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HIPPARIONS OF THE LAETOLIL BEDS, TANZANIA

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With 3 plates

The Laetolil Beds in Tanzania, 20-30 miles south of Olduvai Gorge, have been extensively sampled by parties under the leadership of Mrs. Dr. Mary D. Leakey, who very kindly sent me *Hipparion* material collected in 1974, 1975, and 1976. In a restudy of proboscidean material from these beds described by Dietrich (1942), Maglio (1969) arrived at the conclusion that the Laetolil fauna represents two distinct horizons, one seemingly correlating best with Kanapoi, Yellow Sands (= Mursi Formation), Chemeron, and Kanam, and younger deposits correlating best with the later Omo Beds, possibly antedating Olduvai Bed I but only by a short time interval. This has been confirmed by radiometric dating: the Laetolil Beds with the older fauna are bracketed in time between 3.8 and 3.6 million years whereas the lava flows unconformably overlying them are dated at 2.4 million years. The younger deposits which are to be named Ndolanya Beds, therefore, have an age older than 2.4 million years, and have also produced fossils (Leakey et alii, 1976). The fossiliferous deposits in the Laetolil area have been subdivided into 26 localities from most of which I received *Hipparion* material, all collected in situ. Two localities, 7 East and 18, are in the Ndolanya Beds, while the others are in the Laetolil Beds (Mary Leakey, personal communication). The fossils found in situ are cream coloured or white, sometimes chalky in texture. Surface material also including brown, grey or black specimens, often rolled, has been excluded. It is among the surface material that *Equus* is represented. However, there is no evidence that the equid material from the Laetolil Beds proper includes any genus but *Hipparion*.

I am most grateful to Mrs. Mary Leakey for entrusting this material to me; it comes from a critical time phase in the evolution of African hipparions as will appear from what follows.

Hipparions older than the time interval of the Laetolil Beds have been described from Lothagam-Kanapoi-Ekora, Mpesida, Lukeino, Chemeron, and the Aterir Beds in the Baringo Basin of Kenya, and Mursi at the base of the Omo Group deposits in Ethiopia (Hooijer & Maglio, 1974; Hooijer, 1975: 16-22), ranging from 7 to 4 million years ago. The 7-4 million year *Hipparion* group has been identified as *Hipparion turkanense* Hooijer & Maglio (1974: 8; Hooijer, 1975: 19), *Hipparion primigenium* (Von Meyer) (Hooijer & Maglio, 1974: 13; Hooijer, 1975: 12), and *Hipparion* cf. *sitifense* Pomel (Hooijer & Maglio, 1974: 20; Hooijer, 1975: 25, as ? aff. *sitifense*).

It should be stated at the outset that the range of what I call the Mpesida to Aterir type of *Hipparion* may extend upward beyond the 4 m.y. level, for the Chemeron Formation teeth of *Hipparion primigenium* (Hooijer, 1975: 17-19) are for the best part from locality J.M.493, which belongs to "basal" Chemeron, but so does locality J.M.90 (= J.M.91) the fossils from which suggest an age closer to 2 than to 4 m.y. (Cooke & Maglio, 1972: 327). The age of the Chemeron Formation is best estimated by considering the apparent ages of the bracketing lavas, that is, a probable youngest age of about 4 m.y. for those underlying, and determinations of 2.0 and 1.5 m.y. for those overlying the Chemeron Formation (Chapman & Brook, 1978: 215). The dating of the latest *Hipparion* of the Mpesida to Aterir type remains somewhat uncertain in consequence.

From Olduvai Gorge at the 2 m.y. level comes *Hipparion* cf. *ethiopicum* (Joleaud) (Hooijer, 1975: 26-52). This extremely hypsodont form appears first at Shungura Member C, now dated at 2.6 to 2.4 m.y. (Hooijer, 1975: 61-64).

Hipparions contemporary with those of Laetolil are found in the Omo Group deposits, from the Usno Formation (3.9-3.75 m.y.) on up to Shungura Member C (Hooijer, 1975: 52-64). Identified only as *Hipparion* spec., they do suggest an evolving group, showing increase in crown height and ectostylid expansion as one passes upward along the series of deposits. No characters on which to base a distinct species are available, however.

The cheek teeth of the Olduvai *Hipparion* cf. *ethiopicum* are smaller, on the whole, than those of the 7-4 m.y. *Hipparion*, as will appear from table 1. In this table, culled from Hooijer (1975), the variation ranges in antero-posterior and transverse crown diameters, taken at 2 cm from the base, are seen to overlap in part but the smallest specimens are from Olduvai and the largest from Mpesida to Aterir.

The cheek teeth of the 7-4 m.y. *Hipparion* are less hypsodont and have weaker ectostylids than those of the Olduvai *Hipparion*, but the difference in crown height can be observed only in a handful specimens, viz., those which

are unworn or very nearly so. The M^1 of the Ekora skull has a full crown height of 64 mm and a height/length index of 290 (Hooijer & Maglio, 1974: 13/14), the M_1 of a Lothagam mandible has a total crown height of 60 mm, a weak, narrow ectostylid 45 mm high, and a height/length index of 300 (Hooijer & Maglio, 1974: 18/19). The $P_{3,4}$ from Chemeron is just over 70 mm high with an ectostylid 55 mm high and 4 mm anteroposteriorly; its height/length index is 280 (Hooijer, 1975: 19). On the other hand, the slightly worn $M^{1,3}$ in a maxillary from Olduvai are 70-75 mm high, as are the P^3 and $M^{1,3}$ of the subadult Olduvai skull (Hooijer, 1975: 31-33). The least worn $M_{1,2}$ of Olduvai has a crown height of 78 mm, an ectostylid at

TABLE I

Dental measurements of Olduvai and Mpesida-Aterir *Hipparion* (mm)

	<i>H. cf. ethiopicum</i>	Mpesida-Aterir
P^2 , ant.post.	29-33.5	35-38
transv.	22-24.5	23-25.5
$P^{3,4}$, ant.post.	22.5-25.5	24-29.5
transv.	23-25	25-29.5
$M^{1,2}$, ant.post.	20.5-24.5	22-25
transv.	21-24	23.5-28
M^3 , ant.post.	20-25.5	22-29
transv.	18.5-24	20-25
P_2 , ant.post.	27-32	31
transv.	14-17	16.5
$P_{3,4}$, ant.post.	20-27	23.5-29
transv.	13-18	13.5-18
$M_{1,2}$, ant.post.	20-24.5	20-27
transv.	12-17	13.5-16
M_3 , ant.post.	25-31	30
transv.	10-15	12

least 70 mm high, and a height/length index of at least 325. The $M_{1,2}$ from Shungura Member G, slightly worn, is 80 mm high, has an ectostylid height of 75 mm and a height/length index of 335 (Hooijer, 1975: 46, 70). In Shungura Member K there is marked hypsodonty: uppers 89 mm in height of crown and lowers at least 83 mm high with an ectostylid 75 mm high; two slightly worn Makapansgat Limeworks uppers have crown heights of 83 mm (Hooijer, 1975: 72-73). The ectostylids in the Olduvai *Hipparion cf. ethiopicum* are typically well-developed, their anteroposterior diameters being 7-9 mm in P_2 and $M_{1,2}$ (occasionally 4-5 mm), 7-11 mm in $P_{3,4}$, and 4-6 mm in M_3 (exceptionally 2 mm) (Hooijer, 1975: 43-47). In the 7-4 m.y. *Hipparion* the ectostylids may be lacking altogether; these were the teeth referred to *Hipparion turkanense* Hooijer & Maglio (1974: 17, pl. 7). Loweres with

ectostylids have been referred to *Hipparion primigenium*, but there is no difference in degree of hypsodonty between the two types, nor is the height of crown greater than that in the Vallesian *Hipparion primigenium* (Hooijer, 1975: 19).

The Vallesian *Hipparion primigenium* has what has been called the hipparionid enamel pattern, with rounded loops to the metaconid and (to a less extent) metastylid. The later hipparions have angular, bluntly pointed, metaconid-metastylid loops, the caballoid pattern (Gromova, 1952: 90; French translation, 1955: 73/74). The difference is clear when comparing the Ngorora lowers, which are Vallesian (Hooijer, 1975, pl. 1), with those from Mpesida, Lukeino, Chemeron and Mursi (Hooijer, 1975, pl. 4) as well as with those from Lothagam-Kanapoi-Ekora (Hooijer & Maglio, 1974, pl. 6 fig. 1, pl. 7 figs. 3 and 5). The advanced *Hipparion* cf. *ethiopicum* from Olduvai is also markedly caballoid (Hooijer, 1975, pl. 14 fig. 2). Thus, the caballoid hipparions appear later than the hipparionid hipparions, in the Old World. We find the same in the New World genus *Neohipparion*: the earlier species have more rounded metaconids and metastylids than the advanced (Stirton, 1940: 182). The caballoid pattern clearly must have evolved from the hipparionid, in *Neohipparion* as well as in *Hipparion* of the Old World. Before the "Pliocene" gap in the sedimentary sequence and fossil mammal record in sub-Saharan Africa was bridged (vide Bishop, 1972), the evidence suggested to Forstén (1968: 13) that African caballoid hipparions appear suddenly, as if they were immigrants. The immigration hypothesis cannot be upheld now that we have knowledge of the hipparions in the 7-4 m.y. time range bridging the gap between the Ngorora *Hipparion primigenium*, between 12 and 9 m.y. old, and the advanced *Hipparion* cf. *ethiopicum* emerging at 2.5 m.y. The "intermediate" hipparions have the low hypsodonty of the Vallesian *H. primigenium*, but the caballoid pattern of the higher-crowned Olduvai *Hipparion* cf. *ethiopicum*. Concomitant with this development the ectostylid, small or absent in the earlier forms, expands to its maximum in *Hipparion* cf. *ethiopicum*. The third incisors, both in the upper and in the lower jaw, become much reduced in the advanced hipparion. In the 7-4 m.y. *Hipparion* the reduction of I^3 and I_3 is not yet evident: these elements have the same relative size as those in the Vallesian *Hipparion primigenium*.

In the European *Hipparion primigenium* ectostylids may at a varying frequency be lacking in different populations (Forstén, 1968: 23). The ectostylid development was maximal in the Vallesian, diminishing in later, Pikermian populations (Forstén, 1968: 24). The evidence now available from sub-Saharan Africa suggests that the evolution took a course there different

from that in Europe. The ectostylid continued to develop, witness the Lothagam-Kanapoi specimens which assumed the caballoid enamel pattern. It was only in the 4-2 m.y. interval that the hypsodonty increased together with that of the ectostylid also in anteroposterior direction, and the reduction of the third incisor set in, leading up to the culmination of evolution in *Hipparion* that we find full-fledged at Olduvai and in the Omo Group deposits from Shungura Member F (Hooijer & Maglio, 1974: 30; Hooijer, 1975: 8, 19; Hooijer, 1976: 35). In proposing a derivation of *Hipparion ethiopicum* ultimately from *Hipparion primigenium* we find ourselves in agreement, apart from the nomenclature, with Arambourg (1970: 95): "on peut penser que *Stylohipparion* est le résultat terminal de la ségrégation, sur le continent africain, d'un groupe d'Equidés tridactyles dont *H. africanum* pourrait avoir été l'origine..." (*Stylohipparion* = *Hipparion ethiopicum*, and *H. africanum* = *H. primigenium*).

Having studied the hipparions of the Lower Omo Group deposits, I expressed the hope that more material in the 4 to 2 million year range would become available for study (Hooijer, 1975: 66). The Laetolil collection provides just that, and it will be dealt with by locality in the pages that follow.

Laetolil locality 1: *Hipparion* spec.

Laet.75, 646, M³ dext. worn to 4 cm from the base. The pli count is 5-5-2-1, the pli caballin is double. The protocone measures 10 by 4 mm occlusally, the crown 25.5 by 23.5 mm at 2 cm from the base. This specimen is within the limits of variation of the Mpesida to Aterir specimens and exceptionally large for *H. cf. ethiopicum* (cf. table 1).

Laet.648, is the external portion of a rather worn P^{3,4} sin. in which the fossette plications are numerous and fine (about 10 in the adjoining borders of pre- and postfossette). The anteroposterior diameter is 29 mm at 2 cm from the base, the level to which the crown is worn, within the range of the Mpesida to Aterir P^{3,4} and above that in the Olduvai specimens.

Laetolil locality 2: *Hipparion* spec.

Laet.76, 2-2, an incomplete and much worn crown of an M^{1,2} dext. in which the fossette borders are rather wrinkled. Plis cannot be exactly counted. The protocone is relatively wide (11 mm anteroposteriorly by 8 mm transversely), and has very nearly become confluent with the protoconule. It would have joined the protoconule with a little more wear as happens in senile *Hipparion* teeth. Less than 10 mm of the mesostyle remains; the crown, at this level, measures 26 mm anteroposteriorly (much reduced as a result of interproximal wear), and 31 mm transversely. There is much resemblance to the M^{1,2} dext.

from Kanapoi referred to *Hipparion turkanense* (Hooijer & Maglio, 1974, pl. 5 fig. 4).

Laet.75, 2837, DM^{3,4} dext. worn to 24 mm from the external base. The anteroposterior crown diameter is 32 mm, the transverse, 24 mm, at 15 mm from the base. The protocone is 8.5 mm anteroposteriorly and 4 mm transversely on the occlusal surface but becomes wider down to the enamel base. The plication numbers are 1-4-3-2. On the whole this is a large specimen, with plications less ample than those in the Ekora DM^{3,4} referred to *Hipparion primigenium* (Hooijer & Maglio, 1974: 19, pl. 4). Olduvai DM^{3,4} have higher pli counts in the prefossette (Hooijer, 1975: 48).

Laet.74, 2-11, and Laet.75, 2113, are two P_{3,4} dext. worn to 3.5, and 4 cm from their bases. The external groove is shallow as metaflexid and entoflexid cut it off from the metaconid-metastylid. A ptychostylid is seen in no. 11. There is no trace of an ectostylid in either of the specimens. The crowns are 29-29.5 mm anteroposteriorly, and 18-19.5 mm transversely, taken in the usual manner at a level 2 cm from the base, and are thereby above the limits in *H. cf. ethiopicum*. The smallest of the two Laetolil P_{3,4} represents the maximum found in the Mpesida to Aterir specimens, and the larger surpasses this somewhat (cf. table 1).

Laet.74, 2-13, incomplete P_{3,4} sin., less than 2 cm high as worn, with the same characters as no. 11, measuring 17 mm transversely.

Laet.2-4, M_{1,2} sin. 5.5 cm high as preserved, again without an ectostylid, showing a long ptychostylid. The crown is 28 by 15.5 mm, above the limits of *H. cf. ethiopicum* and just slightly larger than any of the Mpesida to Aterir M_{1,2}.

Laet.76, 3983, a right and a left M₃, worn to 2 cm of height, exact mirror images of each other and certainly of a single individual. Ectostylids are patently absent, crown diameters 31 by 14 mm, almost the maximum in *H. cf. ethiopicum* and exceeding the only known Mpesida to Aterir specimen in size.

Laetolil locality 2 South: *Hipparion* spec.

Laet.75, 634, right upper canine the basal crown diameters of which cannot be taken exactly but which are approximately 13 by 11 mm, larger than those in the holotype skull of *Hipparion turkanense* (8 by 5 mm: Hooijer & Maglio, 1974: 10).

Laetolil locality 3: *Hipparion* spec.

Laet.75, 3473, crown portion of I¹ dext. 18 mm transversely and 10 mm labiolingually at the occlusal surface but 14 by 12 mm at the broken proximal

end; height of fragment 2.5 cm. This tooth tapers too rapidly rootward for the hypsodont *Hipparion* cf. *ethiopicum* I¹, but the less high-crowned *Hipparion turkanense* I¹ resembles the Laetolil specimen closely.

Laet.75, 2761, M³ dext. 5.5 cm high as worn, pli counts 3-8-3-3, small, single pli caballin, protocone 8 by 4 mm, crown 27 by 22 mm, too large for *H. cf. ethiopicum* but within the range found for the Mpesida to Aterir M³.

Laetolil locality 4: *Hipparion* spec.

Laet.75, 2904, M^{1,2} dext. with a height as worn of 4 cm, plis 3-7-4-1, protocone 10 by 5.5 mm, single caballine fold, crown 24 by 27 mm, in the upper part of the range of the Mpesida to Aterir and above the limits found for the Olduvai *Hipparion*.

Laet.74, 4-161, crown portion of P_{3,4} dext. 3.5 mm high as worn, metaconid-metastylid damaged but cabaloid as usual, long ptychostylid and no ectostylid. Crown dimensions 28 by 17 mm, just within the limits found in the Mpesida to Aterir specimens, above those for Olduvai anteroposteriorly.

Laet.74, 4-157, P₂ sin. incomplete in front and without the base, 3.5 cm high as preserved, no ectostylid, transverse crown diameter 15 mm.

Laetolil locality 5: *Hipparion* spec.

Laet.74, 5-195, P² dext. with a height of 4 cm as worn, numbers of plications 6-5-3-1, single, large caballine fold, protocone 10 by 5 mm occlusally, crown diameters 33 by 25 mm. This is a somewhat shorter specimen than the P² of *Hipparion turkanense* as well as that referred to *Hipparion primigenium*, from Lothagam and Kanapoi, respectively. It resembles the latter more than the former (Hooijer & Maglio, 1974, pl. 2; Hooijer, 1975, pl. 6 fig. 1) because it is in the same stage of wear as the *H. primigenium* specimen, as is the Aterir P² (Hooijer, 1975, pl. 2 fig. 4).

Laet.75, 2794, P^{3,4} dext. worn to 4.5 cm of height, pli counts 1-5-4-1, protocone 10 by 4.5 mm, well-developed, single pli caballin, crown 26 by 26.5 mm, above the range observed in the Olduvai but within that found for the Mpesida to Aterir P^{3,4}.

Laet.74, 5-191, M^{1,2} sin. 5.5 cm high as worn, plis 1-5-4-1, protocone 9.5 by 5 mm, crown 23 by 25 mm; relative size as found for preceding P^{3,4}.

Laet.74, 5-287, is a battered right upper cheek tooth, probably P^{3,4}, the crown height of which must have been 65-70 mm, or the maximum observed in the Mpesida to Aterir *Hipparion*. The crown measures 26 mm anteroposteriorly and 26.5 mm transversely, just as in Laet.75, 2794.

Laet.75, 604, a P₃ and a P₄ both of the left side and evidently associated, bases incomplete, ectostylid-less, good ptychostylids, diameters of crown 27-28 by 15 mm, not especially large as such.

Laetolil locality 7: *Hipparion* spec.

Laet.75, 504, P^{3,4} sin. with a height as worn of 2.5 cm, pli counts 1-8-2-1, pli caballin single, protocone very large occlusally, 11.5 by 7 mm, crown 25 by 27 mm, above the range in *H. cf. ethiopicum*.

Laet.75, 3556, extremely worn M³ sin., plis worn out, protocone 11 by 7.5 mm, crown 24.5 by 22 mm occlusally.

Laetolil locality 7 East: *Hipparion* cf. *ethiopicum*

Laet.75, 884, is an M_{1,2} sin. that is slightly worn and has a crown height of no less than 85 mm. This is a very significant specimen, one of the few that permits of a good estimate of the crown height. Such a height is found only in the advanced Olduvai *Hipparion* cf. *ethiopicum*. As it is hardly worn we see small enamel folds posteriorly in the metaflexid as well as anteriorly in the entoflexid. There is a small ptychostylid. The ectostylid tip is not yet touched by wear and is 7 mm below the tip of the least worn main cusp, the metaconid. It is in part covered by cement and measures 7 mm anteroposteriorly over most of its height. The external groove between protoconid and hypoconid reaches the metaconid-metastylid, the "tie", with pointed loops separated by a wide, U-shaped valley. There is a protostylid as a very slender pillar that is free from the crown in the top 2 cm. In the apical portion the crown measures 29.5 by 11.5 mm, but at 2 cm from the base these dimensions are 23 by 13.5 mm. This tooth is fully within the variation limits of *Hipparion* cf. *ethiopicum* from Olduvai Bed II (table 1). The height of the ectostylid in the Olduvai specimens is at least 70 mm, remaining 10-15 mm below the tip of the hypoconid behind it as seen in unworn apical crown portions (none of the Olduvai M_{1,2} is complete from base to tip). A Shungura Member K specimen has an ectostylid height of 75 mm (Hooijer, 1975: 72).

Laet.75, 1021, P_{3,4} sin. in moderate wear, crown height 5.5 cm as preserved, ectostylid well-developed, lenticular, 8.5 by 3.5 mm occlusally, enamel pattern of crown as in preceding specimen except in that the little folds in the two internal flexids do not show any more, and of course in that the external groove does not reach the metaconid-metastylid, a premolar character. The crown is 26 by 16 mm at 2 cm from the base, within the limits of its Olduvai Bed II homologue. The ectostylid is 8.5 mm anteroposteriorly over the entire exposed height. The stage of wear is such that it can safely be concluded that the full crown height well exceeded 5.5 cm: it must have been about 75 mm. Like the preceding M_{1,2} this is a very typical *Hipparion* cf. *ethiopicum* specimen.

Seven incisors in the lot from Laetolil locality 7 East, all isolated and not very well preserved, nevertheless show the advanced characters, such as great

size, grooving, slight curvature, and great transverse diameters near the tip in I_1 and I_2 . Laet.75, 1080, is an I_1 sin. the occlusal width of which is 19 mm (18-23 mm in *Hipparion* cf. *ethiopicum*: Hooijer, 1975: 37/38). Several specimens show the tripartite outline of the cup, or have two enamel islets as shown in the lower portion of the cup, but measurements cannot be taken: Laet.75, 779, 780, 782, and 790. What appears to be an I^1 sin., Laet.75, 769, has the root but not much of the crown, some 40 mm high, 13 mm labiolingually and 8 mm transversely. A rather interesting specimen, Laet.75, 781, is an I^3 sin. fragment only 20 mm high but with a very obliquely worn surface showing a single, cement-filled cup widest medially. The occlusal surface is 14 by 11 mm; the outline of the broken base is subtriangular, 10 mm both ways. This specimen is exceedingly similar in size and curvature to the reduced I^3 in the Olduvai Bed II skull of *Hipparion* cf. *ethiopicum* (Hooijer, 1975, pl. 11 fig. 2), which is 15 by 10 mm occlusally. Thus, at least two of the incisors show clearly that, at locality 7 East, we have to do with *Hipparion* cf. *ethiopicum* and not with the Mpesida to Aterir *Hipparion* which is less high-crowned and in which the third incisor is not reduced in size relative to the centrally placed incisors.

Laetolil locality 8: *Hipparion* spec.

Laet.75, P^{3,4} dext., worn height 5.5 cm with plications numerous and fine: 2-8-5-2, strong pli caballin, protocone 11 by 5.5 mm, crown 29.5 by 26 mm, in the upper part of the range of the Mpesida to Aterir *Hipparion*, and beyond the range seen in *H. cf. ethiopicum*.

Laet.75, 1257, M^{1,2} dext. 3.5 cm high as worn, plis ?-5-5-1, single caballine fold, protocone 12 mm anteroposteriorly, crown 27 by 24.5 mm, on the large side even for the Mpesida to Aterir *Hipparion*.

Laet.75, 1260, incomplete, slightly worn crown of a right upper milk molar of which no measurements can be given.

Laet.74, 8-226, P₂ dext. worn to 2 cm from the base, no ectostylid, crown 32 by 16 mm.

Laet.75, 1269, M_{1,2} sin., 4 cm high as worn, ectostylid absent, 27 by 16 mm in crown diameters, at the upper limit of the Mpesida to Aterir range.

Laet.75, 1261, extremely worn fragment of lower molar.

Laetolil locality 9: *Hipparion* spec.

Laet.74, 9-281, basal portion of crown of I^1 sin., 15 by 14 mm occlusally, at 25 mm above the base, which is only 10 mm transversely and 15 mm labiolingually. This incisor is not of the *Hipparion* cf. *ethiopicum* type, which tapers less rapidly rootward.

Laet.75, 1401, $M^{1,2}$ dext. worn to 6 cm of height with pli numbers 4-6-3-1, pli caballin single, protocone 10 by 5 mm, crown 23 by 23 mm.

Laet.75, 3037, $DM^{3,4}$ dext. with bifid pli caballin, plis not well seen, diameters of protocone 9 by 3.5 mm occlusally but at least 13 mm antero-posteriorly further down to the base, crown 32 by 23 mm, somewhat larger than the Ekora $DM^{3,4}$ (Hooijer & Maglio, 1974: 19).

Laetolil locality 9 South: *Hipparion* spec.

Laet.75, 1479, $M^{1,2}$ sin. worn to 4.5 cm from base, pli counts 2-5-2-1(?), single caballine fold, protocone 9.5 by 4.5 mm, crown 26.5 by 23+ mm (mesostyle incomplete), larger even than Mpesida to Aterir specimens.

Laet.75, 1427, M^3 dext., slightly worn, crown height along mesostyle 60 mm, plis 3-5-?-? (not yet shown in postfossette), single pli caballin, protocone occlusally 11 by 4.5 mm, crown at 2 cm from base 23 by 20 mm, a rather small specimen falling within the limits of both *Hipparion* cf. *ethiopicum* and the Mpesida to Aterir *Hipparion*. However, the crown height, which may not have been more than some 65 mm, is below that in the Olduvai *Hipparion* (75 mm in the subadult skull from Bed II: Hooijer, 1975: 33).

Laet.75, 1559, M^3 sin. 4 cm high as worn, plis 2-6-1-0, single pli caballin, protocone 10.5 by 4 mm, crown diameters 24 by 21 mm.

Laet.75, 1556, $DM^{3,4}$ dext., plis not very distinct, protocone 11 by 5 mm, double pli caballin, crown 32.5 by 24.5 mm, somewhat larger again than the $DM^{3,4}$ of locality 9.

Laet.75, 435, $M_{1,2}$ dext. 6 cm high as worn, no ectostylid, crown 24 by 14 mm.

Laet.75, 1557, $M_{1,2}$ sin. likewise ectostylid-less and 6 cm in worn height, ptychostylid rather well-developed, crown 24.5 by 13 mm.

Laet.75, 1431, $M_{1,2}$ sin. with base incomplete, crown height 4.5 cm as preserved, no ectostylid, weak ptychostylid, crown 26 by 14.5 mm, within the Mpesida to Aterir range and above that for *H. cf. ethiopicum* anteroposteriorly.

Laet.75, 1531, M_3 sin. 6 cm high as preserved but slightly worn (wrinkled enamel in the fossettids), no ectostylid, diameters 29.5 by 12.5 mm.

Laet.75, 1458, DM_3 dext., and Laet.75, 3029, DM_4 dext., evidently associated as they fit exactly on to each other interproximally, carry ectostylids as *Hipparion* lower milk molars invariably do. In the DM_3 , worn to 15 mm from the base, the ectostylid is 7 by 4 mm occlusally; in the less worn DM_4 the exposed tip of the ectostylid is only 5 by 3 mm. The hinder portion of the DM_4 is missing. DM_3 measures 29.5 by 16 mm; the DM_4 is 15 mm wide, dimensions close to the Lothagam $DM_{3,4}$ (Hooijer & Maglio, 1974: 19).

Laetolil locality 10: *Hipparion* spec.

Laet.75, 10-358, P_{3,4} dext. 2 cm high as worn, no ectostylid, crown 27 mm anteroposteriorly but reduced somewhat because of interproximal wear, transverse diameter 16.5 mm.

Laet.75, 3262, damaged crown of P_{3,4} sin. 4.5 cm high as preserved, good ptychostylid but no ectostylid, diameters of crown 28 by 18 mm, just above the *H. cf. ethiopicum* range but within that of the Mpesida to Aterir *Hipparion*.

Laet.75, 2016, M_{1,2} dext. 4 cm in height as worn, ectostylid absent, crown 25 by 14.5 mm.

Laet.75, 1910, a milk incisor showing a long, transverse, cement-filled cup with a partition in the middle, very low-crowned. The enamel is missing medially but it might very well have been a DI¹ sin. The transverse and labiolingual diameters of the occlusal surface are 19 by 9 mm; the external crown height is 13 mm at most. This Laetolil specimen is larger than the DI₂ of *Hipparion cf. ethiopicum* (Hooijer, 1975: 39) but its exact homologue is not available in the Olduvai collection.

Laet.75, 3281, appears to represent a right upper canine again (as in locality 2 South) but it is not very well preserved. The crown diameters are 12 by 9 mm approximately.

Laetolil locality 10 West: *Hipparion* spec.

Laet.75, 1771, P_{3,4} dext. worn to less than 2 cm from the crown base. It has no ectostylid and measures 27 by 16 mm.

Laet.75, 2611, M_{1,2} dext. damaged externally, 4 cm in height as worn, 25 by 15 mm in crown diameters.

Laetolil locality 10 East: *Hipparion* spec.

Laet.75, 2151, M^{1,2} dext., 2 cm high as worn, has pli counts 1-7-4-1, a single pli caballin, protocone 11 by 5 mm, crown 24 by 27 mm, near the upper end of the range of M^{1,2} in the Mpesida to Aterir *Hipparion*.

Laet.75, 2297, is a portion of the mandible holding the damaged roots of all the incisors except I₃ dext. (pl. 1 fig. 2). Although crowns are not preserved, the root of I₃ sin. is seen to be not significantly smaller than that of its neighbour or of the central incisor, which indicates that the specimen belongs to a *Hipparion* with unreduced lateral incisors such as *Hipparion turkanense* or *Hipparion primigenium*, and certainly not to *Hipparion cf. ethiopicum* in which I₃ is a very small affair lying in a groove behind I₂ (vide Hooijer, 1975, pl. 12).

Laet.75, 1878, P_{3,4} sin. worn to 4.5 cm from the base, ectostylid not developed, crown 28.5 by 15.5 mm.

Laet.75, 2260, $M_{1,2}$ dext. 5 cm high as worn, no ectostylid, long ptychostylid, crown 25 by 14 mm.

Laet.75, 1879, M_3 sin. just 2 cm high as worn, again without ectostylid. The crown measures 27.5 by 15 mm.

Laetolil locality 11: *Hipparion* spec.

Laet.76, 3845, I_1 and I_2 dext. of the same individual both with large, wavy in outline, cement-filled cups. The I_1 lacks some of the enamel laterally; it is 19 by 13.5 mm occlusally. The occlusal surface of the I_2 is 19 by 13 mm. The crown of I_1 , some 40 mm high externally to the base of the enamel, tapers markedly: at the base of the crown the diameters are 12 mm transversely and 14 mm labiolingually. Only 1 cm of the root is preserved. The I_2 has 35 mm of the crown preserved and nothing of the root; its basal diameters are 11 by 12 mm. The configuration of these incisors points to the Mpesida to Aterir *Hipparion* and not to *H. cf. ethiopicum* the incisors of which have less taper.

There remain, from Laetolil locality 11, five lower cheek teeth bearing the same field number as the incisors and evidently found in close association with these. All are large and from the left side: P_2 , P_3 , P_4 , M_1 (with a portion of the body of the mandible attached to it), and M_3 . P_2 is 3.5 cm high as worn, P_3 , 4 cm; P_4 , M_1 , and M_3 do not have the base preserved. Ectostylids are wanting in all the teeth. The metaflexid and the entoflexid are in contact in the premolars; in the molars the external fold separates them and almost reaches the bottom of the metaconid-metastylid valley. All this is as usual. The crown dimensions of P_2 are 32 by 18 mm, those of P_3 30 by 19 mm, those of P_4 30 by 18 mm, those of M_1 28 by ? mm, and those of M_3 30 by 13 mm. These measurements exceed those of their homologues in *Hipparion cf. ethiopicum*, M_3 excepted, and agree with those found for the Mpesida to Aterir *Hipparion* cheek teeth.

Laet.75, 852, is a milk incisor almost identical with the DI^1 of Laetolil locality 10 and likewise lacks the root. The crownward expansion is slightly less marked only, and the specimen measures 19 by 8.5 mm occlusally.

Laetolil locality 12: *Hipparion* spec.

Laet.75, 3090, a damaged $M^{1,2}$ sin. some 6 cm high. The caballine fold is single, the protocone 10.5 by 4 mm, the anteroposterior crown diameter 24 mm.

Laet.75, 3089, $M_{1,2}$ dext., ectostylid-less, 26 by 17 mm occlusally, 2 cm from the base. This is, again, a specimen at the upper limit of variation in the Mpesida to Aterir *Hipparion*, and above that in the Olduvai *H. cf. ethiopicum*.

Laetolil locality 12 South: *Hipparion* spec.

Laet.75, 1370, comprises four cheek teeth, all from the right lower jaw. P_2 is large, very much worn down and incomplete anteriorly. The antero-posterior diameter is a little over 34 mm, the transverse, 15 mm. Like the associated teeth it lacks the ectostylid completely. P_3 measures 27 by 17 mm, as does P_4 which is worn to 2 cm from its base. There remains only the M_3 , 2.5 cm high as worn, and 31 by 15 mm in crown dimensions, the maximum found in *H. cf. ethiopicum*. P_3 and P_4 are within the range of size found for the Mpesida to Aterir *Hipparion*.

Laetolil locality 13: *Hipparion* spec.

Laet.75, 1616, $M^{1,2}$ sin. worn down to 4 cm from the base, with pli counts 2-6-3-1, single pli caballin, protocone 9.5 by 3.5 mm occlusally, crown 24 by 25 mm, a specimen larger than the $M^{1,2}$ of the Olduvai *H. cf. ethiopicum*.

Laetolil locality 14: *Hipparion* spec.

Laet.75, 411, comprises two last lower molars. The best preserved is an M_3 dext. 5 cm high as preserved, lacking any trace of an ectostylid, 28 by 18 mm in crown diameters. The other element is an M_3 sin. of the same individual, with the hypoconulid broken off but the base preserved anteriorly. It shows that the slightly worn crown is about 60 mm high.

Laetolil locality 18: *Hipparion cf. ethiopicum*

Laet.76, 18-253, is the symphyseal portion of the mandible holding the crown of I_1 sin. worn to ca. 25 mm from the external base of the enamel. The occlusal crown diameters are 15 mm transversely and 12.5 mm labiolingually. Both the external and the lingual face show a median groove. I_1 dext. has dropped out of its alveolus, but the second and third incisors are preserved on both sides although their extra-alveolar parts are missing (pl. 1 figs. 1, 3, 4).

This specimen clearly represents the advanced *Hipparion cf. ethiopicum* as the I_3 are small (ca. 10 mm in diameters) and are lying behind the I_2 (cf. Hooijer, 1975, pl. 12). Behind these lateral incisors there are canines the right of which is nearly entire. Much curved upward, with diameters 13 mm anteroposteriorly and 10.5 mm transversely at the alveolar border, the crown is 13-14 mm high, showing an anteroposterior cutting edge which is slightly damaged only. The sides of the crown are convex but for a vertical groove or depression just internally of the anterior edge. The length of the symphysis is 85 mm, the least width, 48 mm. The Olduvai symphyses of *Hipparion cf.*

ethiopicum do not sport canines (Hooijer, 1975, pl. 12), and neither do the Laetolil symphysial portions described by Dietrich (1942: 97, pl. XVI fig. 112). The type specimen of *Eurygnathohippus cornelianus* Van Hoepen (1930) has no canines either: the small elements behind I_2 originally interpreted as such proved to be the I_3 . However, the mandible from Koobi Fora recently referred to *Hipparion ethiopicum* by Eisenmann (1976: 586, pl. 5D) has a canine that looks rather similar to that now found in the Laetolil locality 18 specimen; dimensions have not been given.

Is it possible that the canine-bearing advanced hipparions represent male individuals, and those devoid of canines females? In ordinary hipparions canines do develop in either sex, with a slight secondary sexual difference: those of the females are smaller and more rounded than those of the males (Pirlot, 1952). The type skull of *Hipparion turkanense* has canines, of the "male" type, and *Hipparion primigenium* also has them (Hooijer & Maglio, 1974, pl. 1; Hooijer, 1975: 13). The Langebaanweg *Hipparion* cf. *baardi* has an upper canine, but no trace of a canine in the mandible (Hooijer, 1976: 8, 20). It is, at any rate, now a foregone conclusion (Hooijer, 1976: 19) that canines are absent in either sex in the advanced *Hipparion*, at least at Laetolil, or at Koobi Fora.

The most diagnostic isolated cheek tooth from Laetolil locality 18 is Laet.76, 18-599, an $M^{1,2}$ dext. that is very slightly worn. The plications are 1-6-14-(?)1, the protocone is lenticular, 10.5 by 3 mm occlusally, and the single pli caballin extends nearly across the protoconal valley. The height of the crown from the closed bases of the fossettes is 82 mm; the crown diameters, 25.5 by 22.5 at the top, are 23 by 23 mm at 2 cm from the base. The excessive height of the crown points indubitably to *Hipparion* cf. *ethiopicum*, and in crown and protocone dimensions the Laetolil $M^{1,2}$ is within the variation limits of its homologues from Olduvai Bed II and Shungura Members G and K (Hooijer, 1975: 41, 69, 72).

The remaining cheek teeth from Laetolil locality 18 are more worn, and the characteristic hypsodonty, therefore, cannot be determined. These are as follows:

Laet.76, 18-487A, $P^{3,4}$ dext., worn to 5.5 cm of height, pli counts 6-5-5-1, double caballine fold, protocone 9.5 by 4 mm occlusally, anteroposterior and transverse diameters of crown at 2 cm from the base, 24 mm, and 25 mm, respectively.

Laet.76, 18-366, $P^{3,4}$ sin. about 5 cm in worn height, plis indistinctly shown, protocone ca. 9 by 4 mm, crown 26 by 27 mm, larger than the preceding and the following specimen, and above the range found for *H. cf. ethiopicum* of Olduvai.

Laet.76, 18-268, P^{3,4} sin. worn down to less than 2 cm from base, yet with protocone still isolated, 11 by 5 mm, and crown 24.5 by 24 mm occlusally.

Laet.76, 18-363, M^{1,2} dext. 5.5 cm high as worn, pli counts 4-7-4-3, duplicated caballine fold, protocone 7.5 by 3.5 mm, crown 22 by 23 mm.

Laet.76, 18-364, section of crown of M^{1,2} dext. 3.5 cm in height, pli counts 4-8-3-2, single pli caballin, basal diameters of fragment 22.5 by 21.5 mm.

Laet.76, 18-365, M^{1,2} dext. 6 cm high as worn, pli counts 2-7-6-2, trilobate pli caballin, protocone damaged occlusally.

Laet.76, 18-361, M^{1,2} sin., worn height 5.5 cm, pli counts 4-6-5-(?)1, double pli caballin, protocone 8.5 by 4.5 mm, crown 24 by 25 mm.

Laet.76, 18-591, three lower cheek teeth with ectostylids well-developed: a P₂ dext. in ramus fragment, much worn down, metaflexid and entoflexid very nearly cut off from internal border as enamel islands, ectostylid 5 by 3 mm, crown damaged fore and aft, width across ectostylid 14.5 mm; an M₂ sin. 2.5 cm high as worn, ectostylid 5 by 2.5 mm occlusally, crown 23.5 by 14 mm, and an M₃ 3.5 cm high as worn, ectostylid broken but ca. 4 mm anteroposteriorly, crown dimensions 27 by 14 mm.

Laet.76, 18-246, DM^{3,4} sin. just touched by wear but base incomplete; crown at metacone ca. 30 mm high, protocone 21 mm high with blunt tip, maximal crown diameters 31 by 23.5 mm.

Laet.76, 18-461, DM_{3,4} dext., slightly worn but incomplete at base and behind, ptychostylid and ectostylid showing, width of crown 11.5 mm.

Laetolil locality 22: *Hipparion* spec.

Laet.75, 3666, M^{1,2} dext. incomplete at base and 4.5 cm high as preserved. Pli counts 3-6-3-1, single pli caballin, protocone 8.5 by 4 mm, crown 24 by 24 mm.

Laet.75, 631, comprises four lower cheek teeth, all lacking the ectostylid. They are from the right side, P₃-M₂ dext., associated (pl. 3 figs. 1-2). The P₃, 5 cm high as worn, is incomplete postero-externally; the crown is 28 by 16.5 mm. The P₄, the preserved crown portion of which is 4 cm high, is 28.5 by 16 mm in crown diameters. The M₁, 5 cm high as preserved, measures 26 by 14.5 mm, and the M₂, preserved for 5.5 cm, measures 25.5 by 15 mm. These teeth are larger than those of *Hipparion* cf. *ethiopicum* but fall within the limits of the Mpesida to Aterir *Hipparion*.

Two lower cheek dentitions, although of unknown locality, were sent along with the localized specimens by Mrs. Mary Leakey. Both belong to the Mpesida to Aterir type of *Hipparion*, and are well worth recording because they are so complete.

Laet.75, 491, is a right lower cheek dentition, P_2 - M_3 dext., in situ in a hemimandible the lower border of which, however, is not preserved, and neither are the symphyseal portion or the ascending ramus (pl. 2 figs. 1-2). Ectostylid enamel figures show in the external cement investment in all the teeth except for the P_2 . An ancient fracture passes between P_3 and P_4 , allowing for the crown height of the worn premolars to be taken: 3.5 cm for P_3 , and 4 cm for P_4 . Another fracture exposes M_2 anteriorly; it is worn to 4 cm from the base of the crown. The crown height of the M_3 , exposed behind and internally, is 3.5 cm. This gives a measure for the heights of the ectostylids as they start at the bases of the crowns.

The enamel figure formed by the tip of the ectostylid of P_3 is small, reniform, 4 mm anteroposteriorly and 2.5 mm transversely. In the P_4 this figure is somewhat larger, 5 by 3 mm, with a bifid anterior end. Since P_4 erupts later than P_3 it is less worn, and the larger ectostylid figure indicates that the ectostylid is more developed in P_4 than in P_3 . The height of the ectostylid in P_4 is a little over 40 mm, that of P_3 very slightly more than 35 mm. M_1 shows an ectostylid figure 4.5 by 3.5 mm in diameters; the crown of M_1 is worn to a level closer to the base than that in any of the other cheek teeth. M_2 has a figure formed by the tip of the ectostylid of the same size as that in M_1 , and since it is worn to a height of 4 cm it is likely that the ectostylid height was some 45 to 50 mm, not more. The M_3 has the tip of the ectostylid barely exposed on the cement surface: its height must have been just about 35 mm.

Thus, the present Laetolil *Hipparion* dentition has ectostylids that are some 4-5 mm anteroposteriorly and that are most 45-50 mm high, certainly not much more than 35 mm in M_3 , and even less in P_2 : the P_2 is worn more than P_3 (which has a crown height as worn of 3.5 cm) and does not show the ectostylid occlusally. This stage of development of the ectostylids is comparable to that in teeth from Kanapoi and Lothagam (Hooijer & Maglio, 1974: 16, 18) in which the ectostylid is some 40-50 mm high and the crown does not exceed 60 mm in total height. It is also comparable to the stage of development of ectostylids seen in a Shungura Formation Member B11 mandible (Hooijer, 1975: 52/53, pl. 14 fig. 1) with an age somewhat less than 3 million years (Shungura Formation Member B has a palaeomagnetic age of 2.95-2.65 m.y.; midpoint age of Member B10-12 2.7 m.y. according to Dr. Frank Brown as of October, 1975). In the Shungura B11 cheek teeth, which are worn to about the same extent as those from Laetolil, the ectostylid figures are close in size to those seen in the Laetolil dentition.

Therefore, the present (unlocalized) Laetolil dentition shows resemblance in ectostylid development to certain Lothagam and Kanapoi specimens (6-4

m.y.) as well as to a specimen the age of which is some 3 m.y. In the advanced *Hipparion* cf. *ethiopicum* of Olduvai the ectostylids are typically 7 mm anteroposteriorly and over 70 mm high.

TABLE 2

Measurements of teeth of Laetolil mandibles (mm)

	no. 491	no. 2559		no. 491	no. 2559
P ₂ , ant.post.	32	—	M ₁ , ant.post.	25	26
transv.	16.5	—	transv.	15	17
P ₃ , ant.post.	27.5	26	M ₂ , ant.post.	25	26
transv.	18	19	transv.	15	16.5
P ₄ , ant.post.	27	26	M ₃ , ant.post.	31	31
transv.	18	19	transv.	14	14.5

On comparing the measurements of the mandibular teeth from Laetolil with those of the Mpesida to Aterir *Hipparion* (tables 2 and 1) we find that the Laetolil teeth are to the higher side of the ranges of their homologues, or even exceeding them, while some teeth are above the ranges found for *Hipparion* cf. *ethiopicum*, which are smaller, on the whole, than the older teeth. They conform to the many isolated teeth from known sites in the Laetolil area that are here identified as *Hipparion* spec. In previous papers (Hooijer & Maglio, 1974; Hooijer, 1975) we have referred lower cheek teeth to either *Hipparion turkanense* (Mpesida, Lukeino, Lothagam, and Mursi) or *Hipparion primigenium* (Kanapoi-Ekora, Chemeron, and Aterir) mainly on the basis of absence or presence of ectostylids. The constancy of occurrence of ectostylids may be remarkable in some areas (e.g., none of the Langebaanweg Baard's and "E" Quarries lower cheek teeth shows them; they occur in a set of lower premolars from a site between "E" and "" Quarries, and only there: Hooijer, 1976: 26, 37), but as has been pointed out by Forstén (1968: 23/24) the frequency of occurrence of ectostylids varies in different populations of *Hipparion primigenium*, and it is perhaps better to abstain from specific determinations of isolated *Hipparion* teeth or even tooththrows, as I did when dealing with the Lower Omo Group deposits *Hipparion* teeth (Hooijer, 1975: 52-66).

There is, lastly, in the Laetolil collection sent to me an unlocalized left lower cheek dentition, marked Laet.75, 2559. It is less well preserved than no. 491 and somewhat more worn. The height of M₃ is reduced to a mere 20 mm. P₂ is incomplete anteriorly as well as on the external surface. It is clear from the remaining teeth that ectostylids had not developed at all in this specimen. The measurements are given in table 2 and are seen to conform

well with those of mandible no. 491. The entire lower cheek dentitions allow for the length P_2-M_3 to be taken; at the alveolar borders the toothrow length is 169 mm in no. 491, and 172 mm in no. 2559, of the same order as that in the Shungura Member B11 mandible (163 mm).

This completes the study of the Laetolil *Hipparion* collection entrusted to me by Mrs. Mary Leakey. The *Hipparion* is either of the Mpesida to Aterir type, with or without ectostylids, or of the Olduvai type, with well-developed ectostylids. The former type is evidently more generalized, and somewhat larger-toothed, than the latter. At no locality in the Laetolil area there is a mixture of the two *Hipparion* types. It is, therefore, clear that there are two faunal levels at Laetolil. Most of the localities yield the Mpesida to Aterir type of *Hipparion* of the 7-4 million year range, while two localities, 7 East and 18, yield the Olduvai type of *Hipparion* which I called *Hipparion* cf. *ethiopicum*, emerging in the series of Omo Group deposits at 2.5 million years. It is just these two localities that are in the Ndolanya Beds, with a youngest age of 2.4 million years. It is gratifying to be able to state that the conclusions based by Maglio (1969) on the Laetolil elephants are fully borne out by the study of the hipparions.

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EXPLANATION OF THE PLATES

PLATE 1

Figs. 1, 3, and 4, *Hipparion* cf. *ethiopicum* (Joleaud), symphyseal portion of mandible, Laetolil locality 18, no. 253; fig. 1, dorsal view; fig. 3, left lateral view; fig. 4, right lateral view, $\times 1.2$. Fig. 2, *Hipparion* spec., roots of I_{1-2} dext. and I_{1-3} sin., Laetolil locality 10 East, no. 2297, dorsal view, $\times 1.3$.

PLATE 2

Hipparion spec., right mandibular ramus with P_2 - M_3 , Laetolil, no. 491; fig. 1, crown view; fig. 2, internal view, $\times 0.8$.

PLATE 3

Hipparion spec., P_3 - M_2 dext., associated, Laetolil locality 22, no. 631; fig. 1, crown view; fig. 2, external view, $\times 1.2$.





