

2667, 4054, and the uppers KNM-ER 1263, 3985, 4083, 5335, and 5359); the others could belong to either species. Most of the teeth assigned to *Hipparion* sp. B have been recovered from the *Metridiochoerus andrewsi* zone or from uncertain horizons. For the moment there is nothing to add to the diagnosis of *Hipparion* sp. B except that the upper cheek teeth are not very plicated. There are no conspicuous morphological differences between the teeth of *H. cf. ethiopicum* and *Hipparion* sp. B, just size differences. Skulls, incisors, and limb bones are unknown from east of Lake Turkana. Similar teeth have been found in the Shungura Formation (Hooijer 1975, p. 23; Eisenmann in press) in Members C to G, mostly F. Some fragmentary upper incisors and limb bones have been referred to the same species.

Hooijer and Maglio (1974, p. 20) referred to *H. cf. sitifense* some specimens of the Lothagam-Kanapoi-Ekora collections that are older than the Koobi Fora ones. The size of the limb bones and of the teeth seem to be the same but the lower cheek teeth lack ectostylids (except one  $M_3$  from Kanapoi); the morphology of the double knot is difficult to interpret on the two  $M_3$ 's figured by Hooijer and Maglio (1974, Plate 8, Fig. 2 and 3), but is probably intermediate between the typical hipparionine and the typical caballine. *Hipparion cf. sitifense* may be an ancestral form to *H. sp. B* but its relation to the true *Hipparion sitifense* of North Africa is not clear: if the North African species is of Pliocene age, its 'primitive' double knot precludes its derivation from the more 'advanced' *H. cf. sitifense*; if, as I suppose, *H. sitifense* is a Miocene species, it could perhaps have given rise to the *H. cf. sitifense*—*Hipparion* sp. B lineage.

## DISCUSSION

### Biostratigraphy

The hipparion material from the Pliocene and Early Pleistocene sequence east of Lake Turkana represents several species characterized mostly by their size and the development of ectostylids.

In the Kubi Algi Formation, *H. hasumense* is a large sized hipparion with small ectostylids. *H. hasumense*, which on the basis of an isolated  $P^2$  may persist in the Koobi Fora Formation, is found also in the Hadar Formation and perhaps in the Chemeron Formation.

In the Koobi Fora Formation, *H. cf. ethiopicum* is a medium-sized hipparion with large and complicated ectostylids. *H. cf. ethiopicum* occurs also in the Shungura Formation and at Olduvai. A cranium

from the Lower Member of the Koobi Fora Formation has been attributed to *H. cornelianum*, a species defined by the morphology of its incisors. *H. cf. ethiopicum* may prove to be a synonym of *H. cornelianum* when the incisors of the former and the lower cheek teeth of the latter are known. Another species with cheek teeth smaller than those of *H. cf. ethiopicum* is possibly present in the Koobi Fora Formation. This material is temporarily referred to *Hipparion* sp. B; it clearly does not belong to the North African *H. sitifense*.

A few lower cheek teeth have ectostylids intermediate in size and morphology between those of *H. hasumense* and *H. cf. ethiopicum* and have been referred to *Hipparion* sp. A. One of them was collected from zone C of the Kubi Algi Formation, others from the Koobi Fora Formation, another from the Guomde Formation, which shows that the morphology of single teeth is not reliable in matters of biostratigraphy.

But when one considers the sample of lower cheek teeth from the Kubi Algi Formation versus that from the Koobi Fora Formation, there are such differences in the relative size of the ectostylids that one may postulate a large amount of time separating the two formations (Eisenmann 1977, p. 78). Such an interpretation is supported by the study of other mammals (White and Harris 1977, p. 17).

### Anatomy and evolution

Examination of the Koobi Fora hipparion material confirms the impression I gained from the study of other material, that there is no single isolated morphological character that may be used to identify or date a fossil species of equid. It seems that different species have inherited the same evolutive capacities but that they do not necessarily express them in association. Thus hipparions with very similar upper and lower cheek tooth patterns may or may not develop ectostylids, may lose or retain preorbital fossae, etc. The simplest, and usual, way to interpret such differences is to rank them with regard to a theoretical order of change; thus the species lacking ectostylids may 'not yet have acquired them', species with preorbital fossae would 'not yet have lost them'. Such a mandatory sequence of changes is not altogether supported by available chronostratigraphic information. Moreover there are anatomical features which appear logically to be linked but perhaps are not. Take for example the reduction of the third incisors. The same trend (reduction and loss of  $I_3$ ) seems to occur in two different lineages at different times: first in *H.*

*hasumense* of the Pliocene Hadar Formation where the slightly atrophied third incisor is associated with relatively small first and second incisors, and later in *H. cornelianum* of the Pleistocene of East and South Africa, where the greatly atrophied third incisors are associated with very large first and second ones. From cranial evidence the ancestral form to *H. cornelianum* appears to be not *H. hasumense* but rather *H. afarensis*, a contemporary form in which a fully developed third incisor is associated with very large first and second incisors.

Another evolutive trend probably manifested by several species is the lessening of biometrical and morphological differences between  $P_{3-4}$  and  $M_{1-2}$ . In Pliocene specimens there are differences of about 3 mm in the occlusal lengths of the premolars and molars (most of the Hadar Formation specimens, Shungura Formation Member C). In Pliocene-Pleistocene forms (Shungura Members E-F, Koobi Fora Formation) the difference is reduced to about 1 mm. This helps explain why one gets such disconcerting results when comparing the sizes of different cheek teeth; two or three size clusters of premolars may be distinguished when only one size group of molars might be recognized. Here again, the trend is probably not restricted to particular species. Morphologically, the lessening of the differences between the premolars and molars is expressed by the trend manifested by the molars (first  $M_3$ , then  $M_2$ , and perhaps  $M_1$ ) to develop shallow vestibular grooves instead of deep ones (Eisenmann 1977). In the Lower Member of the Koobi Fora Formation the vestibular groove extends to the lingual in one  $M_3$  out of three and six anterior molars ( $M_{1 \text{ or } 2}$ ) out of nine. In the Upper Member none of the six known third molars possesses a deep groove and it is present in only four of eleven anterior molars. It is possible therefore that this character may be considered an advanced one (*H. ethiopicum* being more progressive than *H. cf. ethiopicum*), but on its own is insufficient to distinguish one species from another.

### Phylogeny

The study of the Koobi Fora fossils has greatly improved our knowledge of the cranial anatomy of the recent African hipparions. The cranium recovered in the *Notochocerus scotti* zone, though immature, possesses such incisors as to justify its attribution to *H. cornelianum*. In addition, morphological similarities between this cranium and that of the Pliocene *H. afarensis* indicate a close relationship between the two species.

Unfortunately many other problems of systematics and phylogeny remain to be settled, mostly because of the lack of sufficiently abundant and associated material. Given the present state of our knowledge, the only points that seem fairly probable are the following: *H. cornelianum*, present both in East and South Africa, has evolved from *H. afarensis*; *H. sitifense* in North Africa and *H. cf. baardi* in South Africa (and perhaps in East Africa) may have evolved from *H. africanum*. The time for more comprehensive phylogenetical trees of African hipparions has not yet come.

### *Equus* Linn., 1758

*Diagnosis.* Monodactyl extant and fossil equids with protocones connected to protoconules on the upper cheek teeth.

The accuracy of identification of bones and teeth of both fossil and modern examples of *Equus* is largely dependent on the quality and quantity of specimens. Skulls in a good state of preservation can be reliably identified; entire cheek teeth series, especially if numerous, provide some useful indications of relationships; limb bones are more difficult to identify; isolated cheek teeth are, in general, useless. Characters that are particularly useful are discussed below.

The multivariate analysis of 350 skulls of modern *Equus* showed that a dozen measurements out of the 33 initially studied are most discriminant (Eisenmann and Turlot 1978; Eisenmann 1979a, 1980). The comparison of individual skulls is facilitated by the 'ratio diagrams' (Simpson 1941) using these measurements. In the present paper (Figs. 5.5 and 5.6) the values of the cranial measurements of *E. hemionus* are chosen as the standard (zero line); differences in the logarithms of measurements characterize different species. Cranial measurements are as in Eisenmann and De Giuli (1974, pp. 513-14) and Eisenmann (1980b, Fig. 4.6).

The study of the upper cheek teeth of some 300 individuals belonging to modern species of *Equus* showed a considerable overlap of absolute dimensions and protoconal indices. On the other hand, if the average protoconal indices of each species are plotted separately for each tooth of the series ( $P^2$ ,  $P^3$ ,  $P^4$ , etc.), different patterns are found. Similar or other patterns may be determined for fossil series (Eisenmann 1979a, 1980b).

As in the upper teeth, the lower cheek teeth of modern *Equus* species show a considerable overlap of

Upper cheek teeth are listed with their measurements and provenances in Table 5.4 and figured in Plate 5.4, B-F and H; lower cheek teeth in Table 5.5 and Plate 5.4, J-K, and Plate 5.5, A-C and F-O. There are in addition two fragmentary mandibles (Eisenmann 1976a, Plate V, B and D) already discussed in the section on *H. cornelianum*; one very worn upper incisor (Plate 5.4, D); six astragali (Table 5.8); three distal ends of lateral metapodials (Plate 5.4, L-N); a distal fragment of tibia (Table 5.9) and two distal fragments of metatarsal III (Table 5.9).

As in *H. ethiopicum*, the lower molars are of similar size to those of *H. hasumense* but the premolars have shorter occlusal lengths. The Koobi Fora teeth differ from those of *H. ethiopicum* by being narrower. The ectostylids are large (Eisenmann 1977, Fig. 2) but in general not as wide as in *H. ethiopicum*; in most of the teeth, ectostylids reach the top of the crown. The  $M_3$  may have shallow vestibular grooves (Plate 5.5H, L, N) but in contrast to *H. ethiopicum* moderately worn  $M_1$  and  $M_2$  generally have deep vestibular grooves coming in contact with the lingual grooves (Plate 5.5B, C).

No upper cheek teeth were associated with the lectotype of *H. ethiopicum* and it is difficult to assess which, if any, of the upper dentitions recovered subsequently from the Shungura Formation could or should be attributed to this species. Only a few upper cheek teeth from the Koobi Fora Formation are here referred to *H. cf. ethiopicum*. Of these specimens  $P^{3-4}$  are notably smaller than those of *H. hasumense*; in contrast  $M^{1-2}$  are only slightly smaller or of similar size. The premolar/molar ratio would be similar to that of *H. ethiopicum* lowers, namely relatively large molars and relatively small premolars.  $M^3$  is smaller than in *H. hasumense*.

The six astragali have similar dimensions, noticeably smaller than KNM-ER 2789 from the Kubi Algi Formation which is assigned to *H. hasumense*, and than AL 155-6 from the Hadar Formation referred to *H. cf. hasumense* (Table 5.8). One distal end of lateral metapodial from the *Notochoerus scotti* zone has an anteroposterior articular diameter of 19 mm; two others, from the *Metridiochoerus andrewsi* zone, are smaller: 14 and 16 mm. Two distal ends of third metatarsals from the *Met. andrewsi* zone have similar dimensions to metapodials from Oued el Hammam (Eisenmann 1980a) and from the Shungura Formation Members F (Eisenmann in press) and G (Hooijer 1975, p. 71).

As I have stated elsewhere (Eisenmann in press), fossil material retrieved by recent French expeditions to the Omo Basin does not include lower cheek teeth that are exactly similar to the type material of *H. ethiopicum*. The recently collected specimens that come closest in their morphology to the lectotype and associated lower cheek teeth were collected from the base of Shungura Member G; these specimens exhibit similar morphology of the ectostylids but have a deep vestibular groove on the  $M_2$  (Eisenmann in press, Plate 2, Figs. 12-16). Material figured by Hooijer from Olduvai Gorge includes a lower series which shows the same features—large and complicated ectostylids and deep vestibular groove on the  $M_2$  (Hooijer 1975, Plate 14, Fig. 2). We shall come back later to the problem of the molar vestibular grooves, but if I am right to consider the shallowness of these grooves as an evolved character (Eisenmann 1977, pp. 74-5), and if we persist with the diagnosis of *H. ethiopicum* as combining large and complicated ectostylids, molars and premolars with nearly similar occlusal length and shallow vestibular grooves on  $M_3$  and  $M_2$ , then some of the *Hipparion* material from east of Lake Turkana, Olduvai, and the recent French collections from the Omo may be assigned to *H. cf. ethiopicum* but not to *H. ethiopicum*.

Several small specimens in the East Turkana collections could represent one extreme of a single species highly variable in size or a second smaller one. They will be referred to *Hipparion* sp. B.

#### ***Hipparion* sp. B**

1975 *Hipparion* ?aff. *sitifense*; Hooijer: 22

1978 *Hipparion sitifense* (partim); Churcher and Richardson: 394

*Diagnosis.* Small to middle-sized hipparion with caballine lower cheek teeth and ectostylids.

Specimens of this species have been referred to *H. ?aff. sitifense* by Hooijer and to *H. sitifense* by Churcher and Richardson. The true North African *H. sitifense* is smaller and has hipparionine lower cheek teeth lacking ectostylids (Eisenmann 1980a); the synonymy proposed by Churcher and Richardson does not seem justified.

Upper and lower cheek teeth referable to this small hipparion are listed in Tables 5.6 and 5.7 together with their measurements and places of collecting. Some of them are certainly too small to belong to *H. cf. ethiopicum* (the lowers KNM-ER 336, 1268,

least 20 per cent). In as much as one may judge from only four *E. quagga* skeletons, metacarpal III differs from that of *E. burchelli* by its greater proximal width while metatarsal III also has a lesser distal articular width; both the latter characters make the metatarsal III of *E. quagga* look more like that of *E. przewalskii*.

In summary, *E. quagga* was probably a distinct species from *E. burchelli* but close to it (Eisenmann 1979b); the characters shared with horses may be accounted for by symplesiomorphies. Contrary to the assertions of Churcher and Richardson (1978, p. 417), there is no apparent cline of variation from *E. quagga* through *E. zebra* to *E. burchelli*; *E. zebra* is a totally different species.

The skulls of *E. zebra* have some features in common with the other zebras but in practice problems of discrimination arise only with *E. burchelli* (not *E. quagga*) and with *E. africanus* or *E. asinus*. The upper molars are large with respect to the premolars (the difference between  $P^4$  and  $M^1$  is relatively small). The protoconal indices for  $P^2$ ,  $P^3$ , and  $M^3$  of *E. zebra* are smaller than those of *E. quagga*; they are equal for  $M^1$  and greater for  $P^4$  and  $M^2$ . The protoconal indices of all the upper cheek teeth of *E. zebra* are smaller than those of *E. burchelli*. On the lower cheek teeth, the lingual groove is usually shallow, particularly on the premolars. The vestibular groove is rarely shallow in the molars. The postflexid index is nearly as great on  $P_2$  as on  $P_3$  and less on  $M_2$  than on  $M_1$ . Perfect cups are constant on  $I_{1,2}$  and very frequent (90 per cent at the second stage of wear) on  $I_3$ .

*E. zebra* metacarpals have similarities with those of *E. burchelli* and *E. quagga* but the metatarsals are more like those of *E. grevyi*. Distal articular keels are moderately developed. As already pointed out by Hoffstetter (1952, p. 274), the volar surface of the third phalanx is usually flat. On the posterior face of the astragalus the central calcaneal facet is separated by a groove of several millimetres width from the navicular facet on the distal face of the bone.

The skulls of *E. africanus* are intermediate in morphology between those of *E. zebra* and those of *E. hemionus-E. kiang*. As Groves (1974, p. 161) has already observed, the skulls of *E. africanus africanus* seem less different from the skulls of *E. asinus* than those of *E. africanus somaliensis*; however the material available is not very abundant and the subspecific differences are difficult to assess.

In the upper tooth row  $M^3$  is slightly larger than  $M^2$ . On  $M^1$  the protocones are much shorter than on

$P^4$  and the protoconal indices of  $M^1$  are usually smaller than in  $P^4$ ; these characters discriminate *E. africanus* from all zebras except *E. zebra*. As in *E. grevyi*, and in contrast to other species, the postfossettes rarely or never open backwards on the  $M^3$ . On the same tooth, hypoglyphs are isolated in 60 per cent of the specimens.

On the lower cheek teeth the lingual groove is usually deep. The vestibular groove is shallow in many examples of  $M_1$  (77 per cent) and in most of the lower second and third molars (95 per cent), this character distinguishing *E. africanus* from most of the zebras. Postflexid indices are smaller on  $P_3$  than on  $P_2$ . Cups are present on  $I_1$  and  $I_2$  but may be absent from  $I_3$ .

Metapodials are relatively slender, but less so than in *E. hemionus* or *E. kiang*. Distal keels are poorly developed. On metacarpal III, the magnum facet and the posterior unciform facet are relatively large; on metatarsal III the proximal width and articular surface for the cuboid are also relatively large. The *E. africanus* astragali may exhibit the same characters as those of *E. zebra*.

#### Systematics of fossil *Equus* species

Many fossil species from Africa have been recorded in the literature but few of them are adequately described. At present it seems worthwhile considering five species only—*E. capensis*, *E. oldowayensis*, *E. numidicus*, *E. tabeti*, and *E. mauritanicus*. As frequent references must be made to the European species *E. stenonis*, a brief discussion of this species will precede treatment of the African taxa. *Equus stenonis*, *E. numidicus*, *E. tabeti*, and *E. mauritanicus* have all been analysed previously with respect to their crania and upper cheek teeth (Eisenmann 1979a, 1980b), lower cheek teeth (Eisenmann 1976b, 1981), incisors (Eisenmann 1979d), metapodials (not *E. numidicus*; Eisenmann 1979e) and phylogenetic problems (Eisenmann 1979b), and for the sake of brevity no further bibliographical reference will be made to these papers.

The best material of *Equus stenonis* comes from the Villafranchian of France (Saint-Vallier, Seneze) and Spain (La Puebla de Valverde). The crania of *E. stenonis* have a long palate, short broad muzzle and an asinine vomerine index; all these characters are probably primitive. The relatively wide occipital crest may be considered as a progressive feature. Although they have characters in common, the crania of *E. stenonis*, *E. simplicidens* and *E. grevyi* are quite different (Figs. 5.5–5.6). The protoconal indices of *E. stenonis* are small (smaller than in *E.*

*simplicidens*) and they generally increase from the P<sup>2</sup> to the M<sup>3</sup>; the postprotoconal groove is very deep. Lower cheek teeth are stenorine (obviously), with deep lingual grooves; vestibular grooves may be shallow on some molars (as in asses and unlike most zebras). No protostylid was observed on P<sub>2</sub> or dP<sub>2</sub> from Saint-Vallier or La Puebla de Valverde, but was present on some teeth from the younger site of Seneze. Cups are well developed on I<sub>1</sub> and I<sub>2</sub>. Metapodials, and especially those of *E. stenonis* cf. *vireti* from La Puebla de Valverde, have nearly the same proportions as in *E. burchelli* but are larger (Figs. 5.9 and 5.10). The investigation of what may be primitive (plesiomorphous) or advanced (apomorphous) characters has led me to infer that *E. stenonis* cannot be the common ancestor of the Old World modern equids and that it probably represents a lateral offshoot of the quagga (*E. burchelli*-*E. quagga*) lineage.

The original description of *Equus capensis* by Broom (1909) was discussed by Cooke (1950, p. 441) who chose a neotype and referred additional material. From the information now available it appears that *E. capensis* is characterized by its large teeth (Broom 1909), its broad muzzle and its massive metatarsal (Broom 1913). No upper cheek teeth series can be safely ascribed to this species. In a moderately worn lower series (Cooke 1950, Fig. 19), the cheek teeth are stenorine with a deep lingual groove; P<sub>2</sub> is relatively short and bears no protostylid; the postflexid indices are subequal on P<sub>2</sub> and P<sub>3</sub> and smaller on M<sub>2</sub> than on M<sub>1</sub>; vestibular grooves are very deep on M<sub>1</sub> and M<sub>2</sub>. Most of these characters agree more closely with *E. zebra* than with *E. grevyi* but a single lower series is not sufficient to settle the question. Judging from the cast of a moderately worn upper premolar from Langebaanweg (L2: SAM 11714), kindly supplied by Hendey, the dimensions of the occlusal surface (35 × 35 mm) have no match in the North and East African Plio-Pleistocene and Middle Pleistocene equid material I have seen. This is in agreement with Hendey (1978, p. 6) that *E. capensis* is probably a Late Pleistocene giant species; its possible South African Middle Pleistocene ancestor had smaller teeth. It seems unwise to conjecture about the lineage leading to the giant South African species until our knowledge of both *E. capensis* and the other African Pleistocene species has measurably improved.

*Equus oldowayensis*, described by Hopwood (1937), is characterized by teeth of similar size to those of *E. grevyi* but by a much broader muzzle. Unfortunately

the type of this species was destroyed in the Second World War. A large collection of equid material was subsequently retrieved from Olduvai Gorge and is now being studied by Churcher, having previously been in the care of first Stirton and then Hooijer. I have not seen this new material and can comment only on specimens from the early Olduvai collections now housed in the British Museum (Natural History).

A moderately worn lower cheek tooth row (BM 14184) is 177 mm long, which is indeed near the mean value for *E. grevyi* (173.5 mm; range of variation 156–187 mm), and some 20 mm less than the probable length of *E. capensis* (more than 200 mm long). As in *E. grevyi*, and unlike *E. zebra* and *E. capensis*, the postflexid index is much higher for P<sub>3</sub> than P<sub>2</sub> and for M<sub>2</sub> than for M<sub>1</sub>. Unlike most *E. grevyi*, there is no protostylid on the P<sub>2</sub> and the vestibular groove is rather shallow on the M<sub>1</sub>. The metacarpals I have seen (M.14434 and M.14436) are closer to those of *E. grevyi* than to those of *E. stenonis* or the other zebras; the main differences are the much larger size, the relatively greater supra-articular distal width, and relatively greater size of the anterior unciform facet in *E. oldowayensis* (cf. Fig. 5.7 with Eisenmann 1979c, Fig. 9.11). There seems to be a notable discrepancy between the size of the metacarpal III and of the lower cheek teeth. Known metatarsals (M.14135 and 14445) more closely resemble *E. grevyi* than the other zebras or *E. stenonis* (cf. Fig. 5.8 with Eisenmann 1979e, Figs. 10–12); the main difference is the greater supra-articular width in *E. oldowayensis*.

It will be interesting to learn if *E. oldowayensis* is present throughout the Olduvai sequence and of any evolutionary trends; a tendency to increase or decrease in size through the sequence could account for the observed discrepancy in the size of the metapodials versus that of the mandible if they can be shown to come from different levels.

*Equus numidicus* was described by Pomel (1897, p. 19, Plate II, Figs. 5–6) from a little-worn upper cheek tooth from Beni Fouda (= Aïn Boucherit of Arambourg 1970, p. 20). The species was redescribed by Arambourg (1970) on the basis of further material now housed in the Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris. The material now comprises 19 upper cheek teeth, 15 lowers, 10 metapodials, and several other limb bones collected at Aïn Boucherit. The upper premolars are 29.5–33 mm long (mean 31 mm), the molars 25–29 mm long (mean 27); the mean protoconal indices are 33.5 for the premolars

and 36.2 for the molars. The upper cheek teeth look like those of *E. stenonis vireti* (Saint-Vallier, France) on the bases of size and of depth of the postprotoconal valley but the protoconal indices are smaller. In the lower cheek teeth  $P_2$  (two specimens) bears no protostylid and the vestibular groove may be rather shallow (three out of six specimens of  $M_{1,2}$ ); the same is true of *E. stenonis vireti* and of *E. oldowayensis* (BM 14184). The metacarpals (six specimens) look like those of *E. grevyi* but have better developed distal keels and larger unciform facets. The metatarsals (four specimens) resemble both *E. grevyi* (proportions of the diaphysis) and *E. oldowayensis* (great supra-articular width); they are quite different from those of *E. stenonis* of France (Saint-Vallier) or Spain (La Puebla de Valverde).

At present it would seem that *E. numidicus* and *E. oldowayensis* are closely related species. The fauna of Ain Boucherit is possibly of similar age to that from Bed I at Olduvai (Jaeger, personal communication) and the publication of the recently collected Olduvai equids should help throw further light on the relationship of the North and East African specimens. Meanwhile, although better material (particularly crania) would be welcome, the present data already show that *E. numidicus* is a large species, not a 'medium-sized to small horse' as stated by Churcher and Richardson (1978, p. 404) who quote Arambourg (1970) but seem unaware of his descriptions of the limb bones (Arambourg 1970, p. 98-103).

*Equus tabeti*, described by Arambourg (1970), is represented by many specimens collected from Ain Hanech from strata younger than those of Ain Boucherit. Comparison of both samples shows that there is probably a very close relationship between *E. numidicus* and *E. tabeti* (depth of the postprotoconal valley, slenderness of the metapodials) but *E. tabeti* has smaller teeth and limb bones and slenderer metapodials and phalanges. This extraordinarily gracile nature of the limbs is one of the reasons why Arambourg placed *E. tabeti* among the asses rather than the zebras. In fact, the metapodials are even more slender than in the modern *E. africanus* and look more like those of *E. hemionus* (the onager) apart from the larger facets for the unciform on metacarpal III and for the cuboid on metatarsal III. The pattern of the lower cheek teeth is not different from that of *E. stenonis* or most zebras; it differs from that of the asses in that vestibular grooves are deep on most of the molars. However, when one looks at the mean protoconal indices of the upper cheek teeth (calculated on eight

more or less complete series), one finds the usual asinine pattern: protoconal indices greater on  $P^+$  than  $M^+$ . Because of characters seen in the upper cheek teeth and metapodials, I do not agree with Churcher and Richardson (1978, pp. 408-9) that *E. tabeti* is a synonym of *E. burchelli*. Even if *E. tabeti* has no relationship with the asses or onagers, its similarities with *E. numidicus* preclude putting it in one subgenus (*Hippotigris*) and *E. numidicus* in another (*Dolichohippus*) as these authors do.

Pomel (1897) described *Equus mauritanicus* from the site of Ternifine (or Palikao). Arambourg and Hoffstetter later collected much more material comprising several skulls and hundreds of teeth and limb bones. The skulls are very like those of the quaggas *sensu lato* (*E. burchelli*-*E. quagga*), and the upper cheek teeth have characters in common with both the quaggas and *E. stenonis*. Lower cheek teeth have the usual zebrine-stenonine pattern and shallow vestibular grooves in 15 per cent of the anterior molars ( $M_{1,2}$ ). One  $dP_2$  (of three) bears a protostylid but this is unknown in the permanent  $P_2$ . The cups are closed in most known first incisors, 50 per cent of the second incisors and in one third incisor (of 12). The metapodials are very similar to those of *E. stenonis* from La Puebla de Valverde but with a less well developed posterior unciform facet on the third metacarpal and cuboid facet on the third metatarsal. The interpretation of plesiomorphous versus apomorphous characters led me to believe that *E. mauritanicus* is a side branch of the quagga s.l. lineage. (Incidentally, to my knowledge, there are no remains of *Hipparion* from Ternifine (cf. Churcher and Richardson 1978, Table 20.1)).

At present the only fossil species from Africa that are well documented are *Equus mauritanicus* and, to a lesser extent (no skulls), *E. tabeti*. The first may be related to the modern quagga lineage (*E. burchelli*-*E. quagga*), and, like the quaggas, may be readily derived from a *stenonis*-like ancestor. *E. tabeti* is obviously derived from *E. numidicus*; the lack of crania precludes our assessing its relationship to the onagers. The hemionine characters of its metapodials could reflect either parallel evolution or phyletic relationship. *E. tabeti* may also be related to the younger and smaller European *Equus hydruntinus* which also requires revision. For the other species we lack adequate material and/or detailed descriptions.

The differences that we see today between living species of *Equus* will inevitably diminish the further

we are able to trace their lineage back in time. The first *Equus* to appear in Africa closely resembles *E. stenonis* but this is not unexpected as, at this point in time, neither is very far removed from a common ancestor. Clearly, in order to unravel the systematics of the Plio-Pleistocene African *Equus* populations, it will be more profitable to seek differences rather than points of similarity. Equally clearly, meaningful differences will only be ascertained with the aid of large samples of relatively complete material.

## KOObI FORA MATERIAL

*Equus* material from east of Lake Turkana is in general well preserved, has suffered little from post-mortem deformation, and includes several complete cheek teeth series and limb bones. The material is not, however, very abundant and the specimens were collected from many different localities whose precise stratigraphic relationships are sometimes difficult to ascertain (White and Harris 1977, p. 17). The majority of specimens come from the Koobi Fora Formation and number 60 specimens from the *Not. scotti* zone, 120 specimens from the *Met. andrewsi* zone and 25 from the *Met. compactus* zone. A few specimens are known from the Guomde Formation and Galana Boi Beds. Some 50 specimens are from undetermined horizons or unknown localities.

In my treatment of the Koobi Fora material I have identified more than one possible species. I feel it would be useful at this stage to give a new name to one of them but it must be understood that this is only an interim conclusion pending the recovery of further complete and associated material.

### *Equus koobiforensis* sp. nov.

1976 *Equus* sp. nov. A; Eisenmann (1976c): 234

1978 *Equus* sp. A; Harris: 44

**Diagnosis.** Large *Equus* approaching the size of *E. sanmeniensis* of China. Palate relatively long with respect to the muzzle. Upper cheek teeth with deep postprotoconal valleys and relatively small protocones. P<sub>2</sub> at least occasionally bearing protostylid; stenocone double knot on the lower cheek teeth; vestibular grooves at least occasionally shallow on M<sub>2</sub>.

**Holotype.** Cranium of young adult mare, KNM-ER 1484, from the *Notochoerus scotti* zone, below the KBS Tuff in Area 130.

Other specimens known from the *Notochoerus scotti*

and *Metridiochoerus andrewsi* zones of the Koobi Fora Formation; Omo Shungura Formation?; Olduvai Gorge?

**Etymology.** The species name reflects the stratigraphic provenance of the type specimen (Koobi Fora Formation) east of Lake Turkana.

The holotype cranium comes from the *Notochoerus scotti* zone. Dentitions that match the holotype in size were also collected from later levels while others from the *Not. scotti* zone seem too small to be referred to *E. koobiforensis*. Scatter diagrams of the upper and lower cheek teeth indicate: at least two species were probably represented in the sequence; teeth from the *Not. scotti* zone are usually larger than most from the *Met. andrewsi* zone (but large teeth recur at later horizons); there are no precise dimensional or morphological differences which separate the large and small teeth and the attribution of teeth of intermediate size is uncertain.

It would be possible, in light of the variation shown by other *Equus* species, to refer all the *Equus* teeth from east of Lake Turkana to one taxon. It is equally possible, on the basis of size and morphology, to refer one lower series (KNM-ER 4051) to one species (*E. koobiforensis*) and others to another.

The presence of more than one species is suggested also by postcranial evidence. Using known ratios of skull size to limb size in other *Equus* species (Fig. 5.4), one may infer that a horse with a skull equivalent in size to that of *E. koobiforensis* would have very large metapodials with a distal supra-articular width of 50–55 mm. Metapodials of this size have not been found east of Lake Turkana but occur at Omo (lower Member G of the Shungura Formation) and perhaps also at Olduvai. *Equus* metapodials recovered from east of Lake Turkana are only the size of *E. numidicus*—*E. tabeti*; the difference between the smallest of them and the large Omo and Olduvai specimens is too great to be accounted for by intraspecific variation.

Thus, on the basis of evidence provided by the correlation of cranial and metapodial size in living species, more than one *Equus* species appears to be present in the Koobi Fora Formation. It is possible, however, that the attributions provided below may require modification in the future. Upper cheek teeth series and isolated uppers are listed in Tables 5.11–5.12 and lower cheek teeth in Tables 5.13–5.14.

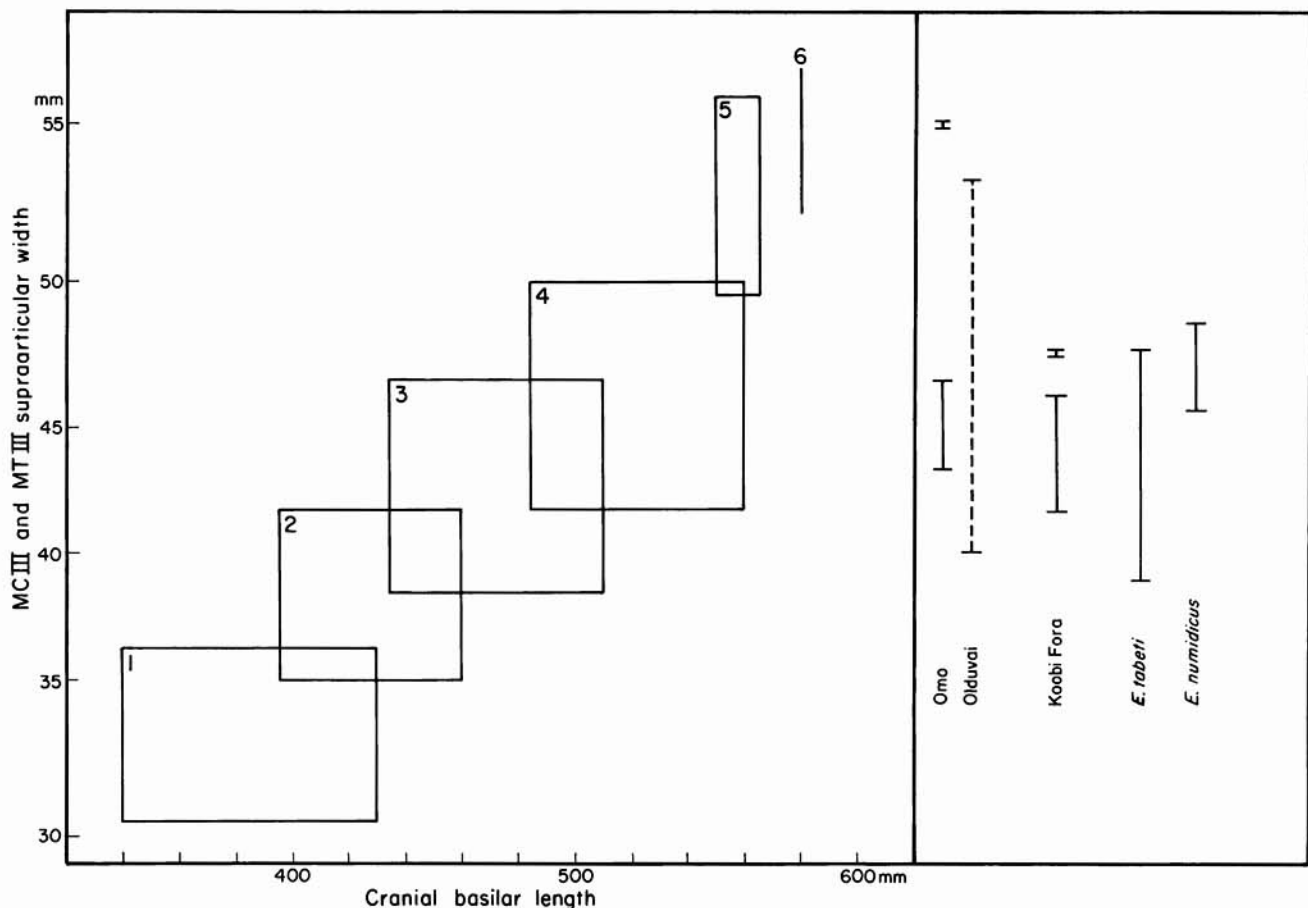


FIG. 5.4. Tentative correlation between metapodial width and cranial length. (1) *E. asinus*; (2) *E. hemionus*; (3) *E. zebra*; (4) *E. grevyi*; (5) *E. stenosis vireti*; (6) *E. samnienensis*. The skull of *E. koobiforensis* is 577 mm long and should have been associated with metapodials 50–55 mm wide. The right part of the figure shows the width of the metapodials actually found in East and North Africa.

The skull KNM-ER 1484 (Plate 5.6) is in a good state of preservation but several parts that would have been important for diagnosis are damaged or missing. For example, the occipital crest is broken, the vomer is damaged and there is no auditory tract. The specimen, detailed measurements of which are given in Table 5.10, is among the largest *Equus* crania I have encountered. Compared to living species it is closer to *E. zebra hartmannae* than to *E. grevyi* in the straightness of its naso-frontal suture, relatively narrow forehead and depth of the nasoincisive notch. However, as seen in Figs. 5.5 and 5.6, the most striking similarities are with *Equus stenonis* and particularly with *E. stenonis* cf. *vireti* from La Puebla de Valverde, Spain, apart from the fact that *E. koobiforensis* is much larger.

An isolated premaxilla (KNM-ER 1239 from the *Met. andrewsi* zone of Area 104) bears five rather

worn incisors. A similar stage of wear is encountered in an 11–13-year-old *E. zebra hartmannae* (Joubert 1972, Plate 19). Two well developed canines are present. The width of the premaxilla behind the  $I^3$  is 63 mm and its minimum width is about 46 mm, measurements that are similar to those of the holotype female (Table 5.10).

As has already been noted, the upper cheek teeth may have very deep postprotoconal valleys (Plates 5.7E,F; 5.8J) as in *E. stenonis*; the protocones are short (Plate 5.8). The proportions of the lengths and protoconal indices of the upper series are very similar to those of *E. stenonis* (based on two complete tooth rows KNM-ER 1484 and 2691).  $P^2$  and  $M^3$  are relatively long and the protoconal index increases from  $P^2$  to  $M^3$ .

Only one lower cheek tooth series (KNM-ER 4051) matches that of the holotype cranium. These



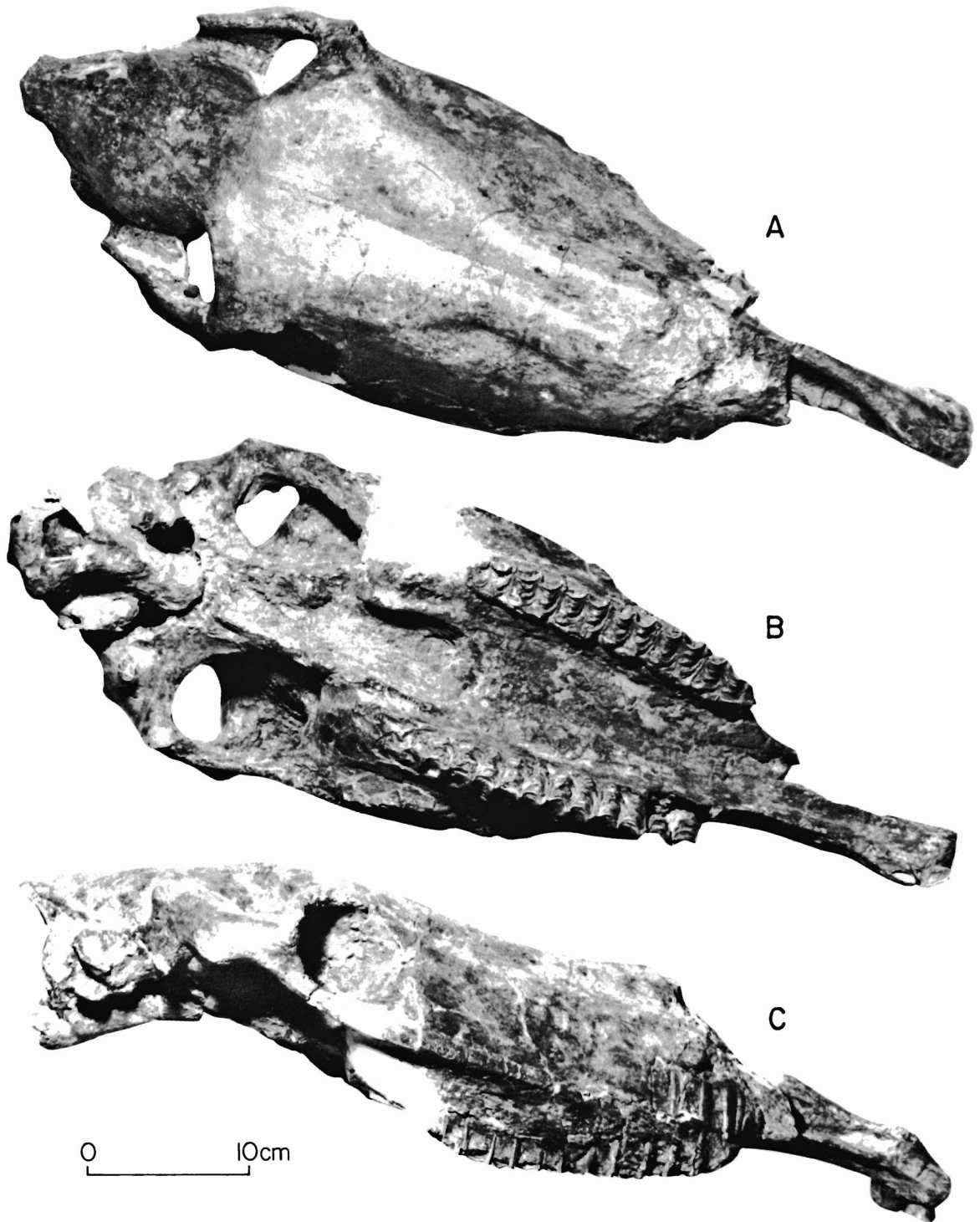


PLATE 5.6. *Equus koobiforensis* cranium (KNM-ER 1484, holotype). (A) dorsal view; (B) ventral; (C) lateral.

teeth are also like those of *E. stenorius* with rounded metaconids and metastylids, deep and pointed lingual grooves, short vestibular grooves on at least some of the molars, and a relatively long  $P_2$  (Plate 5.9E). The presence of a protostylid on  $P_2$  evokes a comparison with *E. grevyi* but the shallow nature of the molar vestibular grooves is rare in the latter species. Other, smaller, series (KNM-ER 5361A, 1582 and perhaps 5360) have pointed metastylids, a shorter  $P_2$ , shallower lingual grooves and deeper vestibular grooves on every molar. The anteroexternal wall of the  $P_2$  may show a kind of angulation (Plate 5.9C). All these features are more frequently found in *E. zebra* than in *E. stenorius*.

The mandible KNM-ER 1582 shows cups on every incisor; this character is common to most species of *Equus* both extant and fossil.

At least two characters of the holotype indicate that *E. koobiforensis* is distinct from, and probably more primitive than, any modern species of *Equus*—the relatively long palate associated with a short muzzle (seen also in *Dinohippus interpolatus*, *D. leidyani*, *Equus simplicidens*, *E. stenorius vireti*, and *E. stenorius senezensis*) and the low protoconal indices

(not very different from those of *E. stenorius*). However, differences in the morphology of the skull are more marked (Figs. 5.5–5.6) between *E. koobiforensis* and *E. stenorius* than among the European subspecies of the latter.

It is almost impossible to compare *E. koobiforensis* with *E. capensis* owing to the lack of precise data for the skull, cheek teeth and limb bones of the South African species. It is, at present, similarly difficult to compare *E. koobiforensis* with *E. oldowayensis* which is being revised by Churcher. If there is only one species at Olduvai, namely *E. oldowayensis*, its metapodials are of suitable size to belong to *E. koobiforensis* which perhaps may therefore end up as a junior synonym of *E. oldowayensis*. This problem will only be fully resolved when and if metapodials similar to those of Omo and Olduvai are recovered from the Koobi Fora Formation. *Equus numidicus* is also too poorly known to make profitable comparisons, being represented by a few limb bones and a few isolated teeth. The protoconal indices of *E. numidicus* are small as in most Pliocene horses and while the metapodials are not *stenorius*-like, they do not match closely the large metapodials from Olduvai (Figs. 5.7, 5.8). It is not beyond the bounds

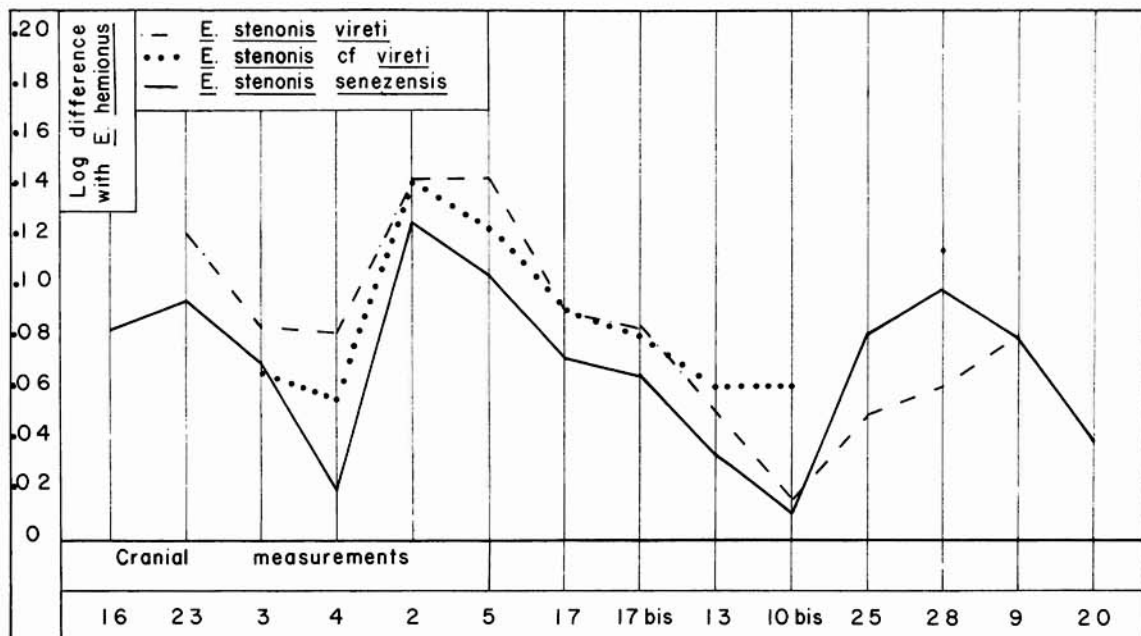


FIG. 5.5. Ratio diagram of some cranial measurements in three subspecies of *E. stenorius*: *E. stenorius vireti*, mean of six fragmentary crania from Saint-Vallier, France; *E. stenorius cf. vireti*, mean of two fragmentary crania from La Puebla de Valverde, Spain; *E. stenorius senezensis*, mean of three fragmentary crania from Senèze, France.

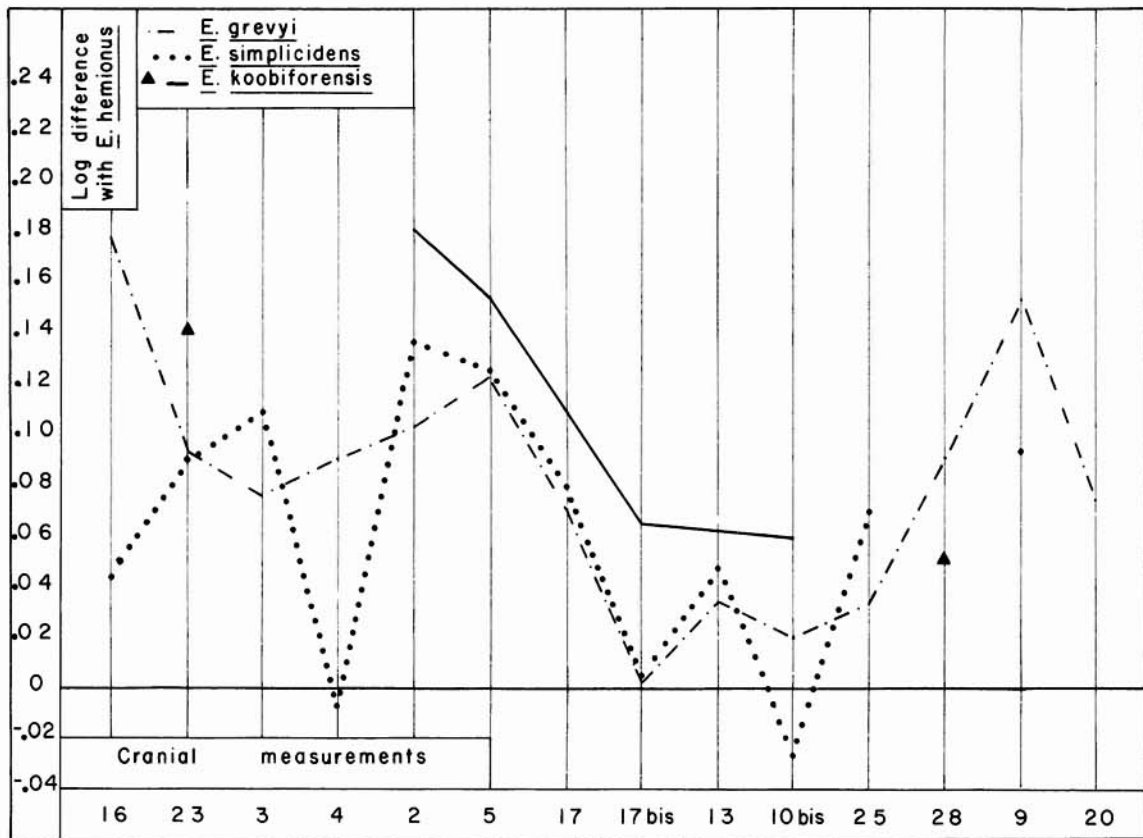


FIG. 5.6. Ratio diagram of some cranial measurements in three species of *Equus*: *E. grevyi*, mean of 50 crania; *E. simplicidens*, mean of eight fragmentary crania from Hagerman Formation and Mount Blanco after data published by Gazin (1936) and Skinner, Hibbard *et al.* (1972); *E. koobiforensis*, one cranium, KNM-ER 1484, Koobi Fora Formation, *Notochoerus scotti* zone.

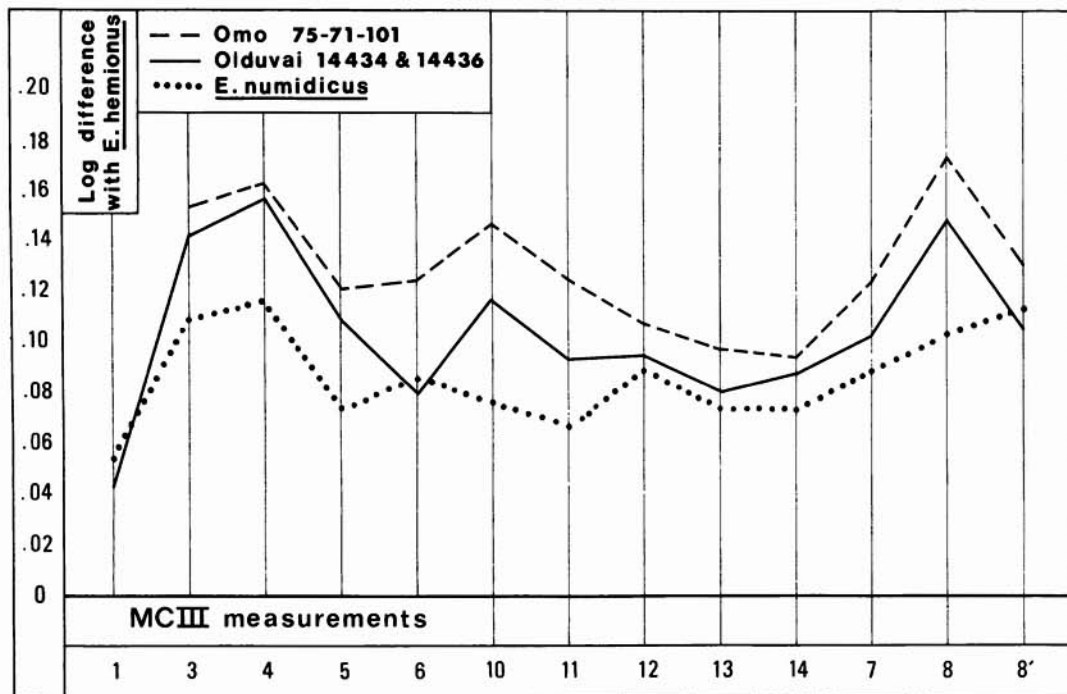


FIG. 5.7. Ratio diagram of dimensions of third metacarpal in *E. cf. koobiforensis* from Omo and Olduvai and in *E. numidicus* (mean of six specimens from Ain Boucherit).

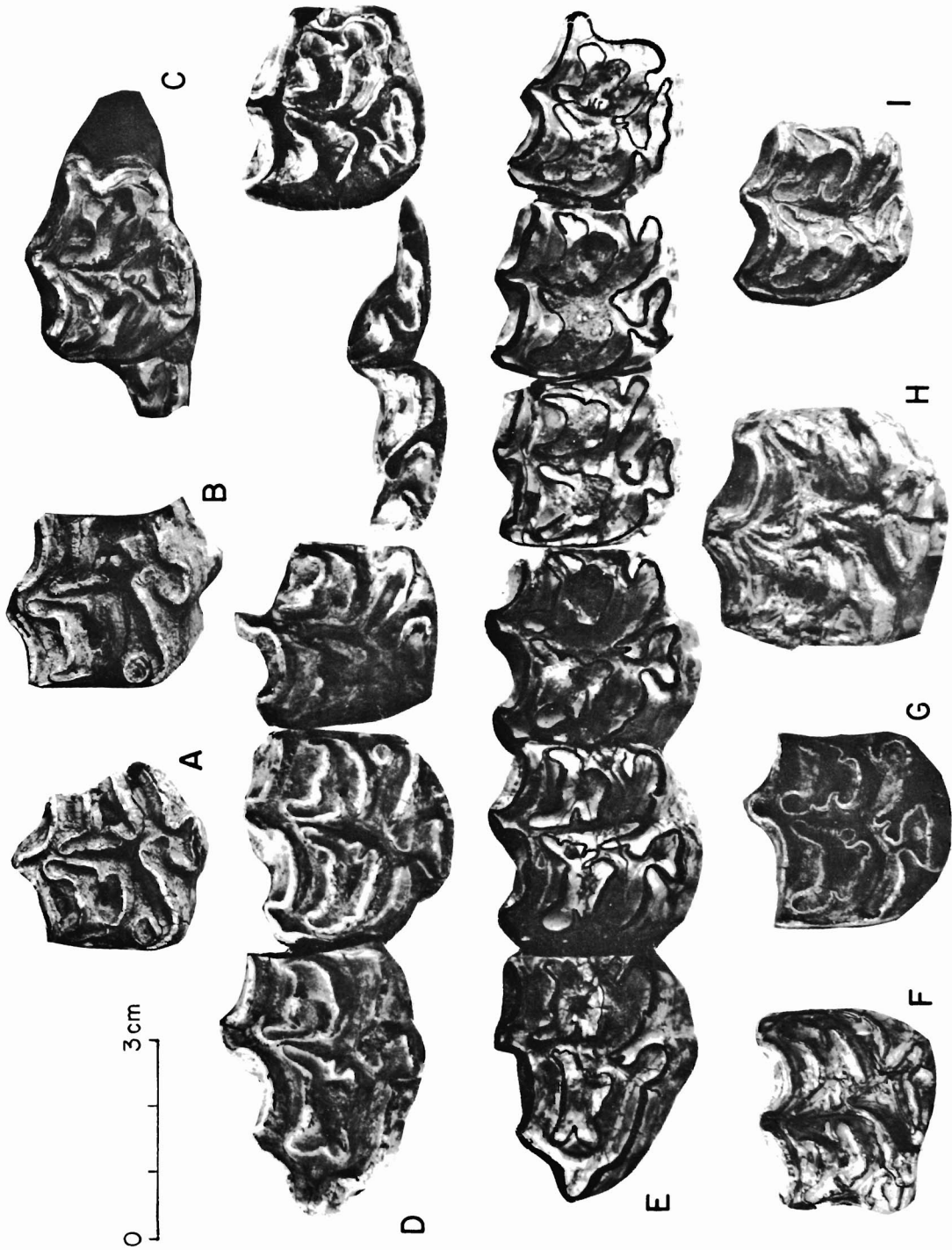


PLATE 5-7. *Equus koobijorensis*.  
 (A) P<sup>3</sup> or P<sup>4</sup>; (B) fragmentary P<sup>2</sup>; (C) M<sup>3</sup> (KNM-ER 5519); (D) fragmentary upper cheek teeth row (KNM-ER 5361B-D); (E) upper cheek teeth row (KNM-ER 2691); (F) M<sup>1</sup> or M<sup>2</sup> (KNM-ER 2687); (G) P<sup>3</sup> or P<sup>4</sup> (KNM-ER 4025); (H) P<sup>1</sup> or P<sup>2</sup> (KNM-ER 1129); (I) M<sup>1</sup> or M<sup>2</sup> (KNM-ER 1255).