

Pliocene vertebrate locality of Çalta, Ankara, Turkey. 7. *Hipparion*

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ABSTRACT

The genus *Hipparion* is represented in the Pliocene of the Western Region, Turkey, at Çalta, by fragmentary skulls, mandibles, teeth and limb bones. Two large species are present; most of the fossils belong to a robust form, which we consider as a new species: *Hipparion heintzi*. A few bones belong to a slender hipparion, *Hipparion* cf. *longipes* Gromova, 1952. Equations to predict body weight using metapodial and tooth variables are proposed. Estimations of body weights based on sections of metapodials (distal breadths multiplied by distal depths) seem less approximative than those based on occlusal tooth surfaces (lengths multiplied by breadths).

KEY WORDS

Pliocene,
Turkey,
Mammalia,
Perissodactyla,
Hipparion heintzi n.sp.,
Hipparion cf. *longipes*,
body weight estimations.

RÉSUMÉ

Le gisement de vertébrés pliocènes de Çalta, Ankara, Turquie. 7. Hipparion. Deux espèces de grande taille sont présentes à Çalta. La plupart du matériel (restes crâniens, dentaires et squelettiques) est rapporté à une nouvelle espèce très robuste, *H. heintzi*, dont on discute les différences avec *H. crassum*. Quelques restes squelettiques appartiennent à *H. cf. longipes* Gromova, 1952, une espèce extrêmement gracile. Leur coexistence et la prédominance de restes robustes sont surprenantes dans un milieu considéré comme steppique. On propose de nouvelles équations d'estimation du poids du corps des équidés à partir de dimensions de métapodes et de la M1 supérieure. Les équations fondées sur le produit d'une largeur distale par un diamètre antéro-postérieur distal semblent moins sujettes à caution que les estimations fondées sur la surface occlusale d'une dent, surtout pour les hipparions graciles.

MOTS CLÉS

Pliocène,
Turquie,
Mammalia,
Perissodactyla,
Hipparion heintzi n.sp.,
Hipparion cf. *longipes*,
estimations du poids corporel.

INTRODUCTION

Within the updated European Land Mammal Zones (MN) of Mein (1990), Çalta is supposed to belong in the MN15 zone. The fauna is rich in fossils, poor in species, and points to a steppic environment (Sen 1977). Preliminary studies of the Çalta hipparions have noted the similarities (but not the identity) of the robust form with *H. crassum* (Ginsburg *et al.* 1974; Sen *et al.* 1974) and referred the rests of the slender form to *H. longipes* (Heintz *et al.* 1975). Both *H. crassum* and *H. longipes* are poorly known species. *H. longipes* was described by Gromova (1952) from Pavlodar, Kazakhstan, and is said to belong in the MN13 zone, in a dry environment (Vangenheim *et al.* 1993). *H. crassum* was described from Perpignan but was also believed to be present at Montpellier (Gervais 1859, 1869; Depéret 1885, 1890). Accordingly it belongs in the MN15 zone, and possibly also in the MN14 (Alberdi & Aymar 1995). The context is humid (Aguilar *et al.* 1998 ; Aymar 1992).

Collections of Çalta are currently housed in the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, France (MNHN), and in MTA (Genel Müdürlüğü Tabiat Tarihi Müzesi), Ankara, Turkey (Forsten 1997).

The material was measured according to the recommendations of the "New York International Hipparion Conference" (Eisenmann *et al.* 1988) with one exception: on the third metapodials, the minimal distal depth (MC13 or MT13) is measured on the medial condyle, not on the lateral. The reason is that most of our metapodials were already measured in this way (Eisenmann 1979) before the New York Conference. Since the minimal depth of the lateral condyle is somewhat smaller than the medial, but not always in the same way, we must stick to the original system if we want to use our data for comparisons. Metrical data are in tables 1 to 14. Scatter diagrams and ratio diagrams (Simpson 1941) are used for comparisons.

Order PERISSODACTYLA Owen, 1848
 Family EQUIDAE Gray, 1821
 Genus *Hipparion* de Christol, 1832

Hipparion cf. *longipes* Gromova, 1952

DESCRIPTION

We refer to *H. cf. longipes* one entire MtIII, a proximal fragment of a juvenile MtIII; a proximal fragment of a McIII; one entire and one fragmentary first phalanges; one entire second phalanx; one entire third phalanx – all from the main digit, and probably all posterior; three tali (Figs 1-3, 15A, B, 16A; Tables 1-3). The entire MtIII is so long and so slender that it obviously cannot belong to the robust hipparion of Çalta. The same is true for the entire first phalanx of the central digit. For other bones the differences between the two hipparions of Çalta are not as big as could be supposed. Indeed, the specific assignment of some second phalanges is doubtful: are ACA-83 and ACA-113 posterior phalanges of *H. heintzi*, or anterior phalanges of *H. cf. longipes* (Table 14, Fig. 13F)?

The entire MtIII was described in detail by Heintz *et al.* (1975). As can be seen from figure 1, the lateral metapodials were situated well at the back of the diaphysis. The diaphysis and the epiphyses are deep: the antero-posterior diameters are large in comparison with the breadths (Fig. 2). Similar proportions (big depth relatively to breadth) characterize all the other limb bones and enable to assign to *H. cf. longipes* three tali and the fragmentary metapodials and first phalanx.

Although the material is poor, it gives information about the limb proportions (Fig. 4): compared to the metatarsal length, the length of the first phalanx is short.

COMPARISONS

Metatarsals of about the same size and proportions (Eisenmann & Sondaar 1989) were found at Pavlodar (*H. longipes*), Karaburun, and Layna (*H. fissurae*). Of similar proportions but smaller size are the MtIII of La Gloria 4 and Kalmakpai (Eisenmann & Mein 1996).

Pavlodar and Kalmakpai are situated in Kazakhstan. Both faunas bear evidence of dry conditions and are supposed to belong in the MN13 zone, although Kalmakpai would be drier and closer to the Mio-Pliocene boundary



FIG. 1. — *H. cf. longipes*, third metatarsal (ACA-214); A, anterior; B, medial; C, lateral; D, posterior views. Scale bar: 10 cm.



FIG. 2. — *H. cf. longipes*, third metatarsal (ACA-214), proximal view. Scale bar: 3 cm.

(Vangenheim *et al.* 1993). At Pavlodar, Gromova (1952) described two species of hipparions: the larger as *H. longipes*, the smaller as *H. elegans*. Both forms are slender-built. Both have long metapodials and short first phalanges relative to the proximal limb bones (Fig. 4, Table 4). The skull of *H. elegans* has a preorbital fossa; there is no skull of *H. longipes*. Gromova insisted on the morphological resemblances between the teeth of both species, which cannot be differentiated otherwise than by the size, while *H. longipes* seems more adapted to a dry and open environment than *H. elegans* [Gromova's argumentation (1952 : 275) is: in *H. longipes*, the metapodials are longer than in *H. elegans*, the third metatarsal facets for the cuneiforms I and II and for the cuboideum are larger, and the trapezoideum is (at least in some cases) articulated with the third metacarpal; therefore the limbs were longer and a smaller part of the body weight was born by the lateral digits; these (and some other characters) indicate a better specialization for running and therefore a drier and more steppic environment than for *H. elegans*]. But Gromova was puzzled by the great degree of the enamel plication, surprising in dry conditions. In short, *H. longipes* looks like a large *H. elegans*, with possibly more weight born by the central digits, and more robust first phalanges. Both species were recently reviewed by Forsten (1997).

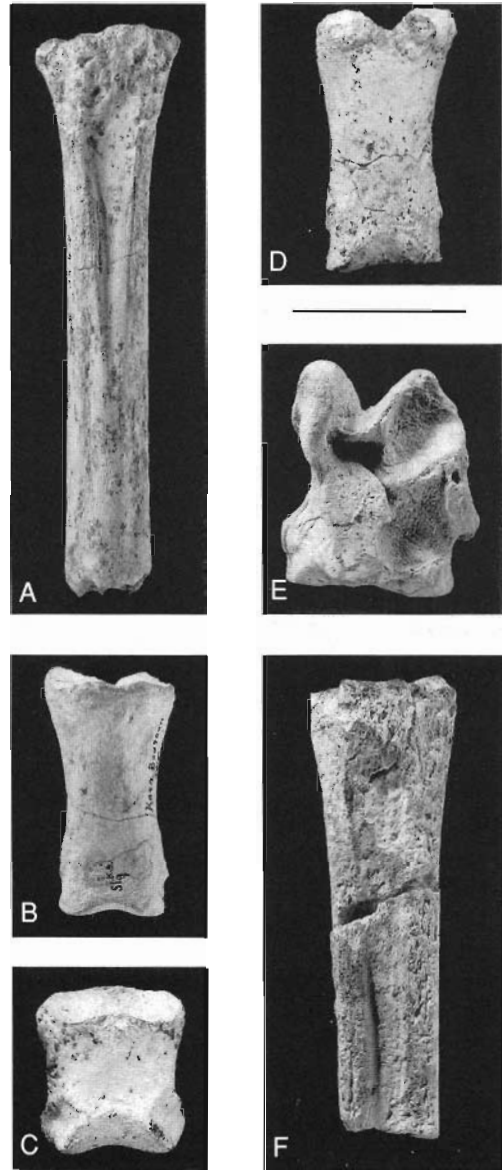


FIG. 3. — *H. cf. longipes*; A, third metatarsal (ACA-55), posterior view; B, first phalanx of the central digit, Karaburun, anterior view; C, posterior (?) second phalanx of the central digit (ACA-84), anterior view; D, first phalanx of the central digit (ACA-82), anterior view; E, talus (ACA-92), posterior view; F, third metacarpal (ACA-56), posterior view. Scale bar: 5 cm.

As can be seen from the table 1, the third metapodials of Pavlodar are slightly smaller than those of Çalta; the same is true for the tali (Table 3). The first phalanges of the central digit are not

only shorter but also more robust (Gromova 1959 : 236).

At Kalmakpai, a few teeth were referred to *H. elegans*, while most of the material, including skulls without fossa, was referred to *H. hippidoidus* by Zhegallo (1978) and to *H. cf. mogoicum* by Forsten (1997). There is some heterogeneity among the metapodials, both in size and in proportions, and some of the metapodials seem too small to fit with the size of the skull (Eisenmann & Mein 1996). Forsten also (1997 : 20) remarked the small size of the limb bones of Kalmakpai, comparative to the large skull. All the upper cheek teeth look alike, however, with rather rounded protocones and a moderately plicated enamel. The lower cheek teeth could be easily referred to *H. crassum*, although, according to Forsten (review of the present paper), the protostylids are better developed in *H. cf. mogoicum*. One first phalanx of the central digit is as long as in *H. longipes* but much more slender. In short, the taxonomy of the hipparion(s) of Kalmakpai is not quite clear.

La Gloria 4 (Spain) is another locality where the fauna indicates dry conditions. It is situated in the middle of MN14 zone. The entire MtIII is like one specimen of Kalmakpai, but the upper cheek teeth are much smaller and have elongated protocones (Eisenmann & Mein 1996). The material is scarce.

H. fissurae of Layna (Crusafont & Sondaar 1971) is not very well known either. Although logically it should be closely related to the hipparion of La Gloria 4 (which was indeed referred to *H. fissurae* by Alberdi & Alcalá 1992), the resemblances are not as marked as could be expected (Eisenmann & Mein 1996). From what is known about the limb bones, *H. fissurae* looks rather like the *H. cf. longipes* of Çalta, but is smaller (Fig. 4). Layna is believed to belong in the top of MN15 (Mein 1990).

The precise age of the MtIII collected from the cliffs of Karaburun (Macedonia) is not known (Sondaar & de Bruijn 1979). From Karaburun, there is also a first phalanx, preserved in the collections of the Laboratoire de Paléontologie, MNHN, Paris (Fig. 3, Table 2). Both the MtIII and the first phalanx are very similar to *H. cf. longipes* of Çalta (Fig. 3, Table 4).

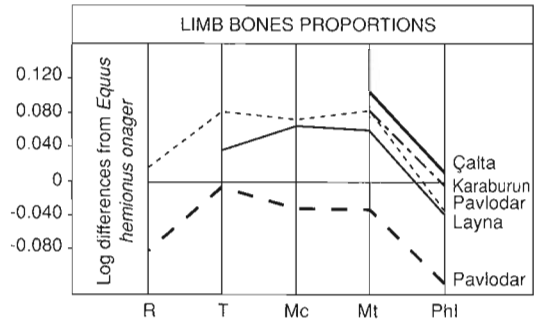


FIG. 4. — Ratio diagrams of lengths of : R, radii; T, tibiae; Mc, third metacarpals; Mt, third metatarsals; Phl, first phalanges. The corresponding data are in table 4. Çalta and Karaburun, *Hipparion cf. longipes*; Pavlodar, *H. longipes* and *H. elegans*; Layna, *H. fissurae*.

CONCLUSION

Except for their remarkable slenderness and sometimes large size, all these Late Turolian or Ruscinian hipparions are very poorly known. They all seem to belong in steppic or desertic faunas, but there is no unequivocal evidence that they were more “grazers” than “browsers”. They may have lacked preorbital fossa – if the Kalmakpai skulls without fossa are indeed associated with the slender limb bones. The *H. cf. longipes* of Çalta resembles most closely the Karaburun hipparion; unfortunately, the precise age of the latter is not known.

THE ROBUST HIPPARION OF ÇALTA

DESCRIPTION

Skull

Although we have no absolute proof that the skull fragments do belong to the robust hipparion of Çalta, their relative abundance renders this attribution most probable. There are three fragmentary skulls (Table 5). One belongs to an old adult; it is restricted to the palate, the upper cheek teeth rows and the facial areas. It has no collection number but it is in Ankara; we know it only by photographs (Fig. 5). The length of the upper cheek teeth can be estimated at about 160 mm (Fig. 6). The other two fragments belong to foals (ACA-336, dP2-dP4, M1 not

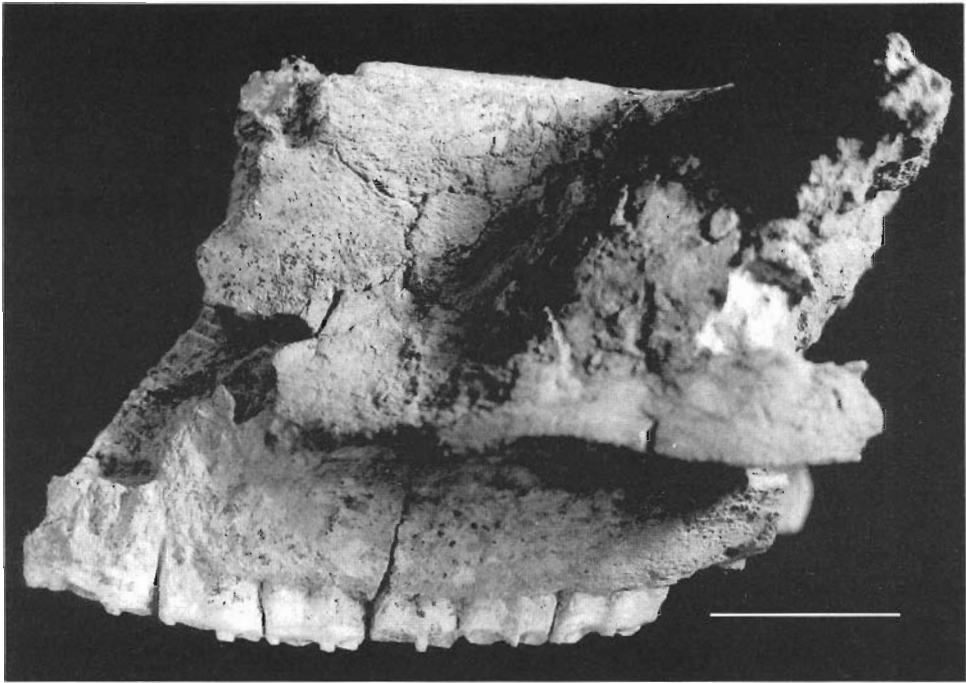


Fig. 5. — Fragment of an adult skull without number, Ankara; profile. Scale bar: 5 cm.

erupted; ACA-337, dP2-M1, M2 erupting, associated with a mandible). The best preserved of them (ACA-336, Fig. 7) is striking by the breadth and height of the face, and by the concavity below the broad and bulging nasals. There is no preorbital fossa. The orbits are placed very high. The overall impression is not unlike that of a camel skull, and suggests an unusual development of the nasal cavity. Another striking character is the thickness of the post-orbital process (about 20 mm), particularly surprising in a juvenile animal. Although the young age and the state of preservation do not allow certainty, it seems that the narial opening was deep (the profile view is slightly reminiscent of *H. dermatorhinum* as illustrated by Sefve 1927, plate I). It seems also that there was a contrast between the width of the nasal opening and the small distance between the premaxillaries, like in *Probosciparion sinense* (Sefve 1927, plates VI, VII).

Mandible

There is one complete mandible (ACA-337)

associated with the eldest foal fragmentary skull. The definitive I1 are erupting; they are grooved and have cups. The ascending ramus is high, and nearly at a straight angle with the horizontal ramus (Fig. 8). The horizontal ramus is relatively high (Table 6).

Upper cheek teeth

In addition to the adult upper cheek series at Ankara (Fig. 6), there are two little worn adult specimens: a left P3 or P4 (ACA-258: 55 mm high, Fig. 9A) and a right M1 or M2 (ACA-72: 51 mm high, Fig. 9B). Both were sectioned at mid-height (Fig. 10A and 10B). The protocones are small, rounded on the vestibular side but flattened on the lingual one. The fossettes are plicated and the pli caballins are multiple. The lacteal upper cheek teeth (Fig. 11A) are large and plicated.

Lower cheek teeth

There is no adult moderately worn specimen. The lacteal teeth are illustrated on figure 11B.

Limb bones

The material is relatively rich (about seventy specimens), with some associations, and well-preserved although some bones are distorted (Tables 7 to 14). As a raphonomical curiosity, it can be noted that out of eight humeri, seven are right, and that out of six tali, five are also right. The limb bones are big and very robust. The occurrence of several entire proximal limb bones brings interesting information as to the limb proportions (Fig. 12). Let us stress that the proportions of a single bone (robustness – gracility) should not be confused with relative limb bone proportions: thus, the first phalanges (Fig. 13D, E, G) are robust, meaning that their width is huge relative to their length; they are also long, when compared to more proximal limb bones (Fig. 12); like the first phalanges, the metapodials are robust (Fig. 13A, C) but they are very short relative to the radii and the tibia (Fig. 12).

Metapodials

The diaphyses of the central metapodials are wide and flat, the depth (antero-posterior diameter) being small relative to the breadth. The attachment areas of the interosseous ligaments uniting the lateral metapodials to the third metacarpal are very wide (Fig. 13A, C). They seem situated more on the lateral side of the central metacarpals than in most hipparions. In this respect, the hipparion of Çalta resembles *H. crassum* from Perpignan. The distal supra-articular tuberosities are more developed than in *H. crassum*. All these characters are more pronounced on the metacarpals than on the metatarsals. The lateral metacarpals are especially large and laterally situated, rather like in *Anchitherium*. On the third metacarpals, the articular facets for the fourth metacarpal are in continuity (not divided in one anterior and one posterior facets). So are the facets for the fourth carpal (Fig. 14A). The facet for the fourth carpal (hamatum) is nearly in the same subhorizontal plane as the facet for the magnum. The angulation between the hamatum facet and the magnum facet is rather like in *Equus*, much less than in most hipparions. The fifth metacarpals seem to be fused with the fourth, and can be seen as a distinct tuberosity on two specimens (ACA-134 and ACA-257) out of four

(Fig. 14A). All second metacarpals bear a small facet for a trapezium.



FIG. 6. — Fragment of an adult skull without collection number, Ankara; left cheek teeth row. Scale bar: 5 cm.

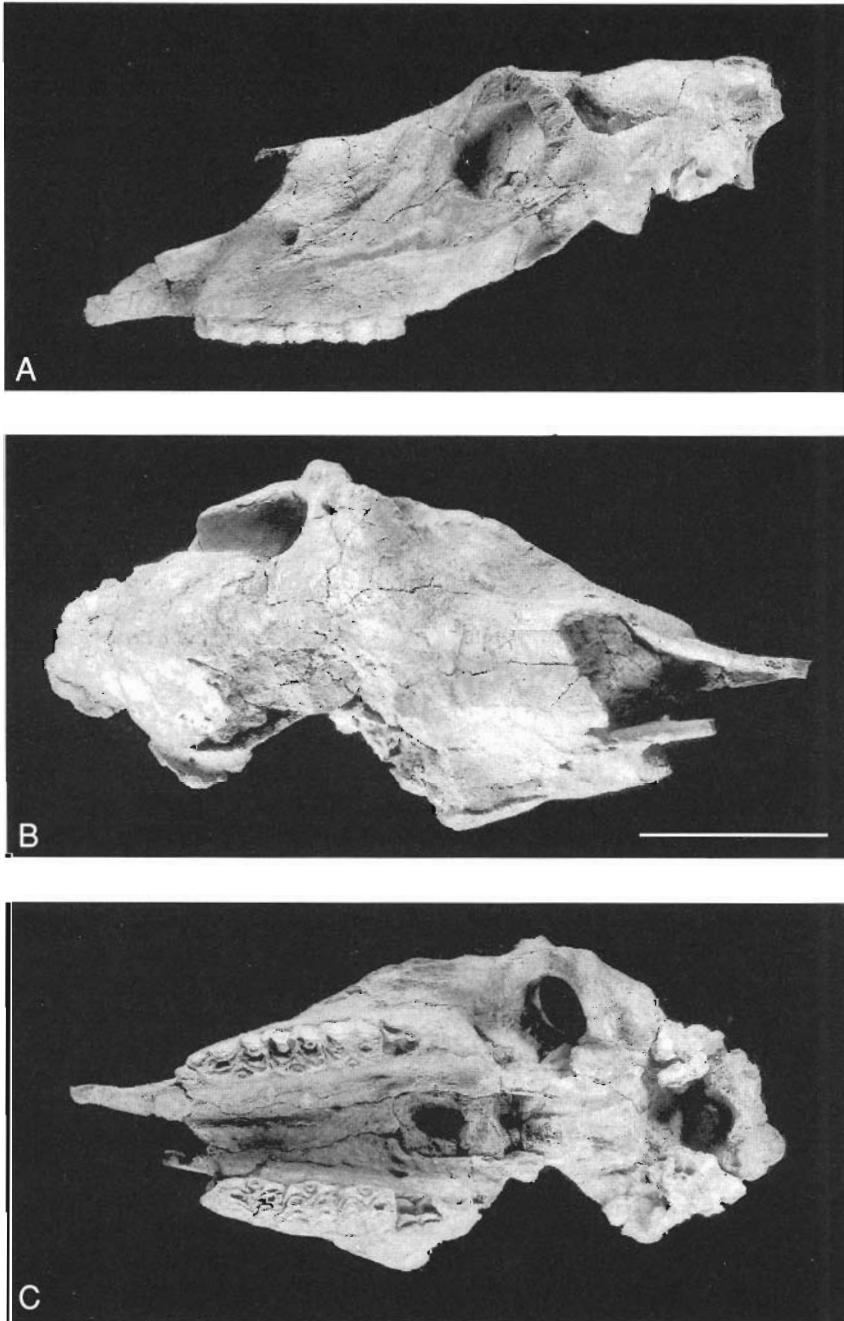


FIG. 7. — Fragment of a juvenile skull (ACA-336); **A**, profile; **B**, dorsal view; **C**, ventral view. Scale bar: 10 cm.

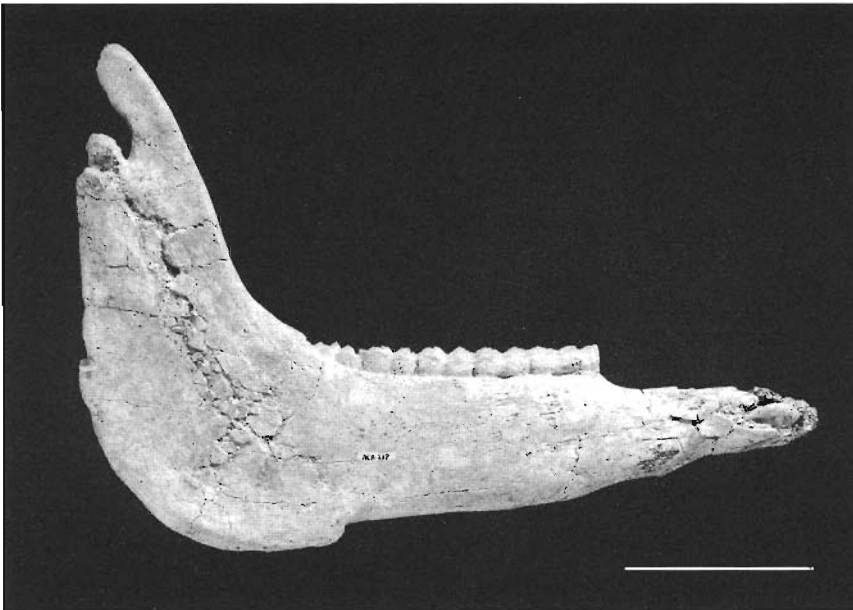


FIG. 8. — Juvenile mandible (ACA-337), profile. Scale bar: 10 cm.

Third phalanges

Both the anterior and posterior third phalanges are very wide (Fig. 16B, C); the sole is nearly flat (Fig. 15D, F), while it is well excavated in *H. cf. longipes* (Fig. 15B). In a lateral view, the sole appears convex (Fig. 15C, E) and the phalanx rocks on a horizontal plane, while it is stable in *H. cf. longipes* (Fig. 15A). The general shape is reminiscent of *Anchitherium* (Fig. 15G, H). Possibly the robust hipparion of Çalta, or at least its front foot, was subunguligrade like *Anchitherium*, with a large surface of contact with the ground. This feature may be of functional significance for walking on soft ground.

The conjunction of all these particularities leads us to propose a new specific name for the robust hipparion of Çalta.

***Hipparion heintzi* n.sp.**
(Fig. 13A)

HOLOTYPE. — Right McIII of the central digit (ACA-49a), associated with the entire McII (ACA-149c) and the proximal part of the McIV (ACA-49b). Collections of the Laboratoire de Paléontologie, MNHN, Paris.

PARATYPE. — Third anterior phalanx of the central digit (ACA-125; Fig. 16C)

DERIVATIO NOMINIS. — In honour of Emile Heintz as a friendly tribute to his work on Neogene Mammals in general, and to his excavations at Çalta in particular.

TYPE LOCALITY. — Çalta, Turkey.

AGE. — Ruscinian.

DISTRIBUTION. — Turkey.

DIAGNOSIS. — Large and robust hipparion, about the size of *H. primigenium* of Höwenegg and *H. brachypus* of Pikermi. Metapodials wide, flat, and extremely short relative to the radii and tibiae. First phalanges of the central digit robust but long relative to the metapodials, radii, and tibiae. Third anterior phalanges extremely wide, flat, and rocking on a horizontal plane, possibly subunguligrade. The fifth metacarpals are fused (or at least tend to be fused) with the fourth. If the skulls do belong to the same species, *H. heintzi* had no preorbital fossa, very high

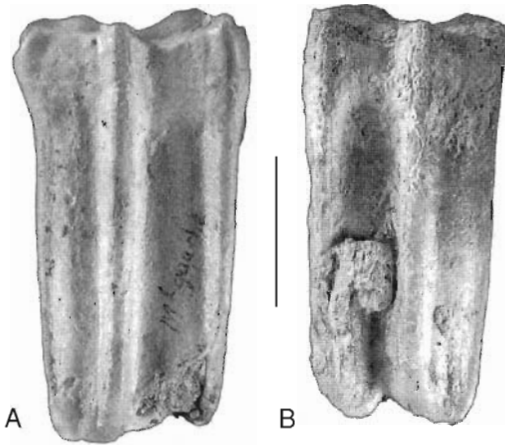


FIG. 9. — **A**, left P3 or P4 (ACA-258), vestibular view; **B**, right M1 or M2 (ACA-72), vestibular. Scale bar: 2 cm.

orbits, and a well-developed nasal cavity. The length of the cheek teeth was about 160 mm. The post-orbital process was very thick (at least it is so on the skull ACA-337). The horizontal ramus of the mandible was high.

COMPARISONS

Large and robust hipparions with wide and flat diaphyses are known in the Vallesian and the Turolian (Eisenmann 1995), as well as in the Pliocene (Eisenmann & Sondaar 1989). The Vallesian *H. primigenium* and the Turolian *H. brachypus* need not be discussed because they had well-developed preorbital fossae while the fossa is lacking in the skulls referred to *H. heintzi*. There is no definitive information about the facial area in *H. tchicoicum* but Zhegallo (1978: 90) supposes the preorbital fossa was present, because of the association of what he believes to be functionally related characters; at all events, the fossa is present in *H. insperatum*, a probably close relative of *H. tchicoicum* (Qiu *et al.* 1988) or may be even a synonym (Forsten 1992). Anyway, *H. tchicoicum* is clearly different from the Çalta robust form: *H. tchicoicum* has a very shallow mandible, and reduced cups, or no cups at all, on the lower incisors (Qiu *et al.* 1987, fig. 29; Eisenmann 1998). The remaining question therefore is whether the robust hipparion of

Çalta may, or may not, be a close relative or maybe even only a subspecies of *H. crassum* (Alberdi & Aymar 1995).

According to the descriptions by Gervais (1859) and Depéret (1885; 1890) *H. crassum* is characterized by its very large size, plicated upper cheek teeth with rounded protocones, not plicated lower cheek teeth, laterally compressed roots on the incisors, and short and robust third metapodials. A complementary description of the presently available material is in preparation but we may already note several points.

The skull of *H. crassum* mentioned by Depéret (1890) and chosen as lectotype by Forsten (1968) was never described in detail and seems lost. In particular, there is no information about the occurrence of a preorbital fossa. The only measurements given by Depéret are the distance between the prosthion and the posterior border of M3 (325 mm) and the length of the upper and lower cheek rows (respectively 170 and 164 mm). The muzzle was therefore about 155 mm in length, the longest recorded in hipparions.

Several fragmentary mandibles belonging to the collections of the Muséum d'Histoire naturelle de Lyon could be found and restored. The extremely elongated and narrow muzzle points to a selective browser diet (Eisenmann 1998). The incisors are long, straight and grooved, very much like those of African evolved hipparions (Eisenmann 1985, pl. I). Like in most hipparions, the cups are well-developed and bordered by a wavy enamel.

The upper cheek teeth have ten to thirty-eight fossette plications, multiple plis caballin, and

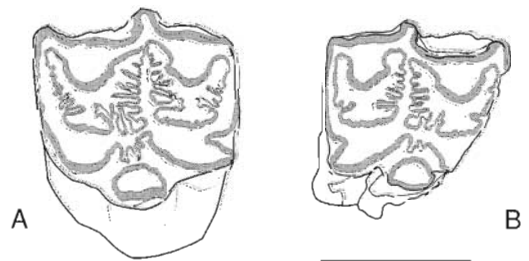


FIG. 10. — **A**, left P3 or P4 (ACA-258), section at mid-height; **B**, right M1 or M2 (ACA-72), section at mid-height. Scale bar: 2 cm.

very short and rounded protocones. The sizes at mid crown vary between 21 mm (smallest M1 or M2) and 29 mm (largest P3 or P4). An unworn premolar is 53 mm high; an unworn molar is 49 mm high.

The lower cheek teeth have quite variable enamel patterns and degrees of plication. Little worn teeth may have a nearly caballoid pattern and wrinkled fossettes. When the teeth are more worn (or cut at mid-crown), the enamel is usually (but not always) less wrinkled. Little worn premolars and molars may be up to 54 mm high.

The metapodials are rather wide and flat, although not all of them to the same degree. They seem short relative to the tibiae and to the first phalanges. The articular facets for the fourth carpal and the fourth metacarpal are continuous (Fig. 14B). The attachment areas of the interosseous ligaments are wide. There is an articular facet for the fifth metacarpal (Fig. 14B) observable on two specimens. The metapodials II and IV were situated laterally to the third.

Of *H. crassum* of Perpignan, there are two probably juvenile third central phalanges. Although the retro-osseous apophyses are not developed (possibly because of the young age), the general aspect is more like in usual hipparions; these phalanges are more stable on a horizontal plane than in *H. heintzi*. The third phalanx illustrated by Depéret (1890, pl. XIX, fig. 10) looks very wide (unfortunately, we have not been able to locate the phalanges illustrated by Depéret on this plate).

As already pointed out by Forsten (1968), *H. crassum* is not unlike *H. primigenium*, and the fossils found in its company point also to humid conditions and forest environment (Aymar 1992; Aguilar *et al.* in press).

DISCUSSION

The large overall size, the robustness, even the upper cheek tooth morphology, are rather similar in *H. crassum* and *H. heintzi*. The main differences are the larger size of *H. heintzi*, its exaggerated tendency to wide and flat metapodials, and a relatively reduced and subhorizontal facet for the hamatum. Actually, the resemblances are very

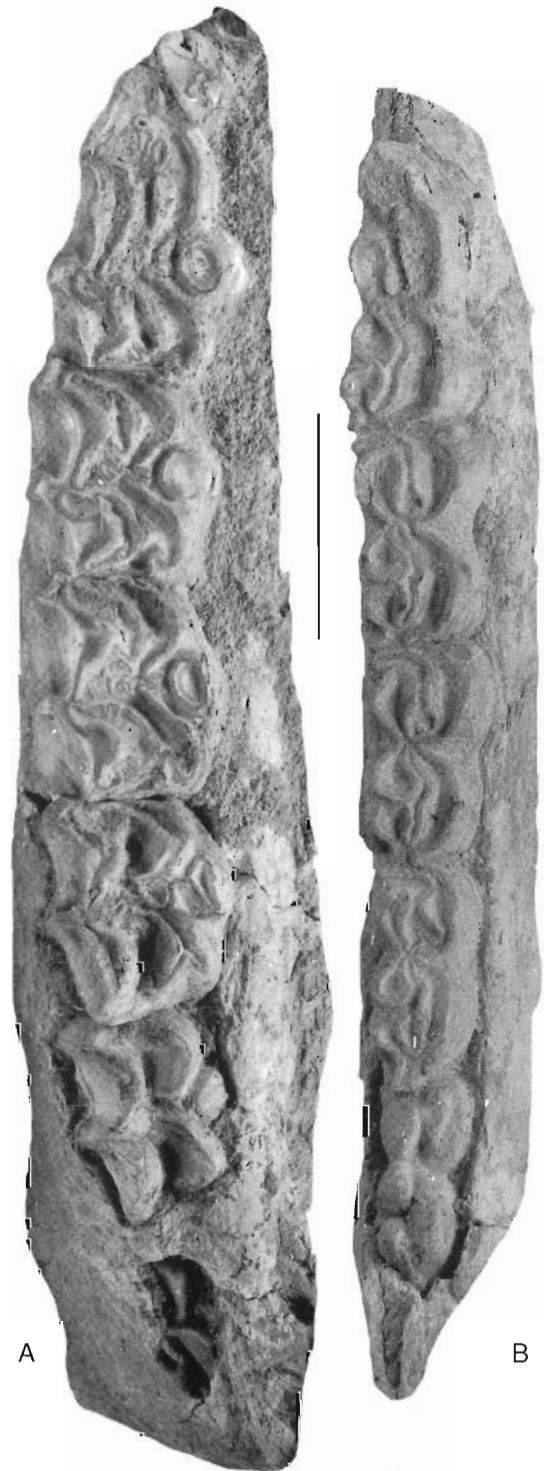


FIG. 11. — A, upper lacteal cheek teeth; B, lower lacteal cheek teeth (ACA-337). Scale bar: 3 cm.

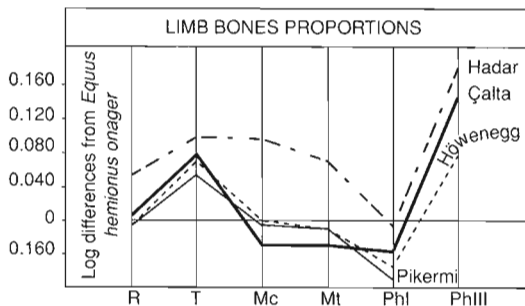


FIG. 12. — Ratio diagrams of lengths of: R, radii, T, tibiae, Mc, third metacarpals, Mt, third metatarsals, PhI, first phalanges. The corresponding data are in table 4. Hadar, *H. cf. afarensis* (AL 155-6); Çalta, *H. heintzi*; Höwenegg, *H. primigenium*; Pikermi, *H. brachypus*.

puzzling in face of the radically different environment evidenced by the associated fauna.

One of the striking characters of *H. heintzi* is the shortness of the metacarpals relatively to the radii. When these lengths are plotted for several hipparions together with the corresponding lengths of mountain and plains zebras (Fig. 17), *H. heintzi* is the only hipparion to come close to the mountain zebra (there are no data for the radius length of *H. crassum*). We were tempted to consider this feature as an evidence of adaptation to climbing steep slopes, as could be also the case of one “capra-like” bovid (Bouvrain, this volume). The shape of the third phalanges is, however, in contradiction with such an interpretation: hooves are usually narrow in climbing unguligrades.

Although the material does not permit quite satisfactory comparisons, the shape of the mandible and of the muzzle were probably different in *H. crassum* and *H. heintzi*. *H. crassum* had an extremely elongated muzzle which can be considered as belonging to a browser (Eisenmann 1998). As much as can be seen from the juvenile mandible referred to *H. heintzi*, the muzzle was shorter. When juvenile mandibles of the same age are compared (ACA-337, Pp 206, Pp 209), the ascending ramus and the horizontal ramus are higher in *H. heintzi* relative to the length dP2-Gonion (Table 6).

BODY WEIGHT ESTIMATIONS

After the present paper was finished, S. Sen asked us for measurements of the lower molars of Çalta hipparions in order to calculate their body weights. The material is very poor or lacking; besides, we were sceptic about the reliability of the technique itself. After some discussion, it was decided that we would estimate body weights, using what techniques we considered to be the best, and compare the results with other authors works.

A previous study (Eisenmann & Karchoud 1982) addressed the question of size correlation between skull and metapodial variables in equids for which one of us (VE) has collected and published numerous data. On a sample of 138 modern equids, it was found that the basicranial length is less correlated with the lengths of metapodials than with their widths (in particular the distal supra-articular width of the third metacarpal: MC10) and depths (in particular the distal minimal depth of the medial condyle of the third metacarpal: MC13). This can be understood intuitively, since the skull is “supported” by the sections of the bones, not by their lengths. We considered to using the “section”, *i.e.* the product of these widths and these depths (MC10 and MC13) to see if the correlation would be better, but we had no time to do it. In a recent paper, Alberdi *et al.* (1995) used skeletal data and data on weights of different extant equids to compute regression lines and predict body weights of fossil species. According to them, the body weights correlate best with the depths of the first phalanges, and the minimal depths of the medial condyle of the third metacarpals (MC13). It is interesting to note that the last one also correlates extremely well with the basicranial length (Eisenmann & Karchoud 1982).

The problem of body weight correlations with skeletal variables is, however, very difficult because of the poor information on body weights. Individual weights of animals to which the skeletons available in osteological collections belonged are, in general, not recorded. The published “average” data on live animals may be given separately for males and females, or lumped. The size



FIG. 13. — A-H, *H. heintzi*; A, metacarpal III (ACA-49A), ventral view; B, talus (ACA-65), ventral view; C, metatarsal III (ACA-52), ventral view; D, first anterior phalanx of the central digit (ACA-106), dorsal view; E, first posterior phalanx of the central digit (ACA-122), dorsal view; F, second phalanx of the central digit (ACA-113), dorsal view. Posterior of *H. heintzi* or anterior of *H. cf. longipes*? G, first anterior phalanx of the central digit (ACA-78), dorsal view; H, second anterior phalanx of the central digit (ACA-81), dorsal view. Scale bar: 5 cm.

of the sample and the range of variation may be not known. Moreover, some published data may be incorrect. Thus a weight of 400 kg for the extinct quagga is very probably excessive: quaggas and plains zebras skeletons and skulls are about the same size; if plains zebras weigh about 235 kg (Alberdi *et al.* 1995; see also Kingdon 1979), quaggas could not weigh nearly the double. One should also consider with caution the value of 350 kg used for Przewalski's horses (Alberdi *et al.* 1995). The most reliable data on

body weight of Przewalski's horses are those recorded for members of the first and second generation at Askania Nova: three adult males weighed 278-297.2 kg; one male, three years old, weighed 260 kg, and two adult females weighed 240 and 280 kg (Groves 1994). We have contacted Dr Zimmermann, a specialist of Przewalski's horses (Zoological Garden of Köln, Germany) who confirmed that, according to her data, the average weight of Przewalski's horses was about 275 kg, not 350 kg.

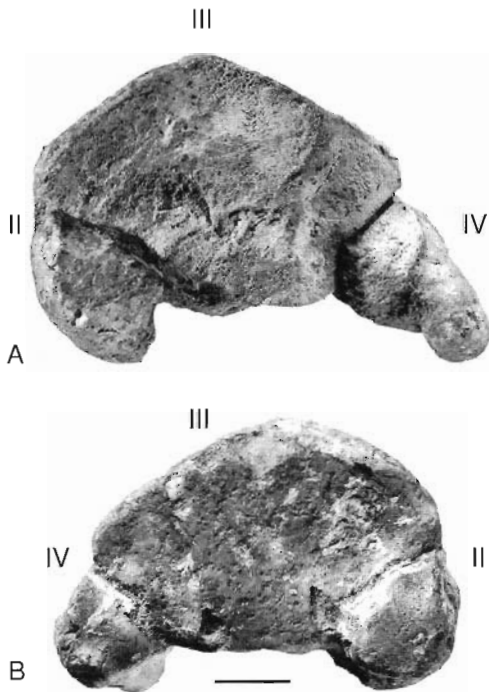


FIG. 14. — A, *H. heintzi*, metacarpals II, III, IV, and V (ACA-257), proximal view; B, *H. crassum*, metacarpals II, III, and IV (PER 48), proximal view. Scale bar: 1 cm.

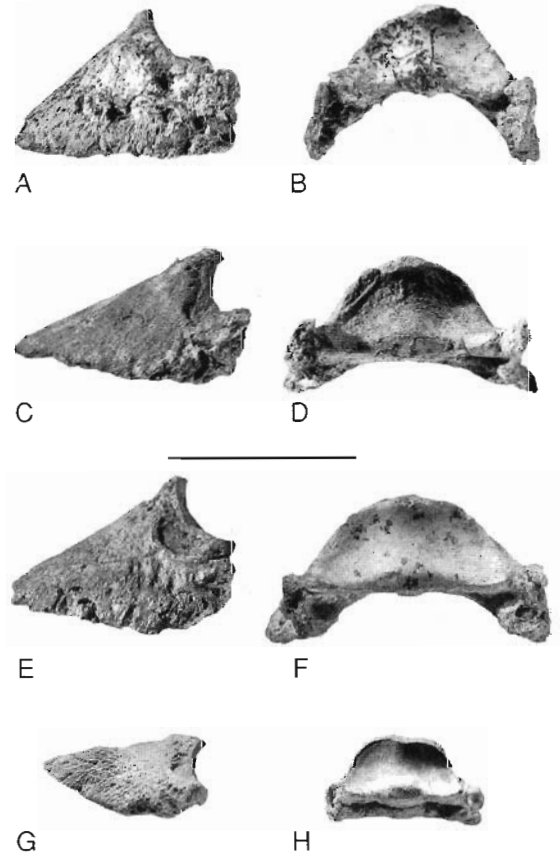


FIG. 15. — *H. cf. longipes*, third posterior (?) phalanx of the central digit (ACA-87); A, profile; B, articular view; *H. heintzi*, third posterior phalanx of the central digit, ACA-89: C, profile; D, articular view. *H. heintzi*, third anterior phalanx of the central digit (ACA-125); E, profile; F, articular view. *Anchitherium aurelianense*, Sansan, third anterior phalanx of the central digit (Sa4997); G, profile; H, articular view. Scale bar: 5 cm.

In spite of all these difficulties, we tried to see what could be done with the information at our disposal that we judged reliable (Table 15). Data on body weights of individual domestic horses and donkeys were found in the collections of the Institut für Haustierkunde of Kiel (Germany), and of the Comparative Anatomy Laboratory, Paris (France). For Przewalski's horses, we accepted an average body weight of 275 kg (Groves 1994; Zimmermann pers. com.). Body weights of Hartmann's zebras come from Joubert (1974) and Penzhorn (1988). Kingdon (1979) reports body weights of plains zebras and Grévy's zebras. The maximum weight of the Poitou donkeys was taken from Audiot (1977). Data on skulls, metapodials, and teeth are our own (most of them published in Eisenmann 1979, 1980). For Przewalski's horses, we have taken care to use only the osteological material of old collections (mostly St Petersburg and Moscow). For moun-

tain zebras, we have used only the data on the subspecies *E. zebra hartmannae* (which is larger than *E. zebra zebra*).

ESTIMATIONS OF BODY WEIGHT BASED ON THE THIRD METACARPALS

Dispersion diagram of weight versus distal depth of McIII (MC13)

Since the data are very scanty, we did not calculate regression lines but just plotted our values (Fig. 18). As can be seen, similar weights (around 140 kg) may be found in animals with different

values of MC13: 19.5 to 22 mm. On the other hand, similar values of MC13 (between 28 and 28.5 mm) may correspond to quite different body weights: 207 kg for a donkey (Kiel No. 1395), 263 kg for a domestic horse (Kiel No. 131431), 275 kg for an average Przewalski's horse, 343 kg (maximum for Hartmann's zebras), and 400 kg for an average Grévy's zebra. Note that the domestic horse plots close to the average Przewalski's horse.

Scatter diagram of weight versus product of distal depth of McIII (MC13) by distal width (MC10)

The values for domestic horses and donkeys are better aligned (Fig. 19) but the wide range of variation discussed above still exists for values of the product comprised between 1200 and 1300 square millimeters. It looks as if donkeys, horses, and plains zebras were on a line with a smaller intercept than the lines of Hartmann's and Grévy's zebras.

One possible reason may lie in the different sizes of the skulls. Indeed, values of 28-28.5 mm of the distal depth of the medial condyle (MC13) correspond to basilar lengths of: 452 mm in the donkey, 492 mm in the domestic horse, an average of 487 mm in eleven Przewalski's horses, a maximum of 510 mm in forty-six Hartmann's zebras, and an average of 532 mm in fifty-one Grévy's zebras (Table 15). Although this particular explanation (skull size) may be incorrect, or play a minor role, it is clear that body weight estimations cannot be accurate if they take into account only one parameter, because one parameter does not reflect the whole anatomical specificity of a taxon.

Computed regressions

Alberdi *et al.* (1995) have published tables of correlation between weights and skull, teeth and limb bone measurements in modern equid species, and given corresponding equations for predicting body weights. According to them, one of the best predictors is a distal depth of the third metacarpal: 9.39% for the Standard Error of the Estimate. Their computations were performed on natural logarithmic values (Ln).

Following the advice of Leslie Marcus, we have tested the equations proposed by Alberdi *et al.*

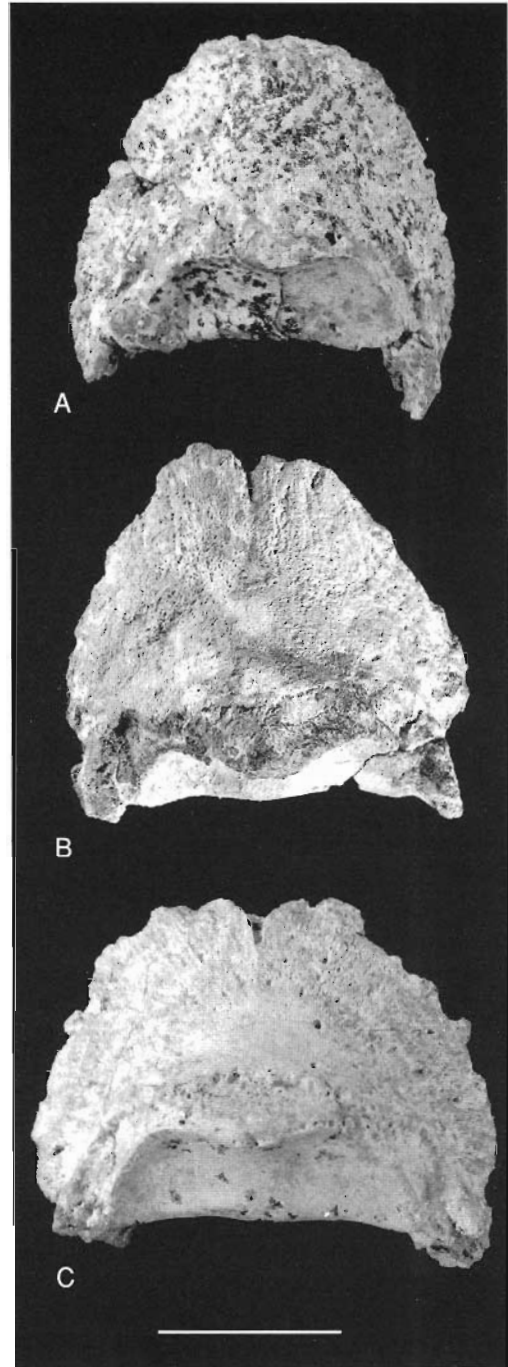


FIG. 16. — A, *H. cf. longipes*, third posterior (?) phalanx of the central digit (ACA-87), dorsal view; B, C, *H. heintzi*; B, third posterior phalanx of the central digit (ACA-89), dorsal view; C, third anterior phalanx of the central digit (ACA-125), dorsal view. Scale bar: 3 cm.

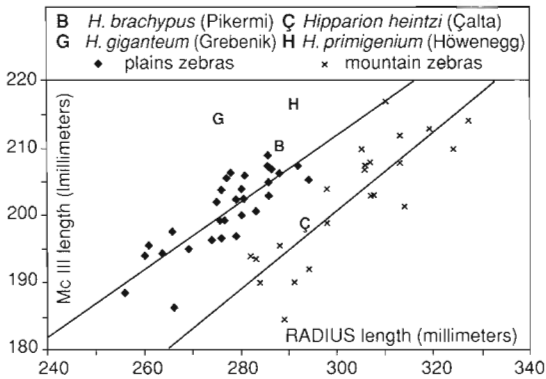


FIG. 17. — Scatter diagram of third metacarpal and radius lengths in equids. In the mountain zebras, the metacarpal is shorter relative to the radius than in the plains zebras. *H. heintzi* is the only "robust" hipparion to plot close to the mountain zebras.

(1995) on the means calculated with the data in our table 15 and on the maximal values for the Poitou donkeys. It is interesting to note (Table 16) that the best estimations are not always obtained with the same variables: MC10 gives less errors for Przewalski's horses, donkeys, and Hartmann's zebras; MC13 gives better estimates for the other forms. The weight of Przewalski's horses is notably overestimated (23.3 and 37.5% error). The percentage of error for the weight of the Poitou donkey is small with MC10 (7.6%) large with MC13 (36.3%).

Using the same data, we have also computed new slopes and intercepts for three metacarpal variables. The equations are:

$$\begin{aligned} \text{Ln of the weight} &= \\ &= -5.768 + 3.011 (\text{Ln MC10}). R = 0.94 \end{aligned}$$

$$\begin{aligned} \text{Ln of the weight} &= \\ &= -3.152 + 2.665 (\text{Ln MC13}). R = 0.92 \end{aligned}$$

$$\begin{aligned} \text{Ln of the weight} &= \\ &= -4.525 + 1.434 (\text{Ln of the product of MC10 by MC13}). R = 0.94 \end{aligned}$$

The correlation is better for MC10 and its product by MC13, than for MC13. As could be

expected, since the animals tested were also used to compute slopes and intercepts, our error percentages are less than those obtained with Alberdi *et al.* (1995) equations (Table 16). For the product of MC10 by MC13, the errors are intermediate between errors for MC10 and errors for MC13. This product does better only for the weight of small donkeys (overestimated by MC13, and underestimated by MC10).

It is more interesting to remark that, whatever the equations used, the weight of Grévy's zebras is underestimated, while the weight of Przewalski's horses is overestimated. As noted above for the diagrams of dispersion, the regression lines of these two forms differ probably by the intercepts; the regression computed for all equids together is a compromise; it cannot provide correct predictions for every species.

ESTIMATIONS OF BODY WEIGHT BASED ON THE THIRD METATARSALS

On the whole, the observations made for third metacarpals are valid for third metatarsals.

The equations computed with our data are:

$$\begin{aligned} \text{Ln of the weight} &= \\ &= -4.362 + 2.634 (\text{Ln MT10}). R = 0.93 \end{aligned}$$

$$\begin{aligned} \text{Ln of the weight} &= \\ &= -4.552 + 3.100 (\text{Ln MT13}). R = 0.94 \end{aligned}$$

$$\begin{aligned} \text{Ln of the weight} &= \\ &= -4.585 + 1.443 (\text{Ln of the product of MT10 by MT13}). R = 0.94 \end{aligned}$$

Error percentages are compared in table 16.

ESTIMATIONS BASED ON A TOOTH

Using the surface of an *Equus* tooth [occlusal length (Ol) multiplied by occlusal breadth (Ob)] to predict weight seems an enterprise doomed to give approximations such as "it is a small horse", or "it is a big horse". There are many reasons for that. First there is the matter of tooth wear, which reduces the occlusal surface; then the technique of measure (with or without cement); then the individual intraspecific variation which is much bigger for teeth than for limb bones. Moreover, some equids are microdont, and others macrodont. For example, the index of the

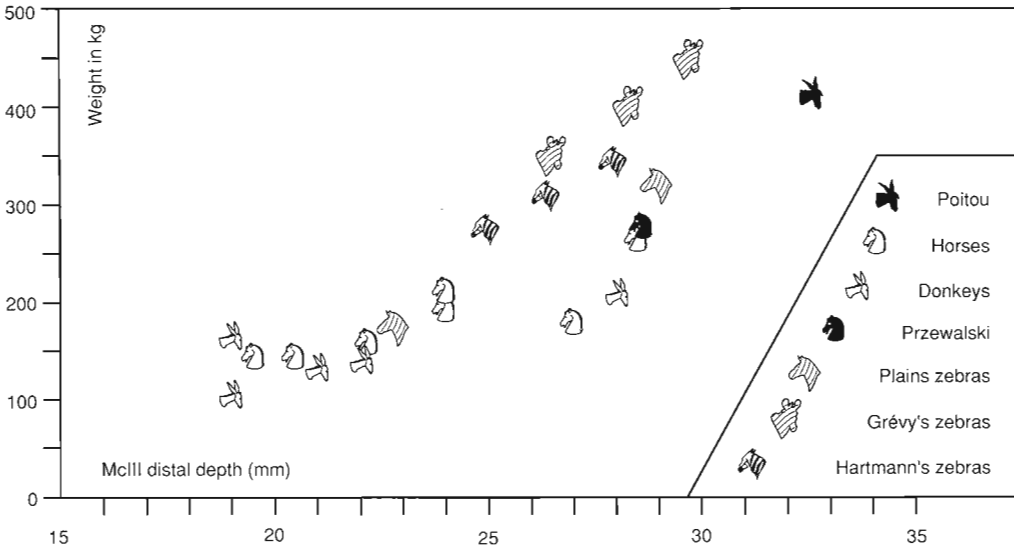


FIG. 18. — Scatter diagram of the body weight versus the distal minimal medial depth of the third metacarpal (MC13).

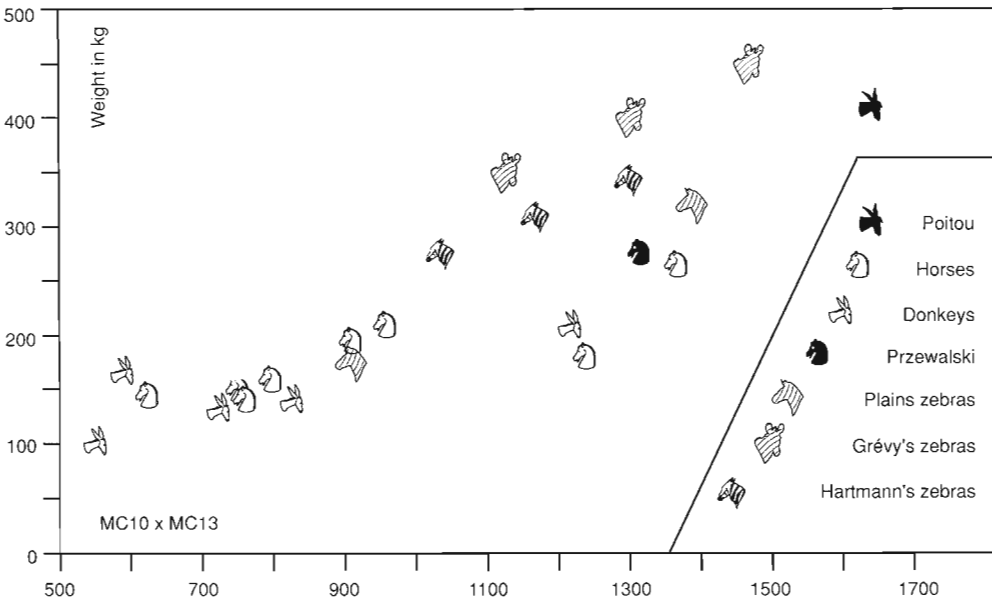


FIG. 19. — Scatter diagram of the body weight versus the product of the distal maximal supra-articular breadth (MC10) by the distal minimal medial depth of the third metacarpal (MC13).

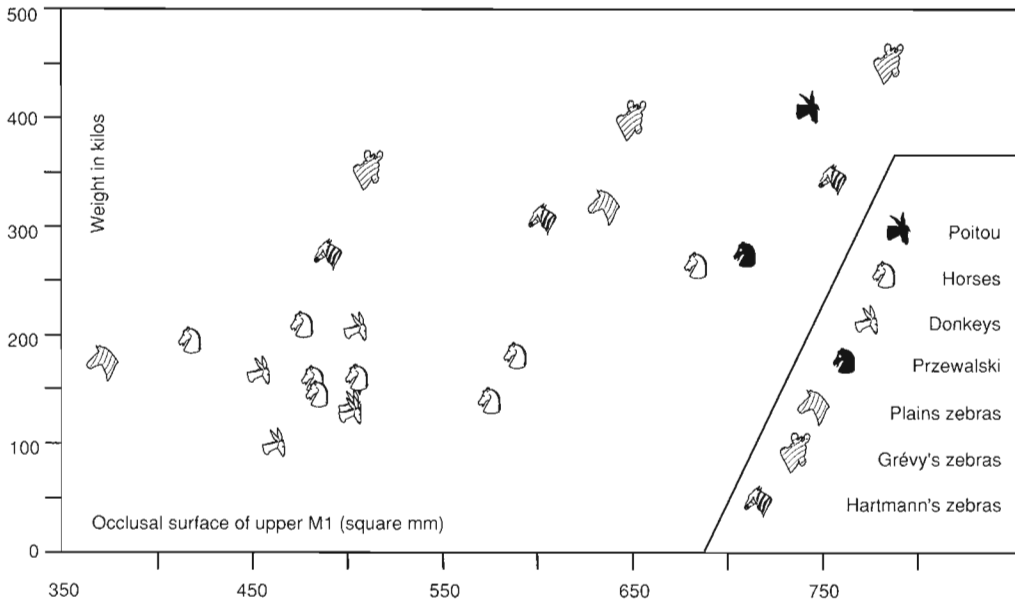


Fig. 20. — Scatter diagram of the body weight versus the occlusal surface of the upper M1.

occlusal surface of M1 to the product $MC10 \times MC13$ is 54% in Przewalski's horses, but less than 50% in Grévy's zebras.

Scatter diagram of weight vs occlusal surface of upper M1

As could be expected, and as can be seen on figure 20, horses tend to have relatively bigger occlusal surfaces than Grévy's zebras. All the points are, however, quite scattered.

Computed regressions

As noted by Alberdi *et al.* (1995), dental variables are not very good to predict body mass. We have compared the percentages of error in the same ways as for the metapodial variables (Table 16). Using the equation of Alberdi *et al.* (1995), weights are quite overestimated for horses and donkeys.

The equation computed with the means calculated on the data of table 15, and on the maximal values for the Poitou donkeys is:

$$\text{Ln of the weight} = -6.388 + 1.873 (\text{Ln surface M1}). R = 0.82$$

It tends to overestimate the weights of horses (because they are relatively macrodont), and underestimate the weights of the (relatively microdont) zebras (Table 16).

Although there exists a correlation ($R = 0.82$) between the occlusal surface of the upper M1 and the body weight, it does not grant an acceptable estimation of the latter.

ESTIMATIONS IN THE HIPPARIONS OF ÇALTA AND PAVLODAR (Fig. 21)

For *H. heintzi*, the techniques based on the metacarpal and metatarsal variables, whatever the equations used, give estimations comprised between 300 and 360 kg. When the estimations are done from the surface of the M1, values of 240 to 280 kg are found. According to the index of the occlusal surface of M1 to the product $MC10 \times MC13$, which is less than 43%, *H. heintzi* is quite microdont, so naturally the weight will be underestimated using tooth size as predictor. For *H. heintzi*, the body weight is probably better estimated by the metapodial variables.

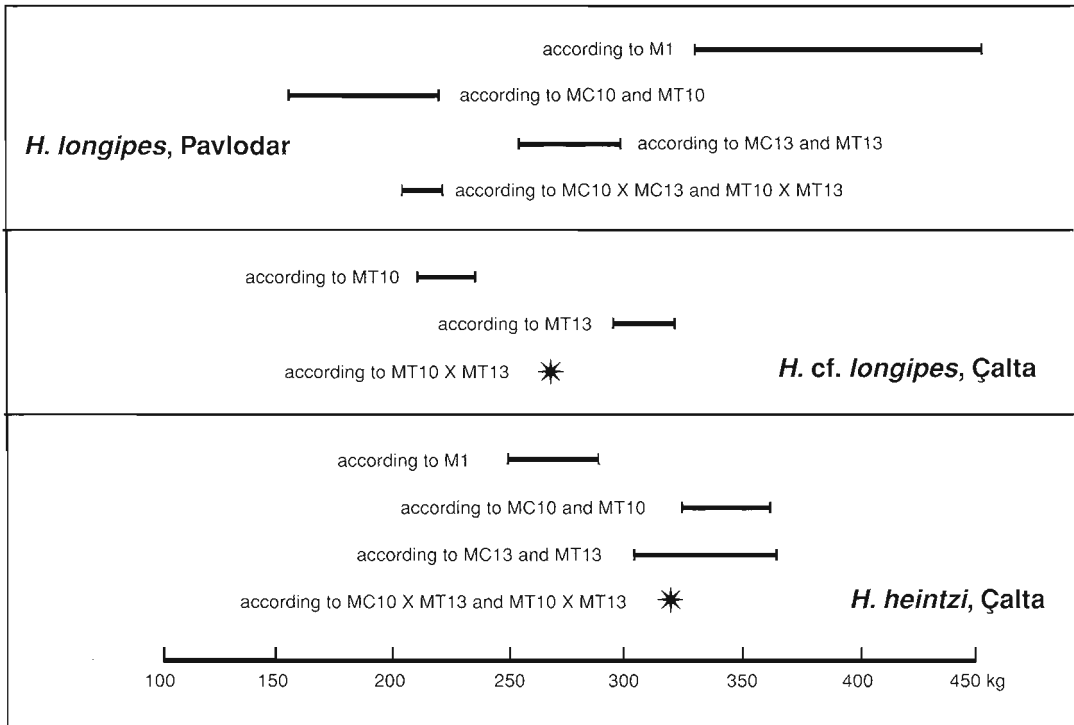


FIG. 21. — Comparison of hipparion body weight estimations based on the surface of the upper M1, and on various metapodial variables: **MC10, MT10**, distal maximal supra-articular breadths of McIII and MtIII; **MC13, MT13**, distal minimal medial depths of McIII and MtIII; **MC10 × MC13 and MT10 × MT13**, products of distal maximal supra-articular breadths by the distal minimal medial depths in McIII and MtIII.

For *H. cf. longipes* of Çalta, using the metatarsal equations (there are no teeth and no distal metacarpals), the estimated weights range from 212 to 323 kg. *H. cf. longipes* differs from all the equids used to compute these equations by a very narrow and very deep distal MtIII. Consequently the equations based on MT10 give much smaller estimations than those based on MT13. In this case, it is probably safer to use the product of MT10 by MT13 and estimate the weight at about 256 kg.

More problems arise in the case of *H. longipes* of Pavlodar. We have no data on the size of its teeth other than those published by Gromova (1952) who has probably included the cement in her measurements. If we use these data, *H. longipes* appears extremely macrodont: the indices of the occlusal surface of M1 to the products MC-MT10 × MC-MT13 are more than 66%. Accordingly, weights estimated on the M1 surfa-

ce range from 331 to 457 kg (more than for *H. heintzi*). On the other hand, weights estimated on MC10 and MT10 range only from 158 to 221 kg. Using the products of MC10 × MC13 and MT10 × MT13 gives a (probably not too bad) weight estimate of 210-222 kg.

CONCLUSIONS

Different forms of *Equus* are not constructed in the same way: some have big heads, some have wide or deep bones, some have small teeth. Equations computed on any variable, for all forms of *Equus*, will result in compromises: the weights of some species will be correctly estimated, the weights of other species will be over- or underestimated. In practice, the tooth surface is among the worse parameters to predict body weight. Estimations based on limb bones widths and/or depths are more reliable. In some cases, it

may be safer to combine width and depth (using their product). In *H. longipes* for example, metapodials are extremely narrow and deep; such morphologies, unknown in modern *Equus*, could not be considered when computing the equations. Thus the *Equus* equations give fantastic indications for the weight of this hipparion: 158 or 177 kg according to the width of the McIII; 263 or 296 kg using the depth of the same bone. Tentatively, we propose weights of 300-350 kg for *H. heintzi*, 250-260 kg for *H. cf. longipes* of Çalta, and 210-220 kg for *H. longipes* of Pavlodar.

As always, the most difficult part of the work is to find reliable data. One must constantly be aware that the use of statistical equations cannot improve poor and rare data. Confidence in the results should be more proportional to the quality of the data, than to the sophistication of the methods.

CONCLUSIONS

The rodents of Çalta (Sen 1977) bear evidence of a steppe environment. The presence of *Pliospalax* (16% of the rodents) and the high number of the gerbilline *Pseudomeriones abbreviatus tchaltaenus* (56.8% of the rodents) are remarkable in this aspect. The low specific diversity of the fauna (but there are two equids) suggests an also somewhat isolated biotope. Both are well in accord with the geographic situation of Çalta (Central Anatolia) and the altitude (more than 1000 m, probably the same now and during the Pliocene). Both are at the opposite of what we know of Perpignan which is located near the Mediterranean and yielded a diversified fauna (but with one equid only) belonging in a forest environment.

During the Pliocene, Old World hipparions become rare in comparison with other large herbivorous ungulates like bovids and cervids (Sen *et al.* 1978). They also show extreme specializations: dolichopodial and slender hipparions like *H. cf. elegans* at La Gloria 4 (Eisenmann & Mein 1996) and *H. fissurae* at Layna (Crusafont & Sondaar 1971) or brachypodial and robust forms like *H. crassum* at Perpignan. The dolichopodial and slender forms are found in arid contexts,

while *H. crassum* is part of a humid fauna. What is unique about Çalta, is the occurrence of a brachypodial and robust hipparion in an arid context. Surprisingly enough, the robust *H. heintzi* is even more abundant than the slender *H. cf. longipes*.

We tentatively propose that *H. heintzi* was a subunguligrade walking on a soft soil. The occurrence and abundance of *Pseudomeriones* and *Pliospalax* (burrowing species) are consistent with this hypothesis. The fragmentary skulls referred to *H. heintzi* may have borne nasal specializations (like what may be found in camels and saigas) consistent with an arid climate. But we are fully aware that our interpretation would have been quite different in other contexts. Had we not had the extremely wide third phalanges at our disposal, we would have interpreted the shortness of the metapodials relative to the proximal limb bones as an adaptation for climbing. Had the rest of the fauna not been so clearly steppic, we would have taken the robustness of the metapodials as evidence of a humid climate.

Inside the same genus, different species frequently associate similar characters in different ways (Eisenmann & Mein 1996; Forsten 1997; Eisenmann 1998). A species may be recognized by its own, peculiar, mosaic of characters but each character taken separately is not diagnostic of the species. At most, an isolated character may give an ecological hint, although some of the classically accepted "hints" do not seem to fit with what we suppose about Çalta: such is the case of the robustness of the bones and the high degree of enamel plication of *H. heintzi* that are usually considered as tokens of humidity.

Acknowledgements

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APPENDIX
MEASUREMENTS AND STATISTICS

TABLE 1. — *H. longipes* (Pavlodar: PIN 2346-6867 and PIN 2413-5030) and *H. cf. longipes* (Çalta, ACA), third metacarpal and third metatarsals, measurements in millimeters. Estimated dimensions between brackets.

McIII or MtIII	McIII ACA-56	McIII Pavlodar	MtIII Pavlodar	MtIII ACA-214	MtIII ACA-209	MtIII ACA-55 juv
Maximal length		255.0	300.0	318.0		
Minimal breadth	29.0	27.0	28.5	29.5	28.3	24.0
Depth at the same level	27.3	26.0	30.0	30.0	27.0	24.0
Proximal articular breadth	[44.5]	42.0	46.0	42.0		42.0
Proximal articular depth	[32]	28.0		35.0		35.0
Distal maximal supra-articular breadth		37.0	39.0	40.0		
Distal maximal articular breadth		36.9	39.0	[37]		
Distal maximal depth of the keel		29.5	33.0	[34]		
Dist. min. depth of the medial condyle		26.7	26.0	28.0		
Dist. maximal depth of med. condyle		27.5	30.0	31.0		
Diameter facet 3rd carpal or tarsal	38.5	36.0	39.0	40.0		39.0
Diameter facet 4th carpal or tarsal	11.5	11.0		11.0		11.0

TABLE 2. — *H. cf. longipes* from Karaburun (Slq) and Çalta (ACA): first, second and third phalanges of the central digit, measurements in millimeters. Estimated dimensions between brackets. **tuber.**, tuberosities.

	PhI ACA-82	PhI ACA-124	PhI Slq 1915	PhII ACA-84	PhIII ACA-87
Maximal length	75.0		74.0	48.0	56.0
Anterior length				37.5	53.5
Maximal breadth					64.0
Minimal breadth	29.0		26.9	36.5	
Proximal breadth	[40]	43.0	39.1	42.5	
Proximal depth	[34]	32.0	33.8	29.0	
Distal breadth at tuber.	[33]			42.0	
Distal articular breadth	[34]		32.0	24.0	
Distal articular depth			19.0		
Articular breadth					39.0
Articular depth					24.0
Circumference					145.0

TABLE 3. — *H. cf. longipes* of Çalta and *H. longipes* of Pavlodar. **Tali**, measurements in millimeters. **Max.**, maximal; **diam.**, diameter. The measurements for *H. longipes* of Pavlodar are average on 9 specimens (Gromova 1952). The first one is not exactly the same (medial height in Gromova).

Tali	ACA-259	ACA-63	ACA-92	<i>H. longipes</i>
Maximal length	65.0	62.5	65.0	[61.1]
Max. diam. medial condyle	63.0	64.0	61.5	
Maximal breadth	52.0	58.0	55.0	55.9
Breadth of trochlea	25.7	25.0	26.5	
Distal articular breadth	45.2	50.0	48.0	45.5
Distal articular depth	40.0	41.0	37.0	34.5
Maximal medial depth	52.0	52.5	49.0	49.1

TABLE 4. — Lengths in millimeters of humeri (H), femora (F), radii (R), tibiae (T), third metacarpals (Mc), third metatarsals (Mt), first phalanges (anterior and posterior) of the central digit (PhI). For the femora of hipparions, the length is from caput femoris to lateral condyle. For the other limb bones, the lengths are maximal. Maximal breadth of the third anterior phalanx of the central digit (PhIII). n, number of specimens.

		H	n	F	n	R	n	T	n
<i>E. hemionus onager</i>		241.3	10	329.7	10	293.5	10	313.0	10
<i>H. longipes</i>	Pavlodar			335.0	1	304.0	1	378.0	1
<i>H. fissurae</i>	Layna							340.0	1
<i>H. elegans</i>	Pavlodar	213.0	2			242.2	5	307.5	2
<i>H. heintzi</i>	Çalta	274.7	3	387.0	2	297.3	7	375.0	1
<i>H. primigenium</i>	Höwenegg	275.0	3	378.3	3	287.5	2	367.5	4
<i>H. brachypus</i>	Pikermi	268.0	1	342.0	1	290.0	2	355.0	2
<i>H. afarense</i> ?	Hadar: AL 155-6	281.0	1			332.5	1	392.5	1

		Mc	n	Mt	n	PhI	n	PhIII	n
<i>E. hemionus onager</i>		214.1	10	250.8	10	73.8	20	54.0	8
<i>H. longipes</i>	Pavlodar	252.0	2	305.3	3	68.5	3		
<i>H. cf. longipes</i>	Çalta			318.0	1	75.0	1		
<i>H. cf. longipes</i>	Karaburun			302.0	1	74.0	1		
<i>H. fissurae</i>	Layna	250.0	1	288.0	1	67.0	2		
<i>H. elegans</i>	Pavlodar	198.3	35	232.2	50	56.4	34	54.0	2
<i>H. heintzi</i>	Çalta	200.4	7	234.7	7	67.6	11	76.0	1
<i>H. primigenium</i>	Höwenegg	214.0	3	245.0	3	65.1	6	64.5	2
<i>H. brachypus</i>	Pikermi	211.8	45	246.8	53	63.2	8		
<i>H. afarense</i> ?	Hadar: AL 155-6	267.0	1	296.0	1	72.8	2	82.0	1

TABLE 5. — Skulls: measurements in millimeters. Estimated dimensions between brackets. **Ant-post.**, antero-posterior; **Dors-ventr.**, dorso-ventral; **For. infraorb.**, foramen infraorbitale; **alveol.**, alveolar.

Skulls	Ankara	ACA-336	ACA-337
P2 to orbit		158	[190]
Palatal length	[125]	110	
Vomerine length		104	
Premolar length	[85]	105	102
Molar length	[71]		[82]
Cheek teeth length	[157]		
Choanal length	[74]	61	
Minimal choanal width		31	
Maximal choanal width	[42]	37	
Palatal width	[70]	70	75
Length of temporal fossa		58	
Frontal width		225	
Bizygomatic width		206	
Basioccipital width		[115]	
Posterior ocular line		[180]	
Height of auditory meatus		13	
Ant-post. orbital diameter		52	
Dors-vent. orbital diameter		47	
For. infraorb. to alveol. border		50	[60]

TABLE 6. — Mandibles: measurements in millimeters. Estimated dimensions between brackets.

Mandibles	<i>H. heintzi</i> ACA-337 dP2-(M2) Çalta	<i>H. crassum</i> Pp 206 dP2-(M2) Perpignan	<i>H. crassum</i> Pp 209 dP2-(M2) Perpignan	<i>H. crassum</i> Pp 210 P2-M2 Perpignan
Maximal length	410.0			
Length Gonion-Infradentale	390.0			
Length P2-Gonion	272.0		290.0	290.0
Height at the condyle	230.0		210.0	245.0
Height at the coronoid				265.0
Height at incisura mandibul.	215.0	216.0	195.0	230.0
Breadth of ascending ramus	122.0		130.0	135.0
Height under M1	77.0	74.0	73.0	80.0
Height between P4 et M1	75.0	71.0	69.0	78.0
Height under P4	75.0	69.0	69.5	76.0
Height under P3	73.0	68.0		65.0
Height in front of P2	61.0	54.5	59.0	55.0
Length of symphysis	87.0			
Muzzle length	[115]			
Diastema P2-I3	67.0			
Alveolar premolar length	97.0	95.0	95.0	90.0
Min. breadth of symphysis	41.0		45.5	

TABLE 7. — Humeri: measurements in millimeters. Estimated dimensions between brackets.

Humerus	ACA-101	ACA-102	ACA-100	ACA-94	ACA-96	ACA-95	ACA-97	ACA-99
Maximal length	[280]	262.0		[282]				
Maximal length from caput	265.0	248.0						
Minimal breadth	35.5		34.0	35.0	36.0		35.0	37.5
Depth at the same level	42.0		45.0	46.0	46.0		42.0	48.0
Prox. depth at median tubercule		[100]		[105]				
Maximal breadth of trochlea	77.0	75.0	76.0	80.0	78.0	76.0	73.0	82.0
Maximal distal depth		[85]						
Maximal trochlear height (medial)		48.0	51.0	50.0	50.0			
Minimal trochlear height	[38]		35.6	40.0	34.0	31.0		39.0
Trochlear height at sagittal crest	47.0		43.0	47.3	40.5	38.0		45.0

TABLE 8. — Radii: measurements in millimeters. Estimated dimensions between brackets.

Radius	ACA-229	ACA-47	ACA-230	ACA-57	ACA-104
Maximal length	306.0	286.0	300.0	302.0	307.0
Medial length	282.0	273.0	281.0	274.0	286.0
Minimal breadth	42.0	[45]	45.0		45.0
Depth at mid-diaphysis	26.0	[31]	30.0		28.0
Proximal maximal breadth	79.0		78.0		76.0
Proximal articular breadth	74.0		76.5		74.0
Proximal articular depth	42.0	[39]	[36]		41.0
Distal maximal breadth	75.0	70.0	69.0		72.0
Distal articular breadth		58.0	60.5		64.0
Distal articular depth	40.0	38.0	40.0		38.0
Breadth radial condyle	26.0	25.0	26.0		28.0
Breadth ulnar condyle		13.5	13.0		14.5

Radius	ACA-107	ACA-105	ACA-108	ACA-148 j
Maximal length	307.0	273.0		
Medial length	287.0	261.0		
Minimal breadth	43.0	44.0		
Depth at mid-diaphysis	34.5	27.5		
Proximal maximal breadth		[83]		
Proximal articular breadth		76.0		
Proximal articular depth	43.0	40.0		
Distal maximal breadth		75.0	71.0	
Distal articular breadth		65.0	65.0	59.0
Distal articular depth		37.0	36.5	
Breadth radial condyle	[25]	26.5	29.0	23.0
Breadth ulnar condyle	15.0	15.0	15.0	15.0

TABLE 9. — Femora: measurements in millimeters. Estimated dimensions between brackets.

Femur	ACA-236	ACA-103	ACA-109	ACA-117
Length from caput to lateral condyle	384.0	390.0		
Minimal breadth	39.0		35.0	40.0
Depth at the same level	50.0		50.0	48.5
Maximal diameter of caput	57.0	58.5		
Maximal distal depth	more than 101	more than 105		

TABLE 10. — Tibiae: measurements in millimeters. Estimated dimensions between brackets. j, juvenile.

Tibia	ACA-115	ACA-59	ACA-151	ACA-112a	ACA-208
Maximal length	382.0				
Medial length	361.0				
Minimal breadth	47.0	45.5	44.0	43.0	42.0
Depth at same level	36.0	30.0	31.5	30.5	30.3
Distal maximal breadth	[76]		74.0	79.0	71.0
Distal maximal depth	[49]		50.0	46.0	48.0
Length of fossa digitalis	58.0				
Breadth of fossa digitalis	19.0				

Tibia	ACA-231	ACA-60	ACA-116 j	ACA-58 j
Maximal length				
Medial length				
Minimal breadth	44.0		41.0	38.0
Depth at same level	32.0	31.0	32.0	27.0
Distal maximal breadth	77.0		71.0	
Distal maximal depth			48.0	46.5
Length of fossa digitalis				
Breadth of fossa digitalis				

TABLE 11. — Tali: measurements in millimeters. Estimated dimensions between brackets.

Talus	ACA-62	ACA-65	ACA-64	ACA-66	ACA-61	ACA-112b
Maximal length	56.5	59.0	63.0	55.5	62.0	58.0
Max. diam. medial condyle	60.0	63.0	65.1	[57]	61.5	61.0
Maximal breadth	63.0	64.0	66.0	60.0	60.5	63.0
Breadth of trochlea	30.0	30.5	30.0	30.0	30.0	31.0
Distal articular breadth	50.5	50.3	51.5	49.0	50.0	50.5
Distal articular depth	39.0	39.0	39.0	[37]		
Maximal medial depth	51.0	52.0	54.0	50.0	51.0	50.0

TABLE 12. — Calcanea: measurements in millimeters. Estimated dimensions between brackets. j, juvenile

Calcaneum	ACA-150	ACA-112b	ACA-67	ACA-73	ACA-62	ACA-61 j
Maximal length	115.5					
Length of proximal part	75.0			[72]		
Minimal breadth	24.0	22.0	24.0	23.0	22.0	
Proximal maximal breadth	35.0					
Proximal maximal depth	52.0			54.0		
Distal maximal breadth	59.0	56.0	60.0		55.0	54.0
Distal maximal depth	53.0	53.0	53.5	54.0	53.0	47.0

TABLE 13. — Third metacarpals (MclII) and metatarsals (MtIII): measurements in millimeters. Estimated dimensions between brackets. art., articular; dist., distal; min., minimal; med., medial.

MclII	ACA-237	ACA-49a	ACA-345	ACA-346	ACA-54	ACA-257	ACA-149a	ACA-238a
Maximal length	199.0	208.0	194.0	200.0	200.0	204.0	198.0	
Minimal breadth	31.0	34.0	34.5	36.0	32.5	32.5	33.0	32.0
Depth at mid-diaphysis	24.0	26.0	24.0	26.8	23.0	24.0	24.0	24.7
Proximal articular breadth	46.5	50.0	50.0	49.0	47.0	49.0	48.5	
Proximal articular depth	29.5	33.0	32.0	33.0	31.5	34.0	32.0	
Distal maximal supra-art. breadth	44.0	49.4	48.0		45.7		48.5	
Distal maximal articular breadth		48.0	44.8	48.0	[43]		45.0	44.0
Distal maximal depth of keel	33.0	35.0	33.0	35.0	32.0		35.0	35.5
Dist. min. depth of medial condyle	26.5	29.0	26.3	30.0			27.3	28.5
Dist. maximal depth of med. condyle	28.0	30.5	28.0	32.0			29.2	31.0
Diameter facet for the 3rd carpal	39.0	41.0	41.0			40.0	41.0	
Diameter facet for the 4th carpal	14.0	15.0	14.0			15.0	14.0	

MtIII	ACA-347	ACA-52	ACA-51	ACA-121a	ACA-53	ACA-48	ACA-50	ACA-112c
Maximal length	242.0	246.0	233.0	234.0	220.0	238.0	230.0	
Minimal breadth	35.0	33.5	29.0	29.0	33.0	32.0	31.0	31.0
Depth at mid-diaphysis	31.5	30.0	27.0		28.5	31.0	31.0	28.0
Proximal articular breadth	50.0	51.0	48.0					49.0
Proximal articular depth	39.0	39.0	37.0					37.0
Distal maximal supra-art. breadth		49.5	43.0	43.0				
Distal maximal articular breadth	44.0	47.0	42.7	42.7	46.0			
Distal maximal depth of keel		37.0	35.0	32.0	36.0			
Dist. min. depth of medial condyle	30.0	30.0	28.0	25.0				
Dist. maximal depth of med. condyle	33.0	32.0	29.5	30.0				
Diameter facet for the 3rd tarsal	47.0	47.0	43.5	44.0				44.0
Diameter facet for the 4th tarsal	12.0	13.0	10.0	11.0		12.0		13.0

TABLE 14. — First, second and third phalanges of the central digit, measurements in millimeters. Estimated dimensions between brackets. **Ant.**, anterior; **Post.**, posterior; **Juv.**, juvenile; **tuber.**, tuberosities.

PhI	Ant. ACA-74	Ant. ACA-78	Ant. ACA-106	Post. ACA-122	Post. ACA-123
Maximal length	69.0	65.5	71.7	66.0	67.5
Anterior length	61.0	57.5	66.0	59.5	59.0
Minimal breadth	34.8	35.0	36.0	34.0	35.0
Proximal breadth		48.0	50.0	46.0	47.7
Proximal depth	34.0	33.0	35.7	35.5	35.5
Distal breadth at tuber.	40.7	41.0	45.0	39.0	39.2
Distal articular breadth	42.5	42.0	44.8	40.0	
Distal articular depth	24.0	22.0	24.0	22.8	

PhII	Ant. ACA-81	Ant. ACA-260	Post. ? ACA-113	Post. ? ACA-83
Maximal length	48.0	47.5	45.0	44.0
Anterior length	39.0	37.0	35.0	35.0
Minimal breadth	44.0	41.0	40.0	39.0
Proximal breadth	52.0	52.0	47.0	[45]
Proximal depth	32.0	31.0	30.0	30.0
Distal articular breadth	51.0	45.5	43.0	42.0
Distal articular depth	25.0		24.0	24.0

PhIII	Ant. ACA-125	Ant. ACA-251	Post. ACA-126	Post. ACA-89	Post. Juv. ACA-88
Maximal length	59.0	[57]	65.0	61.0	[50]
Anterior length	60.0	[55]	65.0	63.5	[54]
Maximal breadth	78.0	76.0	71.5	69.0	58.0
Articular breadth	52.0	48.0	47.0	45.0	40.0
Articular depth	25.0	26.5	25.0	25.5	23.5
Circumference	[170]	[150]	165.0	150.0	[125]

TABLE 15. — Individual and average data on some size indicators in equids. Body weights in kilograms. Basilar lengths (**Basilar L**) and other measurements in millimeters. **MC10**, **MT10**, distal maximal supra-articular breadth of third metacarpals and third metatarsals, **MC13**, **MT13**, distal minimal depth of the medial condyle of third metacarpals and third metatarsals; **M1 OL**, occlusal length of upper M1; **M1 Ob**, occlusal breadth of the upper M1; n, number of specimens.

	Weight	n	MC10	MC13	n	MT10	MT13	n
Donkey, Kiel 9272	98.5	1	29.0	19.0	1	28.7	19.7	1
Donkey, Kiel 29027	130.3	1	34.5	21.0	1	34.6	22.0	1
Donkey, Kiel 1395	207.0	1	43.5	28.0	1	43.5	26.8	1
Donkey, Kiel 1399	138.5	1	37.5	22.0	1	35.5	21.8	1
Donkey, Kiel 26192	163.5	1	31.0	19.0	1	30.6	21.0	1
Horse, Kiel 16449	140.0	1	36.0	21.0	1	36.0	21.0	1
Horse, Kiel 20253	193.0	1	38.0	24.0	1	37.0	22.9	1
Horse, Kiel 20914	158.0	1	36.0	22.2	1	37.0	22.0	1
Horse, Kiel 16438	143.0	1	32.0	19.5	1	33.0	20.0	1
Horse, Kiel 31431	263.0	1	48.0	28.5	1	49.0	29.0	1
Horse, Kiel 16719	209.0	1	40.0	24.0	1	40.0	24.0	1
Horse, Kiel 18146	179.0	1	46.0	27.0	1	46.5	28.0	1
Horse, AC 1937-51	142.0	1	37.0	20.5	1	36.0	20.5	1
Przewalski, average	274.8	5	46.0	28.6	8	47.6	27.7	7
Plains zebra, min	175.0	?	40.0	22.8	26	39.8	23.4	26
Plains zebra, max	320.0	?	48.0	29.0	26	47.0	28.0	26
Hartmann's zebra, min	276.0	?	41.5	25.0	16	43.0	24.0	16
Hartmann's z., average	309.5	?	44.3	26.4	16	44.2	26.1	16
Hartmann's zebra, max	343.0	?	46.5	28.0	16	46.0	27.0	16
Grévy's zebra, min	352.0	?	42.6	26.5	21	41.4	26.4	21
Grévy's zebra, average	400.0	?	46.1	28.3	21	46.5	28.2	21
Grévy's zebra, max.	450.0	?	49.5	29.7	21	49.0	30.0	21
Poitou max.	410.0	?	50.5	32.5	4-5	49.5	30.9	4-5
<i>H. heintzi</i> , Çalta			47.1	27.9	5-6	47.0	27.9	5-6
<i>H. cf. longipes</i> , Çalta						40.0	28.0	1
<i>H. longipes</i> , Pavlodar			36.5	26.4	2	39.0	26.0	1

	Basilar L	n	M1 OL	M1 Ob	n
Donkey, Kiel 9272	352	1	21.0	22.0	1
Donkey, Kiel 29027	383	1	21.0	24.0	1
Donkey, Kiel 1395	452	1	21.0	24.0	1
Donkey, Kiel 1399	410	1	21.0	24.0	1
Donkey, Kiel 26192	350	1	20.3	22.3	1
Horse, Kiel 16449	375	1	24.5	23.5	1
Horse, Kiel 20253	390	1	19.0	22.0	1
Horse, Kiel 20914	370	1	21.0	23.0	1
Horse, Kiel 16438	368	1	22.0	22.0	1
Horse, Kiel 31431	492	1	27.3	25.1	1
Horse, Kiel 16719	395	1	21.0	22.7	1
Horse, Kiel 18146	440	1	23.5	25.0	1
Horse, AC 1937-51	377	1	22.0	23.0	1
Przewalski, average	487	11	25.9	27.4	10
Plains zebra, min.	405	169	18.0	20.7	101
Plains zebra, max.	486	169	24.5	26.0	101
Hartmann's zebra, min.	435	46	21.0	23.4	40
Hartmann's z., average	473	46	23.7	25.5	40
Hartmann's zebra, max	510	46	28.0	27.0	40
Grévy's zebra, min.	485	51	21.0	24.4	44

	Basilar L	n	M1 OL	M1 Ob	n
Grévy's zebra, average	532	51	24.8	26.2	44
Grévy's zebra, max.	560	51	28.0	28.0	44
Poitou max.	538	5	26.5	28.0	5
<i>H. heintzi</i> , Çalta			24.5	23.0	1
<i>H. longipes</i> , Pavlodar			25.8	25.9	10

TABLE 16. — Percentages of error found when different equations are used to estimate average body weights of modern *Equus* from average variables. The averages are either already printed in table 15, or calculated from data printed in table 15. Alberdi *et al.*, paper of 1995, cited in text. MC10, MT10, distal supra-articular breadths of third metacarpals and metatarsals; MC13, MT13, distal minimal depths of the medial condyle of third metacarpals and third metatarsals; MC10 × MC13 and MT10 × MT13, products of the latter. Surface of M1, product of occlusal length by occlusal breadth of the upper first molar.

	Alberdi <i>et al.</i> % error	This paper % error	Alberdi <i>et al.</i> % error	This paper % error	This paper % error
	MC10		MC13		MC10 × MC13
Donkeys	7.2	-4.7	11.7	6.9	0.2
Poitou donkeys	7.6	2.5	36.3	11.6	7.8
Horses	20.2	9.3	13.3	6.1	6.9
Przewalski's horses	23.3	15.4	37.5	18.3	17.0
plains zebras	20.9	12.2	12.8	0.9	5.8
Hartmann's zebras	-1.5	-8.5	-4.4	-15.1	-12.2
Grévy's zebras	-14.7	-20.1	-8.5	-20.9	-20.5

Surface of M1

Donkeys	22.7	22.2
Poitou donkeys	48.8	-2.5
Horses	28.7	18.1
Przewalski's horses	95.5	33.9
plains zebras	-17.9	-21.4
Hartmann's zebras	9.5	-12.1
Grévy's zebras	4.5	-22.0

	MT10		MT13		MT10 × MT13
Donkeys	10.8	-2.9	31.1	8.1	0.8
Poitou donkeys	10.6	3.0	25.4	13.5	8.2
Horses	25.1	11.7	24.3	3.8	7.7
Przewalski's horses	32.4	21.6	29.9	13.6	18.0
plains zebras	16.9	6.0	16.8	0.1	2.9
Hartmann's zebras	-2.2	-11.1	-2.4	-16.1	-13.5
Grévy's zebras	-14.1	-21.4	-6.0	-17.4	-19.6