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THE FOSSIL HIPPOPOTAMUS FROM HOPEFIELD, SOUTH AFRICA

by

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(With Plates XII — XIII)

INTRODUCTION

The fossil remains of *Hippopotamus* from the Pleistocene "Elandsfontein" site near Hopefield, Cape Province, have already been briefly described by Singer and Keen (1955), who found that the material available at the time was not different from the living *Hippopotamus amphibius* L. However, it seems worthwhile to review their status since the *Hippopotamus* material has been considerably increased as a result of recent collecting trips to the site. Not only are there now cranial remains, but also postcranial material, notably carpals, tarsals and metapodials. The purpose of the present note is to place on record all the material at present in the Hopefield collection pertaining to the species in question. The specimens, originally housed in the Anatomy Department, University of Cape Town, have now been transferred to the South African Museum, Cape Town. The specimens' numbers refer to the Hopefield collection catalogue.

Order ARTIODACTYLA Owen
Family HIPPOPOTAMIDAE Gray
Genus HIPPOPOTAMUS Linnaeus
Hippopotamus amphibius L. subsp.

DESCRIPTION OF SKULL AND DENTAL REMAINS

The best preserved cranial remains of the hippopotamus in the Hopefield collection are two posterior parts of skulls, both broken off in front of the

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orbits (the fragments composing the first skull are numbered 1259, 1263, 1264, 4061, 5909, 5925, 5940, 5951, 5966, 5968, and 6021; the fragments of the second specimen bear the following numbers: 5903, 5904, 5908, 5911, 5913, 5914, 5915, 5917, 5919, 5920, 5921, 5923, 5932, 5933, 5935, 5939, 5943, 5945, 5946, 5947, 5952, 5953, 5955, 5970 and 6003). The former group are now designated H. 1., and the latter group as individual H. 2. In H. 1. the vertex is preserved as well as both posterior zygomatic roots, but the base of the occiput is missing. In H. 2. the basioccipital and both condyles are in situ but the vertex is incomplete and only the right zygomatic arch is present (part of the left is preserved but cannot be fitted to the skull). The few measurements that can be given (Table I) are within the limits of variation of the recent *Hippopotamus amphibius* skulls.

TABLE I

Skull measurements of fossil and recent *Hippopotamus amphibius* L. (in mm).

	Hopefield		Recent *H. amphibius* (Hooijer, 1950, table IB)	
	H. 1.	H. 2.	Males	Females
Zygomatic breadth	331	395	361-483	327-411
Horizontal diameter of orbit	—	65	53-75	58-72
Elevation of orbit above level of frontals	46	—	20-50	27-55

Two isolated M^3, one from the right and one from the left side (3998 and 4006 respectively), evidently of the same individual, agree in size with the largest (male) recent M^3 (Table II).

TABLE II

Measurements of M^3 of fossil and recent *Hippopotamus amphibius* L. (in mm).

	Hopefield	Recent *H. amphibius* (Hooijer, 1950, table IB)	
	3998, 4006	Males	Females
Length	63	47-62	47-56
Breadth	58	45-58	49-51

A partial mandible (plate XII), a maxillary and two premaxillaries (3999-4002, 4018 and 4022 respectively) all belong to a single juvenile individual (H. 3.). Only the left M^1 is preserved; it is just in wear (plate XIII). The two DM^4 are in situ, and so is the right DM_4, while the left DM_4 (4014) is separately preserved; it lacks the anterior lobe. DM^3 and DM_3 are lost but their alveoli remain; DM^2 and DM_2 appear to have been shed. Three

of the unerupted premolars, viz., left P^2, right P_3 and left P_2 are embedded in the bone. The (empty) alveoli of DM^1 and DM_1 are small and shallow, as they are in recent skulls of *Hippopotamus amphibius*. The degree of reduction of the anterior milk molars in the fossil specimen is the same as that found in the recent milk dentitions. The canines from the left side are preserved but broken off at their alveolar borders; the right canines are not preserved.

A noteworthy peculiarity of the fossil specimen is the absence of the left I^1. In the right premaxillary the two incisors (I^1 and I^2) are present; they have just erupted and their crowns are only slightly worn. On the left side there is only one incisor, and it corresponds in position to the I^2. It is evident that the absence of the left I^1 is not due to shedding; it has not developed at all.

A case of congenital absence of the upper central incisor in hippopotamus has not been recorded previously. The only cases of missing incisors in *Hippopotamus amphibius* concern the lower lateral incisor, I_2 (Hooijer, 1950, and references cited therein). In these cases the mandible is distinctly narrower between the canines than it is in normal mandibles with the full complement of incisors (Hooijer, l.c., p. 9). Therefore, it is interesting to find that in the Hopefield specimen the left premaxillary (with one incisor only) is narrower than that of the right side; the transverse diameter of the left premaxillary is 55 mm, whereas that of the right premaxillary is 61 mm. It should be noted that the mandible of this individual has the normal set of incisors, two on each side.

In the fossil hippopotami of Asia three incisors develop on each side, both in the upper and in the lower jaw. Some embryological evidence has been brought forward (Hooijer, 1950, p. 10) that the upper incisors normally developing in the recent African species in reality are I^2 and I^3, and that, consequently, the reduction in number of upper incisors to two in *Hippopotamus amphibius* is due to elimination of the central incisor. The two mandibular incisors normally present in the African hippopotamus are I_1 and I_2. I_3 is eliminated, although it is still occasionally present in instances of so-called unilateral hexaprotodontism (Hooijer, 1942). In cases in which there is only one incisor in the right or the left half of the mandible it is invariably the I_2 that has been eliminated.

The fact that the congenitally absent upper incisor in the present fossil skull is the central incisor is in harmony with the view that in the upper jaw of *Hippopotamus amphibius* the reduction in number of incisors has set in at the mesial end of the incisor series instead of at the distal end as is the case in the lower jaw.

Another fossil individual (H. 4.), in a slightly more advanced stage of wear of M^1, is represented by a fragment of the left maxillary with DM^3-M^1 (3997; the left DM^3 is 7743), the posterior half of the right M^1 (4016), and the right DM^{3-4} (5910 and 4013). The measurements of the molars of the two individuals (H. 3. and H. 4.) are very similar, and those of M^1 are near the upper limits of the variation ranges in the recent species (Table III).

TABLE III

Measurements of upper deciduous and first molars of *Hippopotamus amphibius* L. (in mm).

		Hopefield		Recent *H. amphibius* (Hooijer, 1950, table IA)	
		H. 3.	H. 4.	Males	Females
DM^3	breadth	—	24	—	—
DM^4	length	45	45	—	—
	breadth	38	38	—	—
M^1	length	52	53	37-54	37-50
	breadth	46	45	37-48	36-46

Three isolated M^2, all from the right side (4005, 1846 plus 3577, and 2816), present the following dimensions (Table IV).

TABLE IV

Measurements of M^2 of *Hippopotamus amphibius* L. (in mm.).

	Hopefield			Recent *H. amphibius* (Hooijer, 1950, Table IA)	
	4005	1846 3577	2816	Males	Females
Length	59	53	*c.* 55	47-62	47-60
Breadth	50	53	*c.* 53	41-58	44-53

Unfortunately, entire lower permanent molars of the hippopotamus have not been found at Hopefield as yet. The best specimen is a left lower M_3 consisting of 1848 and 1850, the lingual aspect and the talonid of which are incomplete. The length of this M_3 is at least 68 mm; in recent female hippopotami the length of M_3 varies from 64 to 75 mm, but in recent males the maximum length of M_3 is 86 mm (Hooijer, 1950, Table I A).

Fragments of hippopotamus molars of uncertain serial position include 1849, 2699b, 2818, 4003, 4007, 4008, 4020, 4021, 5015 and 5303.

There are two entire isolated premolars, viz., a right P^2 (4015) and a left P^3 (3522), as well as a right P^4 (4009) that is slightly damaged and has part of the maxillary attached to its roots.

Portions of upper canines are 4017 plus 4037, 2699c plus 4036, 1847, 4042 and 4052. Fragments of lower canines are 5023 plus 5025, 5029, 4055 and 2631. Measurements cannot be taken on these specimens.

Three upper incisors, 2805 plus 5648, 5099 and 4004, and one lower lateral incisor 4011, diameter 22 mm, complete the dental material of hippopotamus in the Hopefield collection.

POSTCRANIAL REMAINS

The only bone of the forelimb represented is the distal portion of the right radio-ulna (257). As will be seen from Table V the size of the fossil bone is within the limits of variation of that of the radio-ulna of recent *H. amphibius* (including a specimen from an unnumbered skeleton in the Port Elizabeth Museum, now M 127 on permanent loan to the South African Museum).

TABLE V

Measurements of radio-ulna of *Hippopotamus amphibius* L. (in mm) (P. E. Mus. = Port Elizabeth Museum; A-P = antero-posterior).

		Recent *H. amphibius*		
	Hopefield	P. E. Mus.	Hooijer, 1950, p. 95	
Distal breadth of radius	100	84	107	117
Distal A-P diameter of radius	74	60	78	78
Distal breadth of ulna	50	46	54	55
Distal breadth of radio-ulna	153	142	128	166

The distal end of a right femur (638) agrees well in size with that of a recent femur (Table VI).

TABLE VI

Measurements of femur of *Hippopotamus amphibius* L. (in mm).

	Hopefield	Recent P. E. Mus.
Breadth across condyles	140	133
Distal A-P diameter (medial side)	192	186
Distal A-P diameter (lateral side)	150	140
A-P diameter from middle of trochlea to intercondyloid fossa	104	92

Two carpal bones, the cuneiform and the unciform, are represented by a few specimens each (Tables VII and VIII).

TABLE VII

Measurements of cuneiform of *Hippopotamus amphibius* L. (in mm).

	Hopefield				Recent
	3769 (right)	6507 (left)	600 (left)	6808 (left)	P. E. Mus. (left)
Maximum basal diameter	49	51	48	54	45
Anterior height	50	51	54	61	42
Proximal A-P diameter	54	54	53	63	44

TABLE VIII

Measurements of unciform of *Hippopotamus amphibius* L. (in mm).

	Hopefield			Recent
	603 (left)	5695 (left)	3768 (left)	P. E. Mus. (left)
Vertical diameter	47	44	45	37
Transverse diameter	73	70	73	63
A-P diameter	92	89	93	75

Two tarsals, the astragalus (79, 2699r) and the cuboid (5629) both from the right side, but not from the same individual, do not differ significantly in size from their recent homologues (Tables IX and X).

TABLE IX

Measurements of astragalus of *Hippopotamus amphibius* L. (in mm).

	Hopefield	Recent (Hooijer, 1950, p. 106)	
Median length	96	95	102
Lateral length	106	105	106
Distal breadth	97	91	98
Lateral A-P diameter	60	59	60

TABLE X

Measurements of cuboid of *Hippopotamus amphibius* L. (in mm).

	Hopefield	Recent *H. amphibius* (Hooijer, 1950, p. 108)	
Anterior length	40	52	43
A-P diameter	72	77	78
Transverse diameter	73	76	78

Among the metapodials (Tables XI and XII), there are two specimens that are decidedly smaller than their homologues in the Hopefield collection, viz., 2978-2979, a left third and fourth metacarpal belonging to the same individual. The other fossil metapodials agree well in size with the recent, although a fifth metacarpal (1309) is noticeably more massive than that in

TABLE XI

Measurements of metacarpals of *Hippopotamus amphibius* L. (in mm) (P. E. Mus. = Recent *H. amphibius* in the Port Elizabeth Museum; R = Right; L = Left).

	II		III				IV				V	
	Hopefield	P. E.	Hopefield			P. E.	Hopefield			P. E.	Hopefield	P. E
Metacarpal	1295 (R)	Mus.	3223 (R)	1338 (L)	2978 (L)	Mus.	1297 (R)	1313 (L)	2979 (L)	Mus.	1309 (L)	Mus.
Median length	118	117	121	142	113	143	120	137	104	136	97	108
Maximum length	126	125	129	150	122	155	121	139	108	139	97	108
Proximal diameter: A-P	43	40	48	51	40	45	48	—	—	48	46	37
breadth	35	31	47	55	43	52	50	—	41	48	39	31
Mid-shaft diameter: A-P	21	23	20	23	20	21	27	28	19	22	25	26
breadth	33	29	33	40	31	39	39	41	31	37	38	30
Diameter at distal articular surface: A-P	—	32	34	41	30	37	39	42	31	37	40	35
breadth	—	36	38	46	34	43	43	42	—	42	39	36

TABLE XII

Measurements of metatarsals of *Hippopotamus amphibius* L. (P. E. Mus. = Recent *H. amphibius* in the Port Elizabeth Museum; R = Right; L = Left).

	II				III		IV				V	
	Hopefield			P. E.	Hopefield	P. E.	Hopefield			P. E.	Hopefield	P. E.
Metatarsal	1307 (L)	1344 (L)	6734 (L)	Mus.	6382 (L)	Mus.	1352 (R)	3793 (R)	1311 (L)	Mus.	2980 (R)	Mus.
Median length	99	94	96	95	104	123	128	—	126	129	96	95
Maximum length	102	95	97	95	110	129	128	—	128	130	96	95
Proximal diameter: A-P	36	35	37	27	47	49	64	58	68	57	43	38
breadth	27	27	—	22	37	40	52	—	50	43	33	27
Mid-shaft diameter: A-P	20	25	25	25	21	22	26	26	26	22	30	20
breadth	29	27	27	24	32	37	42	39	41	34	30	24
Diameter at distal articular surface: A-P	—	38	36	33	36	34	46	—	41	36	41	34
breadth	—	35	—	31	38	39	48	—	47	40	35	28

the recent specimen available for comparison. However, the cranial and dental material of hippopotamus in the Hopefield collection does not provide evidence for the existence of more than one species, viz., the living *Hippopotamus amphibius* L. Until further evidence for the presence of "pygmy" or otherwise aberrant forms of hippopotamus at Hopefield is forthcoming the present specimens may be provisionally classed with the others, indicating the extent to which the fossil hippopotamus may vary within the species.

Fossil remains representing varieties or at most races of the living *Hippopotamus amphibius* have been described under various names from all parts of Africa; for an enumeration of these, with references to the literature, the reader is referred to Cooke (1949) and Hooijer (1950, p. 28/29; 1958). An early Pleistocene stage of development of the hippopotamus, slightly more primitive than *H. amphibius* and appropriately named *Hippopotamus protamphibius* by Arambourg (1948) occurs at Omo in East Africa. It differs from the living species in the lesser elevation of the orbits, the separation of the lacrimal from the nasal by an anterior prolongation of the frontal (one of the characters also found in the extinct Asiatic species of hippopotamus), in its more brachyodont dentition and lesser development of cingula, simpler premolars and one-rooted persistent first premolar. In all these points the Hopefield hippopotamus differs from *H. protamphibius* just as does the living *H. amphibius*.

It is a general observation in Pleistocene faunas that forms otherwise identical to their modern counterparts are rather large-sized. At Hopefield this has already been demonstrated, e.g., in the carnivora (Ewer and Singer, 1956), and in the rhinoceroses (Hooijer and Singer, 1960). Apart from its rather larger size (although still within the limits of variation of the living form) there is nothing by which the fossil hippopotamus from Hopefield can be distinguished from recent *H. amphibius*.

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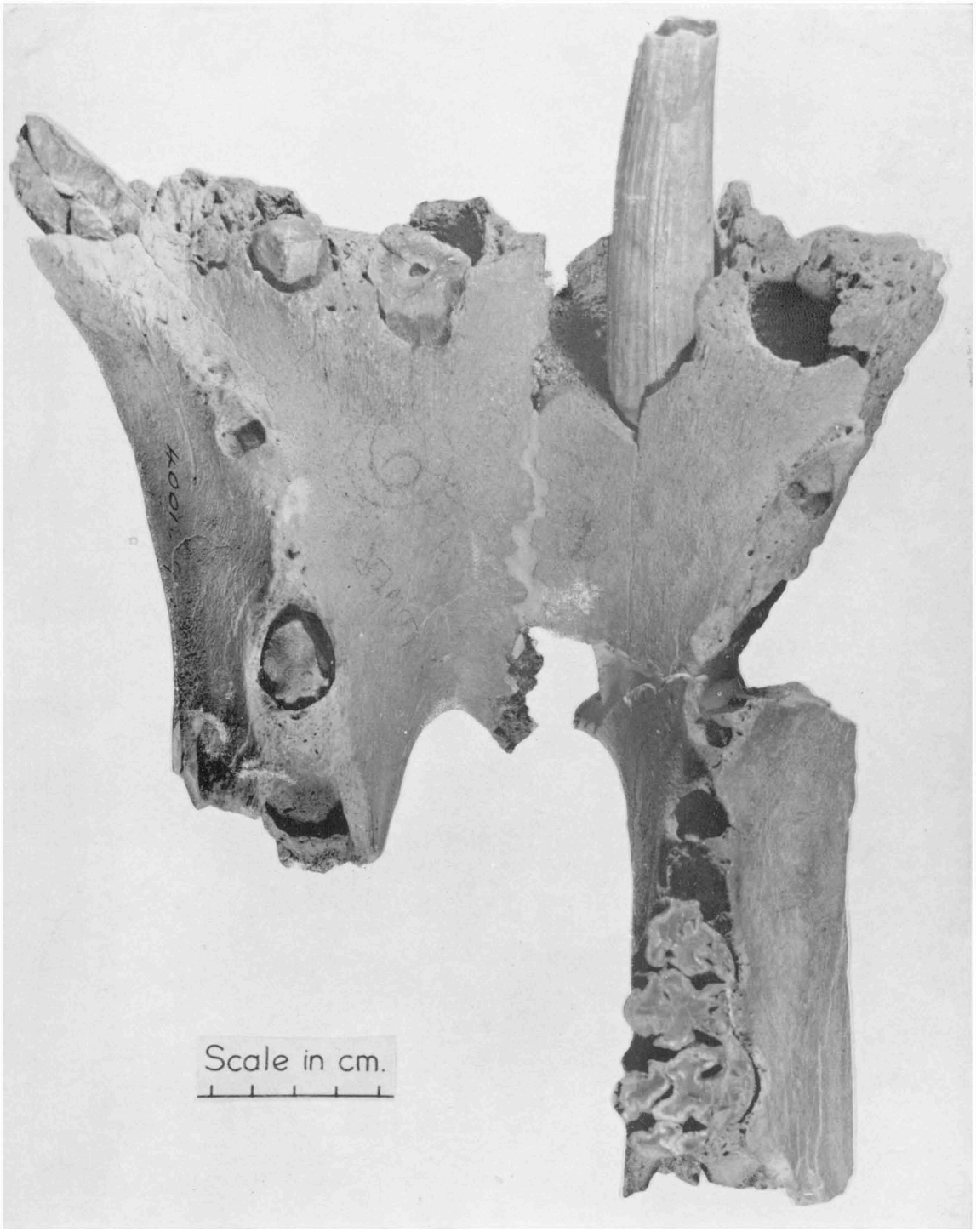
EXPLANATION OF THE PLATES

Plate XII

Superior aspect of portion of a mandible of a fossil *Hippopotamus amphibius* from Hopefield (H. 3.).

Plate XIII

Inferior aspect of portion of a maxilla and premaxillary of a fossil *Hippopotamus amphibius* from Hopefield (H. 3.) showing left M^1, both DM^4, alveolus for left DM^3, left P^2 embedded, shallow alveolus of left DM^1, the left canine broken off at the alveolar border, left I^2, right I^1 and I^2. Note that the left I^1 is absent.


Scale in cm.

Pl. XIII