

On the bi-rooted upper first premolar in some specimens of the Madagascan Holocene Hippopotamidae

SOLWEIG STUENES

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Two double-rooted upper first premolars found in the Madagascan collection of hippopotami in the Palaeontological Museum, Uppsala, are described. Doubt is raised about the value of the double-rooted first premolar as a diagnostic generic character.

Solweig Stuenes, Paleontologiska institutionen. Uppsala universitet. Box 558, S-751 22 Uppsala. Sweden. 29th August, 1980.

Introduction

The family Hippopotamidae is entirely confined to the Old World, where it first appeared towards the end of the Tertiary Period. Today, the family contains two monospecific genera, living in Africa, south of the Sahara. Fossil hippopotami have been found in Africa (including Madagascar), Asia and Europe.

In the Palaeontological Museum, Uppsala University (abbreviated to UM), there is a collection of Holocene subfossil Hippopotamidae from Madagascar. These fossils were collected by Bertil Ljungqvist and brought to Sweden in 1929. The collection consists of nine well preserved calvaria and the same number of mandibles, several parts of the postcranial skeleton, and isolated teeth. This, hitherto undescribed, collection seems to consist of two taxa. The Madagascan hippopotami have generally been treated as one taxon, currently referred to *Hippopotamus madagascariensis* or *Hippopotamus lemerlei*. My revision of the taxonomic status of the material has not yet been completed.

In the present paper, I deal with the double-rooted condition of the upper first premolar in Madagascan hippopotami, a feature not earlier reported in the genus *Hippopotamus*.

Description

The dentition in Hippopotamidae is remarkably conservative throughout their known history. Early forms of the family have a complete dentition, namely, $\frac{3\ 1\ 4\ 3}{3\ 1\ 4\ 3}$. In more advanced forms, the num-

ber of incisors tend to be reduced and the first premolars lost. In adults of the living species, the first milk molars are often retained as persistent deciduous elements in the permanent dentition.

In connexion with my studies on the collection of hippopotami at Uppsala, I found that four of the calvaria constitute a separate morphologic group. In two of these specimens, there are double-rooted upper first premolars. In one of the calvaria, no. M 3963, the left P¹ is in situ (Plate 1, B; Fig. 1). In the second calvarium no. M 3962, the first premolars are lost, but there are distinct alveoles of double-rooted teeth (Plate 1, A). Among the isolated teeth in the collection, there is an upper double-rooted first premolar, that probably belongs to the calvarium no. M 3962, because it fits well into the alveole of the left first premolar (Fig. 2).

The fixed P¹ has, like the isolated P¹, one cusp. The two roots in the isolated P¹ are of subequal size and the same appears to be the case in the fixed P¹. The cingulum is feebly developed, except on the palatinal side of the isolated P¹, where there is a small cingulum; on the buccal side of the same tooth, there is a pattern in the enamel suggesting a possible continuation of the cingulum. In the fixed tooth, the cingulum can be made out only in the middle of the palatinal side. The two premolars have a somewhat different appearance, especially on the palatinal side, where the fixed P¹ has a great many enamel nodules spread over the surface, while the nodules are fewer and smaller in the isolated P¹. Mesially, in the both teeth, the nodules are situated above each other, forming a vertical ridge. Distally, the nodules form a more or less

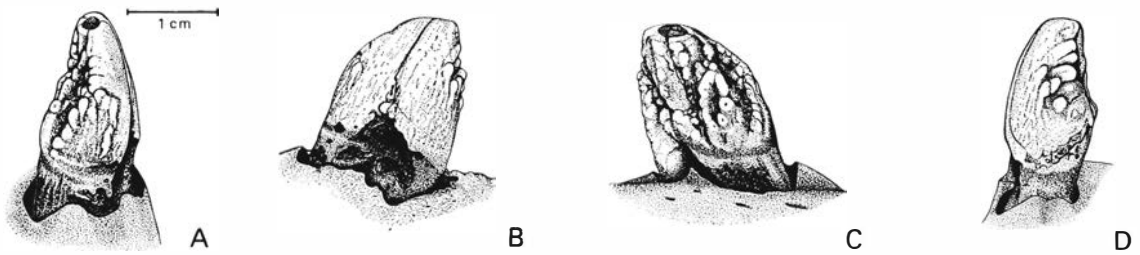


Fig. 1. The upper first premolar in the calvarium UM no. M 3963.
A. Distal view. B. Buccal view. C. Palatinal view. D. Mesial view.

triangular pattern. On the buccal side of the two teeth, at about the same position in each tooth, there is damage, which appears to have been caused by dissolution of the dentine. The wear-facets are oval, in the isolated P¹ 3,5 mm and in the fixed P² 2,8 mm, at their greatest diameter.

It is difficult to make comparisons between P¹ in different species of hippopotami, in cases where very few have been figured. Coryndon (1978) figured two specimens from Kenya, each represented by an isolated premolar (Fig. 3). The first upper premolar (KNM-Lu 014) from the Lukeino Formation appears to have a large wear-facet, different in size from those seen in the two Uppsala specimens. The other P¹ (KNM-Bc 631) figured is from the Chemeron Formation; it has a small, apparently round, wear-facet; the crown has ridges running vertically over the surface.

In the two Uppsala specimens, the P¹ is the least worn tooth in the premolar row.

In the Palaeontological Museum in Oslo (abbreviated to OM), there is a third Madagascan calvarium, no. A 31931, with alveoles of double-rooted first premolars (Plate 1, C and D). (The calvarium is not the same as Guldberg described in 1883.)

I have not seen the lower first premolars in my Madagascan specimens, but judging from the not quite obliterated alveoles, they seem to have been single-rooted. The specimen kept in Oslo agrees in this respect with my specimens. However, in one of the specimens kept in the Laboratoire d'Anatomie Comparée in Paris, one mandible (no. 1937—50) has alveoles of double-rooted first premolars.

Discussion

Linné knew only of the large African hippopotamus, which he named *Hippopotamus amphibius*

(1758). In 1836, Falconer and Cautley established the subgeneric name *Hexaprotodon* for *Hippopotamus (Hexaprotodon) sivalensis*, the large Pleistocene hippopotamus of the Upper Siwalik Beds in India. The subgeneric name refers to the fact that this hippopotamus has six incisors in each jaw. However, later studies have shown that this character is variable and has therefore limited taxonomic value. Falconer and Cautley also observed the large upper first premolars, which later proved to be double-rooted. Colbert (1935) elevated *Hexaprotodon* to generic level. The bi-rooted condition of the first premolar has been assigned a high taxonomic value in the classification of the Hippopotamidae, that is, its presence is taken to be a clear indication of a representative of the genus *Hexaprotodon*. However, there are several African species of that genus which have single-rooted first premolars, if they are present at all. Before the discoveries of fossil hippopotami in East Africa over the last few decades, the double-rooted P¹ was one of the characters, that was said to distinguish the Asiatic hexaprotodons from the African ones (Coryndon 1973).

Coryndon (1977a) suggested that all living and fossil hippopotami should be placed in the two genera, *Hippopotamus* and *Hexaprotodon*.

It was not until 1976, that the double-rooted first premolars were reported from Africa (Coryndon 1976). In the oldest hippopotamus remains, found in the Ngorora Formation, Kenya, dated to be between nine and twelve million years, no premolars have been found. The oldest known lower and upper first premolars, which both have double-roots, have been collected from the Kenyan Lukeino Formation which has been dated at six and a half million years.

In 1977, Coryndon published a description of *Hexaprotodon bavardi*, from Lothagam Hill on the west side of Lake Turkana in Kenya (Coryndon 1977b). This is so far, the earliest hippopotamus cranial material complete enough for de-

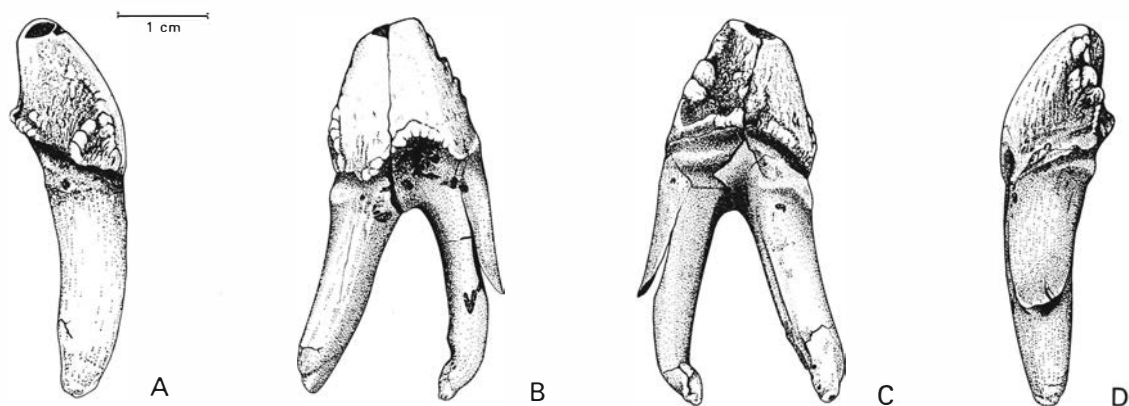


Fig. 2. The isolated upper first premolar in the calvarium UM no. 3962. A. Distal view. B. Buccal view. C. Palatinal view. D. Mesial view.

scription, and it has been dated at about five million years, i.e. Upper Miocene. Double-rooted upper first premolars are present in the holotype (57—67K).

The East African discoveries have shown that double-rooted first premolars are an ancient Miocene feature, that has disappeared in younger Pleistocene members of the Hippopotamidae family in Africa. However, the bi-rooted condition of the first upper premolars remained throughout Pleistocene time in the Asiatic hexaprotodons, and as shown in the present paper, this ancient

feature persisted almost until present times among the Madagascan hippopotami.

The group of Madagascan hippopotami, here dealt with, cannot, without further notice, be placed in the genus *Hexaprotodon*, despite several features diagnostic for this genus, such as the presence of the double-rooted P¹, the shape of the wear-facets in the incisors and the morphology of the upper canines. This group also has several characters typical of *Hippopotamus*, such as the extent of the lachrymal bone and the form of the premaxilla. Careful evaluations of these characters must be made, in order to establish the taxonomic relationships of the Madagascan hippopotami.

The mixture of the generic characters, in one and the same individual of the Madagascan hippopotami, reduces the taxonomic value of the double-rooted P¹. At present, it is doubtful if this feature can be used as a diagnostic generic character in the classification of the family Hippopotamidae.

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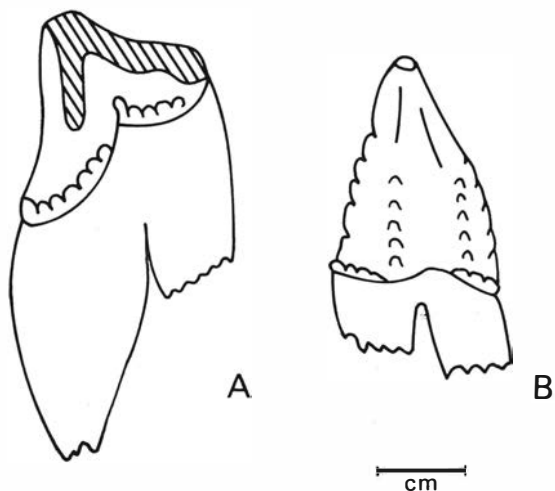


Fig. 3. Isolated upper first premolars from the Baringo Basin, Kenya (from Coryndon 1978).

A. Lukeino KNM-Lu 014 (right) from Late Miocene. B. Chemeron KNM-Bc 631 (left) from Pliocene.

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PLATES

Plate 1

- A. Calvarium UM no. M 3962.
- B. Calvarium UM no. M 3963.
- C. Calvarium Om no. A 31931.
- D. Detail of calvarium in fig. C.

