HIPPARIONS FROM THE LATE MIOCENE AND PLIOCENE OF NORTHWESTERN KENYA

by

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With 2 text-figures and 8 plates

Abstract

The faunas of Lothagam, Kanapoi and Ekora on the west side of Lake Rudolf in Kenya include well-preserved *Hipparion* material. The most interesting species is represented by a skull from Lothagam that is devoid of a preorbital fossa: *Hipparion turkanense* Hooijer & Maglio. The upper cheek teeth have small fossette plications and rather wrinkled anteroposterior fossette borders; the lower cheek teeth also show this wrinkled enamel condition, notably on the buccal wall, and sport no ectostylids. The closest resemblances are with certain Chinese "Pontian" forms described by Sefve.

An equally large *Hipparion* with a preorbital fossa occurs at Kanapoi and Ekora. The upper cheek teeth are richly plicated fore and aft, and the anteroposterior fossette borders are not wrinkled. The lower cheek teeth do possess ectostylids, although these structures do not always show. This species also occurs in the "Pontian" of North Africa: it was described as *Hipparion africanum* Arambourg from Wad el Hammam in Algeria. We designate the Kanapoi-Ekora *Hipparion* as *Hipparion primigenium* (Von Meyer).

A third species represented in the Lothagam-Kanapoi-Ekora collection is of small size; not only the teeth are present but also a set of metacarpals. The isolated teeth present a striking resemblance to those of *Hipparion sitifense* Pomel from deposits of pre-Villafranchian age in North Africa (Saint-Arnaud, Mascara). The median metacarpal is as slender in build as that of *Hipparion mediterraneum* Roth & Wagner from Pikermi, but the distal articulations of metacarpals II and IV are heavier than in that species. We designate the small northwestern Kenya *Hipparion* as *Hipparion* cf. *sitifense* Pomel.

Introduction

In spite of enhanced paleontological field exploration in Africa during the past decade, the late Miocene and Pliocene epochs remain poorly represented. Among the major new localities producing fossils of these ages are Langebaanweg (Hendey, 1970a, 1970b) and the Chiwondo Beds (Mawby, 1970) in southern Africa, Kolinga, Koulá, and Ouadi Derdemy (Coppens, 1962) in Chad, and a variety of sedimentary deposits in eastern Africa. The latter include the Mpesida, Lukeino, Kaperyon and Aterir beds in the Baringo basin (Bishop et al., 1971), the Lothagam, Kanapoi and Ekora formations on the west side of Lake Rudolf (Patterson et al., 1970), the Kubi Algi beds on the eastern side of the Lake (Maglio, 1972), and the Mursi Formation in the Lower Omo Valley. Of these new localities Kanapoi and Lothagam have so far yielded the most complete and best preserved faunas.

Lothagam Hill lies about 35 miles ESE of Lodwar, between the deltas of the Kerio and Turkwel rivers. The tilted fossiliferous sediments rest on a thick sequence of Miocene volcanics dated from 16.8 ± 0.5 m.y. at the bottom to 8.31 ± 0.25 m.y. near the top. Discomformably above these volcanics are more than 480 meters of fluvial-deltaic deposits comprising unit 1 and containing the earliest fossil assemblage at Lothagam. The geology of this succession has already been discussed (Patterson et al., 1970).

Unit 1 is conformably overlain by an 80 meter thick sequence (unit 2) of fine grained lacustrine deposits with only the rare occurrence of fossils. A third unit (unit 3) follows conformably and represents a return to fluvial deposition with 90 meters of section exposed before being covered by recent alluvium. An upper age limit for these deposits is given by a basalt sill some 30 meters thick intruded between units 1 and 2, and apparently postdating the entire Lothagam sequence.

The fauna of unit 1 is clearly much older than those from Olduvai Gorge, Omo or East Rudolf and contains numerous elements that are far more archaic than those from the dated Mursi Formation (4.0 m.y.) and the Kubi Algi beds (4.55 m.y.). This unit 1 fauna correlates best with assemblages from the Mpesida and Kaperyon beds dated at 7.0 and 5.0 m.y. respectively (Bishop et al., 1971). Thus the age of unit 1 may be placed approximately at 6.0 m.y. Although it may be somewhat older than this figure, it is not likely to be much younger.

The fauna from unit 3 shows considerable advance over that of unit 1, and correlates in most details with material from the Mursi Formation and from Kanapoi (see below). This puts the age rather firmly at about 4.0 m.y.

Located about 40 miles to the south, along the drainage of the Kalabatha River, are fossiliferous outcrops of the Kanapoi Formation (fig. 1), consisting of more than 60 meters of fluvial to lacustrine deposits (Patterson et al., 1970). The sequence is capped by a basaltic flow originally dated at 2.5-2.9 m.y. These early samples are now considered to have been altered and a new determination has placed the age of this flow at 4.0 m.y. (F. Fitch, pers. comm.). This confirms fully the faunal evidence which suggests contemporaneity with the Mursi Formation.

Lying conformably above the Kanapoi basalt is the Ekora Formation, exposed some 17 miles to the northeast. The Ekora fauna is rather limited and appears to be approximately of the Kanapoi type.

It is interesting to note that in early publications on these localities Kana-

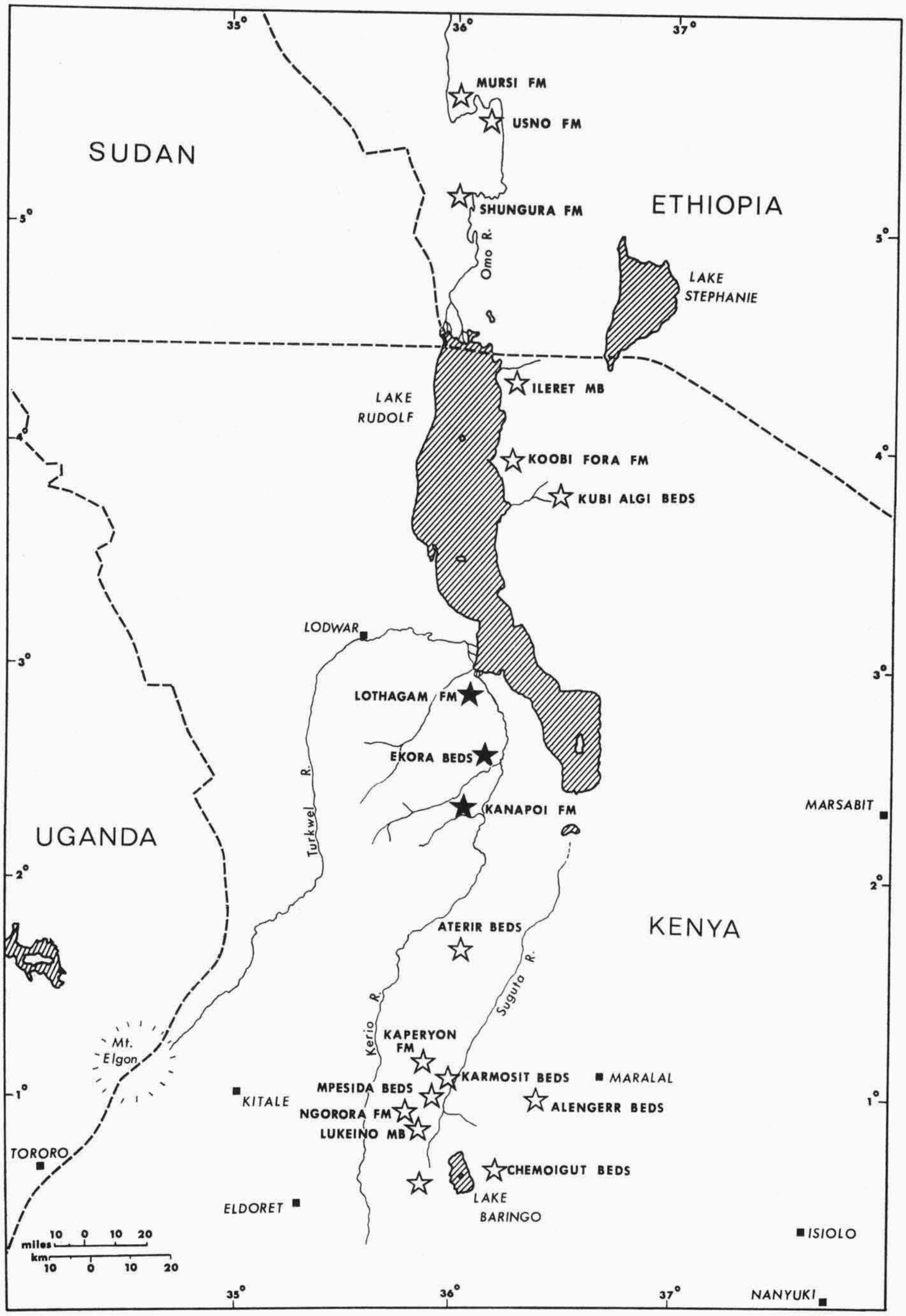

Fig. 1. Map of Kenya showing the geographic relationships of the Lothagam, Kanapoi and Ekora localities to other major fossil sites in East Africa.

poi was considered to be early Pleistocene in age (Patterson, 1966) and Lothagam late Pliocene (Maglio, 1970). As radiometric ages became available for these sites their relative positions within the geological time scale were revised downward with Kanapoi emerging as late Pliocene and Lothagam as Middle Pliocene (Cooke & Ewer, 1972).

Further confusing the picture are new radiometric calibrations of European marine sections upon which these relative time units are based. Such studies indicate a younger age for classic European stages correlated with dated deep-sea cores zoned on planktonic foraminiferal and nannoplanktonic criteria (Blow, 1969; Berggren, 1969; Van Couvering, 1972). If the Miocene/Pliocene boundary is taken within foraminiferal Zone N. 18, the absolute age of the boundary emerges as about 5.0 m.y. (Berggren, 1969). More recently, Bandy (1972) suggested a younger age of 3.0 m.y. for a Mio/Pliocene boundary placed at the base of Zone N. 19.

As for the Pliocene/Pleistocene boundary, similar uncertainty prevails. For European sections, Lyell's boundary has been equated with the base of the marine Calabrian and with the bottom of Foraminiferal Zone N. 22 (Hays et al., 1969), even though underlying Astian sands contain continental fossils of early Villafranchian type (Selli, 1967). Radiometric data for the Zone N. 21-N. 22 boundary give an age of ca. 1.8 m.y. On land mammal criteria Azzaroli (1970) suggested 2.7 m.y. as the age of the Plio/Pleistocene, and Ambrosetti et al. (1972) have placed the boundary between 2.5 m.y. and 3.4 m.y.

It is thus clear that the use of terms such as late Miocene and early Pleistocene will have little objective meaning until arbitrarily set by international agreement. It would seem best to avoid their use altogether, although lacking stage units as an alternative in Africa, these terms are difficult to set aside. For purposes of the present paper we follow Van Couvering (1972) in placing the Mio/Pliocene boundary at 5.0 m.y. and the Plio/Pleistocene boundary at 1.8 m.y. Thus, Lothagam 1 may be considered late Miocene in age and Kanapoi-Ekora as early Pliocene.

The equid material described in the present paper was collected between 1965 and 1972 by expeditions from Harvard and Princeton Universities. The stratigraphic position of each specimen is indicated on the diagrammatic sections given in fig. 2. All specimens are housed in the permanent collections of the National Museum of Kenya, Nairobi.

Acknowledgments

The authors thank Bryan Patterson for his permission to study specimens collected by him in 1965-1967, and the National Museum of Kenya for

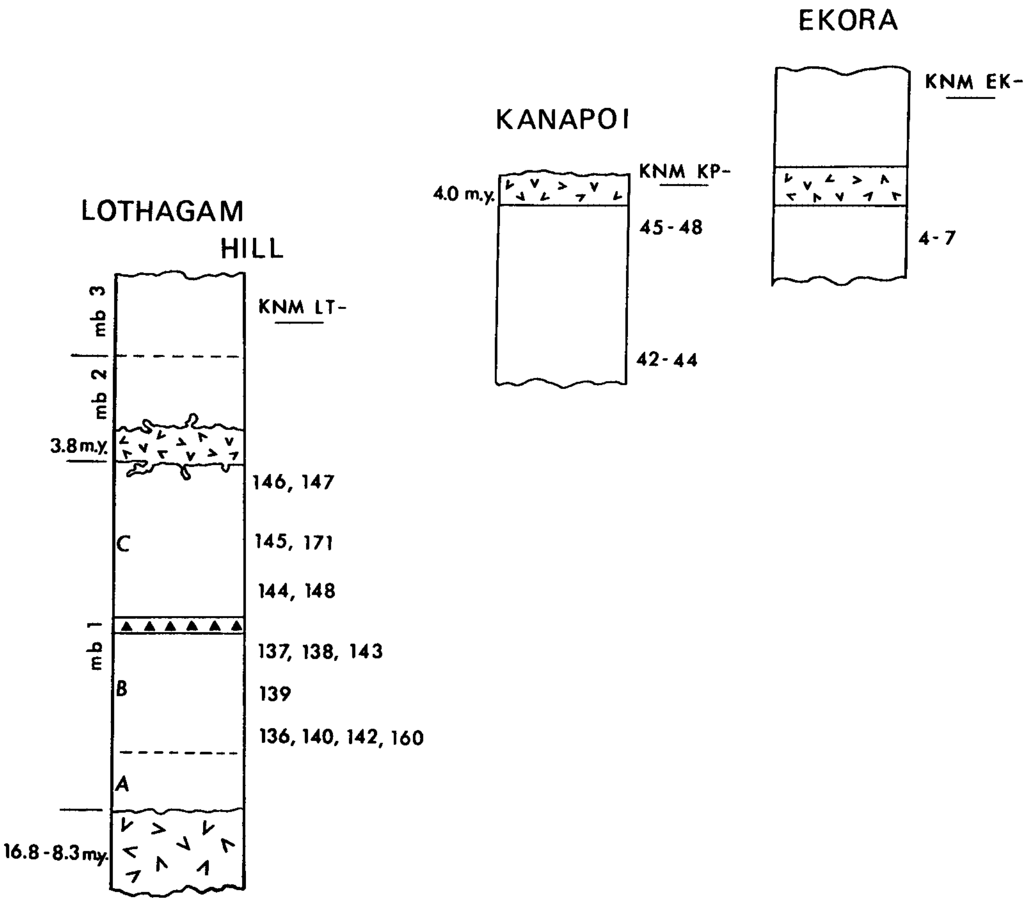

Fig. 2. Diagrammatic section of the Lothagam, Kanapoi and Ekora formations showing the stratigraphic positions of important equid specimens discussed in the text.

allowing the export of material collected in 1968 and 1972. For support of the field work we are indebted to the National Science Foundation (U.S.A.) for grants to B. Patterson (nos. GP-1188 and GA-425), and to the National Geographic Society and the Wenner-Gren Foundation for Anthropological Research for grants to V. Maglio. Funds from Princeton University made possible the visit of D. A. Hooijer for this study. We owe the restoration of the type skull of *Hipparion turkanense* to the dexterity of Mr. Arnie Lewis, Harvard University. Preparation of further *Hipparion* material was done at Princeton by Mr. James Everhart. The following abbreviations are used: KNM, National Museum of Kenya; LT, Lothagam Hill; KP, Kanapoi; EK, Ekora.

Class Mammalia
Order Perissodactyla
Family Equidae

Hipparion turkanense Hooijer & Maglio

A formal diagnosis of the present species has already been presented (Hooijer & Maglio, 1973) as follows: Size large: basilar length of skull 465 mm, length P^2-M^3 165 mm. Muzzle moderately long, nasal notch over P^2, no preorbital fossa. Upper cheek teeth with fossette plications moderate in amplitude, anteroposteriorly oriented enamel borders of fossettes wrinkled, protocones oval but flattened internally. Lower cheek teeth with wrinkled enamel in the entoflexid and buccally, proto- and ptychostylids, but devoid of ectostylids. The holotype is the adult skull, KNM LT-136, figured on pl. 1 of the present paper.

The type skull, KNM LT-136, is rather well preserved on the left side; the right side of the facial part is largely reconstructed except for the tooth-bearing portion of the maxillary. The nasals are likewise modelled in plaster, and their length thus cannot be determined. However, on the left side of the skull the deepest point of the nasal notch is shown; it is formed by the premaxillary bone, which encroaches high on the side of the snout, resulting in the ass-type of naso-premaxillary suture (in the horse the deepest point of the notch is formed by the nasal: Hooijer, 1949: 258)). The lateral notch is situated above the anterior border of P^2. The incisor-bearing portion of the premaxillaries is not complete, but I^3 sin. is in situ, showing that the diastema is neither excessively long nor short (21.5 per cent of the basilar length, within the range of both horses and asses: Hooijer, 1949: 252).

There are small canines placed at two-thirds the distance between P^2 and I^3, in front of P^2. The extent of the palatine fissure cannot be judged, but the posterior end was somewhat in front of P^2. The infraorbital foramen is small and situated above the posterior border of P^2. The facial crest begins to emerge above the anterior border of M^1, and the posterior border of the palatum durum is on a level with the posterior border of M^2 in the median line. On the maxillary bone there is a very shallow depression, only about 4 cm long, beginning 1 cm behind the infraorbital foramen and at most 2 cm high. The bone around it is somewhat broken and distorted, and it seems possible that the depression was even less distinct in the original state. At any rate, a true preorbital fossa is clearly lacking in this skull.

The orbit is distorted, its lower margin being pushed in. The greatest width of the skull is at the glenoid fossa, but might originally have been at the posterior border of the orbit; this is difficult to tell. The cranial base is present for the most part, the left paroccipital process is almost entirely preserved, and both occipital condyles are present and only slightly distorted. The occiput is complete when seen from behind, but the top with the sagittal crest is restored. The dorsal surface of the skull from the postorbital constriction to several cm in front of the orbits is restoration. Measurements are given in table 1.

TABLE 1

Basilar length (prosthion-basion)	465
Prosthion - posterior end palatum durum	250
Prosthion - posterior border of M^3	280
From anterior border of P^2 to orbit	170
Diastema I^3 - P^2	100
Length P^2 - M^3	163
Length P^2 - P^4	89
Length M^1 - M^3	74
Palatal width between M^3	70
Postorbital constriction	ca.70
Greatest width of cranium	ca.90
Zygomatic width	ca.200
Bicondylar width	80
Height of occiput (from basion)	ca.110

Skull measurements of the type skull of *Hipparion turkanense* KNM LT-136 (mm).

The dentition of the adult Lothagam skull is in a good state of preservation apart from the incisors, of which only I^3 sin. is entire; parts of both I^2, and of the right central incisor are preserved. Because of the bad state of preservation, and some restoration it is impossible to give accurate measurements of the incisor crowns, but I^3 evidently is not much smaller than I^2. Only I^2 sin. shows a cup, or mark; the cement has gone. The canine is rather small, 8 mm anteroposteriorly and 5 mm transversely in crown diameters. In front of P^2 there is no alveolus for the vestigial first premolar. The premolar-molar series is entire on both sides, and its relative length (table 1), 35 per cent of the basilar skull length, is within horse as well as ass limits (Hooijer, 1949: 252). The stage of wear is advanced; the crown height of M^1 is only about 12 mm.

P^2, as all premolars, has the anterior horn of the postfossette extending outward markedly beyond the posterior horn of the prefossette. The inner and outer borders of the fossettes are finely wrinkled; this applies to all the cheek teeth and is one of the most characteristic features of this specimen. The anterior and posterior plis of the two fossettes are very minor in amplitude: the most important of them are the pli protoconule, which is barely one mm in extent, and the pli postfossette, which is only slightly longer and double. Development of these plis is never exactly the same in the homologous teeth on either side of the jaw; e.g., the anterior portion of the pli postfossette in P^2 sin., but the posterior portion of the same in P^2 dext., is the larger of the two. There are in all 4 folds in the posterior border of the prefossette, and 3 or 4 in the anterior border of the postfossette. The buccal portion of the postfossette of P^2 dext., which extends toward the mesostyle, is isolated as a fossette, whereas this portion is still confluent with the whole postfossette in P^2 sin.; this emphasizes the high degree of variability in plication pattern of equid teeth even in identical wear stages. The plication numbers given in tables 4 and 5, where we have all or most of the teeth from both sides of the jaw, show that differences of 2 plis between the right and the left tooth of the same serial position may occur.

The protocone, isolated in P^2 sin., is confluent with the protoconule on the occlusal surface in P^2 dext. It is flattened internally and not much longer than wide. There is a rather deep but narrow hypoconal groove, or hypoglyph. A pli hypostyle, in the posterior border of the postfossette, is not present. The anteroposterior borders of both fossettes, especially the buccal ones, are very finely serrated.

P^3 of course lacks the prolongation anterior to the parastyle that characterizes the P^2 but is otherwise similar in dental pattern. The protocone is slightly shorter and thereby relatively wider, the fossette plications are similar, and the hypoglyph is present, but very shallow. This is remarkable since in P^4, which is less worn than P^3 (whereas of course P^2 is more worn than P^3) the development of the hypoglyph is again the same as that in P^2. The protocones of P^3 and P^4 are indistinguishable; they are oval but flattened internally. The fossette plications (those in the posterior border of the prefossette including the pli protoconule and the tinier ones buccal to it, and those in the anterior border of the postfossette including the pli postfossette and the smaller ones on its buccal side) are more numerous than in P^2. The pli hypostyle is not apparent.

The molars differ from the premolars in having a rather smaller parastyle, not broader than the mesostyle as in the premolars, and in their lesser length. There is a gradation in protocone shape as one passes from M^1 to M^3; the protocones as shown on the occlusal surfaces become shorter but even more markedly narrower so that in M^3 the protocone is almost twice as long as wide, but they keep their internal flattening throughout. Plication numbers in the posterior border of the prefossette, and in the anterior border of the postfossette, are the same as those in the premolars, the complexity being greatest in the prefossette, as usual. The pli hypostyle shows in all the molars, be it weakly developed. In M^3 the hypocone is very nearly constricted off by the hypoglyph and by an anterior hypocone fold; the latter fold does not show in M^1 and M^2 or in the premolars.

The measurements of the cheek teeth of the type skull of *Hipparion turkanense* are given in table 2. They have been taken at the alveolar borders, which are close to the crown bases in this aged individual. The protocones, however, are measured at the worn surfaces as they are thickly coated by cement and cannot otherwise be measured. Full plication numbers

TABLE 2

P^2,	ant.-post.		38	35	M^1,	ant.-post.		22	22.5
	transv.		24	23		transv.		27	25
	protocone,	ant.-post.	9.5	7		protocone,	ant.-post.	10	7.5
		transv.	7	4			transv.	6	4
P^3,	ant.-post.		25	26	M^2,	ant.-post.		22	22
	transv.		26	25		transv.		28	23.5
	protocone,	ant.-post.	9	7.5		protocone,	ant.-post.	9.5	7.5
		transv.	7	4			transv.	5	4
P^4,	ant.-post.		26	24	M^3,	ant.-post.		29	24
	transv.		28	25		transv.		25	22
	protocone,	ant.-post.	9	7.5		protocone,	ant.-post.	9	8
		transv.	6.5	4			transv.	5	3.5

Measurements of teeth of type skull of *Hipparion turkanense*, KNM LT-136 (first column) and of the Kanapoi upper dentition of *Hipparion primigenium*, KNM KP-43 (second column) (mm).

are given in table 3; where the right and the left teeth differ, the number is given thus: 4-5.

The adult Lothagam skull KNM LT-136 is slightly larger than that of *Hipparion africanum* Arambourg (1959) from the Vallesian equivalent of Wad el Hammam in North Africa. The prosthion to posterior border of M^3 length of the latter is 260 mm, compared to 280 mm in the Lothagam skull; the I^3-P^2 diastema measures 97 mm, as opposed to 100 mm for

TABLE 3

	prefossette		postfossette		pli caballin
	ant.	post.	ant.	post.	
P^2	2-5	4	3-4	1-2	2
P^3	1-2	5-7	4-5	2-3	1-2
P^4	3	8-9	6	2	1
M^1	2	7-8	6	1-2	2
M^2	3-5	8	6	1-2	2
M^3	2	7-8	5	2	2

Plication numbers in upper cheek teeth of the type skull of *Hipparion turkanense*, KNM LT-136.

Lothagam, and the P^2-M^3 length is 141-154 mm in *H. africanum*, compared to 163 mm in the Lothagam specimen. However, *Hipparion africanum* has a preorbital fossa, which is so conspicuously lacking in our Lothagam skull. *H. africanum* has been synonymized with the classic *Hipparion primigenium* (Von Meyer) of the Vallesian and Pikermian (the "Pontian") of Europe (Forstén, 1968: 15). Species of *Hipparion* without a preorbital fossa are rare; as a matter of fact a preorbital fossa is lacking not in the European but in one of the Chinese "Pontian" forms, viz., *Hipparion hippidiodum* Sefve (1927 : 9) (including in part *H. kreugeri* Sefve and *H. ptychodum* Sefve in the revision by Forstén (1968: 73)). The fossa is also lacking in two Villafranchian forms, the Spanish *Hipparion crusafonti* Villalta (1952; Sondaar, 1961: 261; Forstén, 1968: 63), and the Chinese *Proboscidipparion sinense* Sefve (1927: 55; Forstén, 1968: 82). The dental pattern of the Lothagam skull is very close to that of *H. hippidiodum* and *H. kreugeri* as figured by Sefve (1927: 92), although the internal flattening of the protocones is more marked than that in the Chinese forms. The wrinkling of the inner and outer fossette borders shows very markedly in *Proboscidipparion sinense* (Sefve, 1927: 62), which is of the same size as our Lothagam skull as far as the teeth go (length P^2-M^3 165 mm), although the peculiar development of the nasal bones sets it apart from the ordinary *Hipparion*. We believe that the resemblances noted between the Lothagam form and the Chinese "Pontian" forms may not be taken to indicate specific identity, and, therefore, we have coined a new specific name, *H. turkanense*, for the large Lothagam *Hipparion* (Hooijer & Maglio, 1973).

Hipparion primigenium (Von Meyer)

The next best upper dentition in the Lothagam-Kanapoi-Ekora collection is one represented by P^3-M^3 dext. and P^2, P^4, and M^2 sin. from Kanapoi, KNM KP-43 (pl. 3 figs. 1, 2). It differs markedly from the Lothagam *H. turkanense* dention just described in the greater amplitude of the fossette border plis fore and aft, in the inner and outer fossette borders not being thrown into fine wrinkles, and in the narrower protocones. The Kanapoi dentition is somewhat less worn than the Lothagam dentition: the crown height of M^1 is 36 mm as opposed to only about 12 mm in the Lothagam skull. It is known that protocones tend to become relatively wider with advancing age, and that plications tend to flatten out as wear advances. Nevertheless, the differences between the Lothagam and the Kanapoi adult dentitions would seem to be greater than could be accounted for just by a difference in individual age at the time of fossilization. Data on the Kanapoi teeth are given in table 2; since these are isolated specimens the anteroposterior and transverse crown diameters have been taken near the base (which is damaged in P^4 and M^1 dext. as well as in P^4 sin.), slightly above the crown-root junction. At the "neck" the crown is constricted anteroposteriorly, and the protocone projects far inward so that measurements at this level are not very useful for comparison, e.g., with those taken at the alveolar borders in the Lothagam skull. It will be seen from table 2 that the Kanapoi teeth are a little less wide in the molar region and have relatively more compressed protocones (measured, as always, at the occlusal surface as cement covers them everywhere else). Full plication numbers are given in table 4.

There is a juvenile skull from Ekora, KNM EK-4, with the full milk dentition $DM^{2\text{-}4}$ in wear and $M^{1\text{-}2}$ unerupted. The permanent molars have been taken out of their sockets, and M^1 sectioned at two levels. This molar, which is not yet fully calcified down to the neck, has a full height of 64 mm from the top of the crown to the closed base between the fossettes, and this, by an anteroposterior diameter of 22 mm, gives a height-length index of 290. The transverse diameter is 21.5 mm throughout. The two levels at which the M^1 sin. has been sectioned are at 16 mm and again 36 mm below the top of the crown. The illustrations (pl. 5, figs. 1-3) show that in moving rootward for 20 mm the fossette plis become less great in extent, and the

TABLE 4

	prefossette		postfossette		pli caballin
	ant.	post.	ant.	post.	
P^2	5	6	4	1	1
P^3	8	7	4	1	2
P^4	5-6	8	5-7	1	3
M^1	5	8	5	3	2
M^2	5-6	7-8	5	3	1
M^3	5	7	1	4	1

Plication numbers in upper cheek teeth of *Hipparion primigenium*, KNM KP-43.

numbers change. There are more of them posteriorly in the prefossette (6 in the higher, 8 in the lower section) and anteriorly in the postfossette (4 in the higher, 5 in the lower section), but less of them posteriorly in the postfossette (3 in the higher, 1 in the lower section). The hypocone is constricted somewhat in the higher section, and not so in the lower. The protocone is 7.5 by 4 mm in the higher section, and 7.5 by 4.5 mm in the lower. The pli caballin is double in both sections. As a whole the molar resembles that in the Kanapoi dentition KNM KP-43 rather than that in the Lothagam skull. Therefore, it would seem to us that the juvenile skull from Ekora is conspecific with the Kanapoi dentition, representing a species different from that of the Lothagam skull. The M^2 of the Ekora juvenile is very imperfectly calcified, down to 31 mm along the mesostyle only, and the protocone is not preserved. The Ekora juvenile skull has a preorbital fossa which is placed above DM^3 and DM^4. The fossa is well marked off behind, 4.5 cm in front of the orbit, and measures 3 cm in height and some 5-6 cm in length, flattening out anteriorly. Its greatest depth is 1.5 cm, and it includes the infraorbital foramen, above the parastyle of DM^3. The facial crest begins above the anterior border of DM^4. Only the left side of the skull, but the milk dentition of both sides, is preserved. The snout is broken off just in front of DM^2 so that the skull length cannot be given. The orbital margins are preserved, giving 53 mm for the horizontal, and 46 mm for the vertical diameter of the orbit. The skull bones are "craquelé", broken up into small fragments, which, however, have been kept in their natural positions. The skull base behind the basisphenoid is missing; the occiput incompletely preserved.

The Kanapoi-Ekora *Hipparion* (with the preorbital fossa) has the dental characters of *Hipparion primigenium* (Von Meyer), with which Forstén (1968: 15) synonymized *Hipparion africanum* Arambourg (1959: 75) from the "Pontian" of Wad el Hammam, the earliest African *Hipparion* so far described. The highly plicated upper cheek teeth, the protocone shape, and the unwrinkled inner and outer fossette borders of *H. africanum* are exceedingly similar to those in the Kanapoi-Ekora *Hipparion,* as is the size. Even the multiple caballine folds, trifid in P^4, bifid in M^1 of the Kanapoi dentition, resemble those in *H. africanum* as figured by Arambourg (1959: 82, fig. 36 A-C). Height-width indices in *H. africanum* run from 220 to 290 in four uppers: in our Ekora M^1 the height-width index is 300. The observations by Arambourg (1959: 79) are based on P^2-P^4 and M^3 that are slightly worn, and thus his figures might have been slightly higher if these had been fully unworn teeth. Such indices are generally relied upon for assessing the evolutionary stage of a hipparion, more so than the dental pattern as such.

The skull of *Hipparion primigenium* (including *H. africanum*) has a preorbital fossa of variable shape but usually simple, placed rather far in front of the orbit, and widely open in front; in other words, it is just as in our juvenile Ekora skull. Because of this, and because the Kanapoi teeth and the Ekora skull cannot be distinguished from *Hipparion primigenium* (syn. *H. africanum),* the Kanapoi-Ekora form may be identified as *Hipparion primigenium* (Von Meyer).

As will be mentioned later on, there is a juvenile mandible with DM_{3-4} and an M_1 from Lothagam, KNM LT-143, that can also be referred to *H. primigenium,* again indistinguishable in the teeth, and this suggests that *Hipparion primigenium* also occurred at Lothagam Hill.

Specimens referred to *Hipparion turkanense* Hooijer & Maglio and to *Hipparion primigenium* (Von Meyer)

The most complete lower dentition is in a partial left mandible from Kanapoi, KNM KP-44 (pl. 6, figs. 1, 2). It comprises P_3-M_2 and the anterior portion of M_3, all worn. The crown height of P_3, as exposed in front, is

50 mm. The external cement of P_4 has been removed at the top, and shows an ectostylid that terminates upward just 7 mm from the worn surface. A very long and narrow ptychostylid is present up to the occlusal surface: it is more marked than the ptychostylids in P_3 and M_1-M_2 in all of which there is in addition an ectostylid. That in P_3 and in M_1 is reached by wear, but in M_2 it terminates just a mm or two below the wear surface. Thus, it is clear that in this jaw ectostylids are developed in premolars and molars alike, but that they do not extend the full height of the crowns. In addition, a very clear protostylid is seen in M_1 and in M_2, worn to a tiny enamel ring at the antero-external crown corner. It is harder to see in the two premolars but it is there, too, partially obscured by the cement coating and not yet reached by wear. Therefore, the protostylids in this jaw are not developed to the full height of the crowns either.

Ectostylids as well as protostylids are small pillars the presence of which may be easily overlooked as they may be hidden in the cement coating on the side of the crowns. They show as tiny enamel figures on the occlusal surface only when reached by wear. A case in point is one of the four isolated M_3 of the small *Hipparion* in the present collection, in which the ectostylid is developed only in the basal 23 mm of the crown. This specimen will be discussed further on.

In the P_3-M_2 from Kanapoi the depression between metaconid and metastylid is shallow and U-shaped in the premolars, whereas in the molars it is deeper, and V-shaped. The metastylid is pointed in all the teeth. The external groove between protoconid and hypoconid is shallow in the premolars, but deep in the molars, and concomitant with this the entoflexid is decidedly larger in anteroposterior extent in the premolars than in the molars; this is a character that serves to distinguish premolars from molars. In the present specimen the entoflexid borders as well as those of the metaflexid, and also the external enamel borders, are finely wrinkled, but not excessively so. The measurements of the four teeth that can be measured in the Kanapoi hemimandible, KNM KP-44, are given in table 5.

Table 5

	P_3	P_4	M_1	M_2
Ant.-post.	28	28.5	25.5	27
Transv.	16+	—	16	15

Measurements of teeth of Kanapoi hemimandible, KNM KP-44 (mm).

There are several isolated lower cheek teeth in the Kanapoi collection, KNM KP-42, that show ectostylids up to the occlusal surfaces, but all are worn specimens. These are a P_3 or P_4 sin., 24.5 by 14 mm in crown diameters, an M_1 or M_2 sin. 24 by 13.5 mm in diameters, and another left premolar incomplete in front and 13 mm transversely. In the weak wrinkling of the enamel externally and in the entoflexid and metaflexid borders, in the pointed metastylids, and especially in the well-developed ectostylids these teeth remind strongly of the Kanapoi lower cheek teeth, KNM KP-44.

In the collection there are further three isolated lower cheek teeth that are characterized by their more marked wrinkling of entoflexid and metaflexid borders, while that on the external enamel borders is very marked indeed. These are P_3 or P_4 sin., KNM LT-170 from Lothagam, P_3 or P_4 dext., KNM EK-7, from Ekora, and M_3 dext., KNM LT-171 from Lothagam. The specimens are presented on pl. 7, figs. 1-6. The two premolars measure 27.5 mm anteroposteriorly on the occlusal surface (40, and 55 mm, respectively, above the base), and 26, and 24 mm, respectively, 2 cm above the neck. Their transverse diameters are 14.5, and 13.5 mm, respectively. The M_3, 42 mm high as worn, is 27.5 mm anteroposteriorly at the occlusal surface, and 30 mm anteroposteriorly basally; its transverse diameter is 12 mm throughout. These heavily wrinkled teeth have no ectostylids at all, although protostylids and ptychostylids (weak, because of the wrinkling of the external borders) are in evidence.

Thus, it seems that we have two types of large lower cheek teeth in the collection, of which one shows a heavier wrinkling of the flexid and external borders than the other. The same difference was found between the teeth of the adult Lothagam skull and those of the Kanapoi adult dentition: the first shows wrinkling of the inner and outer fossette borders that the second does not. It would seem, therefore, most expedient to associate the more heavily wrinkled lowers recorded with the Lothagam skull, and to place the Kanapoi hemimandible and the three isolated lowers with well-developed ectostylids with the Kanapoi upper dentition figured on pl. 3.

Isolated permanent teeth remaining in the collection presumably belong to either *Hipparion turkanense* or *H. primigenium.* Most of the Lothagam teeth conform to the Lothagam type skull such as a $P^{3\text{-}4}$ dext., KNM LT-154, and a $P^{3\text{-}4}$ sin., KNM-LT-142 (in which the enamel even of the protocone is wrinkled). Figured in the present paper is an $M^{1\text{-}2}$ dext. from Kanapoi, KNM KP-48, that agrees very well with those of the Lothagam skull in the fossettes with wrinkled inner and outer borders, plis that are not so great in extent though numerous (6-8 in the adjoining fossette borders in the crown center), and a relatively wide protocone (10.5 by 6.5 mm) (pl. 5, fig. 4). Further, an $M^{1\text{-}2}$ sin. from Ekora, KNM EK-5 resembles more closely the Kanapoi and Ekora *Hipparion primigenium* in its more ample folds, non-wrinkled anteroposterior fossette borders, and narrower protocone (6.5

by 4 mm), which is pointed at both ends (pl. 5, figs. 5,6). The Kanapoi M^{1-2} dext. suggests that *H. turkanense* did occur there as well as at Lothagam. The wrinkled P_{3-4} dext. provisionally placed with *H. turkanense* has the same field number, 16-67K, Ekora, as the M^{1-2} sin. referred here to *H. primigenium*, suggesting that *H. turkanense* was associated with *H. primigenium* at Ekora. Not all of the isolated teeth, however, show clear characters one way or the other, and assigning them to a particular species comes close to sophisticated guesswork, which does not so much increase our knowledge of the two large species in question as merely showing that there is individual variation in dental characters in either one of them. Size is of no avail as a criterion as the two species have teeth that are of the same size (see table 2). It is an easy matter to sort out the small upper and lower premolars and molars in the collection, and these are described below as *Hipparion* cf. *sitifense* Pomel. As a matter of fact size seems to be a less variable character for *Hipparion* species than fossette folding or protocone shape. It may be said though that most of the isolated Lothagam molars are closer in overall pattern to those of the Lothagam skull than to the Kanapoi dentition, and that most of the Kanapoi molars are more like the Kanapoi dentition shown on pl. 3. This suggests that *Hipparion turkanense* was the predominant species in Lothagam times, and that *Hipparion primigenium* was more common at the time of deposition of the Kanapoi beds, although both were present through this sequence of deposits in northwestern Kenya.

Lothagam molars that are like those of *Hipparion primigenium* include a P^{3-4} sin., KNM LT-137, an M^{1-2} sin., KNM LT-169, a P^{3-4} sin., KNM LT-172, an M^{1-2} sin., KNM LT-144, and an M^{1-2} dext., KNM LT-147. Kanapoi molars that have the characters of *Hipparion turkanense* include, beside the figured M^{1-2} dext., KNM KP-48, and a few battered specimens in KNM KP-46 and -47.

Deciduous molars are very much the same in the lower jaw of all hipparions: they show ectostylids in addition to the protostylids and ptychostylids even in species that do not have ectostylids in the permanent dentition. Two deciduous molars, DM_3 and DM_4, are in situ in a portion of the left mandible from Lothagam, KNM LT-143 (pl. 6, figs. 3-4). There is also in situ the entire first permanent molar, fully calcified down to the base and with the tips of metaconid and metastylid as well as the anterior edge just touched by wear. The M_1 has been examined on all sides: there is a weak, narrow ectostylid extending upward to 45 mm from the base. Proto- and ptychostylid are developed to the full height of the crown. The total crown height of the M_1 is 60 mm; the anteroposterior diameter at the top, with the posteriorly bulging hypoconulid, is no less than 25.5 mm but the crown steadily reduces in anteroposterior diameters rootward, and just below the middle of the height the anteroposterior diameter is only 20 mm. This figure gives a height/length index of 300.

The milk molars of KNM LT-143 show a slight wrinkling of the external enamel borders, notably in the protoconid of DM_3. In this tooth, the ectostylid is a semilunar enamel figure on the occlusal surface, concave externally, and 6 by 2 mm in diameters. In the DM_4 of the same specimen the ectostylid measures only 3.5 by 2 mm on the wear surface. Measurements are in table 6.

Table 6

	KNM LT-143		KNM EK-4		
	DM_3	DM_4	DM^2	DM^3	DM^4
Ant.-post.	28	30	34	28	30
Transv.	14.5	14.5	22.5	23.5	23

Measurements of deciduous molars from Kanapoi and Ekora (mm).

The upper deciduous molars in the juvenile Ekora skull, KNM EK-4, resemble the permanent first molar in the amplitude of the fossette plications but differ in having rather more rounded protocones (compare pl. 4, fig. 3, with pl. 5, figs. 2, 3). In the Ekora skull, the DM^2 and the DM^4 have almost completely isolated hypocones, the plis caballins are double, with a tendency toward triplication in DM^3. In all respects, including size, they are like the $DM^{3\text{-}4}$ of *Hipparion primigenium* from locality 2 of the Beglia Formation in southern Tunisia figured by Forstén (1972: 12). Measurements are given in table 6.

Postcranial material pertaining to large hipparions is rare in the collection, but we have the distal end of a left metatarsal III from Kanapoi, KNM KP-45, slightly distended by cracks and superficially damaged behind. The length as preserved is 11 cm. The distal articular width is 41 mm, against 33 to 36.5 mm in *H. africanum*, and the shaft width at the middle (top of preserved portion) is 31 mm against 24.5 to 26 mm in *H. africanum* (Arambourg, 1959: 90). Thus, the Kanapoi metatarsal is slightly larger than the sample (of five specimens) from Wad el Hammam, and it is possible that the present bone should be referred to *Hipparion turkanense*, which most probably is present at Kanapoi, and the skull of which slightly exceeds that of *H. africanum* in size.

An astragalus dext. from Lothagam, KNM LT-156, has a distal articular width of 52 mm, and a (medial) height of 64 mm. Arambourg (1959: 89) gives the "largeur" of two astragali from Wad el Hammam (one juvenile) as 55, and 46 mm, respectively, but Forstén (1968: 120) supplies the distal articular width and the height of the largest Wad el Hammam astragalus as 43 mm, and 56 mm, respectively. Thus, the Lothagam astragalus exceeds the single known adult astragalus from Wad el Hammam in size. A slightly smaller astragalus dext. in the Lothagam collection, KNM LT-160, measures ca. 46 mm in distal articular width, and 58 mm in medial height, whereby it is very close to the astragalus of *H. africanum*. Whether the difference in size between these two astragali denotes a specific difference is of course impossible to say. In the same lot as the astragalus dext. from Lothagam there is a calcaneum sin. with a total length of 111 mm; the greatest width cannot be taken as the sustentaculum tali is broken off. Arambourg (1959: 89) gives the length of the calcaneum of *H. africanum* as 107.5 mm, the greatest width as 50 mm; the length is, again, very close to that of the Lothagam calcaneum. The width of a distal tibia fragment, left side, in the same lot as the astragalus and the calcaneum, Lothagam, KNM LT-160, is approximately 70 mm, against 65 mm in *H. africanum* (Arambourg, l.c.).

Hipparion cf. **sitifense** Pomel

There is a third species of *Hipparion* in the Lothagam-Kanapoi-Ekora collection that is characterized mainly by its small size. We have a number of isolated cheek teeth, uppers as well as lowers, but the skull characters of the small hipparion of these localities remain unknown. Fortunately there is also, in the collection from Lothagam, KNM LT-139, most of the right manus of a small *Hipparion*, including an entire metacarpal III. Slender and gracile, its length is 228 mm and the distal articular width is 35 mm, giving a distal width/length index of 15.4. This is an index that is not found in *Hipparion primigenium* (syn. *H. africanum*) from Wad el Hammam, in the metacarpal III of which the distal articular width is slightly greater (35.5-36.5 mm), but the length is less (198-210 mm), resulting in a distal width/length index of 17.1-18.1 (Arambourg, 1959: 87). Thus, the median metacarpal of *H. primigenium* is of a stouter type than that of our small Lothagam hipparion. A distal width/length index of 15.4 is found, however, in *Hipparion mediterraneum* Roth & Wagner from the Pikermian of Pikermi, in which metacarpal III varies in length from 194 to 230 mm, in distal articular width from 31 to 43 mm and in distal articular width/length index from 13.1 to 21.1 (Arambourg, 1959: 87). Our Lothagam metacarpal III falls completely within these limits; the length is to the higher side, the distal width to the lower side of the observed ranges in the Pikermi *H. mediterraneum*, and the index is a little lower than the mean in that species, but distinctly below that seen in *H. primigenium*. Forstén (1968: 30, 80) gives figures in which the distal width of metacarpal III is plotted against the total length, and the Lothagam metacarpal III falls well within the scatter of *H. mediterraneum* and well outside that of *H. primigenium*. The slender limbs of

TABLE 7

	Lothagam				Mascara	
P^2, ant.-post.	28				30	
transv.	20				17	
protocone, ant.-post.	5.5				6.5	
transv.	4				4	
P^{3-4}, ant.-post.	-				20.5	20
transv.	-				19	20
protocone, ant.-post.	7				7	8.5
transv.	4				4	4.5
	(1)	(2)	(3)			
M^{1-2}, ant.-post.	21.5	21.5	20.5		19.5	19
transv.	22.5	21.5	-		19.5	18
protocone, ant.-post.	7	7.5	-		6.5	7.5
transv.	4	3.5	-		3.5	3
	(1)	(2)	(3)			
M^3, ant.-post.	21	22	-		19	
transv.	19	19	18		18.5	
protocone, ant.-post.	-	8	6.5		9	
transv.	-	3.5	3		3	
	(4)	(5)	(6)	(7)		
M^3, ant.-post.	19.5	20	21.5	20	19	
transv.	17	19	18.5	18.5	18.5	
protocone, ant.-post.	7	7.5	6	7	9	
transv.	2.5	3.5	4	4	3	

Dental measurements of Lothagam *Hipparion* cf. *sitifense* and that from Mascara (mm).

H. mediterraneum are generally interpreted as an adaptation to steppe environment, whereas the shorter and relatively more robust bones of *H. primigenium* supposedly denote forest conditions. Adaptational features have also been seen in the teeth: browsing hipparions have lower-crowned teeth but more richly plicated. However, as Forstén (1968: 24) points out, ectostylids in *Hipparion* teeth were probably not an adaptation to a xerophytic environment.

The adaptive significance of the cingular elements in *Hipparion* teeth, which was so stressed by Gromova (1952), was probably not all that significant. It is amusing to read (in Forstén, 1968: 47) that according to Gromova a shallow external depression between protoconid and hypoconid would be an adaptation to the eating of hard steppe grass. If we would believe this to be true, premolars are better adapted to grass eating than molars, for the external depression between protoconid and hypoconid is shallower in the premolars than in the molars. Moreover, since the movement of the jaws in chewing is side to side, it is hard to see how a transverse fold, be it long or short, could increase the effectiveness of the crown in breaking down grass. The strongest enamel ridges, in upper as well as in lower cheek teeth, are, naturally, anteroposteriorly oriented.

Adaptive significances apart, the cheek teeth of *H. mediterraneum* are more hypsodont than those of *H. primigenium,* with lower plication numbers, and an ectostylid is usually rare (Forstén, 1968: 40-41). Those of *H. primigenium* are relatively brachyodont, mostly richly plicated, with well-developed ecto- and protostylids (Forstén, 1968: 15). The size of *H. mediterraneum* is middle sized to small, that of *H. primigenium* is middle sized to large. Another middle sized to small species is *Hipparion sitifense* Pomel. It is said to have the limb proportions of *H. primigenium* but hypsodont teeth moderately to simple plicated (Forstén, 1968: 33). In Spain there occurred an *H. sitifense* that in the morphology of the teeth, in size, and probably in ecology as well, was rather similar to *H. mediterraneum* (Forstén, 1968: 48), but it should not be overlooked that the Spanish material is only referred to that species, and that the type specimen of *Hipparion sitifense* comes from Saint-Arnaud in Algeria, and consists only of a single upper molar. What its limbs were like we do not know.

The above peroration is introductory to the description of the isolated small cheek teeth in the Lothagam-Kanapoi-Ekora collection, which we find exceedingly similar to *H. sitifense* of North Africa. To this species Arambourg (1956) attributed a relatively well-preserved upper dentition from Mascara in Oran. The excellent illustrations in Arambourg (1956, pl. XXVI) are natural size and show the molars from the right side as well as the left cheek tooth series from Mascara, the type specimen of *H. sitifense* Pomel, and three teeth from Ain el Hadj Baba originally referred to *Hipparion gracile* by Thomas, all now referred to *Hipparion sitifense.* It is in this material that we find the closest approximation in size and characters to our small hipparion from the northwestern Kenya sites.

To begin with the upper dentition, there is one perfect P^2 sin. from Lothagam, KNM LT-158 that measures only 28 mm anteroposteriorly, and 20 mm transversely (across protocone and mesostyle), or four-fifth the linear dimensions of P^2 in the Kanapoi dentition KNM KP-43 (table 2, second column). In the Mascara dentition P^2 measures 30 by (?) 17 mm (the outer wall is lost), with a protocone height, as worn, of only 5 mm (Arambourg, 1956: 818, 820). In our Lothagam P^2, which is much less worn (mesostyle height, as worn, 33 mm; protocone height, as worn, 25 mm), the mesostyle is bifid, but would show a single edge a few mm further down, prefossette and postfossette have an open connection, there is a deep hypoglyph, which is flattened out at 5 mm above the base, and the protocone is blunt in front, flat internally, and pointed behind on the internal side. It is relatively shorter anteroposteriorly than that in the Mascara P^2 (measurements and pli counts are given in tables 5 and 6 along with those of the Mascara dentition). The well-worn protocone in the Mascara P^2 is more pointed in front than behind.

There is only one P^3 or P^4 dext. of the small hipparion in the Lothagam-Ekora collection, and not a very good one at that. It is from Lothagam, and lacks the enamel layer externally and behind so that the crown diameters cannot be given although pli counts can. It is worn down to a height of approximately 33 mm. The anterior horn of the postfossette extends outward beyond the posterior horn of the prefossette, as usual, and the adjoining fossette borders are entire, not confluent as in the P^2 just described, showing a very high number of plis in the prefossette posteriorly (table 8). The protocone is suboval, more flattened internally than externally. The more worn P^3 and P^4 of the Mascara dentition (protocone heights only 6 and 8 mm, respectively) have fewer plis; the protocone of P^3 and the long, single pli caballin of P^4 are as in our Lothagam specimen.

Of M^{1-2} there are three small specimens, (1) M^{1-2} dext., Lothagam, KNM LT-141, 56 mm high as worn; (2) M^{1-2} sin., Lothagam, KMN LT-146, worn to a height of 53 mm, and (3) M^{1-2} sin., Lothagam, KNM LT-140, worn down to 32 mm from the base. The latter lacks the external portion of the protocone. Plication numbers are very much the same throughout, slightly higher in the anterior border of the postfossette than in M^1 and M^2 from Mascara, as judged by Arambourg's 1956 illustrations. The Mascara material is but slightly smaller, but the protocones are as elongated as in the Lothagam sample, with long plis caballins extending quite close to them.

The last upper molar is numerically best represented in the small Lothagam hipparion: There are seven specimens, as follows: (1) M^3 sin., KNM LT-137, just touched by wear but base incomplete, height preserved 48 mm;

TABLE 8

	prefossette		postfossette		pli caballin
	ant.	post.	ant.	post.	
P^2 sin.	5	5	1+	1	2
P^{3-4} dext.	2	9	3	1	1
M^{1-2} dext. (1)	2	5	2	1	1
M^{1-2} sin. (2)	2	5	4	1	1
M^{1-2} sin. (3)	1	4	5	2	1
M^3 sin. (1)	-	-	-	-	-
M^3 sin. (2)	4	8	4	1	1
M^3 sin. (3)	2	6	6	1	3
M^3 dext. (4)	1	-	-	-	1
M^3 dext. (5)	7	7	4	1	3
M^3 sin. (6)	1	5	5	1	1
M^3 sin. (7)	1	5	4	1	2
Mascara (after Arambourg, 1956, fig. 2)					
P^2	3 [5]	3	1	1	2
P^3	1	4	1	1	2
P^4	1	5	4	1	1
M^1	1	5	3	1	1
M^2	1	-	3	1	1
M^3	-	-	-	-	2

Plication numbers of upper teeth of Lothagam *Hipparion* cf. *sitifense*. Specimens as discussed in text are given in parentheses.

(2) M^3 sin., KNM LT-145, worn down to 45 mm from base, external enamel behind mesostyle broken off; (3) M^3 sin., KNM LT-140, enamel lacking fore and aft, worn to same height; (4) M^3 dext., KNM KP-490, most of mesostyle and metastyle lacking, height 43 mm as preserved; (5) M^3 dext., KNM LT-138, height 40 mm as worn; (6) M^3 sin., KNM KP-496, worn down

to 30 mm, and (7) M^3 sin., KNM LT-148, worn down to 15 mm from base. Of (1) the plication numbers cannot be given, and in (4) they are obscured by erosion in the center, but in the other M^3 the folds are numerous and well-developed, especially in (5) (pl. 8, fig. 7). The most worn specimen is hardly inferior in complexity of folding to the others. The protocones are quite elongated although the protocone in the Mascara M^3 is longer still. The sizes tally well with the Mascara M^3 but fossette foldings of this tooth are obscured in the figures presented by Arambourg (1956). The hypocone in the Mascara M^3, as emphasized by Arambourg, is almost completely pinched off, but this condition is also seen in the Lothagam M^3 (2), (3), and notably in specimen (5). Multiple caballine folds characterize the Lothagam M^3 as well as that from Mascara.

The type upper molar of *Hipparion sitifense* is even more like our Lothagam small *Hipparion*. Arambourg (1956: 822, fig. 3A) redescribes and figures it as an M^1 or M^2 sin. measuring 23 by 22.5 mm (on the occlusal surface), and with fossette pli counts 5-5-6-1, prominent pli caballin and oval protocone, a tooth that can be exactly duplicated in our Lothagam series (tables 7, 8). The dimensions of the $M^{1\text{-}2}$ dext., KNM LT-141, are 22.5 by 22 mm occlusally, and the configuration of the fossettes, e.g., in the M^3 (2) and (5), leaves nothing to be desired for closeness to the type specimen of *Hipparion sitifense* Pomel. The same holds for the Aïn el Hadj Baba uppers (Arambourg, 1956: 824, pl. XXVI figs. 3-5).

There are also a number of small lower molars of *Hipparion* in the present collection, including one from Ekora KNM EK-6, found in beds of the Kanapoi Formation, beneath the capping lava. This tooth, and M_1 or M_2 sin., is decidely smaller than those of the large Lothagam and Kanapoi-Ekora hipparions; it measures only 21 mm anteroposteriorly and 11 mm transversely. It is worn to a height of 34 mm, has a small protostylid and a distinct ptychostylid but lacks the ectostylid completely. The absence of ectostylids is one of the leading characteristics of *Hipparion sitifense*; we have seen that they occur, though not along the full height, in the large lower molars from Kanapoi, which are one-fourth greater in dimensions. Another M_1 or M_2 sin., from Lothagam, KNM LT-150, likewise 21 mm long, and 11.5 mm wide, worn down to the same height, has a protostylid, a (weak) ptychostylid, and no trace of an ectostylid. Apart from some fragments of teeth that may represent this small form there are four specimens of M_3: (1) M_3 dext., KNM LT-138, worn to a height of 55 mm; (2) M_3 sin., (same number) worn to the same height; (3) M_3 dext., KNM KP-42, worn down to 50 mm, and a particularly small specimen, (4), M_3 dext., KNM LT-161, also worn down to 50 mm of height. Characteristic of three out of four of these last lower molars is the absence of ectostylids. Protostylids are present but they do not reach upward to the occlusal surface except in the third specimen, KNM KP-42, where it is just touched by wear; in the other M_3 it remains a few mm below the level of wear. Ptychostylids are present and show on the occlusal surfaces in all specimens. The ectostylid, present only in one specimen out of the four, KNM KP-42 (pl. 8, figs. 3, 4), is seen to extend from the base upward to a height of 23 mm, where it terminates. If a tooth like this had been present in a mandible the ectostylid would not have been noticed until wear had been sufficiently advanced to reach its apex. Metaconid and metastylid are widely spaced in all four M_3, but the fourth specimen presents an irregularity; the metastylid is an isolated column and the metaconid consists of two unequal enamel figures nearly separate from each other. The measurements are given in table 9.

Table 9

	Lothagam		Kanapoi	Lothagam
	(1)	(2)	(3)	(4)
Ant.-post.	24.5	25	25	22.5
Transv.	10	9.5	10.5	9.5

Measurements of lower last molars of *Hipparion* cf. *sitifense* from Kenya (mm).

Lower cheek teeth recovered at Saint-Arnaud, the type locality of *Hipparion sitifense*, by Arambourg (1956: 822), correspond to the uppers in their small size, and lack ectostylids. Arambourg does not provide measurements of the lower cheek teeth of *H. sitifense* but the lower molars in the present collection just recorded are at least four-fifths the linear dimensions of the homologues in the large forms represented by skulls, as was true in the upper cheek teeth of the small form as well (compare tables 2 and 7). Unless the small uppers and the small lowers represent different species, which seems most unlikely, the assemblage of small *Hipparion* teeth in the Lothagam-Kanapoi-Ekora collection represents a single species. Size as well as the structural characters of the uppers (plication frequency, flattened protocones), and the absence or rarity of ectostylids in the lowers, make the small *Hipparion* teeth of the present collection very similar to *Hipparion sitifense* Pomel, so that we may provisionally record them as *Hipparion* cf. *sitifense.*

The stratigraphical position of *Hipparion sitifense* is just below the Lower Villafranchian of Ain Boucherit and Ain Jourdel, hence "Upper Pliocene" according to Arambourg (1956: 826). This "true" ("vrai") *Hipparion* without (or almost without) ectostylids we now know from Saint-Arnaud, Ain el Hadj Baba, and Mascara in North Africa (see also Arambourg, 1970: 23, 92 [1]), and the material from Lothagam and from the Kanapoi level at Ekora shows almost conclusively that the same species occurred at an even earlier date in northwestern Kenya, extending over a time spanning from over 6 to about 4 million years ago [2]).

Four astragali in the collection are smaller than the two provisionally referred to *Hipparion turkanense* c.q. *Hipparion primigenium*. These are: (1) astragalus sin., Lothagam KNM LT-149; (2) astragalus dext., Lothagam, KNM LT-157; (3), astragalus sin., Lothagam, KNM LT-158; and (4) astragalus sin., Ekora KNM EK-8. The last mentioned specimen lacks most of the lateral trochlea ridge and the medial part of the distal articular surface. In table 10 the measurements are compared with those of *H. mediterraneum* from Pikermi (after Forstén, 1968: 123) and those of referred material of *H. sitifense* from Piera and Concud in Spain (after Forstén, 1968: 122).

Table 10

	Lothagam (1)	Lothagam (2)	Lothagam (3)	Ekora (4)	Pikermi	Piera	Concud
Distal articular width	42	42.5	38	—	35-41	41.5-42	36-45
Height (medially)	54	54	51	ca. 48	48.5-53	52-53	46-59.5

Measurements of astragalus of small *Hipparion* (mm).

It is seen that the Lothagam and Ekora astragali are close to the referred material of *H. sitifense,* although the ranges of the Concud sample (60, and 55 specimens) almost include the smaller of the two Lothagam astragali that we refer to the larger species (above, p. 20).

The Concud *Hipparion* was long identified as *H. mediterraneum,* the Pikermi species, but Forstén transferred it to *H. sitifense*. The two species are indeed very close, and the similarity of the teeth of *H. sitifense* to those of *H. mediterraneum,* both uppers and lowers, is noted (Forstén, 1968: 35).

1) It should be remarked that the illustration of the upper dentition of *Hipparion sitifense* from Mascara as given in Arambourg's 1970 paper (l.c., 92, fig. 54) is not natural size as stated in the caption to that figure; the actual length P^2-M^3 is 129 mm (Arambourg, 1956: 818). The length in the 1970 illustration is 143 mm.

2) In the assemblage of teeth of *Hipparion albertense* Hopwood from the Kaiso Formation, Cooke & Coryndon (1970: 139, fig. 5J) include a very small left lower molar from South Nyabrogo. The tooth is of the size as our lower molars of *Hipparion* cf. *sitifense* from Lothagam and the Kanapoi level at Ekora, and it is probable that the specimen, which is from Earlier Kaiso, belongs to our small form from Lothagam rather than to *H. albertense.* The Earlier Kaiso fauna is placed at about 5 million year level (Cooke & Coryndon, 1970: 184), that is, between Lothagam and Kanapoi in age.

For priority reasons, the name *H. sitifense* is used rather than *H. mediterraneum*, "although the African form is rather little known" (Forstén, 1968: 34). We now have, for the first time, a good metacarpal of the small African *Hipparion*, as already mentioned at the beginning of the present chapter. There is no good reason to suspect that it belongs to a species of small *Hipparion* other than that of the small cheek teeth from the same site (Lothagam), which we refer to as *Hipparion* cf. *sitifense*. This bone, then, shows that the African small hipparion has the metacarpal proportions of *H. mediterraneum* of Pikermi (above, p. 20), but we prefer to use the African name, *H.* cf. *sitifense*, for this material as we did for the teeth.

The entire metacarpal III dext. is associated with the distal end of metacarpal IV, the proximal and distal parts of metacarpal II, phalanx I and II of the median digit, and the three small phalanges of the second digit. To this lot, KNM LT-139, may belong the proximal end of a radius dext. The measurements of these bones are given in table 11.

The median metacarpal is as slender in build as that in *H. mediterraneum* from Pikermi (the distal articular width/length index of the Lothagam bone is 15.4, that in *H. mediterraneum* varies from 13.1 to 21.1: Arambourg, 1959: 87). The length range of Mc. III in this species is given by Arambourg as 194-230 mm. However, the distal articulations of the second and fourth metacarpals are more strongly developed in the Lothagam *Hipparion* cf. *sitifense* than in *H. mediterraneum*, in which the distal anteroposterior diameters of metacarpal II and IV are 14.5-16 mm (Arambourg, 1959: 88). On the other hand, in *H. africanum*, with a shorter and stouter metacarpal III than our Lothagam bone, the distal articulations of metacarpals II and IV are heavier (anteroposterior diameters for metacarpal II, 18.7 and 18.5 mm; for metacarpal IV, 19 and 19.5 mm: Arambourg, l.c.) Thus, the conformity of the Lothagam set of metacarpals to that of *H. mediterraneum* is not complete.

The *Hipparion* spec. described from the Villafranchian of Bethlehem, Israel (Hooijer, 1958: 280-281, pl. 35 figs. 3-6) is as small as our *Hipparion* cf. *sitifense* described in the present paper: the M_3 measures 25 mm anteroposteriorly, and 9.5 mm transversely, exclusive of cement, and the distal articulation of the lateral metapodial (II or IV) measures 17 by 8 mm. It is not a "*Stylohipparion*", and the associated elephant is an early form of *Elephas planifrons* Falconer & Cautley and was very probably derived from a stage of *Elephas ekorensis* Maglio comparable to that occurring at Kanapoi and Ekora, dated at about 4 million years. The Bethlehem elephant is the lowest-crowned form found in association with a Villafranchian fauna and

TABLE II

Metacarpal III, length	228	Metacarpal IV, distal width	9
Proximal width	39	distal ant.-post. diameter	17.5
proximal ant.-post.	28	Metacarpal II, proximal width	11
mid-shaft width	26	proximal ant.-post.	16.5
ant.-post., same level	22.5	distal width	9
greatest distal width	34.5	distal ant.-post. diameter	17.5
distal articular width	35	Phalanx I, digit II, length	39
distal crest, ant.-post.	29	proximal width	11.5
Phalanx I, digit III, length	61	proximal ant.-post.	18.5
proximal width	37.5	distal width	11
proximal ant.-post.	28	distal ant.-post.	15
least width of shaft	24	Phalanx II, digit II, length	17
least ant.-post. diameter	15.5	proximal width	13
greatest distal width	29.5	proximal ant.-post.	18.5
distal articular width	31	distal width	11.5
distal ant.-post. diameter	19.5	distal ant.-post.	12.5
Phalanx II, digit III, length (max.)	40.5	Phalanx III, digit IV length	ca. 24
proximal width	36	proximal width	13
proximal ant.-post.	24.5	proximal ant.-post.	ca.33
least width of shaft	28		
least ant.-post. diameter	17		
distal articular width	ca.33.5		
distal ant.-post. diameter	20		

Measurements of metacarpals and phalanges of *Hipparion* cf. *sitifense,* KNM LT-139 (mm).

is considered an immigrant from Africa. With our new finds at Lothagam and Kanapoi (Ekora) the Bethlehem *Hipparion* may be regarded as another immigrant from Africa, as *Hipparion* cf. *sitifense*.

POSTSCRIPT

Since the present paper was submitted for publication, continued research in the Baringo area of Kenya by the East African Geological Research Unit (EAGRU) based at Bedford College, University of London, under the direction of Professor B. C. King, has led to the discovery of *Hipparion* remains in the Ngorora Formation, which is between 12 and 9 million years old. Although good skull material is lacking, the molar pattern is very characteristic and points to *Hipparion primigenium* (Von Meyer), which is the primordial Old World species that appears in the Vallesian of North Africa (Wad el Hammam, Beglia Formation) as related above. Consequently, it would appear that one and the same species, *Hipparion primigenium,* emerged pretty much all over the Old World, not only in Eurasia but also in Africa both north and south of the Sahara, at about the 12 million year level, and the time lag in the dispersion of the genus *Hipparion* to sub-Saharan Africa (Bishop et al., 1971: 391; Hooijer & Maglio, 1973: 313) appears illusory.

The morphology of the Ngorora lowers agrees full well with that of the Vallesian *H. primigenium* of Eppelsheim in Germany and Wad el Hammam in Algeria: the metaconid and metastylid loops are rounded, and the ectostylid, if shown, is rather small. In one of the Ngorora teeth there is an ectostylid 15 mm high, and in the others it does not show, although it may be hidden in the thick cement investment on the buccal face, as may be the case in the Wad el Hammam specimens, too. Arambourg (1959) did not observe ectostylids in his *Hipparion africanum,* but these are teeth in situ and probably not worn enough to show the ectostylids, if any. In the Eurasian *H. primigenium* it seems that the ectostylid as well as the protostylid were maximally developed in the earliest, Vallesian, populations and diminished in later, Pikermian, *H. primigenium* (Forstén, 1968: 24). The development in sub-Saharan Africa, however, appears to have been different: the ectostylid continued to develop, witness the Lothagam and Kanapoi specimens described in the present paper. The pattern of the "tie" (i.e., metaconid and metastylid) became more "caballoid", with pointed rather than rounded loops, a progressive feature common to most African hipparions, although the hypsodonty remained the same as in the Vallesian *H. primigenium.* It was this development, in Africa, that led to the emergence of "*Stylohipparion*" in the Villafranchian, as will be documented in a subsequent paper.

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Plate 1

Hipparion turkanense Hooijer & Maglio, skull (holotype), Lothagam, KNM LT-136. Fig. 1, dorsal view; fig. 2, left lateral view; fig. 3, ventral view. × 0.25.

Plate 2

Hipparion turkanense Hooijer & Maglio, P^2-M^3 dext. et sin. of holotype skull, Lothagam, KNM LT-136; crown view. × 0.9.

Plate 3

Hipparion primigenium (Von Meyer), P^3-M^3 dext., Kanapoi, KNM KP-43. Fig. 1, external view; fig. 2, crown view. × 1.3.

Plate 4

Hipparion primigenium (Von Meyer), juvenile skull, Ekora, KNM EK-4. Fig. 1, dorsal view; fig. 2, left lateral view; fig. 3, ventral view. × 0.4.

Plate 5

Fig. 1-3, *Hipparion primigenium* (Von Meyer), unworn M^1 sin., Ekora, KNM EK-4. Fig. 1, crown view; fig. 2, cross section at 16 mm from top; fig. 3, cross section at 36 mm from top. × 1.3.

Fig. 4, *Hipparion turkanense* Hooijer & Maglio, $M^{1\text{-}2}$ dext., Kanapoi, KNM KP-48; crown view. × 1.3.

Figs. 5-6, *Hipparion primigenium* (Von Meyer), $M^{1\text{-}2}$ sin., Ekora, KNM EK-5. Fig. 5, crown view; fig. 6, internal view. × 1.3.

Fig. 7, *Hipparion* cf. *sitifense* Pomel, metacarpal II-IV dext. and phalanges, Lothagam, KNM LT-139; dorsal view. × 0.5.

Plate 6

Figs. 1-2, *Hipparion primigenium* (Von Meyer), P_3-M_3 sin. in situ, Kanapoi, KNM KP-44. Fig. 1, crown view; fig. 2, external view. × 0.8.

Figs. 3-4, *Hipparion primigenium* (Von Meyer), juvenile mandible with $DM_{3\text{-}4}$ and M_1 sin., Lothagam, KNM LT-143. Fig. 3, crown view; fig. 4, internal view. × 0.8.

Plate 7

Hipparion turkanense Hooijer & Maglio. Figs. 1-2, M_3 dext., Lothagam, KNM LT-171. Fig. 1, crown view; fig. 2, external view. Figs. 3-4, $P_{3\text{-}4}$ sin., Lothagam, KNM LT-170. Fig. 3, crown view; fig. 4, external view. Figs. 5-6, $P_{3\text{-}4}$ dext., Ekora, KNM EK-7. Fig. 5, crown view; fig. 6, external view. All figs. × 1.3.

Plate 8

Hipparion cf. *sitifense* Pomel. Fig. 1, M_3 dext. (4), Lothagam, KNM LT-161; external view. Fig. 2, M_{1-2} sin., Lothagam, KNM LT-150; crown view. Figs. 3-4, M_3 dext. (3), Kanapoi, KNM KP-42. Fig. 3, crown view; fig. 4, external view. Figs. 5-6, M^3 sin. (3), Lothagam, KNM LT-140. Fig. 5, crown view; fig. 6, internal view. Fig. 7, M^3 dext. (5), Lothagam, KNM LT-138; crown view. Fig. 8, M^3 sin. (7), Lothagam, KNM LT-148; crown view. All figs. $\times$ 1.3.

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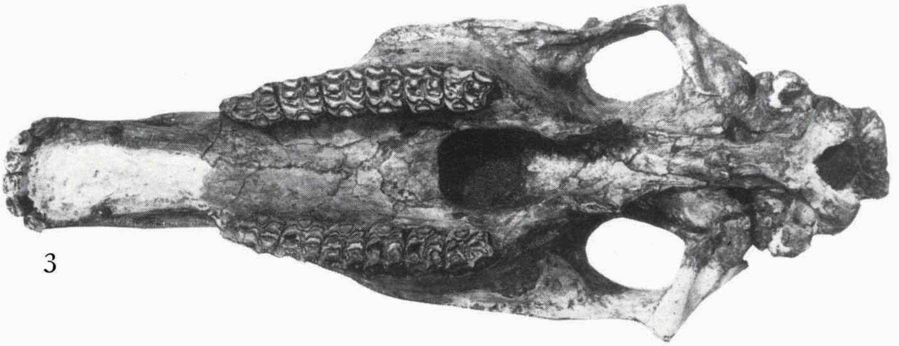

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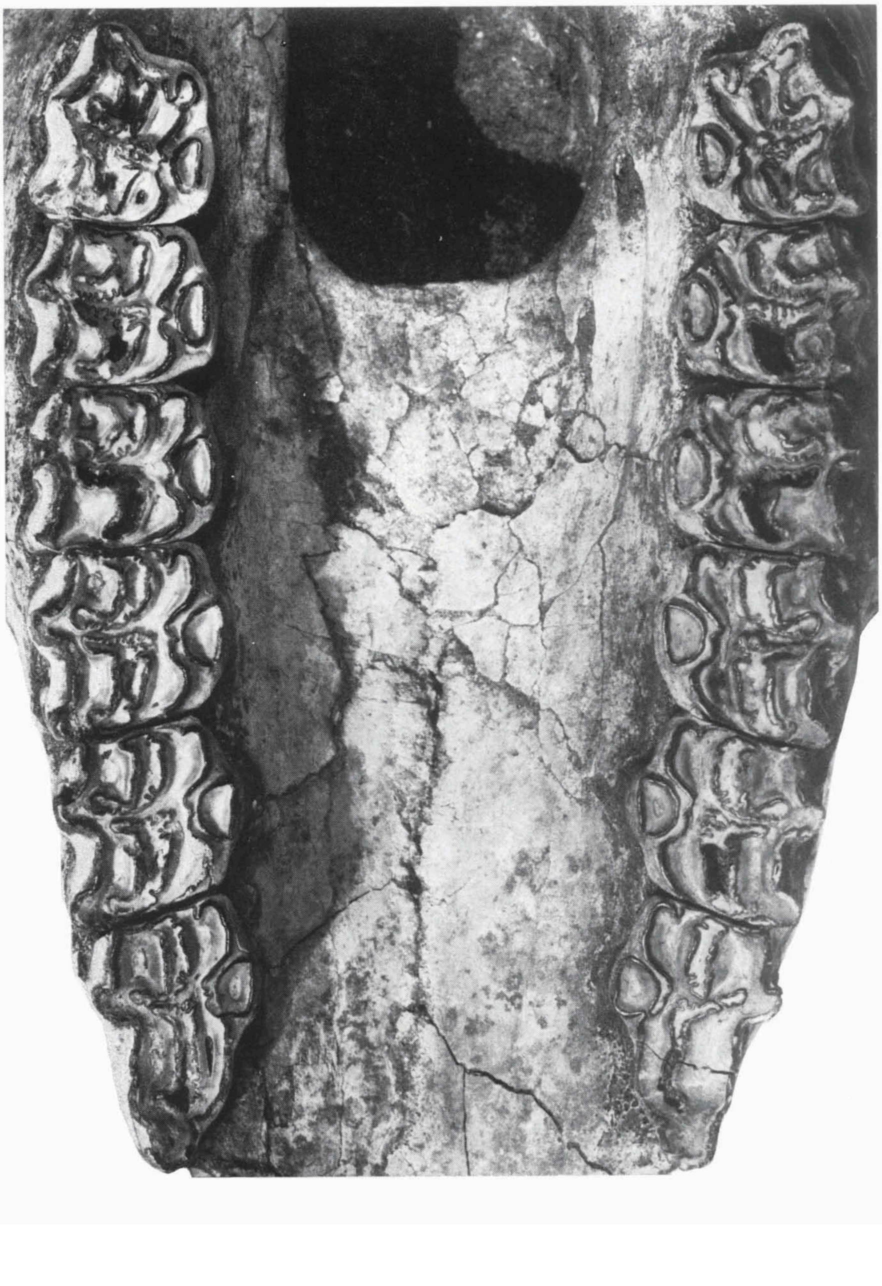

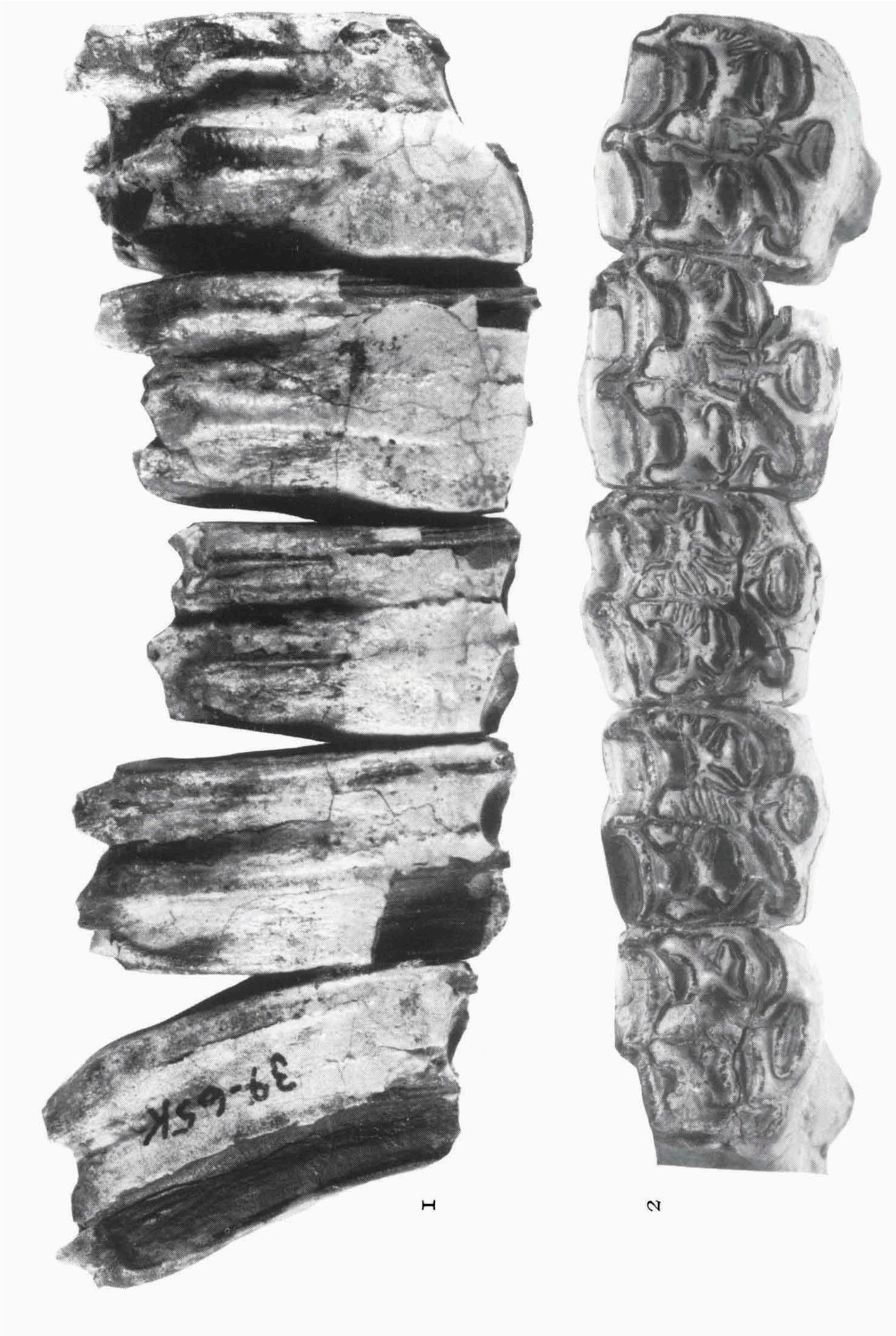

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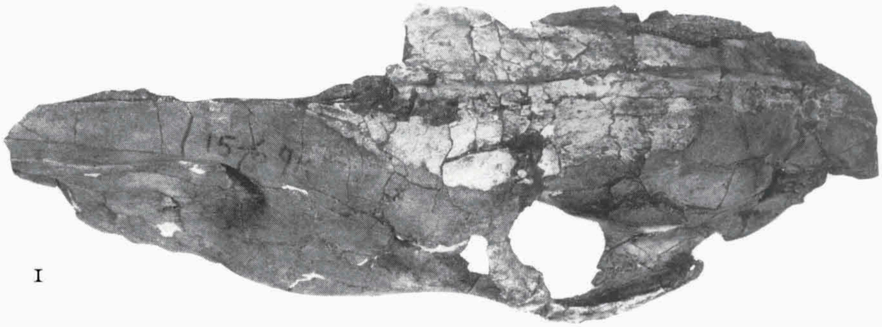

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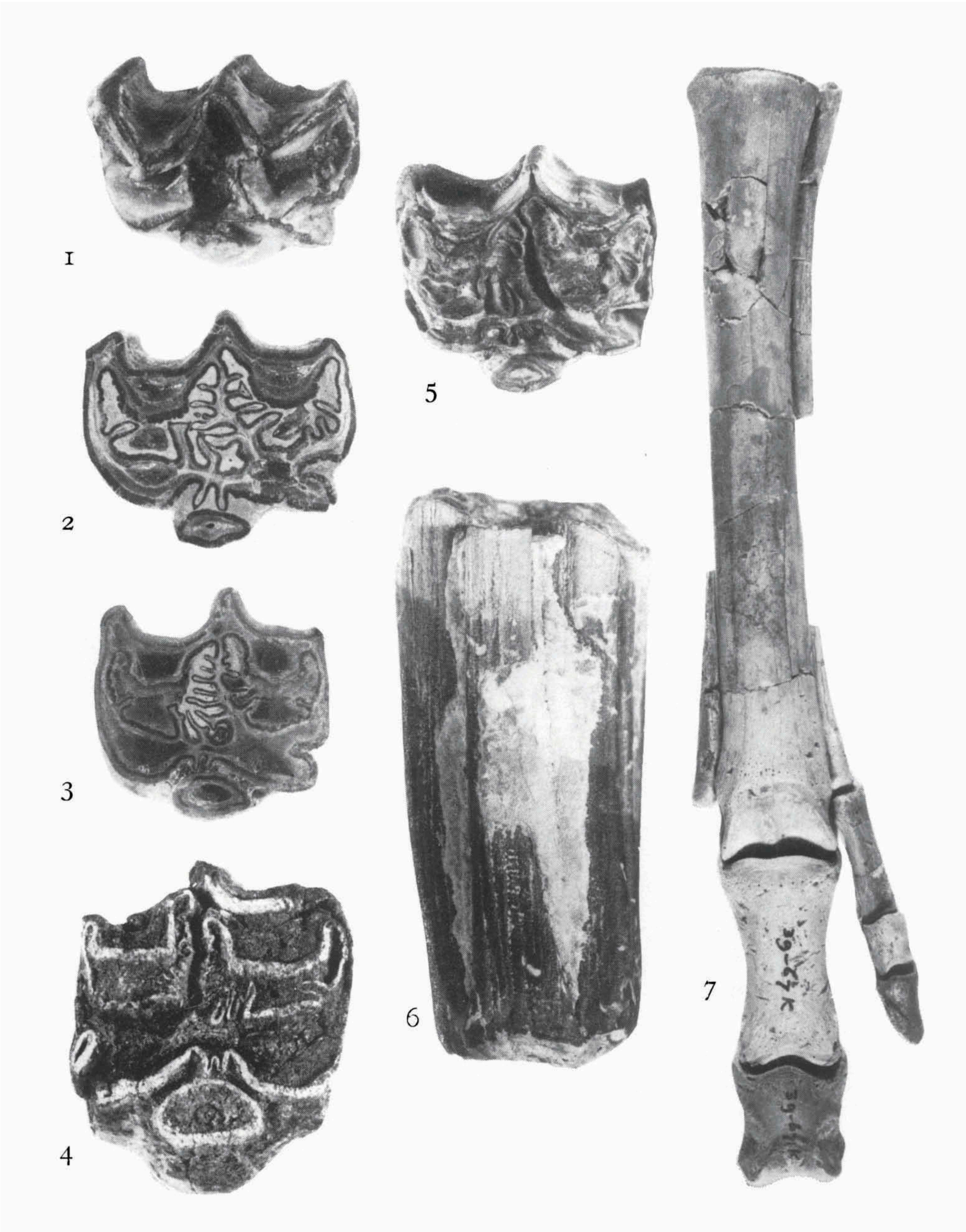
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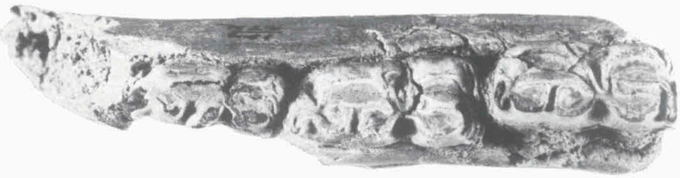

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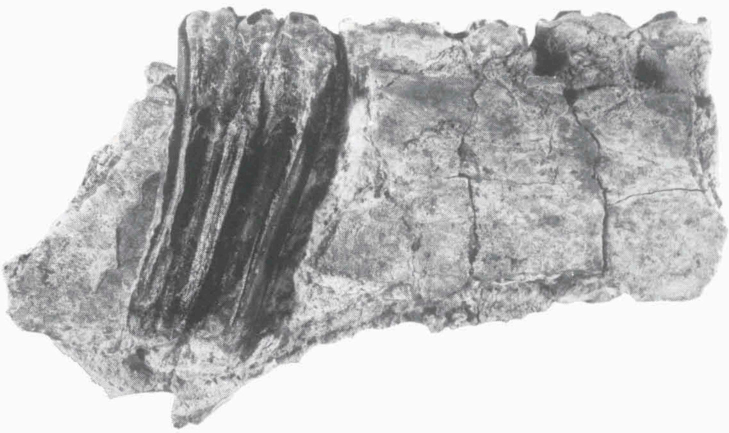

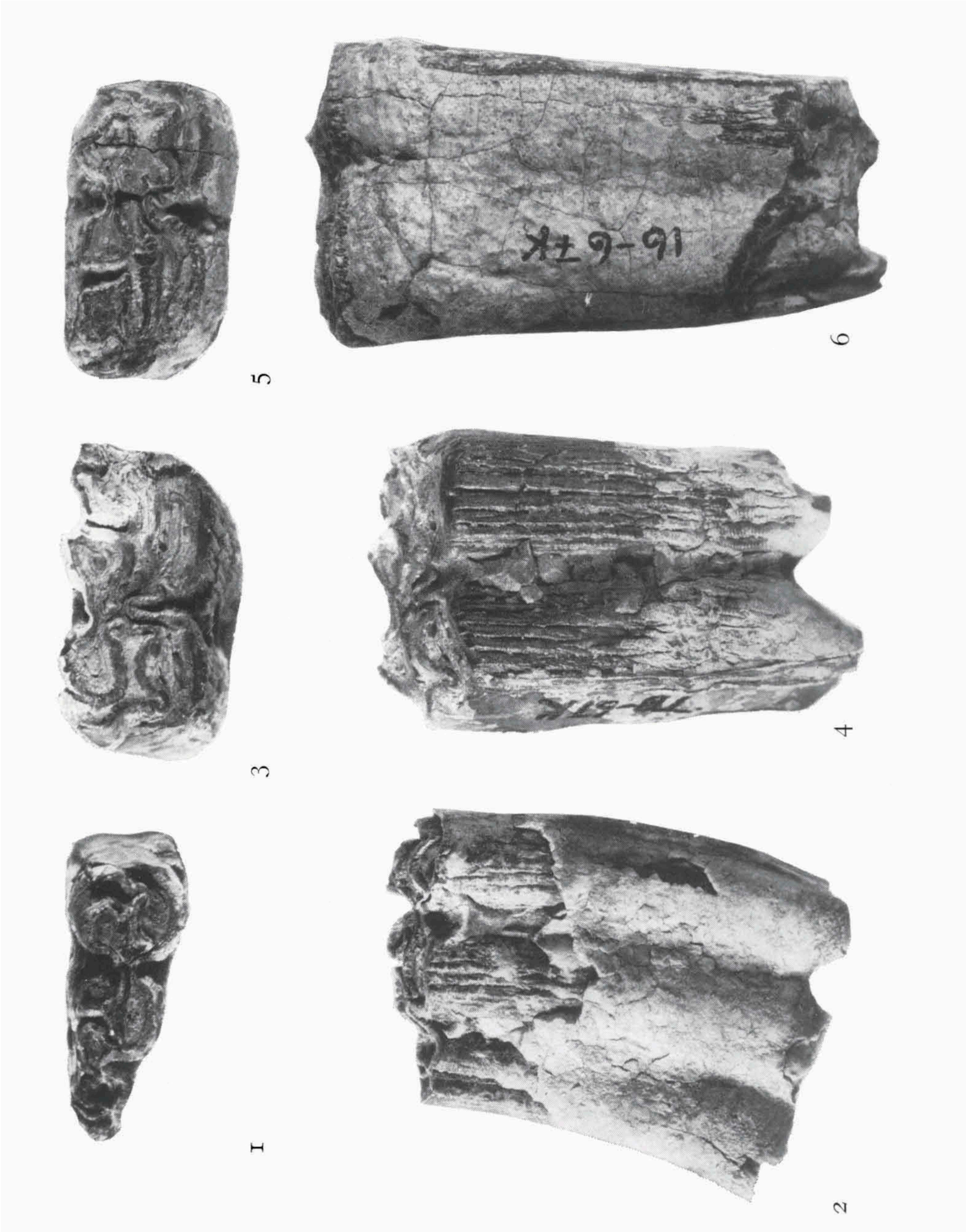

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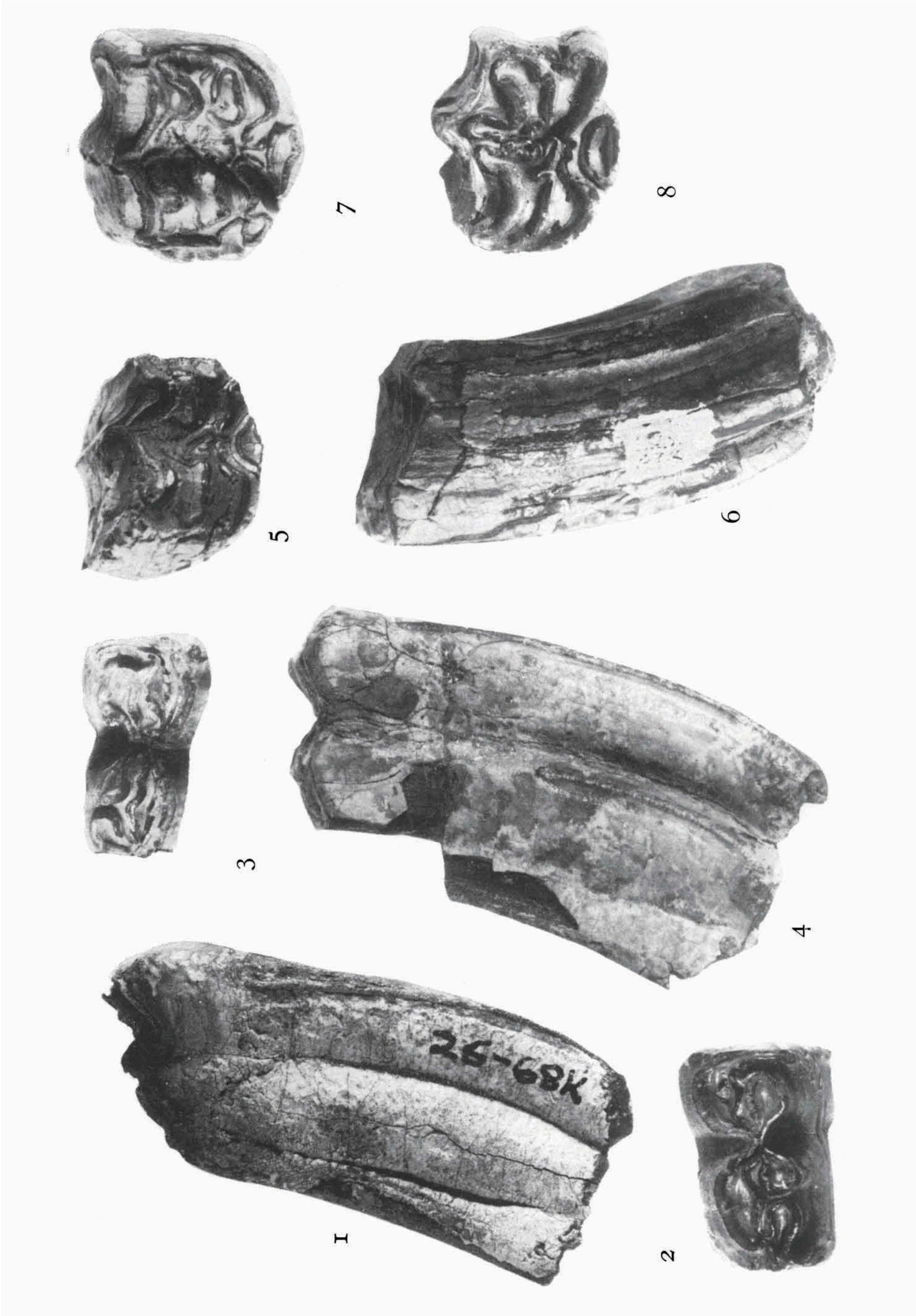
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