dentition. In the upper jaw, however, P_1 seems to develop in very exceptional cases. In the left maxillary of a specimen in the Amsterdam Museum (no. 518), in which M_2 is in use, anteriorly to P_2 a single alveolus occurs with a depth of not less than 45 mm! The tooth is unfortunately lost. In all other respects this skull is quite normal.

we have thus another striking example of the great variability of the pd_1 .

6. In the lower jaw from a ♂ neonatus that lived in the Zoological Garden at Amsterdam May 12th-20th 1939 at the medio-posterior side of cd also a calcified cap was found, somewhat larger than in the foregoing specimen.

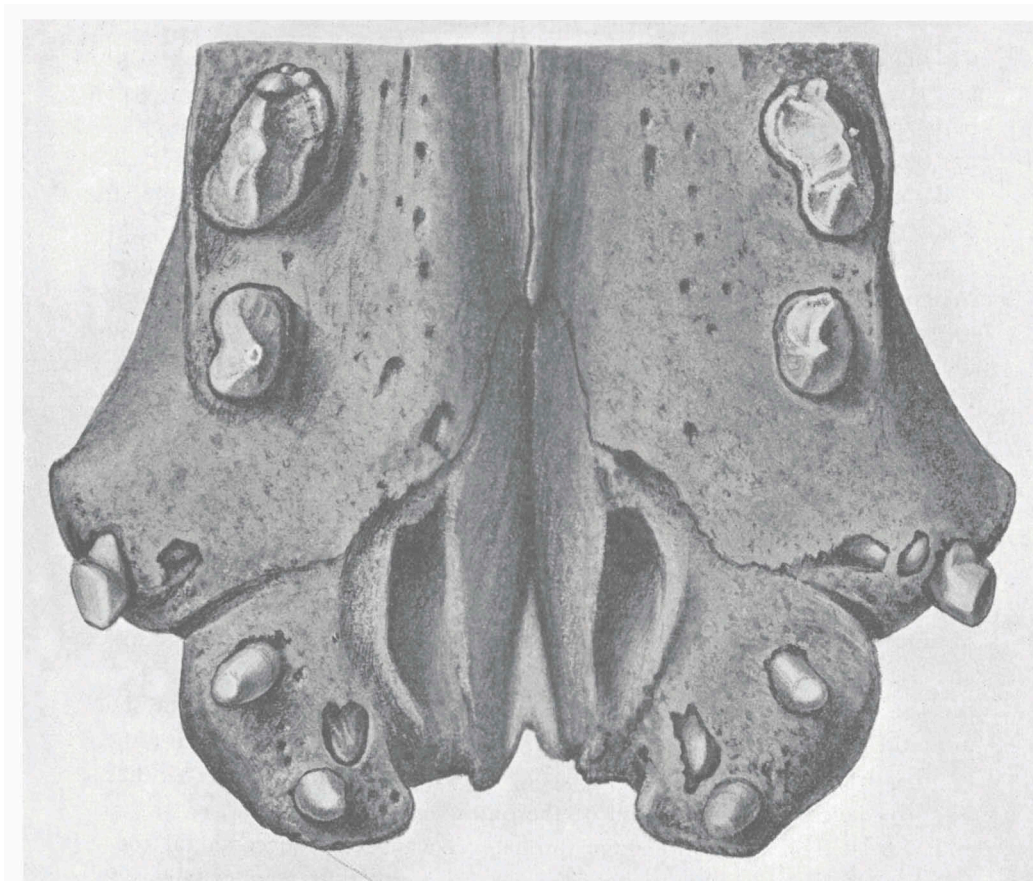


Fig. 1. *Hippopotamus amphibius* L. Frontal part of upper jaw of specimen 7, viewed from below. The tips of I_1 and C are seen at the lingual side of their predecessors.
Nat. size.

The other teeth call for no special comment; the premolars have not yet developed their roots.

7. A young ♂ skull with pd_4 erupting (Leiden Museum, reg. no. 1658) is in possession of the whole milk dentition (pl. VIII). The incisors and canini are worn. At the medio-posterior side of the lower cd , as in both foregoing specimens, an enamel cap is visible. From the röntgenogram it

became evident that this is the extremity of the germ of the lower C. It is more developed than that of I_1 , also buried up in the jaw: the former measures 60 mm, the latter 35 mm, the breadth at base of both calcified enamel caps is about 21 mm. The germ of I_2 is not yet visible in the röntgenogram.

When we look at the upper jaw of this specimen (text-fig. 1) we see at the lingual side of id_1 and cd the unworn extremities of the germs of I_1 and C. There is nothing peculiar in this arrangement, the permanent teeth being typically developed on the inner side of their milk predecessors and not below them.

8. In a young skull with pd_4 fully in place (Amsterdam Museum, no data) the lower cd have been shed and C appears above the alveolar margin (pl. IX). The alveolus is much larger than that in the preceding specimen. When we compare specimens 7 and 8 we see the future alveolar border already marked in specimen 7 by a groove in the bone around cd , enclosing the spot in which the extremity of C is visible. So it becomes apparent that when cd is shed the surrounding bone is suppressed and C erupts, possibly slightly behind its predecessor; the same occurs in connection with id_1 (of which the right has already been shed): the tip of I_1 is seen at the lingual side of its predecessor. In the upper jaw of this specimen C has also cut the jaw, the milk canine and its successor are present side by side.

The lower C, projecting about 10 mm, measures about 120 mm and I_1 75 mm. The germ of I_2 is also visible in the röntgenogram and measures 12 mm. The development of this incisor is retarded in comparison to C and I_1 . Sigel (1883, p. 11) records that the lower cd and id_1 are shed at the age of about $1\frac{1}{6}$ year and $1\frac{1}{3}$ year respectively. The id_2 is not shed until the age of $2\frac{1}{2}$ year (Sigel, 1884, p. 35). A lower jaw was described and figured by me (Hooijer, 1941), in which the left id_1 must have been displaced behind the level of the outer incisors as a result of trauma and subsisted in the adult stage, probably because the successional tooth became devitalised. The right lower I_1 did erupt, but also considerably behind the level of the outer incisors, which are larger than normally. This ascertained endostomatic situation of a part of the milk dentition, not to be explained by some disease or a narrowing of the jaw, I believe to be a condition unique among Mammals, except in Man (l.c., p. 1148).

The incisors of specimen 8 are larger than those of specimen 7, the latter, however, is a ♂ skull, the sex of specimen 8 is unknown. In both specimens id_2 is slightly larger than id_1 , this peculiarity is also stated by Stromer (1914, p. 9) and Dietrich (1928, p. 22).

9. Finally I examined a skull (Zoological Museum Utrecht, no data) with

M_1 protruding (pl. X). The lower I_1 projects about 25 mm, I_2 has not yet erupted. In this skull the upper right pd_1 has two roots. In the lower jaw, on both sides in the position of pd_1 two small malformed conical teeth occur, each of them placed in a separate alveolus. The alveoli on each side are closely approximated like those for the anterior and posterior root of one and the same tooth. The teeth are provided with enamel cappings, which are partly worn off. In the upper left maxillary also a double pd_1 occurs of which the anterior, however, is lost.

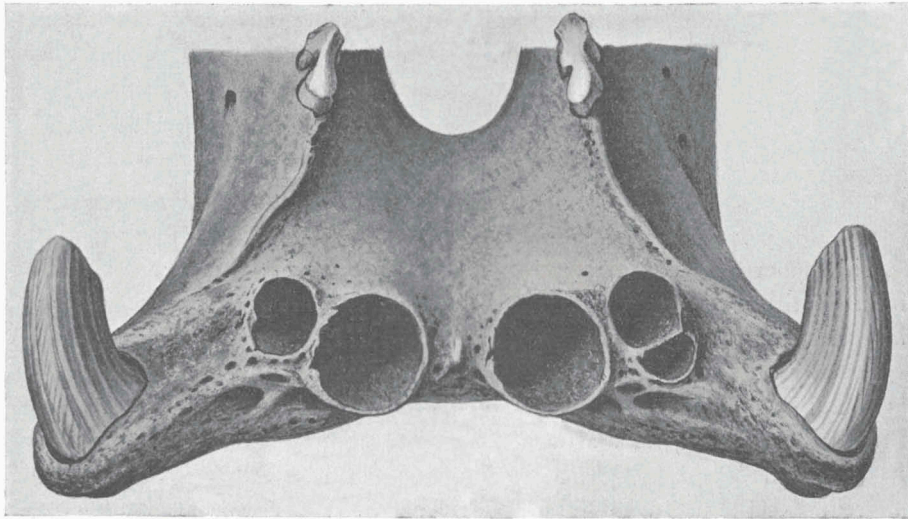


Fig. 2. *Hippopotamus amphibius* L. (Leiden Museum, cat. ost. d, adult ♀). Frontal part of the mandible showing a supernumerary alveolus at the left side, close to that of I_2 . About $\frac{1}{3}$ nat. size.

It is evident that the tooth germ invariably situated medio-posteriorly of the lower cd , shown in specimens 5 (pl. VII fig. 2), 6, and 7 (pl. VIII), which Blainville, Joleaud, Reynolds and with them Weber and Van der Maarel, regarded as the missing lower incisor, in reality constitutes the germ of the C, which is the first developing tooth in the second dentition. I agree with Dietrich in this respect, but I cannot see, however, why he states that "schon lange" supernumerary I, on either side of both upper and lower jaw or only at one side, are known in "*H. amphibius recens*" (Dietrich, 1928, p. 24). Certainly supernumerary incisors are known to develop occasionally in the permanent dentition of *Hippopotamus amphibius* L., but only at one side and only in the lower jaw. Falconer (1868, p. 406 footnote) was the first to mention this interesting anomaly. He described

a small malformed incisor, occurring in the right half of a lower jaw between I_2 and C and projecting about an inch. Gaudry (1876, p. 504) states that he saw "dans le Musée de Paris une mâchoire d'Hippopotame où les incisives sont à droite en même nombre que chez les *Hexaprotodon*, et à gauche en même nombre que chez les *Tetraprotodon*". In all probability Harger (1932, non vidi) mentioned the same anomaly.

A new case of this unilateral hexaprotodontism I found in the collection of the Rijksmuseum van Natuurlijke Historie at Leiden (text-fig. 2). In cat. ost. d, a fully adult ♀ skull from S. Africa, in the left lower jaw between I_2 and C, close to the alveolus of the former, an alveolus is present. The measurements of this supernumerary alveolus indicate an incisor, much larger than a milk incisor. The measurements are as follows (mm):

alveolus of	diameter	depth
I_1	41	125
I_2	28	75
I_3	19	58

This supernumerary incisor in all probability had no predecessor in the milk dentition, for in human dentition a similar tooth is but very rarely known to be preceded by a milk element.

Exactly the same arrangement of the lower incisors in the left lower jaw is found in an adult ♂ skull of *Hippopotamus liberiensis* Morton (Leiden Museum, cat. ost. a, Büttikofer and Stämpfli 1887). In this species normally only I_1 develops in the lower jaw, though the presence of an I_2 is not a great exception. In this skull, however, there are two supernumerary incisors at one side; they do not differ much in size (mm):

	diameter	depth of alveolus
I_1	15	70
I_2	vert. 8, hor. 9	38
I_3	vert. 8, hor. 7	36

At the right side, as usual, only I_1 is developed. This case has already been mentioned by Jentink (1888, p. 31).

In all upper jaws of *Hippopotamus amphibius* L. examined by me no third incisor could be traced. Jentink (1888, p. 31/32) states that cat. ost. b shows "in each ramus (sic) of the upper jaw two well developed incisors and an alveolus for a third incisor, which however is lost". In the upper jaw of *Hippopotamus amphibius* L., at the inner side of I_1 always narrow channels are present, in the living animal containing nerves or bloodvessels. In cat. ost. b these openings indeed are somewhat larger than normally, but by no means they represent alveoli!

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EXPLANATION OF THE PLATES

PLATE VII

Fig. 1. *Hippopotamus amphibius* L. Mandible of specimen 2, in which the tooth germs are partly exposed. Note the presence of a double pd_1 in both rami. The outer of the second pair of cusps (protoconid) of pd_4 is the most prominent. Nat. size.

Fig. 2. *Hippopotamus amphibius* L. Mandible of specimen 5. In the left ramus the bone has partly been removed to show the tooth germs. At the medio-posterior side of the right cd the germ of C is already visible. The corresponding left germ has been removed for further examination. Note the absence of a left pd_1 . About $\frac{2}{3}$ nat. size.

PLATE VIII

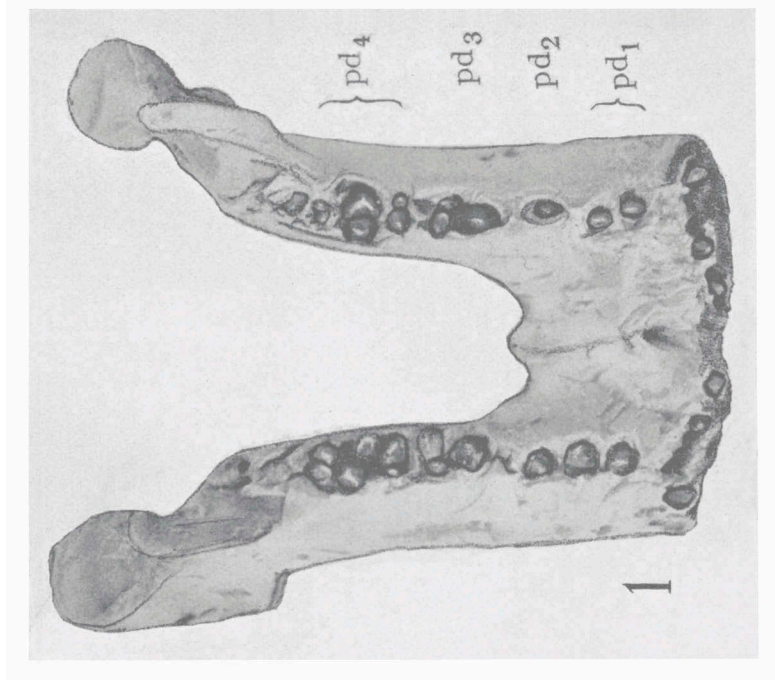
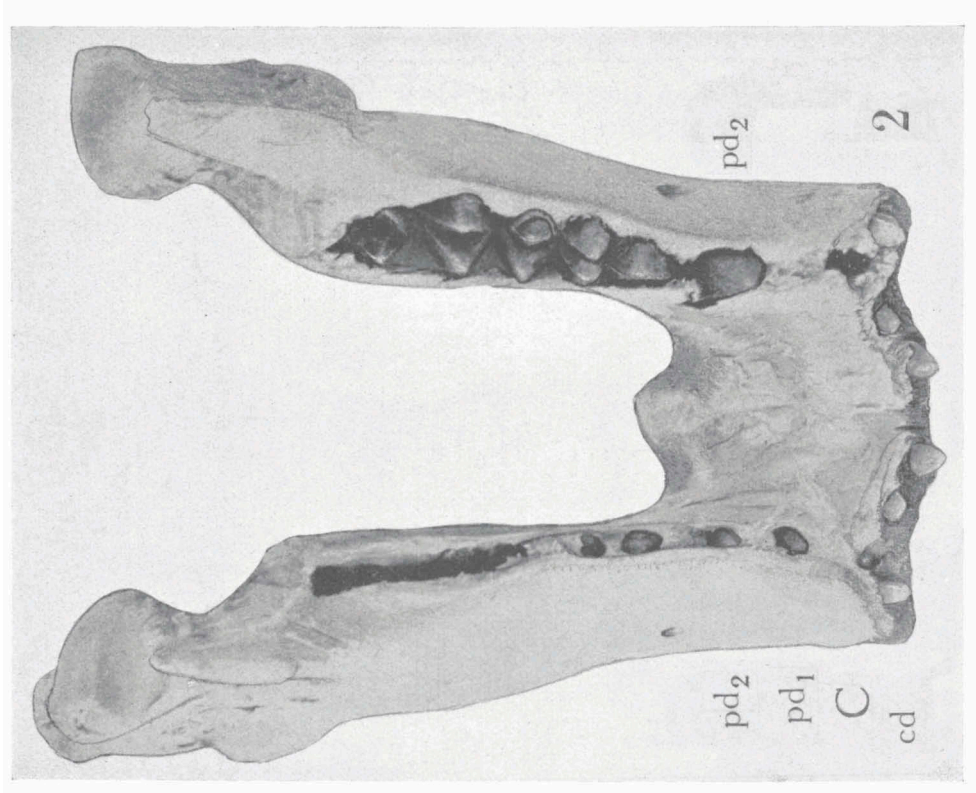
Hippopotamus amphibius L. Mandible of specimen 7 with complete milk dentition. The unworn extremity of C is seen at the medio-posterior side of cd . About $\frac{2}{3}$ nat. size.

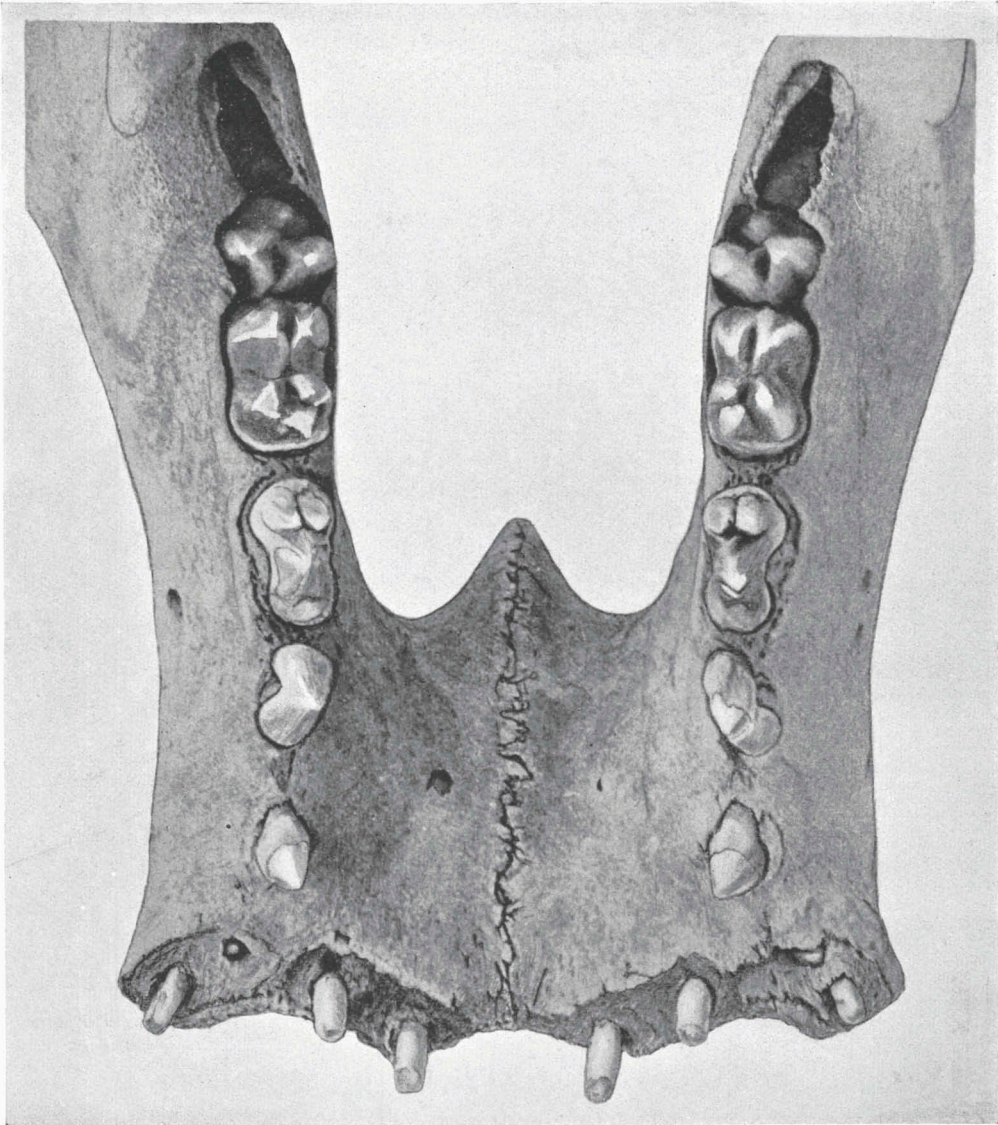
PLATE IX

Hippopotamus amphibius L. Mandible of specimen 8. Milk dentition in a stage slightly in advance of that shown on pl. VIII; the right and left cd and the right id_1 have been shed, the alveoli are enlarged. About $\frac{5}{7}$ nat. size.

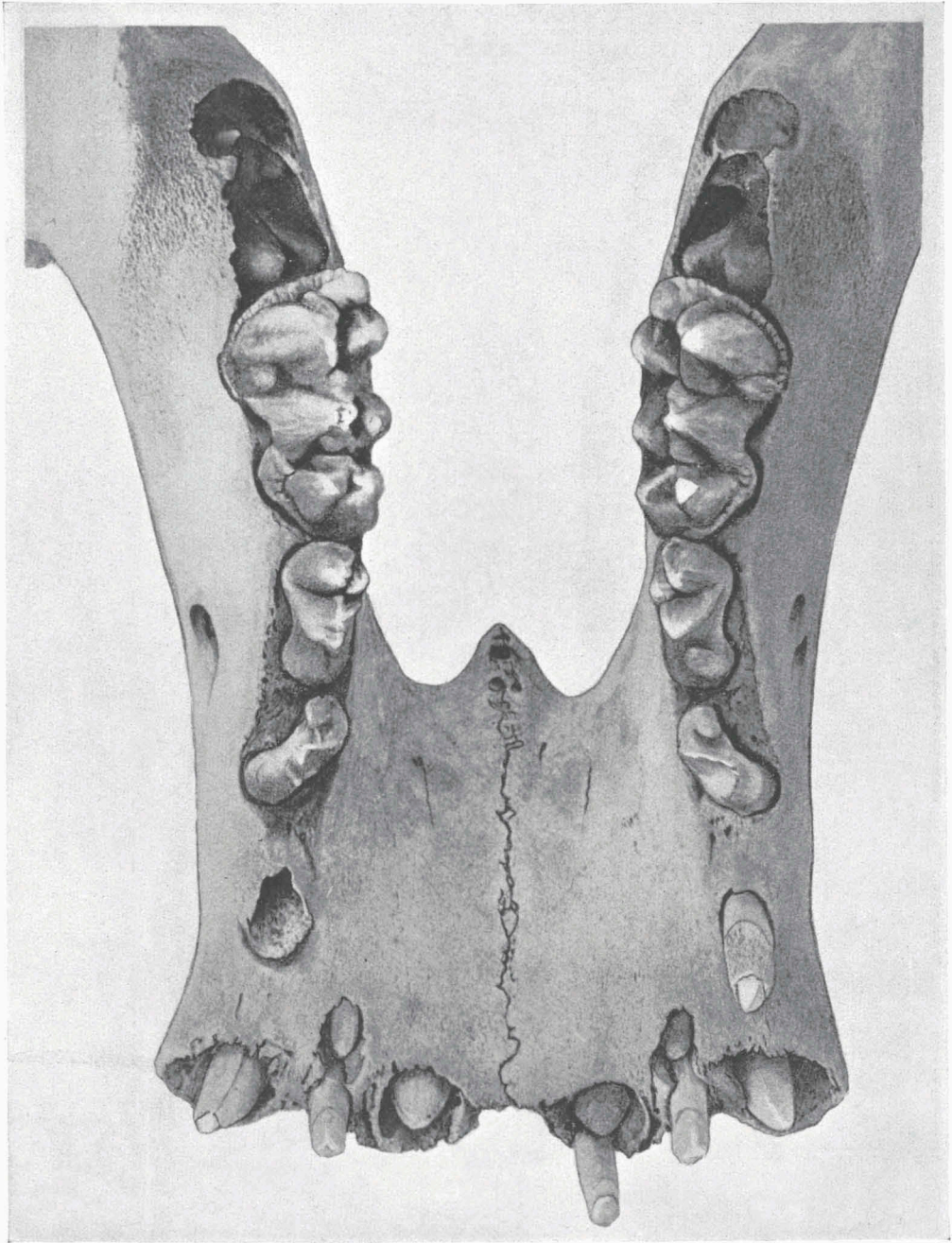
PLATE X

Hippopotamus amphibius L. Mandible of specimen 9. Two malformed conical teeth occur in the position of pd_1 . About $\frac{1}{2}$ nat. size.

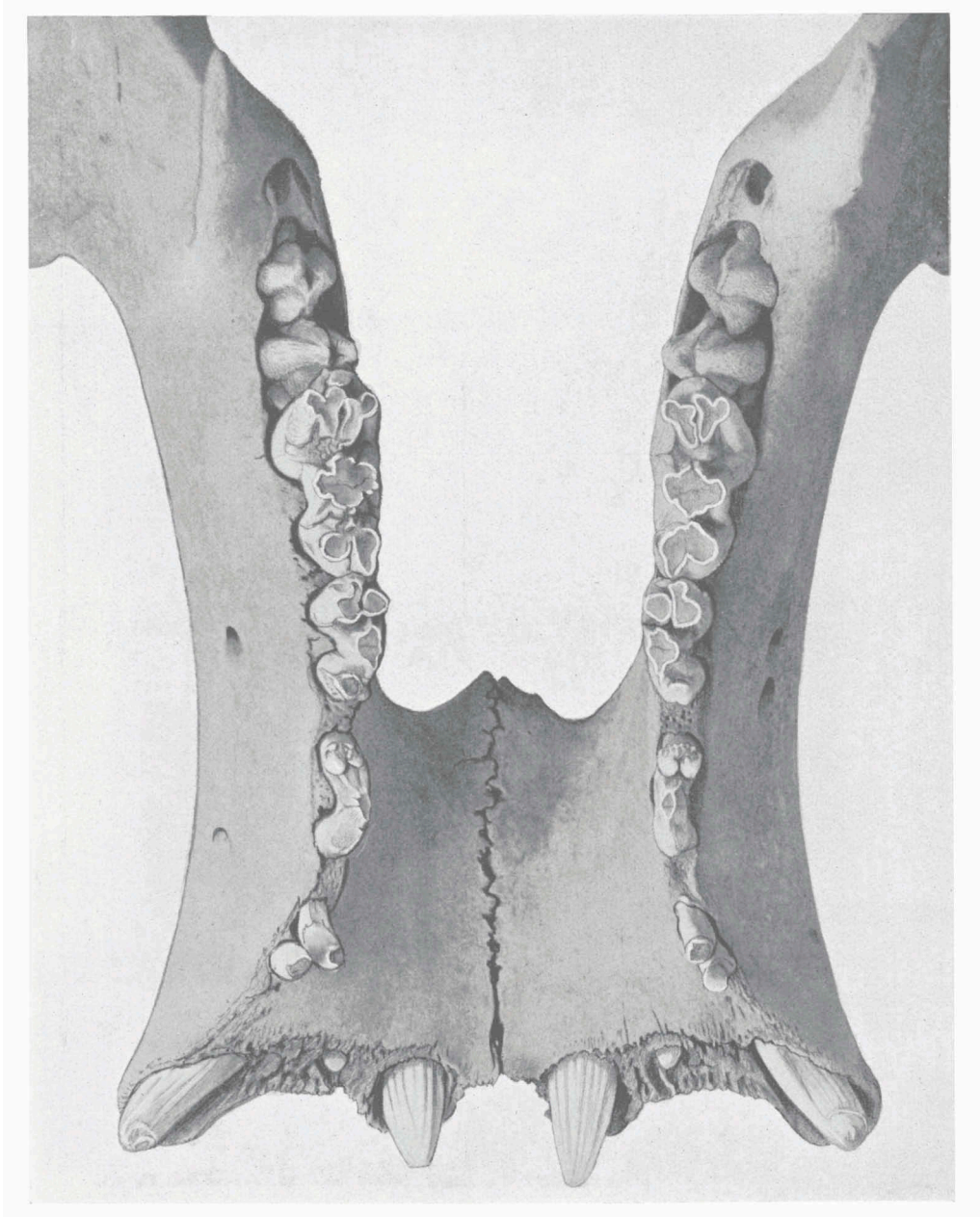




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