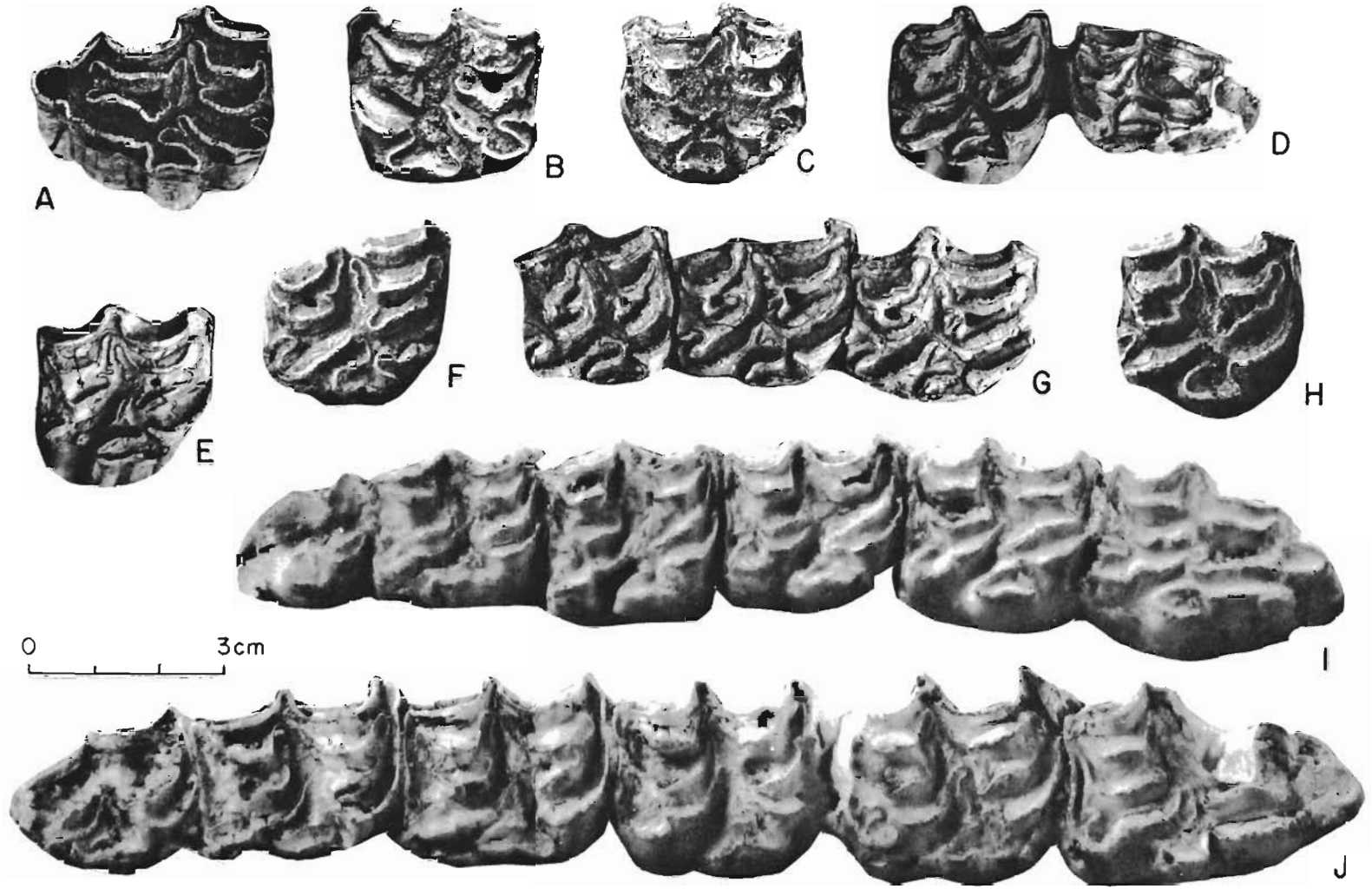


PLATE 5.8. *Equus* sp. indet.
(A) $P^2$ (KNM-ER 2062); (B) $P^3$ or $P^4$ (KNM-ER 4000); (C) $P^3$ or $P^4$ (KNM-ER 2688); (D) associated $M^1$ or $M^2$ and $M^3$ (KNM-ER 1281); (E) $P^3$ or $P^4$ (KNM-ER 1226); (F) $P^3$ or $P^4$ (KNM-ER 1258); (G) associated $P^3$ $P^4$ $M^1$ (KNM-ER 1211); (H) $P^3$ or $P^4$ (KNM-ER 2681); (I) upper cheek teeth row (KNM-ER 1211); (J) upper cheek teeth row (KNM-ER 1484).

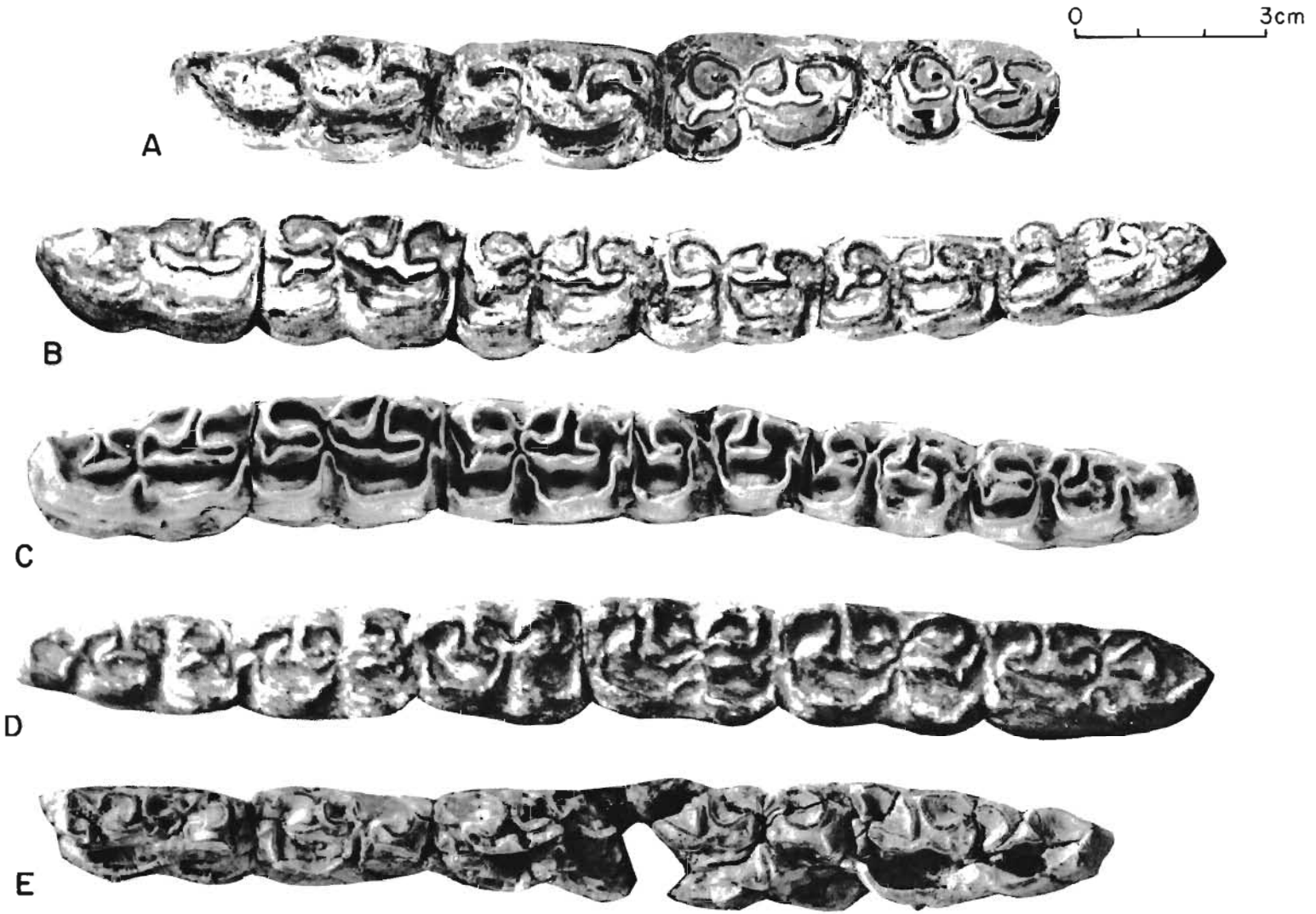


PLATE 5.9. *Equus koobiforensis*.
(A) $P_2$ $P_3$ $P_4$ $M_1$ ($P_4$ and $M_1$ sectioned at about 2 cm below the occlusal surface) (KNM-ER 333); (B) lower cheek teeth row (KNM-ER 5360); (C) lower cheek teeth row (KNM-ER 5361A); (D) lower cheek teeth row (KNM-ER 1582); (E) $P_2$ $P_3$ $P_4$ $M_1$ $M_2$ (KNM-ER 4051).

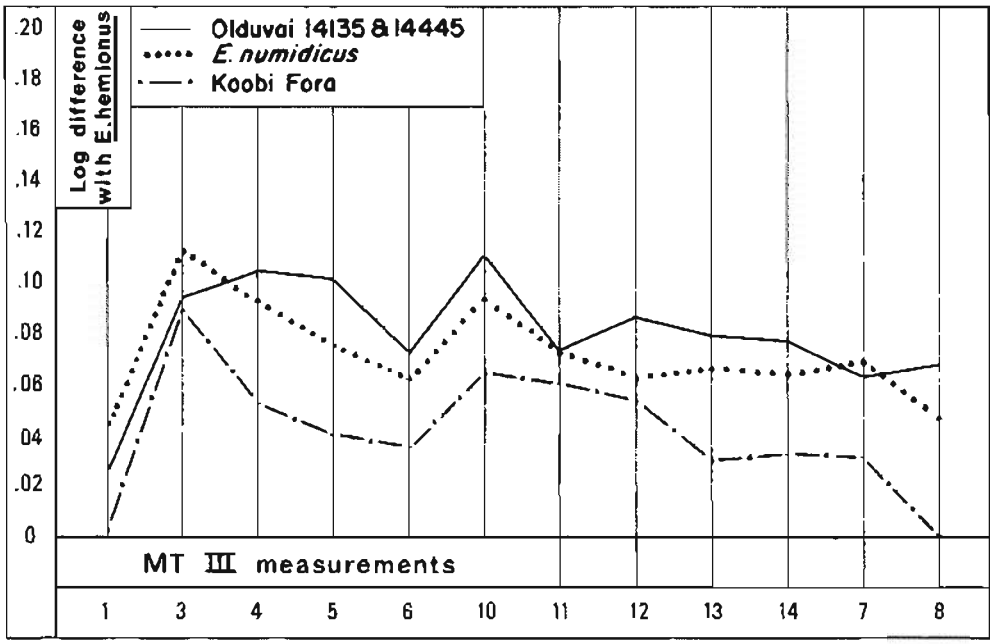


FIG. 5.8. Ratio diagram of dimensions of the third metatarsal in *E.* cf. *koobiforensis* from Olduvai (two specimens), *E. numidicus* (mean of four specimens from Ain Boucherit) and *Equus* sp. indet. from Koobi Fora (mean of five fragmentary specimens).

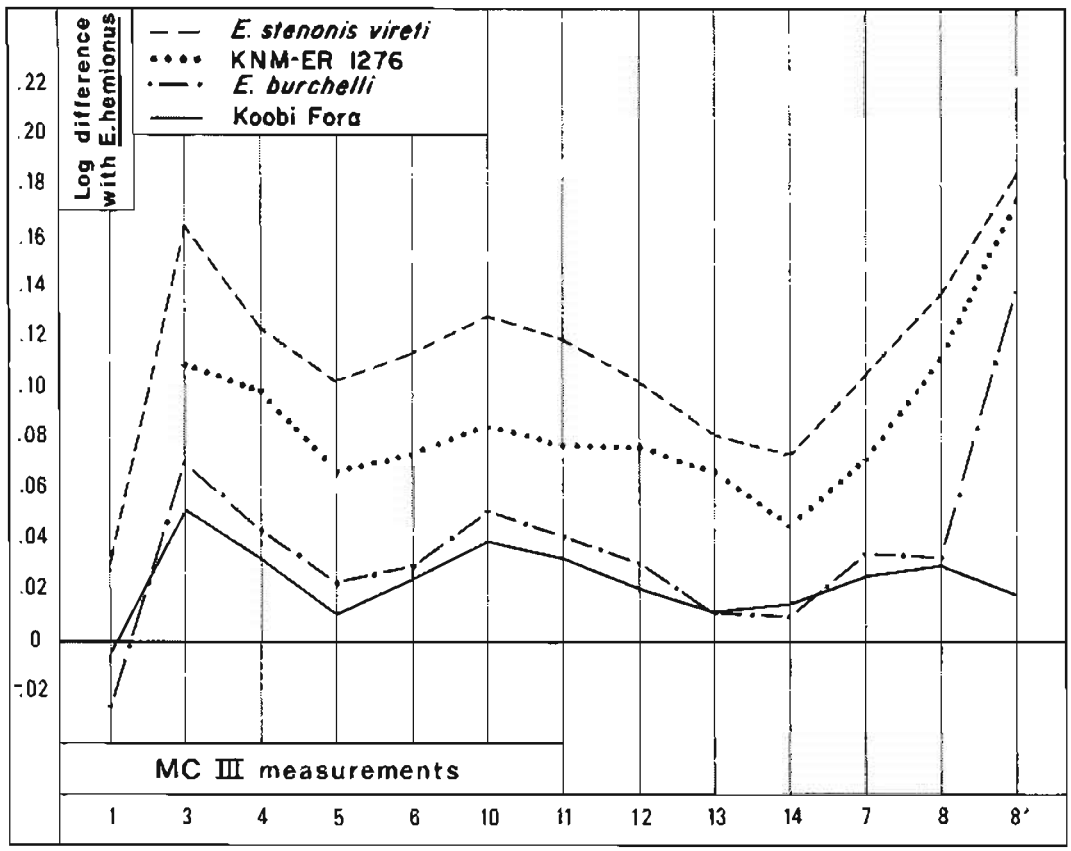


FIG. 5.9. Ratio diagram of dimensions of the third metacarpal in *E. stenonis vireti* (mean of 34–50 specimens from Saint-Vallier), *E.* cf. *koobiforensis* (one specimen, KNM-ER 1276), *E. burchelli* (mean of 25 specimens) and *Equus* sp. indet. from Koobi Fora (mean of five fragmentary specimens).

of possibility that *E. koobiforensis* was conspecific with either or both *E. oldowayensis* and *E. numidicus* but it would serve little purpose at present to synonymize the relatively well documented Koobi Fora species with the other more fragmentary material.

*E. koobiforensis* is clearly distinct from the two best known fossil *Equus* species of Africa. *E. tabeti* has relatively small cheek teeth and very slender metapodials, both characters distinguishing it from *E. koobiforensis*. *E. mauritanicus* has a smaller skull and possesses undoubted quagga characteristics.

### *Equus* cf. *koobiforensis*

As previously noted, metapodials of a size suitable to belong to the *E. koobiforensis* cranium have been found at Omo and Olduvai but not, as yet, in the Koobi Fora Formation. Figure 5.7 shows the great similarity between third metacarpals from Omo and Olduvai; these are clearly closer to those of *E. grevyi* and *E. numidicus* than to those of *E. stenonis*. Other, somewhat smaller, metapodials have been recovered from east of Lake Turkana; these more closely resemble those of *E. stenonis* and *E. burchelli* (Figs. 5.9 and 5.10). Although both kinds of metapodials (the Omo-Olduvai type and the Koobi Fora type) are here referred to *Equus* cf. *koobiforensis*, their conspecificity may be questioned. If so, which specimens are more likely to truly represent *E. koobiforensis*—the *stenonis*-like metapodials from Koobi Fora fitting with a *stenonis*-like cranium but undersized, or the large metapodials from Omo and Olduvai which match the cranium for size but lack *stenonis*-like affinities seen in the cranium?

Because no answer can be made now to this question, I am provisionally referring to *E.* cf. *koobiforensis* the third metacarpals KNM-ER 1275L and 1276 and the third metatarsals KNM-ER 1275G, 4052, and 5358, all except 1275 from the *Not. scotti* zone. I include also within the hypodigm the third

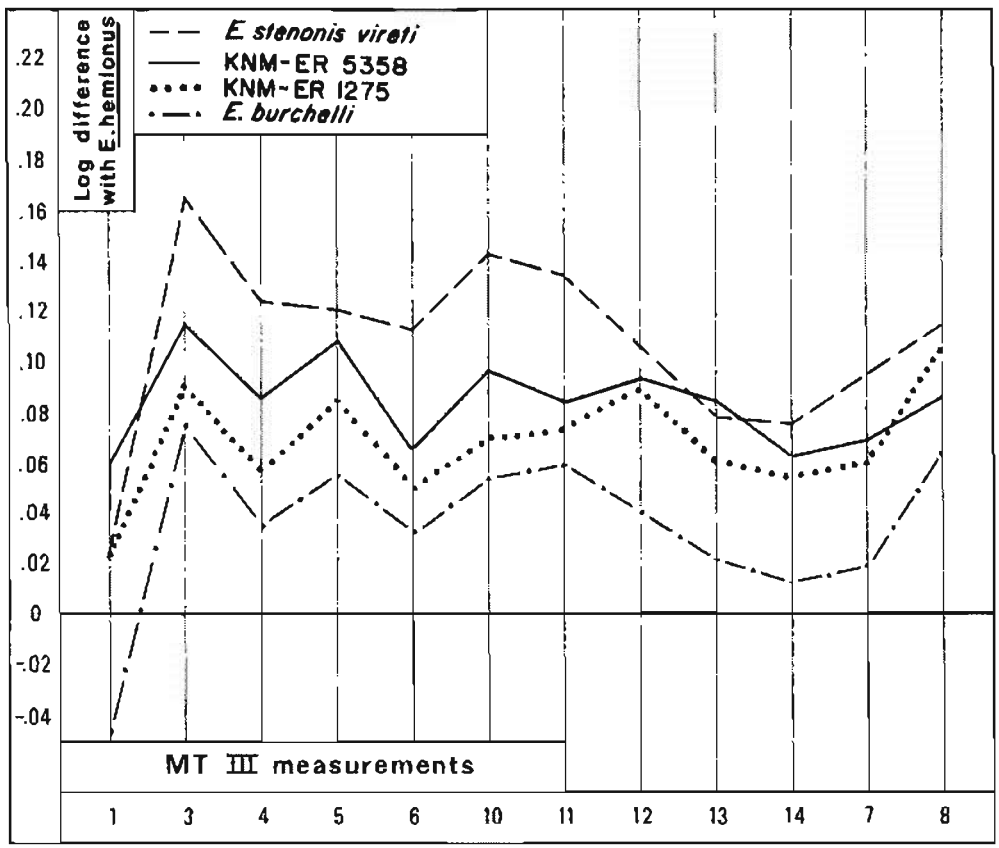


FIG. 5.10. Ratio diagram of dimensions of the third metatarsal in *E. stenosis vireti* (mean of 59–80 specimens from Saint-Vallier), *E.* cf. *koobiforensis* (2 specimens) and *E. burchelli* (mean of 25 specimens).

metacarpal 75-71-101 from Omo and the metapodials BM 14135, 14434, 14436, 14445, and 25510 from Olduvai. It follows that limb bones associated with these metapodials must also be referred to the same taxon and I therefore include KNM-ER 1275A–D second phalanges, 1275E first posterior phalanx, 1275I navicular, 1275J astragalus, 1275K calcaneum, 1275M lateral metapodial fragment, 1276B radius fragment, 1276C humerus fragment, 1276E second phalanx, 1276F first phalanx, 1276I navicular, 1276J lunar, 1276K unciform, 1276L magnum. Other specimens that might also belong to *E.* cf. *koobiforensis* because of their large size are the radii KNM-ER 3998 from Area 102 and 2054 from Area 123 (both from the *Met. andrewsi* zone) and the astragali KNM-ER 2625 and 2317.

The humerus has a distal articular width of 77 mm; the radius a proximal articular width of 74–79 mm and a distal articular width of 60–62 mm. The calcaneum is at least 110 mm long and the astragali have distal articular widths of 47–50 mm and distal anteroposterior diameters of 34–37 mm. A first anterior phalanx (1276F) is 88 mm long with a minimum width of 32 mm; the corresponding measurements on a first posterior phalanx (1275E) are 78 mm and 29 mm. The second phalanges are 46–48 mm long. The humerus, radius, and phalanges are of similar size to those of *E. numidicus*.

***Equus tabeti*** Arambourg, 1970

***Equus* cf. *tabeti***

1976 *Equus* sp. nov. B; Eisenmann (1976*c*): 237
1978 *Equus* sp. indet.; Harris: 44

As already noted, *E. tabeti* is a North African early Pleistocene species of moderate size, mostly characterized by slender limb bones, asinine upper cheek teeth and stenonine lowers. No skull is known. A few specimens from the Koobi Fora Formation show similarities to *E. tabeti* but their attribution remains uncertain.

The fragmentary cranium KNM-ER 1211 is that of a young adult; the third molars are not fully erupted and the remaining cheek teeth are not very worn (Plate 5.8I). The cranium is poorly preserved and only the length of the tooth row (169 mm), the distance between the palate and vomer (107 mm) and width at the facial crest (154 mm) can be measured.

In the cranium the protoconal index of $M^1$ is lower than that of $P^4$ (Table 5.15). The same is true of the associated very worn teeth KNM-ER 5565–6 and in the moderately worn KNM-ER 325 (Tables 5.15–5.17). The upper incisors (KNM-ER 5567) are very worn; they no longer bear cups and have reached the triangular stage of wear corresponding in modern horses to an age in excess of 18 years.

The lower cheek teeth of KNM-ER 325 are fragmentary except for the $M_3$ (Table 5.18) whose vestibular groove is deep and comes into contact with the lingual groove.

The length of the fragmentary metacarpal from Area 103 (KNM-ER 2069) cannot be measured but its other measurements indicate a species of medium size (Table 5.19). The first phalanges associated with this specimen are 75 and 81 mm long and 26 and 27 mm wide at the middle of the shaft.

The other metacarpal from Area 103 (KNM-ER 2067) is small and exceedingly slender and resembles no other modern *Equus* metacarpal that I have seen. Its epiphyses are fused to the diaphysis and in consequence its small size and slender nature cannot be attributed to immaturity. It is possible that the size and appearance of the bone is pathological, and such an interpretation might be supported by a small hollow (1–2 mm deep and 6–7 mm wide) occurring two thirds of the way down the anterior face of the bone; this pit might be cicatricial in origin.

Previous studies have shown that the protoconal index is usually smaller on $M^1$ than on $P^4$ in asses and onagers whereas the reverse is true in caballine species and most zebras. The mean protoconal indices of *E. tabeti* show an asinine pattern and so do the three specimens referred here to *E.* cf. *tabeti*. Exceptions do exist to the rule and thus the interpretation given here is plausible but not certain. The dimensions of the teeth are similar: the premolar length of *E. tabeti* ranges from 82 to 95 mm versus 91 mm in KNM-ER 1211; the molar length of *E. tabeti* ranges from 70–81 mm versus 78 mm in KNM-ER 1211 and 73 mm in KNM-ER 325. The sole lower third molar has a deep vestibular groove like most $M_3$'s of *E. tabeti* but in contrast to modern asses.

The dimensions of the non-pathologic third metacarpal (KNM-ER 2069) are not very different from those of *E. tabeti* except for the unciform facet that, as in modern *E. africanus*, is smaller (Eisenmann 1979*e*, Table 9, Figs. 13, 17). The first phalanges (KNM-ER 2069) are small and slender enough to fall within the range of *E. tabeti*; KNM-ER 1237 is slightly smaller but has the same slenderness.

On the basis of the third metacarpal and the first phalanges, the presence of an asinine species of *Equus* in the Koobi Fora Formation is probable. The upper cheek teeth here identified as *Equus* cf. *tabeti* would support such an interpretation. The rest of the material is less diagnostic and it is entirely possible that some of the lower teeth and limb bones have been erroneously attributed to the other species that occur at the same levels in the Koobi Fora Formation.

***Equus*** sp. indet.

1976 *Equus oldowayensis*; Eisenmann (1976*c*): 234
1978 *Equus* cf. *numidicus*; Harris: 44

*Diagnosis.* Medium-sized *Equus* with mean protoconal indices larger than in *E. stenonis* and smaller than in modern quaggas and *E. grevyi*. The size of the teeth and of the metapodials is intermediate between those of *E. grevyi* and those of *E. burchelli* and notably smaller than in *E. stenonis vireti* and *E. koobiforensis*. Lower cheek teeth with the usual zebrine-stenonine pattern; in most specimens the vestibular groove of the molars is deep.

Referred material occurs throughout the Koobi Fora Formation but comes mainly from the *Met. andrewsi* zone.

The biometrics of the cheek teeth are given in Tables 5.15–5.18. In the upper cheek teeth the postprotoconal valleys may be deep (Plate 5.8E). The mean protoconal indices are 36·7 for $P^{3-4}$, 40·9 for $M^{1-2}$ and 43·9 for $M^3$. In the two specimens where $P^4$ and $M^1$ are associated the protoconal index is larger for $M^1$ than for $P^4$.

Most lower cheek teeth have the usual stenonine pattern with deep lingual grooves. Some specimens (Plate 5.10B–C) have shallower lingual grooves and even a hemionine pattern (Plate 5.10B). On most molars the vestibular groove is deep and extends to contact the lingual one; occasionally the vestibular groove is shallow (Plate 5.10A, D). A protostylid is present on the sole $dP_2$ but not on $P_2$ (Plate 5.10L).

Five more or less complete specimens each of third metacarpals and metatarsals are listed and figured in Tables 5.19–5.20, Figs. 5.8–5.9. The fragmentary radii have a maximum distal width of 62–64 mm, a distal articular width of 52–55 mm and a distal articular anteroposterior diameter of 30–33 mm. The tibia is 327 mm long. The calcanea are 100–111 mm long. The astragali have a maximum height of 50–58 mm and a maximum width of 51–54·5 mm.

The cheek teeth of *Equus* sp. indet. overlap in size with both *E. grevyi* and the quaggas but the protoconal indices, especially that of the $M^3$, are smaller than in the modern species; they approach more closely those of *E. quagga* than the other species. In comparison with fossil species, *Equus* sp. indet. teeth are in general smaller than *E. numidicus* or *E. mauritanicus* and larger than *E. tabeti* but overlap with all three species. The mean protoconal indices of the associated teeth are similar to those of *E. mauritanicus* but the mean calculated from isolated teeth is larger for the $M^{1/2}$ of *E. mauritanicus* (44·2) than for *Equus* sp indet. (40·9).

Most of the cheek teeth are smaller than those of *E. koobiforensis* but the two species overlap in size. The mean protoconal indices of $P^{3-4}$ of *Equus* sp. indet. (36·7) are larger than those for $P^{3-4}$ of *E. koobiforensis* (32·2); they are similar for $M^{1-2}$ and $M^3$ of both species (40·9 v. 41·3 and 43·9 v. 43·7 respectively). If *Equus* sp. indet. evolved from *E. koobiforensis*, which is conceivable given their stratigraphic provenance, the transition would have involved a reduction in size for both premolars and molars, a lengthening of the premolar protocones and shortening of the molar protocones. An alternative interpretation is that the species are not related; *E. koobiforensis* with larger protocones on $M^{1-2}$ than on $P^{3-4}$ resembling *E. tabeti*, *E. mauritanicus*, *E. zebra* and the quaggas, while *Equus* sp. indet., with its subsequal protocones, would be more like *E. stenonis* and *E. grevyi*. The lower cheek teeth of *Equus* sp. indet. resemble those of *E. koobiforensis* in their deep lingual grooves, in the occurrence of a protostylid on $dP_2$, and by the occurrence of molars with shallow vestibular grooves; however, the same characters may be found in the quaggas and *E. grevyi* among the modern equids and in *E. stenonis* and *E. mauritanicus* among the fossil forms.

The third metacarpal of *Equus* sp. indet., known from five specimens, is slightly longer than that of *E. burchelli* but a more striking difference is in the size of the posterior unciform facet which is much larger in *E. burchelli* (Fig. 5.9). The metacarpals of *E. mauritanicus* (Eisenmann 1979*e*, Fig. 17) are notably stouter but otherwise not very different. The third metatarsal, known from five specimens resembles more those of *E. numidicus* (Fig. 5.8) than those of *E. burchelli* (Fig. 5.10); the third metatarsals of *E. mauritanicus* (Eisenmann 1979*e*, Fig. 18) are notably stouter.

The radii of *Equus* sp. indet. are smaller than those of *E. grevyi* and *E. koobiforensis* and fall within the range of variation of *E. burchelli*. The tibia is

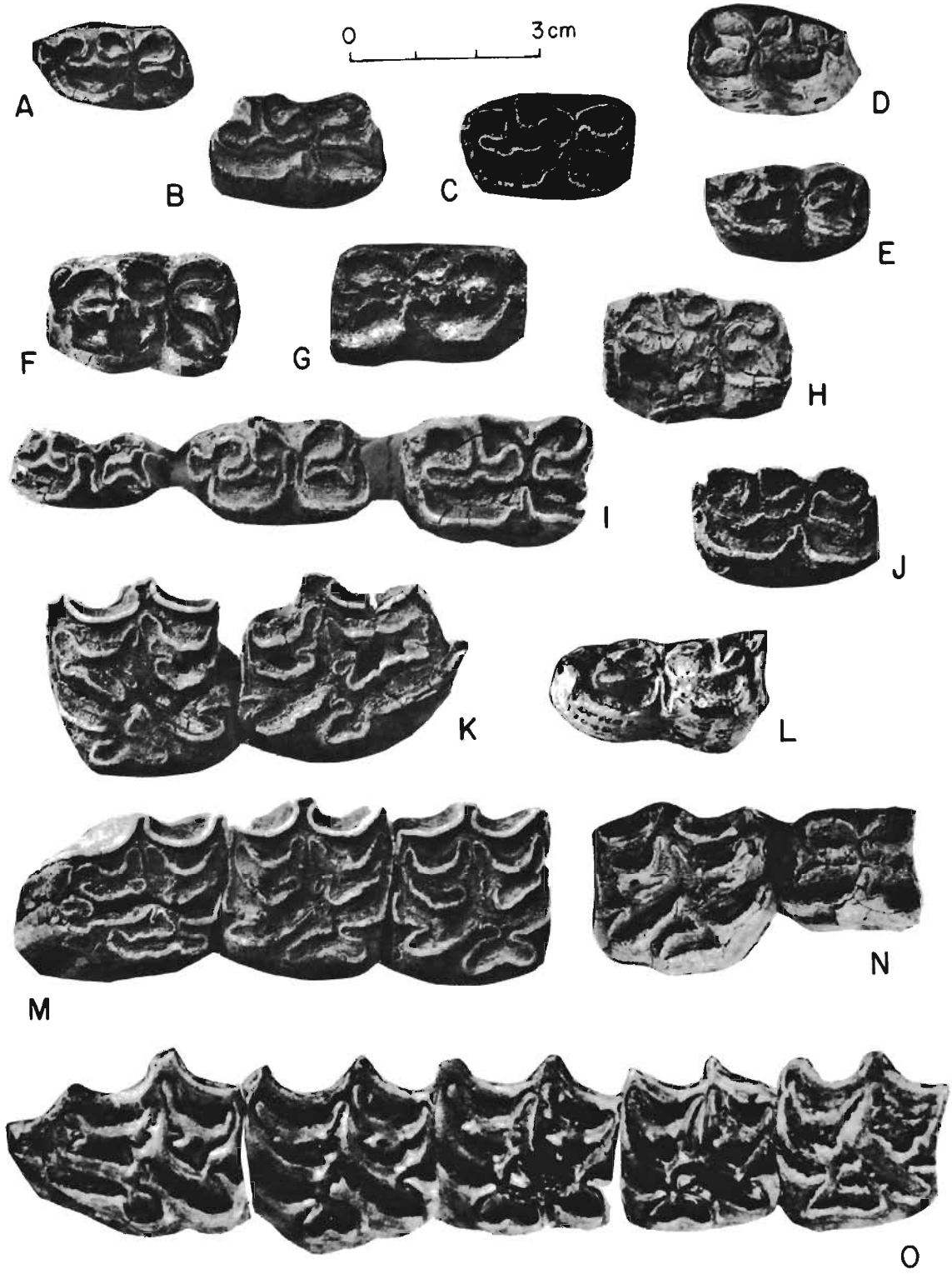


PLATE 5.10. *Equus* sp. indet.
(A) $M_1$ or $M_2$ (KNM-ER 3994); (B) $P_3$ or $P_4$ (KNM-ER 2655); (C) $P_3$ or $P_4$ (KNM-ER 4023); (D) $M_1$ or $M_2$ (KNM-ER 1288); (L) $dP_2$ (KNM-ER 1245).
*Equus koobiforensis*.
(E) $M_1$ or $M_2$ (KNM-ER 4026); (F) $P_3$ or $P_4$ (KNM-ER 3986); (G) $P_3$ or $P_4$ (KNM-ER 4015); (H) $P_3$ or $P_4$ (KNM-ER 4027); (J) $P_3$ or $P_4$ (KNM-ER 4046).
*Equus* cf. *grevyi*.
(I) $P_3$ or $P_4$ and associated fragmentary molars (KNM-ER 4055); (K) $P^2$ and $P^3$ or $P^4$ (KNM-ER 4055); (M) $M^1$ $M^2$ $M^3$ (KNM-ER 4055); (N) associated upper and lower P3 or P4 KNM-ER 2652); (O) $P^2$ $P^3$ $P^4$ $M^1$ $M^2$ (KNM-ER 1457).

intermediate in length between those of *E. grevyi* (328–363 mm) and those of *E. burchelli* (291–325 mm). The calcanea are of the length of the biggest *E. burchelli* and the astragali too fall into the range of variation of this species.

The material from east of Lake Turkana exemplifies the difficulty encountered in investigating Quaternary equids. African fossil and living *Equus* species can be unequivocally distinguished only on the basis of large samples of complete and associated material. When the available specimens do not include skulls, the cheek teeth are isolated or comprise only incomplete and immature or very worn series, when the limb bones are very few and damaged, and when, furthermore, the small and incomplete fossil sample may contain more than one species, identification and interpretation becomes almost impossible; every skeletal element has resemblances to more than one other species, different elements resemble different combinations of species, and no overall attribution can be positively made. In this particular instance I consider *Equus* sp. indet. to have probably evolved from *E. koobiforensis*. It does not seem to be related to *E. zebra* but its relationships with *E. grevyi* or the quaggas are unclear and cannot at present be clarified further.

***Equus grevyi*** Oustalet, 1882

***Equus*** cf. ***grevyi***

Grevy's Zebra (*Equus grevyi*) is the large, narrow-striped zebra of the semidesert regions of East Africa and is characterized by a large skull, large teeth, moderate protoconal indices subequal on $M^1$ and $M^2$, and stenonine lower cheek teeth with deep lingual grooves and frequent protostylids on $P_2$ and $dP_2$. A few equid fossils from the upper parts of the sequence east of Lake Turkana are of similar size to the modern species but their attribution remains uncertain either because the diagnostic characters cannot be observed on the referred material or because they are different.

Referred material comes from the *Met. compactus* zone, the Guomde Formation and the Galana Boi Beds. The upper and lower cheek teeth are listed in Tables 5.21, 5.22. In addition, a single radius KNM-ER (2302), a surface specimen from Area 102 and which may have been derived either from the *Met. compactus* zone or the Galana Boi Beds, can be attributed to this species.

The associated upper and lower cheek teeth of KNM-ER 4055 are rather large (Tables 5.21–5.22; Plate 5.10I, K, M) with protoconal indices increasing from $P^4$ to $M^3$; the $M^3$ bears an isolated hypoglyph (Plate 5.10M). The lower premolar has a deep lingual groove while the molars have deep vestibular grooves coming to the contact of the lingual ones. On one fragmentary molar of this specimen ($M_3$?) there is a rudimentary 'bridge' as described by Groves and Mazak (1967, p. 325) for *E. africanus* and *E. grevyi* and which I have personally observed to be present in no specimens of *E. burchelli* (Eisenmann, 1981, p. 139).

The upper cheek teeth of KNM-ER 1457 are of similar size to those of the previous specimen (Table 5.21, Plate 5.10O) but with smaller protocones. Protoconal indices increase from the $P^2$ to $M^2$; there is no $M^3$.

The radius is 331 mm long and 39 mm wide; the maximum distal width is 69 mm and the distal articular width 57 mm; the distal articular anteroposterior diameter is 37 mm.

All the upper premolars fall within the range of variation of a sample of 40 individuals of *E. grevyi*; some molars (KNM-ER 4055) are at the upper limit or are slightly larger. In KNM-ER 4055 the protoconal indices of $P^4$ and $M^1$ are similar to the mean observed in *E. grevyi* but they are larger for $M^2$ and, especially, $M^3$, which more closely resembles *E. burchelli*. The protoconal indices are notably larger than those of *E. koobiforensis* and *Equus* sp. indet. The only other more or less complete tooth row (KNM-ER 1457) is nearly as large as the previous specimen but its protoconal indices are not very different from those of *Equus* sp. indet. except on the $M^2$ where they approach the mean observed in *E. grevyi*. The great difference between the protoconal indices on $M^1$ and $M^2$ is not characteristic of *E. grevyi*.

The few isolated lower cheek teeth attributed to this taxon do not provide any useful information. Unfortunately the state of preservation of the $P_2$ precludes any observation of a protostylid.

The measurements of the radius fall within the range of variation of 20 specimens of *E. grevyi* except for the distal widths that are slightly smaller.

In summary, the attribution of these specimens to *E.* cf. *grevyi* is largely based on the size (bigger than in *Equus* sp. indet. and than in the quaggas). Further and more diagnostic material will be necessary to substantiate this identification.

***Equus burchelli*** (Gray), 1824

***Equus*** cf. ***burchelli***

*Equus burchelli* is a small to medium-sized zebra with a widespread distribution in eastern Africa from

Kenya to South Africa. The skull, teeth and limb bones of this species are smaller than those of *E. grevyi* but the size ranges of the two species overlap. The first phalanges of both species are rather similar in shape.

Referred material comprises two posterior first phalanges from the *Met. compactus* zone of Area 6A. They were associated together in the field but do not belong to the same individual. The larger, KNM-ER 2678, is 75 mm long and 29 mm wide; the smaller, KNM-ER 5700, is 71 mm long and 27·5 mm wide.

The smallest of a sample of 20 posterior first phalanges of *Equus grevyi* is 75 mm long and 28 mm wide and in general *E. grevyi* phalanges are longer and somewhat more slender (range of variation 75–87 mm in length and 27·5–31·5 mm in width). In the northern forms of *E. burchelli* the range of variation for 21 posterior phalanges is 66·5–77·5 for the length and 27·5–31·5 for the width. Thus, the two Koobi Fora phalanges might thus be better assigned to *E. burchelli* than to *E. grevyi* even if the larger one might have belonged to a very small and rather stout *E. grevyi*! Both phalanges are stouter than the ones assigned to *E.* cf. *koobiforensis* and *E.* cf. *tabeti*; they are smaller than those of *E. mauritanicus*.

Some upper and lower cheek teeth found at the same locality (KNM-ER 2652, 2672, 2684) are bigger than the teeth of *E. burchelli* but fall within the range of variation of *E. grevyi* and were accordingly referred to *E.* cf. *grevyi*. The attribution of all the teeth to one species and of all the limb bones to another is certainly unsatisfactory but cannot be helped in the present state of our knowledge.

## DISCUSSION

It is generally assumed that the genus *Equus* is better adapted than *Hipparion* to a siliceous diet because of its extreme hypsodonty, and to running on hard ground because of its more perfect monodactyly. If it is indeed right to assume that their overall way of life led them to compete directly, it would in consequence be logical for *Equus* to evict *Hipparion* wherever the two genera coincided. The eviction and demise of *Hipparion* seems to have occurred very rapidly in Europe but not in Africa, which leads to a number of questions concerning the African hipparions. Did they compete directly for the same nutritional sources as *Equus*? If so, does their persistence after the immigration of *Equus* relate to their being more hypsodont and more cursorial than their Eurasian relatives? Again, if so, were these characters acquired before the arrival of *Equus* and would they explain the persistence of *Hipparion* or, on the contrary, are they the consequence of a protracted evolution of hipparions in Africa, whatever the cause of this persistence may be? As is often the case, the answer to these theoretical questions is hindered by very practical problems such as how to estimate hypsodonty (or better, how to quantify it?) or how to estimate and compare success at cursorial locomotion?

Hypsodonty is usually quantified as a percentage of the ratio between the height of unworn cheek teeth in the middle of the tooth row ($P^4$, $M^1$, $M^2$) and the anteroposterior diameter of the tooth. However, different authors do not measure heights and diameters in the same way; in consequence the index of the same tooth measured by the techniques recommended by Gromova (1952, p. 33), Sondaar (1962, pp. 226–7), Forstén (1968, p. 7) and Hooijer (1975, p. 6) varies from 200 to 319. Given these variations, direct comparison of data published by different authors is often very difficult. Moreover, unworn cheek teeth are rare so that the range of variation in a single species is usually poorly known. Furthermore, even using the same technique of measurement, the definition of the precise junction between the crown and roots is often so difficult that I have found differences of 10–15 units after having calculated several times the hypsodonty index of the same tooth. With these restrictions in mind, it is still possible to estimate the hypsodonty of some of the African hipparions. Using the measurement of height suggested by Forstén and that of the anteroposterior diameter proposed by Hooijer, *Hipparion* hypsodonty indices for the Omo Shungura Formation range from 256–313 in Members B and C, 291–370 in Members F and G with a single index for Member L of 350. Single indices of 300 were obtained for an unworn molar (KNM-ER 1979) in the *Met. andrewsi* zone of the Koobi Fora Formation (younger than Shungura G but older than Shungura L), for a little worn molar (AL 214-4) from the Sidi Hakoma Member of the Hadar Formation (older than Shungura B) and for an unworn molar (Hooijer and Maglio 1974, p. 19) from Lothagam (older than the Hadar Formation). These results indicate a trend for increase in hypsodonty through the Shungura Formation but indicate also that the Pliocene African hipparions were already quite hypsodont and perhaps more so than contemporary and later European species; at Alcoy (Spain) the

hypsodonty index (exaggerated by Alberdi's technique) is only 256 while at Villaroya (Spain) the hypsodonty indices range between 200 and 300 (Alberdi 1974, Table 50).

Evaluation of the degree of cursorial adaptation is even more difficult. According to Camp and Smith (1942), Gromova (1952), and Sondaar (1968), the main functional differences between *Equus* and *Hipparion* are related to the straightening of the limbs—resulting in the loss of function of the lateral digits and their atrophy. Many anatomical features appear to be linked to this functional shift: shape and relative length of the central first phalanges, position of the lateral digits with respect to the central one, modification of the carpal and tarsal articular facets, etc. To date the functional anatomy of the most recent African hipparions has not been intensively studied. It seems, however, on the basis of material retrieved from the Hadar Formation, that at least some African hipparions had first phalanges closely comparable to those of *Equus* and that their lateral digits occupied a quite posterior position; both characters may be considered as progressive. Further information about the locomotion of African hipparions might be provided by the Pliocene footprints and tracks found recently at Laetoli (Leakey and Hay 1979) and presently being studied by Sondaar and his students.

It seems likely to me that the feeding and locomotory adaptations of the African hipparions were probably more advanced than those of their Eurasian relatives. More material and further study is needed to establish if the progressive features of the African hipparions were attained prior to the arrival of *Equus*.

In the preceeding paragraphs we have assumed that *Equus* and *Hipparion* were in broad competition, leading the same kind of life and feeding on the same kind of food. This assumption is probably justified although patently impossible to prove at the present degree of knowledge. Both genera are represented by several species which must have led also to intrageneric competition. From studies conducted on European Villafranchian cervids (Heintz 1970, p. 293) and Plio-Pleistocene African suids (Harris and White 1979, Appendix I), it appears that at least three species of the same genus can be associated at the same level of a single locality. At Koobi Fora three species of *Hipparion* seem to be associated in the *Nolochoerus scotti* zone. We know little about these species as yet but we may suppose that their ecological 'niches' were somewhat different: *Hipparion* sp. B was probably a very small species, *H. cornelianum* had a broad and angulated incisor region perhaps specialized in the cutting of grass, and *H. ethiopicum* may have had a less specialized premaxilla and symphysis and could have been a browser. With regard to *Equus* I believe that *E. koobiforensis* probably evolved into the smaller *Equus* sp indet. but, if not, the large and small teeth occasionally associated in the same levels would indicate that two species coexisted—the large one mainly present in the *Not. scotti* zone and the smaller mostly in the *Met. andrewsi* zone. Moreover, in the *Met. andrewsi* zone a species with possible asinine affinities, *E.* cf. *tabeti*, coexisted with the other(s) which had more usual stenonine/zebrine features. The eventual coexistence of three species of *Equus* is not particularly surprising as in the northeast of Africa today the range of *E. africanus* overlaps with that of *E. grevyi* and the latter with that of *E. burchelli*. For the same reason the presence together of *E.* cf. *grevyi* and *E.* cf. *burchelli* in the *Met. compactus* zone should not be entirely unexpected; mixed herds of these species are seen today in the Ileret region, *E. burchelli* occurring along the grassy lake shores while *E. grevyi* inhabits the semidesert scrubland to the east of the lake.

Although the question of the attribution of some of the Koobi Fora fossils to *E. grevyi* or *E. burchelli* arose, these species or their immediate ancestors cannot be positively identified in the fossil assemblages. The two living species differ mostly by their size, shape of the crania, shape of the metapodials and in the development of cups on the lower incisors; in the upper cheek teeth morphological differences can be discerned only when a large sample of associated teeth is available while morphological differences in the lower teeth are virtually restricted to the frequency of the protostylid on $P_2$ and $dP_2$. The criterion of size is of dubious value in palaeontology as it is evident that individuals of the same species may increase or decrease in size through time. For example, Gentry and Gentry (1978, pp. 55–6) found that some Olduvai bovids were larger than the living representatives of the same species and Guérin (1979, p. 287) showed that some species of East African rhinoceroses grew smaller during the Pleistocene. The size of the most abundant species in the Koobi Fora fossil assemblages is intermediate between that of *E. grevyi* and that of *E. burchelli*. Even at the level where specimens of this species are most abundant, the *Met. andrewsi* zone, there is no cranium, lower second premolars and associated

upper cheek teeth are rare, and evidence from the few, damaged metapodials is equivocal—they resemble most closely those of *E. burchelli* but are more slender and exhibit differences in the size of the articular facets that may or may not prove to be significant depending on whether these differences persist when a larger sample is available. Today only one African fossil *Equus* species, *Equus mauritanicus*, can be demonstrated to show a close relationship with extant species, in this instance the quaggas. *E. mauritanicus* happens to be represented by several skulls and hundreds of teeth and metapodials. I would maintain that, given the variation present in both extant and fossil equid species, precise and reliable systematic interpretations depend on the availability of adequate samples. I would further advocate that no useful purpose would be served by attempting to over-simplify fossil equid systematics in the interim.

The material collected from east of Lake Turkana has already provided new and important information about the Plio-Pleistocene representatives of both *Equus* and *Hipparion*. However, more material, and in particular more metapodials, will be necessary to improve our understanding of the relationships between the Miocene hipparions and their specialized representatives in the African Pleistocene, and between the Pliocene stenonine forms of *Equus* and the extant African zebras.

# SPECIMEN LISTS AND TABLES

## ABBREVIATIONS TO TABLES

Areas are shown in parentheses after KNM-ER numbers, followed by zones.

| | |
|---|---|
| A | zone A |
| B | zone B |
| C | zone C |
| KF IIA | Koobi Fora IIA (see p. 7 and Fig. 1.4) |
| KF IIB | Koobi Fora IIB |
| KF III | Koobi Fora III |
| N.s | *Notochoerus scotti* zone |
| M.a | *Metridiochoerus andrewsi* zone |
| M.c | *Metridiochoerus compactus* zone |
| GB | Galana Boi Beds |
| GF | Guomde Formation |
| * | specimen measured at mid height |
| ( ) | estimated measurement |
| ant | anterior |
| ap | anteroposterior length |
| diap ap | diaphysis minimum anteroposterior diameter |
| diap tr | diaphysis minimum width |
| dist | distal |
| dist ap | distal articular anteroposterior diameter |
| dist sup tr | distal supra-articular width |
| dist tr | distal articular width |
| ect | ectostylid occlusal length |
| ht | height of crown |
| int | internal |
| max | maximum |
| min | minimum |
| oc ap | occlusal length |
| oc tr | occlusal width |
| PI | protoconal index |
| plic | number of plications including caballine folds |
| post | posterior |
| prox ap | proximal anteroposterior articular diameter |
| prox tr | proximal articular width |
| ptc | protocone occlusal length |
| tr | maximum width |

Teeth measurements are taken at the occlusal surface unless otherwise indicated.

Equid 3rd and 4th premolars and 1st and 2nd molars are often difficult to differentiate on isolated teeth, and measurements of the posterior premolars and anterior molars have been grouped together in the tables. Where two sets of measurements are listed under the same accession number, the first set is for $P_3$ (or $M_1$) and the second for $P_4$ (or $M_2$).

TABLE 5.2.
*Hipparion hasumense* sp. nov. lower cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr | ect | ht |
|---|---|---|---|---|---|
| $P_2$ | 2768A (203 B) | 27·5 | 14 | 2·5 | 37 |
| | 2788A (117 C) | 33 | 14 | — | 38 |
| $P_{3-4}$ | 2776** (204B) | 26 | 15 | 4 | 27 |
| | 2776** (204B) | 25·5 | 15 | 4 | 35 |
| | 2786A (117 C) | 30 | 18 | 4·5 | 58 |
| | 2788C (117C) | 27 | 16 | 2·5 | 47 |
| | 2921 (117 B) | 28·5 | 15 | 3·5 | — |
| | 4073 (117C) | 27 | 15 | — | 56 |
| | 4074 (117 B) | 24 | 15 | 4 | 25 |
| | 4077 (129 B) | — | 16 | — | 31 |
| | 4080 (129 B) | 28 | 17 | 4 | 34 |
| | 4080 (129 B) | 26·5 | 15 | 4 | 41 |
| | 4084 (129 B) | 29 | 16·5 | 5 | — |
| | 4084 (129 B) | 31 | 15 | — | 62 |
| | 4093 (116 B) | 30 | 14 | — | 68 |
| $M_{1-2}$ | 2776** (204 B) | 22 | 12 | 3 | 29 |
| | 2776** (204 B) | 22·5 | 11 | 1 | 31 |
| | 2788B (117 C) | 24 | 12 | 4 | 50 |
| | 2788D (117C) | 26·5 | 11 | — | 55 |
| | 4080 (129 B) | 25 | 14 | 2·5 | 30 |
| | 4084 (129 B) | 27 | 15 | 5 | 50 |
| | 4084 (129 B) | 27 | 14 | 5 | 52 |
| | 4092 (116 B?) | 28 | 13·5 | 4 | 59 |
| $M_3$ | 2768B (203 B) | 26·5 | 9·5 | — | (47) |
| | 2787 (117 C) | 27 | 11·5 | 4 | 43 |
| | 4084 (129 B) | (27) | 9·5 | — | 56 |

** Holotype.

***Hipparion* sp. A**

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| Zone C | 2766 | 203 | Lt $P_{3-4}$ |
| Guomde formation | 1234 | 6A | Lt $P_{3-4}$ |
| Horizon indet. | 335 | 7A | Rt $P_{3-4}$, Rt $M_{1-2}$, Rt $M_3$ |
| | 673 | KF III | $dP_2$, Rt $P_4$, Rt $M_2$ |

TABLE 5.3.
*Hipparion* sp. A lower cheek teeth measurements (mm)

| | KNMR-ER No., area and zone | oc ap | oc tr | ect | ht |
|---|---|---|---|---|---|
| $P_{3-4}$ | 673A (KF III) | 26·2 | 16 | 6 | 51 |
| | 1234 (6A GF) | 23 | 15·5 | 5 | 30 |
| | 2766 (203 C) | (28·5) | 17 | 5 | 45 |
| $M_{1-2}$ | 673B (KF III) | 24 | 10·3 | — | 60 |
| | 335B (7A?) | 25·1 | 14 | 4·6 | 52 |

***Hipparion cornelianum***

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Notochoerus scotti* zone | 3539 | 105 | immature cranium |

***Hipparion* cf. *ethiopicum***

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| Zone B | 4095 | 116 | Rt astragalus |
| *Notochoerus scotti* zone | 1230 | 105 | Rt maxilla frag ($P^4$–$M^1$) |
| | 1626 | 105 | Lt and Rt mandible |
| | 1770 | 131 | $M_{1/2}$ |
| | 2071 | 129 | Rt $M^3$ |
| | 2072 | 130 | Lt $M^{1/2}$ |
| | 2751 | 14 | Rt $P_{3/4}$ |
| | 2752 | 14 | Rt $M_{1/2}$ |
| | 2753 | 14 | Rt $M_3$ |
| | 3990 | 102 | Rt maxilla frag ($P^{2-3}$) |
| | 4076 | 14 | Lt $P_{3/4}$ |
| | 4079 | 105 | Lt $M^{1/2}$ |
| | 4082 | 105 | Rt mandible frag ($P_{2-3}$) |
| | 4084 | 129 | Rt $P_3$–$M_3$ |
| | 4086 | 14 | Lt $P^{3/4}$ |
| | 4087 | 14 | Lt $M_3$ |
| | 4088 | 14 | Lt $M_{1/2}$ |
| | 4089 | 129 | Rt $M^3$ |
| | 4090 | 129 | Rt $M_{1/2}$ |
| | 4091 | 129 | I, Lt $P^{3/4}$, Lt $M^{1/2}$ |
| | 4094 | 116 | Lt $M^3$ |
| | 5353 | 100 | Lt $M^3$ |
| | 5354 | 100 | Lt $M_{1/2}$ |
| | 5357 | 104 | $P_{3/4}$ |
| *Metridiochoerus andrewsi* zone | 776 | 103 | $P_2$–$M_3$ |
| | 1232 | 8A | Lt $M^3$ |
| | 1235 | 8A | dist. 3rd metatarsal |
| | 1236 | 104 | Rt $M_{1/2}$ |
| | 1238 | 6A | dist. tibia |
| | 1244 | 102 | Rt $M_{1/2}$ |
| | 1264 | 10 | Lt $M_{1/2}$ |
| | 1294 | 103 | Rt $M_3$ |
| | 1295 | 103 | Rt astragalus |
| | 1345 | 6A | dist. 3rd metatarsal |
| | 1456 | 104 | Lt mandible frags ($I_2$, $P_{3-4}$, $M_3$) |
| | 1981 | 12 | Lt $M_{1/2}$ |
| | 2047 | 123 | astragalus |
| | 2053 | 103 | prox. lateral metapodial |
| | 2070 | 103 | Lt $M^{1/2}$ |
| | 2242 | 103 | lateral metapodial frag |

***Hipparion* cf. *ethiopicum*** *cont.*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| | 2264 | 104 | Rt $P_{3/4}$ |
| | 2638 | 8B | Rt $P_{3/4}$ |
| | 3989 | 119 | Rt $M_{1/2}$ |
| | 4005 | 103 | Rt $M_3$ |
| | 4053 | 101 | Lt $M_{1/2}$ and M frags |
| | 5355 | 103 | Rt astragalus |
| | 5356 | 104 | Lt astragalus |
| *Metridiochoerus compactus* zone | 1278 | 103 | Rt $M^{1/2}$ |
| | 2069 | 103 | $M_{1/2}$ and associated posteranials |
| | 2656 | 1A | Lt and Rt $M_3$ |
| | 2668 | 11 | $P^2$ |
| | 2690 | 8 | Lt astragalus |
| | 5715 | 103 | $M_{1/2}$ |
| Guomde Formation | 1234 | 6 | Lt $P_{3/4}$ |

TABLE 5.4.
*Hipparion* cf. *ethiopicum* and *H. cornelianum* upper cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr | ptc | ht | plic |
|---|---|---|---|---|---|---|
| $P^2$ | 3990 (102 N.s) | 30 | 21 | 7·5 | (28) | 13 |
| | 2668 (11 M.c) | 32 | 22 | 8 | 47 | 13 |
| $P^{3-4}$ | 1230 (105 N.s) | 25 | 26·5 | 11 | 42 | 18 |
| | 4086 (14 N.s) | 25 | 24 | 7 | 59 | (11) |
| | 4091 (129 N.s) | 24 | 27 | 9 | 21 | — |
| $M^{1-2}$ | 1230 (105 N.s) | 23 | 24 | 9 | 42 | 14 |
| | 2072 (130 N.s) | 23 | 22 | 9 | 66 | 14 |
| | †3539 (105 N.s) | (25·5) | (24) | 9 | — | — |
| | 4079 (105 N.s) | 23 | 22 | 9 | 63 | (6) |
| | 4091 (129 N.s) | 23·5 | 23 | 8 | 30 | (10) |
| | 2070 (103 M.a) | 22·5 | 22 | — | 57 | 10 |
| | 1278 (103 M.c) | 24 | 23 | 9 | 50 | 18 |
| $M^3$ | 2071 (129 N.s) | 22·5 | 18 | 7 | 56 | (8) |
| | 4089 (129 N.s) | 23·5 | — | 10 | 55 | — |
| | 4094 (116 N.s) | 23* | 21·5* | (9) | 60 | — |
| | 1232 (8A M.a) | 22 | 21 | 9·5 | 35 | 8 |
| | 4005 (103 M.a) | 23 | 20 | 8 | (40) | (10) |

† *Hipparion cornelianum.*

TABLE 5.5.
*Hipparion ethiopicum* and *H.* cf. *ethiopicum* lower cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr | ect | ht |
|---|---|---|---|---|---|
| $P_2$ | 1626 (105 N.s) | 28 | 15 | 6 | — |
| | 4082 (105 N.s) | 29 | 16 | 4 | — |
| | 1626 (105 N.s) | 24·5 | 16·5 | 8 | — |
| | 1626 (105 N.s) | 23·5 | 14 | 6 | (30) |
| | 2751 (14 N.s) | 26·5 | 14 | 2 | 61 |
| | 4076 (14 N.s) | 24·5 | 15 | 6 | 45 |
| | 4082 (105 N.s) | 25 | 17 | 6·5 | — |
| | 4084 (14 N.s) | 24 | 15·5 | 6 | 26 |
| | 5357 (104 N.s) | 23·5 | — | — | 64 |
| | 776 (103 M.a?) | 28·5 | 13·5 | 3·5 | 40·5 |
| $P_{3,4}$ | 776 (103 M.a?) | 24·5 | 16 | 6·5 | 45 |
| | 1456 (104 M.a) | 24 | 16·5 | 8·5 | 38 |
| | 1456 (104 M.a) | 24 | 15 | 7 | 35 |
| | 2264 (104 M.a) | 25 | 16 | 6 | 42 |
| | 2638 (8B M.a) | 24·5 | 15 | 7 | 61 |
| | 1234 (6 GF) | 23 | 15·5 | 5 | 30 |
| | 1951.4.128**(Omo) | 23·5 | 16·5 | 7·2 | — |
| $M_{1,2}$ | 1626 (105 N.s) | 23 | 13·5 | 7 | — |
| | 1626 (105 N.s) | 22 | 12·5 | 5 | — |
| | 1770 (131 N.s) | 23·5 | 13·5 | 5·5 | 28 |
| | 2752 (14 N.s | 25 | 11·5 | 2 | 62 |
| | 4088 (14 N.s) | 23 | 14 | 6 | 24 |
| | 4090 (129 N.s) | 23·5 | 11·5 | 5·5 | — |
| | 1236 (104 M.a) | 21 | 14 | 6·5 | 19 |
| | 1264 (10 M.a) | 22 | 12 | 5 | 46 |
| | 1456 (104 M.a) | (25) | 11 | — | 38 |
| | 1981 (12 M.a) | 22·5 | 14 | 6 | 41 |
| | 6100 (101 M.a) | 23 | 13 | 6 | 45 |
| | 5354 (100 M.a) | 22 | 13·5 | 6 | 37 |
| | 5715 (103 M.c) | 24 | (11·5) | — | 60 |
| | 776 (103 M.a?) | 22·5 | 12·5 | 4·5 | 51 |
| | 776 (103 M.a?) | 24 | 11 | 0·5 | (56) |
| | 1244 (102 M.a?) | 24 | (11) | 2 | — |
| | 3989 (119 M.a) | (21·5) | 14 | 6·5 | 29 |
| | 1951.4.129**(Omo) | 23 | 15 | 6·2 | 41 |
| | 1951.4.131**(Omo) | 23·5 | 14·7 | 7·5 | 44 |
| $M_3$ | 1626 (105 N.s) | 26 | 11 | 1 | — |
| | 2753 (14 N.s) | 25* | 10 | 2 | 54 |
| | 4087 (14 N.s) | (23) | 9 | — | 57 |
| | 1294 (103 M.a) | 25·5 | — | — | — |
| | 1456 (104 M.a) | (26) | 11 | — | 40 |
| | 5353 (100 M.a) | 27 | 11 | 4·5 | — |
| | 776 (103 M.a?) | (24) | — | — | — |
| | 2656 (1A M.c) | 25 | 11 | 1·5 | 56 |
| | 1951.4.127** | 27 | 12·7 | 5 | 42 |

** *Hipparion ethiopicum* lectotype and associated teeth, Omo, level unknown.

***Hipparion* sp. B**

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Notochoerus scotti* zone | 1268 | 130 | Rt $P_{3,4}$ |
| | 3985 | 129 | Lt $M^3$ |
| | 4096 | 130(?) | $P_{3,4}$ |
| *Metridiochoerus andrewsi* zone | 1231 | 8A | Rt $M^{1,2}$ |
| | 1263 | 10 | Rt $M^3$ |
| | 2073 | 131 | Rt $M^{1,2}$ |
| | 2263 | 104 | Rt $M^{1,2}$ |
| | 2667 | 8B | Lt $P_{3,4}$ |
| | 3988 | 102 | Lt $P^3/^4$ |
| | 4054 | 101 | Lt $P_2$, Lt $P_{3,4}$ |
| | 4083 | 15 | Rt $M^3$ frag |
| | 5335 | 10 | $M^3$ |
| | 5359 | 102 | Rt$M^{1,2}$ |
| Horizon indet. | 336 | 104 | $P_{3,4}$ |

TABLE 5.6.
*Hipparion* sp. B upper cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr | ptc | ht | plic |
|---|---|---|---|---|---|---|
| $P^{3,4}$ | 3988 (102 M.a?) | 23 | 22 | 7 | 66 | — |
| $M^{1-2}$ | 1231 (8A M.a) | 23 | (19) | 8·5 | 73 | — |
| | 2073 (131 M.a) | 23 | 21 | 10 | 70 | 12 |
| | 2263 (104 M.a) | 22 | 21 | 11·5 | 69 | (11) |
| | 5359 (102 M.a) | 20·5 | 20 | 7·3 | 55 | (13) |
| $M^3$ | 3985 (129 N.s) | 19 | 16 | 8 | 35 | — |
| | 1263 (10 M.a) | 20* | 18* | 8* | 58 | — |
| | 5335 (10 M.a) | 20* | 17* | 8* | 52 | — |
| | 4083 (15 M.a) | 18 | 15 | 7 | 46 | — |

TABLE 5.7.
*Hipparion* sp. B lower cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr | ect | ht |
|---|---|---|---|---|---|
| $P_2$ | 4054 (101 M.a) | 27 | 10 | - | - |
| $P_3$-$_4$ | 1268 (130 N.s) | 22·5 | 13 | 7 | 40 |
| | 4096 (130 N.s) | 24 | 13 | 7·5 | - |
| | 4054 (101 M.a) | 22·5 | 12·5 | 6·5 | 41 |
| | 2667 (8B M.a) | 22 | 15 | 7·2 | 23 |
| | 336 (KF IIB) | 22·2 | 13·9 | - | 21 |

TABLE 5.8.
*Hipparion hasumense* (KNM-ER 2789 and AL 155–6) and *Hipparion* cf. *ethiopicum* (others) astragali measurements (mm)

| KNM-ER No., area and zone | length | max tr | art dist tr | art dist ap |
|---|---|---|---|---|
| 4095 (116 B) | 58 | – | 38 | 30 |
| 2789 (117 C) | 65 | 61 | 47 | 35 |
| 1295 (103 M.a) | 55 | 48 | 41 | 28 |
| 2047 (123 M.a) | 60 | 54 | 45 | 32 |
| 5355 (103 M.a) | 48 | 45 | 41 | - |
| 5356 (104 M.a) | 57 | 49·5 | 41 | 30 |
| 2690 (8 M.c) | (55) | (50) | 42·5 | (30) |
| AL 155–6 (DDM) | (66·5) | (64) | (50) | 36 |

DDM = Denen Dora Member of the Hadar Formation.

TABLE 5.9. *Hipparion* cf. *ethiopicum* postcranial measurements (mm)

| | KNM-ER No., area and zone | diap tr | diap ap | dist sup tr | dist art tr | dist art ap |
|---|---|---|---|---|---|---|
| Metatarsal III | 1235 (8A M.a) | 27 | (24) | 37·5 | 35 | 30·5 |
| | 1345 (6A M.a) | (30) | (28) | 40·5 | 37 | 29 |
| Tibia | 1238 (6A M.a) | 38 | 27·5 | | 61* | 41* |

* Tibia measurements are maximum not articular.

### *Hipparion* sp. indet.

| KNM-ER No. | Area | | Specimen |
|---|---|---|---|
| Zone B | 4077 | 129 | P frag |
| *Metridiochoerus andrewsi* zone | 3987 | 102 | upper cheek tooth frag |
| | 3993 | 103 | $P_2$ frag |

## *Equus koobiforensis*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Notochoerus scotti* zone | 326 | 105 | Rt mandible ($P_2$–$M_3$) and Lt mandible frag ($P_2$–$M_2$) |
| | 337 | 105 | Rt $M_{1/2}$ |
| | 1129 | 129 | $P^{3/4}$ |
| | 1256 | 105 | Rt $M^3$ |
| | 1265 | 130 | Rt $P^{3/4}$ |
| | 1266 | 130 | Lt $M^{1/2}$ |
| | 1271 | 105 | Rt $M^{1/2}$ |
| | 1272 | 105 | Rt $M^3$ |
| | 1484 | 130 | cranium (Lt $I^2$–$M^3$, Rt $P^2$–$M^3$) |
| | 1518 | 105 | Lt mandible ($P_2$–$M_3$) and Rt $M_{1/2}$ |
| | 2224 | 131 | Lt $P^{3/4}$ |
| | 2687 | 105 | $M^{1/2}$ |
| | 2716 | 129 | Lt $P_{3/4}$ |
| | 2740 | 14 | Rt $M^{1/2}$ |
| | 2741 | 14 | $P_{3/4}$ |
| | 3986 | 129 | Rt $P_{3/4}$ |
| | 4011 | 14 | Lt $P_{3/4}$ |
| | 4014 | 14 | Lt $M^{1/2}$ |
| | 4015 | 100 | Lt $P_{3/4}$ |
| | 4019 | 14 | Lt $M_3$ |
| | 4020 | 102 | Lt $M^{1/2}$ |
| | 4026 | 129 | Rt $M_{1/2}$ |
| | 4027 | 129 | Rt $P_{3/4}$ |
| | 4028 | 116 | Rt $P_2$ |
| | 4034 | 130 | $M^{1/2}$ |
| | 4036 | 129 | Rt $M_{1/2}$ |
| | 4037 | 129 | Rt $P_{2-3}$ |
| | 4043 | 129 | Lt $P^{3/4}$ |
| | 4044 | 129 | Rt $P^{3/4}$ |
| | 4046 | 100 | Rt $P_4$, Rt $M_1$ |
| | 4051 | 115 | Rt mandible frag ($P_2$–$M_2$) |
| | 4520 | 104 | cranium (Lt and Rt $M^{1-3}$) |
| | 5360 | 130 | Rt mandible frag ($P_2$–$M_3$) |
| | 5361 | 100 | Lt and Rt mandibles ($I_1$–$M_3$) cranial frags ($P^{2-4}$, $M^3$) |
| | 5519 | 102 | maxilla frags ($P^{2-4}$, $M^3$) |
| *Metridiochoerus andrewsi zone* | 1239 | 104 | premaxilla ($I^1$–C) |
| | 1242 | 102 | Rt $M^3$ |
| | 1243 | 102 | $P_{3/4}$ |
| | 1249 | 104 | Rt $M_3$ |
| | 1250 | 104 | Rt $M^3$ |
| | 1255 | 105 | Lt $M^2$ |
| | 1260 | 6A | Rt $P^{3-4}$ |
| | 1269 | 105 | Lt and Rt $M_1$ |
| | 1582 | 104 | Rt mandible and symphysis (Lt $I_{1-3}$, Rt $I_1$–$M_3$) |

## *Equus koobiforensis* *cont.*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| | 2061 | 104 | $M_3$ |
| | 2248 | 105 | Lt $P_{3/4}$ |
| | 2613 | 7 | Rt $M^3$ |
| | 2618 | 105 | Rt $M^3$ |
| | 2670 | 129 | Lt $M^{1/2}$ |
| | 2691 | 12A | Lt maxilla frags ($P^2$–$M^3$) |
| | 3992 | 101 | Lt $M_{1/2}$ |
| | 4006 | 103 | Rt $M_{1/2}$ |
| | 4025 | 105 | Lt $P^{3/4}$ |
| Guomde Formation | 333 | 105 | Lt mandible frag ($P_2$–$M_2$) |
| Galana Boi Beds | 2931 | 117 | $M_{1-2}$ |
| Horizon indet. | 320 | S. of Koobi Fora Ridge | Lt mandible frag ($P_{3-4}$) |
| | 321 | S. of Koobi Fora Ridge | Rt $P_{3-4}$ |
| | 322 | S. of Koobi Fora Ridge | Rt $P_{3-4}$ |
| | 672 | 103 | Lt $P^2$ |
| | 674 | 103? | $M^3$ |
| | 676 | 102 | Lt $M^{1-2}$ |
| | 679 | 102 | Rt $P^{3-4}$ |
| | 680 | KF IIB | Lt $P_{3-4}$ |
| | 681 | KF IIB | Lt $P_{3-4}$ |
| | 690 | KF III | Lt mandible frag ($M_{1-2}$) |
| | 3986 | 129 | Rt $P_{3-4}$ |

## *Equus* cf. *koobiforensis*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Notochoerus scotti* zone | 1276 | 105 | associated limb bones (see pp. 187–188) |
| | 4052 | 100 | Rt 3rd metatarsal |
| | 5358 | 100 | Lt 3rd metatarsal |
| *Metridiochoerus andrewsi* zone | 1275 | 105 | associated limb bones (see pp. 187–188) |
| | 2054 | 123 | Rt distal radius |
| | 2625 | 7 | Rt astragalus |
| | 3998 | 102 | prox. and dist. Rt radius |
| Horizon indet. | 2317 | ? | astragalus |

TABLE 5.10. *Equus koobiforensis* cranial measurements (mm)

| | KNM-ER 1484 (130 N.s) *E. koobiforensis* | NIH 002* *E. sanmeniensis* | QSV 226† *E. stenonis vireti* | SEN 336‡ *E. stenonis senezensis* | *E. grevyi* (mean of c.50 specimens) |
|---|---|---|---|---|---|
| 1 | 577 | 580 | 550 | 535 | 531·5 |
| 2 | 325 | 308 | 300 | 297 | 272·5 |
| 3 | — | (152) | — | 135 | 133 |
| 4 | — | (116) | — | 110 | 130·5 |
| 5 | 150 | 158 | 145 | 140 | 140·5 |
| 6 | 107 | 125 | 118 | 97 | 111·5 |
| 7 | 110 | 103 | 100 | 104 | 95·5 |
| 7 bis | 91·5 | 90·5 | 84 | 83 | 78·5 |
| 8 | 202 | 192 | 186 | 187 | 173·5 |
| 9 | — | — | — | — | 83·5 |
| 10 | 53 | — | 47 | 50 | 48·5 |
| 10 bis | 44 | — | 37 | 42·5 | 40 |
| 11 | 178 | 156 | 166 | 166 | 157 |
| 12 | 426 | 420 | 400 | 400 | 394 |
| 13 | 225 | — | 226 | 236 | 212 |
| 14 | 213 | — | 216 | 229 | 210 |
| 15 | 111 | — | 104 | 108 | 106 |
| 16 | — | — | — | 69 | 85 |
| 17 | (64) | 64·4 | 69 | 71 | 58 |
| 17 bis | (46) | — | 50 | 44 | 40 |
| 18 | — | — | — | 600 | 597·5 |
| 19 | 13 | 16 | 14·5 | 18 | 14 |
| 20 | — | — | — | — | 17 |
| 21 | 77 | 69 | 61·5 | 67 | 63·5 |
| 22 | 61 | 56·5 | 57 | 60 | 60 |
| 23 | 472 | 480 | 445 | 438 | 420·5 |
| 24 | — | (226) | — | 232 | 213·5 |
| 25 | — | 130 | — | — | 106·5 |
| 26 | 140 | 143 | 126 | 128 | 138 |
| 27 | 140 | — | 124 | 144 | 147·5 |
| 28 | 98 | — | 96 | 110 | 108 |
| 29 | 81 | 97 | 92 | 93 | 80·5 |
| 30 | 36 | 40 | 42 | 39 | 35·5 |

* Collections of the Institut de Paléontologie, Paris.
† Collections of the Musée d'Histoire Naturelle, Lyon.
‡ Collections of the Naturhistorisches Museum, Basel.

TABLE 5.10. *cont.*

Methods of measurement from Eisenmann and De Giuli 1974; Eisenmann and Turlot 1978; Eisenmann in press *c*.

| | | | |
|---|---|---|---|
| 1 | basilar length | 16 | maximum width of occipital crest |
| 2 | palatal length | 17 | muzzle width |
| 3 | distance from palate to vomer | 17 bis | minimum muzzle width |
| 4 | distance from vomer to basion | 18 | vertex length |
| 5 | muzzle length | 19 | infraorbital height |
| 6 | length of diastema | 20 | height of external auditory meatus |
| 7 | length of premolars ($P^{2-4}$) | 21 | anteroposterior diameter of orbit |
| 7 bis | length of molars | 22 | vertical diameter of orbit |
| 8 | length of upper cheek teeth row | 23 | anterior ocular line |
| 9 | choanal length | 24 | posterior ocular line |
| 10 | choanal maximum width | 25 | height of face in front of $P^2$ |
| 10 bis | choanal width between pterygoid processes | 26 | height of face between $P^4$ and $M^1$ |
| 11 | width maxilla at facial crests | 27 | height of face behind $M^3$ |
| 12 | basilar length minus muzzle length | 28 | height of cranium behind orbits |
| 13 | frontal width | 29 | width of occipital condyles |
| 14 | bizygomatic width | 30 | width of foramen magnum |
| 15 | maximum width cranial vault | | |

TABLE 5.11. *Equus koobiforensis* upper cheek teeth series measurements (mm)

| KNM-ER No., area and zone | | $P^2$ | $P^3$ | $P^4$ | $M^1$ | $M^2$ | $M^3$ |
|---|---|---|---|---|---|---|---|
| 1484 (130 N.s) | oc ap | 44 | 32·5 | 32 | 30·5 | 30 | 30 |
| | ptc | 8 | 11·5 | 11 | 11·6 | 12·6 | 12·7 |
| | oc tr | 29·5 | 29 | 28·5 | 28 | 26 | (23) |
| | PI | 18·2 | 35·4 | 34·4 | 38 | 42 | 42·3 |
| 5361B (100 N.s) | oc ap | 40 | 32 | (28) | — | — | 29 |
| | ptc | 7 | 9·3 | 10 | — | — | 11 |
| | oc tr | 29 | 31 | 30 | — | — | 26 |
| | PI | 17·5 | 29·1 | (35·7) | — | — | 37·9 |
| 2691 (12A M.a) | oc ap | 37 | 30·5 | 30 | 26·5 | 26·5 | 29 |
| | ptc | 6·5 | 8 | 10 | 9·5 | 10 | 13 |
| | oc tr | 27 | 30 | 30 | 28 | 27 | 24 |
| | PI | 17·5 | 26·2 | 33·3 | 35·8 | 37·7 | 44·8 |

TABLE 5.12.
*Equus koobiforensis* isolated upper cheek teeth measurements (mm)

| | KNM-ER No. | oc ap | ptc | oc tr | PI |
|---|---|---|---|---|---|
| $P^2$ | 672 (103 KF III) | 40·5 | 8·6 | 25·8 | 21·2 |
| $P^{3-4}$ | 1265 (130 N.s) | 30 | 11 | — | 36·7 |
| | 2224 (131 N.s) | 31 | 10·5 | — | 33·9 |
| | 4043 (129 N.s) | 33 | 11·5 | 29 | 34·8 |
| | 4044 (129 N.s) | (35) | — | 33 | — |
| | 5519 (102 N.s) | 31 | 9 | 30·5 | 29 |
| | 1260 (6A M.a) | 32 | 9 | 28 | 28·1 |
| | 4025 (105 M.a) | 30 | 10 | 30 | 33·3 |
| | 679 (102?) | 30·5 | 8·8 | 28·3 | 28·8 |
| $M^{1-2}$ | 1266 (130 N.s) | 30 | 13·5 | 27 | 45 |
| | 1271 (105 N.s) | 27·5 | 10 | 29 | 36·4 |
| | 2687 (105 N.s) | 30 | 14·5 | 28 | 48·3 |
| | 2740 (14 N.s) | 29·5 | 14 | 27·5 | 47·4 |
| | 4014 (14 N.s) | 26·5 | 11 | 28 | 41·5 |
| | 4020 (102 N.s) | 30 | 14·5 | 26 | 48·3 |
| | 4034 (130 N.s) | 27 | 10·2 | 28·5 | 37·8 |
| | 1255 (105 M.a) | 27·5 | 12 | 27 | 43·6 |
| | 2670 (129 M.a?) | 32 | 12 | 27 | 37·5 |
| | 676 (102?) | 28·5 | 11 | 26·5 | 38·6 |
| $M^3$ | 1256 (105 N.s) | (27·5) | 13 | 24 | (47·3) |
| | 1272 (105 N.s) | 29 | 13 | 24 | 44·8 |
| | 4520 (104 N.s) | (33) | — | (25) | — |
| | 5519 (102 N.s) | 29 | 12 | 25 | 41·4 |
| | 1242 (102 M.a) | 29 | 13 | 24·5 | 44·8 |
| | 1250 (104 M.a) | 28·5 | 13·5 | 25 | 47·4 |
| | 2613 (7 M.a) | 27·5 | 15·5 | 25 | 56·4 |
| | 2618 (105 M.a) | 29 | 10 | 24 | 34·5 |
| | 674A (103 KF III) | 28·2 | 11 | 24 | 39 |

$M^3$ measurements include cement cover and were taken at a height of approximately 30 mm above the roots.

TABLE 5.13. *Equus koobiforensis* lower cheek teeth series measurements (mm)

| KNM-ER No., area and zone | | $P_2$ | $P_3$ | $P_4$ | $M_1$ | $M_2$ | $M_3$ |
|---|---|---|---|---|---|---|---|
| 1518 (105 N.s) | oc ap | 31 | 28·5 | 29 | 25·5 | 26·5 | 36·5 |
| | oc tr | 14 | 17 | 16·5 | 15·5 | 15 | 14 |
| 4051 (115 N.s) | oc ap | 36 | 34 | 30 | 27·5 | 29 | (36) |
| | oc tr | 17 | 17·5 | (17) | 14·5 | 15 | (15) |
| 5360 (130 N.s) | oc ap | 35·5 | 32 | 30 | 28 | 28 | 35 |
| | oc tr | 16 | 17 | 17·5 | 15 | 14·5 | — |
| 5361A (100 N.s) | oc ap | 32 | 30 | 29 | 27 | 27 | 32 |
| | oc tr | 16 | 17 | 16·5 | 14 | 13·5 | 13 |
| 1582 (104 M.a) | oc ap | 36 | 34 | 33 | 28 | 28 | 33 |
| | oc tr | 15 | 18 | 18 | 16·5 | 15 | 14 |
| 326–333 (KF IIA) | oc ap | 35 | 31·1 | 30·3 | 26·3 | 28·5 | 29·3 |
| | oc tr | 16·4 | 16 | 16·3 | 14 | 13 | — |

TABLE 5.14.
*Equus koobiforensis* isolated lower cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr |
|---|---|---|---|
| $P_2$ | 4028 (116 N.s) | 37·7 | 16·2 |
| | 4037 (129 N.s) | (37) | — |
| $P_{3-4}$ | 2716 (129 N.s) | 32 | 15 |
| | 2741 (14 N.s) | 28 | 16·5 |
| | 3986 (129 N.s) | 31·5 | 17·5 |
| | 4011 (14 N.s) | 30 | 16 |
| | 4015 (100 N.s) | 33 | 17 |
| | 4027 (129 N.s) | 32 | 15·5 |
| | 4037 (129 N.s) | 33 | 17 |
| | 1243 (102 M.a) | 28 | 17 |
| | 2248 (104 M.a) | 28 | 17 |
| | 4046 (100 M.a) | 30 | 16 |
| | 680 (KF IIB) | 30·2 | 16 |
| | 681 (KF IIB) | 29·5 | 17 |
| | 776E (KF III) | 29·6 | 16·5 |
| | 320 (S. of Koobi Fora Ridge) | 30·2 | 15·2 |
| | 321 (S. of Koobi Fora Ridge) | 30·2 | 16·2 |
| | 322 (S. of Koobi Fora Ridge) | 31·2 | 16·2 |
| $M_{1-2}$ | 337 (105 N.s) | 30·5 | 12 |
| | 4026 (129 N.s) | 29 | 12 |
| | 4036 (129 N.s) | 28·5 | 14 |
| | 1269 (105 M.a) | 30 | 13 |
| | 3992 (101 M.a) | 25 | 14·5 |
| | 4006 (103 M.a) | 26 | 14 |
| | 690 (KF III) | 29·2 | 15·2 |
| | 690 (KF III) | 26·2 | 14·7 |
| | 2931 (117 GB) | 28 | 13·5 |
| $M_3$ | 4019 (14 N.s) | (32) | 14 |
| | 1249 (104 M.a) | 32 | 12·5 |
| | 2061 (104 M.a) | 31 | 13 |

***Equus* cf. *tabeti***

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Metridiochoerus andrewsi* zone | 1211 | 1 | partial cranium (Lt $P^3$–$M^3$, Rt $P^2$–$M^3$) |
| | 1237 | 6A | prox, anterior 1st phalanx |
| | 5565 | 130 | Lt $P^4$ |
| | 5566 | 130 | Lt $M^1$ |
| | 5567 | 130 | Lt and Rt $I^{1-3}$ |
| *Metridiochoerus compactus* zone | 2067 | 103 | 3rd metacarpal (pathological?) |
| | 2069 | 103 | 3rd metacarpal frags, anterior and posterior 1st phalanges |
| Horizon indet. | 325 | Karari Ridge | Lt and Rt maxilla and Lt and Rt mandible frags |

***Equus* sp. indet.**

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| Zone C | 4002 | 102 | $M_{1/2}$ |
| *Notochoerus scotti* zone | 1254 | 105 | Lt $M^{1/2}$ |
| | 1258 | 105 | Rt $P^{3/4}$ |
| | 1267 | 130 | Lt $M^{1/2}$ |
| | 1270 | 105 | Rt $M^3$ |
| | 1273 | 105 | Lt $P^4$ |
| | 2052 | 104 | upper cheek tooth |
| | 2059 | 100 | $M_2$ |
| | 2655 | 105 | Rt $P_{3/4}$ |
| | 2681 | 105 | Rt $P^{3/4}$ |
| | 3855 | 102 | lower cheek tooth frag |
| | 4012 | 14 | Rt $M^{1/2}$ |
| | 4018 | 102 | $I^1$ |
| | 4021 | 105 | $M^{1/2}$ |
| | 4029 | 129 | $M^{1/2}$ |
| | 4032 | 130 | upper dM or dP frag |
| | 4040 | 129 | Lt $M_3$ |
| | 4046 | 100 | Rt $M_{1-2}$ |
| | 5669 | 105 | $P^{3/4}$ |
| | 5670 | 105 | $M^{1/2}$ |

(*continued overleaf*)

***Equus* sp. indet.** *cont.*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Metridiochoerus andrewsi* zone | 661 | 103 | astragalus and calcaneum |
| | 685 | 103 | astagalus, calcaneum, prox. metapodial, lateral metapodial |
| | 901 | 8 | cranium (Lt $M^{1-3}$), Rt $M^3$ and isolated upper teeth |
| | 1222 | 1 | Rt mandible frag ($P_{3-4}$) |
| | 1223 | 1 | Lt $P_4$, Lt $M_3$ |
| | 1224 | 6 | Lt $P_2$ |
| | 1225 | 8 | Lt $P^{3/4}$, Rt M frag |
| | 1226 | 8 | Lt $P^{3-4}$, Lt $M^3$ |
| | 1229 | 8A | Rt $M^{1/2}$ |
| | 1241 | 104 | Rt maxilla frag ($P^3$–$M^1$) and Lt maxilla frag ($P^4$–$M^2$) |
| | 1245 | 104 | Lt $dP_2$, Rt $M_3$ |
| | 1246 | 104 | Lt $P_2$ |
| | 1251 | 104 | Rt $P^4$, Rt $M^1$ |
| | 1252 | 104 | Lt $P_{3/4}$ |
| | 1253 | 102 | Rt $P_{3/4}$ |
| | 1257 | 105 | Lt $M^1$ |
| | 1259 | 6A | Lt $P^3$–$M^1$, Rt $P^3$ |
| | 1261 | 10 | Lt $M^{1/2}$ |
| | 1262 | 8B | $M^{1/2}$ |
| | 1274 | 105 | Lt 3rd metacarpal |
| | 1277 | 103 | Rt tibia |
| | 1280 | 103 | Rt $P^{3/4}$ |
| | 1281 | 103 | Rt $M^{1/2}$, Lt $M^3$ |
| | 1282 | 103 | $M^{1/2}$ |
| | 1284 | 102 | Lt $P_{3/4}$ |
| | 1286 | 103 | Rt maxilla frag ($M^3$) |
| | 1287 | 104 | $P_2$ |
| | 1288 | 103 | Lt $M_{1/2}$ |
| | 1289 | 102 | $M_3$ |
| | 1290 | 103 | Lt astragalus |
| | 1291 | 103 | dist. 3rd metatarsal, cuneiform |
| | 1292 | 103 | dist. 3rd metatarsal |
| | 1293 | 103 | Rt $M^{1/2}$ |
| | 1296 | 103 | Lt astragalus |
| | 1297 | 103 | prox. and dist. 3rd metacarpal |
| | 1349 | 8 | dist. Rt radius |
| | 1385 | 6A | astragalus |
| | 1717 | 103 | prox. 3rd metacarpal |
| | 1980 | 121 | $M^{1/2}$ |
| | 1982 | 10 | $M^{1/2}$ |
| | 2048 | 104 | astragalus |
| | 2049 | 104 | astragalus |
| | 2050 | 121 | 3rd metacarpal |
| | 2055 | 104 | dist. radius |
| | 2057 | 104 | prox. and dist. 3rd metatarsal |
| | 2062 | 104 | $P^2$ |
| | 2063 | 102 | Rt $P^{3/4}$, Lt $M^{1/2}$, Lt $M^3$ |
| | 2064 | 103 | Rt $P^{3/4}$ |
| | 2065 | 103 | Lt $M^{1/2}$ |
| | 2068 | 121 | Rt $P^{2-3}$, Lt $P^2$, Lt $P^4$, Lt $M^1$, Lt $M^3$ |

***Equus* sp. indet.** *cont.*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| | 2140 | 123 | dist. Lt radius |
| | 2148 | 104 | $P_{3/4}$ |
| | 2215 | 103 | juvenile Lt 3rd metacarpal |
| | 2238 | 130 | prox. Lt 3rd metatarsal |
| | 2301 | 131 | 3rd metatarsal, phalanx |
| | 2642 | 8B | Lt $M^3$ |
| | 2664 | 10 | Lt $M^3$ |
| | 2685 | 15 | Rt $P^2$ |
| | 2688 | 8B | Lt $P^{3/4}$ |
| | 3994 | 102 | Rt $M_{1/2}$ |
| | 3996 | 12 | Lt $M^{1/2}$ |
| | 3997 | 104 | $P_2$ |
| | 4000 | 103 | Lt $P^2$ |
| | 4007 | 102 | $P_2$, $P_{3-4}$ |
| | 4009 | 102 | Lt $M_{1-2}$, Lt $M^{1-2}$ |
| | 4010 | 102 | Lt $P_2$ |
| | 4022 | 105 | Rt $M_{1-2}$ |
| | 4023 | 105 | Rt $P_{3-4}$ |
| | 4030 | 101 | $M^{1-2}$ |
| | 4033 | 101 | $M^{1-2}$ |
| | 4038 | 105 | lower cheek tooth frag |
| | 4039 | 103 | $M^3$ |
| | 4041 | 103 | Rt astragalus |
| | 4045 | 104 | lower tooth series |
| | 4049 | 104 | mandibular symphysis with 2I, C |
| | 4050 | 102 | Rt $M^{1-2}$, Lt $M^3$ |
| | 4056 | 103 | Rt $I^2$, Rt $P^{2-3}$, Rt $M^3$ |
| | 4065 | 8B | $P^{3/4}$ |
| | 4078 | 102 | $M^{1/2}$ |
| | 5189 | 104 | Lt $M^{1/2}$ |
| | 5668 | 104 | $M^{1/2}$ |
| | 5886 | 105 | $P_2$ |
| *Metridiochoerus compactus* zone | 1228 | 3 | Lt $M^{1-2}$ |
| | 2630 | 8 | Lt $M^{1-2}$, Rt and Lt $M_3$ |
| | 2637 | 6A | Rt $P_2$ |
| | 2640 | 6A | Rt mandible frag ($P_3$–$M_2$) |
| | 2654 | 6A | Rt $M^3$ |
| | 2676 | 6A | Rt $P_{3-4}$ |
| | 2695 | 6 | Lt $M^3$ |
| Horizon indet. | 318 | S. of Karari Ridge | Rt mandible frag ($M_{2-3}$) |
| | 319 | S. of Karari Ridge | Rt mandible frag ($P_{3-4}$) |
| | 334 | 103 | $P^{2-4}$, $M^{2-3}$ |
| | 335 | 1 | $P_4$, $M_3$ |
| | 665 | KF III | $P_2$ |
| | 647 | KF III | $M^3$ |
| | 678 | 130 | Lt $P^{3/4}$ |
| | 684 | KF III | $P^{3-4}$, $M^{1/2}$, $M^3$ |
| | 689 | 103 | Rt mandible frag ($P_{2-4}$) |
| | 1288 | 103 | Lt $M_{1/2}$ |
| | 5887 | KF III | $M^3$ |

TABLE 5.15. Koobi Fora *Equus* cf. *tabeti* and *E.* sp. associated upper cheek teeth measurements (mm)

| KNM-ER No., area and zone | | $P^2$ | $P^3$ | $P^4$ | $M^1$ | $M^2$ | $M^3$* |
|---|---|---|---|---|---|---|---|
| 325 (Karari Ridge) *E.* cf. *tabeti* | oc ap | | | 28 | 24·5 | 24·3 | 25·5 |
| | ptc | | | 9·7 | 7·8 | 9 | 11 |
| | oc tr | | | 29 | 26·2 | 25·7 | 22·2 |
| | PI | | | 34·6 | 31·8 | 37 | 43·1 |
| 1211 (1 M.a) *E.* cf. *tabeti* | oc ap | 36 | 28 | 27 | 26 | 26 | 26 |
| | ptc | 8 | 9·5 | 10 | 9 | 10·5 | — |
| | oc tr | 26 | 26 | 23 | 25·5 | 23 | 22 |
| | PI | 22·2 | 33·9 | 37 | 34·6 | 39·6 | — |
| 334 (KF III) *E.* sp. indet. | oc ap | 38 | 28 | 26·2 | | 24·6 | 25 |
| | ptc | 7·5 | 8·7 | 10·9 | | 11 | 12 |
| | oc tr | (25·5) | 27·8 | 26·9 | | 25 | 21 |
| | PI | 19·7 | 31·1 | 41·6 | | 44·7 | 48 |
| 901 (8B M.a) *E.* sp. indet. | oc ap | | | | 24·5 | 25 | 24 |
| | ptc | | | | 11 | 10·5 | 10·5 |
| | oc tr | | | | 24·5 | 24 | 20·5 |
| | PI | | | | 44·9 | 42 | 43·7 |
| 1241 (104 M.a) *E.* sp. indet. | oc ap | | 29·5 | 27 | 24 | 25 | |
| | ptc | | 10 | 10·5 | 10 | 11 | |
| | oc tr | | 27·5 | 28·5 | 25·5 | 25·5 | |
| | PI | | 33·9 | 38·9 | 41·7 | 44 | |
| 1259 (6A M.a) *E.* sp. indet. | oc ap | | 28 | 26 | 25 | | |
| | ptc | | 9 | 9·5 | 11 | | |
| | oc tr | | 28 | 26·5 | 25 | | |
| | PI | | 32·1 | 36·5 | 44 | | |
| 2068 (121 M.a) *E.* sp. indet. | oc ap | — | 27 | 26 | | 24 | 24 |
| | ptc | 6 | 10 | 10 | | 10 | 11·5 |
| | oc tr | 23·5 | 25 | 26 | | 22·5 | 21 |
| | PI | — | 37 | 38·5 | | 41·7 | 47·9 |
| 4056 (103 M.a) *E.* sp. indet. | oc ap | — | 31 | | | | 26 |
| | ptc | 7 | 9 | | | | 10·5 |
| | oc tr | 28 | — | | | | 21·5 |
| | PI | — | 29 | | | | 40·4 |

* $M^3$ measurements include cement cover and were taken at a height of approximately 30 mm above the roots.

TABLE 5.16.
Koobi Fora *Equus* cf. *tabeti* and *E.* sp. isolated upper premolars measurements (mm)

| | KNM-ER No., area and zone | oc ap | ptc | oc tr | PI |
|---|---|---|---|---|---|
| $P^2$ | 2062 (104 M.a) | 40 | 9 | 26 | 22·5 |
| | 2685 (15 M.a) | 37 | 6·5 | 24 | 17·5 |
| $P^{3-4}$ | 1258 (105 N.s) | 30 | 11·5 | — | 38·3 |
| | 1273 (105 N.s) | 28 | 12 | 27 | 42·8 |
| | 2681 (105 N.s) | 27·5 | 9 | 28·5 | 32·7 |
| | 5669 (105 N.s) | 30 | — | 27·5 | — |
| | 1225 (8 M.a) | 27 | 10 | 25 | 37 |
| | 1226 (8 M.a) | 27 | 12·5 | 25 | 46·3 |
| | 1251 (104B M.a.) | 29 | 13 | 27 | 44·8 |
| | 1280 (103 M.a) | 30 | 12·2 | 28 | 40·7 |
| | 2063 (102 M.a) | 28·5 | 9 | 26 | 31·6 |
| | 2064 (103 M.a) | 30 | 8 | 27 | 26·7 |
| | 2688 (8B M.a?) | 28 | 8 | 27 | 28·6 |
| | 4000 (103 M.a) | 30 | 12 | 26 | 40 |
| | 4033 (102 M.a) | 30 | 10 | 27 | 33·3 |
| | 4065 (8A M.a) | 25 | 9·5 | 25·3 | 38 |
| | **5565 (130 M.a.) | 25 | 8 | 26 | 40 |
| | 678 (130 KF IIA) | 30·6 | 9 | 27·5 | 29·4 |
| | 684A (105 KF III) | 29·4 | 14 | 26·3 | 47·6 |
| | 684D (105 KF III | 29·5 | 13 | 26·5 | 44·1 |

** *Equus* cf. *tabeti*. (All others *Equus* sp. indet.).

TABLE 5.17.
Koobi Fora *Equus* cf. *tabeti* and *E.* sp. isolated upper molars measurements (mm)

| | KNM-ER No., area and zone | oc ap | ptc | oc tr | PI |
|---|---|---|---|---|---|
| $M^{1-2}$ | 1254 (105 N.s) | 26 | 10·5 | 25 | 40·4 |
| | 1267 (130 N.s) | 25·5 | 11 | — | 43·1 |
| | 4012 (14 N.s) | 26 | 10·3 | 25·5 | 39·6 |
| | 4021 (105 N.s) | 27 | 10 | 25 | 37 |
| | 4029 (129 N.s) | 24 | 10 | 25 | 41·2 |
| | 5670 (105 N.s) | 24 | — | — | — |
| | 901 (8A M.a) | 26 | 10 | 25 | 38·5 |
| | 1229 (8A M.a) | 26 | 8·5 | 25 | 32·7 |
| | 1251 (104B M.a) | 27 | 14·5 | 25·5 | 53·7 |
| | 1257 (105 M.a) | 26 | 11 | 24 | 42·3 |
| | 1261 (10 M.a) | 25 | 10 | 24 | 40 |
| | 1262 (8B M.a) | 24 | 11 | 25 | 45·8 |
| | 1281 (103 M.a) | 27 | 10 | 27 | 37 |
| | 1282 (103 M.a) | 23·5 | 7·5 | 24 | 31·9 |
| | 1293 (103 M.a) | 25 | 12·2 | 26 | 48·8 |
| | 1980 (121 M.a) | 24 | 9 | 23 | 37·5 |
| | 1982 (10 M.a) | 23 | 11·5 | 23 | 50 |
| | 2063 (102 M.a) | 27 | 10·2 | 24 | 37·8 |
| | 2065 (103 M.a) | 25·2 | 10·2 | 26 | 40·5 |
| | 3996 (12 M.a) | 24·5 | 10·5 | 23 | 42·8 |
| | 4030 (101 M.a) | 25·5 | 13·5 | 23·5 | 52·9 |
| | 4050 (102 M.a) | 28·5 | 9·5 | 25 | 37·2 |
| | 4078 (102 M.a) | 26·5 | 9·5 | 24 | 35·8 |
| | 5189 (104 M.a?) | 24·5 | 10 | 24·8 | 40·8 |
| | 5668 (104 M.a) | 25 | 9 | — | 36 |
| | 1228 (3 M.c) | 24 | 10·5 | 24 | 43·7 |
| | 2630 (8 M.c) | 24 | 10 | 25 | 41·7 |
| | 684B (103 KF III) | 26·4 | 11·7 | 25·9 | 44·3 |
| | **5566 (130 M.a) | 22 | 8 | 25 | 36·4 |
| $M^3$ | 1270 (105 N.s) | 26 | — | 20 | — |
| | 1226 (8 M.a) | 26 | — | 19·5 | — |
| | 1281B (103 M.a) | 25 | 11 | 20 | 44 |
| | 1286 (103 M.a) | 25 | 9·5 | 22 | 36 |
| | 2063A (102 M.a) | 26 | 10·5 | 22 | 40·4 |
| | 2642 (8B M.a) | 25·5 | 10·5 | 21·5 | 41·2 |
| | 2664 (10 M.a) | 27 | 11 | 22 | 40·7 |
| | 4039 (103 M.a) | 27 | 14 | 22 | 51·8 |
| | 4050 (102 M.a) | 26 | 12 | 23 | 46·1 |
| | 2654 (6A M.c) | 26 | 11·5 | 21 | 44·2 |
| | 2695 (6A M.c) | 24 | 12 | 21 | 50 |
| | 334 (103 KF III) | 27 | 12 | 21 | 44·4 |
| | 5887 (103 KF III) | 26 | 10 | 21 | 38·5 |
| | 684C (103 KF III) | (22·5) | — | 20·3 | — |

** *Equus* cf. *tabeti*. (All others *Equus* sp. indet.).

TABLE 5.18.
Koobi Fora *Equus* cf. *tabeti* and *E.* sp. lower cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr |
|---|---|---|---|
| $P_2$ | 1224 (6 M.a) | 32 | 15 |
| | 1246 (104 M.a) | 33 | 15·3 |
| | 5886 (105 M.a) | 33·5 | 14·5 |
| | 1287 (104 M.a) | (32) | 14 |
| | 4007 (102 M.a) | 34 | 15·5 |
| | 4010 (102 M.a) | 34 | 16 |
| | 2637 (6A M.c) | 32·5 | 15 |
| | 665 (103 KF III) | 33·9 | 14·5 |
| | 689 (103 KF III) | 30·2 | 13·2 |
| $P_{3-4}$ | 2655 (105 N.s) | 29 | 15 |
| | 1222 (1 M.a) | 27 | 15 |
| | 1223B (1 M.a) | 27·5 | 15·5 |
| | 1252 (104B M.a) | 27 | (14·5) |
| | 1253 (102 M.a) | 28 | (15) |
| | 1284 (102 M.a) | 27 | 13 |
| | 2148 (104 M.a) | 26 | 15 |
| | 4007 (102 M.a) | 29 | 17 |
| | 4023 (105 M.a) | 27 | 15·5 |
| | 2640 (6A M.c) | 29 | 14·5 |
| | 2640 (6A M.c) | 25 | 14·5 |
| | 2676 (6A M.c) | 27 | 14 |
| | 319 (2 S. of Koobi Fora Ridge) | (28·5) | — |
| | 319 (2 S. of Koobi Fora Ridge) | 27 | — |
| | 689 (103 KF II) | 26·5 | 14·8 |
| $M_{1-2}$ | 2059 (100 N.s) | 25·5 | 12 |
| | 1288 (103 M.a?) | 25 | 12 |
| | 3994 (102 M.a) | 26 | 12 |
| | 4009 (102 M.a) | 25 | 12·5 |
| | 4022 (105 M.a) | 26 | 13 |
| | 4046 (100 M.a) | 24 | 13 |
| | 2640 (6A M.c) | 23 | 14 |
| | 2640 (6A M.c) | 22·5 | 13 |
| | 2676 (6A M.c) | 24 | 14·5 |
| $M_3$ | 4040 (129 N.s) | 31 | 12 |
| | 1223A (1 M.a) | 28·5 | 13 |
| | 2630 (8 M.c) | 29 | 12 |
| | 318 (4 S. of Koobi Fora Ridge) | 32 | 14 |
| | *325 (4 Karari Ridge) | 30·3 | 12·9 |

* *Equus* cf. *tabeti*. (All others *Equus* sp. indet.).

TABLE 5.19. Koobi Fora *Equus* species third metacarpal measurements (mm)

| KNM-ER No., area and zone | max length | diap tr* | diap ap† | prox art tr | prox art ap | magnum facet tr | ant unciform facet tr | post unciform facet tr | dist sup tr | dist art tr | dist art ap | min ap int condyle | max ap int condyle |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1275L (105 M.a) *E.* cf. *koobiforensis* | — | 31 | 24·5 | 49·5 | 32 | 41 | 15·5 | - | — | — | — | — | -- |
| 1276 (105 N.s) *E.* cf. *koobiforensis* | — | (33) | (26·5) | 50·5 | 32 | 40 | 16·5 | 10 | 47·2 | 46·3 | 35 | 28·5 | 29 |
| 2067 (103 M.c) *E.* cf. *tabeti* | 199 | 22·3 | 18 | (33) | (24) | 28·5 | — | — | 33 | 33 | — | 20 | 22 |
| 2069 (103 M.c) *E.* cf. *tabeti* | — | 29·5 | 24 | 44 | 28·5 | 37 | 13 | 7 | 41 | 41 | 32 | 25·5 | 27·5 |
| 1274 (105 M.a) *E.* sp indet. | 213 | 28·5 | 23 | 46 | 29 | 36 | 15 | 6 | 41·5 | 40 | 31·5 | 25 | 27·5 |
| 1297 (103 M.a) *E.* sp indet. | — | 27·5 | 22·5 | 43 | 27 | 34·5 | 13 | 8 | 42 | 41 | 30 | 25 | 26·5 |
| 1717 (103 M.a) *E.* sp indet. | — | 29·5 | 22·5 | 43 | 28·5 | 35·5 | 14 | 6 | — | — | — | -- | -- |
| 2050 (121 M.a) *E.* sp indet. | 208 | 30 | 23 | 46 | 29 | 37 | 13·5 | 6 | 44 | 44 | — | — | 27 |
| 2215 (103 M.a) *E.* sp indet. | (215) | — | — | 43·5 | 30 | 38 | 13 | 9 | — | — | — | — | — |

* Diaphysis minimum width.
† Diaphysis minimum anteroposterior diameter.

TABLE 5.20. Koobi Fora *Equus* species third metatarsal measurements (mm)

| KNM-ER No., area and zone | length | diap tr | diap ap | prox max tr | prox max ap | ecto-cuneiform facet tr | cuboid facet ap | dist sup tr | dist art tr | dist art ap | min ap int condyle | max ap int condyle |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 5358 (100 N.s) *E.* cf. *koobiforensis* | 287·5 | 33 | 31 | 52 | 41 | 45 | 11 | 47·5 | 45·5 | 37 | 29 | 30·5 |
| 4052 (100 N.s) *E.* cf. *koobiforensis* | — | 30 | — | 49·5 | 40 | — | — | 47·5 | 44 | 35 | 29 | 30·5 |
| 1275G (105 M.a) *E.* cf. *koobiforensis* | 266 | 31·1 | 29 | 49 | 39·5 | 44 | 11·5 | 44·5 | 44·2 | 36·7 | 27·5 | 30 |
| 1291A (103 M.a) *E.* sp indet. | — | 30 | 29 | — | — | — | — | 44 | 44 | 33·5 | 25·5 | 28 |
| 1292 (103 M.a) *E.* sp indet. | — | — | — | — | — | — | — | 44 | 42·5 | 34·5 | 25·5 | 28·5 |
| 2057 (104 M.a) *E.* sp indet. | — | 33·5 | 29 | 46 | 41·5 | 42 | 9 | 44·5 | 43·5 | 33·5 | 25·5 | (28·5) |
| 2238 (130 N.s) *E.* sp indet. | — | — | — | 45·5 | 37·5 | 40·5 | 9 | — | — | — | — | — |
| 2301B (131 N.s) *E.* sp indet. | 253·5 | 30 | 28 | (42) | (36) | — | — | 44 | 42·5 | — | 26 | 29 |

### *Equus* cf. *grevyi*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Metridiochoerus compactus* zone | 1227 | 1 | Rt $P^{3-4}$ |
| | 1457 | 103 | maxilla (Lt and Rt $P^{3}$–$M^{3}$) |
| | 2056 | 118 | Rt mandible frag ($P_{2-4}$) |
| | 2066 | 103 | Lt $M^{1-2}$ |
| | 2652 | 6A | Lt $P^{3-4}$, Lt $P_{3-4}$ |
| | 2672 | 6A | $M^{1-2}$ |
| | 2680 | 3 | Rt $P^{3-4}$ |
| | 2684 | 6A | Rt $P^{3-4}$ |
| Guomde Formation | 4066 | 6A | $M_{1-2}$ |
| Galana Boi Beds | 4055 | 117 | associated upper and lower teeth (Rt $P^{2}$, Rt $M^{1-2}$, Lt $P^{4}$, Lt $M^{1-3}$, Rt $P_{3-4}$, $M_{1-2}$) |
| Horizon indet. | 677 | | $P^{3-4}$ |
| | 2302 | 102 | radius |

TABLE 5.21. *Equus* cf. *grevyi* upper cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | ptc | oc tr | PI |
|---|---|---|---|---|---|
| $P^{2}$ | 1457 (103 M.c) | 40 | 6·5 | 29 | 16·2 |
| | 4055 (117 GB) | (40) | 8 | 29 | (20) |
| $P^{3-4}$ | 1457 (103 M.c) | 31 | 10·5 | 30 | 33·9 |
| | 1457 (103 M.c) | 30 | 11 | 29 | 36·7 |
| | 4055 (117 GB) | 30 | 13 | 31 | 43·3 |
| | 1227 (1 M.c | 30·5 | 11 | — | 36·1 |
| | 2652 (6A M.c) | 29 | 11 | 28 | 37·9 |
| | 2680 (3 M.c. | 30 | 10 | 30 | 33·3 |
| | 2684 (6A M.c) | 30·5 | 11 | (26) | 36·1 |
| | 677 (KF 11B) | 29·8 | 13 | 29·5 | 43·6 |
| $M^{1}$ | 1457 (103 M.c) | 27 | 11 | 27·5 | 40·7 |
| | 4055 (117 GB) | 28 | 13 | 29 | 46·4 |
| $M^{2}$ | 1457 (103 M.c) | 28 | 13 | 27 | 46·4 |
| | 4055 (117 GB) | 27·5 | 13·5 | 28 | 49·1 |
| $M^{1-2}$ | 2066 (103 M.c) | 27 | 12 | 28 | 44·4 |
| | 2672 (6A M.c) | 28 | 12·5 | 25 | 44·6 |

TABLE 5.22.
*Equus* cf. *grevyi* lower cheek teeth measurements (mm)

| | KNM-ER No., area and zone | oc ap | oc tr |
|---|---|---|---|
| $P_{2}$ | 2056 (108 M.c) | 35·5 | 16 |
| $P_{3}$ | 2056 (108 M.c) | 30 | 18 |
| | 4055 (117 GB) | (34) | 19 |
| $P_{4}$ | 2056 (108 M.c) | 29·5 | 18 |
| $M_{1}$ | 4055 (117 GB) | 29 | 15·5 |
| $M_{1-2}$ | 4066 (6A GF) | (28) | 12·5 |

### *Equus* cf. *burchelli*

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| *Metridiochoerus compactus* zone | 2678 | 6A | posterior 1st phalanx |
| | 3700 | 6A | posterior 1st phalanx |

### *Equidae* gen. and sp. indet.

| | KNM-ER No. | Area | Specimen |
|---|---|---|---|
| Zone B/C | 4001 | 130 | upper cheek tooth frag |
| | 4057 | 116 | $dP_{3-4}$ |
| *Notochoerus scotti* zone | 4004 | 102 | $dP^{2}$ |
| | 4013 | 105 | $M^{3}$ |
| | 4042 | 105 | dist. frag radius |
| *Metridiochoerus andrewsi* zone | 2300 | 102 | prox. frag femur |
| *Metridiochoerus compactus* zone | 2677 | 6A | $dP_{3}$ |
| | 2683 | 6A | $\overline{dP}$ or $\overline{dM}$ |
| Horizon indet. | 930 | 102 | skull frag |

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