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Plio-Pleistocene Hippopotamidae from the Upper Semliki

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Abstract. The sample size of the fossil hippopotamid material recovered in the Upper Semliki is second only to bovids. The majority of the sample consists of well preserved isolated teeth. The most complete specimens include a mandible fragmented anteriorly to P_4 and an opisthocranium. The taxa present are *Hexaprotodon* cf. *H. imagunculus* in the Lusso Beds and *Hippopotamus* aff. *H. amphibius* in every deposit. The first taxon is very similar to *Hex. imagunculus* from the Kaiso Formation in Uganda. However, the taxon *Hex. imagunculus* is poorly sampled at the type site and at Upper Semliki. The Upper Semliki sample is assigned to *Hex.* cf. *H. imagunculus*, with *Hex. imagunculus* maintained only for the type material. The second species is similar to *Hip. kaisensis* and *Hip. amphibius*. A study of a sample of cranial and dental measurements of modern *Hip. amphibius* (N=34) and the entire *Hip. kaisensis* hypodigm showed that the known metric and nonmetric morphological characteristics of *Hip. kaisensis* are not distinguishable at the species level from *Hip. amphibius*. I included the large hippopotamid form from the Upper Semliki into the taxon *Hip.* aff. *H. amphibius* until further material and a major revision of the family Hippopotamidae define the proper taxonomic status of the Western Rift Plio-Pleistocene *Hippopotamus* taxa.

Résumé. L'abondance des restes d'Hippopotamidés provenant de la Haute-Semliki ne le cède qu'à ceux de Bovidés. La plupart sont des dents isolées bien conservées; le specimen le plus complet comprend une portion de mandibule antérieure à P_4 et un opisthocranium. Deux espèces représentées sont *Hexaprotodon* cf. *H. imagunculus* dans les Couches de Lusso et *Hippopotamus* aff. *H. amphibius* dans toute la séquence. Le premier taxon est fort semblable à *Hex. imagunculus* de la Formation de Kaiso (Uganda). Toutefois les échantillons sont déficients de part et d'autre. Notre attribution *Hex.* cf. *imagunculus* en Haute-Semliki ne laisse la détermination *Hex. imagunculus* qu'au type. La second espèce est semblable à *Hip. kaisensis* et *Hip. amphibius*. Après avoir comparé les caractères dentaires et craniaux de 34 *Hip. amphibius* specimens à ceux de l'hypodigme total de *Hip. kaisensis*, nous jugons que les deux espèces, n'en font qu'une, tant d'après les caractéristiques métriques que non-metriques. Notre dénomination *Hip.* aff. *amphibius* est provisionelle, dans l'attente d'une revision majeure de la famille Hippopotamidae.

INTRODUCTION

This report presents the systematics of the hippopotamid material recovered by the SRE in the field seasons 1983-86. Much of the paleontological work in the Western Rift has taken place in Uganda, carried out between 1920 and 1960 by Wayland, O'Brien, Fuchs, and Bishop, and has produced a sizable fossil mammalian fauna (Hopwood, 1926, 1939; Fuchs, 1934; Bishop, 1969; Cooke and Coryndon, 1970). An updated mammalian faunal list can be found in Pavlakis (1987). Fossil mammals have been collected primarily in the areas of Kaiso Village on the eastern shore of Lake Mobutu, Kisegi-Wasa, and Kazinga Channel. The first site is the type locality of two hippopotamid species: *Hexaprotodon imagunculus* Hopwood, a pygmy, possibly hexaprotodont species, and *Hippopotamus kaisensis* Hopwood, a large tetraprotodont hippo (Hopwood, 1926; Cooke and Coryndon, 1970). Bishop, Gautier, and de Heinzelin (Gautier, 1967) established the Kaiso Formation, which included the major localities of Kaiso Village, Nyawiega, Behanga I/II, and North and South Nyabrogo. These have been biochronologically dated by the large mammal concurrent biochron range method (Hedberg, 1976), and the stage-of-evolution method based on Suidae, Elephantidae, and Bovidae taxa between 3.0 and 1.8 my BP (Pavlakis, 1987). In addition, application of the computerized temporal biostratigraphy method (Shuey et al., 1978) showed best fit dates for these faunas to range from 2.6-2.3 my BP (Pavlakis, 1987).

The valley of the Upper Semliki produced its first mammalian fossils in 1935-1936 (Damas, 1940). However, no reports exist citing fossil hippopotamids in that collection. Between 1938 and 1940, Lepersonne (1949) made a detailed geological study of the Western Rift from Lake Rutanzige to Lake Mobutu. In addition, he collected mammalian fossil hippopotamids.

Specimen No. 683 is a well preserved first front phalanx of a large hippopotamid recovered from locality L311 at Katanda, 6-8 m above the Semliki River, in deposits equivalent to Ugandan middle Pleistocene formations (Hooijer, 1963:22; de Heinzelin, 1955:47; Lepersonne, 1949:30). Hooijer (1963:58) referred this specimen to "*Hippopotamus amphibius* cf. *gorgops*" Dietrich, and noted that the specimen is much larger than the small *Hexaprotodon imagunculus* of the Kaiso Formation in Uganda. He thought that ". . . (the specimen) may be referred to the living *H. amphibius*, a fossil race of which from the early and middle Pleistocene of East Africa has been described as *H. gorgops* by Dietrich (1962, 1928), and as *H. amphibius kaisensis* by Hopwood (1926:23)" (Hooijer, 1963:59). He believed that the two taxa were equivalent and that the former name had priority. Also, he noticed that this extinct "race" is very similar in morphology to the recent hippopotamus. J. de Heinzelin (1955:47) had attributed this specimen to *Hip. amphibius*. Thus, the very first hippopotamid specimen recovered in the Upper Semliki presented the full scale of the controversy involved in the taxonomic status of the Western Rift *Hippopotamus*.

Subsequently, de Heinzelin directed geological and archaeological research in the Upper Semliki Valley, from 1950 to 1960 (de Heinzelin, 1955, 1957, 1961a,b). Among other discoveries, he found fossil remains of both *Hippotamus amphibius* and *Hexaprotodon imagunculus*, at the presumably Lusso Bed locality of Kanyatsi on the northern margin of Lake Rutanzige (de Heinzelin, 1955:84, 85; Adam and Lepersonne, 1959:113, 114).

The deposits in the valley consist of lacustrine and alluvial or colluvial sediments. In some parts they are covered by recent ash from nearby volcanoes. There are Plio-Pleistocene and Holocene sediments in the area outcropping on the margins of the lake and river, as well as at most tributary streams and ravines from the rift wall to the river. The oldest deposits in the Upper Semliki are currently referred to as "Lusso Beds" (Verniers and de Heinzelin, this volume). Younger deposits comprise the Semliki Beds of probable middle Pleistocene age overlain by terrace complexes and the Katwe Ash, of late Pleistocene to Holocene age (Verniers and de Heinzelin, this volume, Table 1; see also preliminary stratigraphic definitions).

The mammalian fauna recovered so far from all formations in the Upper Semliki includes rodents, primates, proboscideans, equids, suids, hippotamids, and bovids (see contributions in this volume). The faunal inventory from the Semliki Beds is rather small,

Table 1. Comparison of *Hippopotamus* aff. *H. amphibius* mandibular fragment Kt2-8 dimensions. Teeth dimensions in mm; measurements of mandibular ramus in cm.
  Abbreviations: X = mean; R^+ = observed variation above mean; R^- = observed variation below mean; N = sample size.
  Other abbreviations as given in the text.

		$LC-P_1$	RP_1-P_2	RP_2-P_3	h_1	l_1	l_2	l_3	e_1	e_4
Hip. amphibius	X	59.94	26.48	10.83	12.53	32.48	22.58	21.72	6.45	17.27
	R^+	97.98	73.44	18.02	16.70	45.00	27.80	24.90	9.00	21.00
	R^-	38.50	5.92	2.72	7.20	21.00	16.10	17.80	4.10	12.80
	N	15	14	23	33	33	33	33	33	33
Hip. kaisensis	X	--	38.06	9.64	--	22.20	--	--	--	16.05
	R^+	--	42.26	10.00	--	24.00	--	--	--	17.10
	R^-	--	34.32	9.28	--	20.40	--	--	--	15.00
	N	--	3	2	--	2	--	--	--	2
Hip. gorgops	X	--	--	26.08	--	--	37.30	--	--	17.50
	N	--	--	1	--	--	1	--	--	1
Hip. aethiopicus	X	23.00	16.00	--	--	--	--	--	--	6.30
	N	1	1	1	--	--	--	--	--	1
Kt2-8		84.45	55.00	11.00	16.30	44.80	30.60	26.40	8	14.80

due possibly to the fact that these deposits are less abundant than either Lusso or higher beds. The sizable terrace complex/Katwe fauna essentially has a modern aspect. Biochronological correlations of the Lusso Beds and Kaiso Formation mammalian faunas indicate that the Lusso fauna is correlative to Kaiso Village and Behanga I/II, and may have a chronologic range between 2.3 and 1.8 my BP (Pavlakis, 1987).

ABBREVATIONS AND DEFINITIONS

Abbreviations and definitions used in the current work are listed below.

SRE: Semliki Research Expedition
VNMH: Virginia Museum of Natural History
BMNH: British Museum (Natural History)
AMNH: American Museum of Natural History
NMNH: National Museum of Natural History (Smithsonian)

Measurements (in mm unless otherwise indicated)

Cranium:
l_c=min. postorbital constriction
l_m=max. distance of zygapophyses
l_o=max. distance of occipital condyles
l_p=max. width of occipital plane
e_a=max. width of rt. glenoid cavity
h_c=min. height of rt. zygomatic process
h_d=max. height of supraoccipital tuberosity
h_k=height of right occipital condyle

Mandible:
l_1=max. width at of canine tuberosities
l_2=min. intercanine distance at root level
l_3=min. width at level of P_3
l_6=mesiolabial distance of P_2
e_1=min. thickness of canine apophysis
e_2=thickness of horizontal ramus at P_3
e_4=length of mandibular symphysis
h_1=height of horizontal ramus anterior to P_2

Teeth:
L=max. mesiodistal length
l_1=max. mesial width
l_2=max. distal width
l_3=min. width of buccolingual constriction
h=height
d_1=max. diameter of anterior teeth
d_2=min. diameter of anterior teeth

Astragali:
H_1=medial length parallel to long axis
H_2=distance of center of proximal groove to distal interarticular ridge
H_3=lateral length parallel to long axis
L_1=proximal width
L_2=distal width
e_1=max. length of medial-proximal articular surface
e_2=min. length of medial-distal articular surface

SYSTEMATICS OF THE UPPER SEMLIKI FOSSIL HIPPOPOTAMIDS
Overview of the Collection

The sample of fossil hippopotamid material is second in size only to that of bovids. It consists of 97 specimens, both cranio-dental (66) and postcranial (31). The majority of the specimens are teeth (64); anterior teeth (36) are always fragmented; postcanine teeth (28) occasionally present complete crowns. Cranial fragments include four fairly complete specimens. Kt2-8, after reconstruction, is the most complete specimen in the collection. It is the anterior portion of a large mandible including the mandibular symphysis, the complete right canine, and both tooth rows up to and including the P_4's (Fig. 1A). Ks3-2 is part of an opisthocranium recovered in one piece imbedded in hard, cement-like sediment. It preserves also the majority of the brain case (Fig. 1B). Mnl-1 and Sn5A-720 are parts of hemimandibles including premolars and molars. The 31 postcranial fragments are distributed as follows: ten carpal/tarsal fragments, seven phalanges, four long bone fragments, three vertebral fragments, two pelvic fragments, two scapular fragments, one rib fragment, one complete astragalus, and one complete patella. Most of the specimens (74) were recovered from Lusso Beds deposits, and 23 from younger deposits.

The condition of preservation of the material is generally good. Most of the Lusso Bed specimens had the characteristic ironstone sediments on them, with dark reddish colora-
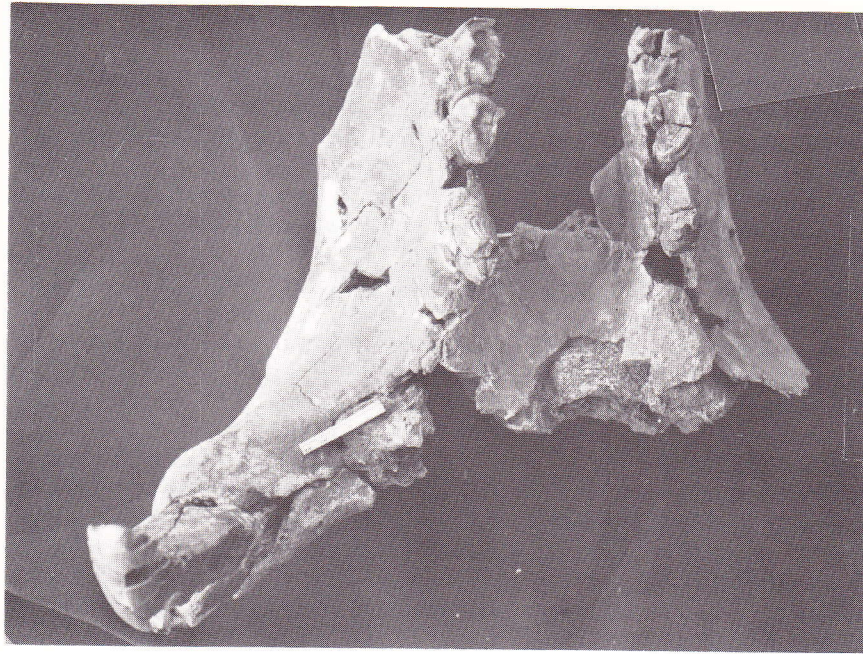
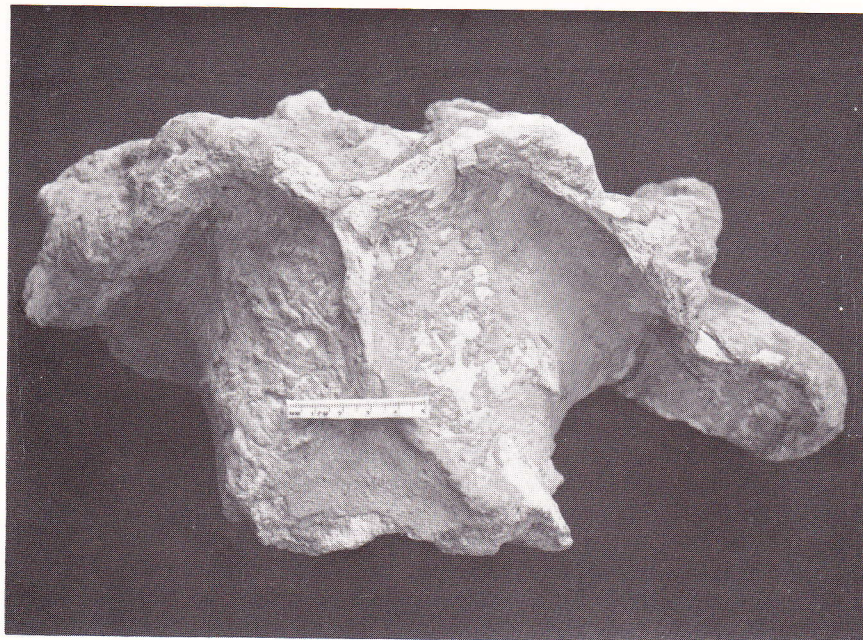Figure 1(A). *Hippopotamus* aff. *H. amphibius* mandibular fragment Kt2-8.

Figure 1(B). Opisthocranium fragment Ks3-2.

tion. The majority of the Lusso Bed specimens do not show weathered surfaces, except the evidence of rolling in some specimens, as indicated by their rounded surfaces. Most of the fossils from the Semliki or terrace/Katwe deposits have light coloration. Their surfaces show extensive weathering (cracking), while some of them are encrusted in hard sediment.

Methodology

The ironstone sediment was removed from the specimens using an airscribe in the laboratory. All measurements were taken using a Helios 0.05 mm sliding caliper, or a Seritex steel tape. The Upper Semliki material was compared with that of *Hex. imagunculus* and *Hip. kaisensis* material from Uganda (BMNH). All dental and most postcranial specimens in the collection were measured. Additionally, every specimen from the Upper Semliki was compared with data of most East African Plio-Pleistocene hippopotamid species. Major sources include Gèze (1980, 1985), Coryndon (1970, 1976, 1977a, 1977b, 1978), Coryndon and Coppens (1973, 1975), Cooke and Coryndon (1970), and Corbet (1969). Furthermore, the Division of Mammals of the NMNH provided on loan two skeletons of modern *Hippopotamus amphibius*, as well as a skeleton of *Hexaprotodon liberiensis*. They were used for morphological comparison with the fossil hippopotamid material under study. In order to estimate the range of variation of the metric and nonmetric dental and cranial characteristics of the species *Hippopotamus amphibius*, I measured a sample of 34 modern hippo skulls housed in the AMNH and NMNH. A total of 78 measurements were taken on each cranium (35), mandible (19), and each of the teeth (three on premolar and five on molars), based on Gèze (1980) and Hooijer (1950). The cusp nomenclature used for description is that used by Gèze (1985, 1980), Hooijer (1950), and Osborn (1907). I do acknowledge, however, Gaziry's (1987) question of such nomenclature. Discussion of this matter is beyond the scope of this study. For the syntax of taxonomic statements I follow Lucas (1986). I use *Hex.* and *Hip.* for *Hexaprotodon* and *Hippopotamus* generic initials, respectively.

Systematic Description

Order Artiodactyla Owen, 1848
Family Hippopotamidae Gray, 1821
Genus *Hexaprotodon* Falconer and Cautley, 1836
Species *Hexaprotodon* cf. *H. imagunculus* Hopwood, 1926

Horizon: Lusso Beds; Plio-Pleistocene Age

Material: Sn6-2 LM^3, Lu1-30 LP^3, Kn2-45/47 RC/, Kt1-23 RC/, Sn13B-1 ?L/C, Kn3-7 LC/, Sn5A-628 L/C, Lu1-29 RC/, Sn16A-1 LC/, Kn2-14 /C, Kn2-46 L/C, Ks4-11 L/C, Kn2-5 L/C, Kn2-1 RP_4, Kn4-1 RP_4, Kt8-1 RP_4, Sn5A-720 LM_1-LM_2, Sn6-3 RM_2, Sn5A-34 RM_2, Lu2-13 ?LM_2, Sn5A-158 ?M_2, Kv7-1 molar, Kn2-17 lt. calcaneum, Kn3-15 rt. scaphoid.

Referred specimens: Kt1-4 LI^1, Ks2-5 ?I^1, Kt3-10 LC, Ks2-22 RP^4, Kt1-22 molars, Ks2-2 ulna, Lu2-14 dm_1.

Comparison

Upper canines: The sample of five canines comes from the Lusso Beds, and presents the following taxonomically salient characters: large and deep posterior groove not covered by enamel, triangular cross section, and finely striated enamel. The sample shows definite *Hexaprotodon* characteristics, and is most similar in morphology and size to *Hex. imagunculus*, specimen M25130 (Cooke and Coryndon, 1970:172, Pl. 12a). Size comparison, however, is not particularly helpful in distinguishing upper canines of *Hexaprotodon* species .

Upper P3: Morphological comparison of Lu1-30, an LP^3, the only upper premolar recognized in the sample, with available East African hippopotamid species plus the two extant hippos, revealed that Lu1-30 approaches more the *Hex. imagunculus* condition than any other species. It shares the following characters: one main cusp with incipient distolingual accessory cusp, triangular but widening distally tooth outline, mesially strong and indentate cingulum, and rugose enamel surface. It is specifically very similar to *Hex. imagunculus* (M12619,) an LP3 from Kaiso Village (Cooke

and Coryndon, 1970, Pl. 12b). A plot of L/l_3 index for fossil hippopotamid species shows that Lu1-30 is close to, but shorter than the mean of five P^3's included in the *Hex. imagunculus* hypodigm (Pavlakis, 1987), probably caused by the fact that Lu1-30 is broken at the distal end.

Upper M3: Sn6-2, an LM^3, is the only M^3 in the sample. Hippopotamid molars are morphologically conservative and are not particularly useful in taxonomy, especially when they are isolated. Nevertheless, Sn6-2 differs in taxonomically important morphological characters from *Trilobophorus* and *Hippopotamus*. These differences include triangular occlusal enamel pattern, tapering upwards from the cusps, and a deep transverse valley. There is limited morphological difference of taxonomic value between Sn6-2 and the modern pygmy hippo's M^3 (Pavlakis, 1987). The presence of a cingulum in the labial aspect of the transverse valley in Sn6-2 is certainly a unique character, but evaluation of its consistency must await the recovery of further material.

Hex. shungurensis and *Hex. karumensis* have more well-developed cingula than does Sn6-2; the former species has a cingulum lingually and labially, and the latter all around the crown (Pavlakis, 1987). Sn6-2 M^3 fits exactly the diagnosis of *Hex. imagunculus* in the conical shape of the cusps, and the shape of the cingulum. Comparions of Sn6-2 with M26328, a right maxilla with M^2 and M^3 in place (Cooke and Coryndon, 1970, Pl. 13a,b), shows that they are morphologically almost identical. The metacone and metaconule have the same conical shape, their occlusal surface is clearly triangular, and the teeth are similarly narrow near their occlusal surface and wider at the cingulum level. A mesostyle is present on the labial side of M26328, exactly as in Sn6-2. In addition, both specimens seem to have similar transverse valleys with pairs of mesial and distal cusps slightly touching each other. No comparison can be made with *Hex. coryndoni* as no description of M^3 is available. From photographs in Gèze (1980) the M^3 is shown quite robust with long cusps. The bivariate plot of the length-width index is shown in Figure 2. As with P^3, the M^3 has an index of L/l_2 closer to *Hex. imagunculus* than to any other species.

Lower canines: There are seven lower canines included in the sample of the Upper Semliki small fossil hippo. They are all typical *Hexaprotodon*, since they present the characteristic parallel enamel ridges (Coryndon, 1977a, 1978). All specimens conform mostly with the morphology of *Hex. imagunculus* lower canines by presenting fine enamel striations, the characteristic bean-shape cross section, and shallow mesial groove. A bivariate plot of lower canine cross section dimensions fails to show clear metric relations between the species, due to the small available sample size for most *Hexaprotodon* species. It is concluded that on morphological grounds the Upper Semliki sample of lower canines is close to *Hex. imagunculus*.

Lower P4: There are three RP_4's in the sample. Hippo P_4's are morphologically variable. The Upper Semliki sample of P_4's contains a robust main cusp triangular in cross section and an auxiliary cusp attached to it. They compare closely with the three P_4's in the *Hex. imagunculus* hypodigm; specifically M26330 to Kn2-1 and M12621 to Kt8-1 (Fig. 3A,B, and Cooke and Coryndon, 1970, Pls. 14d and 14c, respectively). The size relationships of the East African Plio-Pleistocene hippopotamid species is shown in Figure 4. The similarity in dimensions between Kt8-1 and Kn2-1 (x) to M12921 and M26330 (i) is clear.

Lower M2: There are five M_2's in the Lusso sample. As with lower molars, the uppers are conservative and do not show significant interspecific change. However, *Hexaprotodon* lower molars differ from *Hippopotamus* in having a conical shape, occlusal surface divided by a lingually and labially deep transverse valley, triangular occlusal enamel pattern, and low cingulum (Coryndon, 1977a, 1978; Corbet, 1969; Gèze, 1980; Fig. 3C,D, and 5A). These characters, however, are present in all *Hexaprotodon* species. Distinguishing *Hexaprotodon* species on morphological characters of isolated M_2's, therefore, is not certain. Figure 6 shows the bivariate plot of M_2 L/l_1 index for many hippopotamid species. The Lusso sample is very close to *Hex. imagunculus*.

Postcrania: Kn3-15, a complete right scaphoid, is the most complete postcranial specimen in the sample (Fig. 5B). It is not
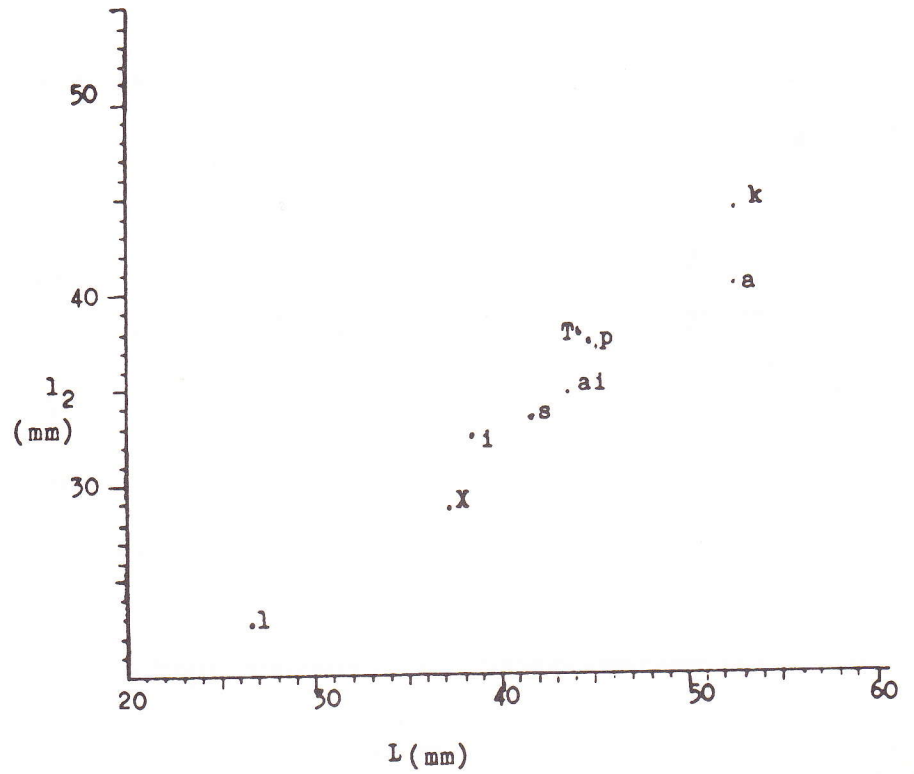
Figure 2. Bivariate plot of *Hexaprotodon* cf. *H. imagunculus* M^3 maximum distal width (l_2) to maximum mesiodistal length (L).

	N	I	RANGE	l_2	RANGE
l : *Hex. liberiensis*	12	26.63	22.64 - 30.52	22.93	20.40 - 25.48
i : *Hex. imagunculus*	4	38.39	37.78 - 39.20	32.60	30.08 - 36.94
p : *Hex. protamphibius*	37	44.87	56.00 - 39.00	37.42	42.00 - 31.20
s : *Hex shungurensis*	3	41.80	38.40 - 44.00	34.00	33.00 - 38.00
k : *Hex. karumensis*	3	52.03	47.60 - 57.00	44.33	34.00 - 51.00
T : *T. afarensis*	11	44.04	39.00 - 49.50	37.95	34.00 - 44.50
ai : *Hip. kaisensis*	3	43.88	40.88 - 45.74	34.99	32.00 - 39.96
a : *Hip. amphibius*	14	52.40	47.16 - 60.36	41.49	33.56 - 50.78
x : Sn6-2		37.10	-	28.95	-

Figure 3. *Hexaprotodon* cf. *H. imagunculus* RP4 Kn2-1(a), RP4 Kt8-1(b), and RM$_2$ Sn5-34(c,d).
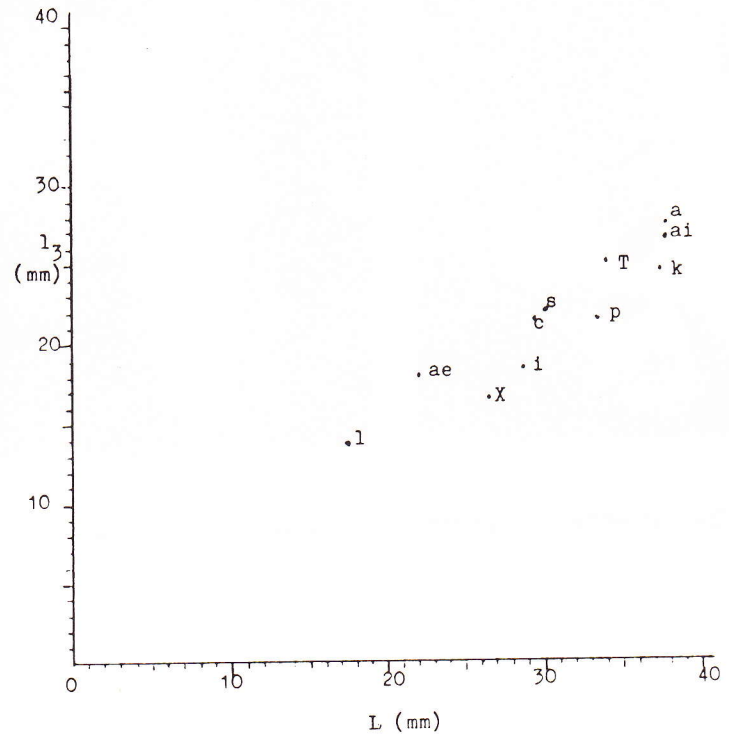
Figure 4. Bivariate plot of *Hexaprotodon* cf. *H. imagunculus* P_4 minimum width of buccolingual constriction (l_3) to maximum mesiodistal length (L).

	N	L	RANGE	l_3	RANGE
l : *Hex. liberiensis*	9	17.52	16.46 - 20.00	13.98	11.56 - 19.82
i : *Hex. imagunculus*	3	28.91	26.34 - 30.60	18.65	16.32 - 19.84
p : *Hex. protamphibius*	1	33.25	-	21.60	-
s : *Hex shungurensis*	1	30.00	-	22.00	-
k : *Hex. karumensis*	3	37.33	31.00 - 41.00	24.66	19.00 - 29.00
c : *Hex. coryndoni*	1	29.35	-	21.30	-
T : *T. afarensis*	9	33.90	28.00 - 40.00	25.00	23.00 - 28.00
ai : *Hip. kaisensis*	2	37.83	37.50 - 38.16	26.81	26.42 - 27.20
ae : *Hip. aethiopicus*	1	22.00	-	18.00	-
a : *Hip. amphibius*	19	37.88	30.48 - 51.92	27.13	19.32 - 32.02
x : Lusso specimens	3	26.48	24.25 - 30.80	16.20	13.35 - 18.75

Figure 5(A). *Hippopotamus* aff. *H. amphibius* RM2 Lu2-1 (left) compared to *Hexaprotodon* cf. *H. imagunculus* LM2 Lu2-13 (right).

Figure 5(B). *Hippopotamus* aff. *H. amphibius* left scaphoid Ky-20 (left) compared to *Hexaprotodon* cf. *H. imagunculus* right scaphoid Kn3-15 (right).

distinguishable from *Hex. imagunculus* (M12631), *Hip. amphibius* (NMNH 162976), or *Hip. kaisensis* (M12634).Comparison with *Hex. liberiensis* (NMNH 444361), however, showed that the medial crest of the articular surface with the magnum extends anteriorly more than in Kn3-15. Comparison of the Kn3-15 length index of articular surfaces with radius and magnum, over the dimension perpen-

dicular to it (0.983), however, showed that it is closer to that for *Hex. imagunculus* M12631 (0.976) than any other hippopotamid species (Pavlakis, 1987).

**Genus *Hippopotamus* Linnaeus, 1758
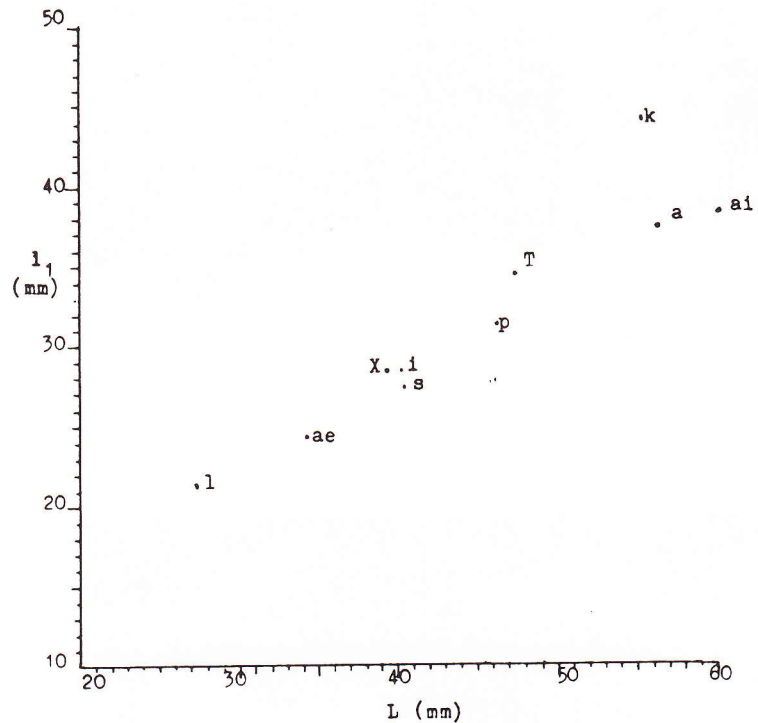Species *Hippopotamus* aff. *H. amphibius* Linnaeus, 1758**

Figure 6. Bivariate plot of *Hexaprotodon* cf. *H. imagunculus* M_2 maximum mesial width (l_1) to maximum mesiodistal length (L).

	N	L	RANGE	l_1	RANGE
l : *Hex. liberiensis*	11	27.69	25.74 - 30.56	21.28	18.58 - 29.50
i : *Hex. imagunculus*	9	40.18	34.48 - 49.58	28.57	25.50 - 32.62
p : *Hex. protamphibius*	37	46.26	43.00 - 50.00	31.10	26.00 - 36.50
s : *Hex shungurensis*	3	40.33	34.00 - 46.00	27.30	23.00 - 30.00
k : *Hex. karumensis*	3	55.33	52.00 - 58.00	44.00	40.00 - 47.00
T : *T. afarensis*	18	47.50	41.00 - 56.00	34.56	30.00 - 43.00
ai : *Hip. kaisensis*	5	60.20	58.48 - 61.70	38.19	36.26 - 41.60
ae: *Hip. aethiopicus*	2	34.00	-	24.25	24.00 - 24.50
a : *Hip. amphibius*	29	56.32	46.46 - 61.72	37.10	31.36 - 43.08
x : Lusso specimens	5	39.13	33.30 - 44.30	28.33	24.80 - 30.80

Horizon: Lusso Beds, Semliki Beds, terrace/Katwe levels; late Pliocene-late Pleistocene Age.

Material: Is8-5 RI^2; Kt5-1 RC/; Sn5A-106 RC/; Kt3-1 ?RC/; Kt1-3 I_1; Ky5-1 ?I_1;l Ky7-48 LI_1; Ks1-3 LI_2?; Kv8-1 RI_2; Kt4-11 R/C; Kv3-1 L/C; Is2-12 R/C; Is2-13 L/C; Kt2-11 L/C; Mn1-39 L/C; Ky6-2 R/C; Is2-18 R/C; Mn1-40 /C; Kt1-12 LP_3; Ky10-1 LP^4; Ky7-57

Lower P2: The only two P_2's in the sample belong to the Kt2-8 mandibular fragment (Fig. 1A). They are single-cusped, bi-rooted, present a strong cingulum anteroposteriorly, and have longitudinal enamel ridges at the distal slope of the cusp. These are characteristics of *Hip. kaisensis* and *Hip. amphibius*, whose P_2's are morphologically indistinguishable. There are no P_2's available for *Hip. gorgops*. The Lusso P_2's and those of *Hip. kaisensis* are also positioned within the 95% confidence ellipse of the *Hip. amphibius* sample for the L/l_2 index (Fig. 7). The RP_2 is not complete.

Lower P3: There are four P_3's in the sample, two in the Kt2-8 mandibular fragment(Fig. 1A). All present a single robust cusp with a strong cingulum mesially and distally. The RP_3 of the Kt2-8 mandible presents also a small lingual accessory cusp. This is a variable character within hippopotamid species. In general, isolated P_3's are not easily distinguishable to taxa. Kt2-8 left and right P_3's of course are part of a huge mandible whose sizes and shape exclude them from *Hexaprotodon* and *Trilobophorus*. The dimensions of the four Upper Semliki specimens are within the range of the *Hip. amphibius* sample, as are *Hip. kaisensis* and *Hip. gorgops*. They cannot, however, be assigned to *Hip. gorgops* because they do not have a talonid (Coryndon, 1976). *T. afarensis* P_3's are bicuspid and give the tooth a triangular shape (Gèze, 1985), much wider in the middle and in general with a quite different configuration from that shown by the Lusso sample. Figure 7 shows that the Upper Semliki sample, as well as the four P_3's known for *Hip. kaisensis*, falls within the 95% confidence ellipse for the *Hip. amphibius* sample.

P4: The right and left P_4's of mandibular fragment Kt2-8 are the only P_4's in the sample (Fig. 1A). They present one large triangular cusp with high cingulum distally. This is a point of dissimilarity with *Hip. gorgops*. In addition *T. afarensis* P_4's have low mesial and distal cingula. *Hip. amphibius* P_4's are indistinguishable from *Hip. kaisensis*, and both species from the Upper Semliki sample. In size, the sample of Upper Semliki P_4's is similar to *Hip. kaisensis*, and both are included in the *Hip. amphibius* range of LP_4's (Fig. 7). The Upper Semliki sample is smaller than *Hip. gorgops*, and substantially larger than *Hip. aethiopicus* (Pavlakis, 1987). Ky10-1, the only P^4, is missing the entire mesiolabial part. It is bicuspid with wide cingulum and circular perimeter, resembling in size and morphology *Hip. amphibius*. Ky10-1, a fragmented LP_4, is the only upper premolar in the sample. It is circular, bicuspid, and has a pronounced cingulum. It is similar in morphology to *Hip. amphibius*. No dimensions could be taken.

Molars: Five specimens are referred to *Hip.* aff. *H. amphibius* but they are badly fragmented. The eight lower molars resemble *Hip. kaisensis* in overall morphology, especially on their occlusal surfaces. They have thick and rugose enamel and, less clearly defined, a trefoil enamel pattern. They contrast with *Hip. gorgops* in the enamel pattern and the weak cingulum without pustulate ridges. The Upper Semliki molar sample could not be assigned to *Hexaprotodon* or *T. afarensis*. The dimensions of the molars in the sample are much larger, and the crown morphology is very different from the small, conical *Hexaprotodon* and *Trilobophorus* lower molars with the tapering upwards cusps and deep transverse valleys. The comparison of dimensions of the Lusso lower molar sample with species of *Hippopotamus* showed that it could not be assigned to *Hip. aethiopicus* on the basis of size, or to *Hip. gorgops* on the basis of the occlusal enamel pattern and the shape and size of the cingulum (Pavlakis, 1987). As shown in Figure 7, however, the *Hip.* aff. *H. amphibius* sample of lower molars is located within the 95% confidence ellipse of the *Hip. amphibius* sample, except for one M_2 which falls outside the ellipse because of the length (L) dimension. It is taxonomically significant that the *Hip. kaisensis* lower molars are also included within the *Hip. amphibius* range. Ky 7-57, the only upper
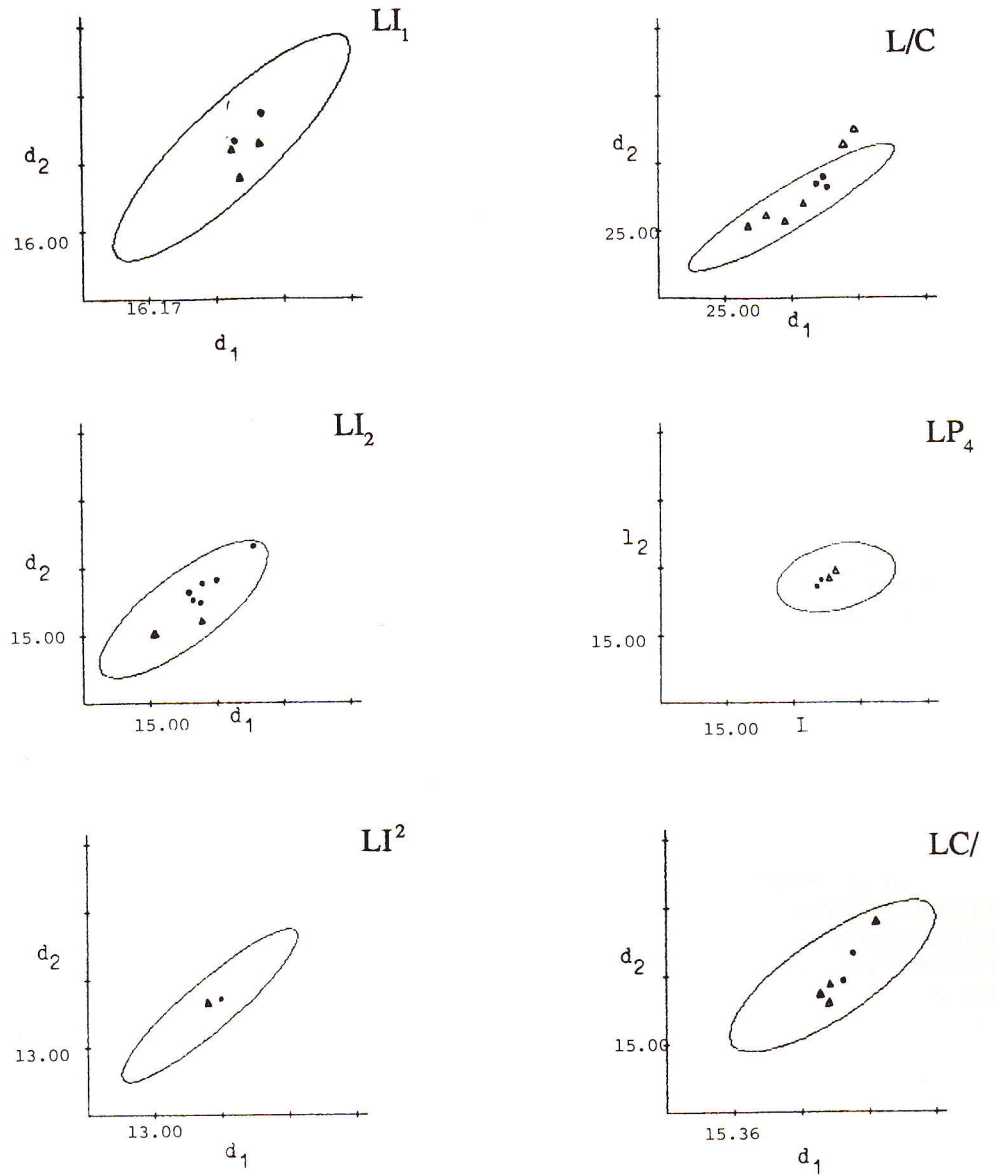
Figure 7. 95% confidence ellipses on dental measurements of the modern *Hippopotamus amphibius* sample of crania (N=34). Triangles represent specimens of the *Hippopotamus* aff. *H. amphibius* sample, and points are specimens of the *Hippopotamus kaisensis* hypodigm. For anterior teeth minimum diameter width (d_2) is plotted against maximum diameter (d_1). For cheek teeth maximum distal width (l_2) is plotted against maximum mesiodistal length (L). Other plots shown are: maximum mandibular width at canine tuberosities (l_1) to length of mandibular symphysis (e_4); height of right occipital condyle (h_k) to maximum distance between occipital condyles (l_o); maximum width of occipital plane (l_p) to maximum height of supraoccipital tuberosity (h_d); minimum height of right zygomatic process (h_c) to maximum width of right glenoid cavity (e_a); and maximum distance of zygapophyses (l_m) to minimum postorbital constriction (l_c). There is close correspondence among the samples.
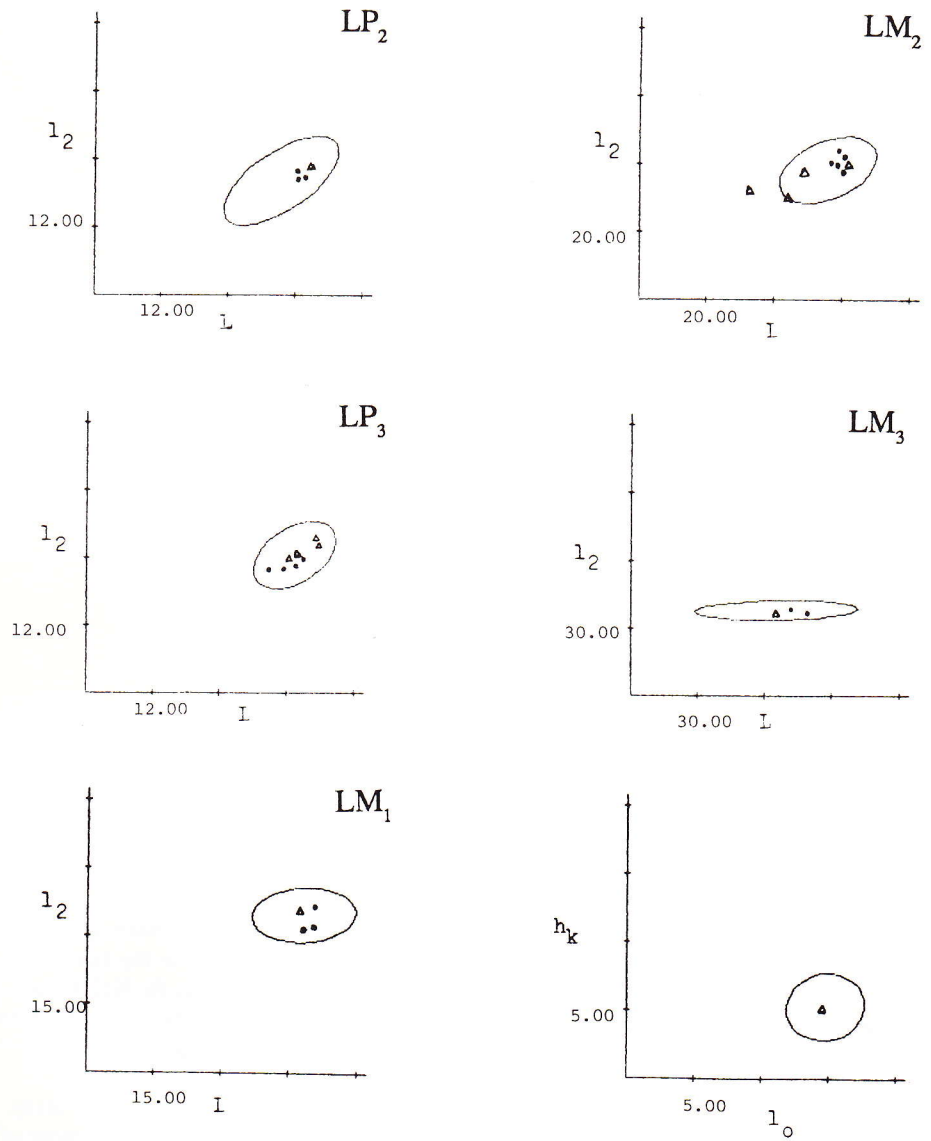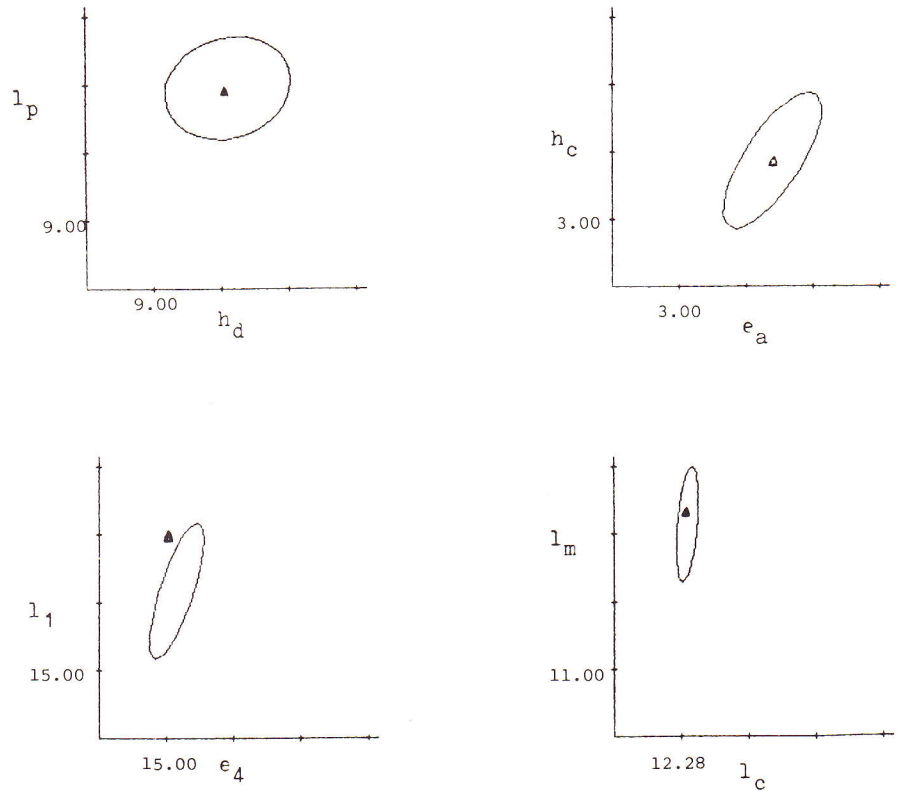
Figure 7 continued

Figure 7 continued

molar in the Upper Semliki large hippo sample, is indistinguishable from *Hip. amphibius* in size and morphology.

Kt2-8 mandibular fragment: Kt2-8 (Fig. 1A) is clearly tetraprotodont and, besides the size similarity, presents typical *Hippopotamus* canine characters (*T. afarensis* is hexaprotodont). Table 1 compares the dimensions of Kt2-8 with available samples of *Hippopotamus* species. *Hip. aethiopicus* is removed from any consideration due to its very small size (Coppens and Coryndon, 1975). In addition, the Kt2-8 P_4 differs substantially in the occlusal morphology from *Hip. gorgops*, as discussed previously. Kt2-8 is within the *Hip. amphibius* range of dimensions except for the mandibular ramus width (e_2) at P_3, and the intercanine distance (l_1), which falls outside the upper range of the *Hip. amphibius* sample. It is evident from the size of the alveolus that the second incisor is not much smaller than the first, thus approaching the *Hip. kaisensis* condition more than the *Hip. amphibius*. The

dimensions of the Kt2-8 canine and third premolar exceed the *Hip. kaisensis* range, but are included in the *Hip. amphibius* range. The 95% confidence ellipse for the l_1/e_4 index of modern hippos relative to the Kt2-8 mandible is shown in Figure 7. The large intercanine distance (l_1) puts Kt2-8 just outside the 95% ellipse.

Ks3-2 opisthocranium: Comparing the dimensions of Ks3-2 (Fig. 1B) with those of the *Hip. amphibius* sample, we note in most measurements a close similarity to the mean of the sample. Furthermore, morphologically, Ks3-2 is very similar to *Hip. amphibius*. The glenoid cavity is wide, with the paroccipital process protruding beyond the level of the occipital condyle. The foramen magnum is quite narrow and superiorly there is no high crest. The frontal and the fronto-parietal sutures are flat. The only material comparable to Ks3-2 in the *Hip. kaisensis* hypodigm is a fragment of the left otic region (Cooke and Coryndon, 1970:192). It presents a more compressed post-glenoid area

than in Ks3-2 or *Hip. amphibius*.

In addition, *Hip. gorgops* presents a different configuration of the occipital part than Ks3-2, with the extreme elevation of the supraoccipital apophyses. Comparing Ks3-2 to *Hip. aethiopicus*, the most notable difference is that the latter taxon has a *Hexaprotodon*-like lateral cranial shape with the postorbital part of the cranium ascending towards the orbits. The 95% confidence ellipses of the modern hippo sample for available Ks3-2 indices are shown in Figure 7 (indices h_k/l_o, l_p/h_d, h_c/e_a, l_m/l_c). They illustrate the close similarity of Ks3-2 to *Hip. amphibius*. In all graphs Ks3-2 fits remarkably near the center of the ellipse.

Postcrania: *Hippopotamus* postcrania in general are not easily classified into species. The Upper Semliki postcranial sample is very similar to modern hippo. Specifically, the dimensions of the complete left astragalus Mn1-16 are compared in Table 2 with samples of astragali of most East African hippopotamid species. Mn1-16 is closer to *Hip. amphibius* in the ratio of the dimensions than to any other species. It should be noted that Mn1 is not a Lusso Bed site and is likely late Pleistocene in age, so this result is not unexpected.

DISCUSSION

That there are two hippopotamid species present in the Upper Semliki Plio-Pleistocene to late Pleistocene mammalian fauna, is easily detectable from the size difference between the samples assigned to *Hexaprotodon* cf. *H. imagunculus* and *Hippopotamus* aff. *H. amphibius*. Figure 5A, for example, very clearly demonstrates this size difference. The two molars Lu2-13 (LM$_2$) and Lu2-1 (RM$_2$) would appear to belong to two different taxa. The roughly equal amount of wear shown by both indicates that they were generally of similar age. In addition, the size difference is so large that sexual dimorphism is excluded. The estimated length and width of Lu2-13 fall outside the lower range of the LM$_2$ dimensions in the sample of 34 modern *Hip. amphibius*, while Lu2-1 falls well within the range (Pavlakis, 1987). Even with the large modern *Hip. amphibius* intraspecific variation as scale, it is apparent that Lu2-13 and Lu2-1 do not belong to the same species. The same is also evident

from the scaphoids Ky1-20 and Kn3-15 (Fig. 5B), as well as from most specimens belonging to the two taxa recognized in the Upper Semliki hippopotamid material. The taxonomic assignment, however, of these two samples is not so straightforward.

After the detailed comparison of each specimen with East African hippopotamid species, it is evident that the Upper Semliki small hippopotamid sample is very similar to *Hex. imagunculus*. *Hex. imagunculus*, however, is still a poorly known species. Its hypodigm consists of only isolated teeth and fragmentary jaws (Cooke and Coryndon, 1970). No complete skull is yet known, so detailed comparisons are not possible. The relevant material from the Upper Semliki is also very fragmentary and does not contribute to a better understanding of that species. Even though the size of the sample's anterior teeth conformed to the hypodigm of *Hex. imagunculus*, their morphology is quite undiagnostic for taxonomic purposes. For this reason therefore, and in order to stress the fact that *Hex. imagunculus* is not a suitably defined species, I assign the Upper Semliki small hippopotamid sample to *Hexaprotodon* cf. *H. imagunculus* until further material becomes available. I prefer to restrict the nomen *Hex. imagunculus* to the material found in the type locality of the Uganda Kaiso Formation. Biostratigraphically, *Hex.* cf. *H. imagunculus* coexists in Lusso Beds with the large hippopotamid but disappears after Lusso times, as does *Hex. imagunculus* in the Kaiso Formation.

The Upper Semliki large hippopotamid sample is referred here to *Hip.* aff. *H. amphibius*. Hooijer (1950) and Coryndon (1970) established that the taxon *Hip. amphibius* includes a substantial morphological variation. Hooijer (1950) specifically made an analysis of this variation and suggested that the existence at that time of five subspecies within the modern amphibious hippo is without foundation. He concluded that *Hip. amphibius* is a single morphologically continuous taxon and noted that it presents a considerable amount of variation. He applied this observed range of variation to the fossil species *Hex. sivalensis*, to which he included skulls which evolved from an early Pleistocene stage having low orbits, elongated post-orbital region, long low

Table 2. Comparison of *Hippopotamus* aff. *H. amphibius* astragalus Mn1-16 dimensions. Abbreviations as in Table 1.

		H1	H2	H3	L1	L2	e1	e2	H1/L1	H2/L1	H3/L1	H1/L2	H2/L2	H3/L2
Hex. protamphibius	X	82.55	80.47	92.53	59.06	71.12	--	--	1.448	1.362	1.570	1.160	1.130	1.300
	R+	85.00	90.00	98.00	68.00	77.00	--	--						
	R-	62.00	64.00	71.00	51.00	58.00	--	--						
	N	121												
Hex. shungurensis	X	69.50	72.40	78.00	59.40	59.60	--	--	1.170	1.218	1.310	1.170	1.210	1.310
	R+	71.00	76.00	81.00	60.00	63.00	--	--						
	R-	67.00	70.00	76.00	51.00	56.00	--	--						
	N	10												
Hex. karumensis	X	87.00	89.00	96.00	62.00	73.00	--	--	1.312	1.361	1.310	1.190	1.230	1.320
	N	1												
Hex. imagunculus	X	77.88	83.88	--	64.50	64.90	--	--	1.207	1.301	--	1.200	1.290	--
	N	1												
Hex. liberiensis	X	47.15	50.95	54.45	33.10	39.90	45.45	25.35	1.424	1.539	1.650	1.180	1.280	1.360
	N	1												
Hip. gorgops	X	96.50	109.10	108.70	73.50	84.70	--	--	1.312	1.361	1.280	1.140	1.180	1.280
	R+	108.00	105.00	123.00	90.00	106.00	--	--						
	R-	90.00	92.00	98.00	65.00	73.00	--	--						
	N	10												
Hip. aethiopicus	X	62.75	63.75	68.25	45.75	51.00	--	--	1.371	1.393	1.490	1.230	1.250	1.340
	N	1												
Hip. kaisensis	X	--	93.64	--	67.36	74.06	--	--	--	1.539	--	--	1.260	--
	N	1												
Hip. amphibius	X	76.45	82.20	84.25	63.25	78.20	59.25	33.70	1.208	1.299	1.30	0.980	1.050	1.080
	N	1												
Mn1-16	X	86.20	89.95	93.05	69.20	84.40	67.85	47.75	1.245	1.299	1.340	1.020	1.060	1.100
	N	1												

symphysis and low horizontal ramus, to a late Pleistocene stage having high orbits, shorter postorbital region, narrow and high symphysis, and horizontal ramus. More recently, Gèze (1980, 1985) divided *Hex. protamphibius* into two subspecies, *Hex. p. turkanensis* and *Hex. p. protamphibius*. The range of morphological variation within this species includes: hexaprotodonty to tetraprotodonty, orbits low to moderately high, occipital plane high to lower, cranium long to globular, and brachydont to marked hypsodont postcanine teeth.

Taking into consideration the fact that some fossil hippopotamid species and the modern amphibious hippo include a large amount of morphological variation, as well as my own observations of the close morphological similarity of the *Hip. kaisensis* material to *Hip. amphibius*, I decided to test the validity of *Hip. kaisensis* taxon. For this reason I compared the *Hip. kaisensis* hypodigm with the sample of 34 skulls of modern hippo referred to at the morphological comparison. The statistical analysis applied to the samples of *Hip. kaisensis* and *Hip. amphibius* measurements was employed in order to evaluate the hypothesis that both samples belong to a single population. The two-sided students' t-test (Thomas, 1976) was applied since I actually compared two sample means while the population standard deviation is unknown (Simpson et al., 1960). The results of the metric character analysis showed that 99% of the time each measurement included in the entire *Hip. kaisensis* hypodigm belonged to the *Hip. amphibius* population. This is also supported by the 95% confidence ellipses made on the *Hip. amphibius* sample of 34 crania. Every available cranial measurement of the *Hip. kaisensis* hypodigm falls within the ellipse (Fig. 7, plus indices L/l_2 for LP^3, L/l_1 for LP^4, and the mandibular indices h_2/e_2 and l_6/e_4 which are not shown). Furthermore, the results of the comparison of the available nonmetric characters between the *Hip. kaisensis* entire hypodigm and the 34 *Hip. amphibius* skulls revealed that the existing morphological differences are of a strictly quantitative nature. There is no clean-cut, qualitative morphological difference between the two taxa in the available *Hip. kaisensis* material. Characteristics

typical for *Hip. kaisensis* which are found only rarely in *Hip. amphibius* are the triangular enamel pattern of molars, the mostly bicuspid P_3, and the rugose enamel of the lower molars. In addition, the *Hip. kaisensis* I_2's are not as small relative to the central incisors as in *Hip. amphibius*. Nevertheless, all the above characters were present in about 8% of the sample of 34 modern skulls. All other morphological characteristics of *Hip. kaisensis* that are included in its diagnosis (Cooke and Coryndon, 1970) were present in *Hip. amphibius* for at least 20% of the sample.

In the known morphological characters *Hip. kaisensis* has retained many primitive characteristics: large I_2, lower premolars often with pustulate ridges, P^4 more often bicuspid, molars with triangular enamel pattern, and possibly more slender body proportions than *Hip. amphibius*. *Hip. amphibius* shows a reduction of the I_2 size, simpler premolars, often single-cuspid P_4, molars with trefoil enamel pattern, and possibly with heavier body proportions. All these differences between the two taxa are not clear-cut. Both *Hip. amphibius* and *Hip. kaisensis* present these characters although *Hip. kaisensis* shows the first set of characters more often than does *Hip. amphibius*.

Taking, therefore, the following facts under consideration: (a) according to the current taxonomy of the family Hippopotamidae, fossil species such as *Hex. sivalensis* (Hooijer, 1950) and *Hex. protamphibius* (Gèze, 1985) include a wide range of morphological variation, (b) the modern *Hip. amphibius* is also morphologically substantially variable (Hooijer, 1950; Pavlakis, 1987); and (c) *Hip. kaisensis* in its known morphology is considerably similar to *Hip. amphibius*; the validity of *Hip. kaisensis* taxon is questionable. Therefore, I refer the Upper Semliki large hippopotamid sample close to *Hip. kaisensis* and *Hip. amphibius* to *Hip. aff. H. amphibius*. The oldest fossil record of *Hip. amphibius* is in Member K of the Omo Shungura Formation (Gèze, 1980). The present date of Tuff K is 1.6 my BP (Brown et al., 1985). The oldest record of *Hip. aff. H. amphibius* in the Western Rift is close to 2.3 my BP. The specific taxonomic status of the Western Rift large *Hippopotamus* taxa *Hip. aff. H. amphibius* and *Hip. kaisensis* should await a major revision of the family Hippopotamidae.

Additionally, the recovery of further fossil material for both *Hip. amphibius* and *Hip. kaisensis* will provide data which may help to define better their taxonomic relationships.

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