Early Pleistocene equids (Mammalia, Perissodactyla) of Nalaikha, Mongolia, and the emergence of modern *Equus* Linnaeus, 1758

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ABSTRACT
Evidence is given for the presence of at least three species of *Equus* at Nalaikha, Mongolia. The smallest, *E. nalaikhaensis* Kuznetsova & Zhegallo, 1996, well represented by skull and limb bones, belongs certainly to modern *Equus* (not *Allohippus* Gromova, 1949) and exhibits a mosaic of characters found in extant hemiones, asses, and Grevy's zebras and in fossil *E. altidens* v. Reichenau, 1915 (from Süssenborn) and *E. hipparionoides* Vekua, 1962 (from Akhalkalaki). In accordance with recent biomolecular studies of equids, *E. nalaikhaensis* may be placed after the individualisation of caballines and between the branching points of hemiones and of the ass-zebra lineage. The other species of Nalaikha are not well represented. They may be related to northeastern Siberian fossils of Olyorian age, in particular to caballines and to *E. suessenbornensis* Wüst, 1901 *s.l.* Other true *Equus* (in particular *E. scotti* Gidley, 1900, *E. coliemensis* Lazarev, 1980, *E. apolloniensis* Koufos, Kostopoulos & Sylvestrou 1997, and *E. graziosii* Azzaroli, 1966) are also documented and discussed, stressing the frequent dissociation of characters usually associated in extant species.

KEY WORDS
Mammalia,
Perissodactyla,
Equus,
early Pleistocene,
Mongolia,
Old World,
North America,
craniology,
phylogeny.

RÉSUMÉ
Les équidés (Mammalia, Perissodactyla) du Pléistocène inférieur de Nalaikha (Mongolie) et l'émergence des Equus *Linnaeus, 1758 modernes.*
Parmi les espèces représentées à Nalaikha (Mongolie), la plus petite, *Equus nalaikhaensis* Kuznetsova & Zhegallo, 1996, associe un crâne ressemblant à celui des hémiones et zèbres de Grévy actuels à des métapodes évoquant *E. altidens* v. Reichenau, 1915 de Süssenborn et *E. hipparionoides* Vekua, 1962 d'Akhalkalaki, et des phalanges ressemblant à celles des ânes, des hémiones et des zèbres de Grévy. La confrontation des données paléontologiques avec les résultats des études biomoléculaires récentes suggère pour *E. nalaikhaensis* une place postérieure à l'émergence des caballins et entre les points d'émergence des hémiones et de la lignée commune des ânes et des zèbres. Les autres espèces de Nalaikha sont mal représentées : un caballin probable et un taxon évoquant des équidés de l'Olyorian du nord-est de la Sibérie que nous incluons dans le groupe *E. suessenbornensis* Wüst, 1901 *s.l.* Ce groupe, probablement proche des hémiones, présente aussi des associations curieuses de caractères dentaires, crâniens et post-crâniens. Divers crânes d'*Equus* de l'Ancien Monde (Algérie, Afrique du Sud, Grèce, Italie, Sibérie) et de l'Amérique du Nord (Texas) sont également documentés et discutés.

MOTS CLÉS
Mammalia,
Perissodactyla,
Equus,
Pléistocène inférieur,
Mongolie,
Ancien Monde,
Amérique du Nord,
craniologie,
phylogénie.

THE NALAIKHA LOCALITY

The quarry of Nalaikha (47°N, 107°E) is situated upstream in the valley of Tola, 10 km from Ulan Bator, Mongolia (Fig. 1). Numerous fossils were found in the alluvial sands and sandy clays of the layer 6 and the upper part of layer 7. According to Zhegallo *et al.* (1982) and Sotnikova (1988), micromammals of layer 6, sometimes in anatomical connection, include *Ochotona* sp., *Marmota* sp., *Citellus* sp., *Allactaga* sp.; large mammals include *Mammuthus* sp., *Coelodonta tologojensis* Beljaeva, 1966, two *Equus* sp., *Spirocerus kiakhensis wongi* Teilhard de Chardin & Piveteau, 1930, *Gazella* (*Procapra*) cf. *gutturosa*, *Bison* sp., Megacerini Owen, 1844 gen. indet., *Xenocyon lycaonoides* Kretzoi, 1938, *Canis variabilis* Pei, 1934, *Ursus* sp. ex gr. *deningeri* v. Reichenau, 1904, *Hyaena brevirostris sinensis* Owen, 1870, *Panthera* cf. *tigris palaeosinensis* Zdansky, 1928, and *Felis* sp. Palynological data indicate a mild and humid climate. Although no precise datation is possible, the main fauna is believed to belong in the late lower Pleistocene, not younger than 0.9 Ma (Zhegallo pers. comm.).

THE EQUIDS OF NALAIKHA

Zhegallo *et al.* (1982) recognized a large *Equus* ex gr. *sanmeniensis*, and a smaller *Equus* (*Hemionus*) sp. In subsequent works (Kuznetsova 1996; Kuznetsova & Zhegallo 1996; Kuznetsova & Zhegallo in press), *E. nalaikhaensis* Kuznetsova & Zhegallo, 1996 was described on the basis of a nearly complete skull, and Kuznetsova & Zhegallo (1996) recognized three species.

When some doubt arises about the number of taxa inside a sample, it is convenient to use the Variability Size Index (VSI), one of the size index scaling techniques devised by archeozoologists (Uerpmann 1982, 1990; Meadow 1986, 1999). A sample including all the bones of a taxon is chosen as reference. Mean and standard deviation are calculated for each measurement of this sample. The comparisons are done using the following formula: VSI = 25(x-m)/s where s is the standard deviation of the mean (m) of the measurement series (the "standard") to which another measurement (x) is being compared. The obtained values are plotted on a histogram graduated in one, two, three, or more standard deviations from the standard. As phrased by Meadow

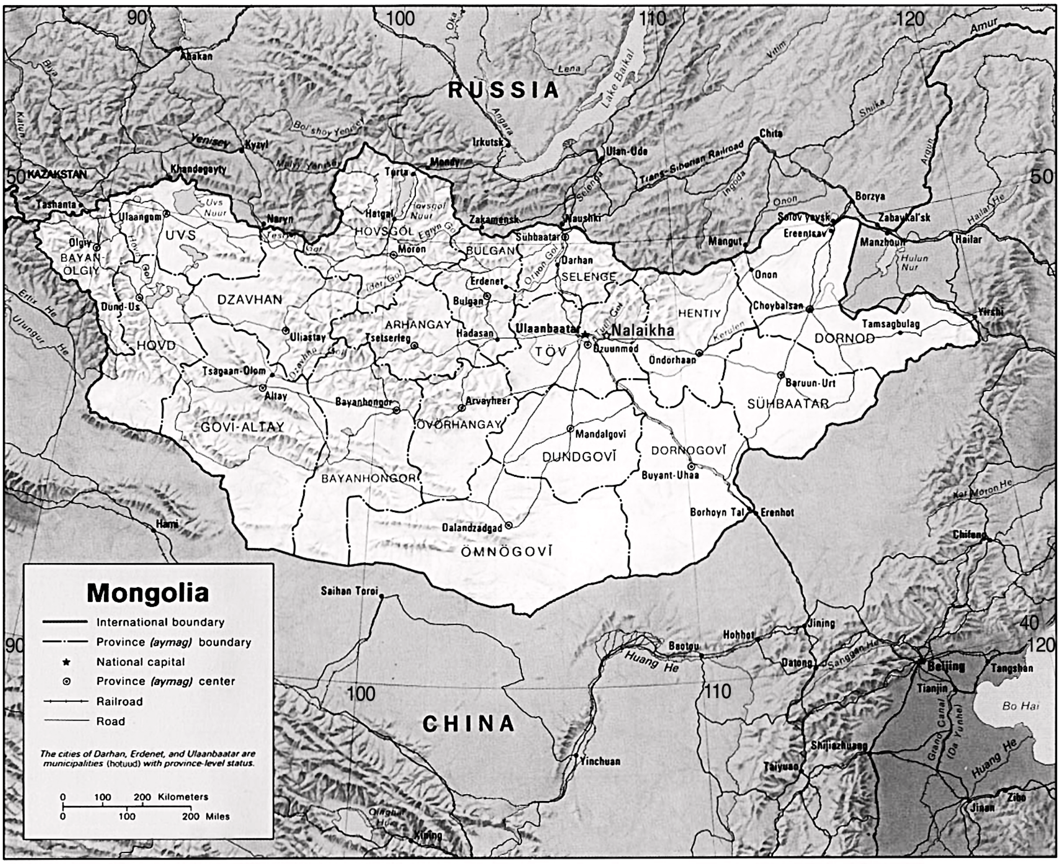

FIG. 1. — Map of Mongolia.

(1986): "Using this formula, the standard dimension is set at zero; a measurement one standard deviation larger than the standard dimension will be plotted at 25, one standard deviation smaller at -25, etc.". Here we have used the monospecific and homogeneous sample of *Allohippus stenonis vireti* Prat, 1964 of Saint-Vallier, France, as reference. We considered separately the lengths and breadths of the adult bones represented inside the Nalaikha sample. Means and standard deviations for Saint-Vallier are in Annexe (Table 1). On Fig. 2, the range of variation and distribution of breadths and lengths inside the Nalaikha sample suggests the presence of three size groups.

Judging by what we know about modern species, size differences cannot be explained by sexual dimorphism. As shown by Fig. 3, the metapodials of male Grevy's zebras, although on the average wider at their distal ends, are very close to, and cluster with, those of female individuals. In the case of Nalaikha, the range of variation is much larger, and there is no overlap between the three groups. Moreover, as will be discussed later, the small metapodials are much slenderer than the middle-sized ones.

Now we have to decide which group of metapodials belong to the skull of *E. nalaikhaensis*. Previous studies have shown that there is a fairly good relation between the basilar length of a skull of *Equus* and the distal breadths of the metapodials (Eisenmann & Karchoud 1982). This relation is represented on Fig. 4, using the metatarsal

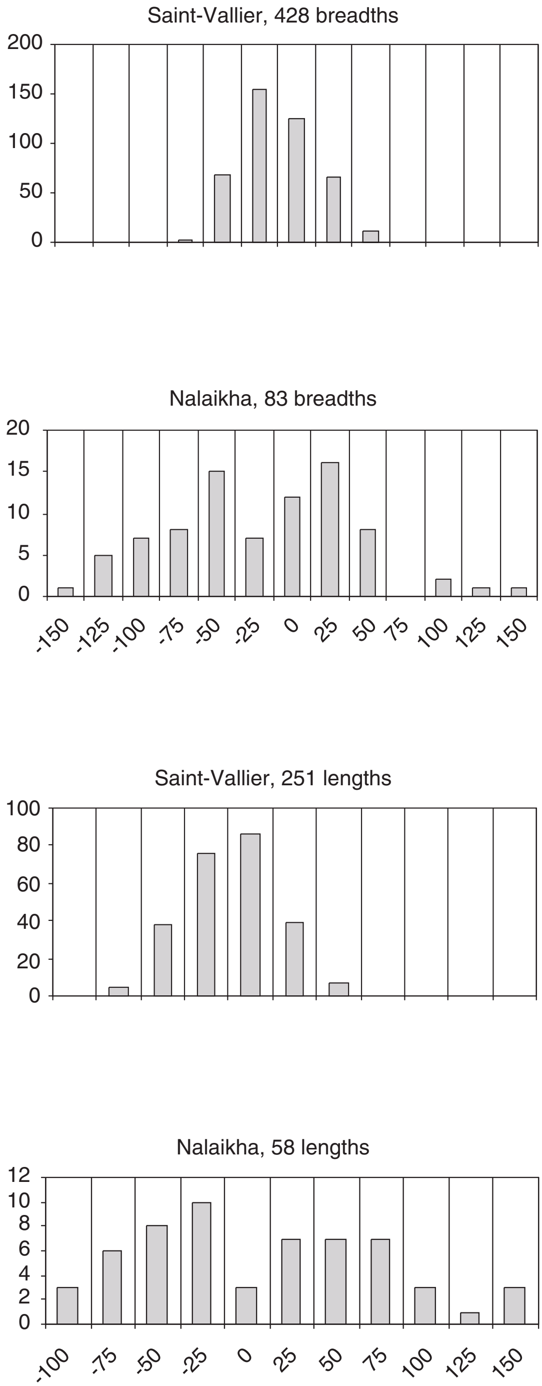

FIG. 2. — Variability Size Indices of *Allohippus stenonis vireti* Prat, 1964 (Saint-Vallier, France) and the sample of equids of Nalaikha (Mongolia).

distal articular breadth of three species of modern *Equus* (*E. hemionus* Pallas, 1777, *E. zebra* Linnaeus, 1758, and *E. grevyi* Oustalet, 1882) and two subspecies of *Allohippus stenonis* Cocchi, 1867 (of Saint-Vallier, and of La Puebla de Valverde, Spain). The basilar length of *E. nalaikhaensis* is 545 mm. It fits best with the small group of MTIII. Extrapolation is difficult for very large metapodials, but it is probable that basilar lengths of about 570 mm can be expected for the middle group (*Equus* sp. A). The biggest MTIII (*Equus* sp. B) would fit with even larger skulls.

ABBREVIATIONS

APL	University of Thessaloniki;
IA	Institute of Geology, Iakutsk;
IGF	Paleontological Institute, Florence;
NMC	National Museum of Canada, Ottawa;
PIN	Paleontological Institute, Moscow;
SI	Severstov Institute, Moscow;
ZIN	Zoological Institute, Sankt-Petersburg;
ZM	Zoological Museum, Cape Town.

Family EQUIDAE Gray, 1821
Genus *Equus* Linnaeus, 1758

Equus nalaikhaensis
Kuznetsova & Zhegallo, 1996

SKULL

An exceptionally well preserved skull (PIN 3747-500) belongs to a very old male (Fig. 5). The basilar length is 545 mm. Among extant wild species, only *E. grevyi* reaches this size. Similar or larger sizes may be observed in Pliocene equids like *Allohippus stenonis* of Saint-Vallier or *Plesippus shoshonensis* Gidley, 1930 of Hagerman Quarry (Idaho, USA). But species belonging to primitive forms such as *Allohippus* and *Plesippus* Matthew, 1924 differ from extant species by basicranial proportions (Eisenmann & Baylac 2000). In extant species the distance between the Basion and the Hormion (Fig. 6) is long relative to the overall palatal length. By that character, the skull of Nalaikha must be considered as modern and referred to *Equus*.

During the middle Pleistocene, the caballine equids were frequently very large. The skulls of

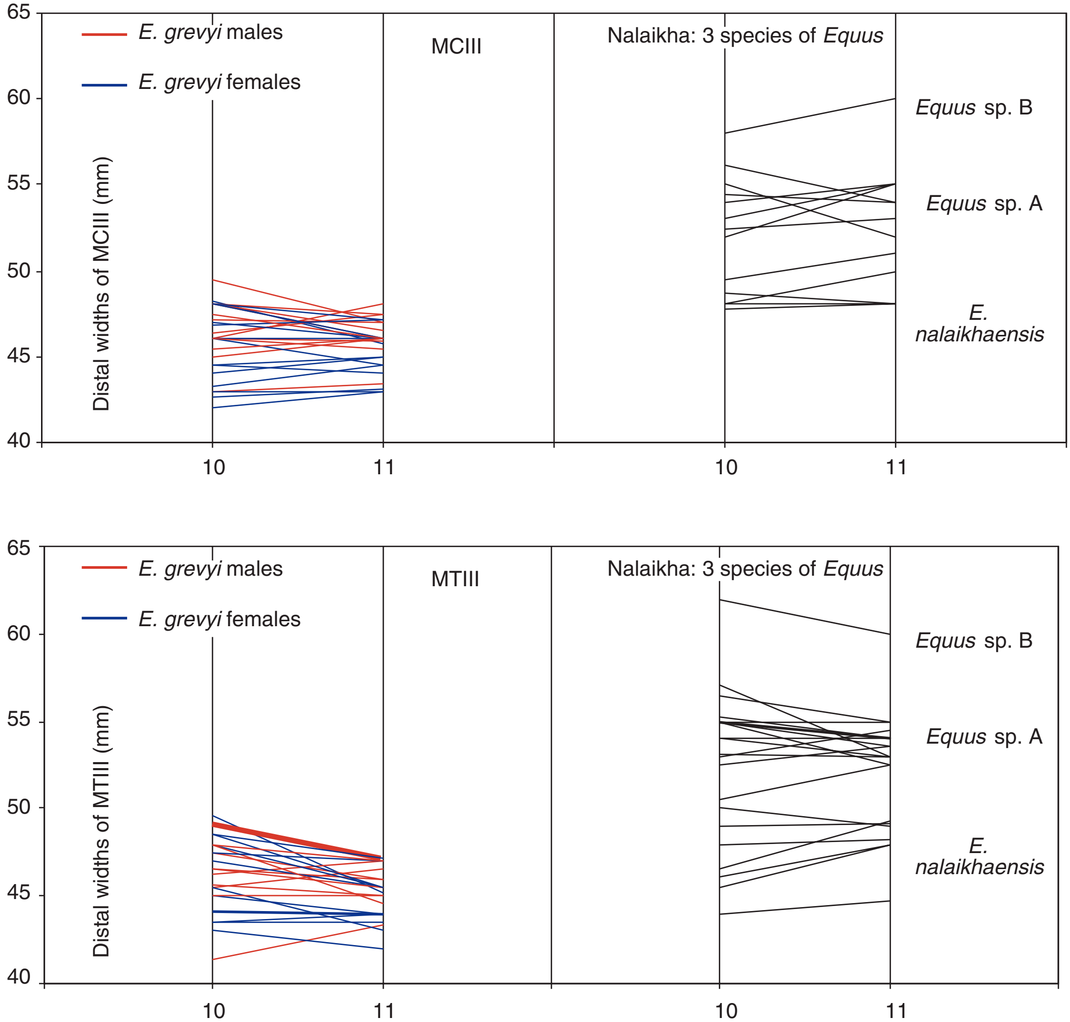

FIG. 3. — Distal supra-articular and articular breadths of metacarpals (MCIII) and metatarsals (MTIII) of extant Grevy's zebras and equids of Nalaikha.

extant caballines wild and domestic (*E. przewalskii* Poliakov, 1881, *E. caballus* Linnaeus, 1758 or *E. ferus* Boddaert, 1785) and fossil caballines may be distingushed from the skulls of asses (wild and domestic) by the so-called Franck's Index. In asses, the distance between the staphylion and the hormion (Fig. 6) is the longest, while in caballines, the longest is the distance between hormion and basion. The separation is not good between caballines and other extant species. Fortunately, the Palatal Index (Eisenmann in press) gives much better discriminations. Both indices indicate that *E. nalaikhaensis* is not a caballine.
Further comparisons were done with non caballine extant *Equus*: Grevy's zebras (*E. grevyi*), plains zebras (*E. burchelli* Gray, 1824 and *E. quagga* Gmelin, 1788), mountain zebras (*E. zebra*), asses (*E. africanus* Heuglin & Fitzinger, 1866 and *E. asinus* Linnaeus, 1758), hemiones (*E. hemionus* and *E. kiang* Moorcroft, 1841). The overall

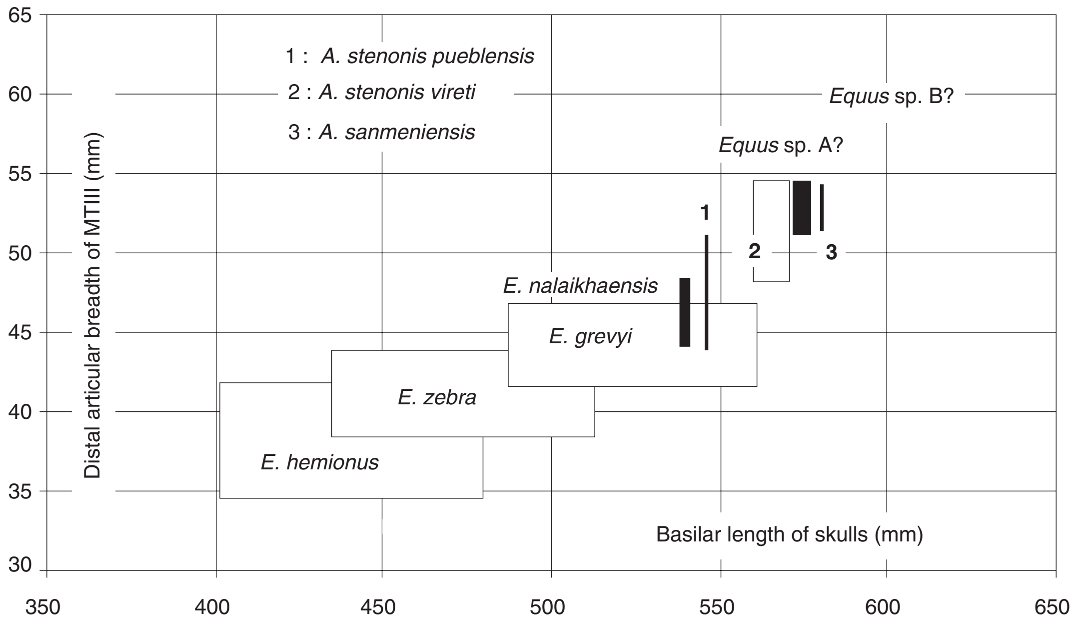

FIG. 4. — Relation between basilar lengths and distal articular breadths of metatarsals (MTIII) in different species of equids. Abbreviations: ***A.***, *Allohippus*; ***E.***, *Equus*.

resemblance of the skull of *E. nalaikhaensis* with that of *E. grevyi* is striking. *E. nalaikhaensis* fits inside the range of variation of *E. grevyi* by almost all its dimensions (Fig. 7; Annexe: Table 2). In particular, like in *E. grevyi* and most other zebras, and contrary to asses and hemiones, the skull is narrow (Fig. 8), even narrower than the average of them. But unlike most zebras and asses, and like in hemiones, the face is high. Moreover, relative to the basilar length, the muzzle is short. Similar shortness is exceptional in extant *Equus*, even in hemiones. Summing up, *E. nalaikhaensis* combines skull characters of extant zebras, asses and hemiones in an altogether original way.

Comparison with three fossil skulls are of special interest. They belong to *E. graziosii*, *E. apolloniensis* and *E. coliemensis*.

1. The type skull of *E. graziosii* is preserved at the Palaeontological Museum of Montevarchi and was described by Azzaroli (1966, 1979) who kindly provided a cast for the former Laboratoire de Paléontologie (Muséum national d'Histoire naturelle, Paris). This skull lacks the posterior part but it is perfectly preserved otherwise. *E. graziosii* (middle-upper Pleistocene) is much smaller than *E. nalaikhaensis* to which it resembles by its face and muzzle proportions; the frontal is however as wide as in *E. grevyi* (Fig. 7; Annexe: Table 2).

2. The type skull (APL 148) of *E. apolloniensis* of latest Villafranchian age (early-middle Pleistocene) excavated in Macedonia, was described by Koufos *et al.* (1997). It is almost entire but laterally compressed which makes comparisons difficult. In particular it is difficult to estimate its frontal width. However, like *E. nalaikhaensis* and *E. graziosii*, it definitely belongs to *Equus* by its basicranial proportions, as already demonstrated by Koufos *et al.* (1997). Like in *E. nalaikhaensis*, the muzzle is very short, but the face looks wider at the frontals (APL 147) and short, and the narial opening is also relatively shorter.

3. The northeastern Siberian skull (IA 1741, Geological Institute, Iakutsk) from Kolyma, probably late-early or early-middle Pleistocene, is the type of *E. coliemensis* and was described by Lazarev (1980). By the basicranial proportions, *E. coliemensis* is

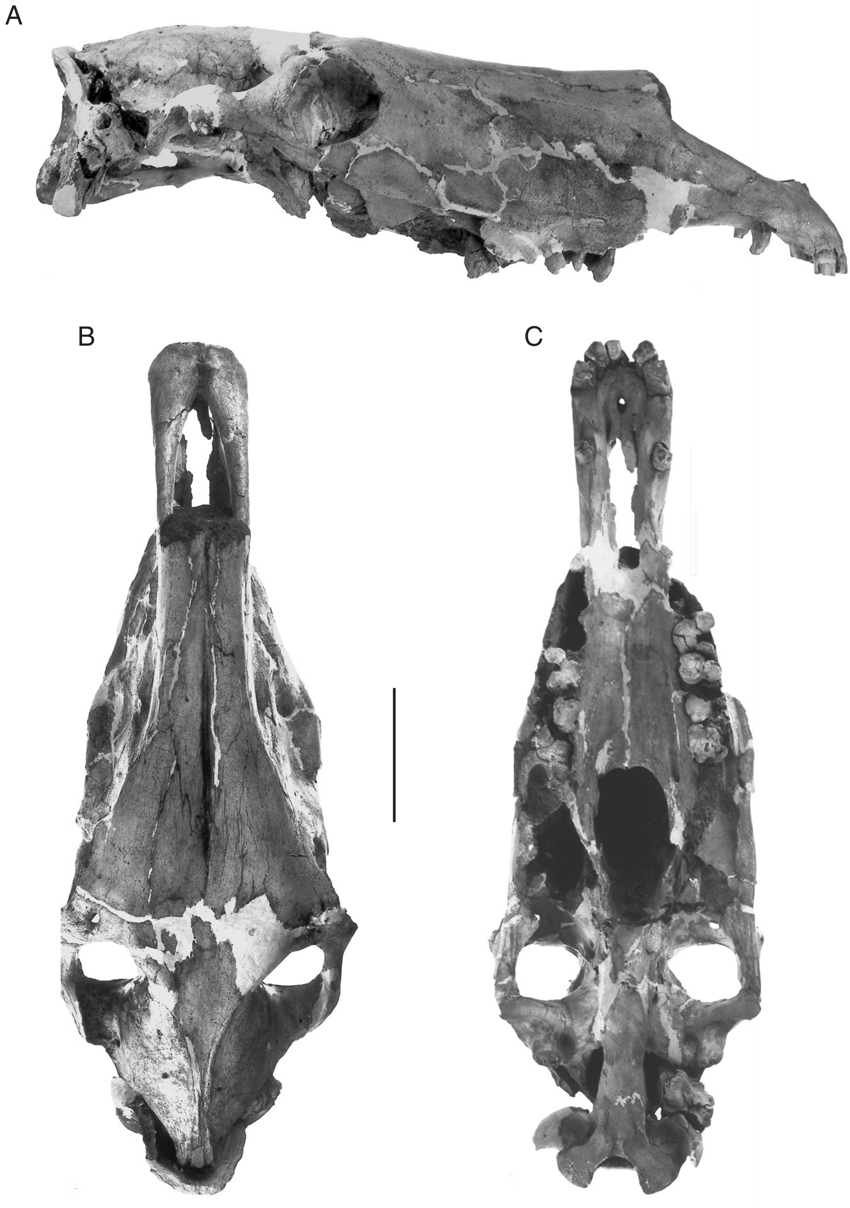

FIG. 5. — Type skull of *Equus nalaikhaensis* Kuznetsova & Zhegallo, 1996 (PIN 3747-500); **A**, profile; **B**, dorsal view; **C**, ventral view. Scale bar: 10 cm.

certainly also an *Equus*. It is about the same size as *E. nalaikhaensis* (basilar length: 538 mm) but different in proportions: the skull is wide at the frontals (Fig. 8), the supra-occipital crest is very narrow, and the muzzle longer and wider. Among extant species, the greatest similarities are with the much smaller *E. hemionus khur* Lesson, 1827 – the Indian hemione (Fig. 19; Annexe: Table 2). In particular, the shape and size of the supra-occipital crest are strikingly similar.

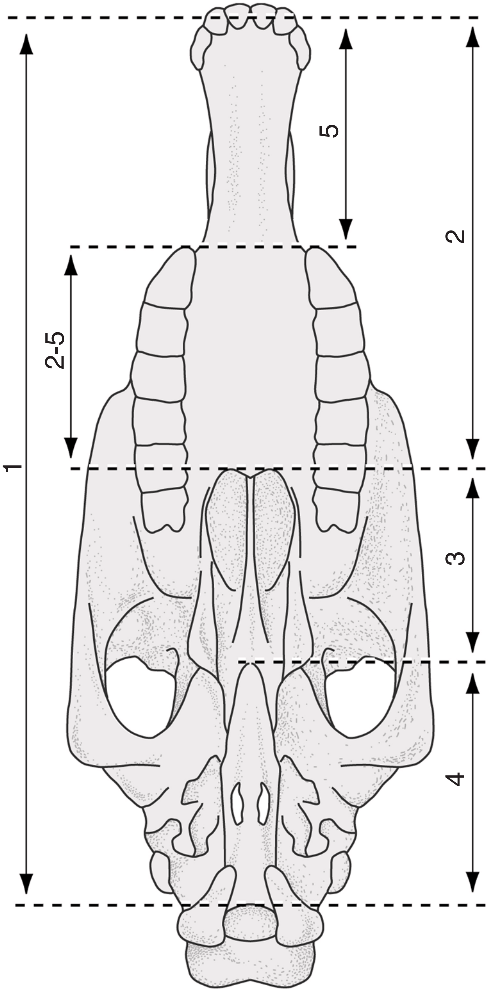

FIG. 6. — Basicranial measurements in *Equus*; **1**, basilar length; **2**, overall palatal length; **2**-**5**, palatal length; **3**, vomerine length; **4**, postvomerine length; **5**, muzzle length.

UPPER CHEEK TEETH

Unfortunately the skull of *E. nalaikhaensis* belongs to a very old animal and its teeth are worn to the roots. Other cheek teeth are extremely variable in size and in protocone length. Figure 9 is a scatter diagram of the protocone length versus the average occlusal diameter (length + width)/2. It shows that the teeth from Nalaikha are larger than in *E. grevyi*. Besides, the wide range of their protocone length implies the presence of more than one taxon as already noted by Kuznetsova (1996) and Kuznetsova & Zhegallo (1996). The sorting into separate taxa is however very difficult. Morphologically, one upper series (Fig. 10B) resembles extraordinarily a Grevy's zebra (Fig. 10A). One rather small premolar PIN 3747-606 (Fig. 10C) resembles modern hemiones by its deep post-protoconal groove. Two associated M2 and M3 (Fig. 10D) have long, flat, and wide protocones, such as found in some caballine horses like the type of *E. lambei* Hay, 1917 from the late Pleistocene of Yukon, the middle Pleistocene *E. orientalis* (Lazarev, 1980: pl. VII-3), and the lectotype ZIN 3966 of the lower-middle Pleistocene *E. nordostensis* Russanov, 1968 (Tcherski 1893: pl. VI-3; Lazarev 1980: pl. VII-2). We cannot presently decide which belonged to *E. nalaikhaensis*.

The upper cheek teeth of *E. graziosii* (Azzaroli 1979: pl. 2) and *E. apolloniensis* (Koufos *et al.* 1997: pl. I) resemble hemiones and some asses by their deep postprotoconal grooves and lack of plis caballins. The teeth of *E. coliemensis* (Lazarev 1980: pl. VII-1) are altogether different. The postprotoconal groove is deep but the plis caballins are very well developed. On P3 and P4 they have the same wide base as some teeth of Akhalkalaki and Süssenborn (Musil 1969: pls XXXIX-1, 3, 6 and others). This pattern was not observed in the Nalaikha sample.

LOWER CHEEK TEETH

They are also variable in size and morphology. Some have a very deep vestibular groove (Fig. 10F) like at Süssenborn (Musil 1969: pls XXXVIII-3, 4). Several have a very shallow lingual groove and a very long bilobated metaconid (Fig. 10G, H). Long and bilobated metaconids are frequent in hemiones, and are also found in *E. granatensis* Alberdi & Ruiz Bustos, 1985 of the lower Pleistocene of Venta Micena (Eisenmann 1999: pl. I-7). Some molars have a shallow vestibular groove (Fig. 10J) like in modern asses. Some may be caballoid. As for the upper cheek teeth, we do not know which belonged to *E. nalaikhaensis*.

The lower teeth of *E. apolloniensis* APL 570 (Koufos *et al.* 1997: pl. III-2) are absolutely ass-like: rounded double knots, shallow ectoflexids on molars. There are no lower cheek teeth associated with the type

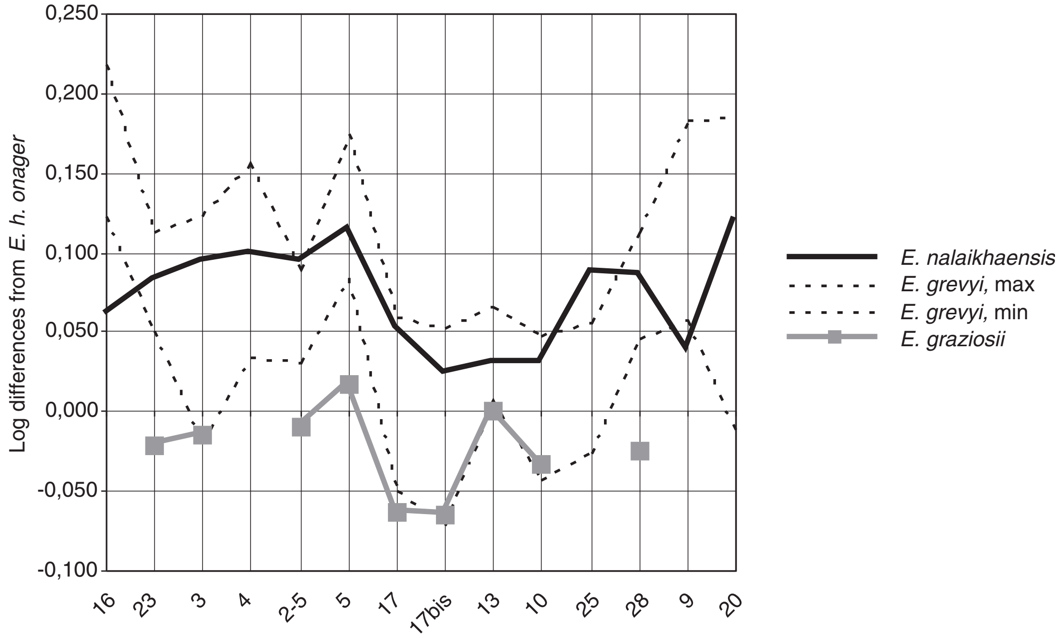

FIG. 7. — Ratio diagrams of skulls of *Equus nalaikhaensis* Kuznetsova & Zhegallo, 1996, extant Grevy's zebras, and late Pleistocene *E. graziosii* Azzaroli, 1966 of Italy. Measurements 16, 23, 3, etc. are defined in Annexe (Table 2).

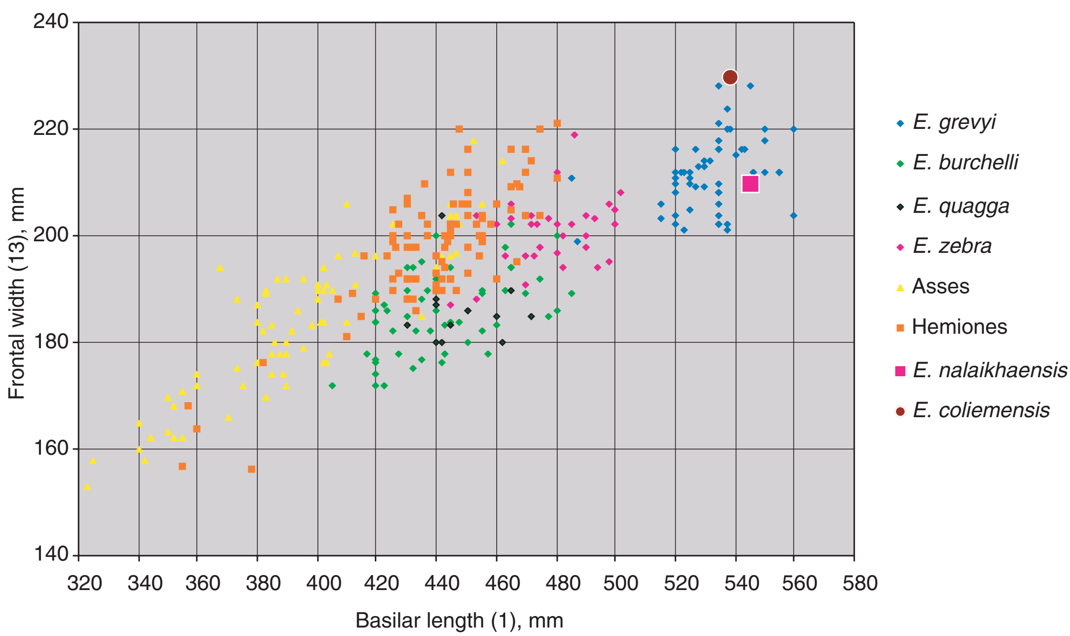

FIG. 8. — Scatter diagram of frontal width versus basilar length in extant *Equus* and in *E. nalaikhaensis* Kuznetsova & Zhegallo, 1996 and *E. coliemensis* Lazarev, 1980.

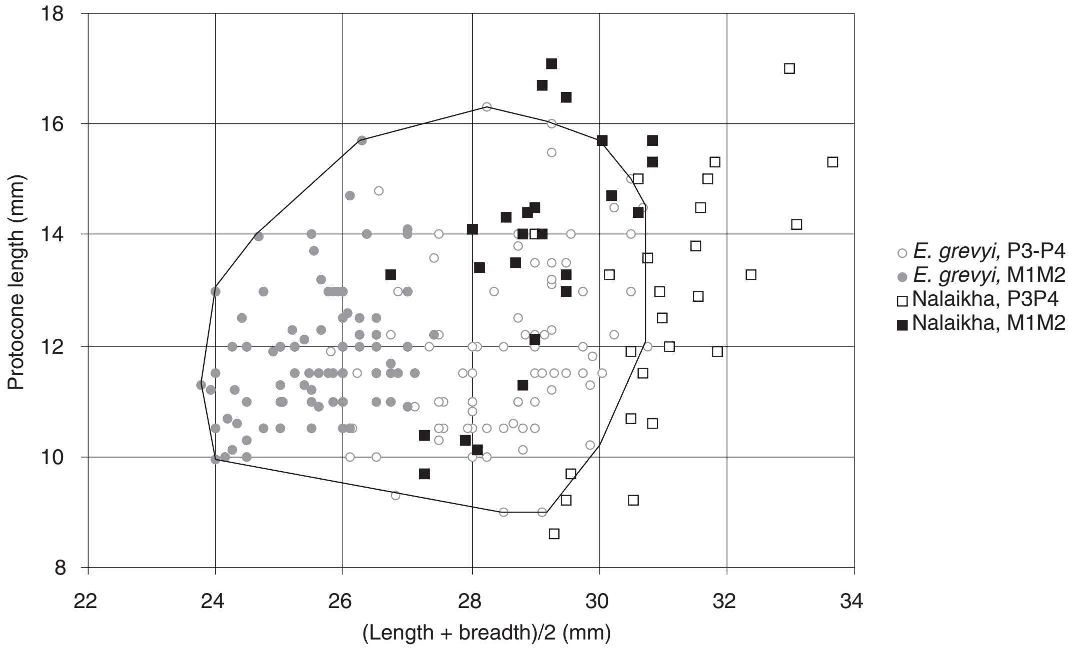

FIG. 9. — Scatter diagram of upper cheek teeth occlusal diameters (occlusal length + occlusal width)/2, observed inside the Nalaikha sample compared to the range observed in extant *Equus grevyi* Oustalet, 1882.

skulls of *E. graziosii* or *E. coliemensis*. Azzaroli (1979: pl. 7) refers to his species a lower mandible that looks rather caballine. Lazarev (1980: pl. VIII-1) refers to *E. coliemensis* a hemione-like worn series lacking the m2.

THIRD METACARPALS

We refer to *E. nalaikhaensis* eight relatively small metacarpals (Annexe: Table 3). Compared to *E. hemionus onager* Boddaert, 1785 (reference line in Fig. 11) *E. nalaikhaensis* has a wider diaphysis. Among fossil metacarpals, the less different are those of *E. hipparionoides* of Akhalkalaki and *E. altidens* of Süssenborn.

THIRD METATARSALS

We refer to *E. nalaikhaensis* eight relatively small metatarsals (Annexe: Table 4) and a few small fragments. Compared to *E. hemionus onager* (Fig. 12), *E. nalaikhaensis* has a wider and deeper diaphysis. Among fossil metatarsals, the less different are again those of *E. hipparionoides* of Akhalakalaki and *E. altidens* of Süssenborn.

FIRST PHALANGES

Most of the first phalanges of Nalaikha have about the same lengths. To sort out the phalanges of *E. nalaikhaensis*, we have used the relation existing between metapodial distal articular breadths and first phalange minimal diaphysis breadths (Fig. 13). We have plotted individual measurements for extant species (where limb bones are associated), and average values for fossil species. We refer to *E. nalaikhaensis* two anterior and six posterior relatively small first phalanges (Annexe: Table 5).

Their proportions are illustrated by ratio diagrams (Fig. 14). One of the anterior phalanges resembles those of some African wild asses while the other is more similar to one specimen of Onager. Among the first posterior phalanges, one is especially interesting to consider because it is associated with the type skull (PIN 3747-500). The ratio diagram shows its resemblance to one Grevy's zebra and one African wild ass. Another posterior phalanx is rather similar to an Onager.

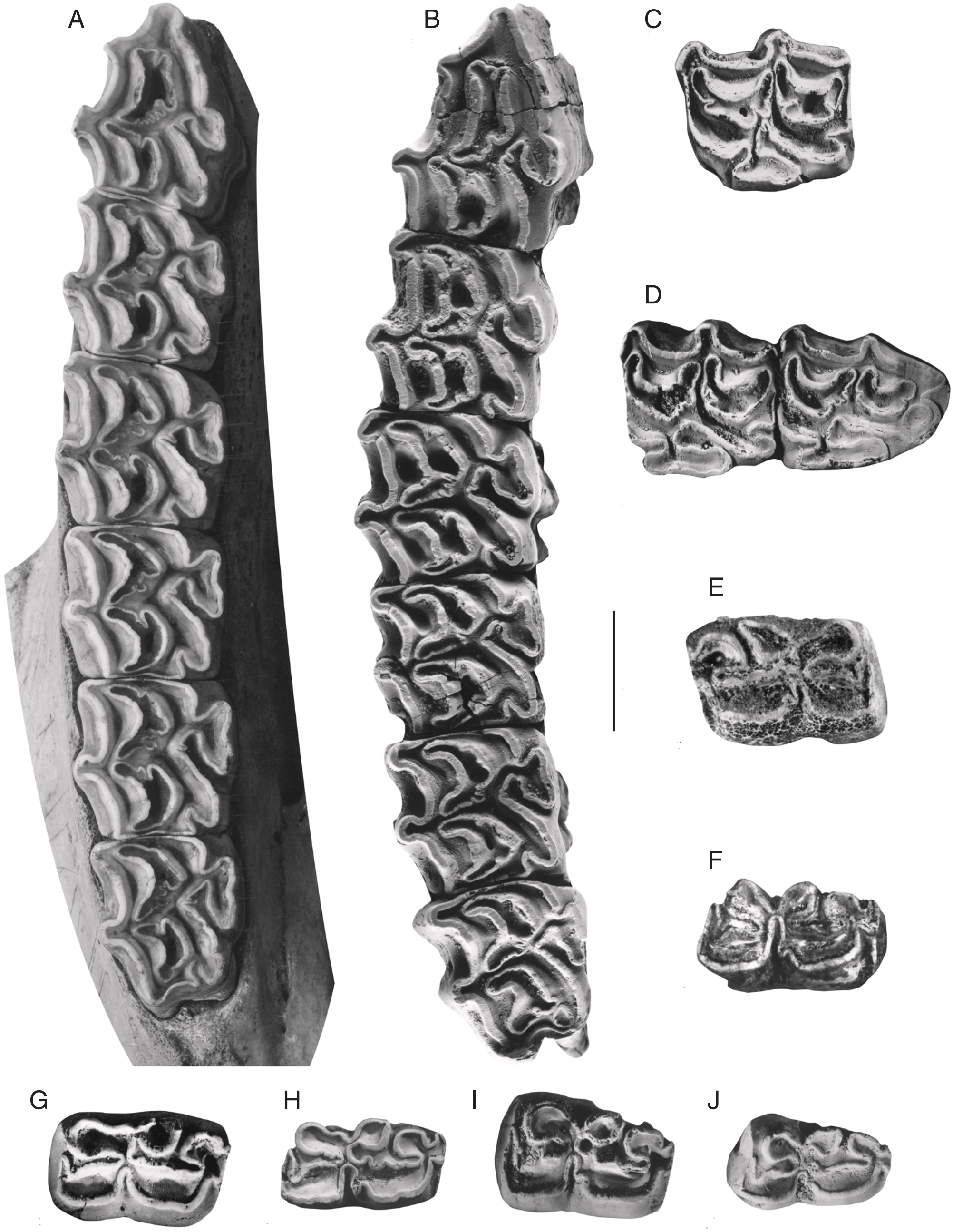

FIG. 10. — Upper and lower cheek teeth of equids of Nalaikha; **A**, upper right cheek teeth series of *Equus grevyi* Oustalet, 1882 (23-10-20-16, British Museum); **B**, upper right associated P2-M3 (PIN 3747-522, 600, 358, 402, 362, 395); **C**, upper left P3 or P4 (PIN 3747-606); **D**, associated upper left M2 and M3 (PIN 3747-457, 458); **E**, lower right p3 or p4 (PIN 3747-491); **F**, lower left m1 or m2 (PIN 3747-345); **G**, lower left p3 or p4 (PIN 3747-394); **H**, lower left m1 or m2? (PIN 3747-300); **I**, lower p3 or p4? (PIN 3746-546); **J**, lower m1 or m2 (PIN 3747-604). Scale bar: 2 cm.

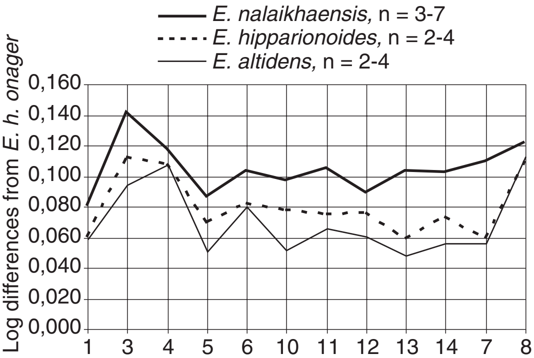

FIG. 11. — Ratio diagrams of third metacarpals of *Equus*. Measurements 1, 3, 4, etc. are defined in Annexe (Table 3).

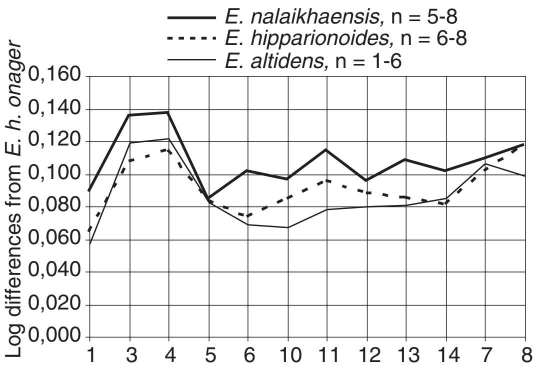

FIG. 12. — Ratio diagrams of third metatarsals of *Equus*. Measurements 1, 3, 4, etc. are defined in Annexe (Table 4).

Second and third phalanges

Second phalanges were sorted into two size groups according to the proximal breadth. We refer to *E. nalaikhaensis* eight specimens (Annexe: Table 6). One posterior phalanx is associated with the type skull (PIN 3747-500). Three other have about the same smallest breadth. The remaining four are considered as anterior.

Most third phalanges may be referred to *E. nalaikhaensis*. The largest (Annexe: Table 7) could belong to *Equus* sp. A. Anterior were distinguished from posterior on the basis of their greater breadths.

Other limb bones

We refer to *E. nalaikhaensis* a proximal fragment of radius (diaphysis breadth: 36 mm, proximal maximal width: 73.1 mm, proximal articular width: about 71 mm, antero-posterior articular depth: 37.1 mm) and a distal fragment possibly of the same individual (distal maximal width: about 80 mm, distal articular width: 66.5 mm, distal antero-posterior depth: 40.3 mm).

Limb segments proportions

The small amount of data does not warrant definitive conclusions. It seems, however, that *E. nalaikhaensis* was a cursorial species with relatively narrow third phalanges. It differs from all extant zebras (less cursorial) and asses (very long posterior first phalanges and very narrow third phalanges). It differs also from extant hemiones and from *E. apolloniensis* by the longer MTIII relative to MCIII and first phalanges.

Body mass

There is no satisfactory way to estimate the body mass of all and any kind of equid by using its cheek teeth (Alberdi *et al.* 1995) or its limb bones dimensions. That is because different species do not plot on the same regression lines. Applying the equations proposed by Eisenmann & Sondaar (1998), the body mass of an equid "in general" can be calculated by using one of the following formulas:

Ln body mass = -4.525 + 1.434 (Ln of the product of MC10 by MC13).

Ln body mass = -4.585 + 1.443 (Ln of the product of MT10 by MT13).

(Ln is the natural logarithm; MC10 and MT10 are the supra-articular distal widths of the third metacarpal and metatarsal, MC13 and MT13 the distal minimal depth of their medial condyles; measurements in mm; body mass in kg).

These formulas are acceptable in a broad way, giving correct estimations for donkeys, domestic horses, and plains zebras, but they overestimate the weights of Przewalski horses and underestimate the weights of mountain and Grevy's zebras. In the case of *E. nalaikhaensis*, the body weights calculated using metacarpals and metatarsals are respectively 381 and 371 kg.

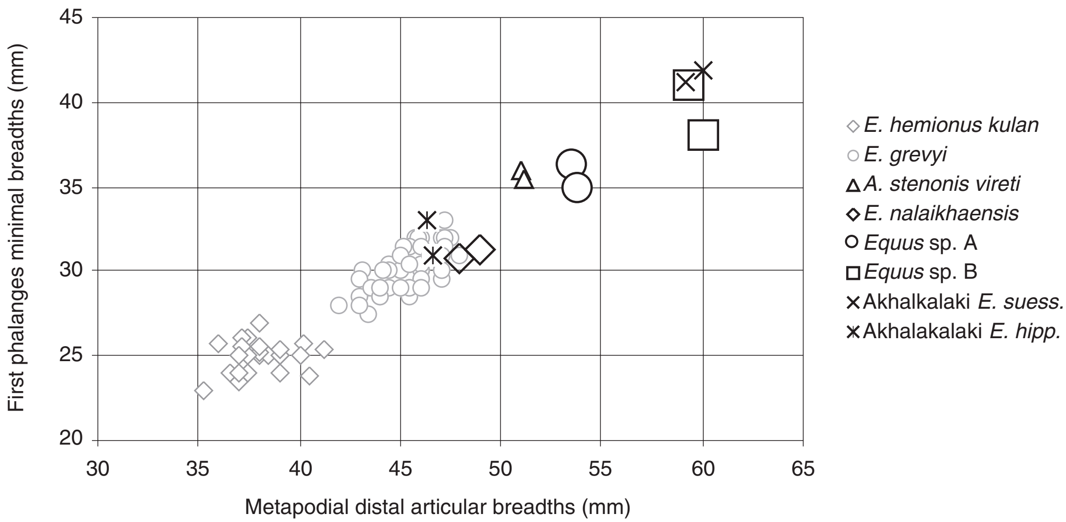

FIG. 13. — Scatter diagram of minimal breadths of first phalanges versus metapodial distal articular breadths. Abbreviations: ***A.***, *Allohippus*; ***E. suess.***, *Equus suessenbornensis*; ***E. hipp.***, *E. hipparionoides*.

ECOLOGICAL PROBLEMS

A long chain of assumptions is used to reconstruct environments from fossil equids. Previous studies have shown the relation that may be established between muzzle proportions and ways of feeding (Solounias & Moelleken 1993; Dompierre & Churcher 1996; Eisenmann 1999). Roughly speaking, square and broad shapes belong to grazers, long and narrow shapes to selective browsers. There are, moreover, numerous intermediary forms that may indicate mixed feedings. Recent grazers like hemiones and Przewalski horses usually feed on abrasive plants that grow in open dry landscapes. Their teeth have high crowns and simple enamel pattern. The proportions of their limb segments are very cursorial.

Palynological data on Nalaikha (Zhegallo *et al.* 1982) give evidence of mixed forest, bushes, forest-prairie, and prairie-steppe vegetation pointing to a mild, humid climate. The long and narrow muzzle of *E. nalaikhaensis* suggests it was a browser. But, if we were right in the referral of the limb bones, it was a rather cursorial species, which is somehow surprising.

Equus sp. A

According to its metapodials and first phalanges (Annexe: Tables 3-7), this species was probably not taller but certainly more robust than *E. nalaikhaensis*. We estimate its body mass at about 490 kg. The metacarpals are similar in size and proportions (Fig. 15) to some specimens collected in north-eastern Siberia, near the Chukochya River in deposits of early and late Olyorian age (Sher 1986, 1987). The metatarsals also resemble specimens of early Olyorian (Fig. 16). The basilar length of the skull is estimated at about 570 mm (Fig. 4).

Equus sp. B

According to the only entire bones – the first phalanges (Annexe: Table 5) –, *Equus* sp. B was both taller and more robust than *E. nalaikhaensis*. Its body mass may be estimated at about 600 kg, close to the estimated weight of *E.* cf. *suessenbornensis* of Akhalkalaki, Georgia (Vekua 1986), and the basilar length of the skull at more than 600 mm (Fig. 4). The fragmentary metapodials (Figs 17; 18)

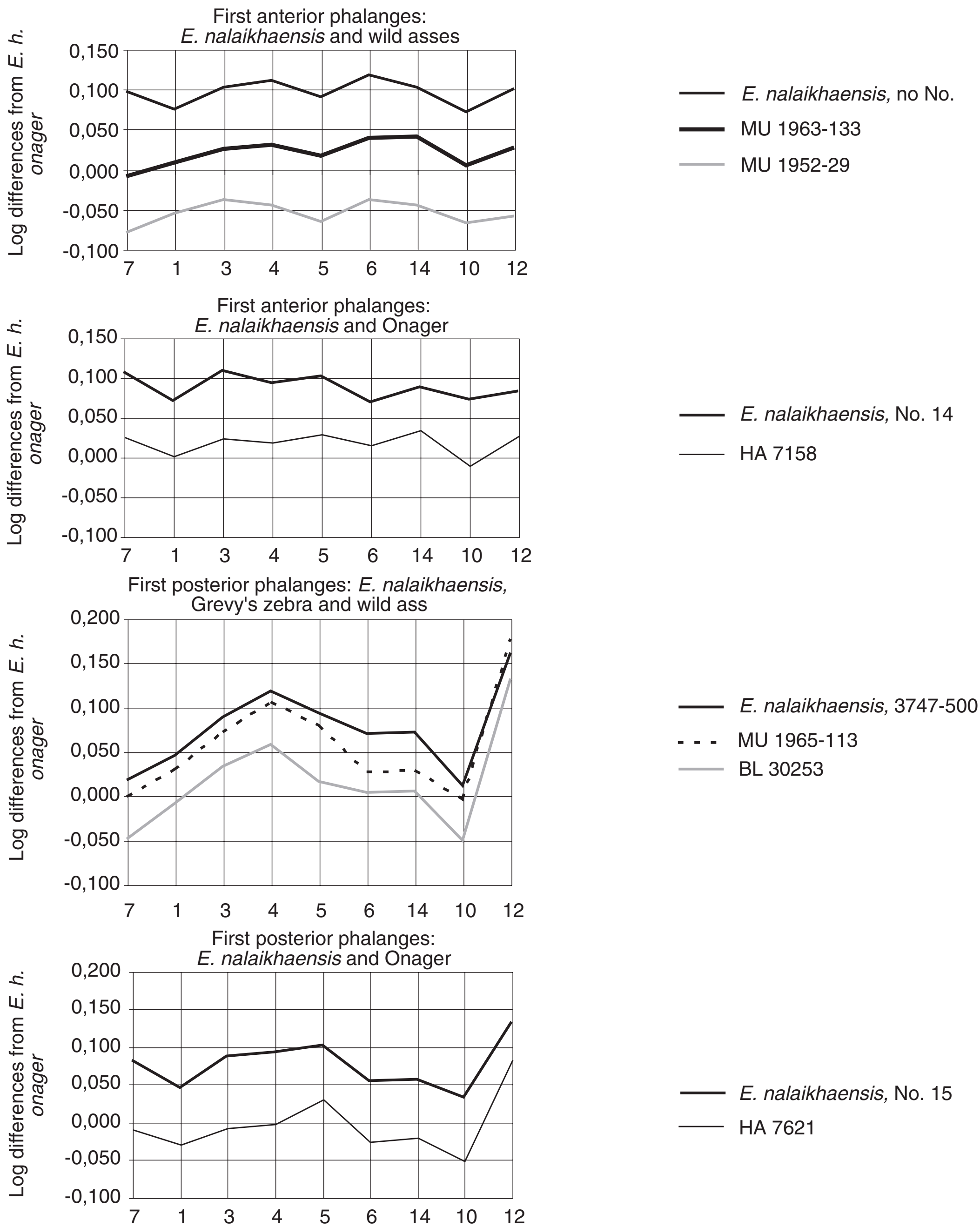

FIG. 14. — Ratio diagrams of first phalanges. Abbreviations: **BL**, Zoologisches Museum der Humboldt Universität, Berlin; **HA**, Zoologisches Institut und zoologisches Museum, Hamburg; **MU**, Zoologische Sammlung des Bayerischen Staates, Munich. Measurements 1, 3, 4, etc. are defined in Annexe (Table 5).

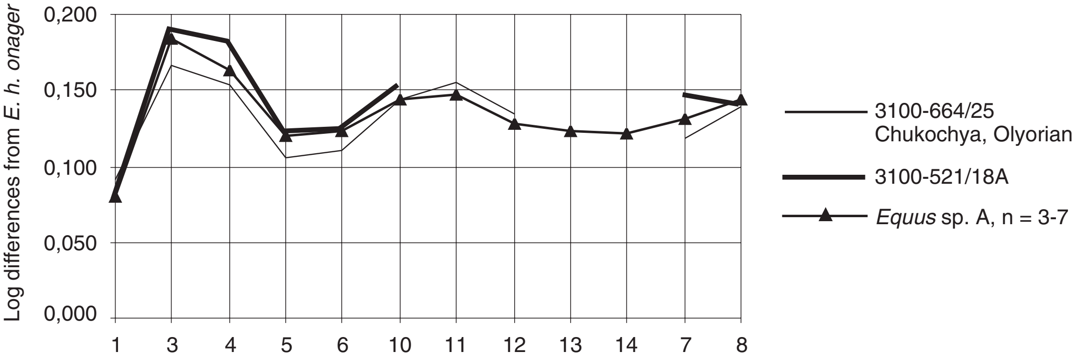

FIG. 15. — Ratio diagrams of third metacarpals (*Equus* sp. A). Measurements 1, 3, 4, etc. are defined in Annexe (Table 3).

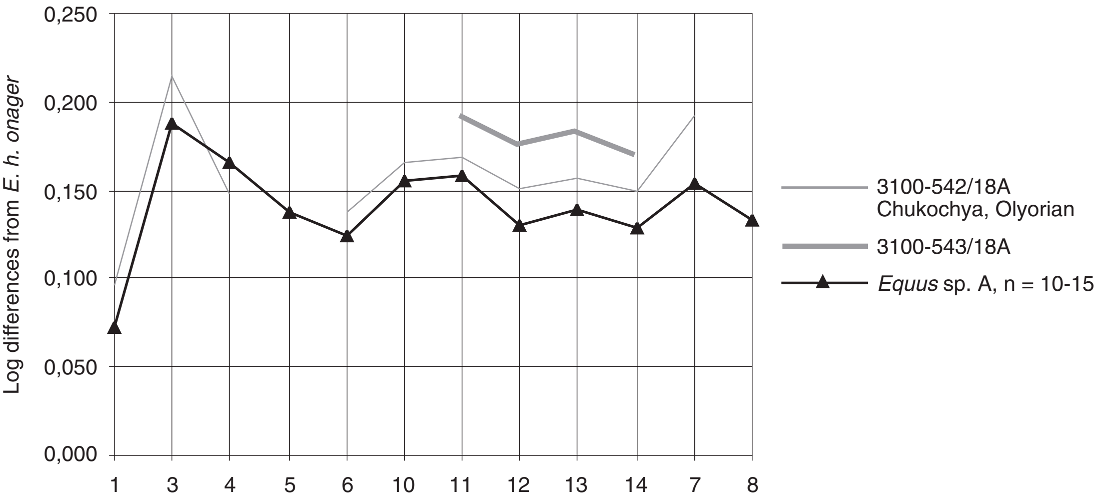

FIG. 16. — Ratio diagrams of third metatarsals (*Equus* sp. A). Measurements 1, 3, 4, etc. are defined in Annexe (Table 4).

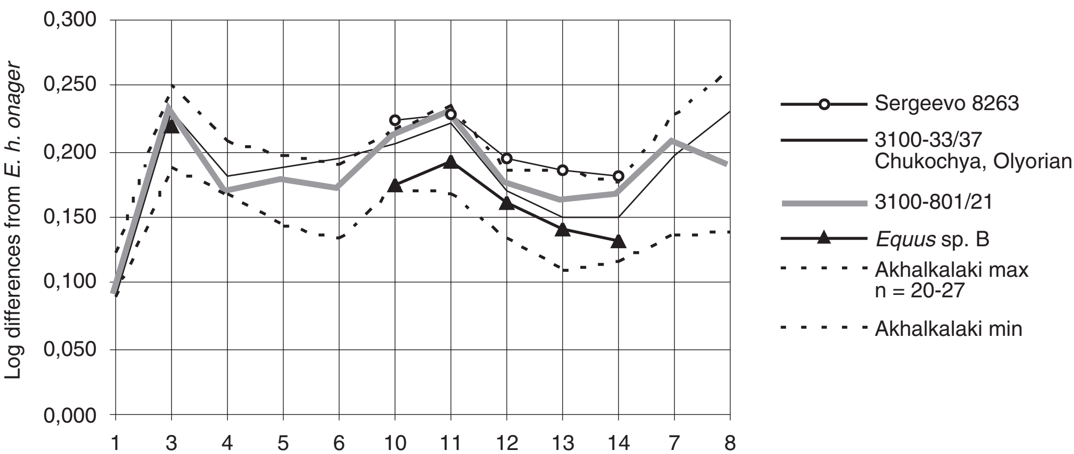

FIG. 17. — Ratio diagrams of third metacarpals (*Equus* sp. B). Measurements 1, 3, 4, etc. are defined in Annexe (Table 3).

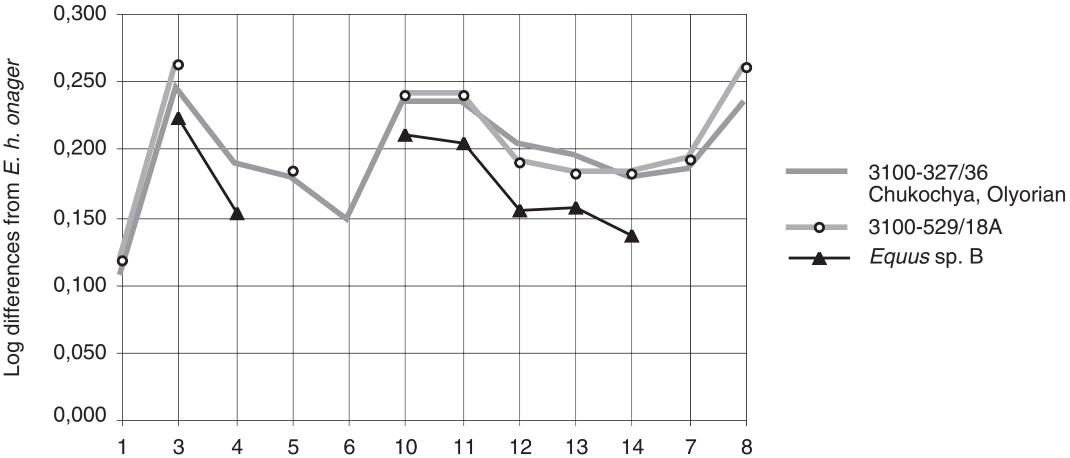

FIG. 18. — Ratio diagrams of third metatarsals (*Equus* sp. B). Measurements 1, 3, 4, etc. are defined in Annexe (Table 4).

are slightly smaller but resemble some of those collected in northeastern Siberia and tentatively referred to *E. verae* Sher, 1971 and a fragmentary MCIII of the early Pleistocene Sergeevo Formation of Kuznetsk Basin referred to *E.* cf. *suessenbornensis* (Foronova 1998, 2001).

EARLY AND MIDDLE PLEISTOCENE *EQUUS*

The current interpretation of the history of monodactyl equids (Azzaroli 1995; Koufos *et al.* 1997; Forsten 1999) assumes an evolution of (at least some) extant *Equus* species from primitive Pliocene or early Pleistocene *Plesippus* (mostly of North America) and/or *Allohippus* (mostly of the Old World). It seems, however, that the early and middle Pleistocene skulls do not show any intermediary morphologies between primitive and modern forms (Koufos *et al.* 1997; Eisenmann & Baylac 2000). On the other hand, any sort of tooth and limb morphologies and proportions may be found both among the primitive (*Plesippus*, *Allohippus*) and the modern (*Equus*) genera (or subgenera). As a consequence, when skull data are lacking, the distinction of species (or species groups) is possible but the generic attribution is subject to controversy. This happens even for late Pleistocene fossils for which the probability of being related to extant species is the greatest. For example, it is only recently that the discovery of a skull associated with a skeleton of *E. hydruntinus* Regalia, 1904 in the late Pleistocene of Crimea made clear that this species is closely related to hemiones (Burke *et al.* 2003) and is definitely not a "relic" of *Allohippus stenonis*. Farther away in time, quite a number of specific groups are too poorly known for generic attributions, let alone phylogenies. That is why skulls of *E. coliemensis*, *E. apolloniensis*, and *E. nalaikhaensis* are so interesting.

Nothing very precise is known about the dates of appearance and the phylogenetical relationship of modern species of *Equus*. Obviously enough, the first good paleontological record probably postdates the emergence of the species but how much?

PALEONTOLOGICAL DATA

Zebras and asses

First fossil skulls very probably related to plains zebras (Fig. 19; Annexe: Table 8) are known from middle Pleistocene in Algeria (*E. mauritanicus* Pomel, 1897 of Ternifine) and in South Africa (*E. capensis* Broom, 1909 at Elandsfontein). A skull (Nakaya pers. comm.) of an equid, possibly related to wild asses was found in older deposits of Kenya.

Caballines

On the basis of the paleontological record, the group of caballoid equids is probably present in North America during the early Irvingtonian (Azzaroli 1998) and certainly present during the middle Irvingtonian where it is well represented, skulls included, by *E. scotti* of Rock Creek, Texas, USA (Eisenmann in press). Compared to the skulls of a late Pleistocene *E. caballus* (IGF 13928 and 835, Val di Chiana, Italy; Azzaroli 1999), the skull of *E. scotti* (NMC 1281, National Museums of Canada, Ottawa) differs mainly by the sharper constriction of the muzzle (Fig. 19; Annexe: Table 8). A skull of broadly contemporaneous age, found in the Akanyan of northwestern Siberia (SI 160-455, Severtsov Institute, Moscow), is very similar to *E. scotti* (Fig. 19; Annexe: Table 8) but with more standard caballine proportions of the muzzle. This Siberian skull was referred to *E. nordostensis* (another large species) by Lazarev (1980). But the fragmentary lectotype of the latter has a shorter muzzle and wide, not bilobated, protocones (like some of Nalaikha: Fig. 10D). *E. scotti* was a large and heavy horse, with long muzzle, long bilobated protocones and complicate enamel on the upper cheek teeth.

Hemiones

North American hemione skulls are not known. Upper cheek teeth of the holotype of *E. excelsus* Leidy, 1869 (Azzaroli 1998: pl. 16-1a) lack pli caballin and have the deep postprotoconal groove and long and wide protocone exhibited by some extant Mongolian hemiones and kiangs. The same sort of pattern is, however, also usual in the late Pleistocene *E. occidentalis* Leidy, 1865 of Rancho La Brea, California. The exact age of *E. excelsus* is not known. Azzaroli (1998) assumes for it an Irvingtonian age and synonymizes *E. scotti* with *E. excelsus*. However, the pattern of the upper cheek teeth of *E. scotti* is quite different. As noted above, *E. scotti* is certainly a caballine, while *E. excelsus* was probably related to *E. occidentalis* (Eisenmann in press). The resemblance of the upper cheek teeth of *E. excelsus* with hemiones may be the result of plesiomorphy or parallel evolution.

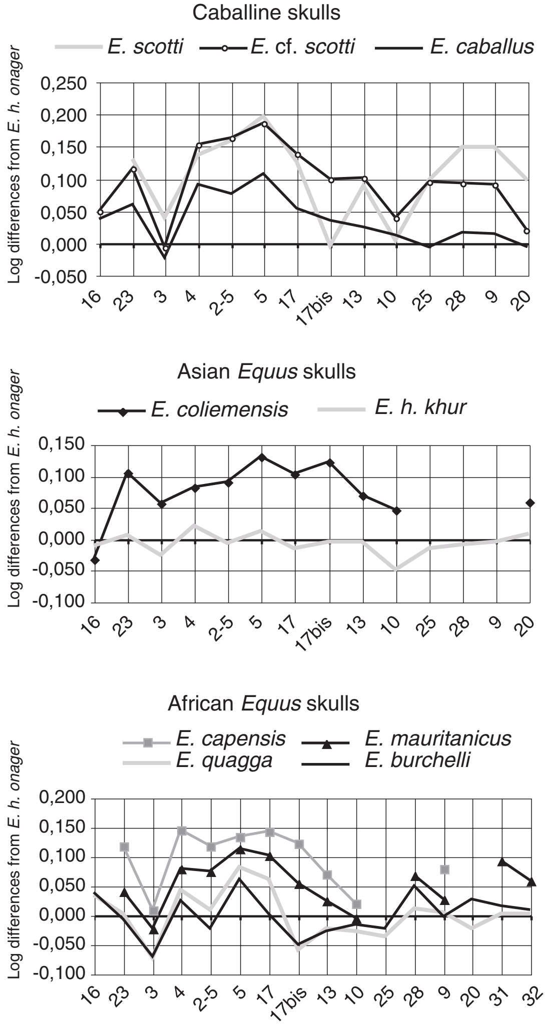

FIG. 19. — Ratio diagrams of *Equus* skulls. Measurements 16, 23, 3, etc. are defined in Annexe (Table 8).

There is a lower cheek series from the late Blancan of Arizona (Azzaroli & Voorhies 1993: pl. 6-6) which shows hemione-like premolars and shallow ectoflexids on all teeth but we have never observed in hemiones the pointed metastylid exhibited by the m2.

Although there are very slender and some times uncommonly large (Eisenmann 2003) "stilt legged" North American Irvingtonian species, limb bones definitely hemione-like are rare and mostly

late Pleistocene. They were found in Alaska and Yukon (Harington & Clulow 1973; Harington 1985), in Wyoming at Natural Trap (Howe pers. comm.), in Texas at Berclair (Pichardo in press). An exception may be the Irvingtonian *Equus* sp. B described by Hulbert (1995) from Leisey Shell Pit A, Florida. It is worth mentioning that there is no evidence of hemione-like metapodials in NE Siberia.
In the Old World, with the exception of *E. hydruntinus* (Burke *et al.* 2003), there are no hemione skulls before the late Pleistocene of Sjara Ossogol, China. During the early or middle Pleistocene, slender limb bones, hemione-like upper or lower cheek teeth are scattered all over Asia (Akhalkalaki, Tologoj), Western Europe (Venta Micena, Süssenborn) Middle East (Ubeidiyeh), North Africa (Aïn Hanech) but the lack of skulls precludes any reliable attribution, not even at the genus *Equus*: *Allohippus* in the Old World (as well as *Plesippus* in North America) may have developed independently (or conserved) cursoriality (Eisenmann 1999, 2003) and hemione-like teeth.

Equus suessenbornensis Wüst, 1901 *s.l.*

During early-middle and middle Pleistocene of the Old World and northwestern America, many fossils point to the existence of a widely distributed but poorly known group, referred here as *E. suessenbornensis* s.l. The limb bones are best represented at Akhalkalaki, Georgia (Vekua 1962, 1986; Gabunia & Vekua 1989). The teeth sample of Süssenborn is richer but unfortunately not homogeneous (Forsten 1986). The same is true for the samples of northeastern Siberia (Chukochya, Adycha) and Yukon (Old Crow). The skull of *E. coliemensis* (northeastern Siberia) is isolated and certainly too small for *E. suessenbornensis* Wüst, 1901 *s.s.* Thus, although very probable, the taxonomical closeness of all these fossils is not absolutely certain.
As noted above, the skull of *E. coliemensis* (Fig. 19; Annexe: Table 2) shows some similarities with hemiones, but it is much larger. The pattern of the upper cheek teeth of *E. coliemensis* is very peculiar, with the extremely complicate enamel and wide plis caballins also observed in *E. verae* and *E. suessenbornensis*. Inside the Süssenborn, Akhalkalaki, northeastern Siberian and Yukon samples, large lower cheek teeth exhibit at times extremely deep ectoflexids and rather shallow, hemione-like lingual valleys. Moreover, some lower teeth of Yukon, Akhalkalaki and northeasten Siberia display isolated ectostylids – an exceptional feature for monodactyl equids. If we rightly referred the large and robust metapodials of Chukochya to *E. verae*, and if the teeth resemblances do indicate a close relationship, *E. suessenbornensis* s.l. had a rather hemione-like skull but unlike-hemione cheek teeth and limb bones and ranged from Beringida to Western Europe.

Molecular biology

Biomolecular studies bring additional insight. On the basis of an age of 0.7 Ma for *E. mauritanicus* (Geraads *et al.* 1986), Oakenfull *et al.* (2000) calculate an age of about 2 Ma for the emergence of the first *Equus*. This is considerably less than the frequently cited age of 3.5 Ma (or more), based on the assumption that *Plesippus* of North America was the ancestor of modern *Equus*. As noted above, *Plesippus* and *Allohippus* were side lineages, not at the origin of modern *Equus*. Again according to Oakenfull *et al.* (2000), caballine equids were the first to branch out of the common line, and they did it shortly after the emergence of *Equus*. That may be so, but there is no sound paleontological proof of that, since the first clearly caballine fossils are younger. The next to branch out would have been the hemiones, possibly about 1 Ma ago. By skull characters, *E. coliemensis* could be close to the emergence of this group in Eurasia. Still according to Oakenfull *et al.* (2000), asses, Grevy's zebras, and mountain zebras diverged two or three hundred thousand years later, and very close to each other, just before the emergence of plains zebras (the reference point in time).

Equus nalaikhaensis, *E. coliemensis* and *E. apolloniensis*

These last points are very interesting in relation to the osteology of *E. nalaikhaensis*. We have noted above in this species a mixture of similarities: the skull has both hemione and zebra characters, some lower cheek teeth resemble extant hemiones, first phalanges at times look like Grevy's zebras, or like hemiones, or like asses. One explanation for this mosaic would be that *E. nalaikhaensis* was close in time to the branching out of true hemiones and to the common ancestor of *E. africanus* and zebras.

The following attempt at more precision is very tentative. If we accept as plesiomorphic the skull proportions of hemiones, asses and all zebras share a wider supra-occipital tuberosity and a lower face. Only zebras share a shorter vomer, and a narrower skull.

E. nalaikhaensis had the narrow skull of zebras but the face was high and the supra-occipital crest narrow. Accordingly, it would best be considered as branching out before the hypothetical common ancestor of asses and zebras but developing skull parallellisms with zebras.

The skull of *E. graziosii* lacks the occiput so that important points like Franck's Index and width of the supra-occipital tuberosity are uncertain. Some points are clear: the muzzle is very narrow and constricted and the frontal is wide (like in some extant zebras, in particular *E. grevyi*) but the vomer is long like in hemiones and asses. The author of the species (Azzaroli 1966, 1979) believes *E. graziosii* to be an ass. If so, it is another case of parallel evolution with zebras.

Unlike the two species above, *E. coliemensis* shows no zebra-like tendency: the muzzle is rather broad, even at the constriction, and thus resembles asses. The supra-occipital crest, however, is very narrow – more like hemiones. Accordingly, it should be best considered as branching out before the common ass-zebra ancestor, but in a rather ass-like way.

Because of its imperfect preservation, all that can be said about *E. apolloniensis* skull is that it does belong to an *Equus* (Koufos *et al.* 1997) and that it differs both from *E. coliemensis* and *E. nalaikhaensis*.

CONCLUSIONS

As already pointed previously (Eisenmann 1999), associations of characters are not stable in equids. At some point in the past, animals could have had hemione-like skulls without hemione-like teeth or limb bones, or the reverse. In consequence, the understanding of a species cannot be simply extrapolated from single parts of its anatomy (Eisenmann & Sondaar 1998) and attribution of isolated teeth or bones is quite uncertain. For this reason, the resemblances between metapodials of *E. nalaikhaensis*, *E. hipparionoides* (Akhalkalaki, Georgia) and *E. altidens* (Süssenborn, Germany) are no absolute proof of their belonging to the same lineage. Nor can we be absolutely sure that *Equus* sp. A and B were closely related to the NE Siberian fossils, or that *Equus* sp. B, *E. coliemensis*, *E. verae* were part of the *E. suessenbornensis* s.l. group.

However, judging from its skull morphology, the Mongolian *E. nalaikhaensis* was a modern *Equus*, quite different from *Plesippus* and *Allohippus*. It was also certainly not caballine. The skull shows a mosaic of characters that can be interpreted by placing it close to the branching out of hemiones, before the hypothetical common ancestor of asses and zebras, and by assuming that it developed skull parallellisms with zebras.

Thus, *E. nalaikhaensis* is one of the three first certain *Equus* of the Ancient World. The exact position of the Macedonian *E. apolloniensis* is yet unknown, although it shows some ass characters. The northeastern Siberian *E. coliemensis* was probably part of the widespread (Yukon to Western Europe) *E. suessenbornensis* s.l. group with some skull characters of hemiones.

The frequency with which "hemione-like" upper and/or lower tooth characters are evidenced in fossils of the New and Old worlds is probably an indication of their plesiomorphy. It would be in accordance with the data of molecular biology: after the individualisation of caballines, hemiones are the first to branch out of the common stem, possibly around 1 Ma ago, before asses and zebras. At that moment, it would be natural to find either caballines or "cocktail" species always including hemione-like characters. Such is the case of *E. nalaikhaensis*, *E. coliemensis*, and probably *E. apolloniensis*.

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ANNEXE

TABLE 1. — Limb bones dimensions, in mm, of *Allohippus stenonis vireti* Prat, 1964 (Saint-Vallier, France) used for the calculation of Variability Size Indices. Abbreviations: **n**, number of specimens; **x**, mean; **s**, standard deviation; **v**, coefficient of variation (v = 100 s/x); **A**, anterior; **D**, diameter; **DT**, transverse diameter; **MC**, third metacarpal; **MT**, third metatarsal; **P**, posterior; **PhI**, first phalanx; **PhII**, second phalanx; **PhIII**, third phalanx.

	n	x	s	v
Scapula, D collum	7	64.2	5.99	9.33
Humerus, maximal length	3	302.7	3.21	1.06
Humerus, DT diaphysis	27	39.2	1.44	3.66
Humerus, DT distal	22	82.3	2.23	2.71
Femur, maximal length	3	406.8	2.75	0.68
Femur, DT diaphysis	19	43.9	2.56	5.84
Radius, length	16	342.9	8.06	2.35
Radius, DT proximal articular	20	81.0	3.95	4.87
Radius, DT distal articular	29	68.8	2.61	3.79
MC, length	38	229.7	7.12	3.10
MC, DT proximal articular	44	54.8	1.82	3.33
MC, DT distal articular	42	51.0	1.56	3.06
Tibia, maximal length	5	367.6	11.55	3.14
Tibia, DT distal	21	80.5	3.00	3.73
Talus, D medial	109	65.5	2.35	3.58
Talus, DT distal articular	102	54.9	1.77	3.21
Calcaneum, length	20	120.0	3.32	2.77
Calcaneum, DT proximal	20	36.7	1.91	5.20
Calcaneum, DT distal maximal	25	56.2	1.88	3.34
MT, length	65	264.5	6.15	2.33
MT, DT proximal articular	70	53.5	1.92	3.59
MT, DT distal articular	68	51.1	1.48	2.89
PhIAP, maximal length	73	83.9	2.94	3.50
PhIAP, DT minimal	74	35.8	1.24	3.46
PhIIAP, maximal length	54	50.0	1.95	3.91
PhIIAP, DT minimal	54	47.4	2.21	4.67
PhIIIAP, maximal length	21	56.9	2.90	5.13
PhIIIAP, DT articular	27	49.5	2.50	5.05
Total	1078			

TABLE 2. — Skull dimensions, in mm, of *Equus*. Abbreviations: **n**, number of specimens; **x**, mean; ***h.***, *hemionus*; *****, approximate.

	E. h. onager n = 21-36	***E. grevyi*** n = 40-61			***E. graziosii***	***E. nalaikhaensis*** PIN 3747-500	***E. coliemensis*** IA 1741	***E. h. khur*** n = 24-33
		min	x	max				
16. Supraoccipital crest breadth	56.6	75.0	85.0	93.5		65	53	55.8
23. Anterior ocular line	347.0	390.0	420.6	450.0	330	420	440	350.4
3. Vomerine length	116.8	111.5	133.0	155.0	113*	145	135*	111.6
4. Postvomerine length	101.9	110.0	130.3	146.0		128	123*	106.6
2-5. Palatal length *s.s.*	115.7	124.0	132.2	142.0	113	144	140	112.0
5. Muzzle length	103.7	126.0	140.3	155.0	108	135	140*	107.0
17. Muzzle breadth	54.9	49.0	57.8	63.0	47.5	62	70	53.3
17 bis. Minimal muzzle breadth	40.7	34.5	40.0	46.0	35	43	55	41.0
13. Frontal breadth	195.8	199.0	211.9	228.0	196	210	230	193.4
10. Choanal maximal breadth	47.5	43.0	48.7	53.0	44	51	53	42.5
25. Facial height	102.0	96.0	106.3	116.0		125		98.2
28. Cranial height	90.1	100.0	107.8	117.0	85	110		87.7
9. Choanal length	63.0	72.0	83.3	96.0		69		61.7
20. Meatus auditivus externus height	14.4	14.0	16.8	22.0		19	17	14.7
31. Nasoincisival notch length	142.9	180.0	185.7	192.0	141	172		138.5
32. Cheek length	160.0	181.0	190.9	206.0	148	209		163.7
1. Basilar length	435.2	485.0	533.4	560.0	410*	545	538	431.0
8. Upper cheek teeth length	158.7	160.0	174.0	195.0	153	155*	180	159.0

TABLE 3. — Third metacarpal dimensions, in mm, of *Equus*. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; ***E. hippar.***, *E. hipparionoides*; **n**, number of specimens; *****, approximate.

	E. nalaikhaensis								***E.* sp. B**	***E. hippar.***
	PIN 3747-583	3747-584	"4"	3747	"1"	"5"	"10"	"11"	"8"	n = 2-4
1. Greatest length	255.0	252.0	257.0							243.0
3. Mid-shaft breadth (DT)	36.0	35.0	37.0			38.0	33.2			33.5
4. Mid-shaft depth (DAP)	28.0	29.0	27.0	27.0			27.0			27.0
5. DT proximal articular	54.0	52.0	53.5				51.0			50.7
6. DAP proximal articular	35.5	35.0	34.0				33.0			32.7
10. DT distal maximal	48.7	47.7	48.0	48.0		49.5				46.3
11. DT distal articular	48.0	48.0	48.0	50.0	49.0	51.0			58.5	45.7
12. DAP distal maximal	35.0	36.5	36.1	36.1	34.0	38.7			41.5	35.0
13. Medial condyle DAP minimal	29.0	31.5	30.1	31.7	29.5	32.1		30.0	34.0	27.6
14. Medial condyle DAP maximal	31.5	33.5	32.0	34.5	32.0	34.0		32.1	36.5	30.7
7. DT articular facet for carpale	47.5	43.5	44.5				41			39.2
8. DT articular facet for carpale	16.5	16.0	15.1	17.0			17			15.9
	***E.* sp. A**									***E. altidens***
	PIN 3747-581	3747-585	3747	3747 bis	"7" ter	"6"	"2"	"3"	"9"	n = 2-4
1. Greatest length	250.0	261.0	252.0							242.5
3. Mid-shaft breadth (DT)	39.0	41.0	36.0	42.0					43.0*	32.2
4. Mid-shaft depth (DAP)	30.1	31.0	30.5	31.0						27.0
5. DT proximal articular	55.5	60.0	55.0							48.5
6. DAP proximal articular	35.0	37.0	36.0							32.6
10. DT distal maximal	52.0	54.5	52.5		55.0	56.1	53.0	54.0	58.0	43.7
11. DT distal articular	55.1	54.0	53.0		52.0	54.0	55.0	55.0	60.0	44.8
12. DAP distal maximal	39.5	40.5	38.0		37.5	40.7	40.1	42.5	33.8	
13. Medial condyle DAP minimal	33.0	32.2	32.0		28.5	33.0	32.0	33.0	33.3	26.9
14. Medial condyle DAP maximal	36.0	35.2	33.3		32.0	35.0	33.0*	36.0	35.1	29.5
7. DT articular facet for carpale	45.0	49.0	45.0							39.0
8. DT articular facet for carpale	16.0	18.0	17.5							16.0

TABLE 4. — Third metatarsal dimensions, in mm, of *Equus*. Abbreviations: **DAP**, antero-posterior diameter; **DT**, transverse diameter; ***E. hippar.***, *E. hipparionoides*; **n**, number of specimens; *, approximate.

	***E.* sp. A**													***E. hippar.***
	PIN 3747-568	571	572	579	580	970/71-2	3747 "5"	567	569	570	573	574	575	n = 6-9
1. Greatest length	294.0	312	312.0	310.0		300.0		295.0	282.0	292.0	300.0	292.0	292.0	286.4
3. Mid-shaft breadth (DT)		36	35.0	33.0	34.0	32.0	32.5	37.0	35.1	38.2	40.0*	39.5	33.0	32.1
4. Mid-shaft depth (DAP)	33.0	36	33.0	38.0*	36.0	31.5		36.0	37.0	34.3	40.0*	37.0	35.0	32.9
5. DT proximal	46.0	52		49.0	47.0	47.0		54.0	54.0	56.5	56.5	54.0	54.5	49.1
6. DAP proximal	42.0	46	47.0	45.0	42.5	42.0		46.0	46.0	46.0	48.0	47.0	45.0	41.4
10. DT distal maximal	48.0	50	49.0	46.5		44.0	45.5	55.0	55.0	54.0	55.0	53.0	50.5	46.4
11. DT distal articular	48.2	49	49.1	49.3		44.7	48.0	52.5	53.5	54.0	55.0	54.5	52.5	46.6
12. DAP distal maximal	38.0	36	38.0	38.0		35.0	37.1	40.0	41.0	41.0	42.0	40.0	40.0	36.8
13. Medial condyle DAP minimal	30.0	32	32.0	30.0		27.5	30.0	33.0	32.0	32.0	32.5	34.0	31.0	28.8
14. Medial condyle DAP maximal	33.0	34	34.5	33.5		31.0	32.8	35.0	35.0	36.0	35.0	35.0	33.0	31.6
7. DT articular facet for tarsale III	43.0	48		47.0		43.0		50.0	50.5	52.0	51.0	50.5	50.0	45.4
8. DT articular facet for tarsale IV	9.0	13	14.0	11.0		12.0		11.0	10.0	10.2	12.0	13.0	10.0	11.5

	***E.* sp. A**												***E.* sp. B**	***E. altidens***
	PIN 3747-575	576	577	578	3747	"1"	970/71-1	"3"	"4"	"6"	"8"	"12"	"5"	n = 1-6
1. Greatest length	292.0	291.0	283.0	302.0	282.0		297.0							282.0
3. Mid-shaft breadth (DT)	38.2	38.0	39.0	38.0	40.0	37.5	39.0			40.0	41		42*	33.0
4. Mid-shaft depth (DAP)	34.3	36.0	37.2	36.5	38.0	38.0	38.0			37.0			36*	33.5
5. DT proximal	56.5	55.0	57.0	55.5	57.0		59.0			54.0	55			49.0
6. DAP proximal	46.0	45.0	45.0	47.5			47.5			46.5	48			41.0
10. DT distal maximal	54.0*	55.0	57.0	55.0	52.5	53.1	55.2	54.0	56.5				62	44.6
11. DT distal articular	54.0*	54.0	53.0	54.0	53.5	53.0	54.1	53.0	55.0				60	44.8
12. DAP distal maximal	41.0	40.0	39.0	39.0	42.0	41.0	41.5	40.0	39.0			41.5	43	36.1
13. Medial condyle DAP minimal	32.0	31.5	32.7	32.0	32.0	33.0	31.3	31.5	32.0			33.5	34	28.5
14. Medial condyle DAP maximal	36.0	35.0	35.5	36.0	36.0	34.7	35.2	35.0	35.0			36.0	36	31.9
7. DT articular facet for tarsale III	52.0	50.0	52.0	53.0			52.0			49.0	53			46.0
8. DT articular facet for tarsale IV	10.2	13.0	14.0		11.0		12.0			13.0	12			11.0

TABLE 5. — First phalanx dimensions, in mm, of *Equus*. Abbreviations: **A**, anterior; **DAP**, antero-posterior diameter; **DT**, transverse diameter; **P**, posterior; *****, approximate.

	E. nalaikhaensis		***E.* sp. A**			***E.* sp. B**	
	"14" A	no No. A	"10" A	"13" A	"11" P	"9" A	"12" P
1. Greatest length	90.0	91	91.0	90.0	87.1	93.0	95.0
3. Mid-shaft breadth (DT)	31.5	31	36.5	36.0	35.0	41.0	38.0
4. DT proximal	51.0	53	58.0	54.0	62.0	65.0	63.0
5. DAP proximal	39.0	38	40.1	40.0	42,5	42.0	45.1
6. DT distal maximal	43.0	48	50.5	48.0	49.0	55.0	50.0
7. Greatest length of trigonum phalangis	61.5	60	65.0	60.0	55.0	64.0	65.0
10. Supratuberosital length	69.0	69	69.0	68.0	60.0	70.0	69.0
12. Infratuberosital length	12.5	13	14.0	13.5	18.5	15.0	18.5
14. DT distal articular	43.5	45	47.5	47.0	49.0	52.2	47.5

	E. nalaikhaensis					
	with skull P	no No. P	"16" P	"17" P	"5G" P	"5D" P
1. Greatest length	85.0	85.0	87.0	80.2	82.0	83.1
3. Mid-shaft breadth (DT)	30.1	30.0	32.0	29.0	31.7	
4. DT proximal	54.0	51.0	54.1	50.0	50.0	54.0
5. DAP proximal	38.2	39.0	41.0	36.0	36.0	38.0
6. DT distal maximal	43.0	41.5	42.0	40.5		42.0*
7. Greatest length of trigonum phalangis	50.0	58.0	56.0	55.0	56.0	56.0
10. Supratuberosital length	60.0	63.0	60.0	58.0	60.0	63.0
12. Infratuberosital length	15.0	14.0	18.5	17.0	13.5	11.0
14. DT distal articular	42.0	40,5	40.0	39.0	40.0*	40.0*

TABLE 6. — Second phalanx dimensions, in mm, of *Equus*. *, approximate.

	E. nalaikhaensis				***E.* sp. A**			
Anterior	6	7	8	9	1	2	3	4
Greatest length	48.5	45.5	46.0	47.0	50.1	50.5	53.1	50.0
Anterior length	36.0		33.0		37.0	39.0	41.0	39.0
Smallest breadth	47.0	44.0	45.0	45.0	51.0	52.0	50.0	51.0
Proximal breadth	52.0	50.0	49.5	50.0	57.0	60.1	60.5	60.5
Proximal depth	33.0		32.0	32.0	35.3	33.1	36.0	34.0
Distal articular breadth	49.0	47.0	47.0	46.1	54.0	54.0	57.0	54.0
Posterior	PIN 3747-500	10	11	12	5	13	14	15
Greatest length	50.0	49.0	47.0	49.0	50.0	50.5	51.0	49.3
Anterior length	37.0	38.0	36.5	38.0	37.0	38.0	38.0	37.0
Smallest breadth	41.0	42.0	40.5	42.0	47.0	48.0	48.0	
Proximal breadth	49.0	51.0	49.5	50.0	55.0	58.0	58.0	56.0*
Proximal depth	32.1	34.0	34.0	33.5	34.5	34.0	35.0	33.0
Distal articular breadth	44.0	44.0	40.0	45.5	52.5	50.0	50.2	50.0*

TABLE 7. — Third phalanx dimensions, in mm, of *Equus*. *, approximate.

Anterior	*E. nalaikhaensis*		*E.* sp. A?
Anterior length	54	53.0	59.0
Antero-posterior diameter		60.0	63.0
Height		44.0	42,5
Greatest breadth	72*	73.5	75.0
Articular breadth		48.0	50.0
Articular depth	25.5	28.5	27.0
Distal "circumference"		150.0	174.0

Posterior	*E. nalaikhaensis*		
Anterior length	50	53.0	52.0
Antero-posterior diameter	54	58.0	58.0
Height	41	40.0	43.0
Greatest breadth	68	67.5	63.0*
Articular breadth	47	45.0	43.5
Articular depth	26	26.0	26.0
Distal "circumference"	142	147.0	140.0

TABLE 8. — Skull dimensions, in mm, of *Equus*. Abbreviations: **n**, number of specimens; *, approximate.

	E. scotti NMC 2381	*E.* cf. *scotti* SI 160-455	*E. caballus* n = 1-3	*E. capensis* ZM 21025	*E. mauritanicus* n = 1-3	*E. quagga* n = 12	*E. burchelli* n = 36
16. Supraoccipital crest breadth		64	62			62.0	62.6
23. Anterior ocular line	465	450	395	453	378	347.6	339.5
3. Vomerine length	130	117	113	121	113	100.2	100.8
4. Postvomerine length	139	145	125	142	122	112.5	107.6
2-5. Palatal length *s.s.*	164	165	136	149	135	116.2	107.7
5. Muzzle length	163	159	133	141	135	125.3	119.7
17. Muzzle breadth	74	76	63	77	70	63.6	55.7
17 bis. Minimal Muzzle breadth	41	52	45	55	47	36.3	37.0
13. Frontal breadth	240	247	207	230	208	185.9	184.1
10. Choanal maximal breadth	48	52	49	50	47	44.8	45.8
25. Facial height	127	126*	100			93.2	96.4
28. Cranial height	126	111	93		105	91.8	100.4
9. Choanal length	88	77	65	75	67	63.2	62.1
20. Meatus auditivus externus height	18	15	14			13.7	15.3
31. Nasoincisival notch length	217	210	180		177	143.5	148.3
32. Cheek length	203	191	164		186	163.5	165.5
1. Basilar length	595	585	520	560	492	449.0	431.0
8. Upper cheek teeth length	201	194	165	193	178	154.0	142.0