

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_4 '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 Plio-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 ($M_{1,2}$) 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 scottii* 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. sitifensis* 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 P³⁻⁴ are notably smaller than those of *H. hasumense*; in contrast M¹⁻² 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. M³ 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^3 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. stenorius*, a brief discussion of this species will precede treatment of the African taxa. *Equus stenorius*, *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 stenorius* comes from the Villafranchian of France (Saint-Vallier, Seneze) and Spain (La Puebla de Valverde). The crania of *E. stenorius* 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. stenorius*, *E. simplicidens* and *E. grevyi* are quite different (Figs. 5.5–5.6). The protoconal indices of *E. stenorius* are small (smaller than in *E.*

simplicidens) and they generally increase from the P² to the M³; 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 P₂ or dP₂ 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 I₁ and I₂. 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: P₂ is relatively short and bears no protostylid; the postflexid indices are subequal on P₂ and P₄ and smaller on M₂ than on M₁; vestibular grooves are very deep on M₁ and M₂. 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 P₃ than P₂ and for M₂ than for M₁. Unlike most *E. grevyi*, there is no protostylid on the P₂ and the vestibular groove is rather shallow on the M₁. 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^4 than M^1 . 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. scottii* zone, 120 specimens from the *Met. andreusii* 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. P₂ at least occasionally bearing protostylid; stenoine double knot on the lower cheek teeth; vestibular grooves at least occasionally shallow on M₂.

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

Other specimens known from the *Notochoerus scottii*

and *Metridiochoerus andreusii* 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 scottii* zone. Dentitions that match the holotype in size were also collected from later levels while others from the *Not. scottii* 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. scottii* zone are usually larger than most from the *Met. andreusii* 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. tabei*; 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.

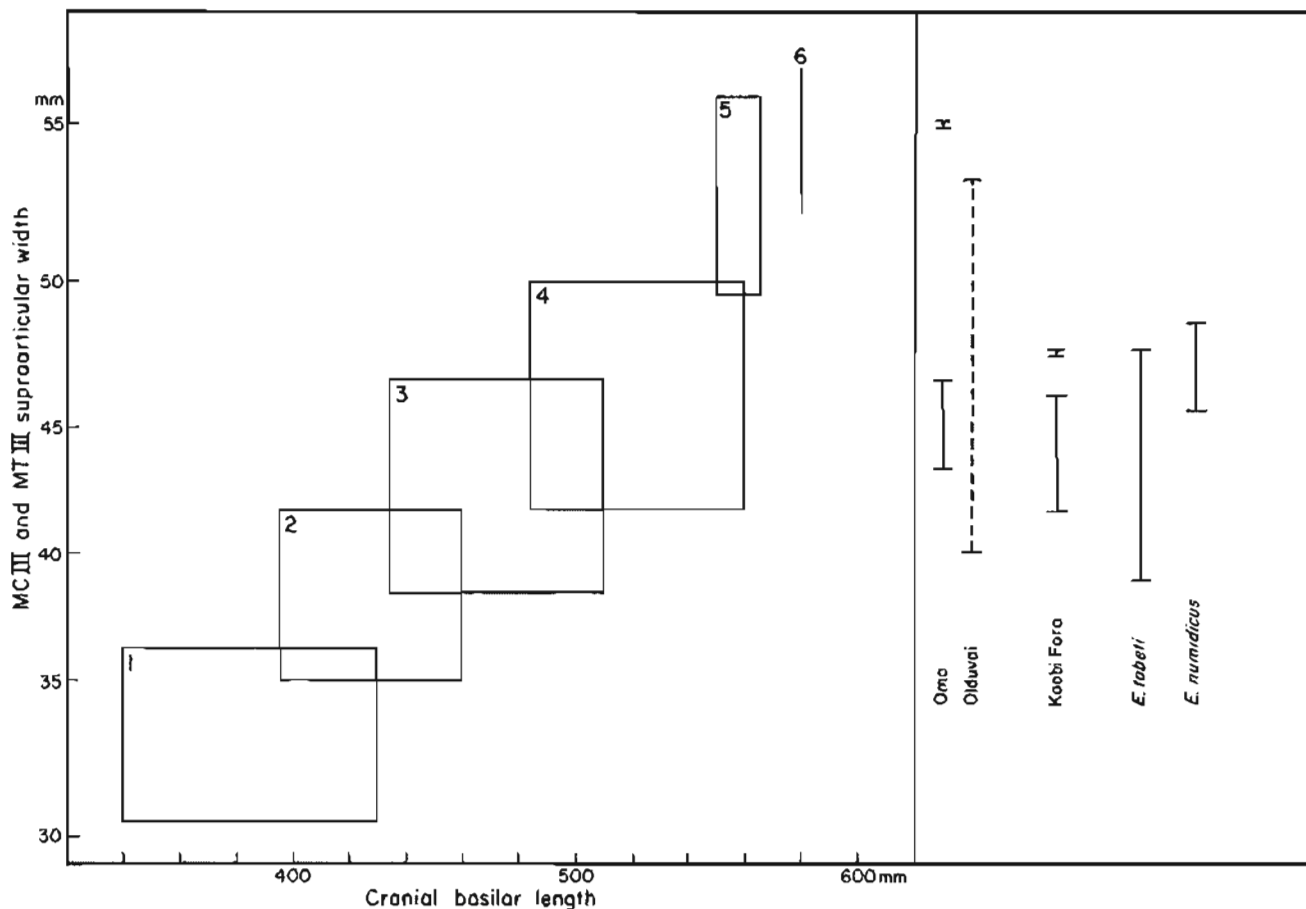


FIG. 5.4. Tentative correlation between metapodial width and cranial length. (1) *E. asinus*; (2) *E. hemionus*; (3) *E. zebra*; (4) *E. grevyi*; (5) *E. stenonis vireti*; (6) *E. sarmenensis*. The skull of *E. koobiforensis* is 577 mm long and should have been associated with metapodials 50–55 mm wide. 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 *Mel. 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

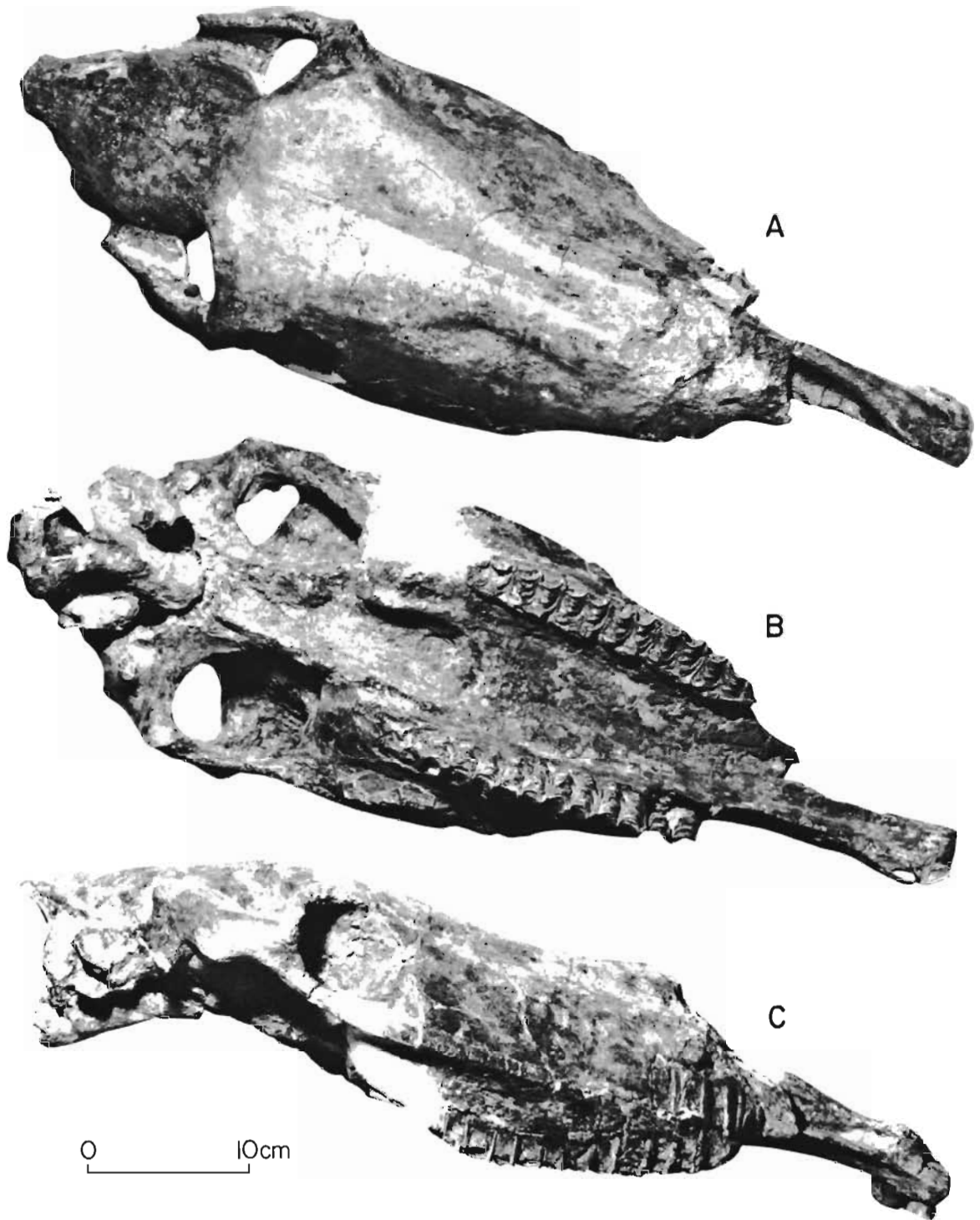


PLATE 5.6. *Equus koobiforensis* cranium (KNM-ER 1484, holotype).
(A) dorsal view; (B) ventral; (C) lateral.

teeth are also like those of *E. stenorhis* 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. stenorhis*.

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. leidymanus*, *Equus simplicidens*, *E. stenorhis vireti*, and *E. stenorhis senezensis*) and the low protoconal indices

(not very different from those of *E. stenorhis*). However, differences in the morphology of the skull are more marked (Figs. 5.5–5.6) between *E. koobiforensis* and *E. stenorhis* 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 *stenorhis*-like, they do not match closely the large metapodials from Olduvai (Figs. 5.7, 5.8). It is not beyond the bounds

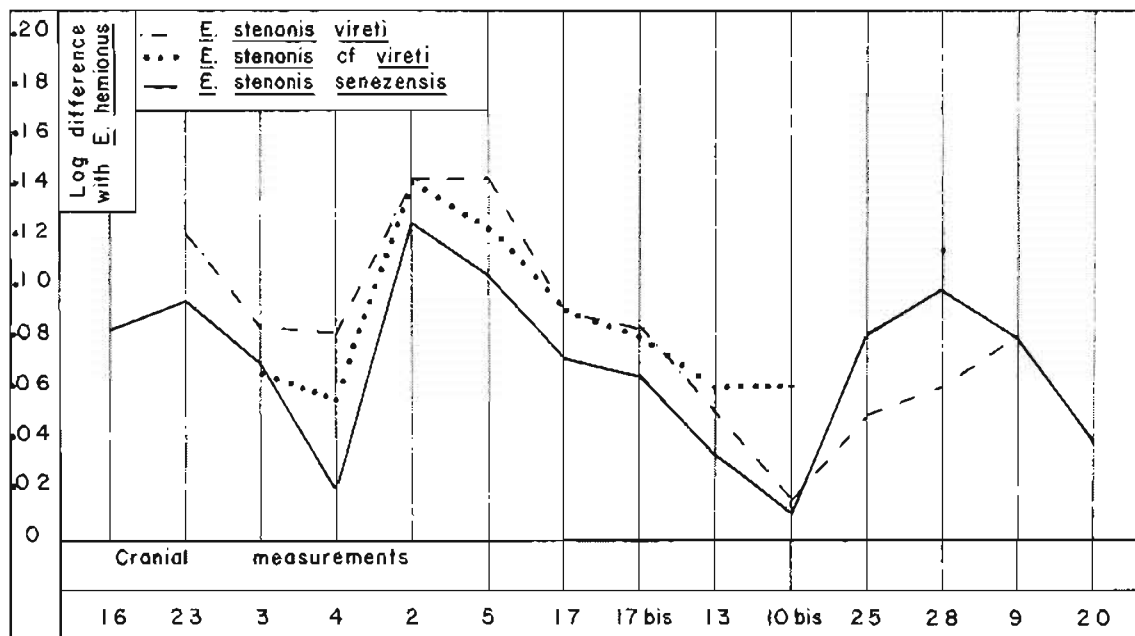


FIG. 5.5. Ratio diagram of some cranial measurements in three subspecies of *E. stenorhis*: *E. stenorhis vireti*, mean of six fragmentary crania from Saint-Vallier, France; *E. stenorhis cf. vireti*, mean of two fragmentary crania from La Puebla de Valverde, Spain; *E. stenorhis senezensis*, mean of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

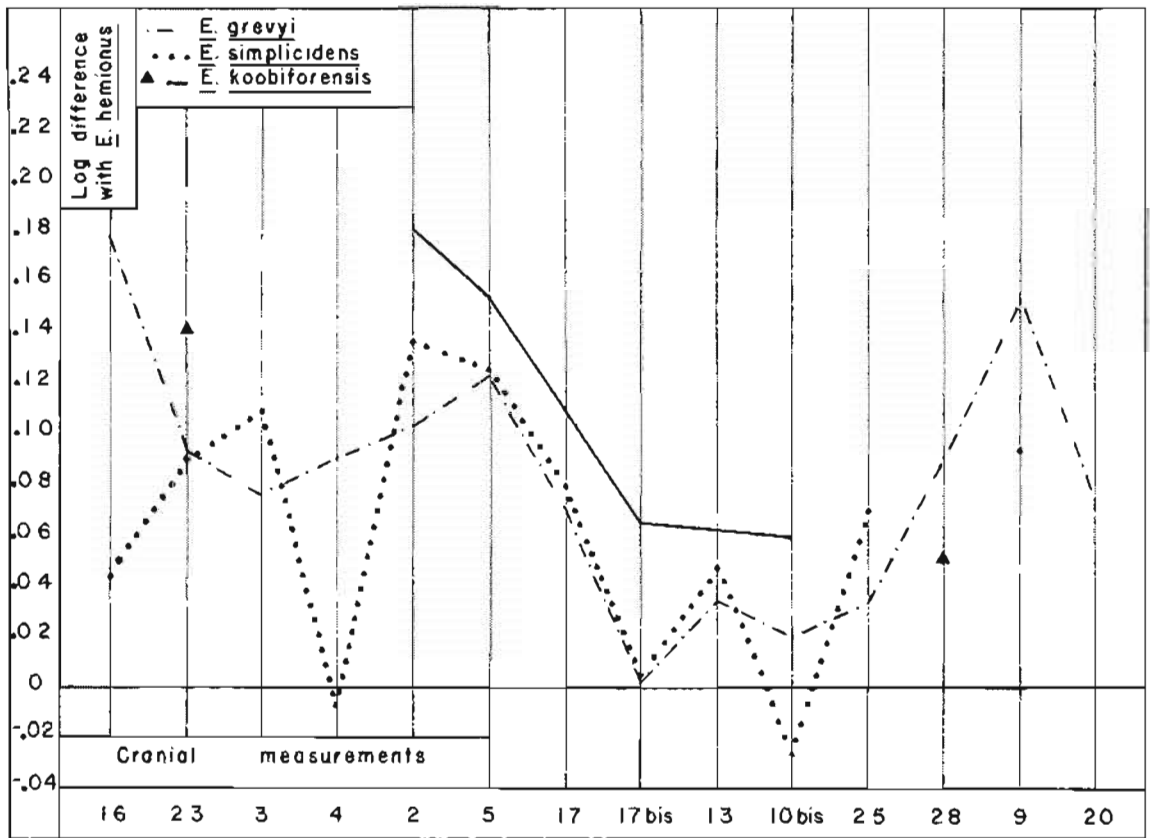


FIG. 5.6. Ratio diagram of some cranial measurements in three species of *Equus*: *E. grevyi*, mean of 50 crania; *E. simplicidens*, mean of eight fragmentary crania from Hagerman Formation and Mount Blanco after data published by Gazin (1936) and Skinner, Hibbard *et al.* (1972); *E. koobiforensis*,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

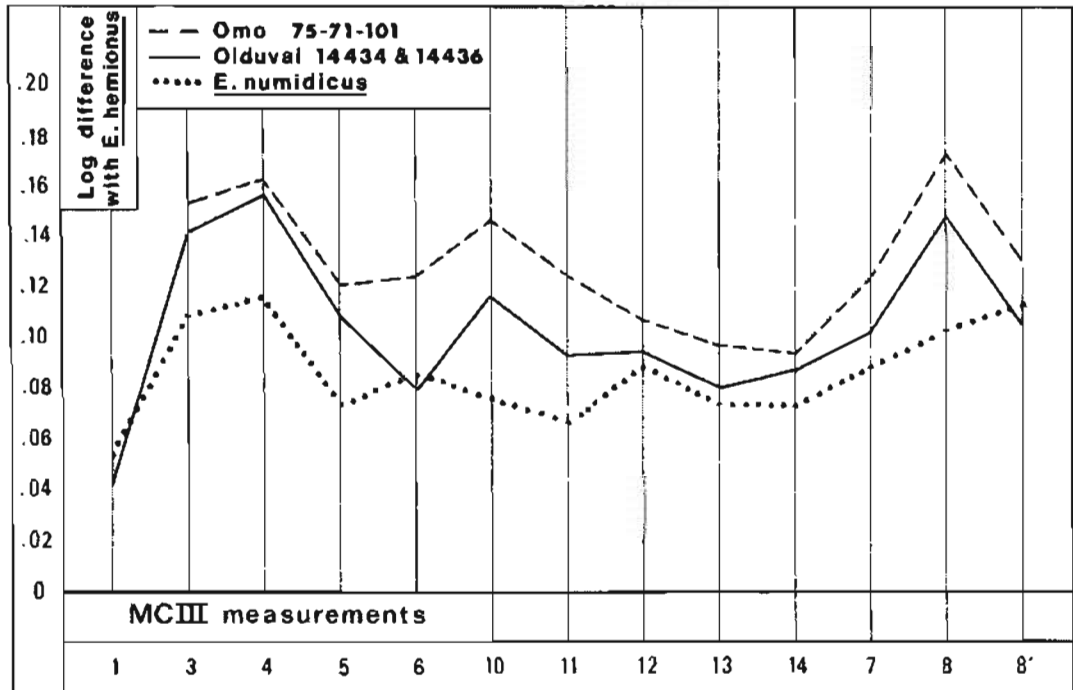


FIG. 5.7. Ratio diagram of dimensions of third metacarpal in *E. cf. koobiforensis* from Omo and Olduvai and in *E. numidicus* (mean of six specimens from Ain Boucherit).

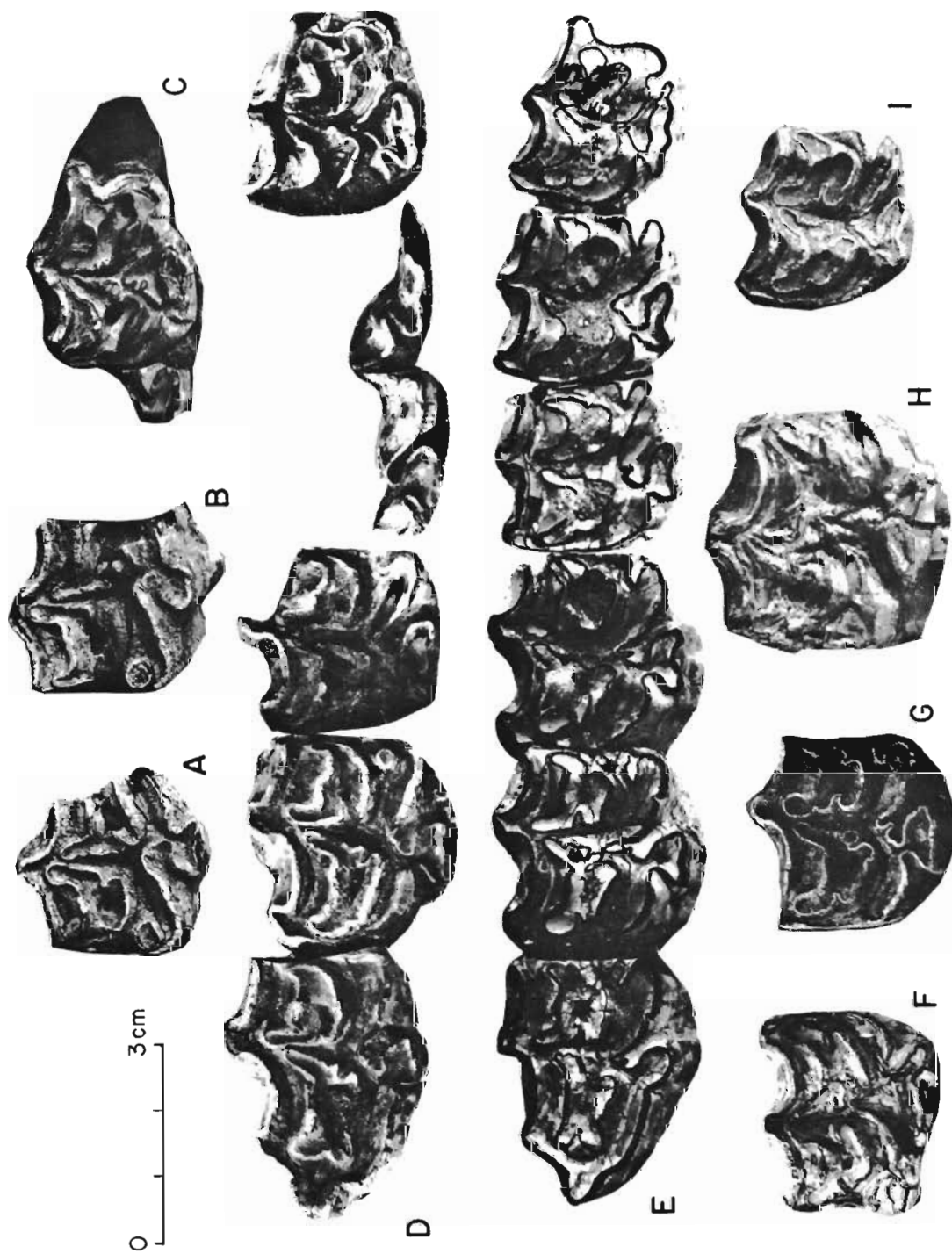


PLATE 5-7. *Equus kumbiformensis*.
 (A) P^2 or P^3 ; (B) fragmentary P^2 ; (C) M^2 (KNM-ER 5519); (D) fragmentary upper cheek teeth row (KNM-ER 5361B-D); (E) upper cheek
 teeth row (KNM-ER 26911); (F) M^1 or M^2 (KNM-ER 2687); (G) P^2 or P^3 (KNM-ER 4025); (H) P^1 or P^2 (KNM-ER 1129); (I) M^1 or M^2
 (KNM-ER 1255).

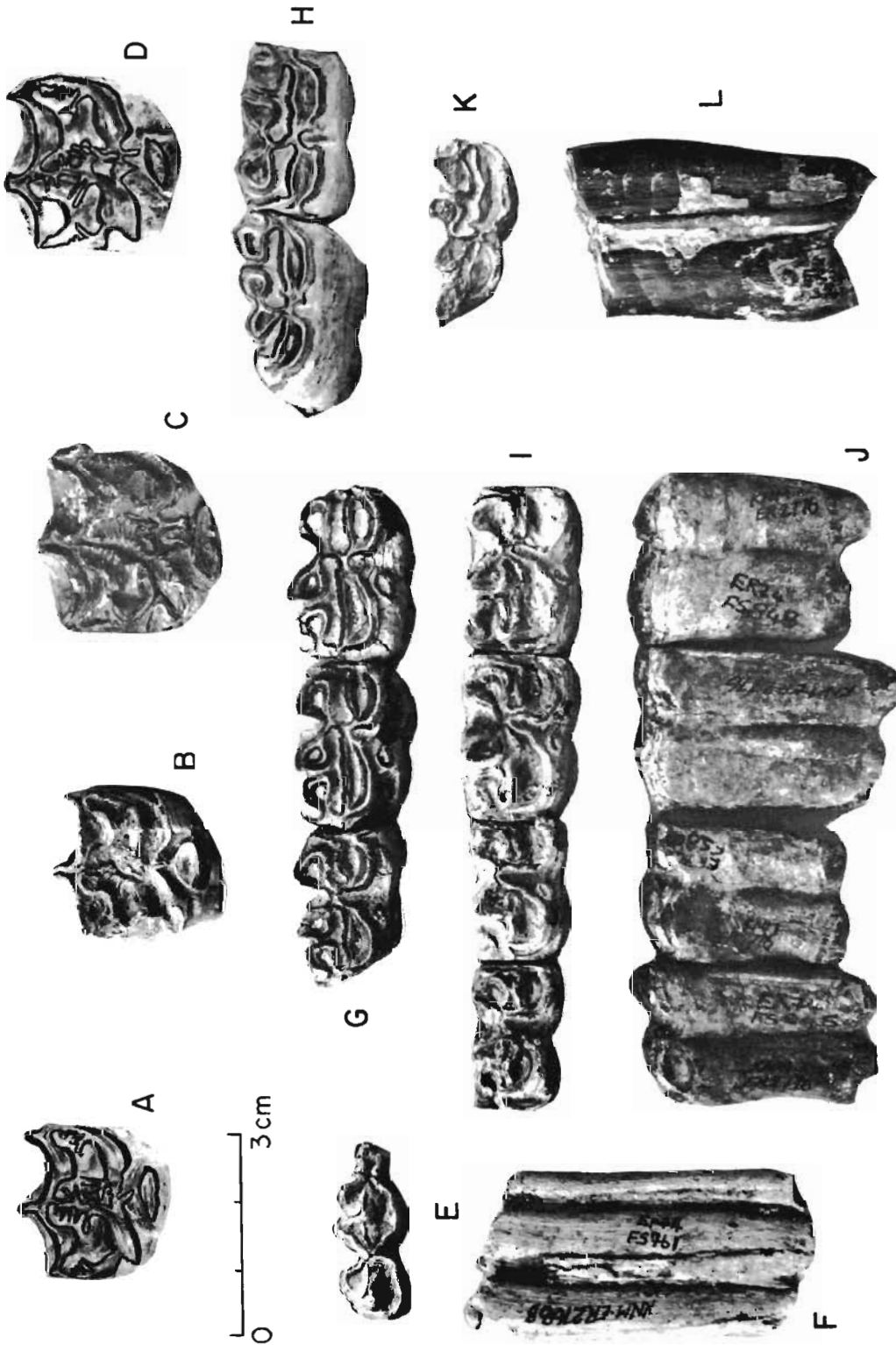


PLATE 5.1. *Hipparion* cf. *hasamense*, Hadar Formation (Dencen Dora Member).

(A) M_2^2 ; (D) P_3^2 ; (H) $P_2P_3^2$.

Hipparion hasamense.

(B) M_1 or M_2^2 (KNM-ER 2923); (C) P_3^2 or P_4^2 (KNM-ER 2785); (E, F) M_1 (KNM-ER 2768B); (G) $P_1P_2M_1$ (KNM-ER 4680); (I, J) $P_3P_4M_1M_2$ (KNM-ER 2776, holotype); (K, L) P_2^2 (KNM-ER 2768).

Hipparion hasumense sp. nov.

- 1974 *Stylohipparion libycum*; Aguirre and Alberdi: 154
 1975 *Hipparion primigenium* (partim); Hooijer: 17
 1975 *Hipparion* aff. *sitifense* (partim); Hooijer, Plate 5,
 Figs. 4, 5.
 1976 *Hipparion* sp.; Eisenmann (1976a): 580

Diagnosis. Moderate to large-sized hipparion with rather caballine lower cheek teeth and deep vestibular grooves on moderately worn molars. Ectostylids probably present in most lower teeth of the species but taper apically and hence more prominent in worn specimens. P_3 and P_4 notably larger than M_1 and M_2 .

Holotype. KNM-ER 2776, associated right P_4 - M_2 and fragments of very worn incisors from beneath the Hasuma Tuff in Area 204 (Plate 5.1, I, J); other specimens are known from zones B and C of the Kubi Algi Formation.

Etymology. The species name reflects the stratigraphic position of the type specimen in the succession east of Lake Turkana.

Specimens attributed to *H. hasumense* from east of Lake Turkana represent a species that has not hitherto been named at any other locality in East or South Africa. Similar specimens have, however, been retrieved from the Chemeron Formation of Kenya and from the Denen Dora Member of the Hadar Formation of Ethiopia.

Lower cheek teeth are listed with their measurements and localities in Table 5.2. I have explained above why upper cheek teeth of hipparions are of limited diagnostic value and it is with caution that I refer to *H. hasumense* the specimens listed in Table 5.1. Other specimens include an astragalus (KNM-ER 2789) from zone C of Area 117, an angular portion of mandible (KNM-ER 4059) from zone B of Area 116 (Eisenmann 1976a, Plate 5C), and two mandibular symphyses lacking incisors (KNM-ER 324 and 1221) from unknown levels south of the Koobi Fora Ridge and in Area 7 respectively (Eisenmann 1976a, Plate 7A, B).

The characteristic features of the lower cheek teeth have already been listed in the species diagnosis. Ectostylids usually reach the top of the crown (except in 5 specimens out of 26). Large and plicated upper cheek teeth that are found in zones B and C are provisionally referred to this species

although there is no known association of upper and lower cheek teeth from east of Lake Turkana.

Measurements of an astragalus are given in Table 5.8.

H. hasumense differs from the evolved hipparions (*H. cornelianum*, *H. steyleri*, *H. libycum*, *H. ethiopicum*) and in particular from *H. ethiopicum* in which the ectostylids are much bigger, the double knots typically caballine, the vestibular grooves shallow in at least some moderately worn molars and in which there is but little difference of size between P_{3-4} and $M_{1,2}$. *H. hasumense* differs also from the South African *H. namaquense* in which the ectostylids are inconstant and minute even at the base of the crown.

Regarding the comparison of *H. hasumense* with *H. afarensis*, one point must be made clear. If it had not been for the difference in size and shape between the muzzle and incisors of the *H. afarensis* type skull and the referred mandible on one hand and the muzzle and incisors of another individual of about the same ontogenetic age on the other, the question of two species in the Hadar Formation would not have arisen because the cheek teeth and limb bones may easily be assigned to a single species. As it is, the variability of the front dentition does not seem compatible with an intraspecific variation and the probability is that there are two species at Afar even if their cheek teeth cannot, for the moment, be told apart (the more so because the lower cheek teeth of the mandible referred to *H. afarensis* are not worn enough to be discussed).

There are some lower cheek teeth from the Hadar Formation referred to *Hipparion* sp. (particularly AL 155-6) that are closely comparable to those of the Kubi Algi Formation. The similarities of size, morphology of the P_2 (Plate 5.1 H, K) and development of ectostylids on all the teeth suggest a very close relationship if not conspecificity. The main difference between comparable specimens from the two formations is that the Hadar teeth (M_1 and M_2 of AL 155-6) have shallow vestibular grooves; it is not apparent whether this is because the Hadar teeth are less worn or if they belong to a slightly more advanced stage of the same lineage. The lower cheek teeth of AL 155-6 were originally associated with incisors, upper cheek teeth and a nearly complete postcranial skeleton, and certainly astragali and upper cheek teeth of *H. hasumense* agree very closely in morphology with equivalent elements from Hadar (Plate 5.1A-D; Table 5.8).

If we can assume that *H. hasumense* is present in

the Denen Dora Member of the Hadar Formation (Aronson *et al.* 1977) it enables us to postulate an age of approximately 3 Ma for zone B of the Kubi Algi Formation. Moreover it provides us with a more complete understanding of the species through the additional information available from the Hadar skeleton. Thus we may infer that metacarpal III and metatarsal III were approximately 267 and 296 mm long respectively, and that the anterior and posterior proximal phalanges were 75 and 70 mm long. We may infer also that the incisors, though neither as large nor as crenulated as in *H. cornelianum*, may exhibit one 'advanced' feature, namely some reduction in size of I_3 .

H. hasumense is perhaps also represented at other East African localities. Lower cheek teeth such as KNM-BC 1157 from the Chemeron Formation (Hooijer 1975, p. 26, Plate 5 Figs. 4, 5) are of similar size and morphology to the type of *H. hasumense*. The presence of *H. hasumense* in the Chemeron Formation is hardly surprising in light of the estimate of its age as 2-4 Ma (Bishop *et al.* 1971). The upper third molar KNM-BC 367(2) (not an M^2 as described by Hooijer (1975, p. 17, Plate 6, Fig. 5) from locality JM 493 is rather similar to the M^3 KNM-ER 2922 from the Kubi Algi Formation (Plate 5.2A) but the latter specimen is bigger with a larger protocone.

Hipparion sp. A

A second species of *Hipparion* may be represented by a damaged lower premolar (KNM-ER 2766, Plate 5.2M) from zone C of the Kubi Algi Formation in Area 203. The ectostylid of KNM-ER 2766 is more prominent than in *H. hasumense*, and its more or less triangular section suggests that its enlarged appearance results from the fusion of several ectostylids of different heights. Similar ectostylid fusion has been recorded in hipparions from the Shungura Formation (Eisenmann in press, Plate 2) and from Aïn Brimba (Arambourg 1970, Plate XVIII, Fig. 3). Although this isolated tooth appears to group with the *H. hasumense* cluster on a scatter diagram of ectostylid length versus occlusal length (Eisenmann 1977, Fig. 2), measurements made on a damaged specimen must be viewed with caution and I believe KNM-ER 2766 to be 'more advanced' than *H. hasumense*. The premolar also displays a peculiar double knot, with a very shallow lingual groove and a very oblique pedicule (stem of the double knot). This combination of characters is seen also in a P_3 from the Sidi Hakoma Member of the Hadar Formation (Plate 5.2L), which is slightly older than the Denen Dora Member, but again also

in an isolated P_3 from the Guomde Formation (Plate 5.2N), which overlies the Koobi Fora Formation at Ileret. Isolated teeth of similar morphology to KNM-ER 2766 are thus known from localities ranging in age from over 3 Ma to less than 1 Ma. These facts stress the caution with which one should use single teeth for establishing time correlations.

An associated molar and premolar, KNM-ER 673A and B, were collected during the early phase of the project from KF III. The molar is little worn and the ectostylid does not reach the occlusal surface. In the premolar the double knot and the size of the ectostylid are strongly reminiscent of those of the zone C and Sidi Hakoma Member specimens, but agree still better with a premolar from Member C of the Omo Shungura Formation (Omo 18-1969-91) which has been interpreted as between 2.4-2.6 Ma (Coppens 1975, p. 1571).

Measurements of these specimens together with that of another (KNM-ER 335B) from an unknown level in Area 7A are given in Table 5.3.

Hipparion cornelianum (Van Hoepen), 1930

- 1930 *Eurygnatohippus cornelianus*; Van Hoepen: 23, Plates 20-22
 1942 *Stylohipparion* sp.; Dietrich: 97
 1963 Chalicotheriidae gen. and sp. indet.; Ewer: 343
 1965 *Hipparion* (*Stylohipparion*) *libycum*; Boné and Singer: 389
 1965 *Stylohipparion* sp.; Leakey: Plate 20
 1975 *Hipparion* cf. *ethiopicum*; Hooijer: Plates 3(8), 7, 11, 12, 13(2)
 1976 *Hipparion* cf. *ethiopicum*; Eisenmann (1976a): 585
 1978 *Hipparion libycum*; Churcher and Richardson: 399

Diagnosis. Species of *Hipparion* with well developed, mesiodistally flattened and crenulated I_1 and I_2 and with atrophied I_3 placed just behind I_2 . The arrangement of the incisors gives a rectangular aspect to the anterior part of the jaw in contrast to the usual rounded morphology.

Holotype. Mandibular symphysis with incisors from the Cornelia Beds, South Africa, described by Van Hoepen (1930, p. 23, Plate 20-22) and Cooke (1950, p. 423, Fig. 8).

In the opinion of Van Hoepen (1930), '*Eurygnatohippus*', the 'horse with the wide jaw', had no third incisors at all. Cooke (1950, p. 423) correctly interpreted the teeth mistaken for canines by Van Hoepen as reduced third incisors and suggested that the 'horse' in question was probably not an *Equus*. It seems that Dietrich (1942, p. 97)

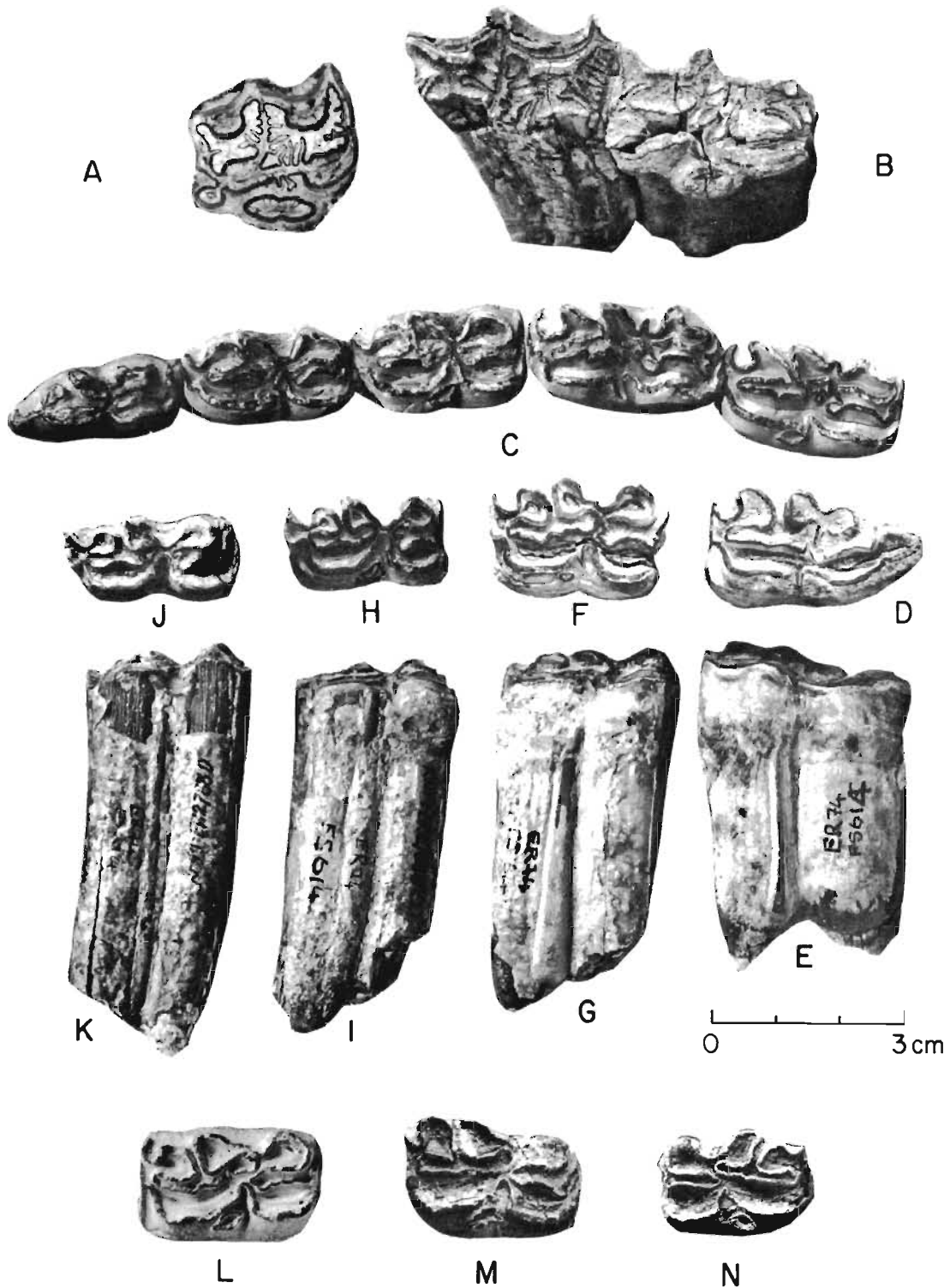


PLATE 5.2. *Hipparion lusitense*.

(A) sectioned M³ (KNM-ER 2922); (B) associated (?) P² and P³ (KNM-ER 2769); (C) P₃, P₄, M₁, M₂, M₃ (KNM-ER 4084); (D, E) P₂; (F, G) P₄ or P₁; (H, I) M₁; (J, K) M₂ (KNM-ER 2788).

Hipparion sp. A.

(L) P₃ (AL 124-51, Hadar Formation, Sidi Hakoma Member); (M) P₄ or P₁ (KNM-ER 2766); (N) P₃ or P₄ (KNM-ER 1234).

was the first author to suggest a synonymy between *Eurygnathohippus* and *Stylohipparion*, followed by Boné and Singer. This hypothesis was proved true when similar specimens were found at Olduvai (Leakey 1965, p. 26), and in particular a skull of *Stylohipparion* with the anterior dentition. The Olduvai specimens were all referred to *H. cf. ethiopicum* by Hooijer (1975, p. 26); however it seems that more than one form of *Hipparion* may be present at Olduvai (Eisenmann in press). As we still do not know what kind of cheek teeth, upper and lower, incisors and limb bones belong together, and as *H. ethiopicum* is known only from lower cheek teeth, it seems best to attribute to *H. cornelianum* such specimens whose incisors fit with the Cornelia type, and to *H. ethiopicum* the lower cheek teeth which fit with the Omo type.

Accordingly, the immature cranium from the *Notochoerus scottii* zone in Area 105, previously described under the name of *H. cf. ethiopicum* (Eisenmann 1976a) is here attributed to *Hipparion cornelianum*. If it should eventually be decided that this cranium and the lower cheek teeth assigned to *H. ethiopicum* are conspecific, the South African taxon will have priority.

The immature skull KNM-ER 3539, the sole specimen to surely belong to *H. cornelianum*, has already been described and its main measurements given (Eisenmann 1976a, Table 1). Its most interesting features pertain to the muzzle, the face and the vomerine region. Although the specimen is immature, the first and second incisors were patently strongly developed and crenulated; there is however no room in the premaxilla for the third incisor, or at most, room for a very atrophied one. The face lacks the preorbital fossa and is relatively short (whereas the face/cranium ratio calculated on a photograph is 250 for *H. cf. baardi*, it is only about 200 for the Koobi Fora specimen). The vomerine ridge is peculiar (Plate 5, 3B) and the vomerine index is very high (150).

Some of the characteristic features of KNM-ER 3539 are also displayed by *H. afarensis* (Eisenmann 1976a, Plates 2 and 6: very large first and second incisors, face devoid of preorbital fossa, acute vomerine ridge and high vomerine index) but *H. afarensis* has a well developed I^3 and the relative length of its face cannot be estimated. It seems highly probable that *H. afarensis* is ancestral to *H. cornelianum*.

H. turkanense shares with KNM-ER 3539 the lack of preorbital fossa (Hooijer and Maglio 1974, Plate

1) and a rather high vomerine index. The face is relatively short. But there seems to be no acute vomerine ridge and the (damaged) incisors seem to have only moderate dimensions. In my opinion it is premature to postulate whether *H. turkanense* was or was not ancestral to *H. afarensis*.

Two skulls were recovered from Olduvai Bed II and described by Hooijer (1975, pp. 28 and 32). Both lack the preorbital fossa but only one is sufficiently preserved to show the large size of I^1 and I^2 and some reduction of the I^3 (Hooijer 1975, Plates 7, 8 and Fig. 2 of Plate 11). The length of the face and the vomerine index cannot be estimated nor have we any data on the shape of the vomer. It is very probable that the skull belongs to the *H. afarensis*—*H. cornelianum* group. The moderate reduction of its third incisors would indicate a closer relationship with *H. afarensis* if it had not been observed that lower incisors are in general more reduced than uppers (Hooijer 1975, p. 35); this enables us to suppose that upper incisors not very different from those of *H. afarensis* may be associated with lower incisors of the *H. cornelianum* kind.

Indeed, lower incisors of the *cornelianum* type are present at Olduvai and include two symphyses identical to the South African one and numerous isolated incisors (Hooijer 1975, pp. 35–8), but some of them, including four specimens collected in Lower Bed II (Hooijer 1975, Plate 13, Fig. 1), are perhaps smaller and less flattened at the root. This slight difference may be related to sexual dimorphism, different stage of wear, different evolutive stage or to mere individual variation without any significance. Anyway, one must note that different kinds of incisors are found together in other East African Plio-Pleistocene sites than Olduvai. In most of these cases the presence or absence of normal or reduced incisors remains unknown.

Lower incisors from the Hadar Formation belonging to individuals of about the same (young adult) age may be very large (*H. afarensis*: AL 363-18 and AL 177-21) or much smaller (*H. hasumense*: AL 155-6) whereas the associated cheek teeth have similar dimensions. Curiously, some degree of reduction is apparent in the *H. hasumense* third incisors, but not in the *H. afarensis* ones.

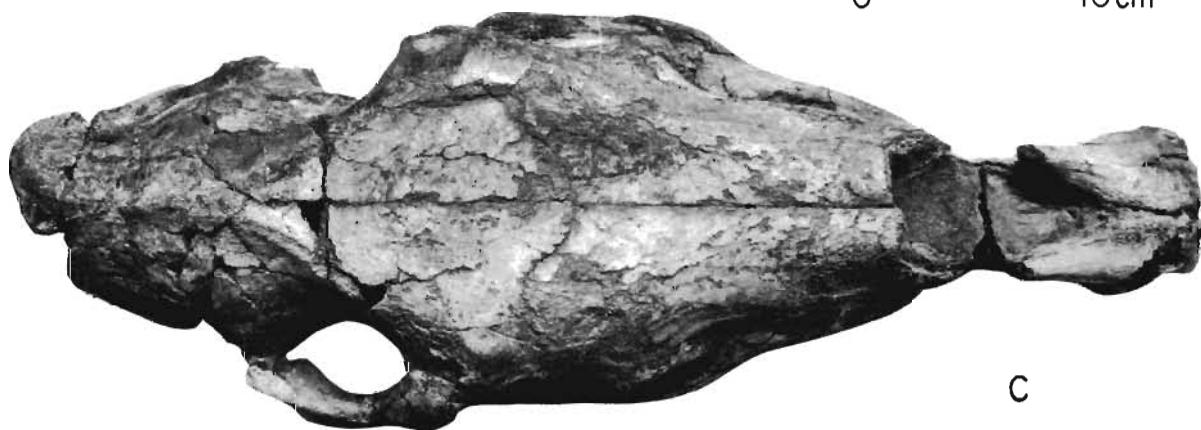
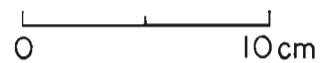
In the Shungura Formation, incisors of the *H. cornelianum* type (large, flattened and crenulated) have been retrieved from the Members D, E, F, G, and L (Hooijer 1975, Plate 3, Fig. 8; Eisenmann in press, Plate 1, Figs. 4–6), whereas smaller and less flattened ones were collected in Members C, F, and G (Hooijer 1975, p. 69: specimen L. 882-4;



A



B



C

PLATE 5.3. *Hipparion cornelianum* skull (KNM-ER 3539).
(A) lateral view; (B) ventral; (C) dorsal.

Eisenmann in press); such a small incisor was figured by Joleaud (1933, Plate I, Fig. 12) among the teeth that served to describe *H. ethiopicum*. We do not know if the lectotype chosen by Hooijer for this species was or was not associated with this incisor but if it was, the question of the synonymy between *H. cornelianum* and *H. ethiopicum* should be reconsidered. Apart from one symphysis from Member C where the third incisor is not reduced, there is no information about the morphology of the third incisors.

Amongst the Koobi Fora material there is one mandible, KNM-ER 1626, collected in the same deposits as the skull referred to *H. cornelianum* (Area 105, *Notochoerus scotti* zone). The symphysis is notably smaller than the typical *H. cornelianum* one (minimal width 45 mm compared with 55 mm in Olduvai 52 no. 067/5344). The front teeth are all missing except the left I_2 and the right canine. The I_2 is smaller than the average *H. cornelianum* ones (17 mm mesiodistal length compared with 20–23 mm). The size of the I_3 cannot be estimated. Mandibular fragments (KNM-ER 1456) from the *Metridiochoerus andrewsi* zone of Area 104 include one I_2 measuring only 16 mm mediolaterally. If these specimens belonged to *H. cornelianum* (as represented at Koobi Fora by the immature cranium) its intraspecific variation would be surprisingly great. At present I prefer to attribute these fragmentary mandibles to *H. cf. ethiopicum* because of general similarities of the lower cheek teeth.

Hipparion ethiopicum (Joleaud) 1933

- 1933 *Libyhipparion ethiopicum*; Joleaud: 7
 1947 *Stylohipparion albertense*; Arambourg: 303
 1965 *Hipparion* (*Stylohipparion*) *libycum* (partim); Boné and Singer: 389
 1970 *Stylohipparion libycum* (partim); Arambourg: 84
 1978 *Hipparion libycum* (partim); Churcher and Richardson: 399

Diagnosis. A species of *Hipparion* with rather large lower cheek teeth (Table 5.5); premolars and molars of nearly the same size. Double knot typically caballine with pointed metastylids. Ectostylids very large and pointed, sometimes accompanied by accessory pillars. Vestibular grooves may be very shallow on part-worn M_2 and M_3 . If the incisor figured by Joleaud (1933, Plate I, Fig. 12) belongs to the species, *H. ethiopicum* possessed incisors much smaller than those of *H. cornelianum*.

Lectotype. A right M_3 (1951-4-127 in the collections of the Muséum National d'Histoire Naturelle, Paris)

from an unknown horizon in the Omo deposits (probably Shungura Formation). This M_3 was figured by Joleaud (1933, Plate I, Figs. 2 and 6). In the same collections are a number of teeth that undoubtedly belong to the same individual: a right and left M_2 (1951-4-130 and 131; Joleaud 1933, Plate I, Figs. 3-4 and 10-11), a left M_1 (1951-4-129; *ibid.* Plate I, Fig. 8), a right P_3 or P_4 (1951-4-128; *ibid.* Plate I, Fig. 1; original lost but cast of the occlusal surface retained in the collections).

The species was described by Joleaud (1933) but the type material listed for the taxon was found to contain representatives of more than one species (Eisenmann in press); in particular there is no certainty about the lower incisor 1951-4-126 figured by Joleaud. In consequence *H. ethiopicum* must be considered as defined only by the lectotype chosen by Hooijer (1975, p. 66) and the associated lower cheek teeth mentioned above.

H. ethiopicum cannot be compared with *H. afarensis* because no lower cheek teeth can be safely ascribed to the latter. From the South African *H. namaquense* it differs by much larger ectostylids. The biometrical comparison with *H. hasumense* from the Kubi Algi Formation shows that: the premolars of *H. ethiopicum* have a similar occlusal width but a shorter occlusal length; the molars of *H. ethiopicum* have a similar occlusal length but a larger occlusal width; the ectostylid length/occlusal length ratio is much greater in *H. ethiopicum* than in *H. hasumense*.

H. ethiopicum is thus characterized by large molars, relatively small premolars, large anteroposterior development of the ectostylid (high ectostylid index), a great vestibulo-lingual development of the ectostylid (great occlusal width). In addition, the ectostylids are complicated, with accessory pillars and some molars have shallow vestibular grooves; this last feature may be considered as an evolved one (Eisenmann 1977, p. 74). The lower row figured by Hooijer (1975, Plate 14, Fig. 2) from Bed II of Olduvai shows most of the characters mentioned. Some of these characters are present in hipparions from the *Notochoerus scotti* and *Metridiochoerus andrewsi* zones from east of Lake Turkana; accordingly the Koobi Fora material will be provisionally assigned to *Hipparion cf. ethiopicum*; no difference was found between the material collected in the two zones.

Hipparion cf. ethiopicum

- 1972 *Hipparion cf. albertense*; Maglio: Table 1
 1976 *Hipparion cf. ethiopicum* partim; Eisenmann (1976c): 234
 1978 *Hipparion cf. ethiopicum* partim; Harris: 44

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. cf. 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,

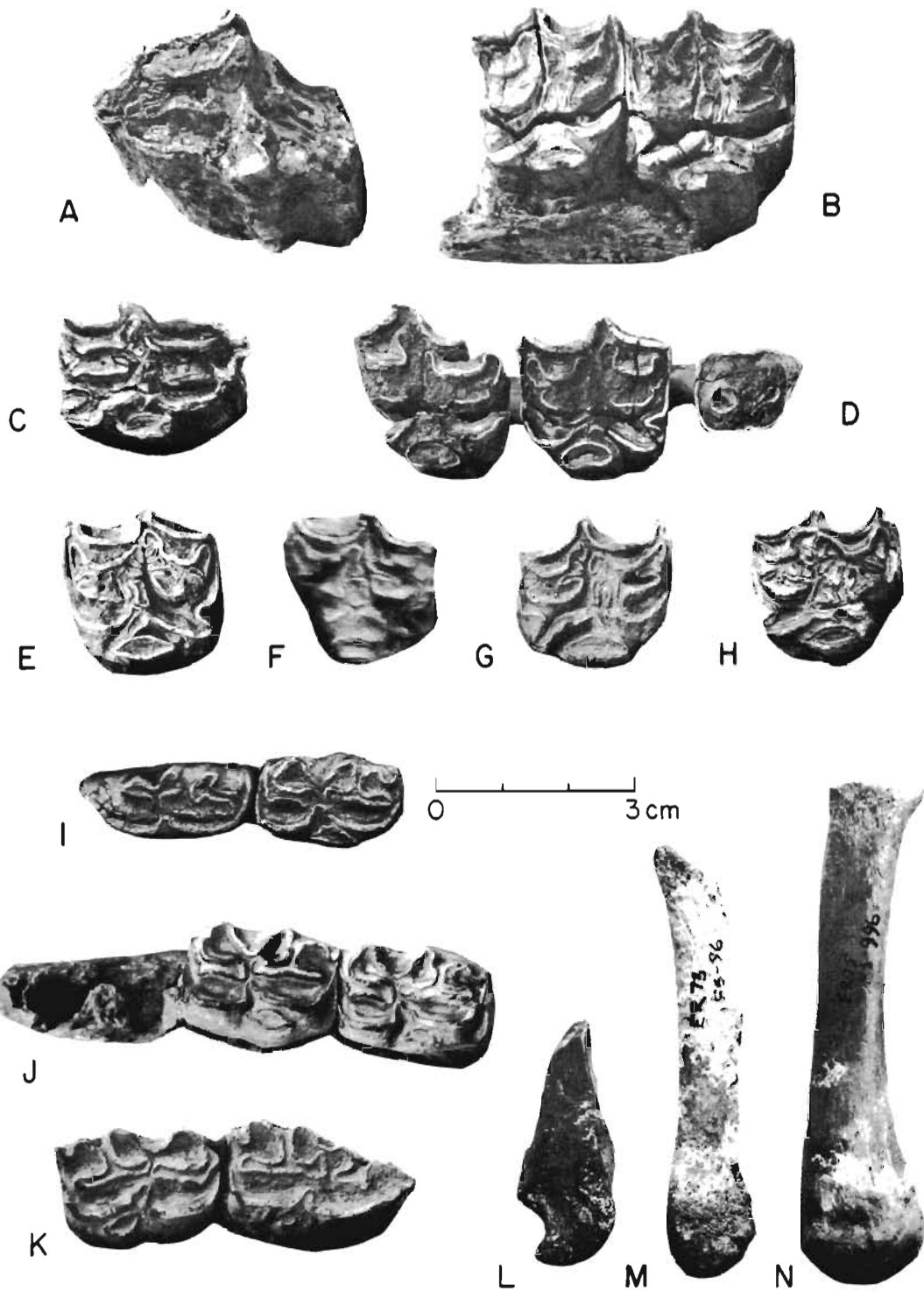


PLATE 54. *Hipparion hasumense*.

(A) P² (KNM-ER 1771).

Hipparion cf. *ethiopicum*.

(B) P³ M¹ (KNM-ER 1230); (C) P² (KNM-ER 2668); (D) associated upper P, M, I (KNM-ER 4091); (E) M¹ or M² (KNM-ER 2072); (F) M¹ or M² (KNM-ER 2070); (H) M¹ or M² (KNM-ER 1278); (J), P₁ P₄ (KNM-ER 1456); (K) P₂ P₄ (KNM-ER 4082).

(L, M, N) distal ends of lateral metapodials: L: KNM-ER 2242, M: KNM-ER 2053, N: KNM-ER 4081.

Hipparion sp. B.

(G) M¹ or M² (KNM-ER 2073); (I) P₂ P₃ (KNM-ER 4054).

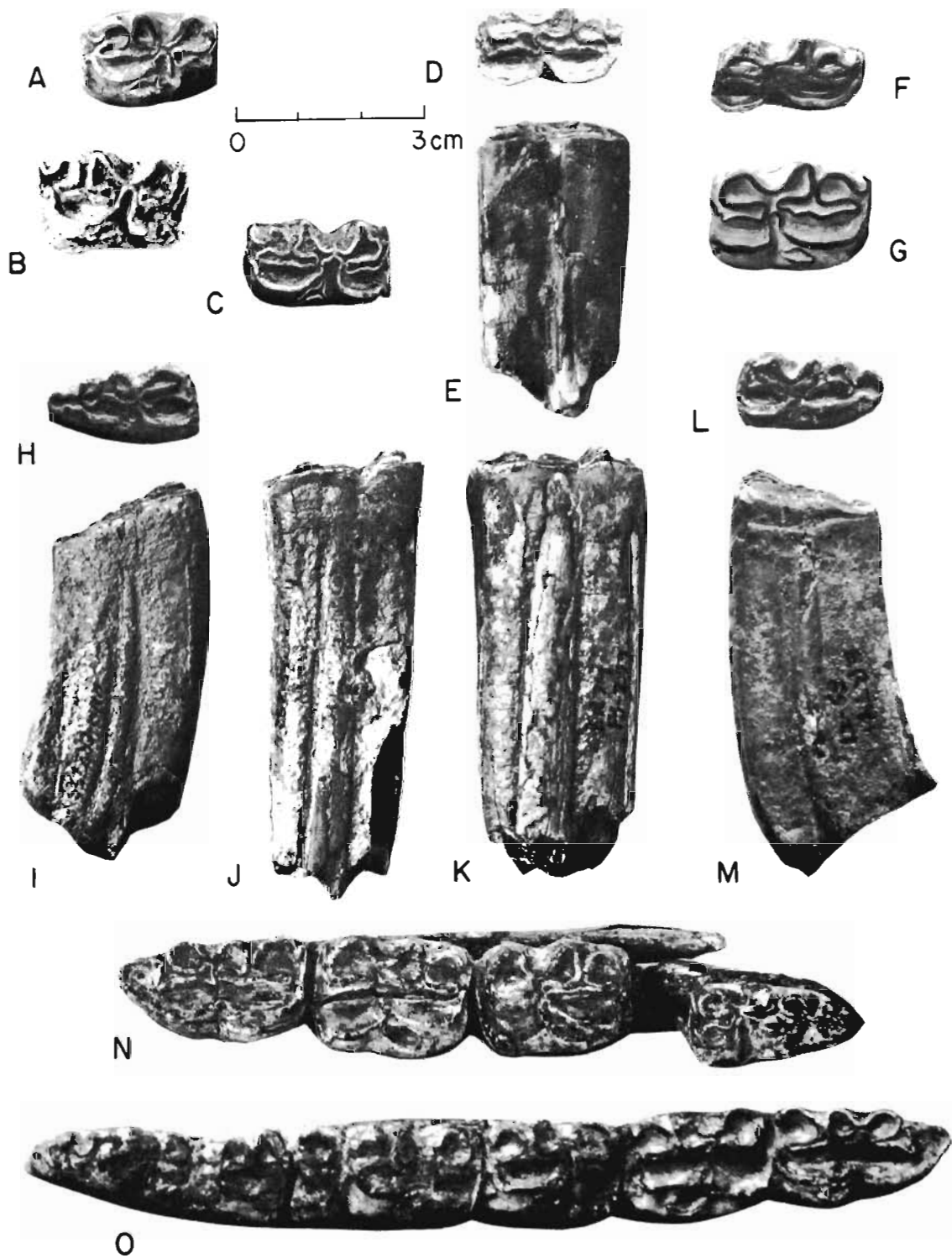


PLATE 5-5. *Hipparion cf. ethiopicum*.

(A) M_1 or M_2 (KNM-ER 5354); (B) M_1 or M_2 (KNM-ER 1770); (C) M_1 or M_2 (KNM-ER 4053); (F) M_1 or M_2 (KNM-ER 2069); (H, I) M_3 ; (J) M_1 or M_2 ; (K) P_3 or P_4 (associated, KNM-ER 2751); (L, M) M_3 (KNM-ER 2656); (N, O) lower cheek teeth KNM-ER 1626).

Hipparion sp. B.

(D, E) P_3 or P_4 (KNM-ER 4096).

EISENMANN V. (1983) .- Family Equidae. In : Harris J.M. (edit), Koobi Fora Research Project, volume 2, The Fossil Ungulates : Proboscidea, Perissodactyla and Suidae,pp. 156-214,10 fig.,10 pl.,22 tabl. Clarendon Press,Oxford.

FAMILY EQUIDAE

V. EISENMANN

African equids are represented by two genera, *Hipparion* and *Equus*. Both are immigrants whose ancestors evolved in North America.

In Eurasia the biostratigraphical significance of the later equids was recognized long ago: *Hipparion* was considered a strictly Tertiary genus whereas the initial appearance of *Equus* was one of the events used to define the beginning of the Quaternary period. Although the onset of the Quaternary is no longer defined in this way, *Equus* remains an important marker in Europe. Its first appearance is at a number of sites which correspond in age to the NM 17 zone defined by Mein (1975, p. 78); furthermore the Villafranchian stenorine *Equus* material is relatively easy to distinguish from the later caballine species. It is rare for *Equus* and *Hipparion* to coexist in Eurasia (Eisenmann and Brunet 1973).

In Africa, hipparions persist at Pleistocene sites and frequently coexist with representatives of *Equus* in sediments that range in age from 2 Ma (first appearance of *Equus* in Africa) to 0.4 Ma (last appearance of *Hipparion* (Eisenmann 1979c)). In Africa it is less easy to differentiate between early Pleistocene and middle to late Pleistocene species of *Equus* than in Europe, partly because of their overall resemblances to the modern zebras and partly because the African fossil material has been less intensively studied.

During the last twenty years the search for fossil hominids in Africa has resulted in the retrieval of large numbers of other fossil mammals including equids. This has helped greatly to improve our knowledge of African *Hipparion* and *Equus*. However, many equid names appearing in faunal lists should be considered *nomina vana* (e.g. *Hipparion albertense*) while others are used despite the fact that detailed descriptions and comparisons with other species have never been published (e.g. *Equus mauritanicus* and *E. oldowayensis*).

Many outstanding studies have been undertaken on equids, and in particular *Hipparion* (Gabunia 1959; Forstén 1968; Sondaar 1968; Alberdi 1974; Zhigallo 1978). However, the standard references for anatomical investigation of *Hipparion* and *Equus* are still those of Gromova (1949a,b, 1952) whose comparison of the skulls, dentitions, and limb bones of these two genera extends to 140 pages and is illustrated by 50 figures (Gromova 1952). For the systems of measurements used here see Table 5.10 (for the cranium) and abbreviations to tables (p. 195 for the teeth. The system of measurements for the metapodials was described in Eisenmann (1979e), for skulls and teeth in Eisenmann (1979a, 1980b).

Figures 5.1 and 5.2 provide a schematic representation of, respectively, an upper left premolar of *Equus* and a lower right premolar of *Hipparion* showing the most important anatomical features. The most important differences between the teeth of the two genera are as follows. The protocone is nearly always isolated in *Hipparion* upper cheek teeth but never so in *Equus*. Ectostylists are frequent in *Hipparion* lower cheek teeth but very rare in those of *Equus*. In *Equus* lower cheek teeth the mesial arm of the preflexid (not the distal arm as

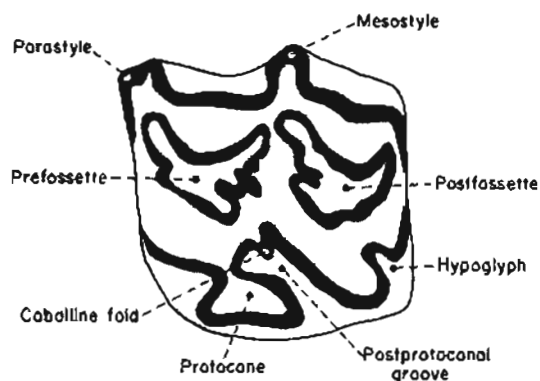


FIG. 5.1. Schematic occlusal view of a left P³ or P⁴ of *Equus*.

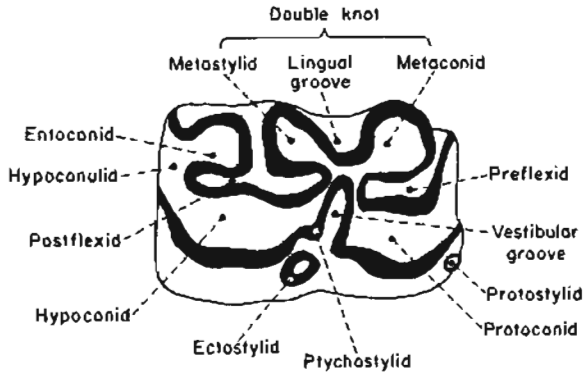


FIG. 5.2. Schematic occlusal view of a right P₄ or P₃ of *Hipparion*.

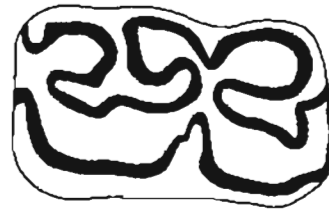
stated by Churcher and Richardson 1978, p. 402) is usually long and oblique (Fig. 5.3B, arrow), whereas in *Hipparion* both arms are short and directed perpendicularly to the mesiodistal axis (Fig. 5.3D). This feature, described by Gromova, is particularly useful for the identification of *Hipparion* teeth when no ectostylids are present.

Figure 5.3 illustrates the principal shapes of the double knots. In the stenonine type (Fig. 5.3A) the vestibular groove is pointed and narrow; it may be of variable depth. In the caballine type (Fig. 5.3B) the vestibular groove is large and angulated; a similar pattern may be found in some hipparions (Fig. 5.2) which are accordingly said to have caballine or caballoid lower cheek teeth. In the hemionine type (Fig. 5.3C) the vestibular groove is wide, rounded, and shallow, sometimes not very different from the hipparionine type (Fig. 5.3D).

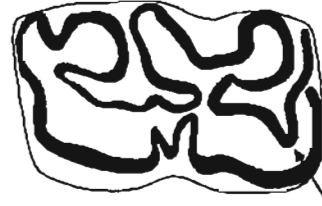
***Hipparion* De Christol 1832**

Diagnosis. Tridactyl extinct equids characterized by isolated protocones on the upper cheek teeth. Many characteristic features of the limb bones are related to the tridactyl mode of locomotion (after Gromova 1952; Sondaar 1968).

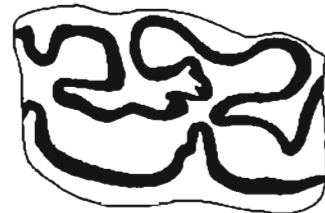
Hipparions are not known in Africa until the Middle to Late Miocene. Thereafter, unlike most of the Eurasian hipparions, they persist until the Late Pleistocene, coexisting with species of the genus *Equus* from the Early Pleistocene onwards. Perhaps because of this protracted existence, they have acquired or developed to the extreme some peculiarities: strong ectostylids, caballine double knots and shallow molar vestibular grooves on the lower cheek teeth; reduction of the third incisors; peculiar vomerine morphology and lack of the



A



B



C



D

FIG. 5.3. Schematic occlusal views of right P₄ or P₃; the pattern of the double knot is: A. zebrine/stenonine; B. caballine; C. hemionine; D. hipparionine.

preorbital fossa in the cranium. Some of these features have motivated the creation of new genera or subgenera: *Eurygnathohippus* (lack of I₃), *Stylohipparion* (well developed ectostylids), *Hypsohipparion* (hypodont cheek teeth without ectostylids). I believe, however, that our present knowledge of the group is not sufficient to warrant such generic distinctions.

Comprehensive revision of hipparionid taxonomy would ideally require access to samples of good material, i.e. specifically and chronologically homogeneous and representative of the entire

anatomy of the species. At the present only one such sample is known, that of Bou Hanifia (or Oued el Hammam) in the Vallesian of Algeria, which provides a good idea of the nature of *H. africanum*. Most of the other species are based on unassociated material retrieved from sites where two or more species of *Hipparion* may have coexisted. These circumstances lead to endless problems of attribution.

Anatomical features

It seems apparent that *Hipparion* species, like those of *Equus* (Eisenmann 1979a), share many morphological features and intergrade in size. Problems are therefore encountered in positive identification of incomplete material, particularly isolated and upper cheek teeth. As Hooijer and others have stressed on several occasions (Hooijer and Maglio 1974; Hooijer 1975), there are striking similarities between the general pattern of hipparionid upper cheek teeth from sites of 9–12 Ma old (Bou Hanifia, Ngorora) and those from sites of only 3–4 Ma old (Aterir, Kanapoi, Chemeron, Ekora, Usno Formation). Moreover Cooke and Coryndon (1970, Fig. 10) have shown that there is no difference in the length and shape indices of the protocone between Vallesian (Bou Hanifia) and Pliocene hipparions (Langebaanweg and Laetoli). In the first case, however, the upper cheek teeth are associated with primitive 'hipparionine' lowers, unreduced third incisors, and preorbital fossae in the crania, whereas in the Pliocene representatives the same kind of upper cheek teeth are in general associated with 'caballine' lowers with ectostylids, crania lacking preorbital fossa but with a peculiar vomerine morphology and third incisors tending to be reduced or lost (Eisenmann 1976a, 1977, 1979c, 1980a, in press). Let us consider the diagnostic value of these features before discussing any systematic framework.

Cranial features. There is some evidence for interpreting the lack of preorbital fossa as an 'advanced' character. Certainly the four youngest *Hipparion* crania from Africa (Hadar Formation, Koobi Fora Formation, Olduvai Bed II) have none. It must be acknowledged, however, that some of the crania lacking preorbital fossae are more or less contemporaneous with others that possess this feature—crania from Lothagam versus Ekora for example, and perhaps also at Hadar (where some specimens are crushed). Is the presence/absence of preorbital fossae in crania from a single locality an

indication of the presence of two distinct species or lineages of hipparion or merely of intraspecific variation? Another feature of potential importance is the shape of the vomerine part of the cranium. Of the four geologically young crania mentioned above, the two best preserved specimens (Hadar and Koobi Fora Formations) exhibit a peculiar bifurcated vomerine ridge and a very high 'hypercaballine' vomerine index (Eisenmann 1976a, p. 387). Unfortunately crania sufficiently well preserved to show such characters are rare; important as such features may be in theory, they have little practical value.

Upper dentition. The apparent stability of the crown morphology in the upper cheek teeth allows several interpretations. One would be that upper cheek teeth do not change during the evolution of a hipparion lineage; they bear evidence for example, to the direct derivation of the Usno hipparion from the form present at Ngorora. In this case the application of the same specific name to samples from both localities may be justified though perhaps confusing (Eisenmann 1977, 1980a).

A second interpretation would be that the pattern of a tooth varies more or less at random and its differences from or similarities to examples from other localities have no temporal or phylogenetic significance. In effect this would mean that upper cheek teeth were totally useless for specific diagnosis.

A third, more hopeful interpretation would be that some morphological characters of the upper cheek teeth are taxonomically diagnostic but we have not yet found which ones. For example, it is possible that hipparion species might display differences in the respective proportions of individual premolars and molars of the upper tooth row. I have already shown that this is the case with some *Equus* species (Eisenmann 1979a, 1980b)—the interspecific differences are more conspicuous if the pattern of the entire row is taken into account (for example, are protoconal indices of P⁴ greater or smaller than protoconal indices of M¹?). I have begun to look for similar differences in hipparion species but my data are still scanty and lack conviction. Nevertheless, I believe that early hipparions (Bou Hanifia and Nombrevilla) are characterized by only a slight difference in occlusal length between P³ and P⁴ but a greater one between P⁴ and M¹. In contrast, in somewhat younger material from Hadar (c. 3 Ma) P³ is rather longer than P⁴ while P⁴ and M¹ are of similar size. It is also possible that species might be separable on the relative mean size of P³ + P⁴ versus M¹ + M².

Naturally these are presently only working hypotheses which need access to larger samples for verification. With regard to the protoconal indices, the only good monospecific sample I have yet studied is from Bou Hanifia; in this sample the means (calculated on ten more or less complete cheek teeth series) increase from the P² (c. 25) to the M¹ (c. 38) and then decrease via the M² (c. 36) to the M³ (c. 31). Again, access to other hipparion populations is necessary before we can test the taxonomic value of these observations.

Given our present state of knowledge, I do not believe that African hipparions may be diagnosed or differentiated on the basis of their upper cheek teeth. This opinion gains support from the fact that the original diagnostic characters separating the upper cheek teeth of *Hipparion turkanense* from Lothagam from those of *H. primigenium* from Kanapoi and Ekora (Hooijer and Maglio 1974, p. 13) have now been abandoned (Hooijer 1976, pp. 12, 15) although the crania of the two species differ by at least one conspicuous feature—the presence (*H. primigenium*) or absence (*H. turkanense*) of a preorbital fossa.

Incisors. The mandibular symphysis of the type specimen of *Hipparion cornelianum* (originally described as *Eurygnathohippus cornelianus* (Van Hoepen 1930)) is very distinctive—the third incisors are atrophied in contrast to I_{1,2} which are very well developed and crenulated. However, it is difficult to be certain whether or not the reduction of I₃ is a secondary sexual character. Hooijer noted (1975, pp. 30, 36) that there are no canines present in the three known symphyses of *H. cornelianum* (the type from Cornelia and two from Olduvai). A much earlier specimen from the Hadar Formation (AL 177-21) has first and second incisors that are very similar in size and crenulation to *H. cornelianum* but possesses both third incisors and canines (Eisenmann 1976a, Plate 7D). Is this specimen a male (the only known male) of *H. cornelianum* or is it representative of the ancestral stock from which *H. cornelianum* evolved by reducing the I₃ and losing the canine?

Lower cheek teeth. The significance and interpretation of the crown morphology, and that of the ectostylids, of hipparion lower cheek teeth have been discussed elsewhere (Eisenmann 1977). Let us merely say here that for the moment, if one has to deal with only isolated teeth, lower cheek teeth are slightly preferable for identifying and dating African hipparion species. However, even lower cheek teeth are poorly known.

Systematic framework

This would not be the place in which to attempt a comprehensive revision of the African hipparions, even if the all necessary information was available. However, a brief review of the principal taxa that have been recognized on the African continent might be helpful before considering in detail the fossil material from east of Lake Turkana.

Apart from *H. albertense* which must be considered as a *nomen vanum* (Hooijer 1975, pp. 6, 27) and whose lower cheek teeth are not known at all, the African hipparions may be considered in terms of two groups—those in general lacking ectostylids and those in general possessing this feature.

1. *Hipparions in general lacking ectostylids:* *Hipparion africanum* is a middle-sized Vallesian species described (Arambourg 1959) from the relatively rich material of Bou Hanifia, Algeria. The crania possess preorbital fossae; the third incisors are normally developed; the cheek teeth are rather hypsodont, the uppers being moderately plicated and the lowers hipparionine without ectostylids; the limb bones are rather slender (Eisenmann 1980a).

Hipparion primigenium Meyer 1833 is an European Vallesian brachydont species with highly plicated upper cheek teeth, hipparionine lowers with occasional ectostylids and rather robust limb bones. Forstén (1968, p. 14) revised the species and extended it geographically and chronologically to African, Asiatic, and Pikermian hipparions, some of which, like *H. africanum*, are notably different as Forstén herself admits (1968, p. 26, 1978b, p. 307). Hooijer (1975, p. 8) went even further than Forstén by using the name *H. primigenium* for African Pliocene fossils. However, Forstén (1978b) does not appear to confirm these last attributions as she refers only to Miocene *H. primigenium* from Bou Hanifia (Forstén 1972), and Ngorora (Hooijer 1975). In agreement with Sondaar (1971, pp. 438–9, 1974, p. 304), and Alberdi (personal communication) I am afraid that such a broad concept of species may lead to oversimplifications and awkward contradictions.

Unlike the European *H. primigenium*, *H. africanum* has slender limb bones, relatively hypsodont teeth, lowers lacking ectostylids, and only moderately plicated uppers. Some other Miocene African hipparions (Eisenmann 1980a) are larger in size than *H. africanum*, have more robust limb bones and have ectostylids on the lower cheek teeth. Whereas these may be referred to an African form of *H. primigenium*, I see no valid reason to similarly refer the well documented and different *H. africanum*. Too

generalized a concept of species leads to contradictions like the one appearing in the 1978 paper of Churcher and Richardson: in the first column of page 391, *H. primigenium* is said to have ectostylids on the permanent lower cheek teeth, while in the second column of page 393 it is the lack of ectostylids that is mentioned to support the similarities between *H. primigenium* and *H. baardi*. Moreover, if the synonymy between *H. africanum* and *H. primigenium* may be defensible, the use of the name of *primigenium* for Pliocene hipparions with caballine lower cheek teeth is totally confusing; in my opinion the morphology of the double knot is a very important character (Eisenmann 1977) not sufficiently taken into account by Hooijer and Churcher and Richardson.

Hipparion sitifense was described by Pomel (1897, p. 14, Plates I-II) on two upper cheek teeth collected at Saint Arnaud, Algeria; this material is now probably lost. Later on, more material was collected at the type locality (Arambourg 1956, p. 822) and recently described (Eisenmann 1980a; Forstén 1978a, p. 295) but the species remains poorly known: no skull, no incisors, few teeth and limb bones. From the data now available, *H. sitifense* is probably a Miocene species with hipparionine lower cheek teeth lacking ectostylids and moderately plicated uppers; it is slightly smaller than *H. africanum* and may be its descendant (Eisenmann 1980a). The East African Mio-Pliocene and Pliocene fossils referred by Hooijer and Maglio (1974, p. 20) to *H. cf. sitifense* and by Hooijer (1975, p. 22) to *H. ? aff. sitifense* are rather larger in size and at least some have caballine double knots and ectostylids. The relationship between the three forms is not yet clear, nor is the relationship with the small Spanish Turolian hipparions referred by Forstén (1968, p. 33, 1978a, p. 295) to *H. sitifense* (Alberdi 1974, p. 122).

Hipparion turkanense was described from localities of about 6 Ma in age and is characterized by a cranium lacking a preorbital fossa, unreduced third incisors (Hooijer and Maglio 1973, 1974), a relatively high vomerine index (VI = 100 calculated on Plate 1 of Hooijer and Maglio 1974), and a relatively short face (ratio of the projections of the distances between the posterior border of the orbit and the occipital crest and between the posterior border of the orbit and the most anterior point of the muzzle calculated on the same plate = approximately 180). Most hipparions have smaller vomerine indices (Eisenmann 1976a, p. 587) and at least one African hipparion has a much longer

face. Unfortunately the upper cheek teeth are worn and there are no associated lower teeth. Three lower teeth from Lothagam attributed to this species (Hooijer and Maglio 1974, p. 17) have no ectostylids but a fourth one has (Hooijer and Maglio 1974, p. 18). The double knot (or tie) is rather caballine.

The hipparion from the Langebaanweg E Quarry was described by Hooijer (1976) under the name of *Hipparion cf. baardi*. The cranium has a preorbital fossa, a 'normal' vomerine index (VI = 86) and a relatively long face (the index mentioned above is approximately 250 instead of 180 in *H. turkanense*). The size is comparable to that of *H. africanum*. The third incisors are not reduced but the arcade is less rounded than in *H. africanum* and the symphysis is broader, though not as much as in some advanced hipparions (Eisenmann 1976a, Fig. 1). The lower cheek teeth have a morphology intermediate between hipparionine and caballine and lack ectostylids. The same species may be present at Ekora (c. 4 Ma) and was assigned by Hooijer and Maglio (1974, p. 13) to *H. primigenium*. The fragmentary and immature cranium has a preorbital fossa; unfortunately the vomerine index and the length of the face cannot be evaluated. The size of the upper cheek teeth seems comparable at Langebaanweg E and Ekora. The lower cheek tooth found at Ekora lacks an ectostylid (Hooijer and Maglio 1974, Plate 7, Fig. 5) and its morphology is intermediate between hipparionine and caballine. *H. cf. baardi* may be derived from *H. africanum*; in agreement with Hendey (1978, p. 11), I believe that the E Quarry species is quite different from *H. baardi*.

Hipparion baardi is an appreciably younger species from Baard's Quarry at Langebaanweg, probably about 2 Ma old (Hendey 1978, Table 5). It has typically caballine lower cheek teeth but without ectostylids (Boné and Singer 1965) and is larger in size. No skull is known.

Hipparion serengetense was described by Dietrich (1942, p. 97) as a subspecies of *H. albertense*, now interpreted as a *nomen vanum*. Though several authors expressed doubts about lower cheek teeth without ectostylids really belonging to an *Hipparion* and not to an *Equus* (Arambourg 1947, p. 306, 1970, p. 94; Hooijer 1975, p. 7), it seems now generally agreed that they do belong to an *Hipparion*. Hooijer (1979) described the teeth collected recently at Laetoli and came to the conclusion that there were in the area two different hipparions: one possessing ectostylids and collected in upper levels, younger than 2.4 Ma, and one lacking ectostylids in levels

about 4 Ma old. Unfortunately the lack of crania leaves it uncertain whether *H. serengelense* (= *Hipparion* sp. Hooijer 1979) is more closely related to *H. turkanense* or to *H. cf. baardi*. The same form with nearly caballine lower cheek teeth seems present at Mpesida and Lukeino (Hooijer 1975, Plate 4 Figs. 4-6; Aguirre and Alberdi 1974, p. 151).

2. *Hipparions* in general possessing ectostylids: *Hipparion namaquense* was described in South Africa by Houghton (1932). The exact locality and horizon are unknown but the teeth are from a single individual. They are very worn and bear very small ectostylids on P_4 , M_1 , and M_2 . The double knot is caballine. The vestibular groove is shallow on the M_3 . Cooke (1950, p. 425) gave the measurements of the row.

Hipparion afarensis from Ethiopia was described in Eisenmann 1976a; it has a cranium characterized by the lack of preorbital fossa, a peculiar vomerine ridge and a very high vomerine index ($VI = 140$); the relative length of the face cannot be estimated. The incisors are large and the third incisors are unreduced. The occlusal length of P^3 is much longer than that of P^4 , that of P^4 is similar to that of M^1 . There are no lower cheek teeth associated with the type cranium; the lower cheek teeth from the Hadar Formation (about 3 Ma old) normally have ectostylids though these are not always well developed (Eisenmann 1977).

Hipparion sp. is another species present in the Hadar Formation. The presence/absence of the preorbital fossa cannot be discussed because the referred crania are either incomplete or crushed; the vomerine index cannot be calculated but the basion-vomer distance is smaller; nor can the relative length of the face be calculated exactly but the face seems long. The muzzle is narrower, with a long and deep gutter on its dorsal face (Eisenmann 1976a, Plate 6, Fig. A). The incisors are notably smaller. The lower cheek teeth are caballine with weakly developed ectostylids.

Hipparion cornelianum (= *Eurygnathohippus cornelianus* Van Hoepen 1930) is based on a mandibular symphysis with I_{1-3} of which I_3 is greatly atrophied. Two similar but more complete specimens were found at Olduvai Bed II and assigned to an hipparion with ectostylids (Leakey 1965, p. 26, Plate 20; Hooijer 1975, p. 26). However, there does not seem to exist a direct association between incisors and lower cheek teeth, which is very troublesome because there is probably more than one species of *Hipparion* at Olduvai (Eisenmann in press).

Hipparion libycum was described by Pomel (1897, p. 8) on the basis of a large lower caballine premolar with a well developed ectostylid collected in the Villafranchian levels of the Carrière Brunie, Oran (Arambourg 1970, p. 92, Fig. 55). The type premolar and the associated fragmentary lower molar are probably lost.

Hipparion ethiopicum (Joleaud 1933) was originally founded on a dozen isolated teeth belonging to different species (and probably different levels) from the Omo deposits (Eisenmann in press). Hooijer (1975, p. 66) selected an M_3 as a lectotype; fortunately the M_3 is associated with three lower molars and possibly one lower premolar of the same individual. These rather large cheek teeth show caballine characters and very well developed ectostylids. The original provenance of the lectotype is unknown.

Hipparion steylleri from the Cornelia deposits (Van Hoepen 1930) is founded upon an upper molar. Lower cheek teeth from this locality resemble those of *H. ethiopicum* but the ectostylids seem more rounded and less developed.

It is conceivable that *H. cornelianum*, *H. libycum*, *H. ethiopicum*, and *H. steylleri* are synonyms but we do not have enough data on the lower cheek teeth to put the last three in synonymy and no certain association between the lower cheek teeth and incisors to put *H. cornelianum* in synonymy with any of the other three species.

KOObI FORA MATERIAL

Hipparion material is apparently not abundant in the Kubi Algi Formation and to date only some 20 specimens have been recovered. A further 60 specimens have been retrieved from the Koobi Fora Formation. Neither sample provides an adequate representation of the several species of *Hipparion* that were present east of Lake Turkana during the Pliocene and Pleistocene—one or two species in the earlier levels and two or three in the upper ones. The samples are, however, sufficient to indicate that there were distinct differences in the assemblages from the two formations and thus render the hipparions useful biostratigraphic zone fossils. As might be expected from the foregoing remarks, some of the material is insufficiently complete to be identified at a species or even a generic level (p. 212). It is also unfortunate that a quarter of the specimens were recovered prior to 1971 and have no certain provenance data.