MIOCENE TO PLEISTOCENE HIPPARIONS OF KENYA, TANZANIA AND ETHIOPIA

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With 1 text-figure and 19 plates

Life is a gift horse in my opinion
J. D. Salinger, Teddy

CONTENTS

INTRODUCTION AND ACKNOWLEDGEMENTS

Hipparion De Christol, 1832, comprises extinct tridactyl equids typified by their isolated protocones, which evolved in North America from *Merychippus* stock, and invaded the Old World 12.5 million years ago. Gone are the days when *Hipparion* was considered ancestral to *Equus*, but to this day sweeping conclusions are being drawn about some reduction in the length of the side metapodials relative to the median metapodial from the oldest to the youngest forms, whereas in reality all there was is allometric growth (cf. Forstén, 1973a). In her plea for the new systematics, with polytypic rather than local and chronologically limited species, Forstén (1973b) observes that since 1829, when the first finds were described by Von Meyer, until about 1930 new species of *Hipparion* have been described at a mean rate of one every three years. Since 1930, the mean rate of increase in the number of species described as new in *Hipparion* has been two every three

years. In her valuable revision of the Old World *Hipparion,* Forstén (1968) regards only nineteen out of a total of sixty-one described species as probably valid. She did not even consider all the described Old World species, leaving out, e.g., those described by Gabuniya (1959), and, of course, those described after 1968, such as *Hipparion nagriensis* Hussain (1971) from the Nagri Formation of the Siwaliks, one more synonym of *Hipparion primigenium* (Von Meyer) of which she had already listed no less than sixteen synonyms (Forstén, 1968: 14/15).

I wish to record my great indebtedness to the late Dr. Louis Leakey and to Mrs. Dr. Mary Leakey who, after having entrusted to me the rhinocerotids kept in the National Museum at Nairobi, gave me the equid material from Olduvai Gorge for study. This contains the first skulls of *"Stylohipparion"* ever found anywhere. I am also much indebted to Dr. F. Clark Howell, who has sent me the equid material from the Omo Group deposits in Ethiopia collected by the American contingent from 1967 to and including 1974. The equids of the Baringo Basin in Kenya collected by the East African Geological Research Unit (EAGRU) based at Bedford College, London, have been sent to me by Dr. Bill Bishop. Dr. Brett Hendey kindly allowed me to study the *Hipparion* from Langebaanweg, South Africa. I have seen casts of *Hipparion* from the Makapansgat Limeworks, Transvaal, through the courtesy of Dr. Alan Walker. The Ngorora Formation *Hipparion* kept in the National Museums of Kenya have been loaned to me by the Ministry of Natural Resources, Nairobi. I have profited much from the collaboration with Dr. Vincent Maglio, then of Princeton, on the Lothagam-Kanapoi-Ekora hipparions collected by Harvard and Princeton University Expeditions to Kenya between 1965 and 1972. Grants-in-aid from the Wenner-Gren Foundation for Anthropological Research, Inc., New York, N.Y., in support of my studies in Africa are gratefully acknowledged.

In thanking my colleagues for their cooperation I can only say that I hope to have achieved some "perfection in the unfinished", for new fossil equids continue to turn up in Africa, and I have not had access to all that is collected to date. The photographs in the present paper are by Mr. C. Hoorn, Leiden.

The major fossil sites in East Africa that have yielded equids are shown in fig. 1.

A word about the terms Miocene, Pliocene, and Pleistocene. These do not mean the same to everyone, and are very confusing to the uninitiated. For the purpose of the present paper I hold the Oligocene/Miocene boundary to be at 25 million years, the Miocene/Pliocene boundary at 5 million years, and the Pliocene/Pleistocene boundary at 2 million years (cf. Van Couvering, 1972).

Some notes on working methods

Hipparion is one of the most interesting genera of equids. It gave its name to the "*Hipparion* fauna", the classic Mediterranean Pontian. However, the relationships between the various species of the genus remain a matter or contention. There is a primordial Old World species, *Hipparion primigenium* (Von Meyer), and it is now becoming clear that the subsequent development in Africa was different from that in Eurasia (Hooijer & Maglio, 1974: 30). The best documented African form is *Hipparion africanum* Arambourg (1959) from the Vallesian of Algeria and Morocco. Its hypodigm includes skulls, mandibles, as well as postcranials; it is identical with *Hipparion primigenium* of the Vallesian of Europe and Asia. We have a skull of *Hipparion turkanense* Hooijer & Maglio from Lothagam, and a juvenile skull of *H. primigenium* from Ekora, both in Kenya (Hooijer & Maglio, 1974: 8-15). There is an (undescribed) skull of *Hipparion baardi* Boné & Singer, but none of *Hipparion namaquense* (Haughton) from southern Africa. We have two skulls of *Hipparion* cf. *ethiopicum* (Joleaud) from Olduvai Gorge. In the Lothagam-Kanapoi-Ekora collections there is a small form of *Hipparion* of which we have no skull, and which consequently we cannot classify properly although there are postcranials of the same size class that may confidently be referred to it. Even toothrows may be difficult to identify specifically. As far as the teeth go, there is no more to them than meets the eye (like any metaphor, this one is not fully adequate as structures called ectostylids, which loom large in phylogenies, may be hidden from view in the cement investment on the external faces of the lower cheek teeth). The enamel borders of the fossettes and flexids form patterns that may appear simple or complex: usually, but not invariably they simplify with advancing wear.

The interpretation of the differences is rather obscure. Complicated tables recording counts of fossette plications fore and aft in the uppers, at various levels of the crown, are given in the literature. Although this method had its values, it tends to overemphasize the significance of such figures, and comparisons between the various forms are rather involved. Moreover, every pli is counted as one no matter whether it is deep or shallow, ample or just a little twist.

Clearly the most important, but likewise the most difficult character to establish in any form of *Hipparion* is the absolute height of the crowns of the teeth. It is a great exception to find a complete crown that is both unworn and has the base calcified, and preserved. The height as worn may be given, but this is of little value for purposes of comparison. If we have crowns

that are just slightly worn a minimum estimate of the full height may be obtained. The relative crown height is the full height expressed as a percentage of either the crown width or the anteroposterior crown diameter: thus we get a height/width index or a height/length index irrespective of the absolute dimensions, and this is of importance in assessing the evolutionary stage: small hypsodont forms may have crowns lower than large, not-so-hypsodont forms. The absolute size of the tooth crowns, anteroposterior and transverse, is of value only when the measurements are taken in a consistent manner and are not dependant upon wear; it should be stated how, at what level of the crown, the measurements are taken. I find that at 2 cm from the base a good measure of the size of the crown is obtained. Third and fourth premolars, and first and second molars become shorter anteroposteriorly as wear proceeds, whereas second premolars and third molars tend to keep the same length or lengthen with advancing wear. The width in the uppers increases with wear at the base, where the protocone is produced, but otherwise the width remains rather constant as in the lowers. Cheek teeth in situ in skulls and mandibles must be measured occlusally if the specimens are not damaged.

Protocone indices will not be found in the present paper, although some authors set considerable store upon such indices. Anyone who handles *Hipparion* teeth should realize how variable and difficult to measure precisely these structures are, and that indices expressing the transverse diameter of the protocone as a percentage of the anteroposterior diameter of the same look fine on paper but are of very limited value (cf. Cooke & Coryndon, 1970: 140-145).

Species of Hipparion in Africa

In a purported revision of African hipparions published ten years ago, Boné & Singer (1965) distinguish the following species: *Hipparion africanum* Arambourg (no subgenus), *Hipparion sitifense* Pomel (no subgenus), *Hipparion* (*Stylohipparion*) *libycum* Pomel, and *Hipparion* (*Hipparion*) *albertense* Hopwood, the last with two subspecies neither one of which is the nominal subspecies.

There must needs be said something against the use of these names. *Hipparion africanum* is a synonym of *Hipparion primigenium* (Von Meyer). *Stylohipparion* Van Hoepen, 1932, is a synonym of *Eurygnathohippus* Van Hoepen, 1930, and the latter name should be used if a subgeneric (or generic) distinction is deemed necessary (for which I see no reason). *Hipparion albertense*, although the name is widely in use, in actual fact is a nomen vanum (in the sense of Simpson, 1945: 27); its type specimen is an in-

complete upper molar, and specific identity with other material cannot by any means be proved to be correct. Lower cheek teeth both with, and without ectostylids have been referred to it, hypsodont, and not-so-hypsodont. I recommend that the name *Hipparion albertense* should be either ignored or listed as indeterminate and without known significance (see p. 27/28).

Hipparion (*Hipparion*) *albertense serengetense* Boné & Singer (1965: 389) has been erected for "*Hypsohipparion*" Dietrich, 1941, with lower cheek teeth devoid of protostylids and ectostylids. These (vide Dietrich, 1942, pl. XIII figs. 89, 90, 93b, pl. XIV fig. 101, pl. XV fig. 106) are indistinguishable from *Equus* and belong there, while the uppers belong to "*Stylohipparion*" (cf. Arambourg, 1947: 306).

Hipparion (*Hipparion*) *albertense baardi* Boné & Singer (1965: 389) from Langebaanweg, Cape Province, lacks ectostylids, too, but has protostylids (unlike in *Equus*). Dr. Brett Hendey (personal communication) informs me that the larger part of a *Hipparion* skull recently recovered at Langebaanweg shows that it is very different from the type of *H. turkanense*, most strikingly in that it has a pronounced preorbital fossa. The Langebaanweg *Hipparion* appears to represent a species in its own right, and it may henceforth be designated as *Hipparion baardi* Boné & Singer. The age of the Langebaanweg form of "E" Quarry, with *Ceratotherium praecox* Hooijer & Patterson (1972) as the most abundant large element (Hooijer, 1972), ranges somewhere in the 7 to 4 million year interval: this is the known temporal range of *C. praecox* (Mpesida Beds to Mursi Formation: Hooijer, 1973: 169).

The first appearance of *Hipparion* in land mammal populations of the northern hemisphere is one of the best documented biochronological events of the Neogene: the genus appears first in the Mediterranean world about 12.5 million years ago (Evernden, Savage, Curtis & James, 1964: 167; Van Couvering & Miller, 1971; Van Couvering, 1972: 256). In France (Guérin, Mein, Philippe & Truc, 1972) its first appearance is Middle to Upper "Helvetian" (ante-"Tortonian").

The evidence available to date supports a 10.5 million year age for the base stratotype Tortonian (Van Couvering, in Bishop & Miller (editors), 1972: 445). This means that the *Hipparion* datum of 12.5 million years is some 2 million years before the Tortonian; in the Vallesian, the dates being what they are, or appear to be.

In Asia, *Hipparion* appears first in the Nagri Formation of the Siwalik Hills (Simons, Pilbeam & Boyer, 1971), about 12 to 10 million years ago. Hussain (1971) described the Nagri Formation *Hipparion* as *Hipparion nagriensis*. However, this appears to be a clear synonym of *Hipparion primi-*

genium: the cheek teeth display the very characteristic pattern, and are of the size of those in this species (cf. Hussain, 1971: 49, 50, pls. 1, 2, and Sondaar, 1961: 273, figs. 21, 22). Hussain (1971: 51) did notice the resemblance of *H. nagriensis* to *Hipparion catalaunicum* Pirlot and *H. koenigswaldi* Sondaar both of which are synonymous with *H. primigenium* (Forstén, 1968: 14, 15).

In North Africa the earliest Hipparion is *H. primigenium*: it was described as *Hipparion africanum* Arambourg (1959: 75, diagnosis: 95) from the Vallesian of Wad el Hamman (also known as Bou Hanifia) and Marceau in Algeria, and further occurs at Camp Berteaux (Melka el Ouidane) in Morocco (Arambourg, 1959: 95/96). This identification was still upheld in 1970 (Arambourg, 1970: 95), although Forstén (1968: 15) had already synonymized *africanum* with *primigenium*. *H. primigenium* has since been recorded from the Vallesian Beglia Formation of Tunisia (Forstén, 1972). Van Couvering (1972: 249) placed Bou Hanifia at about 11.5 million years, and Melka el Ouidane at about 7.5 million years, in which he was followed by Jaeger, Michaux & David (1973).

The discovery of *Hipparion primigenium* in the Ngorora Formation of Kenya, which is between 12 and 9 million years old, greatly reduces the time lag once supposed to exist between the first appearance of *Hipparion* south of the Sahara and that north of the same; it is probably of little or no geological significance.

Teeth indistinguishable from *Hipparion primigenium* have already been described from Kanapoi, in Kenya, and there is a juvenile skull, with a preorbital fossa and teeth of the *H. primigenium* type, from Ekora, also in Kenya, showing that the species lingered on in sub-Saharan Africa till the 4 million year level (Hooijer & Maglio, 1974). There is material pertaining to this species from the Chemeron Formation (between 5.4 and 2 million years old), and from the Aterir Beds (4 million years old), described in the present paper. In the lowers the ectostylid occasionally reaches a height of 45-50 mm, as it does in the Kanapoi hemimandible as well as in a juvenile hemimandible from Lothagam (Hooijer & Maglio, 1974). We interpret this material as an advanced *Hipparion primigenium* in which, contrary to the development in Eurasia (Forstén, 1968: 24), the ectostylid continued to develop since the Vallesian. This may have led to the emergence of "*Stylohipparion*" in the Villafranchian of Africa, the culmination of evolution in the genus *Hipparion*. We find it in its typical development in North Africa, Ethiopia (Shungura Formation from Member F on up), Tanzania (Olduvai Gorge), and in southern Africa including the famous australopithecine sites Swartkrans, Kromdraai, and Makapansgat.

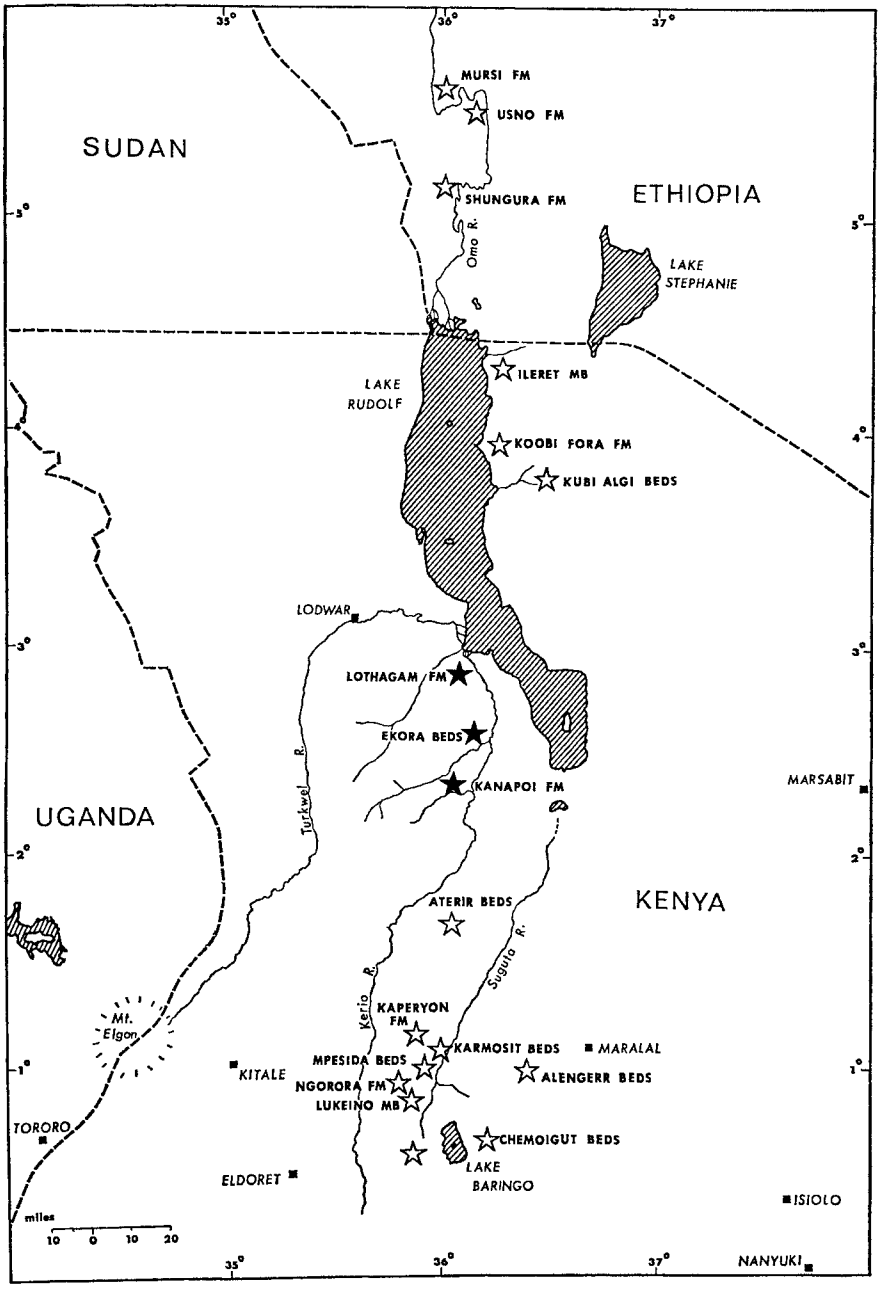

Fig. 1. The major equid sites in East Africa.

The vertical distribution of *Hipparion primigenium* in our interpretation of this species in sub-Saharan Africa is the same as that of *Brachypotherium lewisi* Hooijer & Patterson (1972; Hooijer, 1973: 153): from the Ngorora Formation up into Lothagam Hill, Member C, the 4 million year level.

In South Africa, there is an interesting but unfortunately not well-known *Hipparion* seemingly representing an Early Pliocene stage; it was described as *Notohipparion namaquense* Haughton (1932) from an undated site in Namaqualand. Both Van Hoepen (1932: 31) and Dietrich (1942: 99) regard it as more primitive than *Stylohipparion,* which it undoubtedly is. Cooke (1950: 426) concedes that it may have a bearing on these advanced, Pleistocene forms. Boné & Singer (1965: 389) place it in the synonymy of *Hipparion libycum* Pomel of the Villafranchian of North Africa, which is not justified. The ectostylid development in *Hipparion namaquense* is clearly weaker than in *Stylohipparion*: ectostylids show occlusally in P_4 and M_1, which are worn to 2.5 cm of height, in M_2, worn to 3 cm of height, while the M_3, worn to 3.5 cm of height, does not show it occlusally. In ectostylid development the Namaqualand mandibular teeth (the only teeth known) are slightly inferior to those of the *Hipparion* of the Lower Shungura Formation, particularly a mandible from Shungura Member B11 described in the present paper. The caballoid enamel configuration resembles that of the Shungura form closely.

Hipparion baardi Boné & Singer (1965) from Langebaanweg, Cape Province, is characterized by the absence of ectostylids by a molar crown height of some 7 cm, and the enamel pattern of the molars (except the most worn ones) is rather complex. Ptychostylids are markedly developed. Above all, *H. baardi* has a pronounced preorbital fossa (Q. B. Hendey, in litt.). A symphysial portion of the mandible shows that the third incisor is not reduced, unlike in *"Stylohipparion"* but as in *H. primigenium.* Some entire median metacarpals (none were recorded in the original publication) will be reported upon in the section on the postcranials from Olduvai Gorge.

The skull of *Hipparion turkanense* Hooijer & Maglio (1973, 1974) from Lothagam in Kenya has no preorbital fossa and moderately plicated molars. The anteroposteriorly oriented enamel borders are wrinkled. The referred lower cheek teeth have wrinkled enamel externally and in the flexids, no ectostylids, and the ptychostylids are masked by the conspicuous enamel wrinkling (unlike in *H. baardi*).

Hipparion turkanense seems to have emerged in Africa south of the Sahara some 7 million years ago (Mpesida Beds of Kenya), possibly representing an invasion from Asia in Late Miocene times. It also occurs in the Lukeino Formation (olim Kaperyon Beds) of Kenya, ca 6 million years, and in the

Mursi Formation of southern Ethiopia (dated at 4 million years), as will be recorded below. Its temporal range coincides with that of *Ceratotherium praecox* Hooijer & Patterson (1972; Hooijer, 1973: 168).

In all, then, I distinguish four pre-Pleistocene species of *Hipparion* in sub-Saharan Africa. These are *Hipparion primigenium, Hipparion namaquense, Hipparion baardi,* and *Hipparion turkanense.*

In addition, there are various forms of *Hipparion* of rather small size, in different parts of the range, and none of which represented by a skull. These forms are difficult to classify on the material available: they present problems of nomenclature. If the small teeth cannot be told apart, why then give them separate names? In one case it was possible to establish a significant difference in hypsodonty. Do these forms represent points on a chronocline, a lineage, or did they evolve independently? Are they specifically the same? These questions are hard to solve, and others may disagree with the solution offered. A case in point is the well-known *Hipparion matthewi* Abel (1926a: 163; 1926b: 432, fig. 273) of the Pikermian of Samos, which has a length P^2-M^3 of only 110-112 mm (Forstén, 1968: 125). There is also *Hipparion elegans* Gromova of the Pikermian of Pavlodar in Siberia, which has a P^2-M^3 length of 133-137 mm (Gromova, 1952: 183). *H. elegans* has been tentatively referred to *H. matthewi* because of its size (Forstén, 1968: 53): the Samos skulls are aged, with senile and thus anteroposteriorly short teeth, while skulls measured by Gromova all belong to rather young individuals (in two of them M^3 is only just erupting), and the toothrows accordingly are at their longest (Forstén, 1968: 58/59). We had a small *Hipparion* at Lothagam, Kanapoi and Ekora, and we called it *Hipparion* cf. *sitifense* Pomel (Hooijer & Maglio, 1974: 27). True *Hipparion sitifense* is a North African species, just pre-Villafranchian, around the 3 million year level, and, therefore, later than the material we compared it with from south of the Sahara, which is in the 6 to 4 million year range. It probably occurs in the "Earlier" horizon of the Kaiso Formation in Uganda, between Lothagam and Kanapoi in age, and at Bethlehem in Israel, a very early Villafranchian fauna (Hooijer & Maglio, 1974: 27-29). There is also small *Hipparion* in the Lukeino Formation and in the Chemeron Formation, and in the Omo Group deposits, the latter definitely more hypsodont than the Lothagam-Kanapoi form. This will be described in the present paper.

The *Hipparion* from Olduvai Gorge in Tanzania, "*Stylohipparion*" auctorum, most fortunately is represented by two skulls from Bed II at Olduvai, to be described in the present paper. In the Upper Omo group deposits in southern Ethiopia there is a form that is dentally indistinguishable, and that was described as *Hipparion ethiopicum* (Joleaud, 1933: 7). This is the

advanced, Villafranchian *Hipparion* found in several parts of Africa, from north to south, very hypsodont, with very well-developed ectostylids, and reduced lateral incisors. As Dietrich (1942: 99) surmised, "*Stylohipparion*" is not a genus in its own right, and *H. namaquense* or some such form may be ancestral to it. In the Lower Omo Group deposits there are indications of increase in crown height and ectostylid development with time, as will be documented below.

Hipparion primigenium (Von Meyer)

Geological mapping 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 and Dr. W. W. Bishop, has led to the discovery of the earliest *Hipparion* south of the Sahara. Some isolated teeth of *Hipparion* were first found in the Mpesida Beds, dated at 7 million years (Bishop & Chapman, 1970: 917; Bishop, Chapman, Hill & Miller, 1971: 391; Bishop, 1972: 228; Hooijer & Maglio, 1973: 311), but continued research uncovered *Hipparion* remains in the Ngorora Formation, which is between 12 and 9 million years old (Bishop, 1972: 230). This material, to be described below, represents the primordial *Hipparion* of the Old World, *Hipparion primigenium* (Von Meyer).

The Ngorora Formation rhinocerotids have already been reported upon, and represent *Brachypotherium lewisi* Hooijer & Patterson (see Hooijer & Patterson, 1972: 17; Hooijer, 1973: 153), *Aceratherium acutirostratum* (Deraniyagala) c.q. *Dicerorhinus leakeyi* Hooijer (see Hooijer, 1971: 364), and *Chilotheridium pattersoni* Hooijer (see Hooijer, 1971: 360-362, 365). *Brachypotherium lewisi* ranges from Ngorora to Lothagam Hill, Member C, 12- to 4 million years ago. *Aceratherium acutirostratum* and *Dicerorhinus leakeyi* range from the Early Miocene on up: the latest occurrence of *Dicerorhinus leakeyi* is in the Chemeron Formation (between 5.4 and 2 million years: Bishop, 1972: 230), possibly as reworked material (Hooijer, 1973: 155-156). *Chilotheridium pattersoni* ranges from Loperot to Ngorora, 18 to 12- million years ago. Thus, at Ngorora we have the latest *Chilotheridium* and the earliest *Brachypotherium lewisi.*

The Ngorora Formation *Hipparion* material comprises not only cheek teeth but also incisors, some in situ, and some postcranial bones. The incisors will be dealt with first.

An I^2 and I^3 sin. in situ a premaxillary fragment from Ngorora, KNM-BN 1154 (pl. 2 fig. 5), show that I^3 was not reduced in size as compared to I^2 as it becomes in the later, Pleistocene, *Hipparion.* I^2 is worn down to approximately 20 mm from the crown base. It lacks the apex of the root,

which was about 30 mm long. I^3 has the entire root; the crown is worn to about 20 mm from its base, and the root length is 30 mm. The crown width at the occlusal surface is 18 mm for I^2, and 19 mm for I^3; labiolingually the diameter is 11.5 mm for I^2, and 10.5 mm for I^3. The cup is large in both, the medial third very nearly constricted off in I^2, and cement-filled; there is a very weak longitudinal groove externally, and a median internal depression. A small canine, not more than 10 mm anteroposteriorly and about 6 mm transversely, is in situ in the premaxillary, placed 25 mm behind the I^3. The upper incisors of *H. primigenium* from Wad el Hamman described by Arambourg (1959: 79-80) are of the same shape and size. In the Algerian form the canine is 13 by 9 mm in diameters, and the I^3-C interval is 28-31 mm. In the type skull of *Hipparion turkanense* from Lothagam I^3 is not reduced in size relative to I^2, and the canine is 8 by 5 mm in diameters, placed 30 mm behind I^3 (Hooijer & Maglio, 1974: 9/10). It is rather probable that these laterally compressed canines indicate the male sex: in the females of the Pikermi hipparion the canines are smaller, and round in section (Pirlot, 1952).

From the Aterir Beds there are portions of both premaxillaries, KNM-AT 153-154, associated with cheek teeth indistinguishable from those of *H. primigenium*. I^3 is not reduced in size as compared to I^2. Unfortunately, the two central incisors are not preserved, but I^2 and I^3 dext. are in situ, slightly damaged mesially; I^3 sin. is entire, and I^2 sin. broken off in its alveolus (pl. 2 figs. 2-3). The crowns of the Aterir Beds incisors are worn down to about 25 mm from their bases. The width at the oblique occlusal surface of I^3 is 17 mm, and the basal widths are 12 mm for I^2 and 13 mm for I^3. The labio-lingual diameters of I^2 and I^3 are 12, and 11 mm, respectively.

The lower incisors in the Ngorora collection, apart from fragments (KNM-BN 1124 and 1212), are represented by an I_2 sin., KNM-BN 1211, much worn and wanting the root. The transverse diameter at the occlusal surface is nearly 18 mm, the labio-lingual diameter 11.5 mm. At the base of the crown these diameters are 12.5, and 12.0 mm, respectively, the crown thus assuming a nearly round cross section at base. The height of the crown as preserved is barely 15 mm.

The best preserved upper cheek tooth from Ngorora, KNM-BN 1119 (pl. 3 fig. 1) is a P^3 or P^4 dext. The parastyle is broad, broader than the mesostyle, as is the rule in premolars, and the occlusal surface falls off anteriorly. The crown is worn to a height of only 2 cm internally, and 3.5 cm externally. The isolated protocone measures 8.5 mm anteroposteriorly, and 5.5 mm transversely; the whole crown measures 27.5 anteroposteriorly, and the transverse diameter is exactly the same when measured over meso-

style and protocone occlusally, but 30.0 mm inclusive of the cement that covers the protocone internally. The caballine fold is duplicated, and each of the two folds is forked. The plication pattern of the fossettes is extremely complex, with no less than eight plis in the posterior border of the prefossette (including the pli protoconule) and in the anterior border of the postfossette (including the pli postfossette). In the prefossette there are six anterior plis, and in the postfossette there are four posterior plis. The hypoglyph is narrow but not yet obliterated. Fragmentary upper cheek teeth also from Ngorora (KNM-BN 1205 and 1208), a left premolar and molar, respectively, lack the internal portions of the crown but show the same complex fossette plication pattern. A number of small crown fragments (KNM-BN 1116, 1206, and 1207) conform.

The fossette plication pattern observed in the Ngorora cheek teeth is that of *Hipparion primigenium* (Von Meyer), the primordial Old World *Hipparion*. The upper dentitions from Wad el Hammam described as *H. africanum* by Arambourg (1959: 82, fig. 36 A-C, pl. X fig. 3, pl. XI fig. 3, pl. XIII fig. 2), as well as those from Esselborn in Germany and Nombrevilla in Spain (Sondaar, 1961: 248, fig. 21 A-C; the Nombrevilla dentitions described as *H. koenigswaldi* Sondaar, as synonym of *H. primigenium*: Forstén, 1968: 15) have deep fossette plications, those on the adjoining borders of pre- and postfossette especially narrow and almost parallel. The pattern is rather even and seems to fill the whole fossette. The resemblance of the Ngorora teeth to those of Europe and Algeria, and of the Kanapoi dentition already described (Hooijer & Maglio, 1974, pl. 3) is as close as one could wish it to be.

The lower cheek teeth from Ngorora are likewise indistinguishable from those of *H. primigenium*. There are P_2-M_1 dext., and P_3-P_4 sin. of the same mandible in situ in body fragments, KNM-BN 1117 (pl. 1), excellently preserved. The metaconid and the metastylid are rounded, the metastylid tends to form a point posteriorly, most marked in P_3. The metaconid-metastylid valley is shallow in the premolars, and deeper in M_1. There is much resemblance between the Ngorora lower dentition and that of *Hipparion "africanum"* (= *primigenium*) from Wad el Hamman as figured by Arambourg (1959: 84). In the premolars the entoflexids are larger than those in the molar, as usual: in the molars the external groove between protoconid and hypoconid extends further toward the internal valley, between metaconid and metastylid, than in the premolars. The metaflexid and entoflexid borders are weakly wrinkled. There are very marked protostylids, and traces of ptychostylids, but ectostylids do not show. These may well be hidden in the thick cement that covers the teeth: this was the case with the

Kanapoi P_4 and M_2 before the cement was removed (Hooijer & Maglio, 1974, pl. 6 figs. 1-2). The ectostylids never extend upward to the top of the crown, not even in the most advanced hipparions, but are short by some 10 mm or more. Ectostylids are frequent in *H. primigenium* and differ in frequency in the local populations: Forstén (1968: 24) found that the frequency of occurrence of ectostylids may vary from 14 to 100% in the premolars, and from 24 to 71% in the molars. Arambourg (1959: 84) did not observe them in the teeth of *H. primigenium* from Wad el Hammam but these were teeth in situ and ectostylids may have developed just the same although they are not exposed. As a matter of fact there is a damaged and incomplete right lower cheek tooth from Ngorora, KNM-BN 1283 (pl. 3 fig. 2), of which the external cement has been removed in part, and this tooth shows an ectostylid, extending 15 mm upward (above the front of the M in the photograph). Cement is profusely developed on the cheek teeth: the P_4 measures 18.5 mm transversely, cement included, and only 14.5 mm across the enamel outer and inner borders. The anteroposterior diameters of the cheek teeth are reduced as a result of interproximal wear, but are 30 mm for P_2, 27 mm for P_3 and P_4, and 25 mm for M_1, figures that tally well with those of *H. primigenium* in the literature, including those of the Kanapoi hemimandible. Although cranial material is so far lacking, I have no doubt that the Ngorora *Hipparion* represents *H. primigenium*. No teeth were found in the collection from the Ngorora Formation that represent or resemble those of *Hipparion turkanense* of the Mpesida Beds and Lothagam-1, to mention only the earliest occurrences.

Among the postcranial bones from Ngorora there is first of all the proximal phalanx of a third digit, KNM-BN 1202 (pl. 3 figs. 5-6). Arambourg (1959) had only juvenile phalanges of *H. primigenium* from Wad el Hammam, but Forstén (1972) records six first phalanges of this species from the Beglia Formation in Tunisia, and the Ngorora phalanx I, with a volar length of 54 mm and a least shaft width of 30 mm, is within the limits of these (volar length 50-56 mm; least width 27-33 mm). The Ngorora phalanx is a typical *Hipparion* proximal phalanx, lacking the characteristic, long V-shaped ligamentary scar of its homologue in *Equus*. It is only shorter than the proximal phalanx of the third digit in the Olduvai *Hipparion* cf. *ethiopicum*, which varies in volar length from 63 to 73 mm by a least shaft width of 27 to 36 mm.

The proximal end of a right metacarpal II, KNM-BN 1344, is unmistakable because of the small magnum facet in between the proximal facet and that for metacarpal III, and measures 14 by 19 mm, exactly as in *H. primigenium* from Wad el Hammam (Arambourg, 1959: 88).

There are further, in the Ngorora collection, two entire carpals, viz., a scaphoid dext. (KNM-BN 1343), and a lunar sin. (KNM-BN 1296). According to Hopwood (1942: 81-86)) it is difficult to separate these bones of *Hipparion* from those in recent and fossil *Equus*. The scaphoid of *Hipparion* differs from that of *Equus* in the shape of the inferior facet for the lunar, and this is only a semi-constant difference, while the only difference between the lunar of *Hipparion* and that of *Equus* is that the distal recess for the posterior projection of the magnum is smaller in the former than in the latter. The measuremens of the Ngorora bones are given in table 1.

TABLE 1
Measurements of scaphoid and lunar of *H. primigenium*, Ngorora (mm)

	scaphoid	lunar
Anterior height	31.5	25
Proximal width	30	25
Distal width	28	20
Distal ant. post. diameter	44	31

The upper premolars and molars of the Aterir Beds, KNM-AT 150-152 (pl. 2 figs. 1 and 4) have the *primigenium* pattern, which strikes the eye once it is recognized. There are P^2-M^1 dext. (KNM-AT 150), P^{2-3} sin. (KNM-AT 151), and M^3 sin. (KNM-AT 152), all evidently of the same individual to which belonged the premaxillary portions with the incisors already dealt with above. The measurements and plication counts are given in tables 2 and 3. Since the maxillary portions holding these teeth are incomplete externally it is possible to give the external height of some: P^2, 4.5 cm; P^4, 5.5 cm, and M^3, 6 cm.

TABLE 2
Dental measurements of *H. primigenium*, Aterir, KNM-AT 150-152 (mm)

P^2,	ant. post.	35	M^1,	ant. post.	25
	transv.	25.5		transv.	26
	protocone, ant. post.	9		protocone, ant. post.	8,5
	transv.	4		transv.	4
P^3,	ant. post.	27.5	M^3,	ant. post.	22
	transv.	29		transv.	20
	protocone, ant. post.	10		protocone, ant. post.	9.5
	transv.	4		transv.	3.5
P^4,	ant. post.	27			
	transv.	29.5			
	protocone, ant. post.	10			
	transv.	4.5			

TABLE 3

Plication numbers of upper teeth of *H. primigenium*, Aterir, KNM-AT 150-152

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

Among the material from the Chemeron Formation, locality J.M. 493, there are an M^1 dext., an M^2 sin., and M^3 dext. evidently of the same individual, KNM-BC 367 (1), (2), and (3). The M^1 is very well preserved (pl. 3 fig. 4), and its crown is worn to a height of 5 cm externally. The M^2 lacks the mesostyle (pl. 6 fig. 5), the M^3 has part of the mesostyle at the base, but lacks the metastyle. Their bases are incomplete but the crowns are less worn than that of M^1 and thus were somewhat higher. The Chemeron dentition is worn to the same extent as that from Aterir, but less worn than that from Kanapoi, KNM-KP 43 in which M^1 is worn to a height of 36 mm only (Hooijer & Maglio, 1974: 13, pl. 3). The great depth of the fossette border plis fore and aft, the absence of wrinkling in the inner and outer borders of the fossettes, and the narrow protocones are exactly the same in the three dentitions, and I do not hesitate to refer the Chemeron upper

TABLE 4

Dental measurements of *H. primigenium*, Chemeron, KNM-BC 367 (mm)

M^1,	ant. post.		24
	transv.		24
	protocone,	ant. post.	8
		transv.	4
M^2,	ant. post.		23.5
	transv.		—
	protocone,	ant. post.	8.5
		transv.	4
M^3,	ant. post.		23
	transv.		21
	protocone,	ant. post.	9
		transv.	3.5

cheek teeth to *H. primigenium*. Measurements and plication numbers of the Chemeron M^{1-3} are presented in tables 4 and 5.

TABLE 5

Plication numbers of upper teeth of *H. primigenium*, Chemeron, KNM-BC 367

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

The lower cheek teeth associated with the uppers just mentioned are an M_1 or M_2 dext., KNM-BC 367 (4), and M_1 or M_2 sin., KNM-BC 367 (5) (pl. 4 figs. 1-2, pl. 5 fig. 6). These teeth, from locality J.M. 493, have a deeper metaconid-metastylid valley than the Ngorora teeth, and the metastylid especially is triangular rather than rounded. Thus they display more the caballoid type of the tie (i.e., metaconid and metastylid) than the hipparionid type, with its typically rounded loops, separated by a wide and shallow valley. In the right lower molar, KNM-BC 367 (4), which is incomplete at base but at least 45 mm high as worn, there is an ectostylid extending to the occlusal surface and measuring 4 mm anteroposteriorly. In the left M_{1-2}, which is worn to 40 mm of height, the ectostylid is less developed and nearly entirely hidden in the cement: at the occlusal surface it presents an enamel ring 2 mm in diameter. In both of the molars there is a distinct protostylid, somewhat damaged apically but as marked as that in the Ngorora teeth, and a weak ptychostylid. The crown diameters are 24.5 by 15 mm (without the external cement) for the right, and 27 by 17 mm for the left molar.

A left lower deciduous molar just touched by wear, KNM-BC 368 (pl. 15 fig. 4) from the same locality in the Chemeron Formation (J.M. 493), base incomplete, has a strongly developed protostylid, and, as is invariably the case in milk molars, an ectostylid, which remains 10 mm below the tip of the hypoconid. It measures 30 by 14 mm in crown diameters.

Three specimens of P_3 or P_4 sin. are in collections from other localities in the Chemeron Formation: one, labelled 1/996, has the number KNM-BC 454; the second is numbered 1/998 and is KNM-BC 455, and the third bears the number 1/2002 and is KNM-BC 1158. In all of them there is an ectostylid: in KNM-BC 454, which is worn to a height of 40 mm externally, the tip is just exposed in the cement, and its total height is 38 mm; in KNM-BC 455, a crown portion 30 mm high but with the base incomplete, it is seen all along the height, being 4 mm anteroposteriorly below and 2.5 mm above, while in KNM-BC 1158, 47 mm high as worn, the ectostylid is there

all along, too, and 5 mm anteroposteriorly above. Thus, the ectostylid varies somewhat in dimensions. Protostylids are present in all the premolars, and the ptychostylid can be observed except in KNM-BC 454. The metastylid loop is triangular, that of the metaconid also in KNM-BC 1158, and the metaconid-metastylid valley is rather deep. The anteroposterior diameter of the crowns of P_{3-4} sin. is 26-27.5 mm, the transverse 15-17.5 mm, depending upon the amount of cement: in KNM-BC 455 there is no external cement, and the width, therefore, is minimal.

A very slightly worn P_3 or P_4 dext., KNM-BC 1132, has a crown height of 70 mm; the anteroposterior diameter is 29 mm apically, but only 25 mm just below the middle of the height, giving a height/length index of 280. This figure differs very slightly from that for the height/length index of a Lothagam M_1 (300: Hooijer & Maglio, 1974: 19) that we referred to *Hipparion primigenium*. The ectostylid terminates in the top 15 mm of the crown, and at the base it measures 4 mm anteroposteriorly. Proto- and ptychostylid do show occlusally.

Recently, Aguirre & Alberdi (1974) referred the Chemeron Formation teeth from locality J.M. 493, uppers as well as lowers, to *Stylohipparion libycum*. I do not think his identification is justified, for the crown and the ectostylid are higher in the advanced, Pleistocene *Hipparion*, "*Stylohipparion*", that we find in the Olduvai Gorge as well as in the Omo Group deposits from Shungura Member F on up. I refer them to *Hipparion primigenium* just as we did the Kanapoi and Lothagam hemimandibles (Hooijer & Maglio, 1974), in which the ectostylid height is some 45 to 45 mm. This is an *H. primigenium* more advanced than the Vallesian, in which the ectostylids are not so high, although in hypsodonty it does not exceed the earlier form. If we interpret the post-Vallesian Lothagam, Kanapoi, Aterir Beds, and Chemeron Formation specimens here described as an *H. primigenium* that continued to develop the ectostylid, the development of *H. primigenium* in sub-Saharan Africa is different from that in Eurasia: it seemed to Forstén (1968: 24) 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: 25) further stated *Stylohipparion* to be probably the descendant of forest-hipparion which has retained and even further developed the ectostylid, and this is the development, I believe, that took place in sub-Saharan Africa.

Hipparion turkanense Hooijer & Maglio

In the Mpesida Beds of Kenya, age 7 million years, a few *Hipparion* teeth were found (Bishop & Chapman, 1970: 917; Bishop, Chapman, Hill &

Miller, 1971: 391), which were then thought to be the earliest *Hipparion* south of the Sahara. We referred this material to *Hipparion turkanense* Hooijer & Maglio (1973), a distinct species based on an unusually well preserved skull from Lothagam-1 fully described in 1974 (Hooijer & Maglio, 1974). Only one tooth from Mpesida is entire, a P_3 or P_4 dext., KNM-MP 079 (pl. 4 fig. 4). It has the wrinkled enamel that also characterizes the upper cheek teeth of *H. turkanense*, not only in the entoflexid and buccally but all over. The metaconid and metastylid show little folds, and the entoconid has an irregular outline. The protostylid is well developed, there is a ptychostylid, but no trace of an ectostylid. In all these characters the Mpesida tooth is like those from Lothagam and Ekora, which include specimens of the same serial position (Hooijer & Maglio, 1974: 17, pl. 7). The external wrinkling in these specimens extends all along the height of the crown; the Mpesida tooth, worn to about 5 cm (base incomplete), measures 29 mm anteroposteriorly and 16 mm transversely at the occlusal surface, and 27 by 14.5 mm at 2 cm above the neck. There are two fragments of teeth from the Mpesida Beds, KNM-MP 122, an M_1 or M_2 with a broken crown, and KNM-MP 123, the external anterior portion of another lower cheek tooth, both displaying the wrinkled enamel but other than that not of much value for comparative purposes.

Two well preserved lowers from the Lukeino Formation (olim Kaperyon Beds), age about 6 million years, KNM-KY 79 and 80 (pl. 4 figs. 5-6), may represent *H. turkanense*. KNM-KY 79 is a P_3 or P_4 dext., worn to 5 cm of crown height, diameters 26.5 by 18 mm occlusally, and 23.5 by 16 mm at 2 cm above the neck. KNM-KY 80 is an M_1 or M_2 dext., same height as worn, 26 by 14 mm occlusally, and 22 by 14 mm at 2 cm above the neck of the crown.

An incomplete P_2 sin. from Yellow Sands, the Mursi Formation of southern Ethiopia, YS. 7-3 (pl. 4 fig. 3, pl. 5 fig. 7), may be referred to *H. turkanense*. The entoflexid border is markedly wrinkled, and this crenulation is also seen on the enamel externally. There is no ectostylid but a slender ptychostylid. The Mursi Formation P_2 measures 31 mm anteroposteriorly and 16.5 mm transversely at the occlusal surface, 5.5 cm above the base. The lower part of the crown is incomplete postero-laterally.

In the absence of an ectostylid by a crown height of over 5 cm, probably some 7 cm only when unworn, the teeth of *Hipparion turkanense* resemble those of *Hipparion baardi* from Langebaanweg, Cape Province. Boné & Singer (1965: 374) give the full height of a P^4 as 70 mm by a width of 25.5 mm. The resulting height/width index, 270, is within the limits of *H. primigenium* (220-290: Arambourg, 1959: 79). Boné & Singer (1965:

390) stress the complexity of the enamel pattern and the tendency to form stylids: in the premolars especially there is a marked ptychostylid. However, the typical enamel wrinkling externally on the lowers of *H. turkanense* (Hooijer & Maglio, 1974, pl. 7) is less marked in *H. baardi*. It is this very wrinkling that makes a stylid like the ptychostylid in *H. turkanense* a much less conspicuous element than it is in *H. baardi*.

Boné & Singer (1965: 367-379) present the general features as well as some detailed descriptions of the Langebaanweg teeth, showing that the pattern is more complex than that in *H. turkanense*. In the lower teeth, the wrinkling of the entoflexid is variable, and it may also show buccally. In the absence of a skull from Baard's Quarry the relationships between *H. baardi* and *H. turkanense* must remain obscure, but the dental evidence is suggestive of the two forms being distinct from each other. There is no difference in dental size: the measurements of Lothagam and Kanapoi teeth as well as of those recorded above from Mpesida, the Lukeino Formation, and Mursi agree with those from Langebaanweg (Boné & Singer, 1965: 371, 374). In the holotype skull of *H. turkanense* the incisors are in part preserved, and show that I^3 is not reduced relative to I^2 just as it is in *H. primigenium* (Arambourg, 1959: 80): in the later, Pleistocene *Hipparion* the third incisor is much reduced. The symphysial portion of a mandible from Langebaanweg, S.A. Museum L20553 has an occlusal width of I_3 of 14.5 mm, while that of I_2 is 15 mm, as is the case also in *H. primigenium* (Arambourg, 1959: 84). In the Pleistocene *Hipparion* I_3 is only half as wide as is I_2. Thus, the unreduced third incisor, a feature of both *H. primigenium* and *H. turkanense*, is characteristic of *H. baardi* as well.

As to the origin of *Hipparion turkanense* we have voiced the opinion (Hooijer & Maglio, 1973: 313) that it may represent an invasion from Asia in Late Miocene times: the resemblance with the post-Vallesian *Hipparion hippidiodum* Sefve (1927: 9) of China is striking. We also stated that *H. turkanense* may be ancestral to "*Stylohipparion*". This was because of cranial similarity of *H. turkanense* to the Olduvai *Hipparion*, and also because of the presence of *H. turkanense* right at the bottom of the Omo Group deposits (Mursi Formation). So far no *Hipparion* teeth other than the one referred to *H. turkanense* have been recovered from the Mursi Formation. If *Hipparion turkanense* would be ancestral to "*Stylohipparion*" this would imply that it began developing the ectostylid only after Mursi Formation time. It may also be suggested that *Hipparion primigenium* is the ancestral form (Hooijer & Maglio, 1974: 30); it already had ectostylids in the Vallesian. The preorbital fossa then got lost in the process.

The vertical distribution of *Hipparion turkanense* as here conceived, from

the Mpesida Beds up into the Mursi Formation, from 7 to 4 million years ago, is the same as that of *Ceratotherium praecox* Hooijer & Patterson (1972; Hooijer, 1972; 1973: 168). *C. praecox,* on cranial as well as dental evidence, must be regarded as immediately ancestral to the modern white rhinoceros, *Ceratotherium simum* (Burchell), which occurs in the Shungura Formation as well as at Olduvai Gorge.

Hipparion? aff. **sitifense** Pomel

An almost entire upper cheek dentition, P. 944, from the base of Shungura Member G (contact tuff G and unit G_1), collected in 1972, is rather on the small side. It comprises the right P^2-M^3, $P^{3\text{-}4}$ incomplete internally, and the left P^2, incomplete in front, a portion of the ectoloph of P^3, and further the entire P^4, M^1 and M^3. The amount of wear is not great. The worn crown height of P^4 as well as that of M^3 is 67 mm, that of P^2 47 mm, and that of M^1 57 mm. All the teeth are isolated, but when joined the full length of the toothrow is 136 mm on the occlusal surface; the occlusal length M^1-M^3 is 62 mm. These are toothrow lengths as in *Hipparion sitifense* Pomel of the pre-Villafranchian of North Africa: the length P^2-M^3 is 129 mm in the dentition from Mascara (Arambourg, 1956: 818). There are a number of small teeth in the collection from Lothagam and Kanapoi that we described as *Hipparion* cf. *sitifense* (Hooijer & Maglio, 1974). The Shungura Member G uppers are exceedingly similar to those from Lothagam and Kanapoi in diameters and enamel patterns, but there is one very important difference: the crown height in the Shungura Member G specimens is greater than that in the Lothagam-Kanapoi cheek teeth. One of the M^3 from Lothagam just touched by wear, KNM-LT 137 (no. (1) in Hooijer & Maglio, 1974: 23, table 7), from what is preserved of the base (the closed bottom between the fossettes, and the contact between protocone and hypocone) cannot have exceeded 50 mm in full height, whereas the M^3 from the base of Shungura Member G, with the base complete and only very slightly worn, would have been 70 mm high in the unworn state. There is another M^3 from Shungura Member G, L.16-31, with the crown unworn and enough preserved of the base to show that its unworn height would have been some 70 mm, too. Now this is a difference that, by the same anteroposterior diameter of the crown (21 mm), would give considerable discrepancies in height/length index (240 against 330) between the M^3 of Lothagam and those of Shungura Member G, too much, in fact, for these to be accommodated in a single species. The molars compared are some four million years apart in age (Lothagam 6 million years, Shungura Member G 2 million years at most). The Shungura

Member G small *Hipparion,* the more hypsodont of the two, may have evolved from the Lothagam form, but it is perfectly possible that the later form evolved independently. Unfortunately, the degree of hypsodonty of *Hipparion sitifense* (to which the Lothagam form has been provisionally referred) is not known: the teeth from Saint-Arnaud and Ain el Hadj Baba are worn, and those of Mascara are even of an old individual (Arambourg, 1956). Their age would be around 3 million years. Forstén (1968: 36) gives hypsodonty indices for *H. sitifense* around 260, but these are referred specimens from Spain (Concud, Los Mansuetos and La Fontana), and whether they really represent the same species as that from the North African pre-Villafranchian is not quite certain. The degree of hypsodonty of the referred Spanish material is much the same as that of the Lothagam dwarf *Hipparion,* and that of the Shungura Member G dwarf *Hipparion* is decidedly higher, but we need to know the hypsodonty index of the type *Hipparion sitifense* from North Africa to settle the affinity of the sub-Saharan dwarf form or forms. The Lothagam small *Hipparion* we have named *Hipparion* cf. *sitifense* as this seemed to be the most meaningful designation. There are no lowers associated with the small Shungura Member G uppers of P.944, but there are several isolated lowers as well as uppers, as follows:

L. 1-42a, Shungura Member B, M^{1-2} dext., ant. post. 21.5 mm, transv. 23 mm.

L. 758-1d, Shungura Member C, P^2 sin., ant. post. 30 mm, transv. 20 mm.

L. 27-15B, Shungura Member C, P^{3-4} sin., ant. post. 23 mm, transv. 22 mm.

L. 758-1a, Shungura Member C, M^{1-2} dext., ant.post. 22 mm, internal part wanting.

L. 758-1b, Shungura Member C, M^{1-2} sin., ant. post., 21 mm, transv. 21 mm.

L. 758-1c, Shungura Member C, M^3 dext., ant. post. 20.5 mm, transv. 19 mm.

L. 10-6, Shungura Member E, P^{3-4} dext., ant. post. and transv. 21 mm.

L. 26-71, Shungura Member E, M^3 sin., ant. post. 21 mm, transv. 17+ mm (mesostyle incomplete).

L. 465-69, Shungura Member F, M_3 sin., worn to a height of 53 mm from base; crown incomplete behind except at base, where the ant. post. diameter is 28 mm. The transverse diameter is 11.5 mm. There is an ectostylid, however narrow (only 2.5 mm anteroposteriorly) that extends from the base to 40 mm upwards; there is also a ptychostylid.

L. 465-104, Shungura Member F, M_3 sin., worn and base broken, 35 mm high as preserved, diameters 23 by 9.5 mm; no trace of ectostylid though ptychostylid does show.

L. 65-30, Shungura Member F, is the distal portion of a small third metatarsal, superficially damaged, with an articular width of 35.5 mm, anteroposterior distal crest diameter of 30 mm, and at the broken upper end, 9 cm from the distal articulation, diameters 25.5 by 23 mm (pl. 19 fig. 7). This bone is of the size class of the third metacarpal of *Hipparion* cf. *sitifense* from Lothagam (Hooijer & Maglio, 1974, table 11).

L. 398-1580, Shungura Member F, is the distal end of a third metacarpal, articular width 34 mm, distal crest incomplete behind, to which the same remarks apply.

L. 16-112, Shungura Member G, P^{3-4} sin., ant. post. and transv. 22 mm.

L. 72-71, Shungura Member G, M^{1-2} dext. lacking internal portion, ant. post. 20 mm.

L. 675-2, Shungura Member G, M^3 dext., 70 mm high as worn, ant. post. 21 mm, transv. 20 mm, protocone 9.5 by 3 mm.

L. 16-31, Shungura Member G, external portion of M^3 sin.

L. 7-100, Shungura Member G, M^3 sin., ant. post. 20 mm, transv. 18 mm.

L. 627-215, Shungura Member G, M_{1-2} sin., incomplete behind, 52 mm high as worn; no trace of ectostylid, transv. 10.5 mm.

L. 627-213, Shungura Member G, M_{1-2} sin., worn to 60 mm height, narrow ectostylid (3-4 mm anteroposteriorly); crown ant. post. 21 mm, transv. 12.5 mm.

L. 597-17A, Shungura Member G, M_3 dext., incomplete behind, worn to 60 mm, ectostylid very narrow (1.5-2.5 mm), transv. 12 mm.

These teeth are indistinguishable from those of Kanapoi and Lothagam that we described as *Hipparion* cf. *sitifense* (Hooijer & Maglio, 1974: 20, table 9). Only the crown height and ectostylid development in the Shungura Member F and G specimens is greater than that in the Lothagam-Kanapoi specimens. True *Hipparion sitifense* as described by Arambourg (1956: 823) has no ectostylids, although they may not show as the teeth are in situ.

It is evident that there is a small *Hipparion* in Shungura Members B through G, and it may be related to the species *Hipparion sitifense,* the North African pre-Villafranchian dwarf *Hipparion,* but better material is needed to settle its affinities. For the present I will place it under the head *Hipparion?* aff. *sitifense* Pomel. The measurements and plication frequencies of the Shungura Member G upper dentition are in tables 6 and 7.

There are a few incisor fragments associated with the upper cheek dentition P.944, viz., I^1 dext. (k), I^1 sin. (l), and I^2 sin. (m). The base of the incisor crowns cannot be measured: the transverse and labiolingual diameters at the worn surface are 17.5 by 11 mm for I^1, and 18.5 by ca. 10 mm

TABLE 6

Dental measurements of *H.* ? aff. *sitifense,* Shungura G, P.944 (mm)

P^2,	ant. post.	29	M^1,	ant. post.	22
	transv.	20		transv.	21
	protocone, ant. post.	7		protocone, ant. post.	7.5
	transv.	4		transv.	3.5
P^3,	ant. post.	23	M^2,	ant. post.	21
	transv.	—		transv.	20
	protocone, ant. post.	—		protocone, ant. post.	7
	transv.	—		transv.	3
P^4,	ant. post.	23	M^3,	ant. post.	21
	transv.	22		transv.	19
	protocone, ant. post.	7.5		protocone, ant. post.	7
	transv.	4		transv.	2.5

TABLE 7

Plication numbers of *H.* ? aff. *sitifense,* Shungura G, P.944

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

for I^2. These fragments are not of much value for purpose of comparison but they do represent the dwarf *Hipparion* the incisors of which had not been described previously. As far as direct comparison is possible they do seem to be smaller than the corresponding parts of I^1 and I^2 of the large *"Stylohipparion"* (*Hipparion ethiopicum*) found in the same deposits; as there is no I^3 available of the dwarf form the degree of reduction of this element relative to I^2 cannot be determined.

Small *Hipparion* teeth, of the size of *Hipparion sitifense,* occur in the Lukeino Formation along with those of *Hipparion turkanense,* and in the Chemeron Formation along with *Hipparion primigenium.* The Lukeino Formation material comprises one well-preserved upper molar, KNM-LU 189, an M^{1-2} dext., measuring 20 by 20 mm and worn to 38 mm of height: the fossette plication numbers are 5-8-4-1 (pl. 6 fig. 6). Of a set of three lower cheek teeth, KNM-LU 192 A, B, and C, P_3 and P_4 have a small, narrow ectostylid, only 20, and 25 mm high, respectively. There is none seen in M_1. P_3 measures 22 by 12 mm, P_4 21 by 12 mm, and M_1 21 by

10.5 mm at 2 cm from the base. There are further two distal portions of small median metacarpals, KNM-LU 050 and KNM-LU 187, both incomplete behind, with a greatest distal width of 34, and 36 mm, respectively, and a distal articular width (in KNM-LU 187) of 36 mm. A broken distal end of a lateral metapodial, KNM-LU 051, has an anteroposterior diameter of 16+ mm and measures 11 mm transversely (pl. 19 fig 2). These figures compare well with those of the metacarpals of *Hipparion* cf. *sitifense* from Lothagam (Hooijer & Maglio, 1974, table 11, pl. 18 fig. 3).

In the Chemeron Formation collection there is an M_{1-2} sin., KNM-BC 371, measuring 21.5 by 9.5 mm, which shows no trace of an ectostylid.

However, in another set of lower cheek teeth, P_4-M_2 dext., KNM-BC 1157 (pl. 5 figs. 4-5), from the basal Chemeron, marked 1/2002, there are ectostylids although not very massive ones: their anteroposterior diameters are only 3 mm. The crown of M_1 is worn to 24 mm from the base; the bases of P_4 and M_2 are not clearly seen. The P_4 is incomplete in front: the metastylid is pointed postero-externally, as is also seen in the M_1. There are very distinct protostylids in the two molars, which measure only 23 mm anteroposteriorly, and 13 mm transversely. A set of upper molars, M^1-M^3 sin., marked 1/997, is KNM-BC 450-452. The crowns are unfortunately damaged, and the protocones are not well seen. The enamel pattern of the fossettes is rather complicated, least so that of the last molar, as can be seen in the photograph (pl. 5 fig. 3). The crown diameters of M^1 and M^2 are 20 mm anteroposteriorly, and 22 mm transversely; M^3 measures 21 mm anteroposteriorly, and 18 mm transversely. Such dimensions are those of *Hipparion sitifense* (cf. Hooijer & Maglio, 1974, table 7), which is not to say that the Chemeron teeth necessarily belong here: with only teeth like these a provisional identification is all that can be achieved.

THE OLDUVAI GORGE HIPPARION

Hipparion cf. **ethiopicum** (Joleaud)

There are various names for the advanced, Pleistocene *Hipparion* of Africa characterized by its extreme hypsodonty, well-developed ectostylids, and reduced third incisors, uppers as well as lowers. The North African form is *Hipparion libycum* Pomel, 1897. For southern Africa we have *Hipparion steytleri* Van Hoepen, 1930, *Eurygnathohippus cornelianus* Van Hoepen, 1930, and *Stylohipparion hipkini* Van Hoepen, 1932. For East Africa there is *Libyhipparion ethiopicum* Joleaud, 1933.

In his paper on the Olduvai Gorge *Hipparion,* Hopwood (1937) used the name *Stylohipparion* cf. *albertensis* (Hopwood). The name *Hipparion*

albertensis had been proposed by Hopwood (1926: 17, fig. 4A) for an upper molar worn to 7 cm of height and lacking the internal portion, originating from the Kaiso Bone Beds of Uganda. Although the species could not given a meaningful diagnosis, the same name, *Stylohipparion albertense* (Hopwood), was chosen by Arambourg (1947: 303) for the *Hipparion* of the Omo deposits, listing *Libyhipparion ethiopicum* Joleaud as a synonym. Later (Arambourg, 1970: 84), he relegated *Hipparion albertensis* to the synonymy of *Stylohipparion libycum* (Pomel), which has well-developed ectostylids, and unworn upper premolars 7.5 cm high. In the Olduvai material referred by Hopwood to *Stylohipparion* cf. *albertensis* there was a lower premolar with an ectostylid (Hopwood, 1937: 114), and in the Omo material there were hypsodont upper molars (around 8 cm in crown height), and lowers (Arambourg, 1947: 305, fig. 27, pl. X fig. 3) with large ectostylids.

Thus, both the Olduvai Gorge and the hypsodont Omo *Hipparion* had been identified as *Stylohipparion albertensis,* or *Stylohipparion* cf. *albertensis.* In this Hopwood and Arambourg were originally followed by Cooke (1963: 82), and others. However, in a revision of the Kaiso fauna, Cooke & Coryndon (1970) describe *Hipparion* teeth from both the Earlier and the Later Kaiso, placed at 4-5 million years, and in the 2-3 million year range, respectively. The authors note that those from lower horizons appear to be less hypsodont, with shorter and broader protocones, than those from higher levels, leaving the earlier Kaiso material in *Hipparion albertense* as an early variant. It must be noted though that it is not at all certain that the Earlier Kaiso material belongs to the same species as that from Later Kaiso. It is most probable that there is more than one species of *Hipparion* in the Kaiso deposits, which span several million years. This uncertainty was in fact realized by the authors, who note that the holotype of *Hipparion albertense* "is a very inadequate type specimen and more material is needed from this locality in order that the specific characters may be more clearly defined" (Cooke & Coryndon, 1970: 136/137). They do give an emended diagnosis, in which it is stated that the lower teeth constantly lack the ectostylid, but this statement is not supported by the evidence available. Among the lower cheek teeth there are only two that would show an estostylid, if any, and one of them is so small that we (Hooijer & Maglio, 1974: 27) provisionally referred to it as *Hipparion* cf. *sitifense* (Cooke & Coryndon, 1970: 139, fig. 5J). The problem with the Kaiso *Hipparion* is whether there is more than one species, and which lower molars go with the type.

The *Hipparion* of the Koobi Fora faunal sequence East of Lake Rudolf

in Kenya was named *Stylohipparion albertense* (Maglio, 1971), and then *Hipparion* cf. *albertense* (Maglio, 1972). Nothing is gained by such a denomination. The name *Hipparion albertense,* or *H.* cf. *albertense,* has since been used for not-so-hypsodont teeth albeit with ectostylids from Lukeino, Kaperyon, and Aterir by Aguirre & Alberdi (1974, table I), and from the Usno Formation and Members A, B, and C of the Shungura Formation of southern Ethiopia by Coppens & Howell (1974, Planche I). By now the confusion originating from the inadequacy of the type specimen is complete.

Since *Hipparion albertense* is based on an incomplete, non-characteristic type it is advisable not to use the name al all. It should be kept in the suspense account and not applied to material other than the type. I follow this course in the present paper, and recommend it for the future.

We have, then, *Hipparion ethiopicum* as the earliest available valid name for East African advanced, Pleistocene *Hipparion.* For North Africa there is *H. libycum,* and for southern Africa *H. steytleri.* The teeth of these three named forms are indistinguishable. We do not know their skulls. It is possible that there were various geographic forms in these areas, with certain skull characters permitting of their distinction as such. The Olduvai Beds have provided, for the first time, skulls of the advanced *Hipparion:* it is ironical that this, the Olduvai BK II *Hipparion,* has as yet no valid name of its own.

The skull recovered at Olduvai Gorge in 1973 referred to by L. S. B. Leakey (1965: 26) and by M. D. Leakey (1971: 256) proving that *Stylohipparion* is in fact the same as *Eurygnathohippus,* comes from BK II, pit 6 (Upper Bed II) in two parts both of which are heavily distorted (pls. 7 and 8). No. 2845 has the premaxillaries back to the deepest point of the nasal notch, no nasals, but the sides and ventral portions of the maxillaries to some 4 cm behind the palatine processes of the premaxillaries, where the alveoli for the (missing) P^2 are situated. No. 2846 is the remainder of the skull, broken off behind through the cranial cavity. The right orbit lacks only part of its ventral border but is drawn out anteroposteriorly; part of the right glenoid fossa is preserved. The two portions were sent to me separately, and the only parts positively joining are at the suture between premaxillary and nasal on the left side, just behind the nasal slit. This contact is shown in the left lateral view of the joint specimen. P^3-M^3 are in situ, but because of the distortion the right series is placed a cm or two further back than the left, with unnatural diastemata between the molars.

The crushing of the specimen has been mainly sideways, with the right

side pushed up higher than the left. The skull is indented on the right side between the facial crest and the top, from the infraorbital foramen to the orbit. On the left side this region of the skull is fractured, but the portions are not much displaced, and it is perfectly clear that there was no preorbital fossa. Thus, the Olduvai BK II *Hipparion* shares this feature with *Hipparion turkanense* from Lothagam.

The snout and the six incisors are all there, but the incisor-bearing portion is pulled out sideways and down to the right, the nasal processes of the premaxillaries snapped off and displaced at a fracture 4 cm behind the body. From the fracture to the nasomaxillary notch the right and the left nasal processes are more or less in their natural position; the lateral walls of the nasal cavity are very thin. The ventral surface between I^3 and the alveolus of P^2 is not so much distorted, and the palatine processes of the premaxillaries can be seen to their full extent. By a lucky accident the deepest point of the nasal notch is preserved on the left side: the suture between premaxillary and nasal, along which the two skull portions fit on to each other, is behind the notch, so that the deepest point of the lateral notch is formed by the premaxillary, as is the case in *Hipparion turkanense* (Hooijer & Maglio, 1974). The infraorbital foramina are preserved on both sides, above the posterior border of P^3, and the facial crests emerge above the posterior border of P^4. Between these heavy horizontal ridges and the top of the skull a preorbital fossa, if any, should be in evidence but it is not there at all: even though the lateral surface of the skull is broken there are no traces of such a cavity. Several transverse fractures, the main one just in front of the orbit, along which the bone portions are displaced and warped, render the remainder of the skull unfit for accurate description. On the ventral side, the palate is compressed, but the anterior palatine foramen is seen on a level with the protocone of M^2, and the posterior border of the hard palate is on the same level in the median line. The anterior margins of the orbit are preserved on the right side only; the zygomatic arch behind the orbit carries part of the temporal condyle but does not fit on to the squamous temporal and is warped like the orbit itself. The occipital portion of the skull is lost.

Few measurements can be given: the I^3-P^2 diastema, 100 mm; distance from anterior border of P^2 to anterior border of the orbit, ca. 165 mm, and from prosthion to posterior border of the palatum durum, ca. 260 mm, showing that the Olduvai BK II skull is fully as large as that of *Hipparion turkanense* of Lothagam as recently described by Hooijer & Maglio (1974). The two skulls agree in the absence of a preorbital fossa. The dentition, however, provides the means of distinguishing between the two.

The incisors of the Olduvai skull are of the type of *Eurygnathohippus cornelianus* Van Hoepen (1930): the first and second large, anteriorly flattened, with thick enamel in front and thin enamel lingually, and large cups completely filled with cement. There is a shallow longitudinal groove along the centre of the labial surface of the first incisor, and the second has two such anterior grooves. The lingual surface are grooved also. The third incisor is much reduced. In the Lothagam skull of *H. turkanense* the incisors are smaller, ungrooved, and the third incisor is not reduced in size relative to I^2. There is a small canine in *H. turkanense;* this element is not developed in the Olduvai skull, and it is not present in any of the "*Eurygnathohippus*" specimens from Cornelia, Laetolil, or Olduvai either.

The premolars of the Olduvai skull, the P^2 dropped out of its alveolus, have the anterior horn of the postfossette extending outward beyond the posterior horn of the prefossette. This is less marked in the molars. The inner and outer fossette borders lack the fine wrinkling that characterizes the Lothagam cheek teeth (cf. pl. 2 in Hooijer & Maglio, 1974). The fossette plis vary somewhat in the homologous teeth on the two sides: the counts are given in table 8.

TABLE 8

Plication numbers in upper teeth of Olduvai skull BK II, no. 2846

	prefossette		postfossette		
	ant.	post.	ant.	post.	pli caballin
P^3	1-2	5-6	3-4	1	1
P^4	2-3	5-6	4	1	1-2
M^1	1-2	5-6	2-3	1	1
M^2	2-3	6-7	2-3	0-1	1
M^3	1	3-4	1-2	1	1

The plication counts are very similar to those in the type skull of *Hipparion turkanense* except in the anterior border of the postfossette, 6 in P^4-M^2, and 5 in M^3 of the Lothagam skull of *Hipparion turkanense;* the M^3 of the Lothagam skull even has 7-8 plis in the posterior border of the prefossette. However, the difference is not so much in the number of plis but in their extent, their amplitude: in the Lothagam teeth the plis are very minor, whereas in the Olduvai teeth they are rather long, especially those in the adjoining borders of pre- and postfossette, as shown in the photographs published. The more ample plications characterize "*Stylohipparion*" (cf. Van Hoepen, 1930, figs. 14 and 7, as *Hipparion steytleri,* and Cooke, 1950, fig. 10, as *Stylohipparion steytleri).* The crown height of the M^3 sin. of *Hipparion steytleri,* worn as it is, amounts to 66 mm (Van Hoepen,

1930: 22), and that of the type lower molar of *"Stylohipparion hipkini"*, which is not so much worn, 81 mm (Van Hoepen, 1932: 32). Dental measurements of the BK II skull are given in table 9.

TABLE 9

Dental measurements of Olduvai skull BK II, no. 2846 (mm)

P^3, ant. post.	25.5	M^2, ant. post.	22.5
transv.	25	transv.	22
protocone, ant. post.	8.5	protocone, ant. post.	8
transv.	4.5	transv.	4
P^4, ant. post.	23.5	M^3, ant. post.	22.5
transv.	25	transv.	18.5
protocone, ant. post.	8.5	protocone, ant. post.	7.5
transv.	4	transv.	3.5
M^1, ant. post.	22		
transv.	22.5		
protocone, ant. post.	8.5		
transv.	4		

The cheek teeth of the Olduvai skull are rather similar in size to those of *Hipparion turkanense* and *H. primigenium* from Lothagam and Kanapoi (cf. table 2 in Hooijer & Maglio, 1974) although the M^3 in the Olduvai skull appears rather small; the full range in size of the Olduvai M^3 is given further on, extending it to include the observations on *H. primigenium*. The great anteroposterior diameter of the M^3 in *H. turkanense* is caused by its oblique wear: as it is situ it could not otherwise be measured.

The anterior parastyle fold of *"Stylohipparion"*, specifically mentioned by Van Hoepen (1930: 22) and Cooke (1950: 426) is a general feature of *Hipparion:* the Lothagam and Kanapoi molars show it (Hooijer & Maglio, 1974, pls. 2 and 3) and it does occur in the type and only known molar of *Hipparion albertense* (Hopwood, 1926: 17, fig. 4A; Cooke & Coryndon, 1970: 136, fig. 5A). It runs down into the root region, or stops short of that by a few cm, and is not always very distinct [1]).

A portion of the right maxillary with M^{1-3} in situ, OLD/65, BK II, no. 155, has M^3 just touched by wear, and M^2 and M^1 in early wear. The dimensions at the base cannot be taken, but those at the alveolar border are 22.5 by 23.5 mm for M^1, and 23 by 22.5 mm for M^2; the protocone diameters are 11 by 5 mm for M^1, and 11 by 4 mm for M^2. The plication

1) It is not the parastyle fold of the rhinoceros upper molar, which is placed externally and behind the parastyle, between the parastyle and the paracone style. In the hipparions it is placed internally of the parastyle, separating it from the rest of the protoloph.

numbers in the anterior border of the postfossette (5 for M^1, 4 for M^2) are rather higher than those in the same molars of the adult skull (no. 2846); the other counts are the same. The caballine fold, however, is duplicated in M^1 and M^2 of no. 155 instead of single as in no. 2846. The full height of M^1, taken externally to the base of the enamel between the roots, is 70 mm, that for M^2, 75 mm, and that for M^3, 70 mm in a straight line, in its slightly worn state.

There is a *Hipparion* skull in the Olduvai collection, marked OLD/63, BK II, no. 283, Channel Sand, that lacks the front portion but has the basilar occipital portion. It is not quite adult: DM^4 is still in situ on the right side, and M^3 has not cut the gums yet (pl. 9 fig. 1, pl. 10). On the broken edge of the palate there is seen the posterior notch for the palatine processes of the premaxillaries, and it is 2.5 cm in front of the anterior premolar, P^2. On the left we see the anteriormost deciduous milk molar, DM^1, which is incomplete internally. From this level on backward the skull is compressed from side to side: the palatal portion of the left maxillary is pushed over (dorsally of) the right at the median suture, and the palate as well as the choanae are too narrow though the original palatal width can be determined as the median suture and the median point of the anterior border of the posterior nares are preserved along the undistorted right maxillary and palatine. On the sides of the skull are seen the infraorbital foramina, which are placed above the posterior border of P^3, and the facial crests, which emerge above the middle of the erupting P^4. The top of the skull is again laterally compressed, the nasal bones being squeezed. The orbit is rather well preserved and undistorted on the left side of the skull, and at least the anterior border of the right orbit is in situ. The side surface of the skull between the infraorbital foramen and the orbit, above the facial crest, is tolerably well preserved on either side: the sutures between nasal, maxillary, lacrimal and jugal are shown and the bones are slightly displaced along sutures, which had not yet been completely closed. It is evident from the preservation of this portion of the skull that a preorbital fossa was not developed: there is a slight depression along the naso-maxillary suture in front of the lacrimal but definitely no true preorbital fossa; the naso-maxillary suture may be depressed in *Equus* skulls as well. On the left side of the skull the posterior border of the orbit and the zygomatic arch behind it are intact and in place. Although the cranial region is very imperfect, several bone fragments comprising nearly all of the frontals including the superior border of the right orbit (with the supraorbital foramen) could be assembled and joined. This portion of the top of the skull fits on to the side of the skull in situ above the anterior border of the left orbit, and it

also fits on to what remains of the right orbit in situ. Because of the lateral crushing of the skull it cannot be fitted on to both simultaneously; it is shown, in contact with the right side of the skull, in pl. 10 fig. 2. Thus, the greatest width of the skull can be determined. The parieto-occipital of the skull is missing, but on the ventral surface we have the basilar part of the occipital with the left condyle and paroccipital process that fits on to the body of the sphenoid in situ in the skull, so that the postpalatal length of the skull back to the basion can be taken.

Measurements of the subadult Olduvai BK II skull are given in table 10. The distance from anterior border of P^2 to the anterior border of the orbit is the same as that in the type skull of *Hipparion turkanense* and in the adult BK II skull, and the other measurements also as are as in the Lothagam skull.

The Olduvai skull fortunately shows the extreme hypsodonty quite well: the crown height of the worn P^2, as exposed on the left side, is 60 mm, and that of P^3, as seen on the right side, 75 mm. The full height of the uncut P^4 cannot be determined, but that of the worn M^1, the base of which is exposed in the interior of the skull, is 70 mm, and that of M^2, barely worn and measured in the same way, 75 mm. The unerupted M^3, the base of which is somewhat damaged, has a full crown height, in a straight line, of 75 mm.

TABLE 10

Skull measurements of Olduvai BK II, no. 283 (mm)

From anterior border of P^2 to anterior border of orbit	170
Length P^2-P^4	ca. 90
Palatal width between P^2	50
Idem between M^3	70
Width over posterior borders of orbits	215
Zygomatic width	ca. 200
Postorbital constriction	ca. 65
Greatest width of cranium	ca. 95
Bicondylar width	80

Plication counts can be given only of P^2, P^3, DM^4, M^1, and M^2, as the unworn crowns of P^4 and M^3 do not allow of such observations (table 11).

The highest counts, it will be observed, are in the milk molar. The protocone (table 12) is rather elongated in M^1, longer even that of M^1 and M^2 in the young adult from BK II, 155. The protocones of the premolars have just been touched by wear and appear very small as a result: they are already thickly covered by cement and can be measured only on the occlusal surfaces.

TABLE 11

Plication numbers in upper teeth of Olduvai skull BK II, no. 283

	prefossette		postfossette		
	ant.	post.	ant.	post.	pli caballin
P^2	2-3	3-4	2-3	1	1
P^3	2-3	3-5	1-2	0	1
DM^4	2	7	5	3	2
M^1	1-2	4-5	2-3	1-2	1
M^2	1	3	2	1	1

TABLE 12

Dental measurements of Olduvai skull BK II, no. 283 (mm)

P^2,	ant. post.	34	M^1,	ant. post.	26
	transv.	25		transv.	24.5
	protocone, ant. post.	11		protocone, ant. post.	12
	transv.	3		transv.	3.5
P^3,	ant. post.	30	M^2,	ant. post.	25
	transv.	27		transv.	22.5
	protocone, ant. post.	9		protocone, ant. post.	8.5
	transv.	2.5		transv.	2.5
DM^4,	ant. post.	28			
	transv.	24.5			
	protocone ant. post.	11			
	transv.	5			

The teeth in the subadult skull had to be measured near the top of the crown, whereas those in the adult skull of BK II are measured near the base: the lesser anteroposterior lengths in the more worn teeth are thus accounted for, and there is no doubt that the two skulls are conspecific.

The incisors of *Eurygnathohippus cornelianus* Van Hoepen (1930) are more hypsodont than those of the earlier *Hipparion,* and the third incisor is reduced in size, which is another advanced character. Of the four anterior dentitions of *"Stylohipparion"* figured by Leakey (1965, pl. 20) I have studied three, viz., two lower (upper figs.) and one upper (bottom, left figure). The upper incisors (OLD/55, BK II, no. 264, pl. 11 fig. 1) are less worn than those in situ in skull no. 2845/6 of the same deposit: the width of the central incisors on the occlusal surface is still 22 mm against 20 mm in no. 2845 since the crown narrows rootward in the I^1. The external height of the I^1 from the worn edge to the base of the enamel in no. 264 is 70 mm in a straight line, and 80 mm along the curve; these measurements are 50 mm, and 55 mm, respectively, in no. 2845. At 50 mm from the base of the crown of I^1 in no. 264 the width is reduced to 20 mm,

and the width is only 16 mm at 20 mm from the enamel base externally. I^2 does not taper as markedly toward the base as does I^1: the occlusal width of I^2 is 22 mm both in no. 264 and in no. 2845, and at 20 mm from the crown base the width of I^2 still is 18 mm. I^3 is much reduced and worn very obliquely: its greatest width is 14 mm in no. 264 (15 mm in no. 2845), and its total height no more than 45 to 50 mm. It is placed right behind I^2.

The premaxillaries from the Aterir Beds described above, associated with cheek teeth that belong to *Hipparion primigenium,* show that I^3 is wider than I^2 at identical levels, wheres in the Olduvai *Hipparion* I^3 is narrower than I^2. The incisors from Aterir, however, have thick enamel on the labial surface, thinner enamel lingually, and large cups with a very thin and wavy enamel border and completely filled with cement. Even the longitudinal grooving of the enamel surface is seen in the Aterir specimens. Hence, their is no fundamental difference between the earlier and the later *Hipparion* in the configuration of the incisor marks. The labio-lingual diameters of I^2 and I^3 are 12 mm, and 11 mm, respectively, in the Aterir *Hipparion:* in the Olduvai *Hipparion* specimens from BK II (both no. 264 and no. 2845) these diameters are 13 mm, and 10 mm, respectively. This shows that in *H. primigenium,* as in *H. turkanense,* the reduction in size of the third incisor is less marked than in the later *Hipparion.*

The two lower anterior dentitions of "*Stylohipparion*" from Olduvai BK II (pl. 12 figs. 1-3) are almost exact replicas of the original Van Hoepen *Eurygnathohippus cornelianus* but more complete: the third incisors are entire. They are smaller than those in the upper jaw, only 9-10 mm wide by a width of I_1 of 21 mm, and of I_2 of 22-23 mm. In no. 067/5344 they fit into a posterior groove in I_2 just laterally of the centre of the crown, recurving inward at the tip, while in no. 293 they are slightly more lateral in position. All I_3 have a transversely concave occlusal surface; this concavity is caused by wear against the lateral ridge of its antagonist in the upper jaw. The joined occlusal surfaces of the first and second incisors are slightly convex in the upper, and slightly concave transversely in the lower jaw. Both of the lower incisor dentitions occlude with the upper no. 264 very well, almost as if they had belonged to the same individual. There are a number of isolated *Hipparion* incisors in the Olduvai collection showing something of the amount of individual variation, and these will now be considered.

An I^1 and an I^2 sin., BK II nos. 50 and 52, collected in 1952, belong to the same individual as they fit exactly interproximally, and are much worn down. The crown is worn to 35 mm from the external enamel base, and the tapering roots are 30 mm long. I^1 is 17 mm wide at the oc-

clusal surface, and only 13 mm at the crown base. I^2, with the oblique occlusal surface, shows the lateral posterior groove that lodged I^3. The occlusal surface is 20 mm wide, but the transverse width of the crown at that level is only 17 mm, diminishing only to 16 mm just above the root. Both specimens show that the cup, at this low level, is subdivided by an enamel partition in the centre, leaving two cement-filled enamel islets the lateral of which is the larger in both (pl. 13 fig. 3); the islets are larger in I^1 than in I^2. I^1 has a shallow longitudinal median groove externally, as is also seen in the central incisors of the BK II sets nos. 2845 and 264; in I^2 this groove is so weak as to be practically absent, in the basal part of the crown preserved. Labiolingually the diameters are 14 mm in I^1, and 12.5 mm in I_2, remaining the same down to the root. The dimensions are very much the same as those of I^1 and I^2 in the individually younger sets of BK II already mentioned, taken at the same level. An isolated I^1 sin., OLD/52, GRC. S, no. 553, is 19 mm transversely at the worn surface, 40 mm from the base, intermediate between BK II no. 50 and BK II no. 2845. The width of the cement-filled cup diminishes rootward as does the transverse diameter: 15.5 mm in no. 2845 (50 mm high as worn), 14 mm in no. 553 (40 mm high as worn), and 10.5 mm in no. 50 (35 mm high as worn).

There remain five fragmentary specimens of the upper second incisor, none with the base preserved but showing the asymmetry characteristic of an I^2 and the occlusal surface falling off toward the lateral side, with the posterior lateral groove into which fits the I^3. The specimens, with their transverse and labiolingual diameters, are: I^2 dext., OLD/53, SHK II, no. 243 (21 by 14 mm); I^2 dext., OLD/57, SHK II, no. 438 (20 by 13.5 mm); I^2 sin., OLD, GRK II, no. 1220 (20 by 14 mm); I^2 sin., OLD/55, BK II, no. 180 (21 by — mm), and I^2 sin., OLD/57, SHK II, no. 291 (19.5 by 12.5 mm). One isolated I^3 dext., OLD/62, HWK E II, no. 2889, resembles that in no. 2845 closely, and is only slightly larger (17 by 11 mm; 15 by 10 mm in no. 2845).

Upper and lower *Hipparion* incisors are alike in characters, and differ merely in their degree of curvature: the lowers are less curved. In Van Hoepen's specimen from Cornelia the crowns of I_3 are incomplete, and the Olduvai specimens show for the first time what they look like. Further, the interalveolar border behind I_3 is entire in both specimens to well behind the body of the mandible, the median posterior border of the symphysis, and it shows no trace of a canine, small or large, which may indicate that they represent female individuals unless canines had become completely reduced in both sexes in the advanced *Hipparion*. It will be remembered

that the snout of the adult Olduvai BK II skull no. 2845 does not indicate the presence of canines either. Canines are absent in the Laetolil symphysial portions, too (Dietrich, 1942: 97).

There is one set of right and left first and second lower incisors, certainly from a single individual, collected at Olduvai, HWK II (Lower Bed II) in 1959 (pl. 13 fig. 1). I_1 is worn externally to 30 mm from the enamel base, and I_2 to 42 mm from the base; all show a labiolingual partition in the cup. The specimens, with the transverse and labiolingual diameters at their occlusal surfaces, are: I_1 dext. no. 462, I_1 sin. no. 466 (18 by 11 mm); I_2 dext. no. 465, I_2 sin. no. 461 (19 by 12.5 mm). The external surface of all incisors shows a shallow median groove, while lingually there is a longitudinal ridge, flanked by two fine grooves.

A pair of I_1, fortunately unworn and very nearly entire, lacking only the roots, OLD/57, SHK II, no. 749 (I_1 dext.) and no. 454 (I_1 sin.) (pl. 15 fig. 6), gives a full crown height of 67 mm in a straight line (73 mm along the curve) externally; the width at the top is 21 mm, and is 18 mm at 30 mm from the base, while the labiolingual diameter remains 12 mm down to one cm from the base. The cup in its virgin state is nearly full of cement; the external enamel wall, which is higher than the lingual wall, has a longitudinal groove externally, at about one-third of the width from the median edge, which flattens out only close to the base of the crown. Opposite to this groove, on the inner surface of the enamel, there is a sharp ridge, which in worn teeth makes for an infolding of the cup. A similar but less developed ridge is placed at about one- third of the width from the lateral crown edge. Thus, the tripartite outline of the cup comes into being. The lingual median ridge of the crown, which is narrow apically and forms a point on the unworn crown edge, widens rootward as the grooves flanking it flatten out. These superb specimens (I_1 sin. is damaged along the crown edge medially and lingually, as well as along the base, but I_1 dext. is in its pristine state) demonstrate the extreme hypsodonty of the incisors of the Olduvai *Hipparion*, in perfect harmony with the specializations seen in the cheek teeth. The worn I_1 dext. of the symphysial portion OLD/55, BK II, no. 293, which fortunately can be extracted, has a crown height as such of 53 mm, and at the top measures 20 mm transversely and 12 mm labiolingually, as does the unworn I_1 at the same level. At the base these diameters are 13 by 13 mm in both. The central incisors in the symphysis from BK II, no. 293, therefore, had already lost some 15 mm in height through wear.

Two specimens of the second incisor, I_2 dext., OLD/63, MNK II, no. 2331, and I_2 sin., OLD/63, MNK II, no. 3024, belong to one and the same

individual. Both are worn, though not very much so: the transverse crown width apically is 23 mm. The width is still 18 mm 50 mm lower down, where I_2 dext. has broken off. These I_2 have two grooves externally, with a weak median ridge in between, but the lateral of the grooves is rather weak. The worn I_2 dext. of the symphysial portion OLD/55, BK II, no. 293, which can be taken out of its alveolus, has a height as preserved of 55 mm, 23 mm transversely at the top, and 15 by 13.5 mm at the base: the width is 18 mm at 20 mm above the enamel base. The full height of I_2 when unworn may have been around 70 mm.

One isolated I_1 dext., OLD/57, BK II, no. 1458, slightly worn, measures 70 mm in height in a straight line, 75 mm along the external curve. The transverse and labiolingual diameters are 23 and 11 mm at the top, and 13 and 12 mm at the base of the crown. This specimen is the largest, and most flattened I_1 that I have seen.

Three isolated central lower incisors remaining in the collection are: I_1 dext., OLD/57, BK III E, no. 1440, 20 by 10 mm at the top; OLD/57, SHK II, no. 549, 20 by 12 mm at about 40 mm above the imperfect base, and OLD/63, BK II, no. 1122, a much worn I_1 dext. measuring 14 by 12 mm one cm from the base. The root is preserved in the specimen mentioned last: it is 25 mm long, tapers to a point, but swollen labiolingually, giving a maximum diameter in that direction of no less than 15 mm. In this specimen, the cup is subdivided into three enamel islets by two partitions, of which the lateral is the smallest. The median lingual ridge is still distinct in this basal portion, more so than in any of the other I_1 seen by me.

Six isolated second lower incisors, with incomplete bases, and varying in height as preserved from 25 to 50 mm, with the crown diameters at the top, are: I_2 dext. OLD/59, HWK II, no. 463 (ca. 20 by 13 mm); I_2 sin., OLD/53, BK II Ex., no. 62 (20 by 12.5 mm); I_2 sin., OLD/57, SHK II, no. 597 (23 by 13 mm); I_2 sin., OLD/57, SC II S, no. 360 (22 by 12.5 mm); I_2 sin., OLD/63, TK II, no. 1760 (22 by 13.5 mm), and I_2 sin., OLD/63, FC II, no. 6601 (ca. 22 by 11 mm).

Other than the I_3 in the two symphysial portions nos. 067/5344 and 293 there are no third lower incisors in the Olduvai collection. Their crown height is some 30 mm as worn; the occlusal surface is merely a posterior extension of that of I_2 and less than one-half its width (9-10 mm) by 9 mm labiolingually. The root, which is exposed on the left side in the symphysis OLD/55, BK II, no. 293, is swollen (10.5 by 10 mm) but tapers apically, its length is unknown.

There is a single, isolated milk incisor of *Hipparion* in the Olduvai collection, marked BK II, 4/LS, no. 2774 (pl. 16 fig. 1). That it belongs to

the advanced *Hipparion* of the Olduvai Beds rather than *Equus* is clear from the cement-filled, large cup, in which there is a partition cutting off the medial portion as a separate islet, just as in the permanent lower incisors that have undergone appreciable wear. The specimen is low-crowned, markedly widening apically, and undoubtedly represents DI_2 sin. The transverse and labiolingual diameters of the worn crown are 18 by 8.5 mm. The external crown height is only 12 mm, and the lower margin of the thin enamel is curved upward externally. Of the root no more than 7 mm remain, the remainder has been resorbed and the mark for the developing I_2 behind it is seen in the root portion lingually. An unfigured DI_2 from Aïn Brimba in southern Tunisia (Villafranchian), very similar to the BK II specimen in dimensions, has been recorded as *Stylohipparion libycum* (Pomel) by Arambourg (1970: 85).

There are 17 specimens of P^2 in the Olduvai collection, 10 from the right and 7 from the left side, all isolated and with the base tolerably well preserved. Each series has been arranged according to increasing wear; none of the teeth is unworn. P^2 dext.: 1, OLD/57, BK II, no. 879; 2, OLD/63, BK II, no. 1775; 3, OLD/57, SHK II, no. 339; 4, OLD/57, SHK II, no. 682; 5, OLD/55, BK II, no. 101; 6, OLD/63, BK II, no. 2759; 7, OLD/52, DC II, no. 57; 8, OLD/53, BK II Ex., no 337; 9, OLD/57, SHK II, no. 192; 10, OLD/61, JK2, T; P^2 sin.: 11, OLD/55, BK II, no. 100; 12, OLD/53, BK II; 13, OLD/63, BK II, no. 2688; 14, OLD/62, SHK II, no. 536; 15, OLD/63, FC II W, no. 1207; 16, OLD/57, SHK II; 17, OLD/57, SHK II, no. 451. One of these specimens, 15, has a truncated anterior edge, and its anteroposterior diameter (at 2 cm from base) is only 25 mm; in the others it varies from 29 to 33.5 mm. The transverse crown diameter, likewise at 2 cm from the crown base, runs from 22 to 24.5 mm, a rather uniform series. The pli counts are (1-3)-(2-5)-(2-4)-(1-2), and the pli caballin is invariably single. The protocone is internally flattened, sometimes pointed at both ends, and from 7.5 to 10 mm in length by a width (occlusally) of 3-5 mm. The single P^2 of *Hipparion libycum* from Aïn Brimba (Arambourg, 1970: 87, pl. XVI fig. 7, 7a) is 41 mm anteroposteriorly in its slightly worn state occlusally, but at 2 cm from the base this dimension would not be more than 37 mm; it exceeds all the known Olduvai P^2 in size. The least worn of the Olduvai P^2 (1 and 11) are 6.5 cm high.

A much worn right upper tooth series, lacking the anterior premolar and the last molar, is OLD/55, BK II, no. 222. P^3 and P^4, worn to less than 2 cm of height and exceedingly similar, have a bifid caballine fold and protocones 11 by 5.5 mm in diameters; in M^1 and M^2, which differ from

the premolars in having a narrower parastyle (subequal to the mesostyle) the pli caballin is single, and the protocone 10.5 by 4.5 mm. P^3-M^2 measure 92 mm in length; the width is 26 mm in the premolars and 24.5 mm in the molars.

Isolated P^3 or P^4 are as follows: P^{3-4} dext.: 1, OLD/57, SHK II, no. 189; 2, OLD/59, PDK S, no. 179; 3, OLD/63, BK II, no. 3358; 4, OLD/55, BK II, no. 138; 5, OLD/57, BK II, no. 500; 6, OLD/55, BK II, no. 3; 7, OLD/59, EKK, no. 35; 8, OLD/53, SHK II, no. 238; 9, OLD/57, SHK II, no. 384; 10, OLD/63, MNK II, no. 1519; 11, OLD/53, BK II Ex., no. 340; P^{3-4} sin.: 12, OLD/55, BK II, no. 2; 13, OLD/53, BK II; 14, OLD/57, SHK II, no. 650; 15, OLD/57, BK II, no. 651; 16, OLD/57, FC S, no. 1395; 17, OLD/60, Gully opposite FLK, S; 18, OLD/55, BK II; 19, OLD/57, SHK II, no. 683; 20, OLD/55, BK II, no. 52; 21, OLD/57, SHK II E, no. 1201; 22, OLD/57, SHK II, no. 1301; 23, OLD/52, SWK, no. 572; 24, OLD/61, JK2, 6; 25, OLD/63, MNK II, no. 3404; 26, OLD/61, JK2, T; 27, OLD/57, BK II, no. 1072. The specimens that are least worn (1, 2, 12, 13) are 6.5 to 7 cm in height, with pli counts (2-3)-(5-6)-(2-4)-1; one (13) has a double pli caballin. In specimens worn to about 2 cm of height the plis are no less in number. Two specimens worn to 5 cm (5 and 15) have duplicated caballine folds. The anteroposterior diameters vary from 22.5 to 25.5 mm, and the transverse from 23 to 25 mm, at 2 cm above the base. The protocone is very long (13 by 3 mm) in 5, but 9.5 by 5.5 mm in 7, these two specimens representing approximately the extent of variation. Slightly worn P^{3-4} of *Hipparion libycum* measured 29-32 mm anteroposteriorly and 27.5-31 mm transversely at the top (Arambourg, 1970: 87); those of the subadult BK II skull no. 283, which had be measured near the top, are within these limits (table 11).

The first and second upper molars of Olduvai, right and left, arranged in each series according to increasing wear, are: M^{1-2} dext.: 1, OLD/57, SHK II, no. 544; 2, OLD/63, BK II, no. 319; 3, OLD/52, DC II-III, no. 570; 4, OLD/55, BK II, no. 25; 5, OLD/57, SHK II S, no. 419; 6, OLD/51, BK II, no. 981; 7, OLD/52, BK II, no. 305; 8 OLD/55, BK II, no. 53; 9, OLD/52, BK II, no. 57; 10, OLD/57, BK II, no. 1021; 11, OLD/63, BK II, no. 3387; 12, OLD/53, BK II Ex., no. 339; 13, OLD/63, BK II, no. 2488; 14, OLD/55, BK II, no. 320; 15, OLD/59, KK I, no. 314; 16, OLD/63, TK II, no. 208; 17, OLD/57, SHK II, no. 615; 18, OLD/60, SHK II, no. 068/6149; 19, OLD/63, BK II, no. 2100; 20, OLD/57, BK II, no. 494; M^{1-2} sin.: 21, OLD/52, BK II, no. 58; 22, OLD/55, BK II, no. 140; 23, OLD/55, SHK II, no. 28; 24, OLD/57, SHK II, no. 190; 25, OLD/57, SHK II, no. 252; 26, OLD/57, SHK II,

no. 616; 27, OLD/57, BK II, no. 1357; 28, OLD/57, SHK II, no. 784; 29, OLD/52, BK II, no. 59; 30, OLD/57, SHK S, no. 102; 31, OLD/63, BK II, no. 1623; 32, OLD/?, SWK II base, no. 567; 33, OLD/52, MRC II, no. 569; 34, OLD/57, SHK II, no. 434; 35, OLD/63, BK II, no. 2306; 36, OLD/63, BK II, no. 820; 37, OLD/61, JK2, 6; 38, OLD/63, MNK II, no. 1281; 39, OLD/57, SHK S, no. 78; 40 OLD/63, BK II, no. 13; 41, OLD/63, BK II, no. 2308; 42, OLD/55, BK II, no. 4. The least worn specimens (1-5 and 21-25) have crown heights of 7.5 to 8 cm, taken at the mesostyle. In these molars, the pli counts may be up to 3-7-3-3, with single caballine folds (double in 4), but molars in medium wear may have the same pli numbers, and the complexity of the pattern does not seem to be affected by wear even further than that, as is shown by specimens 17-20 and 41-42, worn to less than 3 cm of height. Protocone diameters also remain rather constant; although the longest protocones (13 mm) are seen in slightly worn molars the anteroposterior diameter does not diminish markedly rootward, while the transverse diameter has a tendency to increase somewhat, as does that of the hypocone, which is more produced basally than apically. The crown diameters, taken as usually at 2 cm from the base, vary from 20.5 to 24.5 mm anteroposteriorly and from 21 to 24 mm transversely. In *Hipparion libycum* (Arambourg, 1970: 89, pl. XVII figs. 5-7) larger anteroposterior diameters are given, but Arambourg took these at the top (as his figures show), and at the level at which I take the measurements his specimens do not exceed my maximum.

The last upper molar is a somewhat more variable element than are M^{1-2}; the metacone may be rather produced basally, increasing the anteroposterior diameter. However, since this posterior metacone bulge is restricted only to the basal cm it does not affect my measurements, which I take at 2 cm from the base. M^3 dext.: 1, OLD/61,JK 2, bottom; 2, OLD/61, JK2, 6; 3, OLD/?, GC III-IV junction, no. 573; 4, OLD/63, TK II, no. 1606; 5, OLD/55, BK II, no. 51; 6, OLD/53, BK II Ex., no. 338; 7, OLD/55, BK II, no. 284; 8, OLD/57, SHK II, no. 253; 9, OLD/62, JK2/Bf P4; 10, OLD/61, JK2, T; 11, OLD/57, SHK II, no. 127; 12, OLD/?, MNK II, I/1, no. 67/1490; M^3 sin.: 13, OLD/53, BK II, no. 8; 14, OLD/62, JK2, A 2918; 15, OLD/55, BK II, no. 50; 16, OLD/57, SHK II, no. 191; 17, OLD/53, SHK II, no. 237. The greatest preserved height, in a straight line at the mesostyle (1, 2, 13) is 6.5 to 7 cm. The crown diameters vary from 20 to 25.5 mm anteroposteriorly, and from 18.5 to 23 mm transversely. Plication numbers are (1-2)-(4-7)-(2-3)-(0-4), and the caballine fold is invariably single. The protocone appears rather compressed laterally,

as a result of the obliquity of the occlusal surface; the hypocone remains well individualized except in the most worn down specimens.

There are several entire lower cheek tooth series in situ as well as series lacking one tooth only, as follows:

OLD/52, BK II, no. 301: P_2-M_3 sin.
OLD/60, FLK I, F 250 (figured in Leakey, 1965, pl. 19): P_2-M_2 dext.
OLD/62, JK2, Geol. Pit 8, no. 1620: P_2-M_2 sin.
OLD/55, BK II, no. 1: P_3-M_3 dext.
OLD/53, BK II Ex., no. 93: P_3-M_3 sin.
OLD/57, SHK II, no. 335: P_2-P_3 erupting, DM_4, M_1-M_2 dext. et sin.

The oldest specimen, from FLK I, the *Zinjanthropus* level, unfortunately is rather worn down so that its hypsodonty cannot be studied: P_2 is worn to 1.5 cm, as in M_2. The ectostylids are 8.5 by 3.5 mm in the premolars, and 6.5 by 2.5 mm in the molars. The metaconid-metastylid loops are angular, especially that of the metastylid, and the valley in between is rather deep, with straight sides, in P_3-M_1, shallower and more rounded in P_2 and M_2. Protostylids show as isolated knobs in P_3 and P_4, and are confluent with the protoconid in M_1 and M_2. Ptychostylids hardly show, in this advanced stage of wear. The length P_2-M_2 is 126 mm along the crown bases. The specimen from JK2, Geol. Pit 8, which is from Bed III and almost certainly from the artefact horizon in Trench 8 (Mrs. M. R. Haldemann-Kleindienst, pers. comm.), is worn to the same degree and the length P_2-M_2 is 120 mm. The ectostylids are slightly smaller (6 by 3 mm in the premolars, and 5 by 2.5 mm in the molars), but the configuration of the "tie" is the same. The three specimens from BK II as well as the many isolated teeth from that level show that this is no more than individual variation among contemporaneous specimens. In the most complete specimen, OLD/52, BK II, no. 301 (pl. 14 fig. 2), which is less worn than the Bed I and Bed III specimens (worn height of M_2 4.5 cm), the length P_2-M_2 is 130 mm along the alveolar border, and the ectostylids form enamel figures that are 10 by 4 mm in P_2-P_3, 8.5 by 3.5 mm in P_4, 6.5 by 3.5 mm in M_1-M_2, and 4 by 2 mm in M_3.

Comparison of OLD/52, BK II, no. 301 with the Shungura Member B11 mandible (L. 1-40), which is likewise worn to a height of M_2 of 4.5 cm (pl. 14 figs. 2 and 1) shows that the ectostylid figures are larger in the Olduvai specimen, which is at least one million years younger than the Shungura Member B11 specimen. The height of the lower jaw of OLD/57, SHK II, no. 335, which is not even adult as M_3 has not cut the gums

yet, is 95 mm at M_1 and 110 mm just behind M_2; these figures are 80 mm, and 90 mm, respectively, in the adult Shungura Member B11 mandible. The ectostylids do not show occlusally in the very slightly worn M_1 and M_2 of the SHK II mandible; evidently the ectostylids do not extend all the way to the top of he crown, even in "*Stylohipparion*" (vide the lower molar of "*Stylohipparion hipkini*" in Van Hoepen, 1932, figs. 14-17). The ptychostylid does show in the M_1-M_2 as a distinct little twist, but the protostylid cannot be seen yet. The measurements, which must needs be taken at the alveolar borders, are presented in table 13.

TABLE 13

Measurements of teeth of Olduvai mandibles (mm)

	P^2	P^3	P^4	M^1	M^2	M^3
BK II, no. 301	30 × 17	25 × 18	23 × 17	23 × 16	21 × 15	25 × 13
FLK I, F 250	27 × 15	23 × 16	23 × 16	22 × 15	24 × 15	——
JK2, Geol. Pit 8, 1620	27 × 15	24 × 16	22 × 15	22 × 15	22 × 15	——
BK II, no. 1	——	— × 14	20 × 15	20 × 14	20 × 13	26 × 12
BK II Ex., no. 93	——	— × 18	23 × 18	22 × 17	23 × 15	31 × 15
SHK II, no. 335	——	——	——	25 × 16	28 × 14	——

Of the anterior lower premolar, P_2, there are the following isolated Olduvai specimens: P_2 dext.: 1, OLD/55, BK II, no. 275; 2, OLD/59, LGK II, no. 391; 3, OLD/53, MNK II, Tr. I S, no. 068/6114; 4, OLD/55, BK II, no. 54; 5, OLD/62, JK2, A 3271/F3; 6, OLD/63, BK II, no. 940; 7, OLD/?, BK II Ex., no. 3171; P_2 sin.: 8, OLD/55, BK II, no. 139; 9, OLD/63, MNK II, no. 2326; 10, OLD/63, BK II, no. 1354; 11, OLD/62, JK2, A 2971; 12, OLD/55, BK II, no. 259. The only unworn specimen (1) is incomplete at the base, and the tip of the ectostylid remains 7 mm below the tip of the hypoconid. The ectostylid is 7-9 mm anteroposteriorly at base, and either remains that long anteroposteriorly for at least 4 cm of height (3, 9, and 10) or tapers to 5 mm anteroposteriorly already 3.5 cm above its base (4). Exceptionally small ectostylids, however, are seen in 2, 7, and (baseless) 5: the anteroposterior diameter is no more than 5 mm at the lower enamel margin. The crown diameters, taken as usual at 2 cm from the base, vary from 27 to 32 mm anteroposteriorly, and from 14 to 17 mm transversely. The metaconid is just a small fold in 10, subequal to the metastylid in most specimens, but rather elongated in 8 and 9. Specimen 2 is peculiar in that the metaflexid and entoflexid are confluent, cutting off the "tie" (metaconid-metastylid) (pl. 16 fig. 2). This specimen is worn to 4.5 cm of height. The pli hypoconid in the anterior portion of the entoflexid is seen in 8 and 12, the latter worn to only 2.5 cm.

A P_2 dext. of *Hipparion libycum* (Arambourg, 1970: 89, pl. XVII fig. 9, 9a) is 34 mm anteroposteriorly, just above the maximum of the Olduvai series.

Isolated P_3 or P_4, arranged according to increasing wear, right and left, are: P_{3-4} dext.: 1, OLD/55, BK II, no. 49; 2, OLD/63, MNK II I/1, no. 486; 3, OLD/63, MNK II, no. 119; 4, OLD/53, BK II Ex., no. 348; 5, OLD/52, BK II, no. 62; 6, OLD/57, SHK II, no. 452; 7, OLD/52, BK II, no. 63; 8, OLD/55, BK II, no. 285; 9, OLD/52, MRC, no 586; 10, OLD/61, JK2, T; 11, OLD/52, SWK, no. 574; 12, OLD/?, BK II, no. 688; 13, OLD/63, BK II, no. 2374; 14, OLD/52, CMK IV, no. 683; 15, OLD/55, BK II; 16, OLD/55, BK II, no. 273; 17, OLD/55, BK II, no. 280; 18, OLD/53, SHK II, no. 239; P_{3-4} sin.: 19, OLD/63, BK II, no. 3363; 20, OLD/57, SHK II, no. 796; 21, OLD/52, CMK IV, no. 837; 22, OLD/57, SHK II, no. 386; 23, OLD/63, MNK II II/1, no. 1586; 24, OLD/63, BK II, no. 2645; 25, OLD/57, SHK II, no. 814; 26, OLD/55, BK II, no. 111; 27, OLD/57, SHK II, no. 220; 28, OLD/55, BK II, no. 321; 29, OLD/63, BK II, no. 938; 30, OLD/57, BK II, no. 1455; 31, OLD/57, SHK II, no. 113; 32, OLD/53, BK II Ex., no. 214; 33, OLD/63, BK II, no. 453; 34, OLD/52, SWK, no. 580; 35, OLD/63, BK II, no. 1608; 36, OLD/62, JK2, A 3000; 37, OLD/62, JK2, Geol. Pit 8, Sec. 3. These premolars vary between wide limits: the anteroposterior diameter from 22 to 27 mm, and the transverse diameter from 13 to 17.5 mm, taken at 2 cm from the base. The ectostylid may vary from 7 to 11 mm anteroposteriorly at base, and the height of this structure, in the least worn specimens (1, 2, 19; 8 on pl. 17 fig. 6) is at least 65 mm, showing an enamel ring or oval at the occlusal surface (none of the specimens is quite unworn). The full height of the Olduvai P_{3-4} may safely be put at 75-80 mm. The protostylid is always well-developed, extending to a few mm from the top of the crown, and the ptychostylid shows best apically although it is still discernible in specimens worn to less than half their original height. One specimen (8) has a deformation in its basal portion: the antero-internal corner of the crown is pushed in (for an internal view, see pl. 16 fig. 5) from 3 cm above the base (preserved externally) on down, the internal anteroposterior diameter thereby reducing from 22 mm to only 16 mm. As a much worn specimen this tooth might have been interpreted as representing a small *Hipparion* like *H. sitifense*. Yet, its ectostylid is 60 mm high as worn, and its enamel figure is still 5 mm anteroposteriorly at the top and 7 mm at its base. A typical, good-sized specimen, P_{3-4} sin., with part of the posterior root, crown height as worn 70 mm, OLD/63, BK II, no. 3363 (19 in the above list) is shown occlusally and buccally in

pl. 16 figs. 3 and 7. The angularity of the metaconid and the metastylid loops is not extremely marked in this specimen; they may form marked internal points also in medium and late wear. The P_3 and P_4 of *Hipparion steytleri* Van Hoepen (1932: 34, figs. 21-23) of Cornelia are 64, and 74 mm high as worn, and the ectostylid shows occlusally in P_3, not in P_4, indicating an ectostylid height of about 70 mm. The M_1 and M_2 of *Hipparion libycum* (Arambourg, 1970: 89, pl. XVII fig. 12, 12a, pl. XVIII figs. 4, 4a, 5) are stated to be 28-30 mm anteroposteriorly, but these diameters have been taken apically: at 2 cm from the base they are within my limits. The ecto- and protostylids are as well-developed as in the Olduvai premolars.

Although there are numerous isolated specimens of the first and second lower molar in the Olduvai collection none of the specimens with the base preserved is unworn, and if the crown is unworn the base is not complete. The specimens, arranged in the same way as the premolars, are as follows: M_{1-2} dext.: 1, OLD/57, SHK II, no. 1300; 2, OLD/63, BK II, no. 477; 3, OLD/53, BK II; 4, OLD/55, BK II, no. 169; 5, OLD/57, SHK II, no. 388; 6, OLD/52, BK II, no. 60; 7, OLD/57, BK II, no. 1456; 8, OLD/55, BK II, no. 14; 9, OLD/61, JK2, 6; 10, OLD/62, JK2, GN61; 11, OLD/57, SHK II, no. 812; 12, OLD/63, BK II, no. 1069; 13, OLD/?, DC III; 14, OLD/57, BK II, no. 1073; 15, OLD/65, MNK, SK/1-2, no. 067/1492; 16, OLD/52, SWK II, no. 578; 17, OLD/61, JK2, 6; 18, OLD/55, BK II, no. 296; 19, OLD/52, SWK, no. 581; 20, OLD/57, BK II, no. 687; 21, OLD/61, JK2, B; 22, OLD/63, FC II W, no. 333; 23, OLD/52, SWK, no. 582; 24, OLD/55, BK II; 25, OLD/?, BK II, 4/CS, no. 067/1663; 26, OLD/62, JK2, Geol. Pit 8, Sec. 5, no. 1569; 27, OLD/52, FC S, 684; 28, OLD/?, FC II W, LS/3, no. 067/5266; 29, OLD/63, FC II W, no. 140; 30, OLD/61, JK2, 6; M_{1-2} sin.: 31, OLD/59,LGK II, no. 394; 32, OLD/57, SHK II, no. 303; 33, OLD/57, SHK II, no. 387; 34, OLD/57, SHK II, no. 194; 35, OLD/?, GC Bed III base, no. 585; 36, OLD/53, BK II Ex., no. 104; 37, OLD/63, BK II, no. 1607; 38, OLD/63, BK II, no. 1610; 39, OLD/63, MNK II, no. 3521; 40, OLD/57, SHK II, no. 195; 41, OLD/57, SHK II, no. 1122; 42, OLD/61, JK2, 6; 43, OLD/55, BK II, no. 202; 44, OLD/63, BK II, no. 1762; 45, OLD/52, BK II, no. 65; 46, OLD/63, BK II, no. 3119; 47, OLD/52, BK II, no. 67; 48, OLD/57, BK IV E, no. 1434; 49, OLD/52, DC II, no. 584; 50, OLD/63, BK II, no. 677; 51, OLD/52, BK II, no. 306; 52, OLD/57, BK II, no. 984; 53, OLD/?, BK II, no. 069/6705; 54, OLD/53, SHK II, no. 248; 55, OLD/62, JK2, A 3273. These specimens range from 20.5 to 24.5 mm anteroposteriorly, and from 12 to 16 mm transversely. The

greatest observed height of crown is 78 mm (1), and the ectostylid in this specimen has a height of at least 70 mm. While the ectostylid is typically some 7-9 mm anteroposteriorly at crown base, one specimen (31) has an ectostylid only 5 mm anteroposteriorly all over its vertical extent (65 mm almost), and there is another (49) in which the ectostylid is only 4 mm anteroposteriorly already 35 mm above the base, the height to which this specimen is worn. The unworn apical crown portions show that the tip of the ectostylid remains 10-15 mm below that of the hypoconid. In slightly worn crowns the enamel spur in the anterior portion of the entoflexid (pli hypoconid) is distinctly seen. Protostylids are very marked, ptychostylids show best in the apical crown portions. The external groove between protoconid and hypoconid always reaches the "tie", which has pointed loops separated by an usually wide and shallow valley.

The lower cheek tooth series of *Hipparion steytleri* Van Hoepen (1932: 34, figs. 21-23) includes M_1 and M_2, which are more worn than our spemen 1 (pl. 16 fig. 6, pl. 17, figs. 1 and 4) for the apical posterior projection of the hypoconulid is already worn off. The heights as given by Van Hoepen are 74, and 73 mm, respectively, and the ectostylids show as enamel rings occlusally, next to the ptychostylids, while the small fold in the anterior portion of the entoflexid (pli hypoconid) in also distinct. These structures are clearly seen occlusally in our specimen 1, which has the base preserved internally at the bottom of the metaconid and the metastylid-entoconid. The lack of cement in this portion of the crown discloses a cingular prominence in the metaconid-metastylid valley that we rarely see: it is a tubercle 6 mm high only. The M_1 and M_2 of *Hipparion libycum* (Arambourg, 1970: 89, pl. XVII fig. 11, 11a, pl. XVIII figs. 2, 3, 3a), of which the M_2 is 69 mm high as worn, are given anteroposterior diameters up to 32 mm, but this is taken apically. Our specimen 1 is 30.5 mm anteroposteriorly at the top but only 24 mm at 2 cm from the base, the level at which I take the measurements. The North and South African "*Stylohipparion*" molars are exceedingly similar to our Olduvai molars in their wide, flattened ectostylids and angular, pointed metaconid-metastylids, in addition to their great crown height.

Of M_3 we have the following specimens: M_3 dext.: 1, OLD/59, LGK II, no. 395; 2, OLD/63, BK II, no. 2442; 3, OLD/52, MRC, no. 588; 4, OLD/62, JK2, A 2956; 5, OLD/63, BK II, no. 1611; 6, OLD/57, SHK II, no. 304; 7, OLD/57, BK II, no. 652; 8, OLD/57, SHK II, no. 432; 9, OLD/57, SHK II, no. 1120; 10, OLD/62, JK2 A 3270/MF2; 11, OLD/63, BK II, no. 191; 12, OLD/52, BK II base, no. 571; M_3 sin.: 13, OLD/63, BK II, no. 2689; 14, OLD/53, SHK II, no. 234; 15, OLD/

57, SHK II, no. 433; 16, OLD/52, BK II, no. 71; 17, OLD/61, JK2 A, T; 18, OLD/57, BK II, no. 1035; 19, OLD/62, JK2, A 3270/EF2; 20, OLD/63, BK II, no. 2712; 21, OLD/63, BK II, no. 704. In this element, the least worn of which (1, 13) are 75 mm high, the ectostylid, although invariably present, may be very slender. Specimen 1 (pl. 16 fig. 4) has an ectostylid only 45 mm high, and 2 mm anteroposteriorly at base, 1 mm at the top. The protostylid is not very well developed in this specimen either, petering out at 55 mm from the base. Normally, however, the ectostylid is 4-6 mm anteroposteriorly at base, terminating, as in M_{1-2}, 10 to 15 mm from the top of the hypoconid. At 2 cm from the base the crown measures 25 to 29 mm anteroposteriorly, and 10 to 13 mm transversely. The M_3 of *Hipparion libycum* (Arambourg, 1970: 89, pl. XVIII fig. 1) is exceedingly similar to the lectotype of *Hipparion ethiopicum* (Joleaud, 1933, pl. I figs. 2, 6), with an ectostylid 5 mm anteroposteriorly, at least 50 mm high, and not markedly narrowing over this height. Such well-developed ectostylids characterize most of the Olduvai M_3.

The Olduvai *Hipparion* is a full-fledged "*Stylohipparion*" that does not differ dentally from either *Hipparion libycum* of the Villafranchian of North Africa or *Hipparion steytleri* (including *Hipparion hipkini)* of southern Africa (Churcher, 1970, has recently recorded a P^{3-4} sin. and an M_{1-2} dext. from the Swartkrans australopithecine site and the Kromdraai type site, respectively). Of neither the North African nor the South African "*Stylohipparion*" we have the skull, which may be different from that of the Olduvai form. The crown height of the lowers is over 80 mm, and the ectostylids may reach a height of over 7 cm; 65 mm has been measured in some teeth showing a worn enamel ring at the tip. The type of *H. hipkini* (Van Hoepen, 1932: 31, figs. 14-17) is 81 mm high, and the ectostylid, as seen from the figure, reaches a height of 75 mm. The height/length index of his important specimen, based on the anteroposterior diameter of 22 mm at 2 cm from the crown base, is at least 370. In lower molars of *Hipparion primigenium* from Lothagam (Hooijer & Maglio, 1974: 18/19, pl. 6 fig. 4) and the Chemeron Formation (this paper, p. 19) indices taken in the same way amount to 280-300, and the ectostylid is maximally 55 mm high. The least worn M_1 or M_2 in the Olduvai collection (OLD/57, SHK II, no. 1300) has a height/length index of at least 325, and its ectostylid reaches a height of 70 mm. In the Shungura Member G collection, as will be mentioned later on, there is an M_1 or M_2 (L. 616-63) slightly worn, 80 mm high, 24 mm anteroposteriorly at 2 cm from the base, giving an index of 335, with an ectostylid height of 75 mm. These figures show the evolutionary advance of *Hipparion ethiopicum* over *Hipparion primigenium.*

The milk cheek dentition in the Olduvai Gorge collection comprises, apart from the fourth deciduous molars in situ in the Olduvai BK II skull no. 283 and in the mandible from SHK II, no. 335, only isolated uppers, and two lower tooth rows plus isolated lowers. The most worn upper, DM^3 or DM^4 sin., OLD/?, FC II W, L. S., no. 067/5254, has a very wide protocone (10 by 5.5 mm) since the protocone widens rootward; the transverse diameter is 24.5 mm, and the plication pattern obscured in part, but posteriorly in the prefossette there are at least 7 of them, as in the milk molar of the skull from BK II, no. 283, that is of the same size (tables 10 and 11). Two specimens of DM^{3-4} sin., OLD/63, BK II, no. 3360, and OLD/?, BK II (no number), are very slightly worn and the plications, therefore, do not show. Their bases are incomplete externally, but the internal crown height is just about 30 mm. The protocones are very massive, 12-12.5 mm anteroposteriorly, depressed internally and only 3 mm transversely on the occlusal surfaces. Their diameters 1 cm from the top are 30-31 mm anteroposteriorly and 22-23 mm transversely. Three specimens of DM^{3-4} dext., OLD/57, FC S, no. 1390, OLD/53, BK II Ex., no. 103, and OLD/63, BK II, no. 3386, worn to 30, 25, and 15 mm externally at the mesostyle, have pli counts (2-4)-(5-7)-(2-3)-(1-3), and the middle specimen has a bifid caballine fold. At 15 mm from the base the crown diameters are 26-30 mm anteroposteriorly. The protocones are 12 mm anteroposteriorly and 4-5 mm transversely, on the occlusal surface. There is a perfect set of right lower milk molars, DM_2-DM_4 sin., OLD/63, BK II, no. 3367 (pl. 15 fig. 5), DM_2 worn to 15 mm, DM_4 to 25 mm, with protostylids, ptychostylids, and massive ectostylids, the latter 8.5-9.5 mm anteroposteriorly and 3.5-4 mm transversely on the occlusal surfaces. In the DM_2 the external groove between protoconid and hypoconid is very shallow, but in DM_3 and DM_4 it is very deep, as in the permanent molars. The length DM_2-DM_4 is 91 mm occlusally and the width 15 mm throughout. A similar set, DM_2-DM_4 sin., is in situ in a hemimandible marked Olduvai S. 4, 1941, F 706; the ectostylid of DM_2 is linked up with the hypoconid by a narrow isthmus. In the remaining, isolated specimens, the ectostylid is always separate from the hypoconid. These specimens are: DM_{3-4} dext.: 1, OLD/52, BK II base, no. 576; 2, OLD/53, SHK II, no. 235; 3, OLD/63, BK II, no. 2098; 4, OLD/55, BK II, no. 125; 5, OLD/57, SHK II, no. 196; 6, OLD/57, BK II, no. 501; 7, OLD/57, FC S, no. 1394; DM_{3-4} sin.: 8, OLD/?, no. 067/1493; 9, OLD/?, EF HR II, LG, no. 067/5411; 10, OLD/57, BK II, no. 626; 11, OLD/52, BK II, no. 64. The ectostylids remain approximately 10 mm below the unworn crown edge, and are sometimes depressed exter-

nally. The crown diameters, at 15 mm from the base, vary from 28 to 31 mm anteroposteriorly, and from 12.5 to 16 mm transversely.

Of the postcranial remains of equids, which abound in the Olduvai collection, I will deal here only with the median and lateral metacarpals and metatarsals of *Hipparion*. Of the third metacarpal there are nine entire specimens the measurements of which are given in table 14. They bear the following notations: 1, OLD/61, FLK N1, Tr. III, no. 7693; 2, OLD/59 I, LGK, no. 366; 3, OLD/57, SHK II, no. 576; 4, OLD/57, SHK II, no. 935; 5, OLD/?, no. F. 345; 6, OLD/60, FLK N1, II/1-2-3, no. 933; 7, OLD/63, BK II, no. 2750; 8, OLD/63, MNK II SK, no. 167, and 9, OLD/55, BK II, no. 45. Nos. 1-4 are from the right side. All are clearly *Hipparion*, and some (nos. 1 and 6, pl. 18) have portions of the lateral metapodials attached to them not, however, in a very good state and lacking the distal articulations.

TABLE 14

Measurements of metacarpal III of *Hipparion*, Olduvai (mm)

No. of specimen	1	2	3	4	5	6	7	8	9
Length	230	213	228	217	205	222	223	210	223
Proximal width	48	43	43	46	45	45	41	42	—
Proximal ant. post. diameter	34	32	30	34	37	33	31	28+	38
Mid-shaft width	33	30	27	32	32	28	27	30	35
Ant. post., same level	27	23	23	25	27	25	22	25	28
Distal width at protuberances	44	41	36	42	47	40	36	—	48
Distal articular width	42	40	39	42	41	41	34	39	—
Distal crest, ant. post.	33	32	31	34	34	34	30	30	37
Distal art. width/length index	18	19	17	19	20	18	15	19	—

Of the median metatarsal from Olduvai there are fewer specimens of which the total length can be taken, as follows: 1, OLD/55, BK II, no. 68; 2, OLD/60, HWK II S, no. 86; 3, OLD/57, SHK II, no. 557; 4, OLD/57, SHK II, no. 729/730; 5, OLD/53, BK II, and 6, OLD/57, SHK II, no. 1177. None of these have lateral metatarsals attached to them; nos. 1 and 2 are from the right side. The measurements are in table 15.

The facet for the meso-entocuneiform is present on nos. 1-5 although quite small in nos. 1 and 2; of no. 6 the proximal surface is damaged.

Few data can be given on the lateral metapodials of the Olduvai *Hipparion*. Metacarpal II attached to metacarpal III no. 1 has a proximal width of 15 mm and an anteroposterior diameter of 19 mm; the shaft remains of an even diameter anteroposteriorly, 15 mm, down to some 8 cm from the upper end, and then reduces slightly in diameter, but it is still 11 mm anteroposteriorly (and 6 mm transversely) at the broken distal end:

TABLE 15

Measurements of metatarsal III of *Hipparion,* Olduvai (mm)

No. of specimen	1	2	3	4	5	6
Length	257	244	253	260	242	254
Proximal width	47	40	47	48	45	—
Proximal ant. post. diameter	40	—	38	38	37	—
Mid-shaft width	31	28	33	33	30	29
Ant. post., same level	34	28	31	33	31	30
Distal width at protuberances	45	38	45	45	44	—
Distal articular width	43	36	44	43	43	41
Distal crest., ant. post.	35	29	35	37	34	33
Distal art. width/length index	17	15	17	17	17	16

the total length as preserved is 16 cm. The second metacarpal attached to metacarpal III no. 6 also has a length as preserved of 16 cm; at the proximal end it is 12 by 17 mm in diameters, and the shaft is more slender, too; the anteroposterior shaft diameter is 13 mm at 2 cm from the proximal end, and reduces gradually to only 7 mm at 13 cm the proximal end. In the distal 3 cm it begins to widen again slightly, and it is 9 mm anteroposteriorly at the broken distal end, the transverse diameter being 5 mm. Metacarpal IV attached to metacarpal III no. 1 is 10 by 16 mm at the proximal articulation, and the shaft, of which only 6 cm are preserved, is still 14 mm anteroposteriorly (and 8 mm transversely) at its broken distal end.

Fortunately, we have at least one distal articulation of a lateral metapodial of the Olduvai *Hipparion:* it is OLD/62, JK 2, B, TTK, and was collected by Miss Maxine Kleindienst (now Mrs. M. R. Haldemann-Kleindienst) in Bed III. The specimen (pl. 19 fig. 1) has been given to me by Dr. Alan Walker. The distal width is 9 mm, the anteroposterior diameter 16.5 mm As such, it is of the same size as those of the small *Hipparion* cf. *sitifense* from the Villafranchian of Bethlehem in Israel (Hooijer, 1958: 281, pl. 35 figs. 5, 6) and from the Late Miocene of Lothagam in Kenya (Hooijer & Maglio, 1974: 29, pl. 19 fig. 5); they resemble the distal end of the lateral metapodial of *Hipparion crustafonti* Villalta (1952, pl. XXIII) of the Villafranchian of Spain. The lateral metapodials of *Hipparion libycum* have not been described (Arambourg, 1970).

While in Nairobi, in September, 1973, Dr. Alan Walker also presented me with casts of distal ends of two *Hipparion* lateral metapodials originating from the Makapansgat Limeworks Dumps, Lower Phase I Breccia. They bear the numbers MLD 20 and MLD 36. MLD 20 has acquired some unjustified fame as it was described by Boné (1955: 88-91) as an acromial fragment of the clavicle of *Australopithecus prometheus* Dart. It is listed

as a clavicle fragment of *Homo africanus* (Dart) by Robinson (1972: 173). Both MLD 20 and MLD 36 are listed as acromial extremities of australopithecine clavicles by Oakley & Campbell (editors, 1967: 63). The *Hipparion* from Makapansgat is listed as *Stylohipparion steytleri* (Cooke, 1963: 94 (with a query); Churcher, 1970: 146). MLD 20 has been exhaustively described by Boné (1955), and MLD 36 is very similar but less complete. The specimens are shown in pl. 19 figs. 3, 4. The distal condyle of the lateral metapodial measures 12 by 21 mm, and thereby is one-third larger in dimensions than the Olduvai Bed III specimen. However, in *H. primigenium* from Wad el Hammam the distal articulation of metatarsals II and IV reaches 20-21 mm anteroposteriorly, while there is also a specimen only 17 mm anteroposteriorly (Arambourg, 1959: 91, 92). Thus, there is variation in the development of the lateral metapodials in *H. primigenium* as well as in "*Stylohipparion*", and we cannot say that there was reduction in the side toes as we pass from the one to the other.

Among the incomplete metapodials of *Hipparion* from Olduvai there is the distal end of a third metacarpal, OLD/41, S 2, no. F. 807, that has a protuberance width of 51 mm by an articular width of 47 mm, while the crest measures 39 mm anteroposteriorly. Two distal ends of median metatarsals, OLD/55, BK II, no. 135, and OLD/63, BK II, no. 620, have a width at the protuberances of 48 mm, distal articular widths of 45 mm, and anteroposterior diameters of the distal crest of 38-39 mm. These bones exceed those listed in tables 14 and 15 in size.

The third metacarpal of *Hipparion libycum* from Lac Ichkeul recorded by Arambourg (1970: 91) is larger than any of the Olduvai third metacarpals: its length is 268 mm and its proximal width 55 mm. In other dimensions the bone of *H. libycum* is not or hardly larger than the maxima in our series. The third metatarsal (Arambourg, l.c.) is likewise 268 mm long, but otherwise does not exceed the maxima found for the corresponding Olduvai bones.

In the early Eurasiatic *H. primigenium* the frequency of third metatarsals lacking the facet for the meso-entocuneiform is relatively high; it seems to diminish in later *H. primigenium* (Forstén, 1968: 15-16). The lengths of the median metapodials in the North African *H. primigenium* are not much less than those in the Olduvai *Hipparion:* metacarpal III 198-210 mm, metatarsal III 232-240 mm, and the distal articular width/length indices are very much the same: 17-18 for the metacarpal, and 14-15 for the metatarsal (Arambourg, 1959: 87, 90). Thus, the evolutionary advance of "*Stylohipparion*" over the primordial Old World *Hipparion primigenium* as shown in the teeth is not manifest in the metapodials although, of course,

the proximal phalanx of the median digit is more elongated in the former than in the latter.

It is, therefore, not to be wondered at that the median metapodials of *Hipparion baardi* from Langebaanweg, Cape Province, which are intermediate between *H. primigenium* and *H. ethiopicum* in geological age, do not differ much in size or proportions from those of either of these. During a visit to Cape Town in 1971, at the instigation of Dr. Brett Hendey, I examined *Hipparion* material from Langebaanweg in the South African Museum. There are two third metacarpals, L 2148 and L 5576: the length is 213-215 mm, the proximal width 41 mm in both, the mid-shaft width 29-31 mm, and the distal articular width 35-36 mm. These bones do not differ significantly from those of table 14, but not from those of *H. primigenium* either. The proximal phalanges of median digits of the Langebaanweg *Hipparion,* L1456 and L1462A (figured in Boné & Singer, 1965, pl. XVI) are 69-71 mm in volar length, and 35-41 mm in least shaft width, longer than those of *H. primigenium.* More material of Langebaanweg will be dealt with at a later date.

THE OMO GROUP HIPPARION

Hipparion spec. and **Hipparion ethiopicum** (Joleaud)

The Mursi Formation *Hipparion turkanense* has already been dealt with under that head. I have seen no material from the Basal Member nor from Member A of the Shungura Formation, but *Hipparion* is represented in the American collection from the Usno Formation and from Shungura Member B on up.

The earlier Omo Group material will be dealt with under the head:

Hipparion spec.

In Coppens, Howell, Isaac & Leakey (editors, in press) there is a survey of the fauna of the Omo Group deposits. My contribution on the Perissodactyla in that volume is based exclusively on the collections made by the U. S. A. contingent since 1967.

The most complete *Hipparion* specimen in the American Omo collection is most of a mandible, with the left and the right cheek dentition in situ. The vertical parts of the rami and the symphysial portion are missing. The specimen is marked L. 1-40 and comes from Shungura Member B11. All the premolars and molars have developed ectostylids: they show as enamel rings or ovals on the occlusal surfaces. Because of ancient fractures it is possible to give the height as worn of several of the teeth: the P_4 is worn

to 4 cm of height, the M_1 to 3.5 cm, and the M_2 to 4.5 cm. The ectostylids of these teeth, therefore, are at least that high. The enamel figures of the ectostylids on the occlusal surfaces are 2 by 2 mm in P_2, 5 by 2.5 mm in P_3, 3 by 2 mm in P_4, 4.5 by 2 mm in M_1, 3.5 by 2 mm in M_2, and 2 by 2 mm in M_3. The hemimandible of *Hipparion* cf. *ethiopicum* from Olduvai BK II (no. 301, pl. 14 fig. 2) is figured beside the same side (left) of the Shungura Member B11 mandible (pl. 14 fig. 1) to show that the ectostylid figures are larger in the Olduvai specimen; the two dentitions are worn down to 4.5 cm of M_2 in both. The Olduvai dentition is more hypsodont than that from Shungura Member B11 as the ramus height shows (above, p. 43). Ptychostylids are hardly visible, but protostylids are there: although the antero-external corner is lost in most of the teeth, or damaged, a protostylid is seen in P_3-M_1, extending all along the height, being free at the apex in P_3. The fold between protoconid and hypoconid is very deep in M_1, extending to the internal valley, between metaconid and metastylid. In M_2 the external fold is slightly less deep, being cut off from the internal valley by the extremities of metaflexid and entoflexid, whereas in M_3, which is in early wear, the external groove extends still less far toward the internal valley, and the entoflexid meets the metaflexid, as in P_3 and P_4. Metaconid and metastylid are angular, and the valley between them is rather deep, hardly less so in P_3 and P_4 than in M_1 and M_2, although this valley is more rounded in the molars. The least worn molar, M_3, has a pointed internal valley, and in this feature, as well as in its shallow external groove, it resembles the posterior two premolars rather than the anterior two molars. The measurements of the crowns are in table 16. Ramus height between P_4 and M_1, 80 mm; below middle of M_3, 90 mm.

TABLE 16

Measurements of teeth of Shungura Member B11 mandible, L. 1-40 (mm)

	P_2	P_3	P_4	M_1	M_2	M_3
Anteroposterior	31	26	25	24.5	25	27
Transverse	17	17.5	17	16	15	14

The length P_2-M_3 is 163 mm; that of the molar series only, 80 mm, taken at the alveolar border. Hence, the length of the lower cheek toothrow is the same as that in *Hipparion africanum* (146-157 mm, Arambourg, 1959: 84) and in *Hipparion koenigswaldi* (163-176 mm, Sondaar, 1961: 250) both of which are synonyms of *H. primigenium* (Forstén, 1968: 15). As mentioned above, Arambourg did not observe ectostylids in *H. africanum*, but these may not be exposed because the teeth are in situ, and

Sondaar mentions the occurrence of ectostylids on a few teeth (P_4, M_1) of *H. koenigswaldi*. Nevertheless, ectostylids are frequent in *H. primigenium:* there is a local population from Gaiselberg in which ectostylids are developed in 100% of P_3-P_4, and one from Vienna sensu stricto in which they occur in 71% of M_1-M_2 (Forstén, 1968: 24). The ectostylids are about 3 cm high in the Namaqualand mandible described by Haughton (1932) as *Notohipparion namaquense*. In teeth from Kanapoi and Lothagam (Hooijer & Maglio, 1974: 16, 18) and in the mandible from Shungura Member B11 the ectostylids are 4-5 cm high, whereas in "*Stylohipparion*" they may reach a height of over 7 cm. This suggests an evolving group, but we badly need skull material to decide what the species are, and we have no skulls yet from the Omo Group deposits. Excluding the small specimens (mentioned under the head *Hipparion ?* aff. *sitifense* Pomel) the Usno Formation specimens, and those from the Shungura Formation Members B through E, will be described in the pages that follow.

USNO FORMATION

The Usno Formation *Hipparion* material consists of some isolated teeth most of which are incomplete. However, in view of the age of the Usno Formation, together with Shungura Member B, probably from 3.9 to 3.75 million years, it is an important collection.

W. 552, Usno Formation, is a P^2 dext. that looks rolled: the anterior and posterior surface as well as the mesostyle and the parastyle are abraded, and the base is incomplete but what remains is smoothly rounded off. This tooth displays the same complex enamel pattern as its homologue in the Kanapoi dentition referred to *H. primigenium* (Hooijer & Maglio, 1974, pl. 3). The P^2 of this dentition is preserved only on the left side, and it is illustrated next to the Usno Formation P^2 on pl. 6 fig. 1. Just in front of the prefossette there is a transverse enamel wall indicating that the Usno specimen was truncated in front rather than pointed, as is the Kanapoi tooth, and as is normal for a P^2 (pl. 6 fig. 2). The anterolingual incurvation in a P^2 lodges the persisting DM^1, which in the Usno specimen may have been rather large. The plications in the two fossettes can be counted in both teeth, and the numbers from front to back (anterior and posterior in the prefossette, and anterior and posterior in the postfossette) are 7-5-5-1 against 5-6-4-1 in the Kanapoi P^2 (Hooijer & Maglio, 1974, table 4). The caballine fold in the Usno P^2 is triple (single in the Kanapoi P^2), and the protocone, measuring 9 by mm, is more flattened than that in the Kanapoi P^2, in which it measures 7 by 4 mm. The Usno P^2 is about 5.5 cm high as worn, the Kanapoi P^2 only 3 cm; the anteroposterior and transverse

diameters of the crown of the Usno specimen appear to be just the same as those of the Kanapoi P^2, 35, and 23 mm, respectively.

There is no way in which the Usno P^2 can be distinguished from that of Kanapoi: the anterior edge (protostyle?) and the protocone of course vary individually to some extent, as is shown by the next specimen.

W. 133, Usno Formation, another P^2 dext. incomplete in front, worn to 3.5 cm of height, pli numbers 5-7-5-1, single pli caballin, protocone 8 by 4 mm. The crown width is 23.5 mm. The anterior edge was certainly more prominent than that in the preceding specimen.

W. 296, Usno Formation, is a P^3 or P^4 dext. worn to a height of 3 cm; the postero-internal angle of the crown is broken off. The complexity of the enamel pattern is striking, the plications filling almost the whole prefossette (pl. 3 fig. 3). Pli numbers 6-8-7-3, even excluding the very minor twists, of the same order as those in P^3 and P^4 of the Kanapoi dentition, which are hardly less worn (3.5, and 4 cm high at the mesostyles); protocone only slightly longer (9 by 4 mm, against 7.5 by 4 mm in the Kanapoi P^3-P^4). The pli caballin has a single point, against 2-3 in the Kanapoi specimens. Crown dimensions 28 by 26 mm.

W. 629, Usno Formation, an entire M^1 or M^2 dext. with a worn height of 5 cm, slighly more numerous plications than in those from Kanapoi, viz., 6-9-6-3, an almost isolated boucle préfossette (prefossette bay) with two invaginations, a single pli caballin, and the protocone 8 by 4 mm across (pl. 5 fig. 1). The crown measures 26 mm anteroposteriorly, and 24.5 mm transversely at 2 cm from the base, whereas the Kanapoi M^1-M^2, measured at the same height, are 22-22.5 mm anteroposteriorly. No other differences can be observed.

B. 139, Usno Formation, the unworn crown of a left upper premolar, lacks the tip of the protocone and a chip postero-externally; the base unfortunately is not preserved. A specimen like this shows that the tips of the buccal cusps (paracone and metacone) are some 5-6 mm higher than those of the lingual (protoconule and hypocone) in their pristine state; the protoloph and metaloph are less high again than the internal cusps, and the enamel projections into pre- and postfossette respectively, the fossette plis, start at the summit of these ridges. Pli counts cannot be given except for those in the anterior border of the profossette, which show as the anterior crown portion is broken 2 cm below the top of the protoloph: they are 7 in number. The protocone can be seen in an oblique section: it is 8 mm long, and the pli caballin is single. The hypoglyph can be followed down the crown so far as preserved, and flattens out 5 cm from the tip of the hypocone. At the antero-buccal angle there is seen a vertical fold

just internally of the parastyle, marking it off from the remainder of the protoloph: this fold is widest at the top. This fold, which may be called the anterior parastyle fold, is present in all hipparions, hypsodont or not, and flattens out rootward. In the already complicated nomenclature of *Hipparion* teeth this fold has no designation of its own, although Van Hoepen (1930: 22) drew attention to it in *Hipparion steytleri,* calling it a peculiar fold in the anterior surface of the anterior style (parastyle).

B. 367, Usno Formation, is a slightly worn DM^4 dext., typified by its thin enamel and very low crown. Unfortunately the base is missing externally, but internally the crown height is not more than 2.5 cm. Enamel plication numbers cannot be given as only the major pli anteriorly in the prefossette and that posteriorly in the postfossette project from the cement that fills the fossettes. The pli caballin is double, and there is a peculiar spur from the protocone, pointing toward the protoconule. The crown measures 34 mm anteroposteriorly and 27 mm transversely, 4 mm more, either way, than the DM^4 of *H. primigenium* from Ekora (Hooijer & Maglio, 1974, table 6).

W. 134, Usno Formation, a right upper milk molar of wich the internal part is missing: either DM^3 of DM^4 dext. This tooth is worn externally to a height of 28 mm, and the anteroposterior diameter of the crown is 30 mm. The mesostyle has a median groove in the top 12 mm, making it a double ridge, but the basal portion is evenly rounded. The parastyle shows the anterior parastyle fold, all the way down to the base of the crown. The specimen is just as large as the Ekora DM^4, but its plication pattern is obscured by cement.

W. 165, Usno Formation, an upper molar fragment showing most of the fossettes, W. 22g, Usno Formation, a fossette, and FS.433, Usno Formation, a protocone portion, are listed merely for the sake of completeness.

HCFN.460, Usno Formation, is a slightly worn P_3 or P_4 sin. preserved to almost the base, 63 mm high as preserved. The protostylid extends all along the height of the crown as a slender pillar, barely 2 mm in diameter; at the apex it is free from the external surface. The ectostylid is also seen to extend to the occlusal surface, where it is as small as the protostylid, but basalward it increases somewhat in diameter. The top portion of 28 mm only is preserved, the basal portion is broken off, and the thin cement investment would not show that an ectostylid had been present: it was evidently free the external surface of the crown except at the very base. The crown projects markedly backward in the upper portion, but the anteroposterior diameter diminishes rootward. The outer surface behind

the ectostylid is broken off in the basal portion (pl. 17 fig. 7). In crown view (pl. 17 fig. 3) the "tie" (metaconid and metastylid) is nearly constricted off by the close approximation of metaflexid and entoflexid, and the external groove between protoconid and hypoconid consequently is shallow; this is a feature of premolars. In the adjoining portions of both flexids there is seen a small spur; such little folds disappear with advancing wear. Metaconid as well as metastylid are not quite rounded, but pointed, mostly so the metastylid, and the valley in between is wide and shallow. The loops would become flatter toward the roots. A tooth like this, even incomplete, is higher than the entire lower molar from Lothagam (Hooijer & Maglio, 1974, pl. 6 fig. 4), which is only 60 mm high in the unworn state, and which has an ectostylid 45 mm high: the Usno specimen is clearly more advanced than that of Lothagam, which is some 2 million years older. The crown is 22 mm anteroposteriorly at the middle of the height, and 12 mm transversely, without cement.

HCFN.458, Usno Formation, a P_3 or P_4 dext. worn to 5 cm of height, has the base not complete. The protostylid is as weak as that in the preceding specimen, but the ectostylid is better developed, 5 mm basally and 4 mm apically in anteroposterior diameter. Its height was at least 5 cm. There is a ptychostylid, and a pli hypoconid, the small spur in the anterior portion of the entoflexid. The configuration of the "tie" is as in HCFN. 460, and the crown diameters are 24 by 14 mm.

W. 621, Usno Formation, is a P_2 dext., entire, and worn down to 1.5 cm from the external enamel base. The ectostylid, 3 by 2 mm in diameters, is there, but no ptychostylid. The metaflexid is quite small, and the metaconid, therefore, not well marked off. The crown diameters are 31 by 15 mm.

W. 742A, Usno Formation, is the basal portion of an M_3 sin. with an ectostylid uniformly 3 mm in diameter extending to the occlusal surface, 3 cm above the base, and a distinct protostylid; the "heel" (hypoconulid) has two small lateral lobes, the crown diameters are 26.5 by 11 mm, exclusive of cement.

W. 23-932, Usno Formation, a crown portion 4 cm high as worn, represents P_3 or P_4 dext. just showing the "tie", the ectostylid strongly developed (6 mm in diameter anteroposteriorly), and a distinct ptychostylid. The crown width is 16 mm.

W. 290, Usno Formation, is an M_1 or M_2 dext. broken off anteriorly through the metaconid, 2 cm high as worn. The ectostylid is 3.5 by 2.5 mm occlusally.

W. 524, Usno Formation, a fragment of an M_1 or M_2 or M_3 sin. broken

off behind the entoconid and incomplete externally. The protostylid is distinct, the ectostylid present but broken in this tooth, only about 1.5 cm high as worn. The crown width (anteriorly) is 14 mm.

HCFN. 459, Usno Formation, is the top portion of an unworn M_3 sin. coated with cement and showing the weak apical portions of ectostylid and protostylid, which are only partially preserved. The fragment is only 4.5 cm high and is still lengthening downward at the broken edge.

FS. 759, Usno Formation, three lower cheek tooth fragments, one of which 5.5 cm high, W. 647, Usno Formation, W. 648, Usno Formation, and HCFN. 461, Usno Formation, all lower cheek tooth fragments, are here recorded only for the sake of completeness.

SHUNGURA MEMBER B

L. 1-42d, Shungura Member B11, is most of a P^2 dext. The portion in front of the parastyle is lost. The plications in the adjoining borders of pre- and postfossette cannot be distinctly seen, but those in the posterior border of the postfossette are at least three in number. The crown is worn to a height of 6 cm externally, measured from the closed base between the fossettes. It displays a weak wrinkling of the anteroposteriorly oriented fossette borders. The protocone diameters are ca. 9, and 3 mm, and the transverse diameter of the crown, over mesostyle and protocone, is 26 mm, exclusive of cement. The pli caballin is single. The hypoglyph is deep occlusally but flattens out toward the base. Thus, this tooth is wider than the Usno Formation P^2, which has a triple caballine fold, and a single pli posteriorly in the postfossette; differences of doubtful significance.

L. 1-42e, Shungura Member B11, is an M^1 or M^2 dext. with a most complex enamel pattern (pl. 3 fig. 7). The plication numbers are 6-8-8-? (the posterior border of the crown is not complete). The eight deep folds in the adjoining borders of pre- and postfossette fill the fossette areas evenly, the typical *H. primigenium* pattern. The height of the crown as worn is 6 cm, and the diameter anteroposteriorly 24 mm, and 24.5 mm transversely, at the middle of the height.

L. 380-4, Shungura Member B, is an M^1 or M^2 dext. worn to 3.5 cm of height, showing just the same complexity of the enamel pattern although the folds are not as well exposed as those in the preceding specimen. The pli caballin is single, the protocone 8 by 4 mm in diameters, lenticular, pointed at both ends. At 2 cm from the base the crown measures 25 by 23 mm in diameters.

L. 1-61, Shungura Member B11, is the external half of an M^1 or M^2 dext., unworn, and with the base preserved. The full height of the crown

at the mesostyle is 65 mm. The anteroposterior diameter, except at the top and at the bottom cm (where it diminishes) is 25.5 mm, giving a height/length index of 255. The height/width index cannot be given, but as the transverse diameter of an upper molar does not differ more than a few mm from the anteroposterior the difference would not be great. In four slightly worn upper premolars and molars of *H. primigenium* from Wad el Hammam the height/width index runs from 220 to 290 (Arambourg, 1959: 79), and the index in the Shungura Member B M^{1-2} was certainly of the same order.

L. 2-21a, Shungura Member B, is a worn M^{1-2} sin. without the base. The hypoglyph is just disappearing at the broken base: at the occlusal surface it is very deep, and the hypocone very nearly constricted off (pl. 6 fig. 3), while the inflection is closed at the root end (the posterior height of the fragment is exactly 30 mm). The crown pattern is somewhat simpler than that in L. 1-42e, with fossette plications numbering 1-5-4-2, and a single caballine fold. The protocone measures 8 by 3 mm, and the crown 23 by 21 mm, exclusive of cement.

L. 2-2b, Shungura Member B, is an M^3 dext. with a worn height of 5 cm, plication numbers 5-4-5-1, pli caballin single, crown and protocone diameters as in the preceding specimen.

L. 2-2c, Shungura Member B, the external half of an M^{1-2} sin., worn height 3.5 cm, plis numbering 5-?-5-3, is interesting for the configuration of the posterior border of the prefossette. The fourth pli from the buccal end is confluent with the pli protoconule, isolating the postero-lingual portion of the fossette as an enamel island, with two small inflections (pl. 5 fig. 2). Such an isolated prefossette bay (boucle préfossette) is occasionally seen, e.g., in the M^2 of the molar series of *H. africanum* figured by Arambourg (1959: 82, fig. 36A). The anteroposterior diameter of the crown is 24 mm.

L. 1-397 a and b, Shungura Member B, are fragments of right upper molars, one the prefossette portion, the other holding the protocone, 8 by 4 mm, and a single pli caballin.

L. 1-21, Shungura Member B11, a protocone portion very similar to the last, but with a triple caballine fold.

L. 2-150, Shungura Member B, is a nearly complete DM^4 dext. closely resembling the Ekora specimen (Hooijer & Maglio, 1974, pl. 4 fig. 3) and that from the Beglia Formation (Forstén, 1972: 12, fig. 2). The plication numbers are 6-10-5-5 against 3-8-3-3 for Ekora and 4-7-4-4 for the Beglia Formation specimen. The pli caballin is bifid, the protocone 9 by 6 mm and intermediate in shape between those of DM^3 and DM^4 of Ekora. The

crown measures 29 mm anteroposteriorly, and the transverse diameter is approximately 25 mm (mesostyle incomplete). Thus, it is somewat smaller than the DM^4 of the Usno Formation (B. 367), but shows the pattern rather nicely (pl. 6 fig. 4).

L. 1-42c, Shungura Member B11, is an entire P_2 dext. with the base preserved (pl. 15 fig. 3). The most conspicuous feature is the ectostylid, which is well-developed, 7 mm anteroposteriorly at base, and gradually tapering to a point that has not yet been touched by wear: its height is 43 mm (pl. 15 fig. 7). In the Usno Formation P_2 (W. 621) the ectostylid is less developed, being only 3 mm anteroposteriorly at 1.5 cm from its base. The ptychostylid is well-marked occlusally but for the most part hidden in cement. In the entoflexid, a slender enamel inflection arising from the hypoconid opposite to the ptychostylid, extends across and touches the metastylid. We see such enamel spurs in slightly worn lowers only; they disappear with advancing wear. The crown measures 31 mm anteroposteriorly and 12 mm transversely at the occlusal surface, but the width increases to 15 mm near the base, where the ectostylid is most prominent; this is exclusive of cement. The Usno Formation P_2 is just as large basally (31 by 15 mm).

L. 2-2d, Shungura Member B, a P_2 sin. worn down to 3.5 cm, has an ectostylid extending to the occlusal surface, on which its enamel ring is 3 mm across; at the base it is 5.5 mm anteroposteriorly. The anteroposterior diameter of the crown is, again, 31 mm, the transverse, 13.5 mm occlusally, and 14.5 mm basally, without cement. The ectostylid in the present specimen, then, is intermediate in size between the preceding and the Usno Formation P_2 ectostylids.

Four lower third or fourth premolars are rather uniform in characters and size: (1) P_{3-4} dext., L. 2-151, Shungura Member B; (2) P_{3-4} sin., L. 2-21b, Shungura Member B; (3) P_{3-4} sin., L. 2-2e, Shungura Member B, and (4) P_{3-4} sin., L. 1-42b, Shungura Member B11. The ectostylid in (1) is 50 mm high, tapering from 5 mm anteroposteriorly at base to 2 mm just below the occlusal surface. In (2), worn to 4 cm of height, the ectostylid is 4 mm anteroposteriorly occlusally. In (3), worn to 3.5 cm, the occlusal diameter is 5 mm, and in (4), worn to the same height, approximately the same (the ectostylid is damaged). In all these teeth the protostylid is a well-marked, slender pillar, while the ptychostylid is not very marked, and metaflexid and entoflexid are unwrinkled. In the least worn specimen (1) the metaconid forms a point lingually but becomes more rounded below, as it is in the other specimens. The crown diameters, taken at 2 cm from the base, are 25-26.5 mm anteroposteriorly, and 15-16 mm transversely.

L. 2-21c, Shungura Member B, is a slightly worn M_{1-2} sin., 5.5 cm high, with the tip of the ectostylid at the occlusal surface. At the base it is 5.5 mm anteroposteriorly but not very prominent. In the entoflexid there is a spur just as we have seen in various other specimens. Both metaconid and metastylid are pointed and far apart on the occlusal surface, becoming more rounded and somewhat closer together basally. The crown diameters are 25.5 by 13 mm.

Of three last lower molars, two, viz., L. 1-172, Shungura Member B11, M_3 sin., and L. 729-5, Shungura Member B, M_3 sin., have an ectostylid, while the third, L. 2-2a, Shungura Member B, M_3 sin., does not have it. L. 1-172 is 5.5 cm high as worn, and the ectostylid is just touched by wear (showing the little spur in the entoflexid). The protostylid is as high as the ectostylid, the ptychostylid marked, at least occlusally. In L. 729-5 the ectostylid is worn to a ring 3.5 mm across at 4 cm from the base. The specimen L. 2-2a, in which the ectostylid is so capriciously absent, differs in no other way from the others. The crown diameters of the three specimens, at 2 cm from their bases, are 30 mm anteroposteriorly, and 12-13 mm transversely.

There remains, from Shungura Member B12, a fragment of left lower cheek tooth, L. 795-14, with metaconid and metastylid, 6 cm high as preserved.

A few postcranial *Hipparion* remains from Shungura Member B11, viz., a navicular sin., L. 1-14, a shaft portion of a femur sin. with the third trochanter, L. 1-66, and the distal end of a tibia sin., L. 1-65, are indistinguishable from series of these bones from Olduvai Gorge representing both *Hipparion* and *Equus*. They will be dealt with along with these remains.

SHUNGURA MEMBER C

It is in this portion of the Shungura Formation sequence, with a provisional age of 2.9 to 2.4 million years, that we begin to encounter very hypsodont cheek teeth that approach "*Stylohipparion*", although the ectostylid development still is somewhat inferior to that seen in full-fledged *Hipparion ethiopicum* and that from Olduvai Bed II. There are some lower incisors first:

L. 132-11 and L. 27-15A, Shungura Member C, are worn I_2 dext. The base is preserved only in L. 132-11, and its worn height is 37 mm. The diameters are 16 by 12.5 mm at the top against 13 mm labiolingually and 9.5 mm transversely at the base. The other I_2, L. 27-15A, a fragment 32 mm

high, is 17 by 12 mm occlusally. There is a median lingual ridge flanked by sharp grooves in both of the I_2, but in L. 132-11 it is seen to flatten out 20 mm from the base. The cup is filled with cement and has a wavy outline.

L. 768-1, Shungura Member C, is an M^3 sin. that is not well preserved, but metacone and hypocone are untouched and the base preserved at least posteriorly. Because of the natural curvature of the crown of this last upper molar, the posterior height (which can be measured exactly as 63 mm, in a straight line) in less than that anteriorly, what with the higher anterior cusps (paracone and protoconule) and the lower base, at the convex side of the curved tooth. The protoconule is not preserved; the paracone has probably lost some 3-5 mm in height because of wear, which makes for a full crown height of approximately 75 mm. The protocone is untouched by wear, and is recurved externally at the tip, against the tip of the likewise untouched hypocone and even curving somewhat over it. Plication patterns of course cannot be seen at this stage yet. The antero-external edge of the crown is damaged, as is most of the apical half of the anterior surface: the basal crown diameters are 27 by 22 mm, whereas one cm from the apex these diameters are 22 by 19 mm. The protocone has a uniform antero-posterior diameter of 11 mm throughout its height. The present tooth is as high as the uncut M^3 in the subadult Olduvai BK II skull (no. 283).

L. 724-3, Shungura Member C, is likewise a slightly worn M^3 sin. but it lacks the apical half of the internal surface and the base is not quite complete. The full height of this specimen is 71 mm, in a straight line, the protocone is 9.5 mm anteroposteriorly and 3.5 mm transversely as seen in section at 3.5 cm from the base, the crown diameters 24 by 20 mm at this level.

L. 724-2, Shungura Member C, is an M^{1-2} sin. that may have belonged to the same individual as the last; unfortunately the external surface is missing. The crown height, as worn, is 67 mm, the pli counts 3-7-2-1, single caballine fold, and protocone 9.5 by 3.5 mm, anteroposterior crown diameter 25 mm.

L. 46-33, Shungura Member C, is a (?rolled) P^{3-4} sin., preserved height 6 cm, pli numbers 1-7-5-1, double pli caballin, protocone incomplete, no diameters can be given.

L. 777-2, Shungura Member C, a portion of a much worn left upper cheek tooth.

L. 27-4, Shungura Member C, external portion of a DM^{3-4} sin., thin enamel, pli counts 4-5-5+-?, external crown height 16 mm.

L. 51-11A, Shungura Member C, is a worn-out DM^{3-4} sin. in which the postfossette is represented by two enamel islands, and the protocone is 9.5

by 5.5 mm, internally flattened. The crown, worn to 7 mm of height, is 22.5 mm transversely.

Among the lower teeth there is a set from Shungura Member C, L. 304-3 (P_2 sin.) and L. 304-21A (M_3 dext.), L. 304-21B (P_3 sin.), L. 304-21C (M_2 sin.), L. 304-21D (M_2 dext.), L. 304-21E (M_1 sin.) plus a few fragments all evidently of one and the same individual. Crown heights as worn are: P_2: 39 mm, P_3: 46 mm, M_1: 57 mm, M_2: 63 mm, and M_3: 66 mm. The ectostylid is present and well-developed in all these teeth, and extends to their occlusal surfaces except in M_3, in which it is only 49 mm high; the basal anteroposterior diameters vary from 6-7 mm and the enamel figures occlusally are from 4 mm (in P_2, the most worn tooth) to 1 mm (in M_2) in diameters. All the teeth have marked protostylids, the metastylid angular and the metaconid more rounded-triangular. Crown diameters are in table 17, and have been taken at 2 cm from the crown base.

TABLE 17

Measurements of teeth from Shungura Member C, L. 304-3, L. 304-21 (mm)

	P_2	P_3	P_4	M_1	M_2	M_3
Anteroposterior	29	26	—	25	24	24
Transverse	14.5	16.5	—	—	13	11

The teeth of the Shungura Member B11 mandible (table 16) are slightly more down, and in the M_3 of this specimen the ectostylid reaches the occlusal surface. In the Shungura Member C lower dentition the ectostylids are at least 60 mm high, as the M_2 shows, whereas that of M_3 barely reaches 50 mm in height. Ptychostylids are present in all the teeth, and show occlusally, while in P_2 as well as in the slightly worn M_2 the enamel spur in the anterior part of the entoflexid is seen; this apical structure that soon vanishes upon wear is not observed in the mandible from Shungura Member B11, another sign that it is more worn than the Shungura Member C teeth: the ectostylid height in the earlier teeth is somewhat in excess of 5 cm, certainly not much at that.

L. 55-29, Shungura Member C, is rather complete M_{1-2} dext., and its crown height is 7 cm. The ectostylid is seen to peter out at at 60 mm from the base, and, therefore, does not show occlusally. This slightly worn tooth is 28 by 13 mm occlusally, because of the posteriorly projecting hypoconulid; at 2 cm from the base it is 23 by 13 mm in diameters.

L. 15-16, Shungura Member C, an M_{1-2} sin., worn height 5.5 cm, has an ectostylid all the way up to the occlusal surface. Crown diameters 21.5 by 12 mm.

L. 327-9, Shungura Member C, is a nearly unworn crown portion of an M_{1-2} dext. in which the apex of the ectostylid is seen to extend just 10 mm short of the crown edge. Diameters as in L. 55-29.

L. 768-19, Shungura Member C, is an M_3 sin. unfortunately incomplete internally, worn to 6.5 cm of height, and 28.5 by 12.5 mm in diameters, at 2 cm from its base.

L. 45-10, Shungura Member C, a much worn P_{3-4} sin. (height only 2 cm), has an ectostylid 8 by 3.5 mm in diameters; the crown is 23.5 mm (reduced as a result of interproximal wear) by 16.5 mm.

L. 768-18, Shungura Member C, a P_{3-4} dext. 4.5 cm high as worn, full ectostylid (5.5 by 2.5 mm occlusally), measures 26 by 16.5 mm at 2 cm from the base.

L. 335-30, Shungura Member C, is a P_{3-4} sin. incomplete on the sides and basally: its anteroposterior diameter is 25 mm at the occlusal surface, about 2 cm from its base, and the ectostylid measures 5.5 by 3 mm.

Remaining lower cheek tooth fragments, from Shungura Member C: L. 27-34, L. 69-11, L. 51-11B, L. 327-24, and L. 355-5 are listed for completeness of record.

The distal portion of a metatarsal III from Shungura Member C, L. 46-34, is *Hipparion;* the distal articular width is 43 mm, and the distal crest measures 34.5 mm anteroposteriorly. An astragalus dext., Shungura Member C, L. 183-26, measures 45 mm in distal articular width, and 61 mm in medial height, and thereby is intermediate in size between the largest and the smaller *Hipparion* astragali from Lothagam (Hooijer & Maglio, 1974: 19, 27).

SHUNGURA MEMBER D

The *Hipparion* specimens from this portion of the Shungura Formation sequence, provisionally dated at 2.4 to 2.1 million years, comprise some incisors as well as cheek teeth, all worn:

L. 36-14, Shungura Member D, is an I_1 dext. 50 mm high as worn, measuring 21.5 by 11.5 mm occlusally. The median lingual ridge is marked (pl. 3 fig. 8); the lateral of the grooves delimiting it is most pronounced. The median external groove shows in the basal 20 mm. The basal width is 13 mm.

L. 9-29, Shungura Member D5, is an I^2 sin. It is worn, with the base incomplete, and the occlusal diameters are 19 by 11 mm.

L. 11-4, Shungura Member D5, an M_3 sin. worn down to 5 cm, in which the ectostylid tip is just touched by wear, giving a height of 50+ mm. Crown diameters 26 by 11 mm.

L. 95-1, Shungura Member D, an M_{1-2} dext., has a worn height of 4.5 cm; the ectostylid as well as the protostylid extend along the full height of the crown, which measures 25 by 13 mm.

L. 581-3, Shungura Member D, an M^{1-2} sin., the only entire upper cheek tooth, 25 by 24 mm in diameters, has plis numbering 3-5-4-?1, a single pli caballin, and a protocone 9 by 4 mm occlusally, at 4.5 cm from the base.

L. 12-3B, Shungura Member D2, an incomplete M^3 dext., about 4.5 cm high as worn, measures 27 by 20 mm. Pli counts cannot be given.

L. 12-3A, Shungura Member D2, a fragment of an M^{1-2} dext. probably of the same individual as the last, worn height at least 5 cm, shows plis numbering 5-8-4-?

L. 11-5, Shungura Member D5, a fragment of an upper left cheek tooth, and L. 12-24A and B, Shungura Member D2, and L. 9-80, Shungura Member D5, three lower cheek tooth fragments, do not add anything of value.

The distal end of a tibia dext., L. 36-13, Shungura Member D, cannot be distinguished from series of *Hipparion* and *Equus* tibiae from Olduvai Gorge to be dealt with in a later paper.

SHUNGURA MEMBER E

This Member, dated provisionally at 2.1 to 2.05 million years, is again not well represented in the *Hipparion* collection, but there is at least one lower cheek tooth that is 70 mm high as worn, with an ectostylid in excess of 65 mm in height:

L. 26-28A, Shungura Member E, an M_{1-2} sin., 7 cm high as worn, the ectostylid forming an island 6 by 2.5 mm in diameters at 65 mm above its base. Small extra spur in anterior portion of entoflexid, metaconid and metastylid rounded triangular and pointed internally, widely spaced, protostylid developed to full height of crown, weak ptychostylid. Crown 23.5 by 13 mm in diameters.

L. 20-17, Shungura Member E, an unworn M_{1-2} dext., base incomplete, with ectostylid extending to 10 mm below the external cusps, 6 mm anteroposteriorly, and basal portion missing.

L. 26-99, Shungura Member E, P^{3-4} dext; worn to 3.5 cm, pli counts 2-6-5-1, single pli caballin, protocone 9 by 4 mm, crown diameters 23 by 25 mm.

L. 206-6, Shungura Member E, P^2 sin., incomplete externally and behind, 4.5 cm high as worn. Plis 1-5-3-2, caballine fold single, protocone 7 by 4 mm.

L. 763-2, Shungura Member E, M^{1-2} dext., worn height 3.5 cm, plis 2-7-3-1, caballine fold single, protocone damaged, crown 22.5 mm anteroposteriorly.

L. 757-1, Shungura Member E, external portion of left upper cheek tooth, and L. 146-101D, Shungura Member E, prefossette portion of left upper cheek tooth.

L. 5/6-63A, Shungura Member E, P_{3-4} dext., worn to 3.5 cm, ectostylid 4 mm anteroposteriorly, crown 25 by 13.5 mm.

L. 5/6-63B, Shungura Member E, M_{1-2} sin., worn to 4.5 cm, ectostylid 5 mm anteroposteriorly, crown 24 by 13.5 mm.

L. 127-30, Shungura Member E, M_{1-2} sin., worn to 1.5 cm, ectostylid 5 by 3 mm, crown 21.5 by 13 mm.

L. 468-3, Shungura Member E, M_{1-2} dext., worn to 2 cm, ectostylid 5.5 by 2 mm, crown 21 by 12 mm.

L. 185-4, Shungura Member E, P_{3-4} sin., worn to 5 cm, external surface missing.

L. 26-28B, Shungura Member E, unworn apical portion of right lower cheek tooth.

L. 147-24, Shungura Member E, posterior portion of left lower cheek tooth.

Two postcranial elements of *Hipparion* are present in the collection of Shungura Member E, viz., an astragalus dext., L. 168-9, with a distal articular width of 45 mm and a medial height exceeding 55 mm, and the proximal portion of a metatarsal III dext., L. 168-10, with a greatest width of some 45 mm (both specimens are damaged).

In the next portion of the Shungura Formation sequence, Shungura Member F, dated provisionally at 2.05 to 1.93 million years, *Hipparion* remains become more numerous. The degree of hypsodonty is such (three uppers, already worn, 75 mm high: L. 79-2A, L. 253-2A, and L. 398-1182) that we have evidently rached the stage of "*Stylohipparion*". It would seem justified, therefore, to use the name *Hipparion ethiopicum* (Joleaud) for the material from Shungura Member F on up, although the species as such may have emerged earlier: we have a very high-crowned molar already in Shungura Member C as noted above. It is hoped that in the future the transitional phase of Usno Formation through Shungura Member E, spanning two million years, will become better documented than it is now.

Hipparion ethiopicum (Joleaud)

Libyhipparion ethiopicum Joleaud (1933), of which I select the M_3 dext. (l.c., pl. I figs. 2, 6) as the type (lectotype), is indistinguishable from

Hipparion libycum and *Hipparion steytleri:* the upper molar described as *Equus* (*Hippotigris*) sp. (l.c., pl. I figs. 9, 13) has an isolated protocone (cf. Arambourg, 1947: 304, pl. XI fig. 4), and hence is not *Equus;* its height is 81 mm. The lowers are characterized by their well-developed ectostylids, angular, pointed metaconid-metastylids, as well as by their hypsodonty. Unfortunately, Arambourg (1947: 303) preferred to ignore the name *Libyhipparion ethiopicum* that was available for the Omo *Hipparion,* and used *Stylohipparion albertense* (Hopwood) instead although we do not know whether the lower cheek teeth of this species do possess ectostylids (above, p. 27). Later (Arambourg, 1970: 84), he placed both *Hipparion albertense* and *Libyhipparion ethiopicum* in the synonymy of *Stylohipparion libycum.* Even the Omo expeditions of 1967-1974 have not recovered skulls of the *Hipparion* from these beds, and full specific identity with the North African Villafranchian *Hipparion libycum* cannot as yet be accepted as definitely established. The teeth from Shungura Member F on up are here placed under the head *Hipparion ethiopicum* as this is the most correct procedure in my opinion.

SHUNGURA MEMBER F

In his paper on "*Libyhipparion ethiopicum*", Joleaud (1933, pl. I fig. 12) figures one incisor. It is an I_1 sin., worn down to about 35 mm from its base, with a partition in the cup, and measuring about 14 mm transversely at the occlusal surface. This specimen is similar to Olduvai specimens worn to the same degree. In the Shungura Formation collection there are several *Hipparion* incisors from Member C on up, and these have been enumerated at the beginning of the present chapter, under *Hipparion* spec. There is no fundamental difference between the incisors of the earlier and the later African hipparions: the later are just more hypsodont, with a more reduced lateral incisor, but the telltale I^3 or I_3 is not represented in the Omo collection.

L. 253-2C and 2B, Sungura Member F, are two upper incisors, I^1 and I^2 dext., of the same individual, worn to 50 mm from the base externally (pl. 13 fig. 2). The transverse and labiolingual diameters at the top are 20 13.5 mm for I^1, and 19 by 13 mm for I^2. At 25 mm from the base widths are reduced to 17 mm, and at the base these are only 10 mm. There is a median ridge lingually, marked off by grooves the lateral of which is very sharp. I^1 has a shallow external longitudinal groove. Such grooving is also seen in Olduvai incisors from BK II (nos. 2845 and 50). Size and hypsodonty are as in the Olduvai I^1 and I^2.

L. 470-3, Shungura Member F, is a P^2 dext. incomplete anteriorly and externally, height 5 cm as preserved, pli counts 1-4-4-1, single pli caballin, protocone 7.5 by 4 mm.

P^3 or P^4 are represented by L. 79-2A and L. 398-1182, both from the right side and 75 mm high as worn. The plication pattern is somewhat obscured, one has a single, the other a double caballine fold, and the protocone is 10 by 3-4.5 mm. The crown diameters, at 2 cm from the base, are 23 mm anteroposteriorly, and 23-26 mm transversely.

Another very hypsodont upper cheek tooth from Shungura Member F, L. 253-2A, is an M^1 or M^2 dext. likewise worn to 75 mm of height. There are two more upper molars, L. 398-1987 and L. 789-3, both M^{1-2} dext. more worn (to 60 mm of height). The pli counts in these three specimens are 1-(4-6)-2-1, with single plis caballins, protocones 9-10.5 by 3.5-4 mm, crown diameters 21 by 21-22 mm.

M^3 is represented in the Shungura Member F collection by three specimens, none of which well preserved: L. 79-2B (M^3 dext.), L. 79-2C and L. 421-1 (both M^3 sin.). They are worn to less than 70 mm of height, and the protocones are quite long (9-10 mm). L. 421-1 is 25 mm anteroposteriorly at 2 cm from its base.

Several upper molar fragments from Shungura Member F, L. 253-2D, L. 399-23, L. 182-11A, and L. 182-11B, are listed for the sake of completeness.

L. 398-13, Shungura Member F, is the distal articulation of a third metacarpal of *Hipparion,* 39 mm transversely, and with an anteroposterior diameter of the distal crest of 32 mm, indistinguisable from those of Olduvai Gorge (table 14).

A P_4 and an M_1 dext., L. 398-11 and 12, Shungura Member F, belong to a single individual. M_1 is worn to 20 mm, P_4 to 25 mm, and in both of them the ectostylid is connected with the hypoconid by a narrow isthmus (pl. 15 fig. 1), an exceptional feature shown in late wear.

Seven specimens of P_3 or P_4 all from Shungura Member F are as follows: P_{3-4} dext.: (1) L. 52-68; (2) L. 465-67; P_{3-4} sin.: (3) L. 79-2D; (4) L. 65-17; (5) L. 465-95; (6) L. 465-68, and (7) L. 467-44. The least worn (1) is 65 mm high, and the ectostylid has a full height of 60 mm. The ectostylids vary from 6 to 8 mm anteroposteriorly at base, and the crown diameters from 22 to 25.5 mm anteroposteriorly and from 13 to 15.5 mm transversely at 2 cm from the base.

Four specimens of M_1 or M_2, Shungura Member F, are: M_{1-2} dext.: (1) L. 420-12; (2) L. 465-70; (3) L. 65-16, and M_{1-2} sin.: (4) L. 65-34.

Specimens 1 and 4 are 55 mm high as worn but their ectostylids were higher. Crown diameters 23-24 by 12-14 mm in this small series.

An unworn crown of a left lower molar, L. 38-3, Shungura Member F, lacks the hypoconid and the ectostylid and the base as well: it is 66 mm high as preserved. A fragment of a right lower premolar, P. 935-2, is listed from completeness.

L. 398-2049, Shungura Member F, is a DM^2 sin. incomplete anteriorly, with a crown height of 23 mm externally, and measuring 20.5 mm transversely at the base. The protocone is very massive, 7.5 by 3 mm occlusally and lengthening and widening rootward.

SHUNGURA MEMBER G

This portion of the Shungura Formation, provisionally dated at 1.93 to 1.83 million years, has a good representation of *Hipparion* teeth, of the "*Stylohipparion*" type. There are a few incisors, as follows:

L. 882-4, Shungura Member G, I_1 dext. worn to 50 mm from base, occlusal diameters 18 by 13 mm; the basal width is no more than 9 mm.

L. 627-216, Shungura Member G, crown portion of slightly worn I_1 sin., 22 by 11.5 mm in diameters occlusally. The cup is wavy in outline, and cement-filled.

These specimens compare very well with their homologues in the Olduvai collection. The I_1 dext. has a median lingual ridge, the I_1 sin. a shallow external groove. Arambourg (1970: 86) makes quite a point of lingual grooves bordered by a ridge on incisors of "*Stylohipparion*" *libycum* from Ain Brimba in Tunisia, but this ridging and grooving is among the variations seen in Olduvai as well as in Omo *Hipparion* incisors.

Among the upper cheek teeth, I single out an M^1 or M^2 sin., L. 627-89, Shungura Member G, unfortunately lacking the internal portion, that is slightly worn, with part of the base preserved externally: the total height as preserved is 84 mm. Even among the extensive collection of upper premolars and molars from Olduvai Gorge there is none worn so slightly and with the base there: the crown height of the Shungura Member G upper molar would have been very close to or at 90 mm in the unworn state. The plication is very complex: 3-7-4-1, the anteroposterior diameter 25 mm at the top and 23 mm at 2 cm from the crown base.

The same complex plication is exhibited in a complete M^1 or M^2 dext., L. 675-3, worn to 6.5 cm of height, 26.5 mm anteroposteriorly at the top and 23 mm at 2 cm from the base, at which level it measures 23.5 mm transversely. The protocone is 9.5 by 4 mm in occlusal diameters, the pli caballin single.

L. 630-6, Shungura Member G, P^2 dext. worn to 4.5 cm, damaged fore and aft, pli numbers 3-4-3-1, single pli caballin, protocone 7 by 4 mm, transverse crown diameter 21 mm.

L. 613-32, Shungura Member G, posterior portion of P^2 sin., protocone 11 mm.

L. 626-36, Shungura Member G, P^3 or P^4 dext., worn height 7.5 cm, pli counts 2-5-2-2, single pli caballin, protocone 11.5 by 3.5 mm.

F. 513-12, Shungura Member G, P^3 or P^4 dext. incomplete at base but almost 7 cm high as preserved, pli counts not clear, protocone 12 by 3 mm, anteroposterior crown diameters diminishing from 25 to 21 mm downward, as in the foregoing specimen.

L. 7-155B and L. 44-16 are from the same Member and serial position, right and left, respectively, worn to 3.5 to 4 cm; state of preservation not so good.

M^{1-2} include, beside L. 627-89 and L. 675-3 already mentioned, the following from Shungura Member G: M^{1-2} dext.: (1) L. 627-212; (2) L. 740-24; (3) F. 267-5; M^{1-2} sin.: (4) L. 616-62; (5) L. 80-77; (6) L. 48-24. These teeth are incomplete in various ways. The least worn (1) and (4) are 7.5 cm high, the protocones up to 10 mm long anteroposteriorly, the anteroposterior crown diameters 20.5 to 23 mm.

Of the last upper molar there are from Shungura Member G: M^3 dext.: (1) L. 534-4; (2) 663-3; (3) L. 627-204; M^3 sin.: (4) L. 627-205; (5) L. 622-22; (6) L. 74-22. The best preserved specimen (1), 70 mm high, increases to 25.5 mm anteroposteriorly basally; the crown diameters of (3) and (5), the only ones that can be measured, are 22-24 mm anteroposteriorly and 18-19 mm transversely at 2 cm from the base.

Remaining incomplete upper molars from Shungura Member G are L. 597-16, L. 25-140, L. 163-3, F. 513-32, and F. 513-33, the last with a crown height of 7.5 cm.

L. 616-63, Shungura Member G, is an M_1 or M_2 sin. (pl. 17 figs. 2,5) that is only very slightly worn. Its crown height is 80 mm, and the anteroposterior diameter, 29 mm apically, is 24 mm at 2 cm from the base, giving a height/lenght index of 335. The ectostylid in this specimen is 75 mm high. These figures compare very well with those of the least worn Olduvai M_1 or M_2, OLD/57, SHK II, no. 1300, which is 78 mm high, 24 mm anteroposteriorly at 2 cm from the base, giving a height/length index of 325; its ectostylid is at least 70 mm high.

The lower premolars from Shungura Member G comprise one P_3 or P_4 dext., L. 627-214, which has lost most of the ectostylid and the hypoconid, 73 mm high as preserved: the others are worn more. The specimens are:

P_{3-4} dext.: (1) L. 627-214; (2) L. 627-203; (3) L. 7-230; P_{3-4} sin.: (4) L. 842-1; (5) L. 74-11; (6) L. 628-191. The ectostylid varies from 7.5 to 9.5 mm anteroposteriorly at base, and remains wide for the greater part of its height: in specimen (4) it rapidly tapers to a point over less than 8 mm of height (the base is not preserved in this specimen). The protostylid is a very distinct, be it narrow, pillar stopping a few mm short of the crown edge; the ptychostylid is always clear occlusally (none of the specimens is worn down to more than 5 cm). The crown diameters, at 2 cm from the crown base, are 24-27 mm anteroposteriorly, and 15-16.5 mm transversely.

Of the M_1 and M_2, one specimen (L. 24-9) is 78 mm high as preserved, with an ectostylid at least 70 mm high and 6 mm in diameter all over. The angularity of the "tie" loops is very marked. In another M_{1-2}, which is from the right side (pl. 15 fig. 2), L. 626-29, the ectostylid is joined to the hypoconid. The crown height as worn is 3.5 cm. On the anterior side of the ectostylid there are two enamel spurs neither of which of course is the ptychostylid. I have not seen anything like this exuberant growth in the external groove of a *Hipparion* lower molar before. The two M_{1-2} are 23-24 mm anteroposteriorly, and 13-14 mm transversely, within the range of the Olduvai series.

Of the last lower molar, there are two specimens from Shungura Member G, viz., M_3 dext., L. 597-17B, incomplete anteriorly, with a narrow ectostylid diminishing in anteroposterior diameter from 5 to 3.5 mm over 3 cm of height, and an M_3 sin., L. 477-6, 70 mm high as worn, with an ectostylid at least 55 mm high but mostly obscured by cement. This M_3 measures 25 by 11 mm at 2 cm from the base.

There remain several worn and broken fragments of lower molars in the Shungura Member G collection as follows: L. 479-8, L. 504-11, L. 613-33, and L. 626-124.

The postcranial remains from Shungura Member G include two indubitable *Hipparion* distal ends of third metatarsals, L. 48-7 and L. 596-22. The distal articular width is 38-39 mm, and the anteroposterior diameter of the crest 33-35 mm, as in specimens from Olduvai Gorge (table 15). There is further the distal portion of a radius sin. with the shaft of the ulna (a not fully reliable distinction from *Equus*), L. 16-57, a calcaneum dext. (F. 513-39), and a portion of a lateral metapodial (F. 513-38), which will be dealt with at a later date. There are entire metapodials attributable to *Equus,* which makes its first appearance in the Shungura Formation at Member G, but these as well as the *Equus* teeth will be reserved for a subsequent paper.

SHUNGURA MEMBER H

From Shungura Member H, including Member I, probable age 1.83 to 1.7 million years, there is one indubitable *Hipparion* lower molar fragment, F. 510-47, with an ectostylid 5 by 2.5 mm in diameters, but the fragment is only 3.5 cm high as preserved. An astragalus sin., P. 955-1, from Shungura Member H5, has a distal articular width of 45 mm and a medial height of 53 mm, close to the smaller *Hipparion* astragali from Lothagam (Hooijer & Maglio, 1974: 27).

SHUNGURA MEMBER J

This Member (age probably between 1.7 and 1.5 million years) yielded one *Hipparion* molar, F. 12-9, an M^1 or M^2 dext., worn down to 5.5 cm, pli numbers 3-7-4-1, single pli caballin, protocone 8.5 by 3.5 mm, crown diameters 21 by 23 mm.

SHUNGURA MEMBER K

From this Member, age probably from 1.5 to 1.3 million years, there come a number of *Hipparion* molar teeth some of which display a marked hypsodonty. They bear the numbers F. 203-2-10, 13, 14 and 59. Two uppers, F. 203-6 and 8, have the closed base between the fosettes and are slightly worn: the crown height as preserved is 89 mm, and the (isolated) protocone is at least 80 mm high and 10 mm anteroposteriorly with a very blunt tip. Two lowers, F. 203-2 and 3, likewise slightly worn, have a crown height of at least 83 mm, the ectostylid forming a pillar 75 mm high and uniformly 7 mm anteroposteriorly, reducing to 5 mm at its worn apex. There are further a central fragment of an upper molar with a very complex pattern, F. 406-9, and a lower molar portion with a trace of the ectostylid basally, F. 407-1.

SHUNGURA MEMBER L

From Shungura Member L. 2, age probably less than 1.3 million years, there is one *Hipparion* tooth, P. 997-19, M^1 or M^2 sin., incomplete on all sides except anteriorly, with a worn height of 5 cm and an extremely complex plication pattern (5-8-5-2), a long, single pli caballin, and a protocone at least 10 mm anteroposteriorly (the internal portion is missing).

ADDENDUM

Two slightly worn upper molars of *Hipparion steytleri* from the Grey Breccia of the Makapansgat Limeworks Site in the Transvaal have been examined by me in the Bernard Price Institute for Palaeontological Research, University of the Witwaters-

rand, Johannesburg, through the courtesy of Dr. A. R. I. Cruickshank and Mrs. J. M. Maguire. M 2475 is an M^{1-2} dext. somewhat damaged occlusally; the full height as preserved is 83 mm. The crown diameters at 2 cm from the base are 25 mm antero-posteriorly, and 23 mm transversely. The protocone is 9.5 by 4 mm in diameters at 2 cm from the occlusal surface, and 10.5 by 6 mm at about one cm from the base; it is completely isolated. An M^{1-2} sin., M 2476, is incomplete at the base, and its height from the closed bases of the fossettes is, again, 83 mm. At the swollen apical portion of the crown the diameters are 30 by 24 mm, and at 2 cm from base the diameters are 25 by 24.5 mm. The protocone is 10 by 4 mm occlusally. These Makapansgat molars are as hypsodont as their homologues in *Hipparion ethiopicum* from Shungura Members G L. 627-89) and K (F. 293-6 and 8) dealt with above. There are no permanent lower cheek teeth of *Hipparion steytleri* available from Makapansgat although milk molars, both uppers and lowers, abound in the collection, as is a feature of the representation of the larger mammals at Makapansgat.

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EXPLANATION OF THE PLATES

Plate 1

Hipparion primigenium (Von Meyer), P_2 — M_1 dext. and P_3 — P_4 sin. in situ, Ngorora Formation, KNM-BN 1117, crown views, × 1.4.

Plate 2

Hipparion primigenium (Von Meyer). Fig. 1, M^3 sin. in maxillary fragment, Aterir Beds, KNM-AT 152, crown view, × 1.4. Figs. 2-3, I^2 and I^3 dext. and I^3 sin., associated, in premaxillary fragments, Aterir Beds, KNM-AT 153 and 154, crown views, × 0.9. Fig. 4, P^2 — M^1 dext., associated, Aterir Beds, KNM-AT 150, crown views, × 0.9. Fig. 5, I^2 and I^3 sin. and C sup. sin. in situ, Ngorora Formation, KNM-BN 1154, crown views, × 0.9.

Plate 3

Figs. 1, 2 and 5-6, *Hipparion primigenium* (Von Meyer), Ngorora Formation; fig. 1, P^3 or P^4 dext., KNM-BN 1119, crown view, × 1.5; fig. 2, right lower cheek tooth showing small ectostylid, KNM-BN 1283, external view, × 1.4; figs. 5-6, proximal phalanx of third digit, KNM-BN 1202; fig. 5, dorsal view; fig. 6, volar view, × 1.1.

Fig. 4, *Hipparion primigenium* (Von Meyer), M^1 dext., Chemeron Formation, KNM-BC 367 (1), crown view, × 1.4.

Figs. 3, 7 and 8, *Hipparion* spec.; fig. 3, P^3 or P^4 dext., Usno Formation, W. 296, crown view, × 1.3; fig. 7, M^1 or M^2 dext., Shungura Formation Member B11, L. 1-42e, crown view, × 1.6; fig. 8, I_1 dext., Shungura Formation Member D, L. 36-14, lingual view, × 1.1.

Plate 4

Figs. 1-2, *Hipparion primigenium* (Von Meyer), Chemeron Formation; fig. 1, M_1 or M_2 dext., KNM-BC 367 (4), crown view, × 2.0; fig. 2, M_1 or M_2 sin., KNM-BC 367 (5), crown view, × 2.0.

Figs. 3-6, *Hipparion turkanense* Hooijer & Maglio; fig. 3, P_2 sin., Mursi Formation, YS. 7-3, crown view, × 2.1; fig. 4, P_3 or P_4 dext., Mpesida Beds, KNM-KP 079, crown view, × 1.9; fig. 5, P_3 or P_4 dext., Lukeino Formation, KNM-KY 79, crown view, × 2.1; fig. 6, M_1 or M_2 dext., Lukeino Formation, KNM-KY 80, crown view, × 2.1.

Plate 5

Figs. 1-2, *Hipparion* spec.; fig. 1, M^1 or M^2 dext., Usno Formation, W. 629, crown view, × 2.0; fig. 2, external half of M^1 or M^2 sin., Shungura Formation Member B, L. 2-2c, crown view, × 1.5.

Figs. 3-5, *Hipparion?* aff. *sitifense* Pomel; fig. 3, M^1 — M^3 sin., associated, Chemeron Formation, KNM-BC 450-452, crowns views, × 1.0; figs. 4-5, P_4 — M_2 dext., associated, Chemeron Formation, basal portion, KNM-BC 1157; fig. 4, crown views; fig. 5, external views, × 1.1.

Fig. 6, *Hipparion primigenium* (Von Meyer), M_1 or M_2 dext., Chemeron Formation, KNM-BC 367 (4), external view, × 1.4.

Fig. 7, *Hipparion turkanense* Hooijer & Maglio, P_2 sin., Mursi Formation, YS. 7-3, external view, × 1.2.

Plate 6

Figs. 1 and 5, *Hipparion primigenium* (Von Meyer); fig. 1, P^2 sin., Kanapoi, KNM-KP 43, crown view, × 1.3; fig. 5, M^2 sin., Chemeron Formation, KNM-BC 367 (2), crown view, × 1.5.

Figs. 2-4, *Hipparion* spec.; fig. 2, P^2 dext., Usno Formation, W. 552, crown view, × 1.2; fig. 3, M^1 or M^2 sin., Shungura Formation Member B, L. 2-21a, crown view, × 1.6; fig. 4, DM^4 dext., Shungura Formation Member B, L. 2-150, crown view, × 1.4.

Fig. 6, *Hipparion?* aff. *sitifense* Pomel, M^1 or M^2 dext., Lukeino Formation, KNM-LU 189, crown view, × 2.0.

Plate 7

Hipparion cf. *ethiopicum* (Joleaud), skull, Olduvai Gorge, 1963, BK II pit 6, nos. 2845-2846; fig. 1, left lateral view; fig. 2, right lateral view, × 0.2.

Plate 8

Hipparion cf. *ethiopicum* (Joleaud), skull, Olduvai Gorge, 1963, BK II pit 6, nos. 2845-2846; fig. 1, ventral view; fig. 2, dorsal view × 0.2.

Plate 9

Hipparion cf. *ethiopicum* (Joleaud), Olduvai Gorge, 1963; fig. 1, upper cheek teeth of skull, BK II, no. 283, Channel Sand, crown views, × 0.7; fig. 2, upper cheek teeth of skull, BK II pit 6, no. 2846, crown views, × 0.7.

Plate 10

Hipparion cf. *ethiopicum* (Joleaud), skull, Olduvai Gorge, 1963, BK II no. 283, Channel Sand; fig. 1, right lateral view; fig. 2, dorsal view; fig. 3, left lateral view, × 0.3.

Plate 11

Hipparion cf. *ethiopicum* (Joleaud), upper incisors, Olduvai Gorge, BK II; fig. 1, OLD/55, no. 264, occlusal view, × 0.9; fig. 2, OLD/63, no. 2845, occlusal view, × 1.0.

Plate 12

Hipparion cf. *ethiopicum* (Joleaud), lower incisors, Olduvai Gorge, BK II; figs. 1-2, OLD/55, no. 293; fig. 1, occlusal view, × 0.5; fig. 2, ventral view, × 0.6; fig. 3, OLD/52, no. 067/5344, occlusal view, × 0.5.

Plate 13

Hipparion cf. *ethiopicum* (Joleaud); fig. 1, set of lower incisors, OLD/59, from left to right: I_2 sin., no. 461; I_1 sin., no. 466; I_1 dext., no. 462; I_2 dext., no. 465, all of one individual, HWK II, upper views, × 1.2; fig. 2, I^1 and I^2 dext. of the same individual, Shungura Formation Member F, L. 253-2C and 2B, lower views, × 1.1; fig. 3, I^1 and I^2 sin. of the same individual, OLD/52, BK II, nos. 50 and 52, lower views, × 1.2.

Plate 14

Fig. 1, *Hipparion* spec., left mandibular ramus with P_2 — M_3, Shungura Formation Member B11, L. 1-40, crown view, × 1.0.

Fig. 2, *Hipparion* cf. *ethiopicum* (Joleaud), left mandibular ramus with P_2 — M_3, OLD/52, BK II, no. 301, crown view, × 0.9.

Plate 15

Figs. 1-2, *Hipparion ethiopicum* (Joleaud); fig. 1, P_4 and M_1 dext. of the same individual, Shungura Formation Member F, L. 398-11 and 12, crown views, × 1.6; fig. 2, M_1 or M_2 dext., Shungura Formation Member G, L. 626-29, crown view, × 1.7.

Figs. 3 and 7, *Hipparion* spec., P_2 dext., Shungura Formation Member B11, L. 1-42c; fig. 3, crown view, × 1.6; fig. 7, external view, × 1.7.

Fig. 4, *Hipparion primigenium* (Von Meyer), left lower DM, Chemeron Formation, KNM-BC 368, crown view, × 1.8.

Figs. 5-6, *Hipparion* cf. *ethiopicum* (Joleaud); fig. 5, DM_2 — DM_4 sin., OLD/63, BK II, no. 3367, crown views, × 0.9; fig. 6, I_1 dext. et sin., OLD/57, SHK II, nos. 749 and 454, external views, × 0.8.

Plate 16

Hipparion cf. *ethiopicum* (Joleaud); fig. 1, DI_2 sin., OLD/?, BK II, 4/LS, no. 2774, crown view, × 2.2; fig. 2, P_2 dext., OLD/59, LGK II, no. 391, crown view, × 1.7; figs. 3 and 7, P_3 or P_4 sin., OLD/63, BK II, no. 3363; fig. 3, crown view, × 1.5; fig. 7, external view, × 1.0; fig. 4, M_3 dext., OLD/59, LGK II, no. 395, external view, × 1.0; fig. 5, P_3 or P_4 dext., OLD/55, BK II, no. 285, internal view, × 1.2; fig. 6, M_1 or M_2 dext., OLD/57, SHK II, no. 1300, internal view, × 1.0.

Plate 17

Figs. 1, 4 and 6, *Hipparion* cf. *ethiopicum* (Joleaud); figs. 1 and 4, M_1 or M_2 dext., OLD/57, SHK II, no. 1300; fig. 1, crown view, × 1.5; fig. 4, external view, × 1.0; fig. 6, P_3 or P_4 dext., OLD/55, BK II, no. 285, external view, × 1.2.

Figs. 2 and 5, *Hipparion ethiopicum* (Joleaud), M_1 or M_2 sin., Shungura Formation Member G, L. 616-63; fig. 2, crown view, × 1.7; fig. 5, external view, × 1.0.

Figs. 3 and 7, *Hipparion* spec., P_3 or P_4 sin., Usno Formation, HCFN. 460; fig. 3, crown view, × 1.3; fig. 7, external view, × 1.3.

Plate 18

Figs. 1-2, *Hipparion* cf. *ethiopicum* (Joleaud); fig. 1, metacarpal III sin. with part of metacarpal II attached to it, OLD/60, FLK N1, II/1-2-3, no. 933, medial view, × 0.7; fig. 2, metacarpal III dext. with parts of metacarpals II and IV attached to it, OLD/61, FLK N1, Tr. III, no. 7693, posterior view, × 0.7.

Fig. 3, *Hipparion* cf. *sitifense* Pomel, metacarpal III dext. with proximal and distal portions of metacarpal II attached to it, Lothagam, KNM-LT 139, medial view, × 0.7.

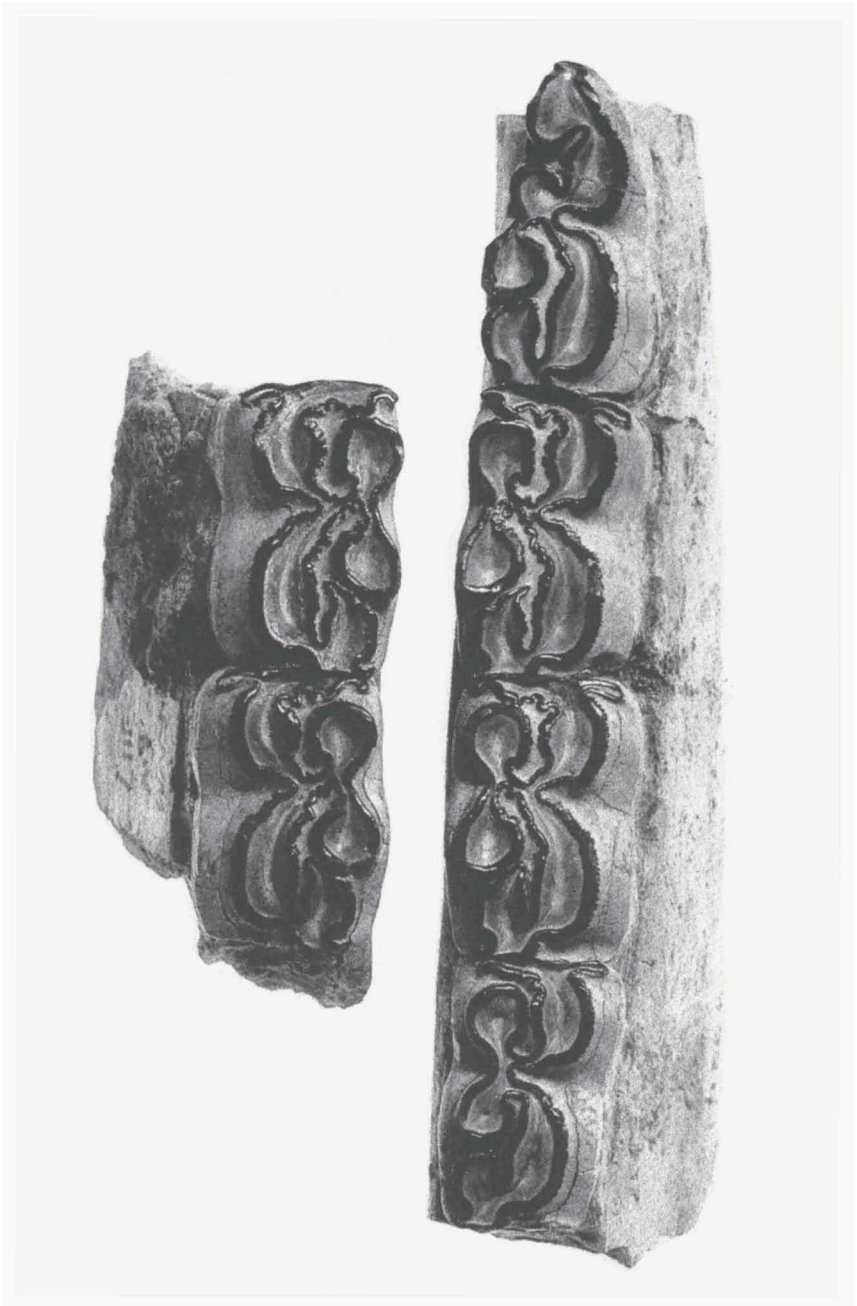
Plate 19

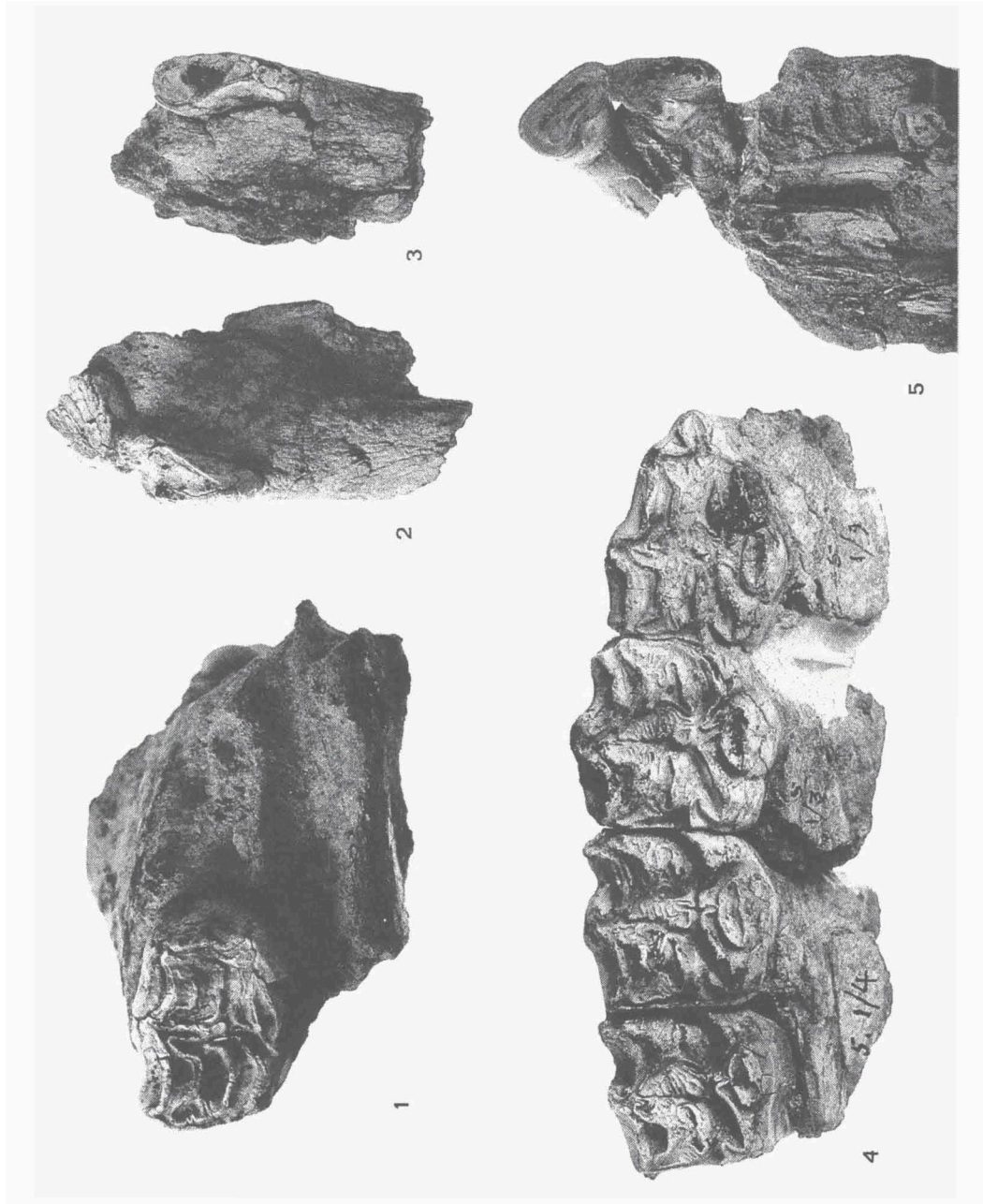
Fig. 1, *Hipparion* cf. *ethiopicum* (Joleaud), distal end of lateral metapodial, OLD/62, JK 2, TTK, lateral view, × 0.9.

Figs. 2, 6, and 7, *Hipparion*? aff. *sitifense* Pomel; fig. 2 distal end of lateral metapodial, Lukeino Formation, KNM-LU 051, lateral view, × 0.9; fig. 6, distal portion of metacarpal III, Lukeino Formation, KNM-LU 187, posterior view, × 0.6; fig. 7, distal portion of metatarsal III, Shungura Formation Member F, L. 65-30, posterior view, × 0.7.

Figs. 3-4, *Hipparion steytleri* Van Hoepen, casts of distal ends of lateral metapodials, Makapansgat; fig. 3, MLD 20, lateral view, × 0.9; fig. 4, MLD 36, lateral view, × 0.9.

Fig. 5. *Hipparion* cf. *sitifense* Pomel, distal portion of metacarpal IV dext., Lothagam, KNM-LT 139, lateral view, × 0.9.

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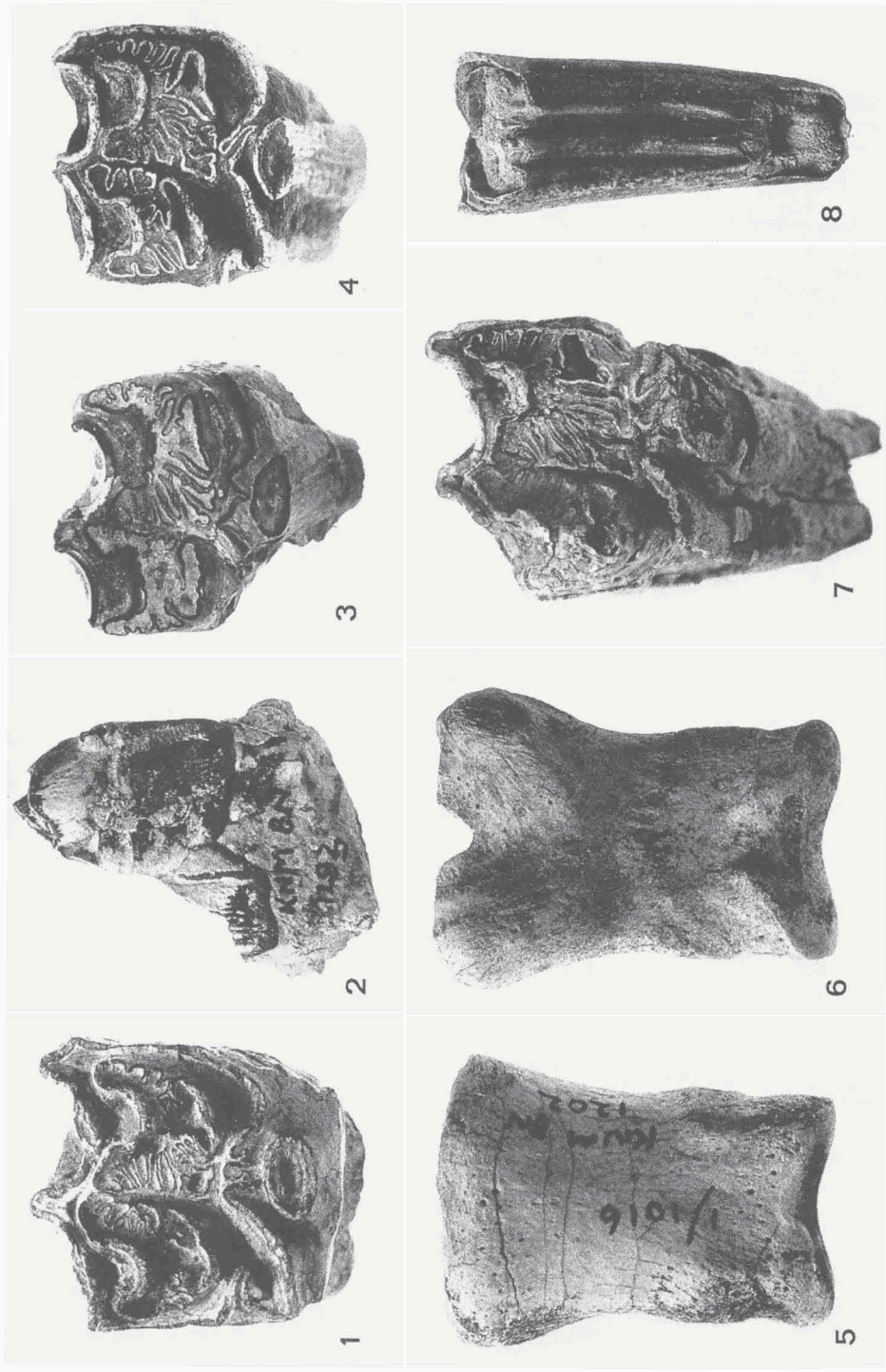
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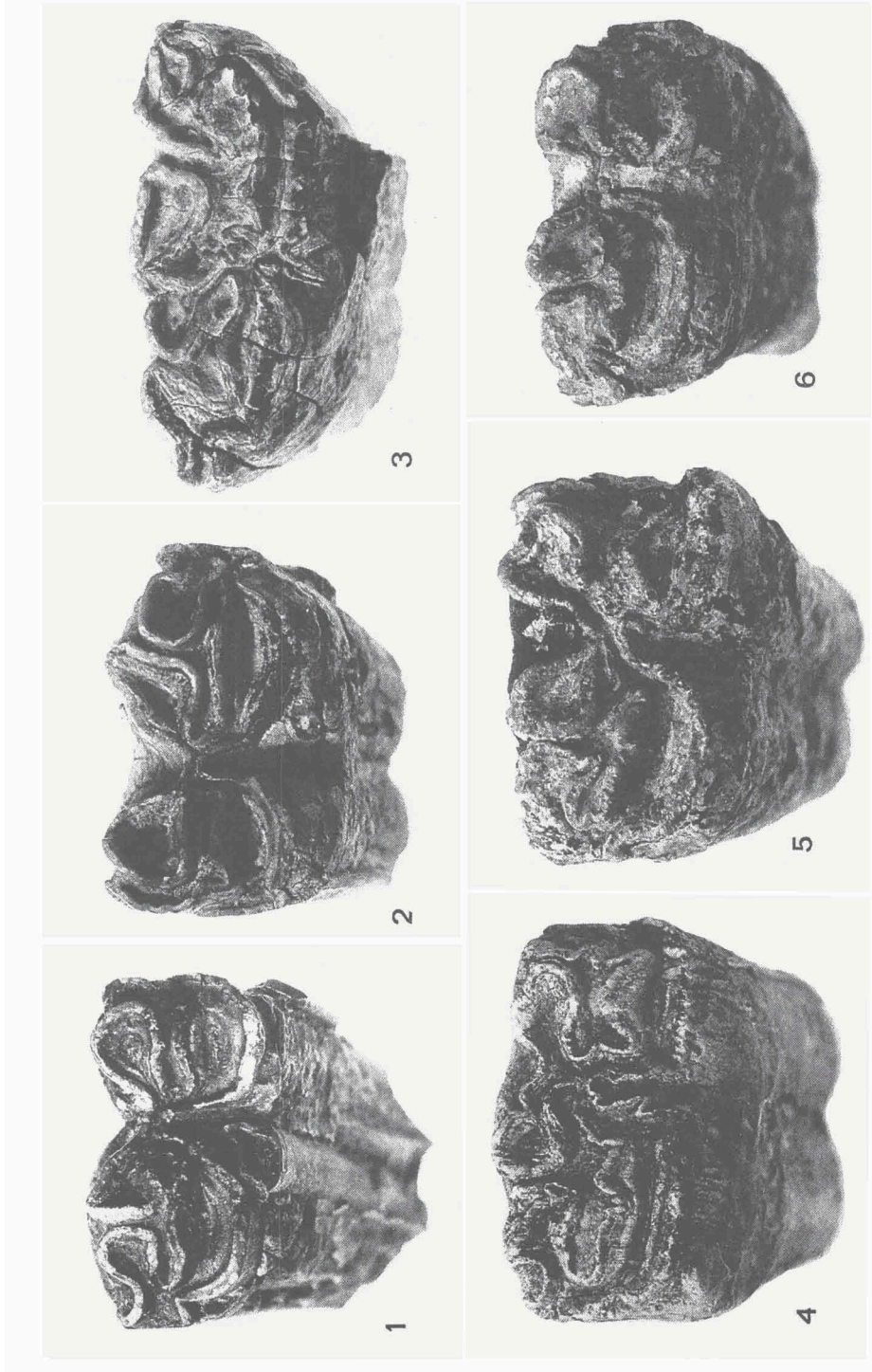
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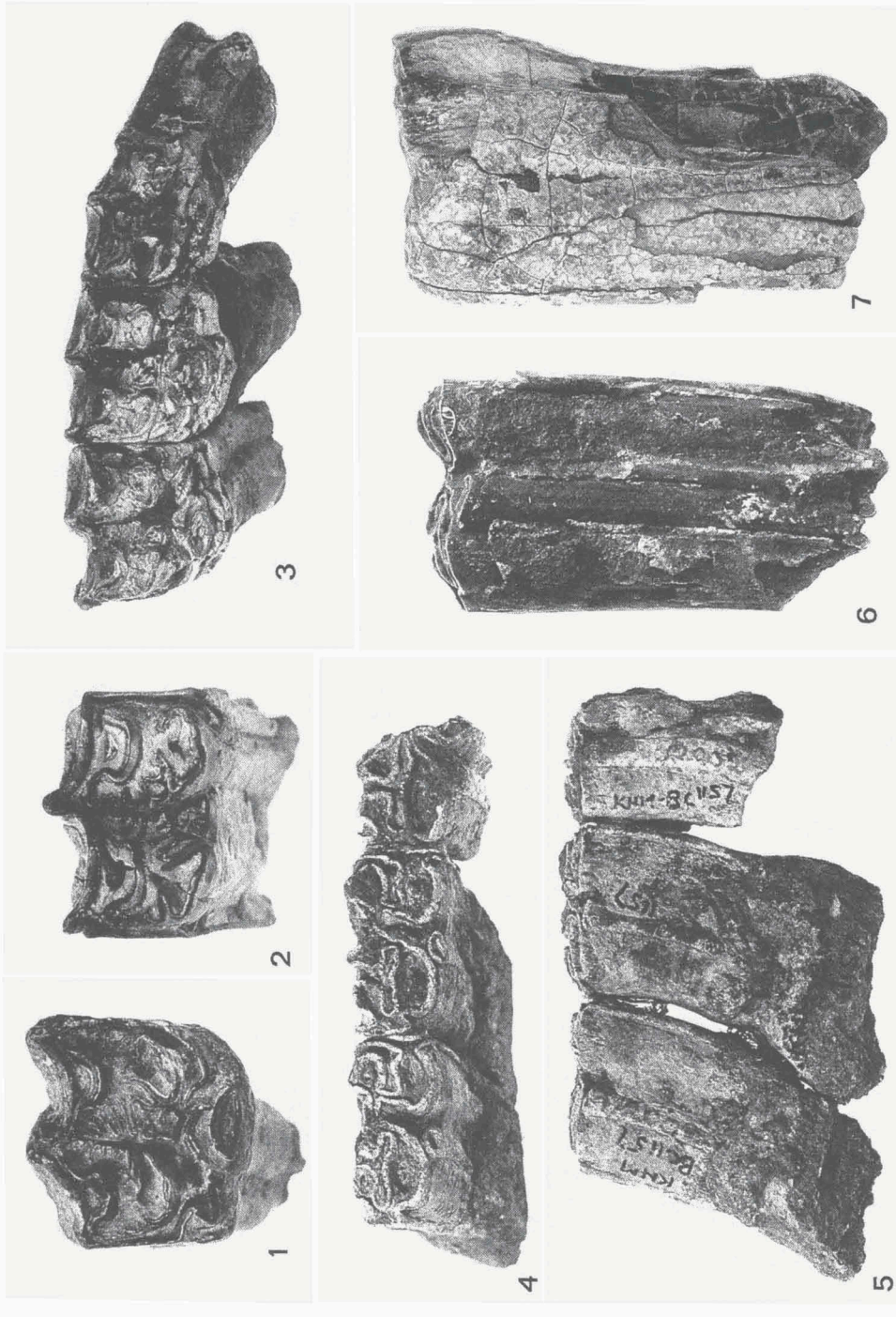
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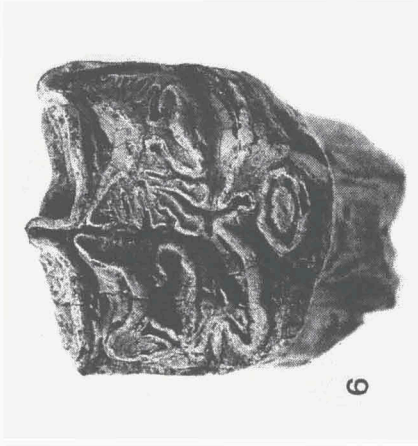
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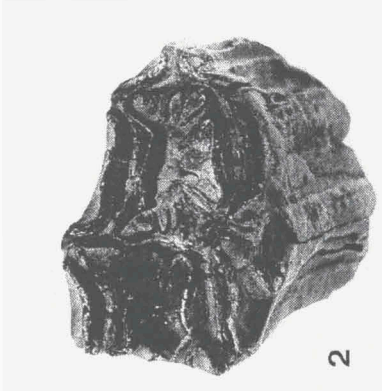
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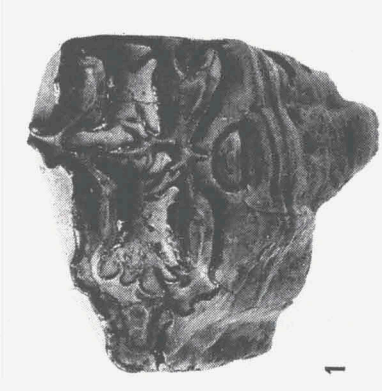
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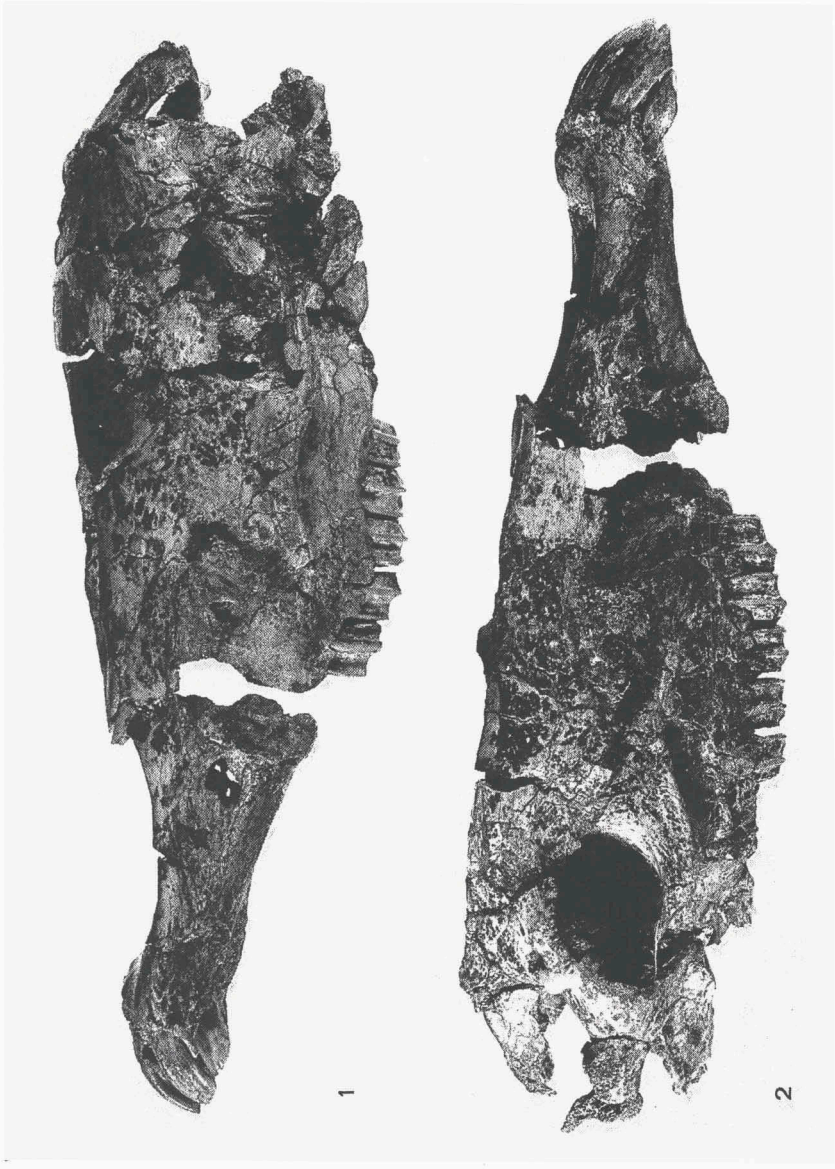
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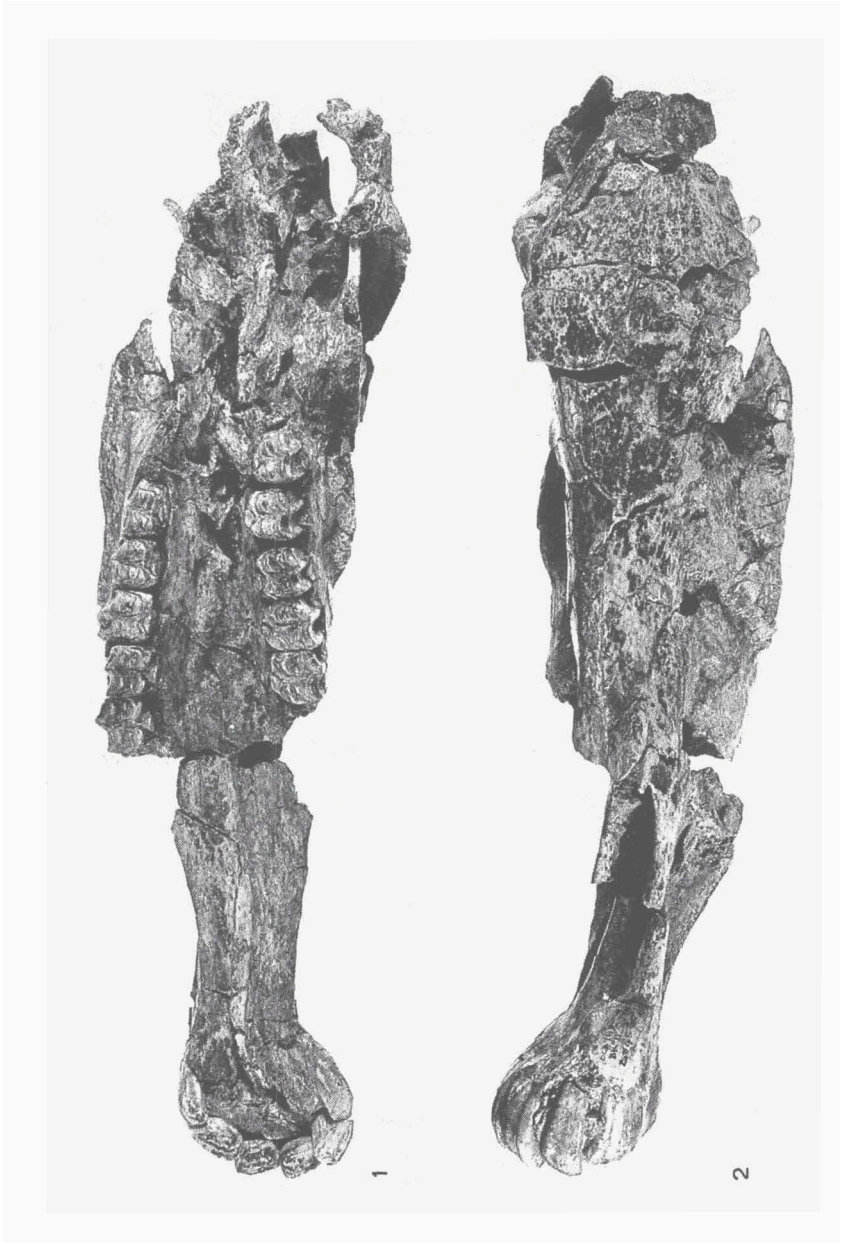
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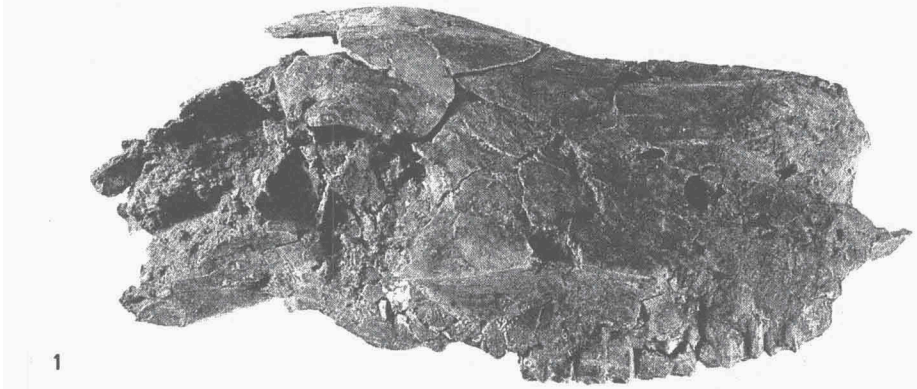

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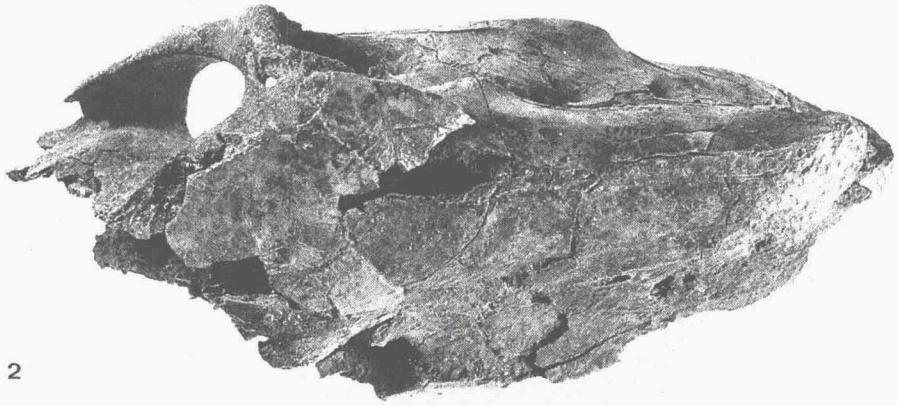

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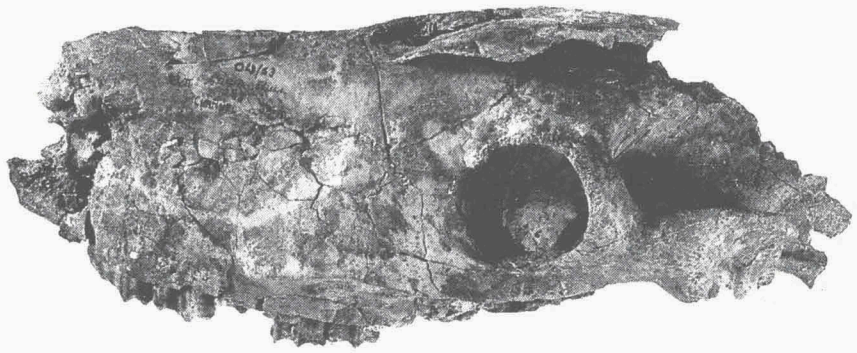

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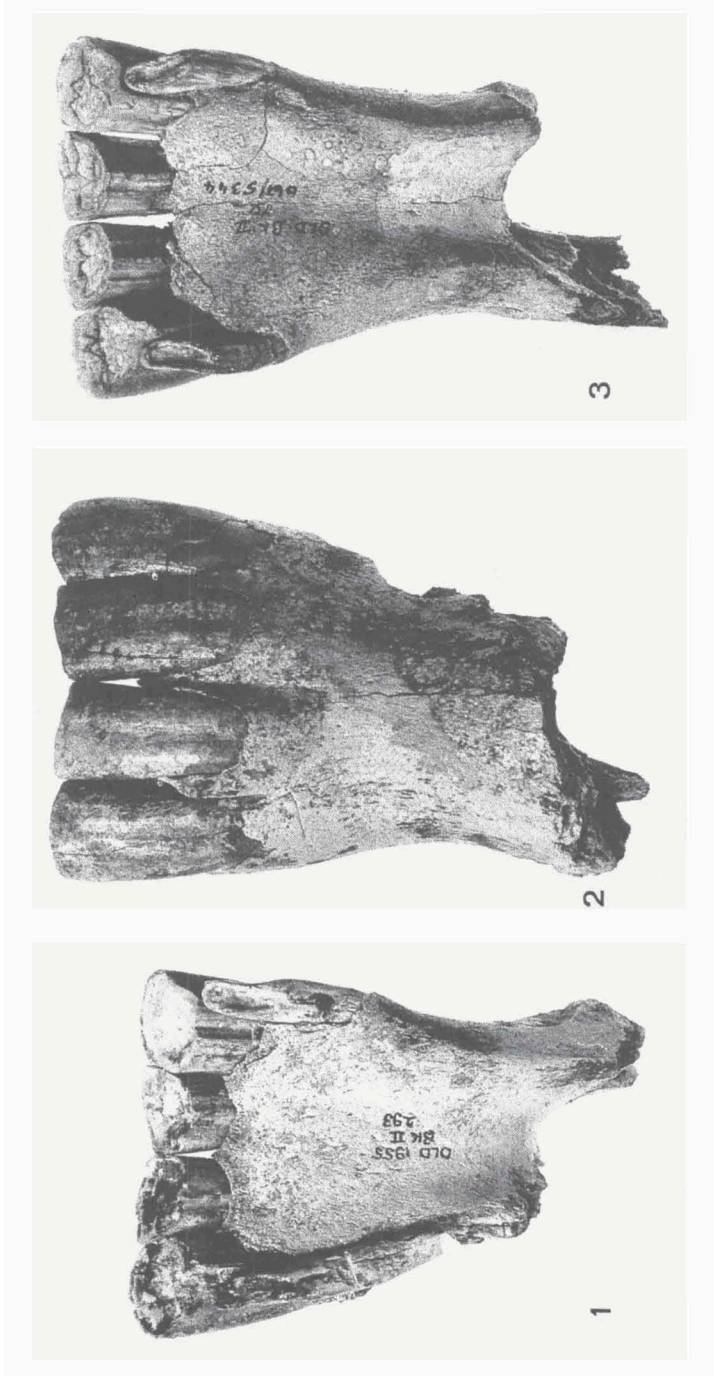
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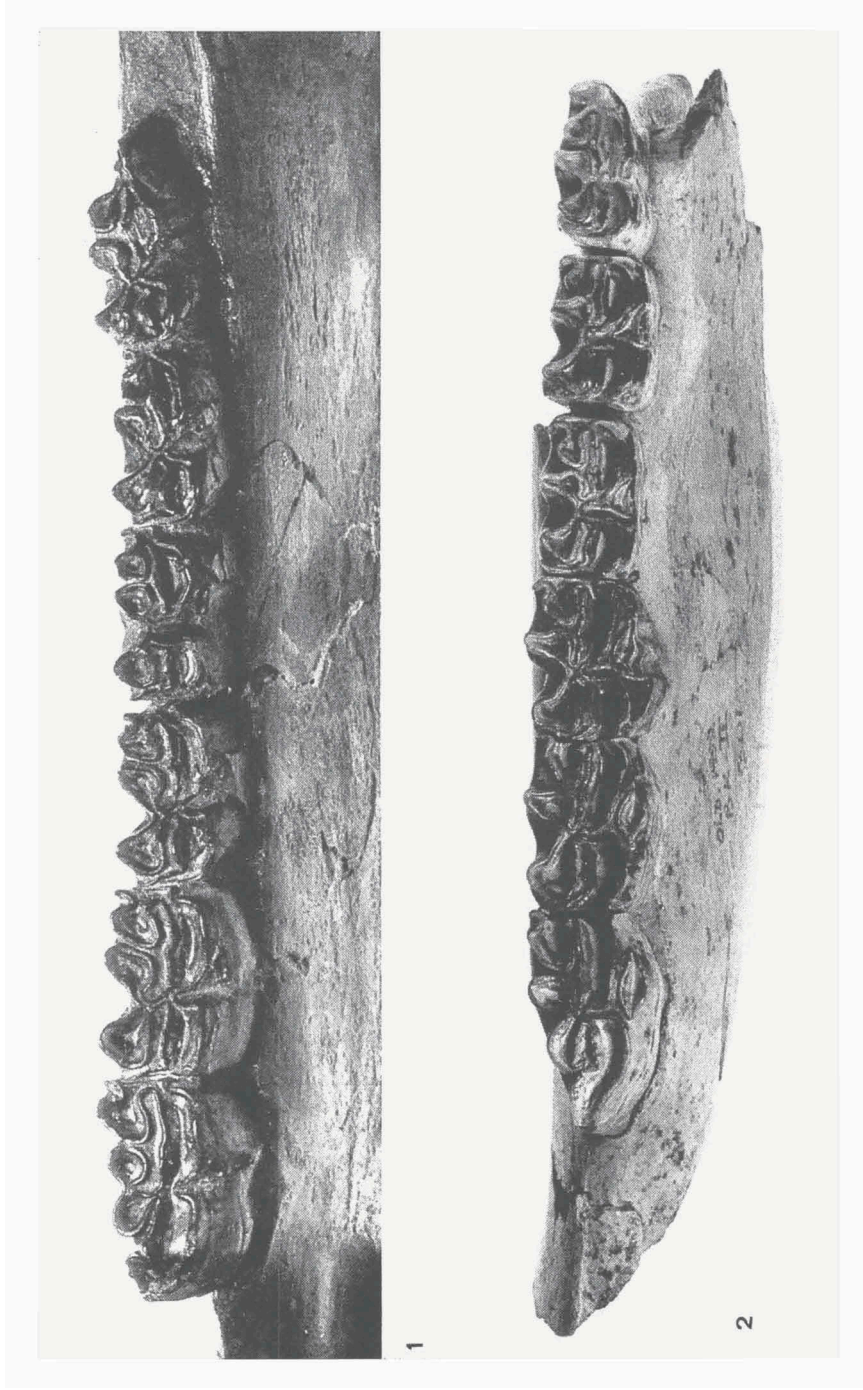
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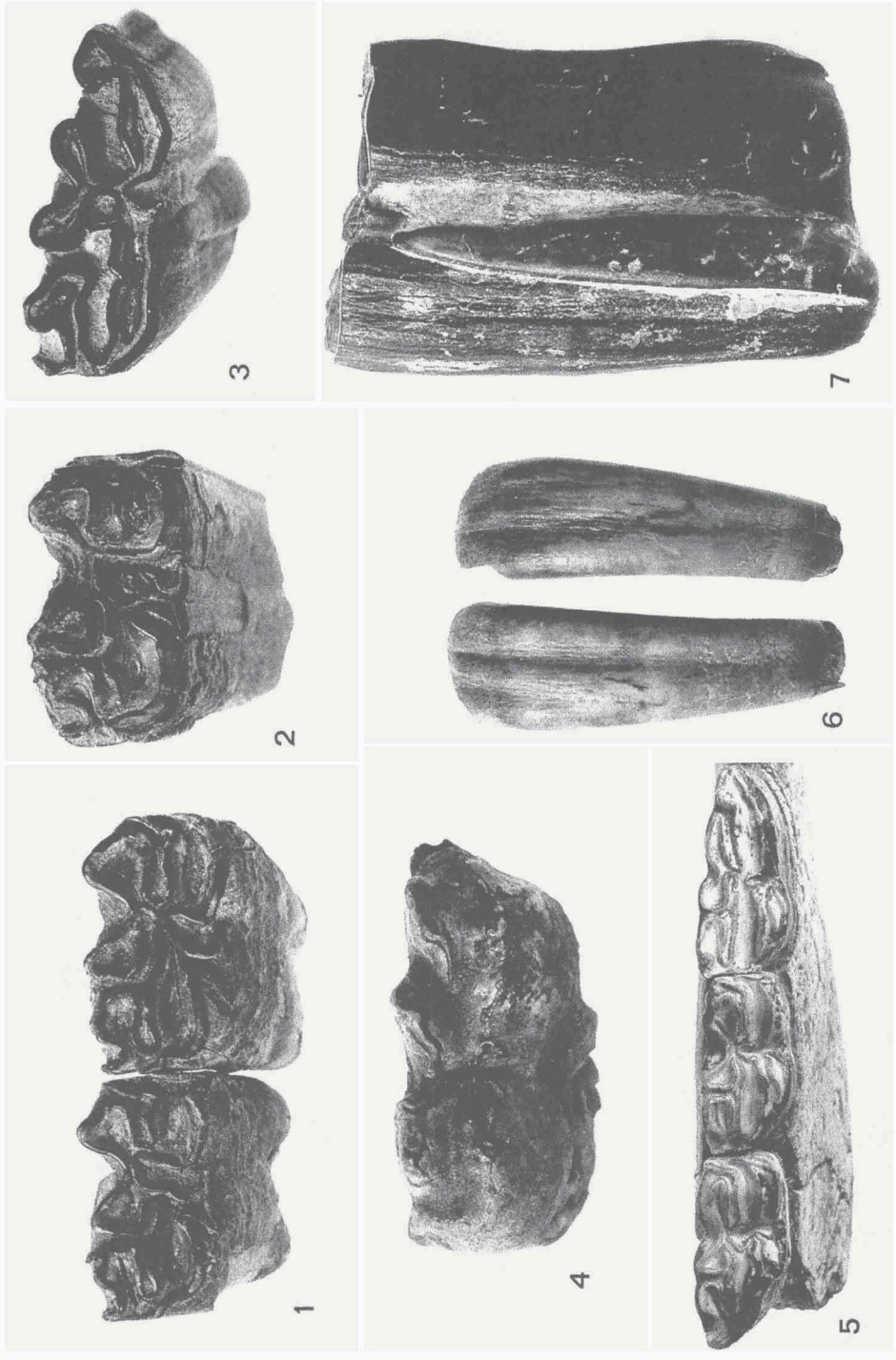
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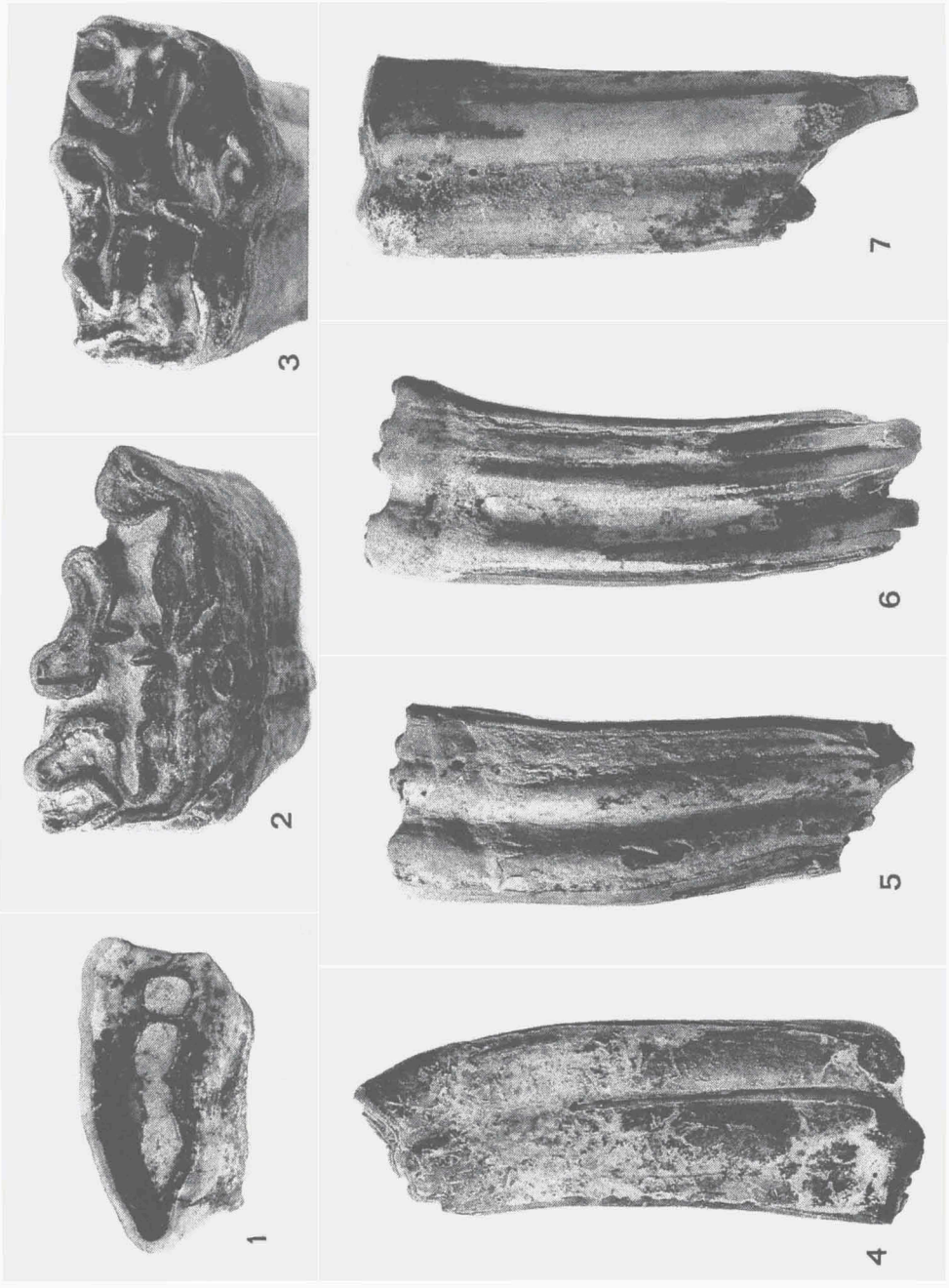
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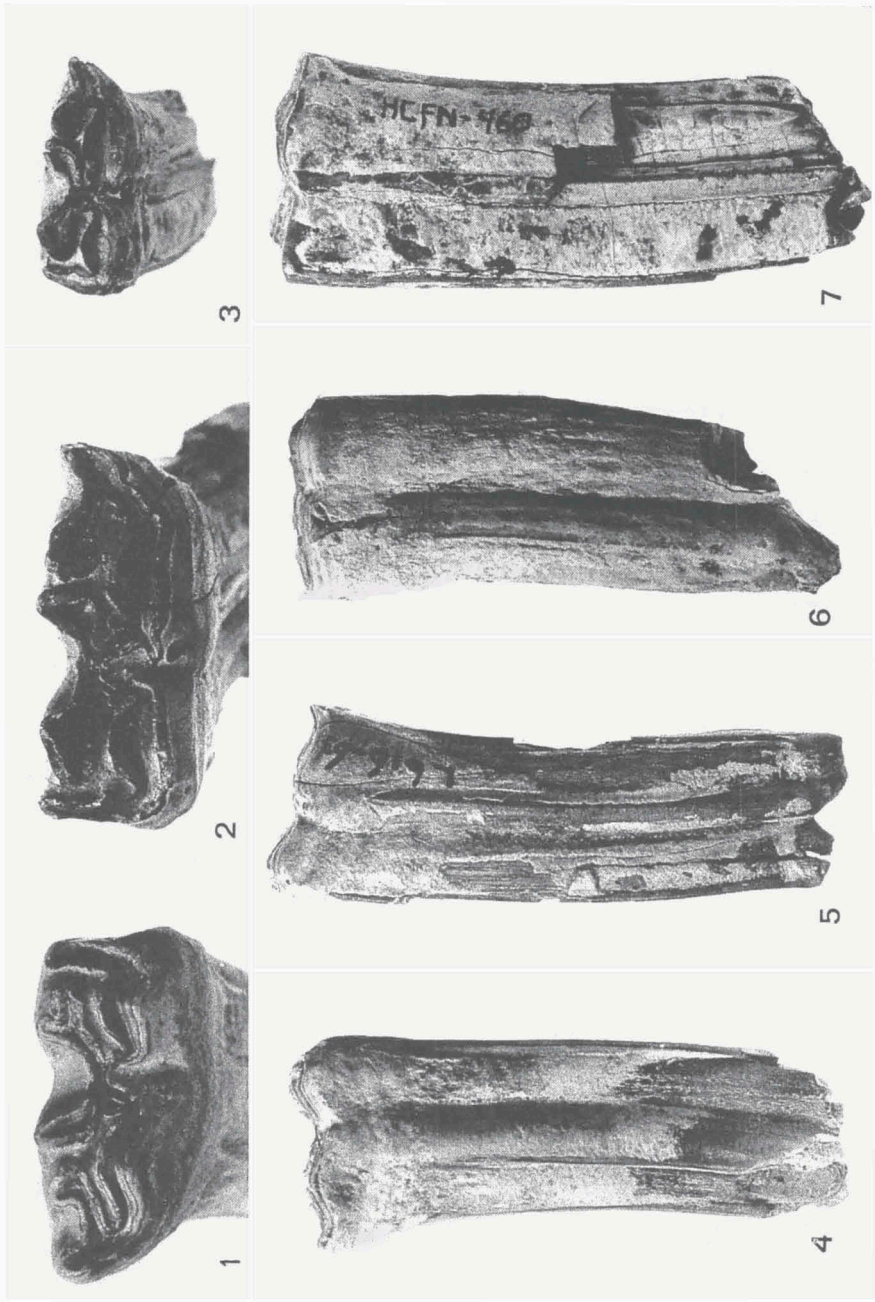
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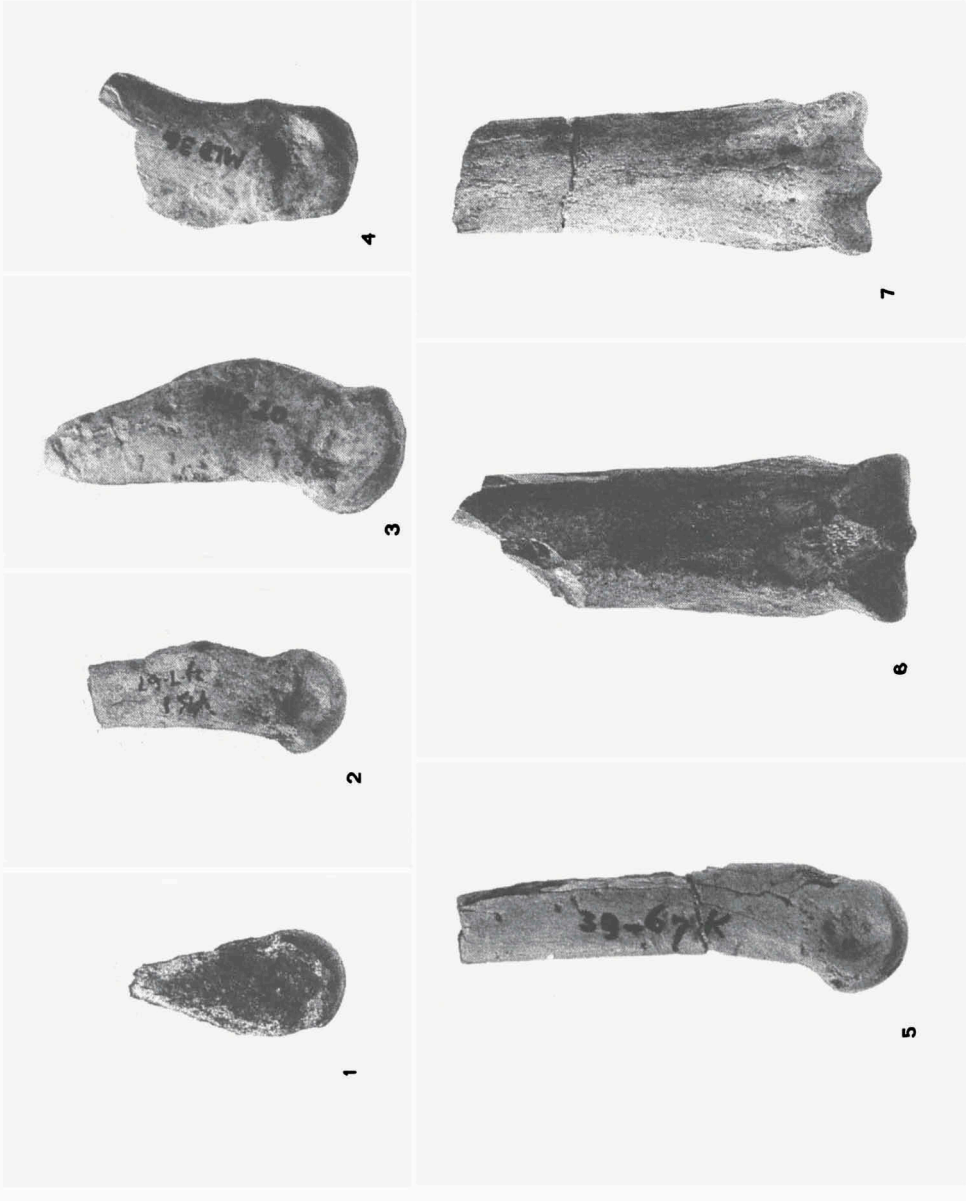
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