THE LATE PLIOCENE EQUIDAE OF LANGEBAANWEG, CAPE PROVINCE, SOUTH AFRICA

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With 8 plates

Introduction

The site of Langebaanweg, situated approximately 32°58′ S, 18°9′ E in the Sandveld region of the southwestern Cape Province, some 105 km NNW of Cape Town, first came into the palaeontological picture in 1958, when the find of a fossil proboscidean, erroneously called *Stegolophodon* (Singer & Hooijer, 1958), was published from this site. The remains of Equidae (*Hipparion*) from Baard's Quarry and from a second quarry, called Varswater, later named 'C' Quarry, were the subject of a paper by Boné & Singer (1965), but better material, mainly from 'E' Quarry, has since been collected. The importance of the 'E' Quarry *Hipparion* material lies in the fact that we now have, for the first time, associated teeth, mandibles, and postcranial bones of single individuals. There is also a skull, but no mandible associated with it. The relationships between the deposits in the area of the mined-out Baard's and the abandoned 'C' Quarries on the one hand, and those of 'E' Quarry have not been satisfactorily resolved. Wolff, Singer & Bishop (1975) hold the view that the Varswater Formation with its three beds, the (Beach)

Gravel Member (= Bed 1), the Fluvial (or Quartzose) Sand Member (= Bed 2), and the Pelletal Phosphorite Member (= Bed 3) as lately described by Tankard (1975) does represent one cyclothem. They also state that there appears to be no valid reason to infer that there would be a major difference in time of deposition between Baard's and 'E' Quarries. Hendey (1976: 241) suggests that there is a time difference: the Baard's Quarry deposits would at least partially postdate those of 'E' Quarry.

In the Baard's Quarry fauna we have *Equus*, which does appear first in East Africa at the 2 million year level (Shungura Formation Member G: Hooijer, 1975). *Equus* has not been found unequivocally at 'E' Quarry: specimens once so identified and recorded from 'E' Quarry (Hendey, 1970a: 102: L 2095, a large *Equus*; L 2545, L 5353, L 10956 and L 10957) have since been considered either doubtfully part of the 'E' Quarry assemblage (L 2095) or have been referred to *Hipparion* (Hendey, 1970b: 124). The large *Equus* upper molar L 2095, although the preservation of the tooth is such that it could be associated with fossils from either quarry (Hendey, 1972: 172), in view of the fact that not a single additional *Equus* specimen has been found at 'E' Quarry, has been retained only in the faunal list for Baard's Quarry (Hendey, 1972: 173; Hendey, 1974: 39/40). When I studied the collection in May and June, 1975, L 10956 and L 10957 had been renumbered and now form part of L 10954, a set of lower cheek teeth, P_2 - M_2 dext., evidently of the same individual, and almost certainly from Bed 3 (pl. 3), representing *Hipparion* cf. *baardi*.

It should be emphasized that negative evidence is always suspect, especially in the case of 'E' Quarry where new species are added to the faunal list each year. Recently (Hendey, 1976: 242), remains of a porcupine, still considered a notable absentee from the Langebaanweg fauna in 1974 (Hendey, 1974: 42), with its characteristic gnaw-marks showing in none of the thousands of bones recovered at Langebaanweg, were found at 'E' Quarry. Further, the hippopotamus, which occurs at Baard's Quarry (Boné & Singer, 1965: 280), and which was still noted as an absentee at 'E' Quarry by Hendey in 1974 (Hendey, 1974: 48), although he said that the depositional environment at Langebaanweg in the Late Pliocene was such that remains of this animal would have been preserved if it had been present, has now been found to occur at 'E' Quarry (Hendey, 1976: 241). The genus *Hippopotamus* goes back in Africa to the Ngorora Formation, which is dated between 12 and 9 million years (Bishop & Pickford, 1975).

The Ngorora Formation in Kenya also contains the earliest *Hipparion* south of the Sahara, the primordial Old World *Hipparion primigenium* (Von Meyer) (Hooijer & Maglio, 1974: 30; Hooijer, 1975: 12-16, pl. 1, pl. 2 fig. 5, pl. 3 figs. 1, 2, 5-6).

The species of rhinoceros found at Baard's Quarry is *Diceros bicornis* (L.): specimens so identified by me in the South African Museum, listed as cf. *Ceratotherium* by Boné & Singer (1965: 280). *Diceros bicornis* is first found in East Africa at Kanam West (Hooijer, 1969: 88) and at Mursi (Hooijer, 1973: 158), at the 4 million year level. So far *Diceros bicornis* has not been identified in the collection from 'E' Quarry: the rhinoceros species at 'E' Quarry is *Ceratotherium praecox* Hooijer & Patterson (1972; Hooijer, 1972), which ranges in East Africa so far as known from 7 to 4 million years ago (Mpesida Beds to Mursi Formation: Hooijer, 1973: 168-169). It may later prove to range earlier and later than that interval of time. *C. praecox* is the immediate ancestor of *Ceratotherium simum* (Burchell), which has not shown up yet either in 'E' or in Baard's Quarry. The transformation from *C. praecox* into *C. simum* took place 4 to 3 million years ago (Hooijer, 1973: 170). The absence of some species at 'E' Quarry may be accidental or due to some ecological barriers existing at the time: this is a consideration that must be borne in mind.

It is supposed that the Gravel Member (= Bed 1) includes elements derived from the underlying Saldana Formation. There is the now defunct 'C' Quarry, which provided some fragmentary permanent, and two well-preserved deciduous *Hipparion* upper molars (recorded by Boné & Singer, 1965: 277 as not from Baard's Quarry but from Varswater, another quarry). In 1975 there were found some extremely interesting *Hipparion* teeth, *H.* cf. *namaquense* (Haughton), at a site between 'E' and 'C' Quarries, in deposits near the contact of the Varswater Formation and the overlying surface sands. These, L 24197 (pl. 7) are now considered to be from the uppermost level of the Pelletal Phosphorite Member (= Bed 3) (Hendey, 1976: 240).

There are certain species that the fauna of Baard's Quarry definitely has in common with that of 'E' Quarry: *Mammuthus subplanifrons* (Osborn) (Maglio & Hendey, 1970), and *Mesembriportax acrae* Gentry (1974). Therefore, Baard's Quarry need not be all younger than 'E' Quarry, as was at one time suggested by Hendey (1974: 57) in a table in which he placed Baard's Quarry above the "Langebaanian". It remains to be determined how large the interval of time at which the two Quarries overlap really is. *Mammuthus subplanifrons* places Langebaanweg between 5 and 4 million years (Maglio, 1973: 70, 79), and the 'E' Quarry, with *Ceratotherium praecox,* would be in the 7 to 4 million year interval if we go by the sound palaeontological practice that sediments with identical species are of the same age. The Baard's Quarry, with *Equus,* would in part at least be less than 2 million years old: *Equus* has not been recorded from beds in Africa indubitably older than this. There are enigmatic aspects of the faunas of 'E' and the other quarries at

Langebaanweg remaining to be solved when the faunas of these deposits have become so well known that no more surprises are to be expected. At the moment of writing, the fossils come principally from the still being mined 'E' Quarry.

Of crucial importance, of course, is the newly found *Hipparion* skull from 'E' Quarry, L 22187, to be described below. We already have *Hipparion albertense baardi* Boné & Singer (1965) of Baard's and 'C' Quarries, which has as holotype a lower premolar, L 946, from Baard's Quarry. This form may be called *Hipparion baardi* as *Hipparion albertense* is a nomen vanum (Hooijer, 1975: 6/7, 27/28). Are the Baard's and the 'E' Quarry hipparions conspecific or not? If they are the same, then we would have another species common to Baard's Quarry and 'E' Quarry, and the main purpose of the present paper is to solve this problem, or at least contribute to its solution.

The specimens mentioned in the present paper are in the Palaeontology Department of the South African Museum. Reference numbers for all begin SAM-PQ-L, followed by a serial number. For the sake of brevity they are here given only as L, followed by the number.

The Hipparion skull from 'E' Quarry

The most important and diagnostic specimen of *Hipparion* to have come from 'E' Quarry, L 22187, is the skull of a fairly aged individual (pl. 1 figs. 1-2). The premolars are very much worn down, and of the first molar only root stumps remain. Behind this molar the tooth-bearing portion of the maxillary is missing on both sides, but the posterior border of the palatum durum is preserved on the right. Much of the sides of the maxillaries and the middle portion of the frontal bones are restored in plaster. This is not a serious defect, however, since the posterior portion of the preorbital fossa on both sides as well as the anterior portion of the facial crest and the infra-orbital foramen on the left side are preserved. The front and back parts of the skull are well preserved.

Of the incisors only the central pair has dropped out. The palatine fissure terminates slightly in front of P^2. The length of the diastema I^3 - P^2 is 110 mm, and since the basilar length of the skull can be determined (455 mm) the diastema index can be given. It is 24, very much the same as that in the type skull of *Hipparion turkanense* Hooijer & Maglio (1974: 8) from Lothagam in Kenya, in which it is 21.5 (in horses this index varies from 19 to 24; lower values are found in zebras and asses: Hooijer, 1949: 252).

The small canines are placed 40 mm behind I^3. The naso-premaxillary notch is above the anterior border of P^2, and the nasals, the tips of which diverge slightly, extend to 70 mm in front of this. In the *H. turkanense*

skull the nasals are reconstructed in plaster, and their length could, therefore, not be determined. The naso-frontal suture is not shown in the Langebaanweg skull, but would have been at about the level of the anterior border of the orbits: the distance from the nasal tips to the orbits is about 250 mm. The infraorbital foramen is placed above the P^4 - M^1 junction, just in front of the facial crest, which emerges above the posterior half of M^1. At 35 mm in front of the anterior orbital margin is seen the posterior boundary of a preorbital fossa, very well-marked and deep, at least 30 mm high and 15 mm deep posteriorly, flattening out anteriorly although its exact length cannot be determined. This is the most striking feature of the Langebaanweg skull. The preorbital fossa probably included or extended close to the infraorbital foramen, which is 70-80 mm in front of the posterior border of the preorbital fossa. Such preorbital fossae characterize most hipparions, and their absence in the type skull of *H. turkanense* from Lothagam in Kenya was one of the main reasons for us to consider the Lothagam skull distinct from *H. primigenium* (Von Meyer), which occurs in an advanced stage alongside *H. turkanense* in the Lothagam-Kanapoi collection (Hooijer & Maglio, 1974). The significance of this feature will be discussed in a later section of the present paper.

The orbital margins of the Langebaanweg skull are entire: the horizontal diameter of the orbit is 60 mm, and the vertical, 50 mm. The supraorbital foramen is relatively large: 8 mm in diameter. The measurements of the Langebaanweg skull are given in table 1 (first column) in conjunction with those of the *H. turkanense* skull (second column). The latter is likewise of an aged individual, and it will be observed that the measurements correspond very closely. The two skulls are of the same size as those of *H. primigenium* from Pikermi and Samos (Forstén 1968: 120-121). The *H. turkanense*

TABLE 1

Measurements of Langebaanweg and Lothagam skulls of *Hipparion* (mm)

	Langebaanweg	Lothagam
Basilar length (prosthion-basion)	455	465
Prosthion to posterior border of hard palate	255	250
From anterior border of P^2 to orbit	ca. 170	170
Diastema I^3 - P^2	110	100
Length P^2 - P^4	77	89
Width over posterior borders of orbits	195	—
Postorbital constriction	72	ca. 70
Greatest width of cranium	100	ca. 90
Zygomatic width	195	ca. 200
Bicondylar width	76	80
Height of occiput (from basion)	105	ca. 110

skull, as said above, is devoid of a preorbital fossa. It is illustrated on pl. 1 of Hooijer & Maglio (1974). A juvenile skull from Ekora in Kenya (l.c.: 14, pl. 4), at the 4 million year level, has a preorbital fossa in the *H. primigenium* fashion, and has been referred to that species. The fossa in the Langebaanweg skull is as well-developed as that in the juvenile Ekora skull, in which it is placed slightly further in front of the orbits. There is a maxillary portion of a juvenile *Hipparion* skull with DM^{2-3} in situ in the Langebaanweg 'E' Quarry collection, L 21823, of slightly younger individual age than the Ekora skull, enough of which is preserved above and behind the infraorbital foramen, placed above the posterior half of DM^3 in both skulls, to show that the Langebaanweg juvenile has a preorbital fossa, too. Thus, so far, two Langebaanweg *Hipparion* skulls present this feature, and they are the only ones in which this feature would show as the remaining Quarry 'E' skull portions do not comprise this critical portion.

The incisors in skull L 22187 are worn down to about 25 mm from their crown bases, and the occlusal surfaces are showing only the nearly worn-out cups, or marks, reduced to tiny, cement-filled pits. At the occlusal surface the width is 14 mm for I^2, and 17 mm for I^3. Labiolingually the occlusal diameter is 11 mm for I^2, and 9.5 mm for I^3. On the external surface of both of these incisors there is a weak median longitudinal groove, flattening out near the base of the crown, while in I^3 there is an internal groove only a few mm from the lateral crown edge. The basal transverse diameters of the incisors are equal, 10 mm, the labiolingual, 12-13 mm. It is thus evident that the third incisor is not reduced relative to the second, just as in *H. primigenium* and also in *H. turkanense*, and quite unlike the condition seen in the advanced, Pleistocene *Hipparion* (*"Stylohipparion"*) in which the third incisor is much reduced (Hooijer, 1975).

The canine is small, with an enamel crown 7 mm anteroposteriorly and about 3 mm transversely: the left C is damaged and the right nearly entire. Canines of the same shape and size are found in the type skull of *H. turkanense*, where they are 8 by 5 mm in diameters (Hooijer & Maglio, 1974: 10).

On the lingual side of the anterior lobe of P^2, which is 65 mm behind the canine, there is in the Langebaanweg skull the stump of the persisting first milk molar. It is retained on the right side only; in the *H. turkanense* skull this vestigial element is missing on both sides. P^2 is worn down to the base of the crown anteriorly, but the posterior border of the crown is about 10 mm high as worn; the occlusal surface of the P^2 is quite concave anteroposteriorly. Only the postfossette shows, as a narrow anteroposterior enamel island, the anterior horn being worn away. The mesostyle and the posterior part of

the protocone can still be distinguished, but no enamel any more on the worn surface anterior to this. In P^3, worn down to 13 mm from the crown base externally, the protocone is confluent with the protoconule, as happens in extremely worn *Hipparion* cheek teeth. The prefossette has a posterior horn extending well outward, and shows three posterior enamel plications. The postfossette is merely a curved enamel island, with the tip of its anterior horn isolated in the left P^3, and worn away in the right. The right P^4 is also more worn than the left, with nothing of the fossettes remaining but a small enamel island of the postfossette, whereas the left P^4 still shows both fossettes, much in the same way as does the right P^3. No plication counts can be given. The P^4 are, of course, normally less worn than the P^3, coming into use later, but in the present instance, since the wear surface of the premolar toothrow is so irregular, highest at P^3 and lower down to the alveolar border both in front and behind, the P^4 are more worn than the P^3. What remains of the M^1 are merely the roots. Unfortunately M^2 and M^3 are not preserved in the Langebaanweg skull so that the full cheek toothrow length cannot be given. The posterior border of the hard palate is 50 mm behind P^4. In the type skull of *H. turkanense* the posterior border of the palate is on a level with the posterior border of M^2. The Lothagam skull of *H. turkanense* is somewhat more senile than that of Langebaanweg L 22187, for the third incisor in the Lothagam skull is worn down more; the irregular wear of the premolar row in the Langebaanweg skull does not permit of the worn height of the crowns to be determined exactly: P^3 is worn down to about 15 mm from the base externally, and P^4 to less than 10 mm, and the heights are not exactly the same on both sides. But it remains the most complete *Hipparion* specimen so far found at Langebaanweg, at 'E' Quarry.

There is, in the 'E' Quarry collection, the maxillary portion of another old individual, L 11751. It holds P^3 - M^1, the anterior portion of the facial crest, and the lower margin of the infraorbital foramen, which is situated above the posterior half of P^4. Unfortunately, in this specimen not enough is preserved to determine whether in this individual there was a preorbital fossa or not. The well-worn teeth in this specimen (pl. 8 fig. 2) are close to those in the type skull of *H. turkanense* (Hooijer & Maglio, 1974, pl. 2). P^3 lacks the postero-external corner of the crown; it is worn down to 13 mm from the crown-root junction externally, and the fossette enamel figures are finely wrinkled along their anteroposterior borders.

There are four posterior plications in the prefossette, and only one remaining in the anterior border of the postfossette. The protocone is rather wide transversely, flattened internally, just as in the type skull of *H. turkanense* the P^3 of which is worn to a very slightly less degree. There is no pli caballin.

TABLE 2

Measurements of Langebaanweg upper cheek teeth (L numbers) and those of *H. turkanense* (KNM-LT 136) and of *H. primigenium* (KNM-KP 43) (mm)

	L 22187	L 11751	L 11222	KNM-LT 136	KNM-KP 43
P^2, ant. post.	—	—	31+	38	35
transv.	—	—	23	24	23
protocone, ant. post.	—	—	8	9.5	7
transv.	—	—	5	7	4
P^3, ant. post.	24	25	25	25	26
transv.	27	28	25	26	25
protocone, ant. post.	—	9.5	7.5	9	7.5
transv.	ca. 6	6	5	7	4
P^4, ant. post.	22	23	23	26	24
transv.	26	—	24	28	25
protocone, ant. post.	—	9	6.5	9	7.5
transv.	ca. 6	6.5	4	6.5	4
M^1, ant. post.	—	21	20.5	22	22.5
transv.	—	27	23.5	27	25
protocone, ant. post.	—	9	7	10	7.5
transv.	—	5.5	4.5	6	4

In the P^4, the external wall of which is lost, the hypoglyph (the fold between hypocone and metaconule) does not show at all; in the less worn P^3 it is still shown as a small enamel island. The inner and outer fossette borders are less wrinkled than those in P^3, and there are traces of about four posterior prefossette plis, an indication of the pli caballin, and a protocone that is still isolated from the protoconule and slightly shorter and wider than that in the P^3. The M^1, which is worn down to 10 mm and lacks only some cement antero-externally and postero-internally, the parastyle is small (a molar character), the mesostyle long and somewhat recurved backward. The fossette plications can be seen only in the adjacent borders of the prefossette and the postfossette as weak folds, similar to those in the P^3 and the P^4: there are about four in the posterior border of the prefossette, and one or two in the anterior border of the postfossette. The protocone is as long as in the premolars but narrower transversely. No hypoglyph is apparent in this very advanced stage of wear, and the wrinkling of the anteroposterior fossette borders is very indistinct. In the M^1 of the type skull of *H. turkanense*, which is slightly less worn down (crown worn to about 12 mm of height), the fossette plications are more numerous, and the protocone a bit larger occlusally. The measurements of the teeth of L 11751 are included in table 2, along with those of the Langebaanweg skull L 22187 and of the Lothagam (*H. turkanense*) and Kanapoi (*H. primigenium*) teeth, the latter taken from

Hooijer & Maglio (1974, table 2). The plication numbers of the Lothagam and Kanapoi cheek teeth are also given in Hooijer & Maglio (1974: 12 and 14); they are of the same order as those in the Langebaanweg specimens dealt with in the present paper; in advanced stages of wear, such as in the type of *H. turkanense* and L 11751, they are smaller, or obliterated.

In Hooijer & Maglio (1974: 13) it was stated that the differences between *H. primigenium* and *H. turkanense* upper cheek teeth are that in the latter the amplitude of the fossette plications is smaller, the anteroposterior fossette borders thrown into small wrinkles, and the protocones somewhat wider than those in *H. primigenium*. These differences were considered possibly the result of the *H. turkanense* dentition being the more worn down of the two, but it was concluded that the two species are distinct, one (*Hipparion primigenium*) having a preorbital fossa, and the other (*H. turkanense*) being devoid of a preorbital fossa. The upper dentition from Kanapoi (KNM-KP 43) agrees in enamel complexity with the juvenile skull from Ekora (KNM-EK 4) that has a preorbital fossa.

Another Langebaanweg upper dentition, L 11222, throws more light on the question as to whether the two species differ in their upper teeth, and this specimen will now be considered.

L 11222 comprises four upper incisors and five upper cheek teeth all evidently of one and the same individual. They derive almost certainly from Bed 3. The incisors, I^{1-3} sin. (pl. 2 fig. 4) and I^3 dext., are less worn than those in skull L 22187, only to some 35-40 mm from their bases externally, and so are the other teeth, P^{2-3} and M^1 sin., and P^{3-4} dext. (pl. 2 fig. 1-3). The crown height of the M^1 is 19 mm externally, and thus the individual age of the dentition is intermediate between that of the Kanapoi dentition referred to *H. primigenium* KNM-KP 43 (worn height of M^1 36 mm) and that of the *H. turkanense* dentition KNM-LT 136 (worn height of M^1 approximately 12 mm). The cups of I^2 and I^3 are much larger than those in skull L 22187; the occlusal width of I^1 (not preserved in L 22187) is 13 mm, that of I^2, 17 mm, and that of I^3, 18 mm. The labiolingual occlusal diameters of I^{1-3} are 12, 11, and 10 mm, respectively. The cement-filled cups are sub-oval, transversely extended, wider labiolingually internally than externally, weakly constricted in the middle. Near the base all three reduce to a transverse diameter of 11 mm, and a labiolingual of 13 mm. Again, it will be seen that I^3 is not reduced in size relative to I^2, as is the case in the advanced Pleistocene hipparions of Africa.

P^2 of L 11222 has three anterior and four posterior plications in the prefossette, and in the postfossette there are three anterior and at least one posterior plication (the posterior border of the postfossette is lost as a result

of interproximal wear). For brevity's sake such plication counts will be given in the following pages thus: 3 - 4 - 3 - 1 +. The protocone is in contact with the protoconule, and thus has very nearly become confluent with the remainder of the crown occlusally. This also occurs in the P^2 of the type of *H. turkanense*: Hooijer & Maglio, 1974, pl. 2. The amplitude of the fossette plis is greater than in the latter specimen, and the prefossette especially is wider. In P^3 the fossette plis number 2 - 6 - 4 - 1, and the protocone is slightly shorter than that in P^2; there is a single pli caballin. The P^4 has a pli count thus: 1 - 5 - 7 - 2; the protocone is even more shortened than that in the preceding tooth. The pli caballin is single. The amplitude of the plications is less great than that in its homologue of the Kanapoi dentition (Hooijer & Maglio, 1974, pl. 3). Finally, M^1, with 1 - 6 - 4 - 1 for the pli count, has a protocone slightly larger than that of P^4. The amplitude of the fossette plications is intermediate between that in the Lothagam and Kanapoi dentitions previously figured (Hooijer & Maglio, 1974, pls. 2 and 3). There is no pli caballin. The crown and protocone measurements are included in table 2 (middle column).

In conclusion, then, the dentition L 11222 is intermediate in enamel pattern complexity between that of the type of *H. turkanense* (the more worn dentition) and that of *H. primigenium* from Kanapoi (the less worn dentition). This is an indication that the difference in enamel complexity between *H. turkanense* and *H. primigenium* as stated in Hooijer & Maglio (1974) is in actual fact the result of individual age differences, and not a character that may be taken as of specific value. This conclusion is further borne out by the study of the remainder of the Langebaanweg upper *Hipparion* teeth, to be given in the pages that follow.

The upper dentition from 'E' Quarry

There are some upper incisors in the 'E' Quarry collection. An I^2 dext., L 10954, is associated with a series of lower cheek teeth $P_2 - M_2$ to be mentioned further on. The incisor is lightly worn; the crown height is 45 mm, and the occlusal surface 18 by 9 mm. An I^3 sin. associated with a mandible and much postcranial material, all numbered L 20541, is 30 mm in worn crown height, 18 by 9 mm occlusally, with a cup subdivided into a large medial and two small lateral portions: in this specimen the basal diameter is 10 mm. An upper anterior premolar, L 20553, likewise belongs to a mandible with teeth and to postcranials bearing the same number. Then, there are isolated P^2, L 2100, L 13314, and L 24611. All these four specimens of P^2 are from the left side, and their dimensions are presented in table 3.

The amount of wear is very different in this series of specimens: the

TABLE 3

Measurements of P^2, 'E' Quarry, Langebaanweg (mm)

	L 20553	L 2100	L 13314	L 24611
Ant. post.	33+	33	32	35
Transv.	24	23	23	24
Protocone, ant. post.	8.5	7	7	8
transv.	5	—	5	—

individually youngest specimen, L 24611, has an external crown height (taken at the mesostyle) of no less than 55 mm; L 13314 is worn to 46 mm of crown height; L 2100 is worn down to 42 mm, and L 20553 to 18 mm as worn. The P^2 of L 11222 is worn to the same height as the last-mentioned specimen, and that of the type skull of *H. turkanense* to only some 10 mm. Therefore, we have a series of six specimens of P^2 of various ages at death. The measurements have been taken at two cm from the crown base (my usual practice, as in Hooijer, 1975), except when the tooth is in situ; it then has to be taken at the alveolar border as, e.g., in the type skull of *H. turkanense*. Some authors take the tooth diameters at the top of the crown, others very close to the base, or just half way the height of the crown no matter how much the crown is worn down. This is one of the difficulties in using the existing data in the literature on *Hipparion*, for measurements should of course be taken in a consistent manner in order for them to be of value for comparison between different forms. The transverse diameter of uppers is taken across protocone and mesostyle, likewise at two cm from the base. The protocone is always measured occlusally, as it is usually covered with cement everywhere else. The plication counts are given in table 4. The P^2 of *H. primigenium* KNM-KP 43 (Hooijer & Maglio, 1974: 14), which is worn to about 35 mm (it has not been figured in Hooijer & Maglio, 1974, but figures in a later paper: Hooijer, 1975, pl. 6 fig. 1), is included in this table between L 20553 and L 2100.

TABLE 4

Plication counts of P^2 from Lothagam, Kanapoi and Langebaanweg

	Prefossette		Postfossette	
	ant.	post.	ant.	post.
KNM-LT 136	2-5	4	3-4	1-2
L 11222	3	4	3	1+
L 20553	4	5	3	2
KNM-KP 43	5	6	4	1
L 2100	5	5	6	1
L 13314	4	3	3	1
L 24611	6	2+	1+	1

The plication counts in KNM-LT 136, the type of *H. turkanense*, are not simple figures as the teeth on both sides of the skull could be measured, and the counts are never exactly the same on the two sides, showing, incidentally, the relative value of such counts. Markedly bifurcated or trifurcated folds are counted as two, or three, but every fold is counted, no matter how small it is. In L 24611 the plis in the adjacent borders of prefossette and postfossette cannot be exactly given because of damage.

The variation in plication numbers appears insignificant, although they are taken at very different wear stages. So are the variations in crown dimensions. The specimen that is worn most, the Lothagam P^2, is at the same time the anteroposteriorly longest specimen, but this is mere coincidence. The variation in anteroposterior diameter, which is from 32 (L 13314) to 38 mm (KNM-LT 136; table 2 of the present paper) is not at all excessive, depending as it does on the development of the prolongation of the crown in front of the parastyle. This development is rather slight in L 13314, and large in L 24611 and KNM-LT 136. In a series of P^2 from Olduvai Bed II representing *Hipparion* cf. *ethiopicum* (Joleaud), the advanced Pleistocene *Hipparion* of Africa, the anteroposterior diameter varies from 25 to 33.5 mm (Hooijer, 1975: 39). The transverse diameter of the Langebaanweg P^2 varies only from 23 to 24 mm; in a P^2 from the Aterir Beds of Kenya, however, (Hooijer, 1975, table 2) the transverse diameter is 25.5 mm; this is a specimen worn to 45 mm of height and it has been referred to *H. primigenium* just as the Kanapoi specimen. In *H.* cf. *ethiopicum* from Bed II of Olduvai the P^2 varies from 22 to 24.5 mm transversely (Hooijer, 1975: 39). It seems, therefore, that the Langebaanweg 'E' Quarry P^2 may all represent the same species, and they are indistinguishable from *H. primigenium* specimens described as such from Kanapoi and the Aterir Beds, as well as from *H. turkanense*.

Among the isolated P^3 and P^4 from 'E' Quarry, with their broad parastyles (broader than the mesostyle), there is a left specimen, L 4768, worn to 45 mm of height, with particularly well-developed plis that seem to fill the whole of the prefossette, in the fashion of the Kanapoi dentition (Hooijer & Maglio, 1974, pl. 3). The pli count is 1 - 8 - 5 - 1, and there is a single, large pli caballin. An incomplete $P^{3,4}$ dext. (the internal portion is missing), L 20260, about 35 mm high as worn, has plis numbering 2 - 7 - 5 - 1, and they are slightly less long than those in the preceding specimen. A $P^{3,4}$ dext., L 11982 (almost certainly from Bed 3), again individually older, worn to 22 mm of height, with plis much the same in number (2 - 7 - 4 - 1) but shorter still, has the pli caballin less long also. In the most worn specimens, the P^{3-4} of the maxillary portion also holding M^1, L 11751, the plis are

minute and the anteroposterior fossette border wrinkling begins to show that is so conspicuous in the P^{3-4} of the type skull of *H. turkanense* KNM-LT 136 (Hooijer & Maglio, 1974, pl. 2). These observations show, once more, that the simplified pattern considered characteristic of the upper cheek teeth of *H. turkanense* may not be considered a specific character but is the result of the very advanced wear of the teeth as compared to those referred to *H. primigenium*.

An almost unworn crown of a $P^{3,4}$ sin., L 3358, has the base preserved between mesostyle and metastyle, and the full height is 65 mm. This tooth is very interesting as it shows how much the anteroposterior crown diameter decreases rootward: it is maximal near the top, 25.5 mm, reducing to 22 mm at two cm from the base, while the transverse diameter is 22.5 mm at the same level. The resulting height/width index is 290. Pli counts cannot be given. There is further the external portion of a $P^{3,4}$ dext., L 21952 (pl. 6 fig. 4), which is from Bed 1, with a complicated enamel pattern (5 - 10 - 7 - 2) looking rather much like those figured by Hooijer & Maglio (1974, pl. 3) from Kanapoi. The anteroposterior diameter, taken as always at two cm from the crown base, is 27 mm (26 mm in the P^3 of the Kanapoi dentition and in the P^4 of the Lothagam dentition). The transverse diameter cannot be given. The height to which the tooth L 21952 is worn is approximately 40 mm. It is evidently at this medium stage of wear that the fossette plications show their greatest development. In the least worn of the $P^{3,4}$ mentioned above, L 4768, the anteroposterior diameter of the crown reduces from 24.5 to 22.5 mm rootward, and the complexity of the fossette pattern on the occlusal surface is striking.

The anteroposterior crown diameters of the $P^{3,4}$ from Langebaanweg 'E' Quarry are thus seen to vary from 22 to 27 mm, always taken at two cm from the base. This is not an unusually wide range of variation: in the $P^{3,4}$ of *H.* cf. *ethiopicum* from Olduvai Bed II this dimension varies from 22.5 to 25.5 mm (Hooijer, 1975: 40).

Among the isolated upper molars of 'E' Quarry, easily recognizable by their parastyles being subequal to the mesostyles, there are a right and a left specimen of $M^{1,2}$, L 6283 and L 9143, of the same individual. The crowns are slightly worn, and the base of the mesostyle fortunately is preserved in the left specimen (L 9143), giving a mesostyle height of 75 mm. From the tips of the external cusps, the paracone and the metacone, a few mm of which are worn off, down to the base the full crown height must have been just 80 mm. The anteroposterior crown diameter reduces from 25 mm apically to 21 mm at two cm from the base, while the transverse diameter remains 21 mm throughout. The height/width index of L 9143, calculated

in the same way as that of the $P^{3,4}$ of the 'E' Quarry L 3358, is 380. This is much higher than that of the premolar, and the result of the actual crown height of the molar being greater, and the transverse diameter being less than that of the premolar. No plications can be observed on the unworn (or nearly unworn) crown surface.

A slightly worn $M^{1,2}$ dext. from the peat bed of the Quartzose Sand Member (= Bed 2), L 21558, has a crown height of 65 mm, with plications 2 - 6 - 4 - (?) 1, and a protocone 10 by 3.5 mm occlusally. The long, single pli caballin extends nearly across the protoconal valley. The crown diameters at two cm from the base are 22 by 22.5 mm. An $M^{1,2}$ sin., L 24842, worn to 43 mm of height, pli count 3 - 9 - 4 - 1, single pli caballin, has a protocone 7 by 4 mm in diameters, and the crown diameters at two cm from the base are 22 by 22.5 mm. An $M^{1,2}$ dext., L 21869, is incomplete at the base and internally except at the top, where the crown dimensions are 26 by 22 mm. In this specimen, which is very slightly worn, the protocone is, again, rather long: 9.5 by 3.5 mm; the plications are just beginning to show and cannot be counted. On the other hand, an $M^{1,2}$ dext., L 25046, worn down to less than 10 mm, has the protocone confluent with the protoconule, and the plications in the fossettes are very minute. The protocone measures 9 by 6 mm. The transverse diameter is 25 mm; the anteroposterior, much reduced because of interproximal wear, only 21 mm, just as in L 11751.

A number of $M^{1,2}$ from 'E' Quarry are not well preserved ($M^{1,2}$ dext.: L 12054, L 12087, and L 22317 (the latter is from Bed 1); $M^{1,2}$ sin.: L 22169, L 21811, and L 21920; the last-mentioned from Bed 1), and no useful information can be gained from them. A rather interesting specimen is L 5353, an $M^{1,2}$ dext. worn to only 15 mm from its base but showing some eight sizable folds posteriorly in the prefossette, while the protocone has just become confluent with the protoconule, as happens in *Hipparion* cheek teeth in extreme wear (such as in the P^3 of skull L 22187). This is why the specimen has originally been regarded as representing *Equus* (Hendey, 1970a: 102, pl. 3 E), and a small species at that, an identification later (Hendey, 1970b: 124) corrected to *Hipparion*. The occlusal crown diameters, taken lower down than usually, viz., at 15 mm against two cm from the base in less worn specimens, are 21 by somewhat over 21 mm (mesostyle not complete occlusally). Although the molar looks rather small, it is not really as small as it appears to be when properly compared to its homologues in the 'E' Quarry collection.

The Bed 1 specimens from 'E' Quarry are not significantly different from those of the other units of the Varswater Formation. There is no evidence for the presence of more than one species of *Hipparion* at 'E' Quarry.

An incomplete $M^{1.2}$ sin. from 'C' Quarry, L 958, is worn to 20 mm of height, and still shows a rich fossette plication pattern (3 - 6 - 3 - 1). The anteroposterior diameter is 22 mm, the transverse cannot be given as the protocone is missing in part. This specimen in itself is indistinguishable from those of 'E' Quarry.

There are two specimens of M^3 in the 'E' Quarry collection. L 25027 is an M^3 dext. worn to 25 mm at the mesostyle, pli counts 1 - 6 - 5 - 2, bifurcated pli caballin, crown dimensions 25 by 23 mm, protocone 9 by 5 mm. L 21066 is much worn down, with a portion of the maxillary attached to its posteriorly recurved roots. This M^3 dext. is worn along an oblique plane, which makes it appear very long: 27 by 22 mm occlusally. The protocone is 11.5 by 5.5 mm. There are three anterior and six posterior plis in the prefossette, but in the postfossette none can be distinguished. The protocone is still isolated although the mesostyle height is less than 10 mm.

The upper milk dentition is represented in the 'E' Quarry collection by the slightly worn DM^{2-3} sin. in situ in a juvenile maxillary fragment with a preorbital fossa, L 21823 (pl. 5 fig. 1) as well as by an isolated DM^3 sin., L 11983, the latter almost certainly from Bed 3. The prolongation anterior to the parastyle is incomplete in the DM^2, and the metastyle of the DM^3 in L 21823 is missing. In their plication pattern these milk molars are rather complex, and also in size they correspond with the Ekora milk molars KNM-EK 4, in which the crowns are somewhat further worn down (Hooijer & Maglio, 1974, pl. 4 fig. 3). The protocones in the Langebaanweg DM^{2-3} are less rounded than those in the Ekora specimen, a result of the more worn stage of the latter. The measurements are given in table 5. Also included in this table are a DM^{3-4} dext. from 'C' Quarry, L 11718 and L 11717. These specimens were described by Boné and Singer (1965: 368-369, pl. VIII B and A) as a right DM^2 and a right DM^3, respectively, while in reality they represent DM^3 and DM^4; the antero-external portion of the DM^3 dext. shown missing in Boné & Singer's illustration (pl. VIII B) has since been recovered and restored to the specimen. Their illustrations are excellent

TABLE 5

Measurements of deciduous upper molars (mm)

	L 21823	L 11983	KNM-EK 4	L 11717/8
DM^2, ant. post.	—	—	34	—
transv.	23.5	—	22.5	—
DM^3, ant. post.	ca. 29	28	28	30.5
transv.	24.5	22	23.5	27.5
DM^4, ant. post.	—	—	30	31.5
transv.	—	—	23	26

otherwise. The plications in the posterior border of the prefossette vary from 6 to 8 in number, those in the anterior border of the postfossette from 2 to 5; the pli caballin may be single or double but always long, almost touching the protocone. The protocone is elongated, becoming more rounded as wear advances. The hypocone is almost completely constricted off in early wear. These are the features of the upper milk molars of *H. primigenium* as figured by Forstén (1972: 12) from the Vallesian Beglia Formation in Tunisia. $DM^{3,4}$ of *Hipparion* cf. *ethiopicum* from Olduvai Bed II vary from 26 to 31 mm anteroposteriorly, and from 22 to 24.5 mm transversely (Hooijer, 1975: 34, 48).

Having finished with the upper dentition of the *Hipparion* from 'E' Quarry, the question to be considered is whether, with the knowledge now gained that the dentitions in the skulls of *H. turkanense* and *H. primigenium* are in fact indistinguishable, the remaining skull distinction, viz., that *H. turkanense* is devoid of a preorbital fossa while *H. primigenium* has one, constitutes a valid character for retaining *H. turkanense* as a distinct species. The lower teeth may be left out at this juncture, although they will be considered later, for the lowers in the Lothagam-Kanapoi collection are merely referred specimens, none of them having been found in direct association with the skull of *H. turkanense* or with that of *H. primigenium*.

The preorbital fossa in *Hipparion* and the later equids in general has received much attention in the literature, but the taxonomic significance of these fossae has been shrouded in doubt and contradiction (Webb, 1969: 135-138). It has been stated that the preorbital fossae are strong in males, and feebly developed in females (Osborn), that they may be subject to considerable individual variation (Pirlot) but also that the fossa is constant, although ranging from shallow to deep, in large single-quarry samples of a single species (Wehrli, Webb). It is even consistent in skulls representing a single species from scattered localities (*Pseudhipparion gratum* (Leidy): Webb, 1969: 136). The interpretation that females lack, and males have the best developed fossae is not supported by available data. In *H. primigenium* the fossae vary but are usually well-developed, placed rather far in front of the orbits (Forstén, 1968: 15), as in the juvenile Ekora skull KNM-EK 4 described by Hooijer & Maglio (1974: 13-15, pl. 4). The teeth of this skull, DM^{2-4} in wear, as well as the sectioned M^1 (l.c.: 14, pl. 5 figs. 1-3), are indistinguishable from those of *H. primigenium*: the M^1 has the same degree of hypsodonty (height/width index 300), and the enamel pattern of that species, the pattern simplifying at levels closer to the base.

It should be mentioned that, if *Hipparion platygenys* Gromova from Taraklia is correctly synonymized with *H. primigenium* by Forstén (1968:

14), then in *H. primigenium* the preorbital fossa may occasionally be lacking altogether; the skull of *H. platygenys* is devoid of a preorbital fossa. This may be an isolated occurrence; the preorbital fossa is lacking, too, in one of the Chinese Pontian forms, *Hipparion hippidiodum* Sefve, in the Chinese Villafranchian *Proboscidipparion sinense* Sefve, and in the Spanish Villafranchian *Hipparion crusafonti* Villalta (Hooijer & Maglio, 1974: 12). To this we may add that in the advanced *Hipparion* of the Pleistocene of Africa, so-called *Stylohipparion*, there is no trace of a preorbital fossa, a character that this form has in common with *H. turkanense* (Hooijer, 1975). In this case, again, it does seem that the fossa is lacking in both sexes, and therefore is not a sex-linked character.

If the difference between the skull of *H. primigenium* and that of *H. turkanense* would be considered merely a secondary sexual difference it should be noted that both the Lothagam type of *H. turkanense* and the otherwise dentally similar skull from Langebaanweg L 22187 do have canines. In modern horses the presence of a big canine is a male character, but in *Hipparion* both sexes do have canines, at least the European Tertiary ones. In this connexion, Pirlot (1952) has suggested that there is sexual dimorphism in these elements; the laterally compressed canines would be indicative of males, while the females would have canines that are smaller, and round in section. Both the type skull of *H. turkanense* and skull L 22187 have laterally compressed canines, of much the same size (*H. turkanense:* 8 by 5 mm; L 22187: 7 by 3+ mm). Therefore, if we accept Pirlot's criterion, both would represent male individuals.

In the advanced, Pleistocene *Hipparion* of Africa canines are not developed at all, neither in the upper nor in the lower jaws from Olduvai Bed II, Cornelia, or Laetolil (Hooijer, 1975: 30). The skulls of the advanced *Hipparion*, characterized by their reduced I^3 and I_3 and great hypsodonty and evidently showing the final trend of evolution in the genus *Hipparion* in Africa, do not show any trace of a preorbital fossa either (Hooijer, 1975: 29, 32). It does seem that canines and preorbital fossae are absent in either sex of the Pleistocene *Hipparion*.

The mandibles from 'E' Quarry

One of the mandibles from 'E' Quarry, L 20541, holds the left I_{1-3} and P_{2-4}, (pl. 6 fig. 2), the body of the mandible being almost completely missing on the right side although P_2 dext. is separately preserved. The left body is broken behind P_4, but the ascending ramus is mostly there, with a large part of the coronoid process, the condyle almost undamaged, while the angle is incomplete. The length of the symphysis is 88 mm, measured ventrally; the

least width, 35 mm; the I_3-P_2 diastema is 95 mm, not very much shorter than the diastema in the skull L 22187. There is no trace of a canine. The height of the symphysis at the mental foramen, which is some 40 mm in front of P_2, is 40 mm; the height of the body at P_3 is 65 mm, measured externally. Another mandible from 'E' Quarry, L 20553, has the full set of incisors (pl. 6 fig. 1) measuring 65 mm transversely over the occlusal surfaces (the width taken over the lateral edges of I^3 in the skull L 22187 is exactly the same). There are no cheek teeth in situ in the symphysial portion, but the alveolus of the right P_2 is partially preserved, and the I_3-P_2 diastema is just 100 mm. There is no trace of a canine. The mandibular height at the mental foramen, 35 mm in front of the alveolus for P_2, is 45 mm. The length of the symphysis, not well preserved at either end, must have been about 80 mm, and the least width of the symphysis is 40 mm. The right M_3 is all that is left of the cheek tooth series from that side, but the left M_{1-3} are in situ in a body fragment without the lower edge (pl. 5 fig. 3) extending to the coronoid process but without the condyle. The portion of the right ascending ramus includes the condyle and the coronoid process. Both mandibles would have fitted the skull L 22187 for size. The length P_{2-4} in L 20541 is 75 mm; the length M_{1-3} in L 20553, just the same, which would make for a total lower cheek toothrow length of 150 mm, certainly not very different from the length P^2-M^3 in skull L 22187 had the full complement of cheek teeth been there. A third mandible in the 'E' Quarry collection, L 13102 (pl. 4 fig. 2) has the DM_4 but with its roots resorbed and P_4 appearing above the alveolar margin; M_3 had just cut the gums. The teeth will be dealt with in a later section. Only the total length P_2-M_3 may be given, which is 160 mm when measured along the alveolar border. As wear advances, the total cheek toothrow shortens as a result of interproximal wear and the anteroposterior diameters of P_3-M_2 decreasing rootward. In addition to the right body of the mandible with the teeth, 67 mm high externally at P_3, there is part of the left ascending ramus with the incomplete coronoid process and the condyle, which measures 50 mm transversely.

The lower dentition from 'E' Quarry

Before we embark upon a discussion of the 'E' Quarry lower *Hipparion* teeth it may be well to review the situation as it was after the publication on the Lothagam-Kanapoi *Hipparion* material by Hooijer & Maglio (1974). In that collection there were two types of lower cheek teeth, unassociated with uppers or with the skulls, of which one without ectostylids and with wrinkled enamel in the flexids and buccally all along the height of the crown (Hooijer & Maglio, 1974, pl. 7), and the other with well-developed ecto-

stylids and less wrinkled enamel. Since *H. turkanense* was taken at the time to differ from *H. primigenium* in the more wrinkled enamel of the upper cheek teeth, and since *H. primigenium* already had some ectostylid development in the Vallesian, it was considered most expedient to associate the first type of lowers with *H. turkanense* and the second with *H. primigenium*. The lower cheek teeth were thus divided amongst these two species (Hooijer & Maglio, 1974: 17), with the exception of the small lowers, which, like the small uppers in the Lothagam-Kanapoi collection, were placed as *H.* cf. *sitifense* Pomel, a pre-Villafranchian North African form the skull of which is unfortunately unknown, and which, therefore, we cannot classify properly.

The *Hipparion* material that was described from the Lothagam-Kanapoi collection, which is in the 6 to 4 million year time interval, may be interpreted in two alternative ways, depending upon whether more value is placed upon ectostylid development, or on that of the preorbital fosa. In the Eurasian *H. primigenium* it seems (Forstén, 1968: 24) that ectostylid and protostylid, maximally developed in the Vallesian population of *H. primigenium*, diminished later, in the populations of the Pikermian. In sub-Saharan Africa, one development may be envisaged in which ectostylids continued to develop, leading up to the advanced, Pleistocene *Hipparion*, "*Stylohipparion*". Then, the preorbital fossa got somehow lost in the process. The other possibility is to derive "*Stylohipparion*" from *H. turkanense*, which is devoid of a preorbital fossa just as is "*Stylohipparion*", and then the ectostylid developed only in the last four million years. In either case the pattern of the "tie" (metaconid-metastylid) became more caballoid, with pointed rather than rounded loops, although the degree of hypsodonty remained much the same as that in the Vallesian *H. primigenium*. The description of the Ngorora Formation *Hipparion*, which is truly Vallesian in age and characters (Hooijer, 1975: 12-15), shows that it is the primordial Old World *H. primigenium*, with rounded metaconid-metastylid loops, and ectostylids, if shown, slightly developed. Lower cheek teeth from the Chemeron Formation resemble Lothagam-Kanapoi specimens referred to *H. primigenium* (Hooijer, 1975: 18). Lowers without ectostylids from the Mpesida Beds, the Lukeino Formation, and the Mursi Formation are like the Lothagam-Kanapoi specimens referred to *H. turkanense* (Hooijer, 1975: 19-22).

The great majority of the Langebaanweg lower cheek teeth show no ectostylids, but they are not invariably absent: some lower premolars found at a site between 'E' and 'C' Quarries in 1975, considered to be from the uppermost level of Bed 3 and identified as *Hipparion* cf. *namaquense* in the present paper, do show them.

In both L 20541 and L 20553, the best 'E' Quarry samples, associated with

postcranial material, there are lower incisors and cheek teeth in situ, the I_{1-3} sin. in L 20541, and those on both sides in L 20553 (pl. 6 fig. 1). These sets show that the third incisors are not reduced in size as compared to the second, which is the same condition as that seen in the upper jaw, and different from that in the advanced, Pleistocene "*Stylohipparion*" in which the lateral incisors are much reduced (Hooijer, 1975: 30, 34-35). On the occlusal surfaces the large, cement-filled pits are seen; the transverse diameters of I_1, I_2, and I_3 are 14.5, 15.5, and 14 mm occlusally in L 20553, and 12, 14, and 15.5 mm in L 20541, the older of the two individuals. The labiolingual diameters decrease slightly as one passes from I_1 to I_3, from 11.5 to 10.5 mm in L 20553, and from 11.5 to 10 mm in L 20541, measured on the occlusal surface.

The Langebaanweg *Hipparion* has been described by Boné & Singer (1965: 390) as characterized by the constant absence of the ectostylid, but, while this holds good for the Baard's and 'E' Quarry specimens this is not always the case (L 24197, vide infra). Attention is further drawn by Boné & Singer to the tendency to form "other additional stylids, especially protostylid extending along the total height of the crown" (l.c.). Now this is not correct: the protostylid is never developed all along the height of the crown. Although they are distinct in all the teeth, unworn specimens show that these antero-external pillars do not quite reach the top of the crown. Protostylids are the distinguishing feature of *Hipparion* lower cheek teeth.

Apart from premolars and molars in situ, there are isolated lower cheek teeth, some of which forming sets that evidently belonged to single individuals. In distinguishing between $P_{3,4}$ and $M_{1,2}$ the following feature should be observed: the anterior and the posterior internal enamel infoldings, metaflexid and entoflexid, approach each other very closely in the premolars, and the outer groove between protoconid and hypoconid is not deep, whereas in the molars the outer groove extends further inward toward the groove between metaconid and metastylid, and separates the two flexids: hence the entoflexid is smaller in the molars than in the premolars. The molars are less wide transversely than the premolars, too, and the curvature is different: the premolars being somewhat recurved forward at their lower end and the molars recurved backward, but these characters are of little avail in isolated or much worn cheek teeth. No attempt has been made to distinguish between P_3 and P_4, or between M_1 and M_2, if unassociated.

The P_2 is the lowest-crowned of the mandibular cheek teeth: the P_2 of the set P_2-M_2 dext., L 10954 (pl. 3) is practically unworn, and its full crown height is only 52 mm, whereas the P_3 of the same set has a full crown height of 63 mm. Since the P_2 is longer anteroposteriorly than the P_3 (28 mm as

opposed to 25.5 mm in P_3, measured at two cm from the crown base), the height/length index of the P_2 is only 190, against 250 in the P_3. The P_4 of the set L 10954, although likewise unworn, is incomplete at the base, but the P_4 of the mandible L 13102 is unworn and has the base preserved: its full height is 75 mm by an anteroposterior diameter of 24.5 mm, giving a height/length index of 310. The M_2 of the set L 10954, again, is slightly worn; its crown height is the same as that of the P_4, 75 mm, but the anteroposterior diameter at two cm from the base is only 21.5 mm, which gives a height/length index of 350. This lower molar from Langebaanweg is higher than an unworn M_1 in situ in a mandible of *H. primigenium* from Lothagam, 60 mm in total crown height and 20 mm anteroposteriorly, height/length index just 300 (Hooijer & Maglio, 1974; 18-19, pl. 6 figs. 3-4). Finally, the unworn M_3 of L 13102 can be measured: it is 65 mm high and 26 mm anteroposteriorly at two cm from the base, giving a height/length index of 250. Thus, the indices are seen to vary considerably depending on the serial position of the tooth.

The vertically wrinkled appearance that characterizes the outer enamel surface of the referred lower cheek teeth of *H. turkanense* (Hooijer & Maglio, 1974, pl. 7) shows, to a less degree, in the set P_2 - M_2 L 10954 (pl. 3), in places where the cement investment is lost. It varies in intensity in the collection of lower cheek teeth. The wrinkled appearance of the enamel borders of the flexids is seen only in early wear stages, and is no longer so marked in cheek teeth that are more worn down.

In the Lothagam-Kanapoi collection some teeth had ectostylids, e.g., the M_1 from Lothagam in situ in a juvenile hemimandible that has a weak, slender ectostylid extending only 45 mm upward from the base of the crown (the total crown height is 60 mm), and there are some worn premolars and a molar with better developed ectostylids; in a mandibular portion with P_3 - M_2 from Kanapoi ectostylids were seen that likewise do not extend along the full height of the crowns, being only some 45 to 50 mm in height (Hooijer & Maglio, 1974: 16-18). In specimens from the Chemeron Formation there are ectostylids, but these are some 50 mm high only, while the full height of a $P_{3,4}$ is just over 70 mm (Hooijer, 1975: 18-19). These specimens have been referred to *H. primigenium* just as the Kanapoi-Lothagam ones with ectostylids. The loops in these teeth, just as those of metaconid-metastylid of the Langebaanweg teeth, are not rounded, but pointed (this is more marked in P_{3-4} than in P_2 of the set L 24197), the caballoid pattern referred to above. The ptychostylid, which is a stylid completely free from the ectostylid, if any (see Hooijer & Maglio, 1974, pl. 6 fig. 2), is best developed in the top portion of the crowns, as the

slightly worn and little cement-invested P_2-M_2 L 10954 show (pl. 3). In lowers with a marked exterior wrinkling of the enamel the ptychostylids are not very conspicuous, and in specimens worn to some degree they may not be evident at all.

L 2546, a mandibular portion with P_3-M_1 in situ, well worn down, shows the pointed loops of metaconid-metastylid; the anteroposterior diameters of the teeth are much as in L 20541 and L 20553, and the molar is narrower than the premolars, as is normal in one and the same dentition. Two teeth, L 13104 and L 13103, evidently belong to a single individual; P_3 is worn to 25 mm, P_4 to 35 mm of height. They slightly exceed those of the other P_{3-4} in dimensions. A left P_4-M_1 in situ, L 22674, is too much damaged for measurement. An isolated P_2 sin. L 20259, worn to 35 mm of height, appears rather large (table 6). However, the variation in size of the lower premolars of *Hipparion* cf. *ethiopicum* from Olduvai Bed II is such (P_2 27-32 mm anteroposteriorly and 14-17 mm transversely; P_{3-4} 22-27 mm anteroposteriorly and 13-17.5 mm transversely: Hooijer, 1975: 43, 44) that the variation in the Langebaanweg premolars does not appear to exceed the limits found in a single population. Two isolated M_3 sin., L 2545 and L 20907, do not differ more in anteroposterior diameter than do those of L 20553 and L 13102. In *H.* cf. *ethiopicum* from Bed II of Olduvai M_3 varies in anteroposterior length from 25 to 29 mm (Hooijer, 1975: 47). Some isolated $P_{3,4}$ and $M_{1,2}$, L 3140, L 12865, L 13423, and L 24610, are also listed in table 6. The measurements of the lower premolars L 24197, which are not from 'E' Quarry, and which possess ectostylids, are given in table 6, too. They tally well in size with those from 'E' Quarry.

A slightly worn $M_{1,2}$ dext. from the peat bed of the Quartzose Sand Member (= Bed 2), L 22547, has a crown height of 65 mm, and reduces in diameters from 27 by 14 mm at the top to 23 by 12 mm at two cm from the base.

The lower deciduous dentition DM_{2-4} is in situ in a mandible L 21571 (pl. 4 fig. 1 and pl. 5 fig. 2). The milk molars have well-marked ectostylids as they do in all species of *Hipparion*, including those that do not sport ectostylids in the permanent dentition. These teeth are slightly worn, and M_1 is unerupted. There are further two isolated $DM_{3,4}$: L 21489, from the right side, and L 10965, from the left. L 21489 is from the peat bed of the Quartzose Sand Member (= Bed 2) as are one upper and one lower $M_{1,2}$ mentioned above, characterized by its dark brown colour. Finally, there is the much worn crown of the DM_4 dext. of the mandible L 13102. The ectostylid in the DM_3 is duplicated, consisting of two separate enamel islets the anterior of which is the smaller. The ectostylid of DM_2 measures 4.5 by

TABLE 6

Measurements of lower cheek teeth, Langebaanweg (mm)

	L 20541	L 20553	L 10954	L 13102	L 24197
P_2, ant. post.	26.5	—	28	28	29
transv.	14.5	—	12.5	14	14
P_3, ant. post.	25.5	—	25.5	26	26
transv.	16	—	13	14.5	15
P_4, ant. post.	24.5	—	25	24.5	25
transv.	16	—	13	13	15
M_1, ant. post.	—	21.5	22	22	—
transv.	—	16.5	12	12.5	—
M_2, ant. post.	—	23	21.5	—	—
transv.	—	16	11	—	—
M_3, ant. post.	—	29.5	—	26	—
transv.	—	15	—	—	—

	L 2546	L 13103/4	L 20259	L 3140	L 12865
P_2, ant. post.	—	—	33	—	—
transv.	—	—	17	—	—
P_3, ant. post.	25.5	28.5	—	25	25
transv.	17.5	16.5	—	15	14
P_4, ant. post.	24	26	—	—	—
transv.	17	15.5	—	—	—

				L 13423	L 24610
M_1, ant. post.	21	—	—	24	24
transv.	15	—	—	13	13

	L 2545	L 20907
M_3, ant. post.	26.5	29
transv.	10.5	13

3 mm occlusally; those of DM_3, 2.5 mm, and those of DM_4, single on the right and double on the left side, a little over 1 mm in diameters. Ptychostylids show in all the teeth, most markedly so in the DM_2, and the protostylids are well-developed in DM_{3-4}. The posterior projection in these low-crowned milk teeth is soon worn off, reducing the anteroposterior diameter considerably; the measurements given in table 7 are taken at the top of the slightly worn crowns, except, of course, those of L 13102.

The DM_{3-4} in situ in a mandible from Lothagam (Hooijer & Maglio, 1974: 18-19, pl. 6 figs. 3-4), worn crowns, are shorter than those of L 21571: the DM_4 is 30 mm long, but when measured below the posterior bulge, slightly below the alveolar margin, the DM_4 of L 21571 is also 30 mm anteroposteriorly. $DM_{3,4}$ of *Hipparion* cf. *ethiopicum* from Olduvai Bed II vary from 28 to 31 mm anteroposteriorly, and from 12.5 to 16 mm transversely

TABLE 7

Measurements of lower deciduous molars (mm)

	L 21571	L 21489	L 10965	L 13102
DM_2, ant. post.	34	—	—	—
transv.	15.5	—	—	—
DM_3, ant. post.	30	31	32	29
transv.	15	15	13.5	16
DM_4, ant. post.	34.5	—	—	—
transv.	14	—	—	—

(Hooijer, 1975: 49). The ectostylids in these specimens terminate in a point about 8-10 mm below the unworn antero-external cusps, and are from 7 to 10 mm anteroposteriorly.

Lower premolars from a site between 'E' and 'C' Quarries

A set of lower premolars, P_{2-4} sin., L 24197, comes from a site between 'E' and 'C' Quarries, and is now considered to be from the uppermost level of Bed 3 (Hendey, 1976: 240). Unfortunately there is no associated material. P_2 is worn to 40 mm, P_3 to 45 mm, and P_4 to 52 mm of height. The teeth (pl. 7 figs. 1-4) are damaged externally, and the thick cement cover is lost in places, showing the enamel to be weakly folded vertically, a grooving that is less marked than that in the teeth referred to *H. turkanense* in Hooijer & Maglio (1974, pl. 7). In contrast to the latter but just as in *Hipparion namaquense* (Haughton), these Langebaanweg P_{2-4} L 24197 possess ectostylids, unlike the other Langebaanweg teeth. They do not show as an enamel point or island on the occlusal surface and were evidently not more than 35 mm high, petering out crownward. The ectostylid in P_4 is cement-covered, but that of P_3 is partially exposed as a very slender stylid, set off from the more yellowish cement. In the type of *Hipparion namaquense*, which is in the South African Museum, ectostylids show occlusally in P_4 dext. (not in P_4 sin.), which are worn to 25 mm of height, as well as in both M_1. In M_2, worn to 30 mm, it still shows on the occlusal surface, but not in M_3, which is 35 mm high as worn. Thus, the ectostylids in *H. namaquense* are only some 30 mm high, or less. The measurements of L 24197 are presented in table 6.

Metapodials from 'E' Quarry

There are several entire median metacarpals and metatarsals in the 'E' Quarry collection. None were mentioned or are available from the Baard's Quarry collection as described by Boné & Singer (1965), and, therefore, they constitute important new material on which to assess the status of the

Langebaanweg *Hipparion*. Of the third metacarpals (table 8) L 20541 is associated with the mandible and teeth and several more limb bones bearing the same number.

TABLE 8

Measurements of median metacarpals from 'E' Quarry (mm)

	L 2148	L 5576	L 20541
Length	217	215	224
Proximal width	40	40	41
Proximal ant. post. diameter	30	32	33
Mid-shaft width	28	31	27
Ant. post., same level	23	24	24
Distal width, greatest	36	36	38
Distal articular width	36	36	37
Distal crest, ant. post.	32	31	32
Distal art. w/l index	17	17	17

Of the four entire median metatarsals from 'E' Quarry (table 9), L 20553 is associated with a mandible and teeth and more postcranials bearing the same number.

TABLE 9

Measurements of median metatarsals from 'E' Quarry (mm)

	L 5899	L 20553	L 21295	L 20554
Length	263	270	260	ca. 260
Proximal width	47	46	42	45
Proximal ant. post. diameter	—	37	35	36
Mid-shaft width	34	29	29	30
Ant. post., same level	33	31	28	30
Distal width, greatest	43	42	37	38
Distal articular width	ca. 42	40	36	38
Distal crest, ant. post.	34	34	33	32
Distal art. w/l index	ca. 16	15	14	ca. 14

As table 10 shows, the Langebaanweg metacarpals are slightly but not significantly longer than those of *H. primigenium* from the Vallesian of Wad el Hammam, and the Langebaanweg metatarsals a little more so. The metacarpals fall within the variation limits of the Olduvai Bed II *H.* cf. *ethiopicum*, which overlap to a small extent those of *H. primigenium* in length but are of the same proportions. The metatarsals are even longer than their homologues in the Olduvai form, which in turn are somewhat longer than the Wad el Hammam specimens, but the proportional width of the shaft is much the same in all. There has evidently been little change in the median metapodials from *H. primigenium* to *H.* cf. *ethiopicum*.

TABLE 10

	H. primigenium Wad el Hammam (Arambourg, 1959)	Langebaanweg Quarry 'E'	*H.* cf. *ethiopicum* Olduvai Bed II (Hooijer, 1975)
Metacarpal III length	198-210	215-224	205-230
Width/length index	17-18	17	15-20
Metatarsal III length	232-240	260-270	242-260
Width/length index	14-15	14-16	15-17

The distal articulation of a lateral metacarpal, L 20541, measures 18 by 8 mm. The distal articulation of a lateral metatarsal, with an incomplete metatarsal, L 21966, measures 16.5 by 7.5 mm. These dimensions are found in *H. primigenium* as well as in *H. ethiopicum*, and from these and other data it is evident that there was no reduction in the side toes as we pass from the one to the other (Hooijer, 1975: 51).

Proximal phalanx from 'E' Quarry

There is a single, entire proximal phalanx of the median digit in the 'E' Quarry collection, L 13832 (pl. 6 fig. 3). This specimen definitely represents *Hipparion*, lacking the long, V-shaped ligamentary scar that characterises *Equus* proximal phalanges. The measurements of this bone are presented in table 11.

TABLE 11

Measurements of proximal median phalanx (mm)

Median length	57	Least width of shaft	27
Volar length	60	Least ant. post. diameter	16
Proximal width	40	Distal articular width	33
Proximal ant. post. diameter	31	Distal ant. post. diameter	21

The proximal phalanx of the 'E' Quarry *Hipparion* is longer than that of the Ngorora Formation Vallesian *H. primigenium*, which is 54 mm in volar length and 30 mm in least shaft width, and it is hardly less elongated than its homologue in the Olduvai Bed II *H.* cf. *ethiopicum*, which varies in volar length from 63 to 73 mm by a least shaft width of 27 to 36 mm (Hooijer, 1975: 15).

Thus, the Langebaanweg *Hipparion*, as judged by the single proximal phalanx available for examination, shows some evolutionary advance over the Vallesian *H. primigenium*: the proximal phalanx became more elongated in the transformation from the primordial Old World *H. primigenium* to the final evolutionary stage of *Hipparion* in Africa: "*Stylohipparion*", whereas the median or the lateral metapodials changed but little in size or proportions (Hooijer, 1975: 15, 51, 52).

Further postcranial bones from 'E' Quarry

Three entire limb bones are in L 20541 of which the metacarpal III has already been recorded (table 8), viz., the humerus sin., the radio-ulna sin. (olecranon incomplete), and the femur dext. Of L 20553 (metatarsal III recorded in table 9) we have the entire astragalus and calcaneum dext. A femur sin., L 21295, is associated with the entire metatarsal III bearing the same number; an associated tibia is incomplete, as are the femur and tibia of L 20553. Of L 20554, however, we have the nearly entire femur and tibia dext. as well as the metatarsal III already recorded (table 9), and the astragalus dext. There are a number of entire astragali, and some calcanea. The measurements of the limb bones are presented in table 12, and those of the tarsals in table 13.

TABLE 12

Measurements of limb bones from 'E' Quarry (mm)

		L 20541	L 20554	L 21295
Humerus,	articular length	230		
	distal width	68		
Radius,	length	280		
	greatest proximal width	68		
	proximal articular width	63		
	greatest distal width	61		
	distal articular width	53		
Femur,	greatest length	360	—	360
	articular length	330	ca. 320	320
	greatest proximal width	100	—	105
	greatest distal width	85	ca. 85	ca. 85
Tibia,	greatest length	—	335	
	proximal width	—	ca. 90	
	distal width	—	65	

TABLE 13

Measurements of astragali and calcanea from 'E' Quarry (mm)

Astragalus,	L 20553	L 20554	L 20178	L 13128
distal articular width	44	46	45	46
medial height	57	57	58	56
Astragalus,	L 13696	L 6249	L 13007	L 13127
distal articular width	41	46	44	40
medial height	57	58	61	51
Calcaneum,	L 20553	L 20178	L 13144	L 7567
greatest diameter	107	107	ca. 105	102
greatest transv. diameter	44	42	44	42

The measurements of radius and tibia are very close to those of *H. primigenium* from the Vallesian of Wad el Hammam (Arambourg, 1959: 87, 89; Forstén, 1968: 119); the humerus from Pikermi is longer (260-267 mm), but the tibia from Pikermi varies in a sample of 14 specimens from 325 to 365 mm (Forstén, 1968: 119), which includes the observation on the Langebaanweg tibia. Of the astragali, one, L 13127, appears rather small as compared to the others, but this must be an immature specimen. There is an astragalus, L 20943, which looks fully formed but which by a fortunate accident of collecting is still attached to the distal epiphysis of the tibia, which is not fused to the shaft and therefore immature. The distal articular width of this astragalus is only 42 mm, and the medial height 51 mm. Since the astragalus ossifies from a single centre there are no epiphysial sutures to show whether the bone is fully grown or not. The largest astragalus from Wad el Hammam is 43 mm in distal articular width, and 56 mm in height (Forstén, 1968: 120), very close to the Langebaanweg astragali, and the length of the calcaneum of *H. primigenium* from Wad el Hammam is given as 107.5 mm (l.c.), again as in the Langebaanweg calcanea.

Hipparion from 'E' Quarry and Baard's Quarry compared

The holotype of *Hipparion albertense baardi* Boné & Singer (1965: 389) is a $P_{3,4}$ dext. from Baard's Quarry, L 946 (l.c., pl. XIV A). It measures 26 by 16 mm at two cm from the base, and thereby is of the dimensions of P_{3-4} L 13103/4 of 'E' Quarry (table 6). There is nothing to distinguish the Baard's Quarry type from those of 'E' Quarry. The other important specimen in the Baard's Quarry collection is the unworn upper cheek tooth, L 11716, identified by Singer & Boné (1965: 374-375, pl. XI D, E) as a left P^4 but which in actual fact is an $M^{1,2}$ sin.; the parastyle is not broader than, but subequal to the mesostyle. The full crown height is 70 mm. The anteroposterior diameter taken at two cm from the base is 24 mm, the transverse, 24.5 mm, at the same level. Boné & Singer record 28.1, and 25.5 mm, respectively, for the crown diameters, but these have been taken near the top of the crown, where the dimensions are maximal. In this way the measurements are not comparable to those of worn specimens, which form the great majority of the collection. In an earlier paper, before having seen the specimen, I copied Boné & Singer's measurements and thus arrived at a height/width index of 270 (Hooijer, 1975: 20), whereas the index taken consistent with those in earlier studies is 290. The height/width index for the Baard's Quarry $M^{1,2}$ is exactly the same as that for the 'E' Quarry $P^{3,4}$ L 3358, 290, and close to that of the Ekora M^1 of *H. primigenium*, 300 (Hooijer & Maglio, 1974: 15). A rather higher and narrower 'E' Quarry

$M^{1,2}$, L 9143, gives a height/width index of 380, as related above. On the whole, the Baard's Quarry cheek teeth are not as well preserved as those from 'E' Quarry, and Boné & Singer (1965) have described and figured most of them. They give hypsodonty indices even of the worn specimens (l.c.: 371, 374), which of course is meaningless as the indices thus taken only indicate the degree to which the teeth are worn down, and are of no value for comparison between the Baard's Quarry and other forms of *Hipparion*.

Moreover, the measurements recorded have not been taken in a manner consistent with that adopted in the present study, and some of the teeth have not been correctly identified. E.g., L 1465F has been identified as an M_3 (l.c.: 369, pl. VIII E), but it is most surely an M_1 or M_2 as it lacks the third lobe, hypoconulid. The anteroposterior diameter, at two cm from the base, is 25 mm, whereas that of L 938, correctly identified as an M_3, is 32 mm. L 949 is also an M_3, but its hypoconulid is broken away, and the anteroposterior diameter, given by Boné & Singer (l.c.: 371) as 24.3 mm (!), is not that of the complete tooth, which would have been approximately 30 mm. Likewise, L 1465B is an M_3 with the hypoconulid broken off, but in this case Boné & Singer (l.c.) correctly omitted the anteroposterior diameter in their table of measurements. A slightly worn M_3 that was put together by Dr. Q. B. Hendey from three fragments, numbered L 1455C, L 1455K, and L 1460B, is about 50 mm high as preserved, and its anteroposterior diameter increases from 29 mm at the top to 32 mm, 40 mm lower down.

In table 14 are presented the measurements of the upper cheek teeth that are sufficiently well preserved for at least one measurement to be taken, at two cm from the base of the crown, consistent with the measurements given for the 'E' Quarry cheek teeth.

Measurements of lower cheek teeth, apart from M_3 already dealt with, are presented in table 15.

TABLE 14

Measurements of upper cheek teeth, Baard's Quarry (mm)

		L 1467D	L 1467E	L 11719	L 942	L 934	L 955	L 950
$P^{3,4}$,	ant. post.	—	27	23.5	24.5	25	25	—
	transv.	25	26.5	25	—	26	25.5	26.5
		L 1467B	L 1453D	L 1455D	L 953	L 954	L 956	
$M^{1,2}$,	ant. post.	23	24	23	22.5	22.5	23	
	transv.	24.5	24	25	25	25	—	
		L 935	L 1461A					
M^3,	ant. post.	25	24					
	transv.	22.5	—					

TABLE 15

Measurements of lower cheek teeth, Baard's Quarry (mm)

		L 947	L 934	L 1465D			
P_2,	ant. post.	32.5	—	—			
	transv.	14	13.5	15			
		L 1465A	L 1451A	L 954	L 957 L 1633A	L 943	
$P_{3,4}$,	ant. post.	28	28	26	27	27.5	
	transv.	15.5	17	17	17	16.5	
		L 1465F	L 1635A	L 1448	L 952	L 959	L 944
$M_{1,2}$,	ant. post.	25	27	26	25	25	26
	transv.	13.5	16	15	15.5	14.5	14

The dimensions of Baard's Quarry $P^{3,4}$ are within the variation limits of their homologues of 'E' Quarry, and the $M^{1,2}$ likewise are not larger than the maximum in the 'E' Quarry series, although most of the Baard's Quarry $M^{1,2}$ are larger than all but one of the 'E' Quarry specimens. The two specimens of M^3 from Baard's Quarry are of the size of those from 'E' Quarry. Of the lower cheek teeth, one P_2 from Baard's Quarry nearly equals L 20259 from 'E' Quarry in anteroposterior diameter; the $P_{3,4}$ likewise remain below the maximum of their homologues in the 'E' Quarry series. The $M_{1,2}$ from Baard's Quarry are mostly larger in one or both dimensions than those from 'E' Quarry. The M_3 from Baard's Quarry vary from ca. 30 to 32 mm anteroposteriorly, whereas the anteroposteriorly longest 'E' Quarry M_3, L 20553, is 29.5 mm. The two sets of lowers from 'E' and Baard's Quarry, therefore, do differ somewhat in size, the latter being on the large side as far as the series of specimens available go. The vertical grooving in the Baard's Quarry lower cheek teeth may be quite as marked as that in L 24197, but this is a variable feature in the collection of lower cheek teeth.

The Baard's Quarry and 'E' Quarry lower cheek teeth, however, agree in the complete absence of ectostylids, which probably indicates that they are closely related, if not fully conspecific. This matter is not to be decided upon these data only; we need more and better material to compare with the skull from 'E' Quarry, L 22187. As long as this is not available from Baard's Quarry, the 'E' Quarry form may be referred to as *Hipparion* cf. *baardi*.

There was some postcranial material in the Baard's Quarry collection described by Boné & Singer, but the only entire specimens were some phalanges, and these have not been positively allocated with either *Hipparion* or *Equus* although the first phalanges would have given no difficulty in assigning them to one taxon or the other. Most unfortunately, the two proximal phalanges of median digits from Baard's Quarry, L 1456 and L 1462A,

figured by Boné & Singer (1965, pl. XVI), and which would seem to represent *Hipparion* and not *Equus*, are no longer in the collection at the South African Museum and probably are housed elsewhere. From the illustrations they are 69-71 mm in volar length and 35-41 mm in least shaft width, and thus longer and more massive than the 'E' Quarry phalanx of table 11, more like the proximal phalanges of the Olduvai Bed II *H.* cf. *ethiopicum*. The original specimens must be examined to settle this point, which has an important bearing on the question as to whether the Baard's Quarry *Hipparion* is conspecific with that of 'E' Quarry.

Equus from Baard's Quarry

The only specimens from Baard's Quarry still in the South African Museum's collection are three largely intact cheek teeth and some fragments, L 2095 and L 2106, M^{2-3} of a single individual (pl. 8 fig. 1), L 866, an $M_{1,2}$, and among the fragments two posterior portions of M^3, L 2109 and L 2129. L 2095 was originally regarded as derived from 'E' Quarry (Hendey, 1970a: 102, pl. 3 D), later stated to be of unknown provenance (Hendey, 1970b: 124), and still later (Hendey, 1972: 172) discounted as from the 'E' Quarry assemblage. "The ore dump from which it was recovered may have included deposit from Baard's Quarry, or the tooth in question may have become accidentally mixed with specimens from 'E' Quarry recovered at the same time" (l.c.). It is, however, clearly of the same individual as L 2106, and an unnumbered fragment in the Baard's Quarry *Equus* collection has the same preservation. In Boné & Singer (1965: 379) it is stated that the *Equus* teeth at Langebaanweg constitute 10% of the total number of equid remains collected thus far at Langebaanweg, so that there must have been more, but these are no longer in the museum collection. Of the equid phalanges several were figured by Boné & Singer (1965, pls. XVI-XIX), and of these the two figured on plate XVII of their paper almost certainly represent *Equus* proximal phalanges. However, there remains in the Baard's Quarry only one, incomplete *Equus* proximal phalanx, L 314, which will be dealt with presently.

The M^{2-3} dext., L 2095 and L 2106, are characterized by their great size and almost certainly belong to *Equus capensis* Broom. The M^2 is worn down to about 60 mm of height, the M^3 to the same degree. The anteroposterior crown diameter is 30 mm for M^2, 37 mm for M^3; the transverse diameter is 32.5 mm for M^2, and 28.5 mm for M^3, taken at two cm from the base. The $M_{1,2}$ dext., L 866, measures 36 by 19.5 mm at the same level; it is 72 mm high as worn. Such dimensions agree well with those of the type lower cheek tooth series of *E. capensis* as restored by Cooke (1950: 444,

fig. 18) and of the neotype and other referred upper cheek teeth figured by the same author (Cooke, 1950: 449, fig. 20). About the structural details little needs to be said; of course the protocone is connected with the protoconule, as is typical of the genus *Equus*, and the fossette plications are simpler than those in *Hipparion*. The pli caballin does not invariably show: it is present in some (L 2095 and L 2106) as a tiny spur, and absent in L 2109, as it varies in the uppers referred to *E. capensis* by Cooke (1950, fig. 20). Of the two incomplete M^3, L 2109 permits of the transverse diameter to be taken, which is 28 mm over protocone and mesostyle; its height as worn is approximately 70 mm. The posterior groove between metastyle and hypostyle begins to form at about 40 mm from the crown base, and therefore does not show occlusally in L 2109 but does in L 2106 the posterior height of which is less than 40 mm.

With only these few teeth at hand, all I can do is refer the Baard's Quarry *Equus* provisionally to *Equus capensis*, and wait for better material. The incomplete proximal phalanx, L 314, less than half of the distal articulation of which is preserved, is about 80 mm long, and 57 mm wide proximally, by a mid-shaft width of about 37 mm. This seems to correspond well with the proximal *Equus* phalanges L 1462 B and L 1462 C, particularly the former, which were figured by Boné & Singer (1965, pl. XVII), but which are not available any more. *Equus* cf. *capensis* has been listed from several Quaternary sites of the south-western Cape Province (Hendey, 1974: 40) and also from the Swartkrans Australopithecine Site and the Kromdraai Faunal Site by Churcher (1970); from the latter site comes a proximal phalanx 76 mm in total length, ca. 51 mm in proximal width, and 32 mm in mid-shaft width (Churcher, l.c., table 5), slightly, but not significantly smaller than our Baard's Quarry specimen.

How many species of Hipparion are represented at Langebaanweg?

The Langebaanweg Quarry 'E' collection has shown that the upper cheek teeth of *H. turkanense* Hooijer & Maglio (1973) are not really distinguishable from those referred to *H. primigenium* by Hooijer & Maglio (1974). If the maxillary fragment with the much worn down P^3-M^1 L 11751 had been with the Lothagam-Kanapoi collection at the time it would have been referred to *H. turkanense*, but the various wear stages represented in the Langebaanweg collection prove that these are merely very old *H. primigenium*-like teeth.

The Langebaanweg Quarry 'E' collection has not solved the problem as to which type of lower cheek teeth go with a skull that has a preorbital fossa such as L 22187. Most unfortunately, there is no mandible positively

associated with that skull. However, since all the lower cheek teeth found to date at 'E' Quarry are devoid of ectostylids it would seem practically certain that the mandible of skull L 22187, had it been found in direct association with the skull, would have had such teeth, ectostylid-less, like those referred to *H. turkanense*.

The only ectostylid-bearing lower premolars in the Langebaanweg collection so far found are not from the 'E' Quarry proper but from a site between 'C' and 'E' Quarries (L 24197), and there is no skull associated with these teeth. If the P_{2-4} L 24197 had been found at the Namaqualand site the type lower dentition of *H. namaquense* (Haughton, 1932) came from, these teeth would have been considered another individual of *H. namaquense*, and incorporated in that species.

As there is no skull or even upper cheek teeth associated with the lowers of *Hipparion namaquense*, the status of this species remains somewhat uncertain. Likewise, there is no material directly associated with the lower premolars L 24197 that are virtually indistinguishable, and which for the time being may be referred to as *Hipparion* cf. *namaquense*. The type material of *H. namaquense* comes from an undated site, and various opinions have been expressed as to its status. While Van Hoepen (1932: 31) and Dietrich (1942: 99) regard it as more primitive than "*Stylohipparion*", and Cooke (1950: 426) concedes that *H. namaquense* may have a bearing on these advanced, Pleistocene forms, Boné & Singer (1965: 389) place it, though with some reservation, in the synonymy of *H. libycum* Pomel of the Villafranchian of North Africa, which is certainly unjustified. In this "*Stylohipparion*" that we find full-fledged at Member F of the Shungura Formation (age probably 2.0 to 1.9 million years) crown heights are up to 90 mm, and the strong, laterally compressed ectostylids are up to 80 mm in full height. The Langebaanweg P_{2-4} L 24197 have an ectostylid development only slightly inferior to that seen in a mandible originating from Member B11 of the Shungura Formation the probable age of which is some 3.9 to 3.75 million years (Hooijer, 1975: 52/53). This would give some indication as to the age of both *H. namaquense* and L 24197 (which latter is considered to be from the uppermost level of Bed 3 of the Varswater Formation), the dates being what they are, or seem to be. Such teeth as those of *Hipparion namaquense* and of L 24197 may be interpreted as representing an *H. primigenium* that continued to develop the ectostylid beyond its development in the Vallesian, and which eventually led to true "*Stylohipparion*", which did emerge sometime between Members C and F of the Shungura Formation, about the 3 to 2 million year interval (Hooijer, 1975: 61-66).

The remarkably constant absence of ectostylids in the Langebaanweg 'E' Quarry cheek teeth, and the fact that the only two skulls of *Hipparion* so far found at that Quarry (the old L 22187 and the juvenile portion L 21823) have preorbital fossae, would seem to make a strong case for preorbital fossae to be associated with lower cheek teeth devoid of ectostylids in one and the same species. This, then, would seem to be the *Hipparion baardi* type of association, perhaps a development independent from that envisaged from the primordial *H. primigenium* into "*Stylohipparion*" (above, p. 21). It is here that *Hipparion turkanense* comes into the picture, *H. turkanense* that dates back to approximately 6 million years, Lothagam, and with which Hooijer & Maglio (1974: 8) associated ectostylid-less lower cheek teeth.

From the previous discussion of the preorbital fossa, the absence of which is the main characteristic of *H. turkanense* as well as of the skull of "*Stylohipparion*" (Hooijer, 1975: 29, 32), the provisional conclusion may be drawn that the non-development of the preorbital fossa may be taken as a specific character. We evidently need more *Hipparion* skulls from the various sites rather than just teeth or mandibles to have a firmer basis for this conclusion, but these are not available at the moment of writing. We do not know for certain as yet which lower teeth go with a skull like the type of *H. turkanense*: which is the *Hipparion turkanense* type of association. It remains a possibility that both types of skull have mandibles with ectostylid-less as well as ectostylid-bearing cheek teeth.

The final solution of this problem, which of the various species based only on skulls, or only on mandibular teeth, are really valid species, may be arrived at upon discoveries of good skulls positively associated with their mandibles, such as we have from Wad el Hammam. *H. primigenium* of the Vallesian of North Africa originally named *H. africanum* by Arambourg (1959) has preorbital fossae but no ectostylids so far as recorded, the same association presumed to be true for the 'E' Quarry *Hipparion, H.* cf. *baardi*. Since the occurrence of positively associated upper and lower jaws is not at all uncommon at 'E' Quarry we might find this in *Hipparion* as the collecting at this Quarry continues.

Conclusion

The *Hipparion* from 'E' Quarry is as hypsodont as, but smaller-toothed than *Hipparion baardi* Boné & Singer from Baard's Quarry, and it shares with it the absence of ectostylids. It has a preorbital fossa in the *Hipparion primigenium* fashion, whereas the cranial characters of the Baard's Quarry *Hipparion* are unknown. It seems best, therefore, to name the 'E' Quarry form *Hipparion* cf. *baardi* Boné & Singer as there is probably a close rela-

tionship. The form from a site between 'E' and 'C' Quarries, L 24197, does have ectostylids, and may be recorded provisionally as *Hipparion* cf. *namaquense* (Haughton). The relationships between various species of *Hipparion* based on either only skulls (such as *H. turkanense* Hooijer & Maglio) or only on mandibular teeth (such as *H. namaquense* (Haughton)) are not to be settled until positively associated skulls and mandibles with their teeth have been found, and it is hoped that such a lucky accident of collecting may occur at 'E' Quarry in the future.

Summary

A wealth of material of what is apparently a single species of *Hipparion* has been described for the first time from the 'E' Quarry at Langebaanweg. It is characterized by having a preorbital fossa, the size of *Hipparion primigenium* (Von Meyer) of the Vallesian of the Old World, and by the apparent constancy in absence of ectostylids in the lower cheek teeth. The lateral incisors are not reduced in size as they are in the advanced, Pleistocene, "*Stylohipparion*" of Africa. The metapodials are not significantly different from those in either *H. primigenium* or "*Stylohipparion*", but the proximal phalanx of the median digit is more elongated than that in the Vallesian *H. primigenium*, and approaches those in the advanced, Pleistocene *Hipparion*, "*Stylohipparion*". The 'E' Quarry *Hipparion* is probably closely related to *Hipparion baardi* Boné & Singer of Baard's and 'C' Quarries at Langebaanweg, and may be recorded as *Hipparion* cf. *baardi*.

Some lower cheek teeth from a site between 'E' and 'C' Quarries, considered to be from the uppermost level of the Varswater Formation, are practically indistinguishable from *Hipparion namaquense* (Haughton). They have been identified as *Hipparion* cf. *namaquense*.

Further research is imperative to elucidate the relationships of the various species of *Hipparion*. The 'E' Quarry of Langebaanweg, which falls in the 7 to 4 million year interval as judged by its most abundant large element, *Ceratotherium praecox* Hooijer & Patterson, may one day provide associated skulls and mandibles of *Hipparion*, which will throw fresh light on such relationships.

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specimens. I wish to express my appreciation to Dr. and Mrs. Hendey and the staff of the Cenozoic Vertebrate Palaeontology Department of the South African Museum for facilities extended to me, and especially to Mr. S. Kannemeyer, who has made the photographs. A grant from the Maatschappij voor Wetenschappelijk Onderzoek in de Tropen (Treub Maatschappij) is gratefully acknowledged.

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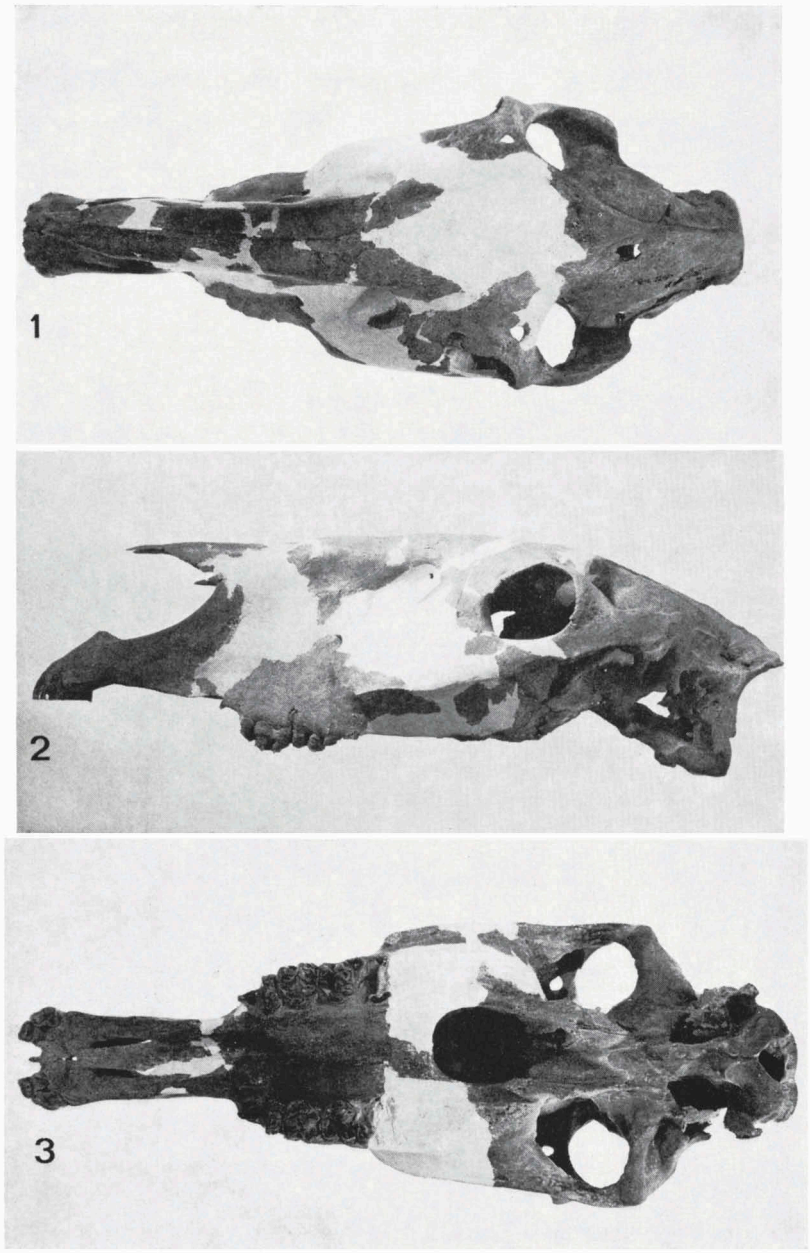
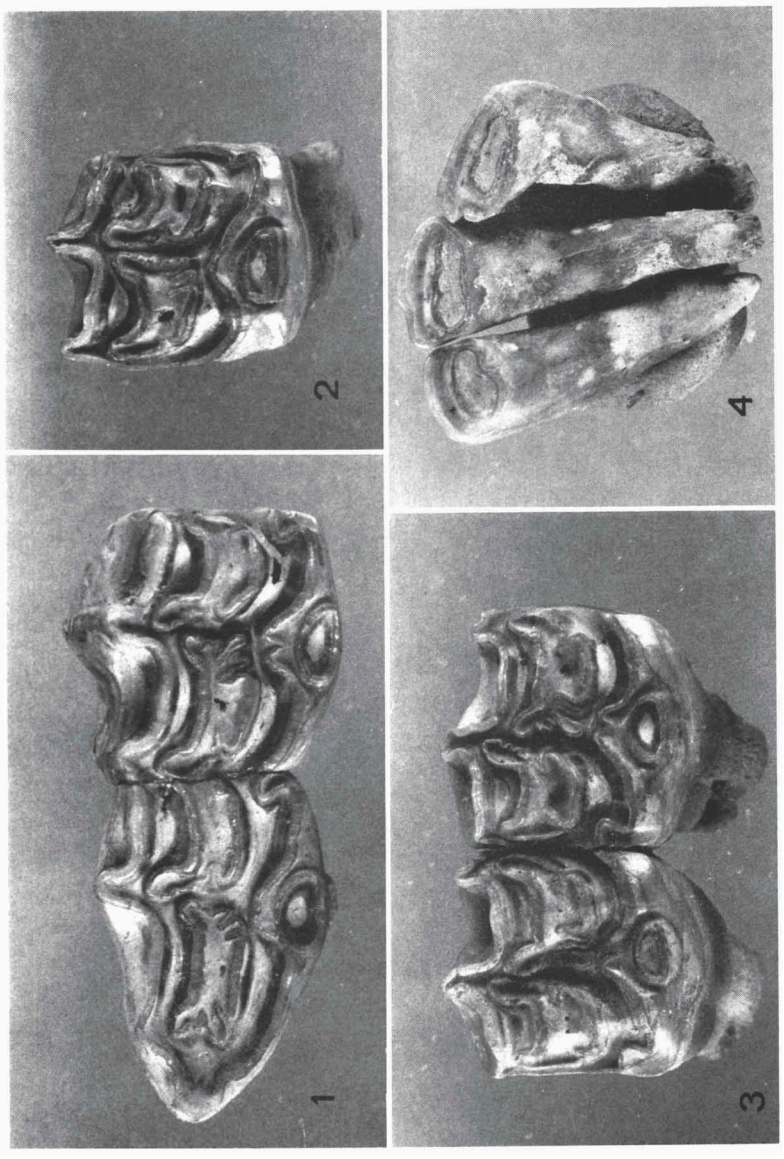
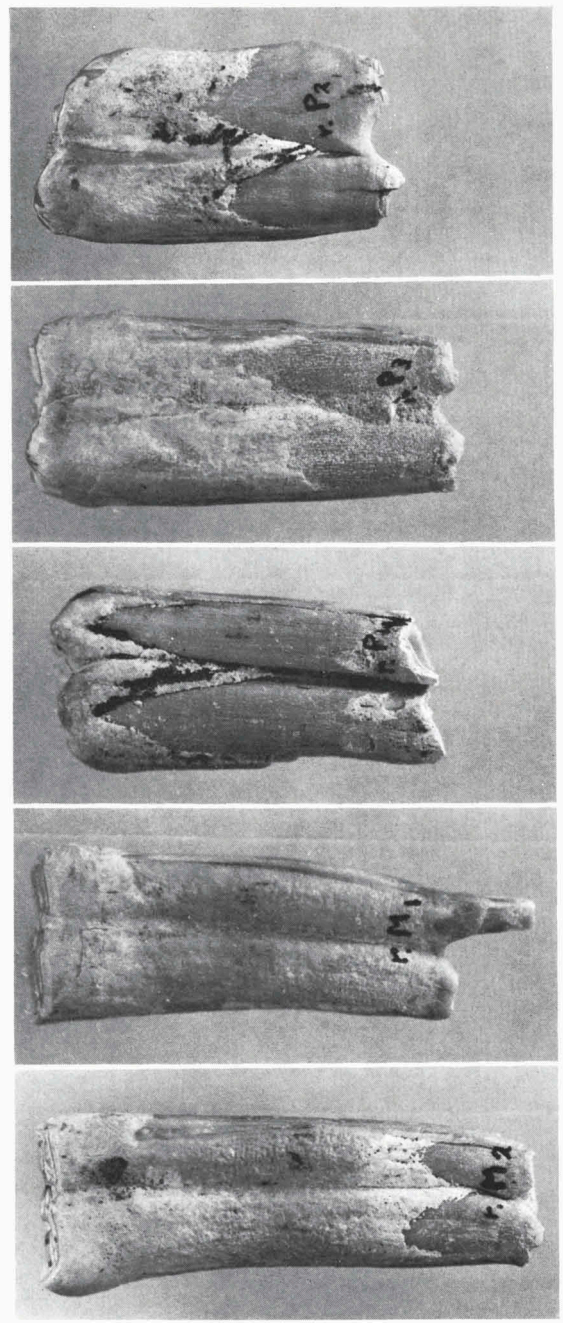


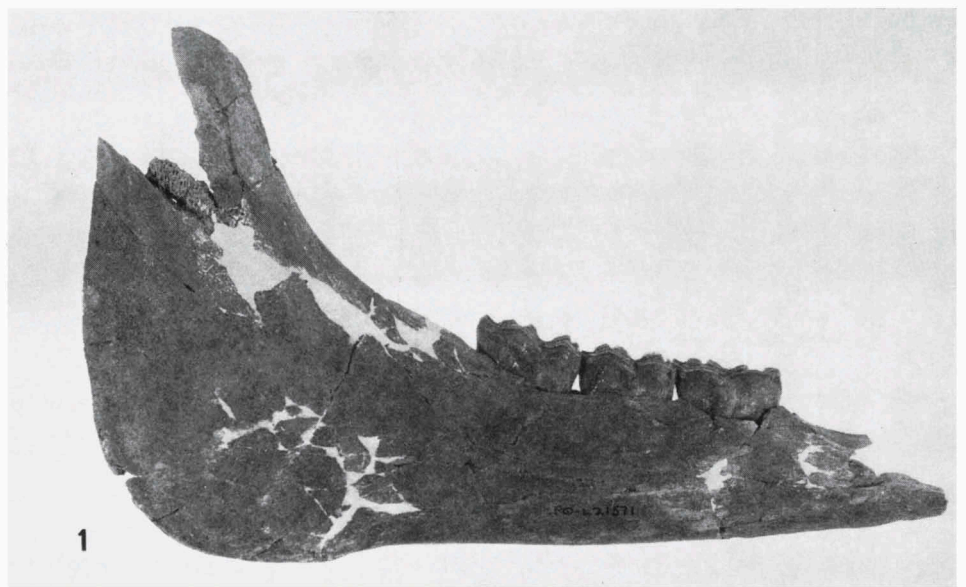
Hipparion cf. *baardi* Boné & Singer, skull, Langebaanweg 'E' Quarry, L 22187. Fig. 1, dorsal view; fig. 2, left lateral view; fig. 3, ventral view. × 0.2.



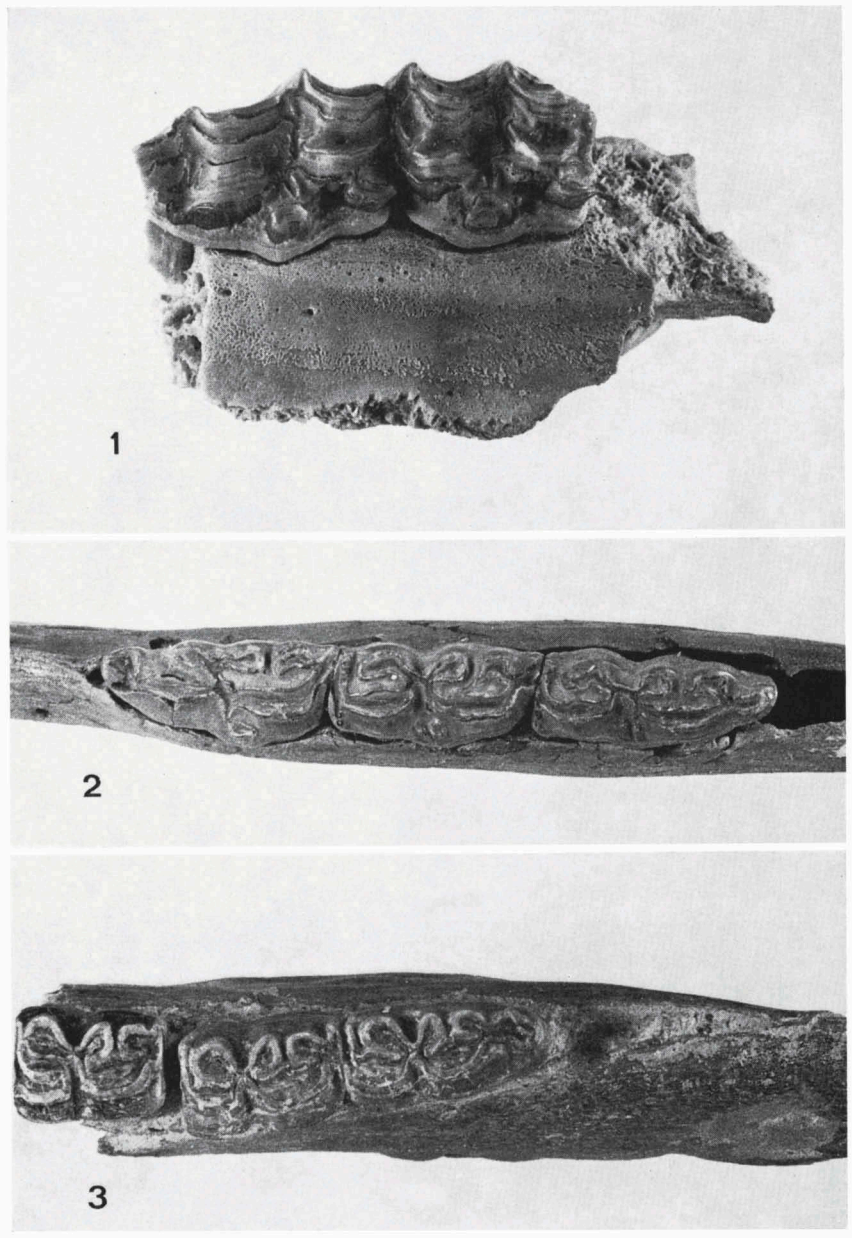
Hipparion cf. *baardi* Boné & Singer, Langebaanweg 'E' Quarry, L 11222. Fig. 1, P^{2-3} sin., crown view; fig. 2, M^1 sin. crown view; fig. 3, P^{3-4} dext., crown view; fig. 4, I^{1-3} sin., occlusal view. Figs. 1-3, × 1.4; fig. 4, × 1.1.



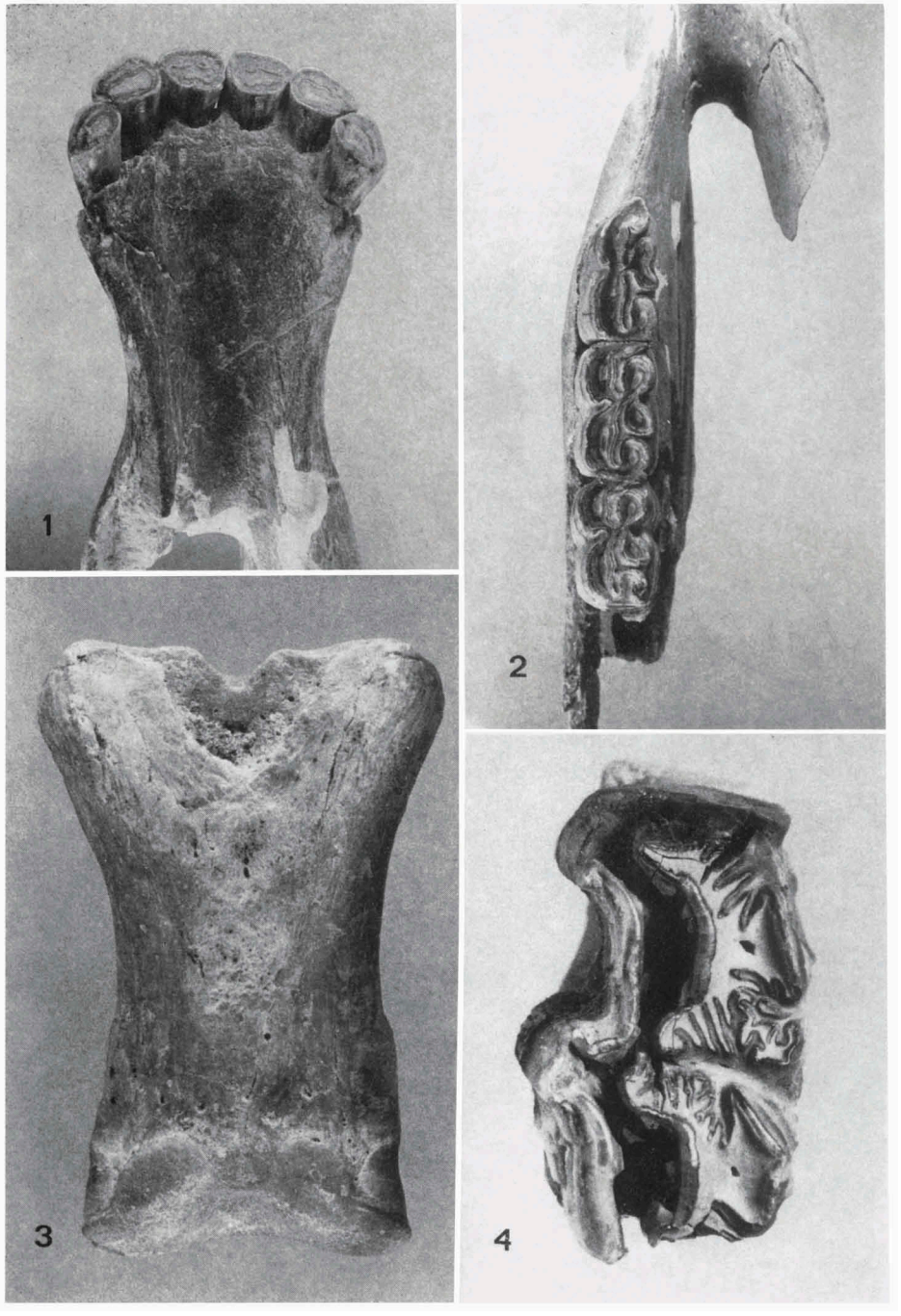
Hipparion cf. *baardi* Boné & Singer, Langebaanweg 'E' Quarry, P_2 - M_2 dext., associated, L 10954, external views. × 1.0.



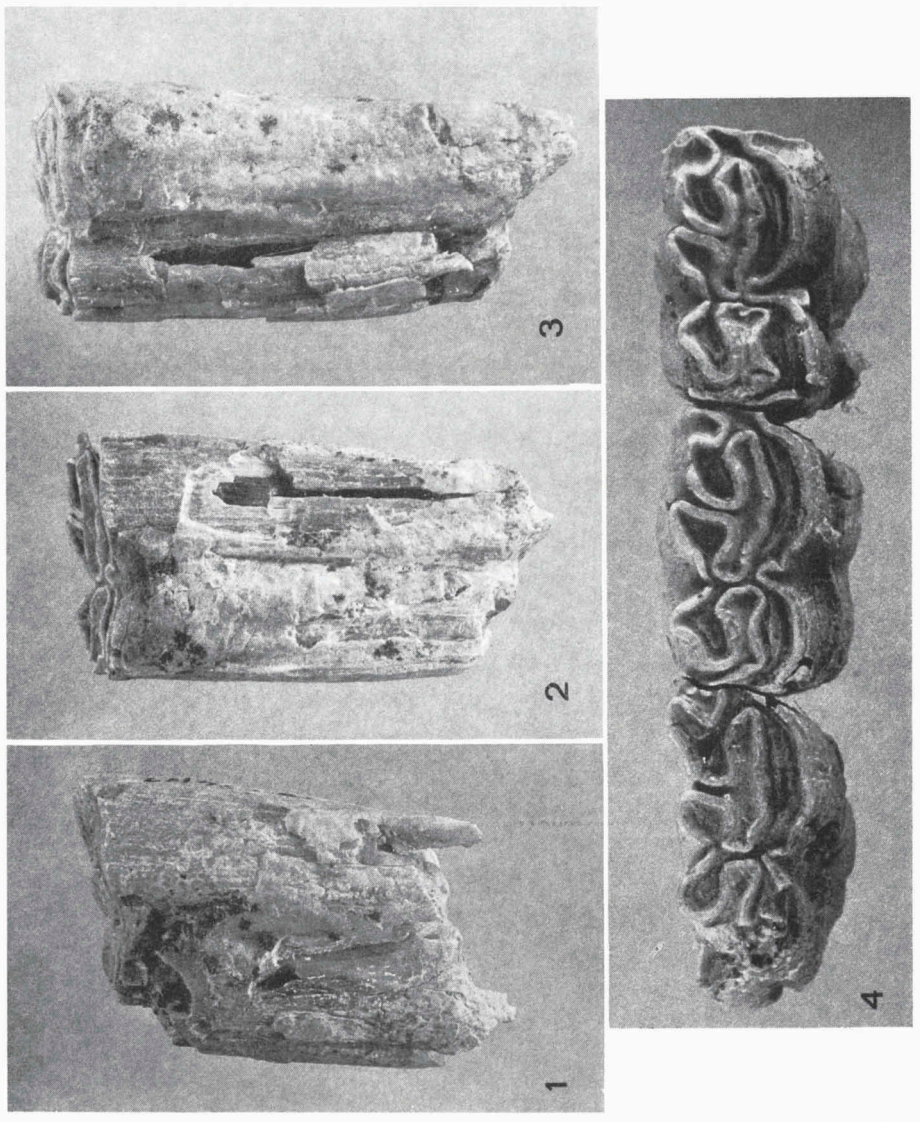
Hipparion cf. *baardi* Boné & Singer, Langebaanweg 'E' Quarry. Fig. 1, right mandibular ramus with DM_{2-4} in situ, L 21571, externalview, × 0.4; fig. 2, right mandibular ramus with P_{2-3}, P_4 erupting, M_{1-3}, L 13102, internal view. × 0.4.



Hipparion cf. *baardi* Boné & Singer, Langebaanweg 'E' Quarry. Fig. 1, DM^{2-3} sin. in situ, L 21823, crown view, × 1.0; fig. 2, DM_{2-4} sin. in situ, L 21571, crown view, × 0.9; fig. 3, M^{1-3} sin. in situ, L 20553, crown view, × 0.9.



Hipparion cf. *baardi* Boné & Singer, Langebaanweg 'E' Quarry. Fig. 1, symphysial portion of mandible with I_{1-3} dext. et sin. in situ, L 20553, occlusal view, × 0.7; fig. 2, P_{2-4} sin. in situ, L 20541, crown view, × 0.7; fig. 3, phalanx I of median digit, L 13832, volar view, × 1.5; fig. 4, external portion of $P^{3,4}$ dext., L 21952, crown view, × 2.5.



Hipparion cf. *namaquense* (Haughton), Langebaan weg, a site between 'E' and 'C' Quarries (considered to be from uppermost level of Varswater Formation), L 24197. Fig. 1, P_2 sin., external view; fig. 2, P_3 sin., external view; fig. 3, P_4 sin., external view; fig. 4, P_{2-4} sin., crown views. × 1.3.

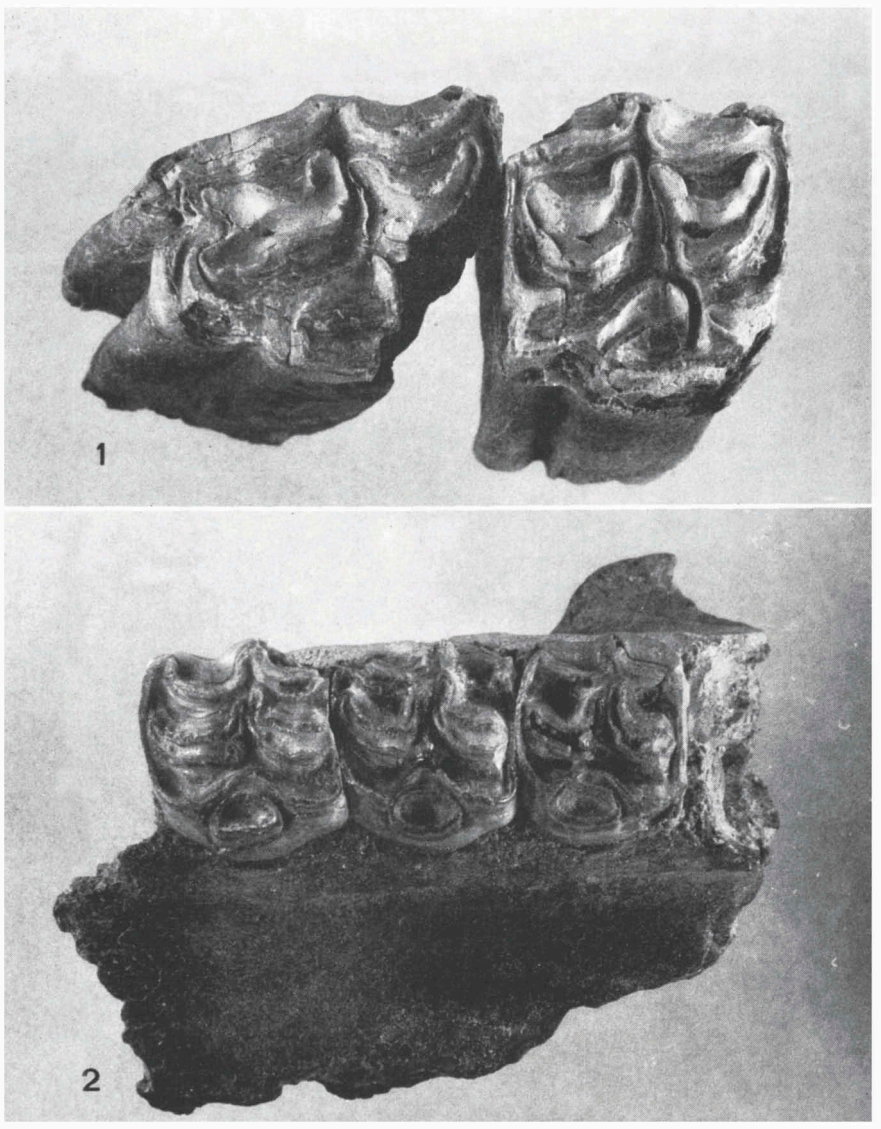


Fig. 1, *Equus* cf. *capensis* Broom, Langebaanweg Baard's Quarry, M^{2-3} dext., L 2095 and L 2106, crown views. × 1.4.

Fig. 2, *Hipparion* cf. *baardi* Boné & Singer, Langebaanweg 'E' Quarry, P^3 - M^1 sin. in situ, L 11751, crown view. × 1.0.