Fossil equids (Mammalia, Equidae) from the Neogene and Pleistocene of Tadzhikistan

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ABSTRACT
Fossil equids from Tadzhikistan are little known outside the former USSR. We here describe the equid samples from a number of fossil localities in this part of central Asia. Because the samples are small, the taxonomic status of the finds in most cases remains uncertain or preliminary.

KEY WORDS
Neogene,
Pleistocene,
equids,
Tadzhikistan.

RÉSUMÉ
Équidés fossiles (Mammalia, Equidae) du Néogène et du Pleistocène de la République du Tadzhikistan.
Les équidés fossiles de la République du Tadzhikistan sont peu connus en dehors de l'ex-URSS. Nous décrivons des restes d'équidés de quelques localités fossilifères de cette région de l'Asie centrale. Dans la majorité des cas, ceux-ci sont peu nombreux et leur statut taxonomique est le plus souvent indéterminé.

MOTS CLÉS
Néogène,
Pleistocène,
équidés,
Tadzhikistan.

INTRODUCTION

In this paper we describe the fossil equids from a number of localities in the Republic of Tadzhikistan. The localities span a period of time from the late Miocene-Turolian to and including the Late Pleistocene. The equids represented belong to the genera *Hipparion* and *Equus*. Fossil material from Tadzhikistan has earlier been described in papers in Russian. Although most local samples are quite small and the equid species represented in them therefore remain taxonomically uncertain, we believe that it may be of general interest to gather, within one paper, the information on the fossil equids from this region of central Asia. The material here described is kept in the Institute of Zoology and Parasitology, Tadzhik Academy of Sciences (IZP), Dushanbe. Material from some of the localities is also kept in the Paleontological and Geological Institutes of the Russian Academy of Sciences (PIN and GIN), Moscow, and in the Institute of Paleontology, Kazakh Academy of Sciences, Almaty.

METHODS

We analyse the material, which consists of single tooth rows, isolated cheek teeth and more or less fragmentary limb bones, using measurements according to Gromova (1949, 1952). The data are depicted in scatterplots and Simpson's ratiodiagrams (Simpson 1941), using the common logarithms of the original measurements. In the diagrams we compare our data with the classical samples from Pikermi (Greece), Valdarno (Italy) and the Indian subcontinent, and with data gleaned from the literature. In the scatterplots (Figs 3-6), we have drawn the 95% equiprobability ellipses (Defriese-Gussenhoven 1955) based on the hypodigm samples (own data) of *Hipparion mediterraneum* Roth & Wagner, 1855, *Equus stenonis* Cocchi, 1867 and *E. stehlini* Azzaroli, 1965. In Simpson's ratiodiagrams on the metapodials and skulls (Figs 7-8; 10-11), we use arbitrary standards (vertical line in the middle of diagram; see figure texts), which allow for the comparison of any sample mean or single specimen (curves to the right depicting sample means/specimens larger than the standard, and curves to the left depicting sample means/specimens smaller than the standard).

DESCRIPTION

THE GENUS *HIPPARION* CHRISTOL, 1831

Late Miocene

Locality Sor. The locality Sor is situated in the western Gissaro-Alai, on the northern slope of the Magian Basin in the Province of Sor, northwestern Tadzhikistan (Fig. 1, A). The locality was discovered in 1971 by the geologist S. A. Nesmeyanov. There are two fossiliferous horizons, in which occur bones of mammals, fishes and reptiles in pale brown aleurites of the Gusar Suite (Fig. 2). Between those two horizons is an approximately ten-metre-thick non-fossiliferous layer of aleurites. The main excavations were done in the upper fossiliferous horizon, from which have been identified Canidae, *Ictitherium* sp., *Hyaena* sp., Felidae, *Chalicotherium* sp., *Chilotherium* sp., *Hipparion garedzicum magianense* Zhegallo 1978, *Samotherium* sp. (= *S. irtyshense* Godina, 1954), *Protoryx tadzhikistanica* Dmitrievna, 1977, *Sogdohyrax magianense* Dubrovo 1978 (Dmitrievna & Nesmeyanov 1982; Zhegallo 1978; Dubrovo 1978). Since 1979 excavations have been carried out in the lower fossiliferous horizon, but only occasionally in the upper one. The hipparion comes from the upper horizon, as the lower one has not, in spite of several years of work, yielded any hipparion material although the rest of the fauna is rich (Sharapov 1982).

This locality with its two fossiliferous horizons has erroneously been dated middle Pliocene (Nesmeyanov 1973) or early Pliocene (Zhegallo 1978; Sharapov 1982; Dmitrievna & Nesmeyanov 1982), but it rather correlates with the late Miocene-Pontian of the eastern Paratethys and the Pannonian-Turolian, as determined on the basis of *Machairodus* cf. *giganteus* (Wagner, 1857), *Adcrocuta eximia* (Roth & Wagner, 1848), *Microstonyx* sp. (Sharapov 1982),

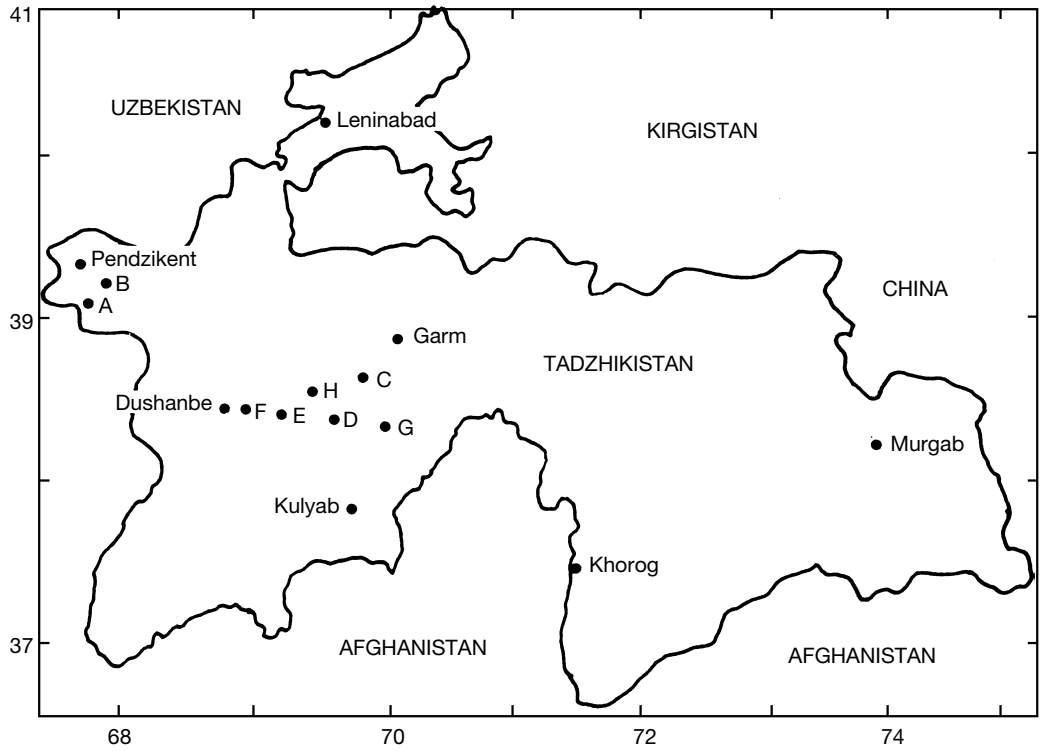

FIG. 1. — Map of the area in Tadzhikistan from whence are described local samples of fossil equids. Localities: **A**, Sor; **B**, Marmar; **C**, Darayaspoon; **D**, Kuruksai; **E**, Karamaidan; **F**, Yakhabed; **G**, Lakhuti 1 and 2; **H**, Obigharm.

and *Hipparion,* the latter identified as belonging in the *H. mediterraneum* group (Forsten 1997).

The hipparion from Sor (PIN 3544) was first listed by Nesmeyanov (1973) as *Hipparion* sp., later by Zhegallo (1978) who referred a subspecies *magianense* to *H. garedzicum* Gabuniya, 1959. Although resembling the hipparion from Bazaleti, Georgia, referred by Meladze (1967) to *H. garedzicum*, hipparion from Sor (and Bazaleti) differs from the hypodigm of the species from Udabno, Georgia, both in morphology and stratigraphic age. *Hipparion garedzicum* from the ?late Vallesian, type locality Udabno, is larger and more massive, with a shorter and broader snout, differently situated and shaped preorbital fossa of the skull, and richly plicated upper cheek teeth with a longer protocone. The hipparions from Sor and Bazaleti do not represent *H. garedzicum*, but resemble *H. mediterraneum* from the Turolian of Pikermi, Greece, although larger than the latter (Forsten 1997) (Fig. 3, Mc, Mt S and without a locality abbreviation). They may be identified as *H. magianense* Zhegallo 1978.

Locality Darayaspoon. The locality Darayaspoon is situated on the right bank of the river Obi-Mazar in the Province Darayaspoon, Afghan-Tadzhik Depression, southeastern Tadzhikistan (Fig. 1, C). It was discovered in 1978 by the geologist S. A. Arvanitaki during prospecting in the river basin.

Fossil mammals occur here in strongly carbonized, hard aleurites of dark and light brown colour. The fossiliferous horizon, which is 20-30 cm thick, lies in the upper part of the section, 40 m above the level of the river and with an inclination of 3-5°S. According to Arvanitaki (pers. comm.) the fossiliferous horizon lies on conglomerates of the early Pliocene Polizak Suite (Fig. 2); a Pliocene age of the latter is supported by fossil pollen (Erzhova, pers. comm.).

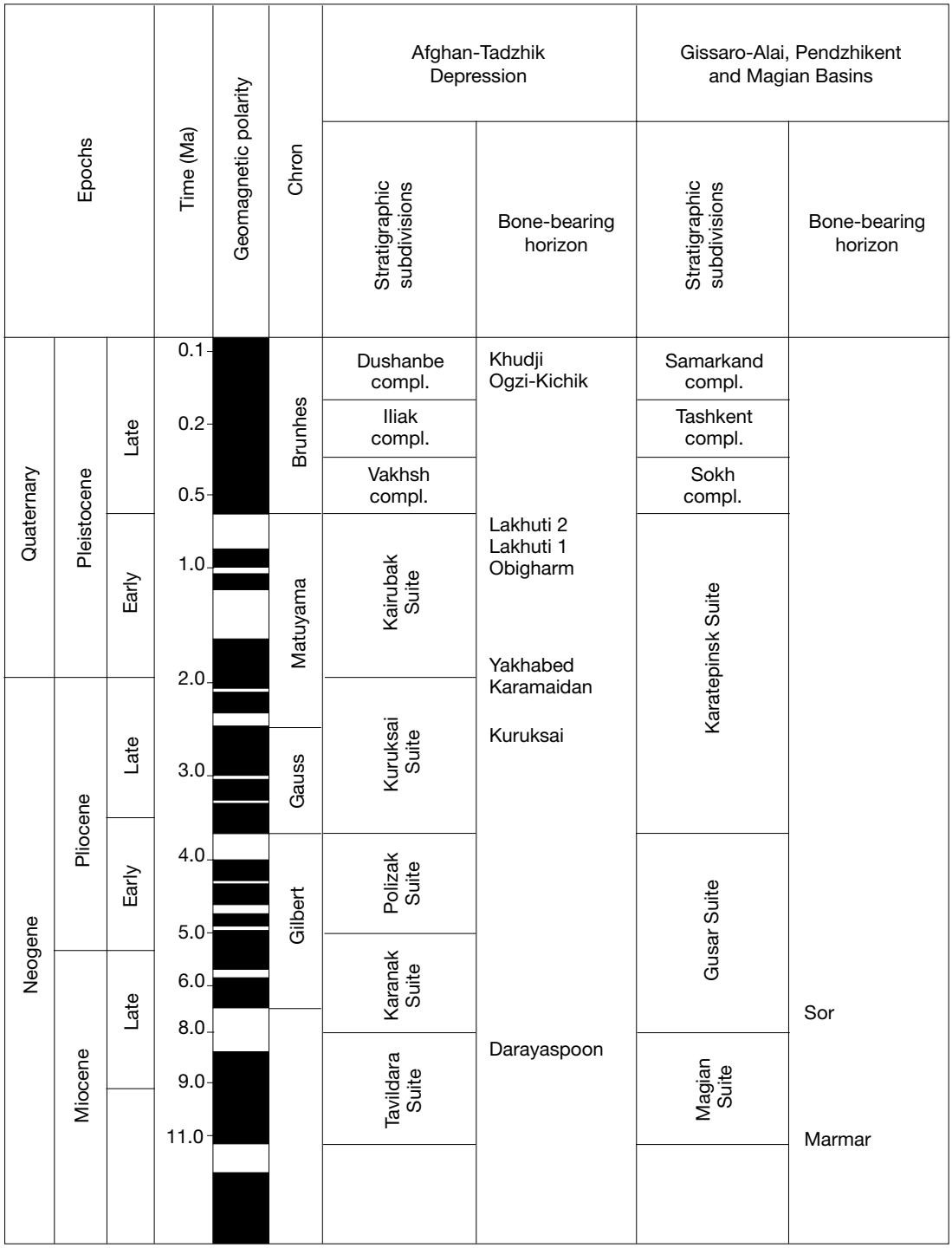

FIG. 2. — Stratigraphic scheme, showing the placement of the fossil localities discussed in this article.

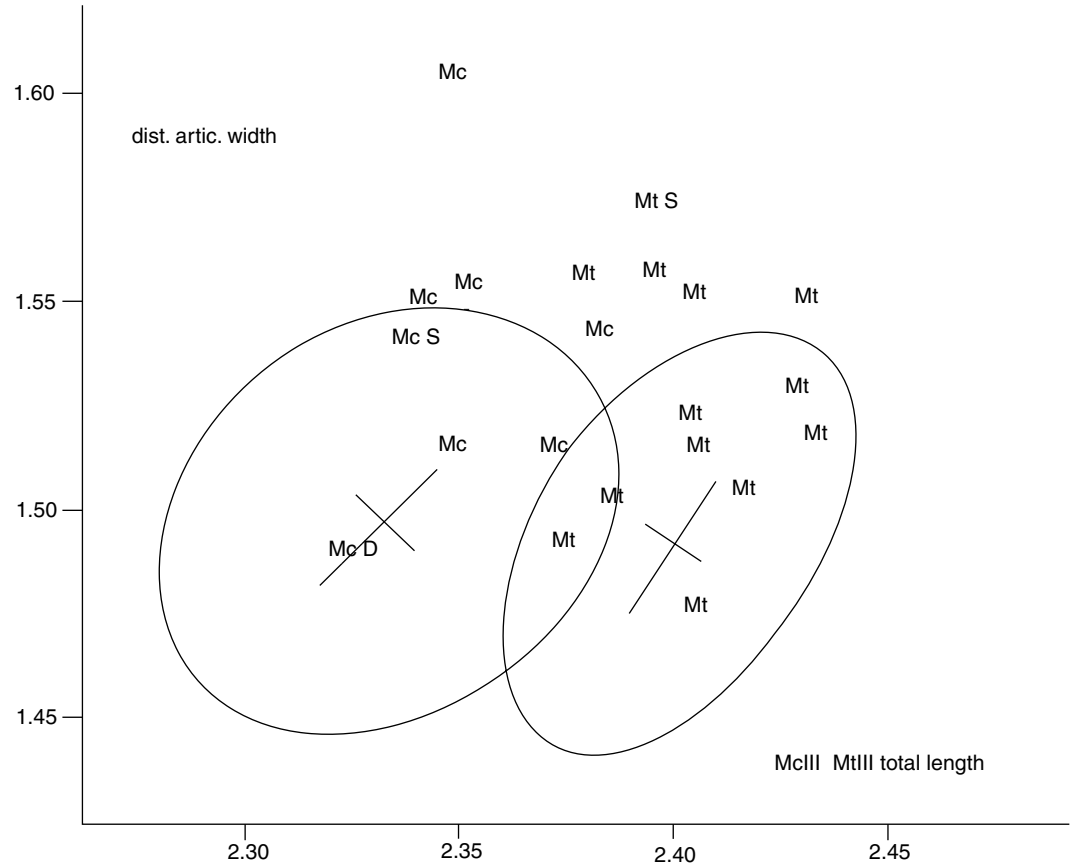

FIG. 3. — Distal articular breadth plotted to total length in Mc and MtIII of hipparions of the *H. mediterraneum* group; log data of measurements in mm. 95% equiprobability ellipses drawn on the hypodigm sample of *H. mediterraneum* from Pikermi. Plotted are specimens from Darayaspoon (**Mc D**), Sor (**Mc**, **Mt S**) and Bazaleti (**Mc**, **Mt** without locality abbreviation).

However, the fauna, which comprises ?*Prospalax* sp., *Ictitherium* sp., Cervidae, Giraffidae, *Gazella* sp., *Chalicotherium* sp. (the latter according to Vangengeim, pers. comm.), and *Hipparion* sp. (Sharapov 1982) indicates a late Miocene-Turolian age corresponding to the Tavildara Suite (Fig. 2). The locality has not yet been fully studied from a stratigraphical and faunal point of view.

Hipparion sp. from Darayaspoon is represented by scant material: there are only an McIII (IZP 11-831/Das) and a right lower m3 (IZP 11-892/Das). Plotted on its distal articular breadth to total length, the McIII falls close to the mean of the hypodigm sample of *H. mediterraneum* from Pikermi (Fig. 3, Mc D). The molar is typically hipparionid and cannot be identified to species. We therefore leave this find as *Hipparion* sp.

Locality Marmar. This is a new, so far unstudied locality, discovered in 1982. It is situated in the Pendzhikent Basin of the western Gissaro-Alai, 10 km south-west of Pendzhikent on the right side of the road to Magian, northwestern Tadzhikistan (Fig. 1, B).

The fossil horizon is part of a succession, from the bottom up, of layers of grey conglomerates, pale brown aleurites and thin layers of sands evidently of the Magian Suite (Fig. 2). The total thickness is approximately 50 m. This section, and with it a unique fauna of fossil mammals, was destroyed by blasting works during the construction of a canal. However, previous excavations at the locality had

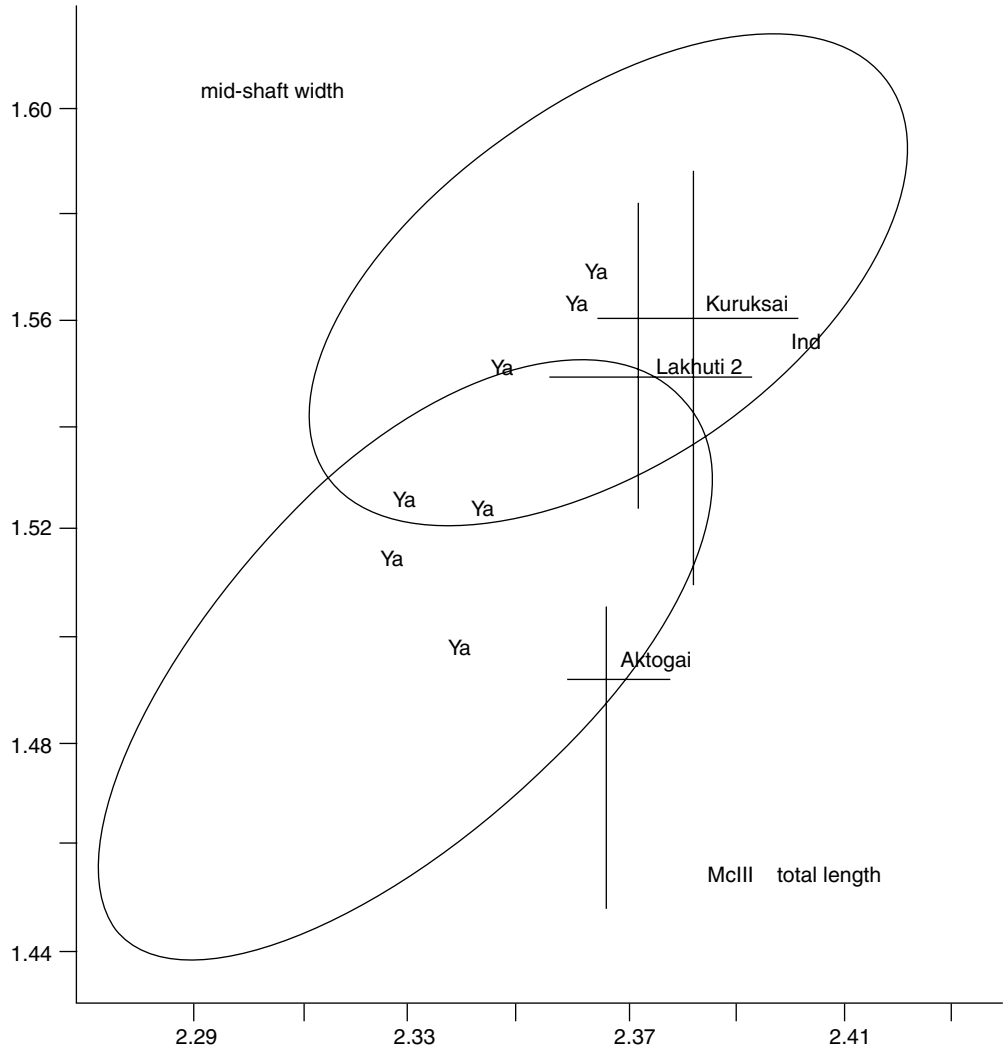

FIG. 4. — McIII midshaft width plotted to total length in *Equus*; log data of measurements in mm. 95% equiprobability ellipses drawn on the hypodigm samples of *E. stenonis* (top) and *E. stehlini* (bottom). Observed ranges and means drawn for Kuruksai, Lakhuti 2 and Aktogai; single observations plotted for *E. sivalensis* (**Ind**) and from Yakhabed (**Ya**).

shown that it is probably of volcanic origin and comprises a great amount of fossils, mainly skulls and jaws of large mammals such as ?*Brachypotherium* sp. (more than 50% of the finds belong to rhinocerotids), mastodonts such as *Platybelodon* sp., and hipparions. There are also egg shells of some large bird (ostrich?), not yet studied. *Platybelodon* sp. could indicate that the fauna is as old as middle Miocene in age (correlated with the Tsokrak Fm. of the eastern Paratethys), but the presence of *Hipparion* shows that it is younger or late Miocene.

The hipparion is represented by scant material: there is a fragmentary and distorted lower snout and right ramus with PM2-PM4 (IZP 10-1132/M) and some isolated teeth. Plotted on its least diastemal width (Gromova's measure No. 11) to symphysial length (Gromova's measure No. 15) (Gromova 1952), the jaw falls beneath the main sample of *H. mediterraneum*

TABLE 1. — Measurements on the limb-bones of *Equus*, Tadzhikistan (in mm). Loc. Kuruksai, small form (IZP collections).

Mc, Mt	total l.	prx. br.	a.-p. prx.	dist. br.	protub. br.	keel diam.
Mc 1-213/N	–	–	–	35.7	41.6	30.4
Mc 1-214/N	–	–	–	38.1	38.6	32.8
Mt 1-216/N	–	41.3	4.07	–	–	–

Astragalus	dist.art.br.	a.-p. dist.	height
1-223/N	> 40.0	30.0	52.7
GIN no No.	–	a.30.8	51.8

from Pikermi, showing that the snout is narrow. The premolar row measures 81 mm.

The premolars of the jaw (IZP 10-1132/M) are typically hipparionid; p3 has a protostylid, p4 only a protostylid seam (for terminology see Fig. 9). All three premolars have a long entoconid tip. Left m2-m3 (IZP 10-1133/M) are so strongly worn that only the enamel periphery remains; both teeth have a protostylid plication. The left lower d2-d4 (IZP 10-1134/M) in early wear have an ectostylid, although not yet reaching the occlusal surface; the deciduous tooth row measures more than 90 mm. Two upper M1-2 (IZP 10-1131/M), probably the left and right tooth of one individual, are in early wear. The teeth are large (basal length 23 and 24 mm) with an oval protocone with pointed ends (protoconal length 8.1 and 8.5 mm); the plication count is rather high (not countable). On the present scant material this rather large hipparion cannot be identified to species and we therefore leave it as *Hipparion* sp.

THE GENUS *EQUUS* LINNAEUS, 1758

Late Pliocene

Locality Kuruksai. This locality, situated 18 km north-east from Baldzhuan in the valley of the river Kuruksai, Afghan-Tadzhik Depression, southeastern Tadzhikistan (Fig. 1, D), was discovered in 1962. Fossil mammals occur here in deposits, which most geologists differentiate into four layers (Dodonov 1973, 1986). The three lower layers consist of conglomerates and aleurites and belong in the Kuruksai Suite (Fig. 2); the second of these layers is the bone-bed. The fourth and uppermost layer mainly consists of loessic clay and belongs in the Kairubak Suite.

Paleomagnetic datings of the Kuruksai deposits indicate that the Gilbert-Gauss boundary probably lies at the base of the Kuruksai Suite; the Gauss-Matuyama boundary lies within this suite. The bone-bed is inversely magnetized and is believed to be older than the Olduvai Episode (Penkov *et al.* 1976; Penkov & Gamov 1980).

Excavations at two points, Kuruksai-Navrukho and -Lagernaya, have yielded a rich fossil material (Sharapov 1986; Vangengeim *et al.* 1988), the main part of which is in PIN and GIN (PIN/GIN 3120, 3848). The fauna from Kuruksai, dated to the middle Villafranchian, was first identified by Kozhamkulova as comprising two equids, i.e. *Equus stenonis* and *E.* cf. *hidruntinus* (sic!) Regalia, 1904 (cited *in* Vangengeim *et al.* 1988). Later a single equid has been identified from Kuruksai, variously referred to as *E.* (*Allohippus*) aff. *sivalensis* Falconer & Cautley, 1849 (Sharapov 1975), *E.* (*Hippotigris*) *pamirensis* n. sp (Sharapov 1986), and *E. stenonis bactrianus* n. ssp. (Zhegallo *in* Vangengeim *et al.* 1988). The common, large horse from Kuruksai is believed to belong to the species *E. stenonis* and corresponds well for the size and proportions of its limb bones to the hypodigm from Valdarno, Italy (Figs 4-7, Kuruksai) (Forsten, 1999). It differs from the European local forms of *E. stenonis* in having larger teeth with a longer protocone and in the shallow ectoflexid of its lower molars (Vangengeim *et al.* 1988, table X: 1-3, XI: 1-4), and from the type form in having a shorter and broader snout and shorter distance choanae-vomer notch (Fig. 8, Kuruksai).

Kozhamkulova's faunal list indicated the presence of a small horse from Kuruksai. A few bones, i.e. an McIII (IZP 1-40/N), proximal and distal MtIII (IZP 1-216/N, 1-213/N), and two fragmentary astragali (IZP 1-223/N, GIN 381/?), from Kuruksai-Navrukho, have been interpreted as belonging to a second, smaller species than the common *E. stenonis* (Sharapov 1980, 1982)

TABLE 2. — Measurements on the limb-bones of *Equus*, Tadzhikistan (in mm). Loc. Karamaidan (IZP collections).

Mt	total l.	prx. br.	a.-p. prx.	dist. br.	protub. br.	keel diam.	midshaft br.
5-1071/Kar	281	53.9	49.6	47.3	49.0	38.4	35.7
5-1072/Kar	274	51.6	43.0	48.0	51.3	36.5	36.3
5-1073/Kar	266	51.0	45.0	47.0	48.7	37.5	35.3
5-1075/Kar	–	54.2	43.3	–	–	–	–

Astragalus	dist.art.br.	a.-p. dist.	height
5-1077/Kar	47.8	35.7	61.7
5-1078/Kar	52.3	33.8	63.6
5-1079/Kar	–	–	63.0

Phal. I	total l.	dors. l.	midshaft br.
5-1076/Kar	80.0	75.6	33.0

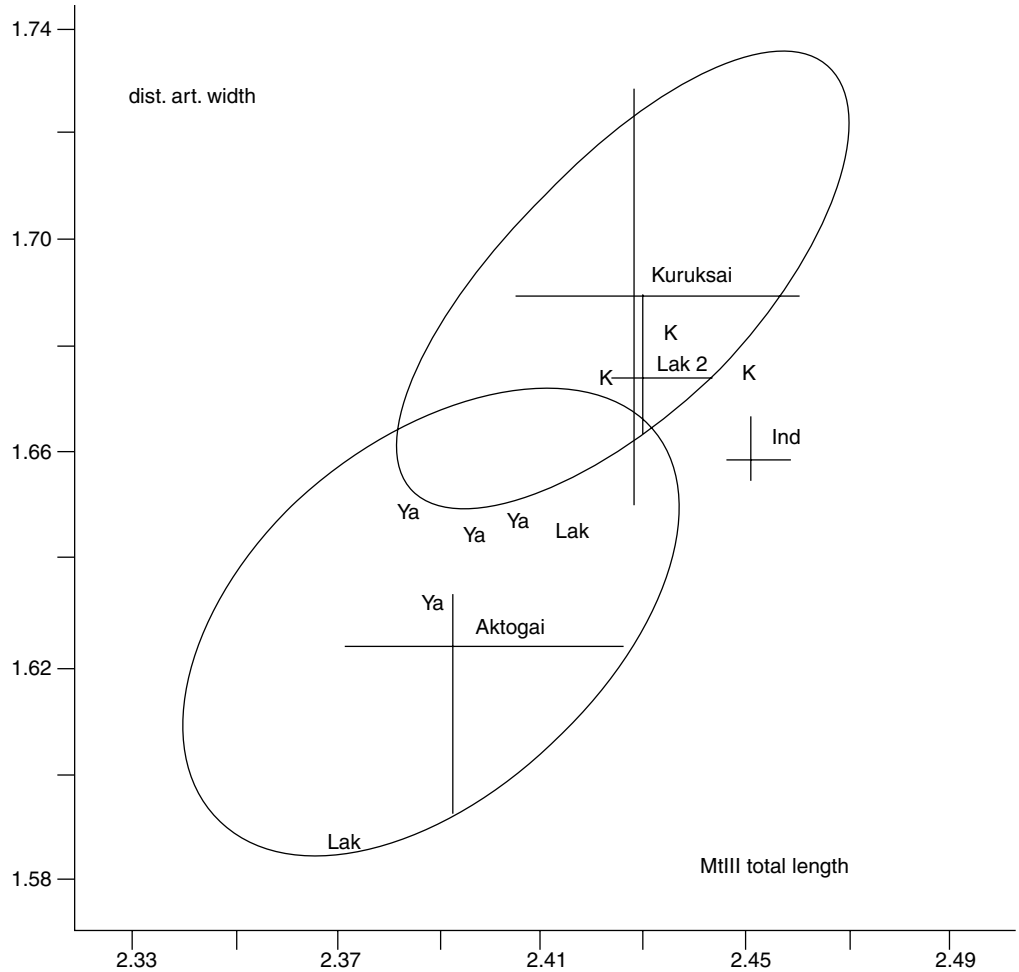

FIG. 5. — MtIII distal articular breadth plotted to total length in *Equus*; log data of measurements in mm. 95% equiprobability ellipses drawn on the hypodigm samples of *E. stenonis* (top) and *E. stehlini* (bottom). Observed ranges and means drawn for Kuruksai, Lakhuti 2 (**Lak 2**), Aktogai and *E. sivalensis* (Ind); single observations plotted from Lakhuti 1 (**Lak**), Yakhabed (**Ya**), Obigharm (**O**) and Karamaidan (**K**).

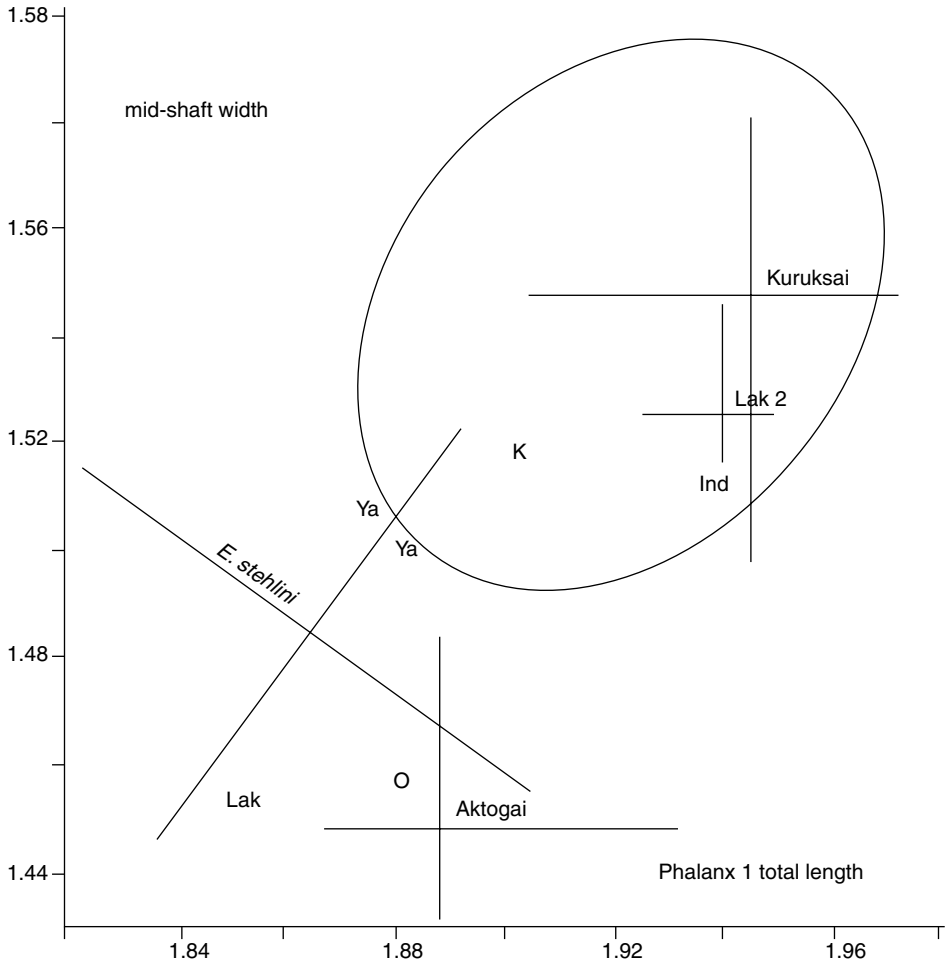

FIG. 6. — Phalanx I mid-shaft width plotted to total length in *Equus*; log data of measurements in mm. 95% equiprobability ellipse drawn for the hypodigm sample of *E. stenonis* (top) and range and mean drawn for the hypodigm sample of *E. stehlini,* Kuruksai, Lakhuti 2 and Aktogai. Single specimens plotted on *E. sivalensis* (**Ind**), Lakhuti 1 (**Lak**), Obigharm (**O**), Yakhabed (**Ya**) and Karamaidan (**K**).

(Table 1). There are no teeth. The Mc, when plotted on its breadths to length, falls in among the smallest specimens of the larger form; we now believe that it may represent an extreme variant of the latter. The Mt proximal and distal fragments correspond in size to those of the smallest stenonid horses known. Although fragmentary, the two astragali when plotted on distal articular width to height would fall within the range of *E. stehlini*; however, they may be juvenile. We tentatively refer to this find as a separate species *E.* sp., indicating sympatry of a large and small stenonid horse at Kuruksai.

Locality Karamaidan. Karamaidan is situated in the southeastern foothills of Karategin, 8-9 km north-west of the city of Faisabad in the valley of the river Djondody, Afghan-Tadzhik Depression (Fig. 1, E). The bone-bearing deposits are found in a narrow gorge on the right bank of the river Djondody. The bone-bearing horizon belongs in the Kairubak Suite (Fig. 2) and is uncovered at two localities, one in the upper, the other in the lower range of the river. The horizon has been dated on paleomagnetics to the interval between the episode Gilsa and the boundary Matuyama-Gauss (Putevoditel 1977, 1981).

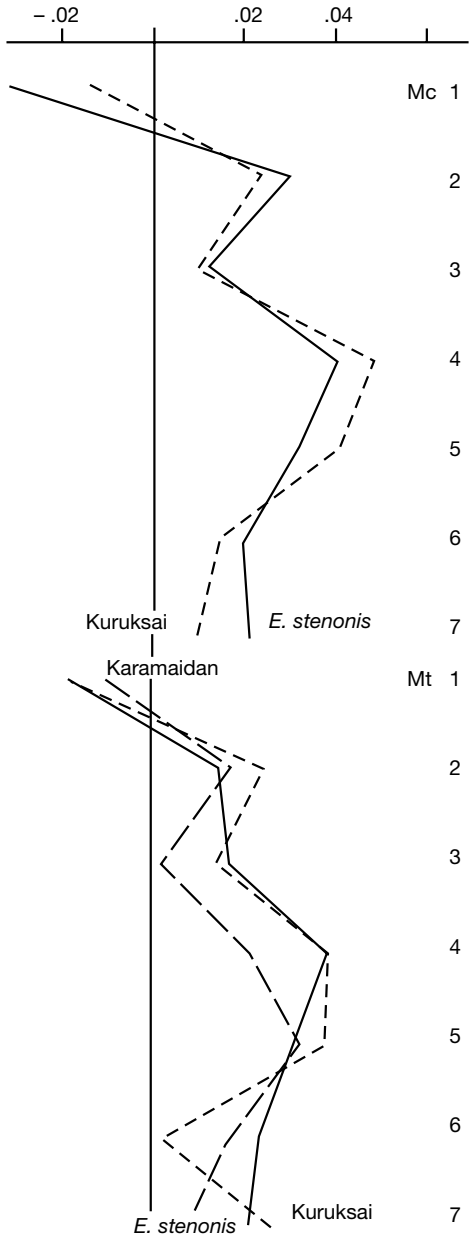

FIG. 7. — Simpson's ratiodiagram, comparing the metapodials (Mc top; Mt bottom) of *E. stenonis* from Valdarno (hypodigm), Kuruksai and Karamaidan, using means of samples. Arbitrary standard (in logs): **Mc**; measure **1**, total l. 2.40; measure **2**, proximal breadth 1.70; measure **3**, proximal diameter 1.54; measure **4**, distal articular breadth 1.65; measure **5**, distal protuberance breadth 1.66; measure **6**, distal keel diameter 1.54; measure **7**, mid-shaft width 1.54; **Mt**; measure **1**, total l. 2.45; measure **2**, proximal breadth 1.70; measure **3**, proximal diameter 1.65; measure **4**, distal articular breadth 1.65; measure **5**, distal protuberance breadth 1.66; measure **6**, distal keel diameter 1.56; measure **7**, mid-shaft width 1.54.

The fossil fauna is believed to be middle Villafranchian in age and comprises *Papio* sp. (Sharapov, unpubl.), *Canis* sp., *Ursus* cf. *etruscus* Cuvier, 1812, *Stephanorhinus* cf. *etruscus* (Falconer, 1859), *Equus* ex. gr. *stenonis, Paracamelus* sp., *Cervus* sp., *Protoryx* cf. *laticeps* Pilgrim & Hopwood, 1928, and *Gazella sinensis* Teilhard & Piveteau, 1930 (Putevoditel 1977).

The material (IZP 5-/Kar) of the horse from Karamaidan consists of a fragmentary skull, upper permanent and deciduous teeth, three MtIII and fragments of metapodials, four astragali and one proximal phalanx (Table 2). In the upper cheek teeth (IZP 5-1097/Kar) of the skull, in which PM2-M3 measures 203 mm, the protocone of the premolars is short, fairly long in the molars (total range in PM3-M2 8.5-13.8 mm), the post-protoconal groove is deep, the hypocone well indented lingually in PM2-PM4 and M3; M3 has a hypostylar foramen (for terminology, see Fig. 9). There is a pli caballin and an additional plication posteriorly on the protoconal stalk; the plication count is 9-11 plications. In PM3 the parastyle is grooved, the mesostyle of the premolars is flattened, in the molars pointed. The upper cheek teeth resemble those of *E. stenonis* from Kuruksai. There are no permanent lower cheek teeth. The astragali and MtIII, plotted on their breadths to length, fall within the range of *E. stenonis*, close to the means of the same bones from Kuruksai (Fig. 5, K, Kuruksai); also for their general proportions, the MtIII resemble those of *E. stenonis* (Fig. 7, Karamaidan). The single proximal phalanx, plotted on its mid-shaft width to total length (Fig. 6, K), falls at the lower limit of the range for Kuruksai. We believe that the horses represented by the two local samples are closely related with one another and with *E. stenonis*.

Late Pliocene-early Pleistocene

Locality Yakhabed. This locality, discovered in 1962, is situated on the left bank of the small river Yakhabed, 15 km north-east of Kafirnigan in the Province of Zulfi, Afghan-Tadzhik Depression (Fig. 1, F). The proluvial sediments, which lie on eroded Neogene sediments of the Karanak Suite (Fig. 2), consist of a succession of

TABLE 3. — Measurements on the limb-bones of *Equus*, Tadzhikistan (in mm). Loc. Yakhabed (IZP collections).

Mc, Mt	total l.	prx. br.	a.-p. prx.	dist. br.	protub. br.	keel diam.	midshaft br.
Mc							
3-1021/Ya	231	51.0	33.8	45.9	48.9	34.5	36.6
3-1022/Ya	213	55.0	33.6	45.6	44.6	32.3	32.7
3-1023/Ya	221	46.3	32.6	44.5	44.2	34.3	33.3
3-1048/Ya	223	52.2	32.2	44.1	48.7	35.5	35.4
Mc (cont.)							
3-1051/Ya	231	53.0	32.6	46.3	46.7	31.7	37.0
3-1049/Ya	213	50.0	28.5	–	44.0	33.8	33.5
3-1050/Ya	217	45.0	31.6	40.3	43.0	33.0	31.6
3-1024/Ya	–	–	–	44.3	47.0	33.4	33.7
Mt							
3-1020/Ya	254	49.8	43.2	44.0	46.2	34.9	37.0
3-1037/Ya	247	48.2	39.6	42.7	47.3	35.0	35.1
3-1047/Ya	252	49.0	37.8	43.7	44.7	32.3	32.8
3-1058/Ya	244	43.0	–	34.6	38.0	32.5	32.0
3-1065/Ya	–	45.7	39.0	–	–	–	–

Astragalus	dist.art.br.	a.-p. dist.	height
3-1027/Ya	48.1	33.7	58.0
3-1028/Ya	43.5	33.0	55.6
3-1025/Ya	48.9	34.2	58.4
3-1039/Ya	46.9	32.0	57.6
3-1066/Ya	47.6	33.8	57.7

Phal. I, II	total l.	dors. l.	midshaft br.
phal. I 3-1057/Ya	76.0	68.6	32.0
phal. I 3-1058/Ya	75.3	65.9	32.2
phal. II 3-1035/Ya	44.3	35.8	39.0

layers of alternating coarse gravel and aleurite. The thickness of each layer is 6-7 m, the total thickness of the sediments is 20 m. The bone-bearing horizon, lying at the base of the sediments, is vertically 1 m thick and extends 5-6 m horizontally. The age of the fauna of the locality, based on the fossil mammals identified as *Equus stenonis, Cervus* cf. *elaphus* Linnaeus, 1758, and *Ovis* sp., was determined as late Pliocene and correlated with the Ilii Complex of Kazakhstan (Loziev & Lim 1962; Kozhamkulova 1970). Excavations since 1971 have uncovered *Canis* cf. *etruscus* Major, 1877, *Vulpes* sp., *Chasmaporthetes* sp., *Pachycrocuta* sp., *Dicerorhinus* sp., *Equus* ex. gr. *stenonis,* Camelidae ind., *Cervus* cf. *philisi* Schaub, 1941, *Leptobos* sp., *Parastrepsiceros* sp. and *Gazella* sp. (Sharapov, unpubl.). This fauna indicates a middle to late Villafranchian age.

Of the fossil horse (IZP 3-/Ya) from Yakhabed there is a fragmentary skull and jaw, isolated teeth, a fragmentary humerus, radius, some Mc and MtIII and their fragments, astragali, calcanea, proximal, second, and third phalanges (Table 3); some of the bones were found in connection. The upper tooth row (IZP 3-1012/Ya) of the skull measures 208 mm (excluding PM1), PM2-PM4 118 mm, and M1-M3 89.4 mm, with a protoconal length range in PM3-M2 of 10.9-14 mm. The plication count varies between six and nine plications. The hypocone in the premolars and M3 is slightly indented lingually. The premolar styles are flat or slightly grooved. The lower cheek teeth (IZP 3-1013/Ya, pm2-m3 measuring 206 mm) have a typically stenonid double-knot, a pli caballinid, but no protostylid; in m2 the ectoflexid is shallow (Fig. 12E). The teeth are large in comparison with the bones.

The metapodials when plotted on their distal and midshaft widths to total length (Figs 4; 5, Ya), fall within the range of *E. stehlini* (Mc) or between *E. stehlini* and *E. stenonis* (Mt). Although larger, they resemble the bones of *E.* ex gr. *steno-*

TABLE 4. — Measurements on the limb-bones of *Equus*, Tadzhikistan (in mm). Loc. Lakhuti 1 (IZP collections).

Mt	total l.	prx. br.	a.-p. prx.	dist. br.	protub. br.	keel diam.	midshaft br.
2-895/L-1	232	39.0	33.9	38.7	40.6	30.3	29.4
2-896/L-1	259	45.0	41.0	44.2	45.4	32.9	33.2

Phal. I, II	total l.	dors. l.	midshaft br.
phal. I 2-896/L-1	71.0	–	28.4
phal. II 2-896/L-1	39.5	30.6	39.0

nis from Aktogai, Kazakhstan (Kochenov & Kozhamkulova 1988: tables 5; 8), in general proportions, being proximally and distally flat like the latter (Fig. 10, Yakhabed, Aktogai). The proximal phalanges fall in the upper part of the range of *E. stehlini* (Fig. 6, Ya), as does the single second phalanx, the calcanea and the astragali.

Early to early middle Pleistocene

Locality Lakhuti 1. The locality Lakhuti 1 is situated on the right bank of the river Obi-Mazar, like Kuruksai a tributary of the river Kyzylsu, Afghan-Tadzhik Depression (Fig. 1, G). The aleurites of the deposits belong in the Kairubak Suite (Fig. 2). The bone-bearing layer is normally magnetized and is believed to date to the Jaramillo Episode (0.95 MA.), corresponding to the late early (late Villafranchian) or early middle (Galerian) Pleistocene (Dodonov 1986). The bone bearing carbonated aleurites contain *Canis lupus mosbachensis* Soergel, 1927, *Paracamelus* cf. *gigas* Schlosser, 1903, *Cervus* (*Rusa*) sp., Bovidae and *Equus* sp. (Putevoditel 1977; Sharapov unpubl.).

From Lakhuti 1 there are a two lower pm3-4 (IZP 2-/L-1) of a stenonid horse, two left MtIII (IZP 2-895/L-1 and 2-896/L-1), a proximal (IZP 2-896/L-1), second (IZP 2-896/L-1) and third phalanx (IZP 2-896/L-1) (Table 4); the three phalanges belong to the Mt with the same number. When plotted on their distal articular/midshaft width to total length, the Mt fall within the range of *E. stehlini* from Italy (Fig. 5, Lak). The smaller and more slender specimen IZP 2-895/L-1 resembles the bones of *E.* ex gr. *stenonis* from Aktogai (Kochenov & Kozhamkulova 1988: table 8), the larger and more massive IZP 2-896/L-1 approaches the bones of *E.* aff. *sivalensis* from Lakhuti 2 (see below). However, both may belong in one sample, especially since phalanx I and II (IZP 2-896/L-1), belonging with the larger Mt, are both small and when plotted on midshaft width to total length, fall in among the bones of *E. stehlini* (Fig. 6, Lak). The phalanges also resemble those from Aktogai (Kochenov & Kozhamkulova 1988: tables 9; 10). The two Mt, like those from Aktogai, are proximally and distally flat (Fig. 10, Lakhuti 1, Aktogai).

Locality Obigharm. This locality is situated on the left slope of the valley of the river Obigharm, at the mouth of the tributary Deshljashkhar, Afghan-Tadzhik Depression (Fig. 1, H). The bone-bearing horizon is a 2 m thick and 5 m long lens within a section, the total thickness of which is 35 m, consisting of hard loess and loesslike sediments with layers of calcareous tuffs; basally the sediments lie on granite. Paleomagnetic data show the bone-bearing horizon to be inversely magnetized; it is believed to be older than 0.7 Ma. (Penkov 1971) (Fig. 2). However, this age is disputed as datings on the basis of uranium have given an age of only 370 000 ± 120 000 years (Cherdyntsev 1969).

Fossil mammals from the bone-bearing layer have been identified as *Equus caballus mosbachensis* Reichenau, 1903, *Dicerorhinus* cf. *etruscus*, *D. mercki* (Jaeger, Kaup 1839, 1841), and *Gazella* sp. (Babaev 1962), indicating a mixed assemblage. More recent excavations have yielded fragmentary remains of Rhinocerotidae, *Gazella* sp., Felidae and *Equus* sp. (small stenonid) (Sharapov 1972). Caballoid horse teeth, showing

TABLE 5. — Measurements on the limb-bones of *Equus*, Tadzhikistan (in mm). Loc. Obigharm (IZP collections).

Mc	prx. br.	a.-p. prx.	dist. br.	protub. br.	keel diam.
4-783/O	47.7	31.1	–	–	–
4-787/O	–	–	37.0	43.0	26.0
4-817/O	–	–	42.0	41.0	31.6
4-754/O	–	–	38.3	40.0	29.0

Mt	total l.	prx. br.	a.-p. prx.	dist. br.	protub. br.	keel diam.	midshaft br.
4-756/O	256	46.5	38.6	38.6	45.5	34.2	31.5
4-750/O	258	47.2	39.4	42.8	43.4	35.1	31.0
4-752/O	250	–	37.0	41.0	42.0	33.0	30.5
4-753/O	–	41.0	35.1	–	–	–	–
4-757/O	–	42.8	38.0	–	–	–	–

Phal. I, II	total l.	dors. l.	midshaft br.
phal. I 4-756/O	76.8	69.3	28.6
phal. II 4-807/O	43.9	34.3	33.8

the presence of *E. caballus* Linnaeus, 1758 have not been found and the earlier identification of this species seems doubtful.

The material (IZP 4-/D) of the small horse from Obigharm comprises single upper and lower cheek teeth and deciduous teeth, three MtIII and proximal and distal parts of metapodials, proximal, second and third phalanges (Table 5) and a distal tibia. The teeth are stenonid, the upper M1-2 (IZP 4-766/D) has a short protocone (9.5 mm) and the lower m1-2 (IZP 4-762/D) has a stenonid double knot, shallow ectoflexid, and a pli caballinid (Fig. 12A). The deciduous left and right lower d3-d4 (IZP 4-815/D and 4-814/D) of one individual have a pronounced protostylid plication; they and their corresponding upper D3-D4 (IZP 4-768/D) are large, each tooth measuring 32-34 mm occlusally. Plotted on their distal articular and mid-shaft breadth to total length, the three MtIII fall within the range of *E. stehlini* (Fig. 5, O), intermediate between the two Mt from Lakhuti 1 and tieing them in with the sample from Aktogai (Kochenov & Kozhamkulova 1988: table 8); the bones are proximally flat (Fig. 10, Obigharm). The proximal and second phalanges, plotted on mid-shaft width to total length (Fig. 6, O), fall close to the sample mean or in the lower range, respectively, of the bones from Aktogai (Kochenov & Kozhamkulova 1988: tables 9-10). Judging from the deciduous teeth, dental size is large in relation to limb bone size.

Middle Pleistocene

Locality Lakhuti 2. This locality is situated near Lakhuti 1, on the tributary Khoshar of the river Obi-Mazar (Fig. 1, G). It belongs in the upper part of the Kairubak Suite (Fig. 2). The bone-bearing horizon is inversely magnetized and is believed to belong in the upper part of the Matuyama Epoch, between the boundary Matuyama-Brunhes and the Jaramillo episode (Dodonov 1986).

The fauna, believed to be early middle Pleistocene (Galerian) in age, comprises *Crocidura* sp., *Cricetulus* sp., *Meriones lakhutensis* Zazhigin, 1988, *Clethrionomys* sp., *Allophaiomys* sp.?, *Microtus* (*Phaiomys*) *lakhutensis* Zazhigin, 1988, *Canis lupus* cf. *mosbachensis, Xenocyon lycaonides* Kretzoi, 1937, *Meles* ex. gr. *meles* (Linnaeus, 1758), *Pachycrocuta brevirostris* (Aymard, 1854?), *Homotherium teilhardi-piveteaui* Sharapov, 1988, *Panthera gombaszögensis* Kretzoi, 1938, *Palaeoloxodon* cf. *antiquus* (Falconer & Cautley, 1846), *Equus* aff. *namadicus* Falconer & Cautley, 1846, Rhinocerotidae, *Camelus* cf. *knoblochi* Poljakoff, 1880, *Sinomegaceros* sp., *Praemegaceros* sp., *Gazellospira* sp. and *Bison* cf. *schoetensacki*

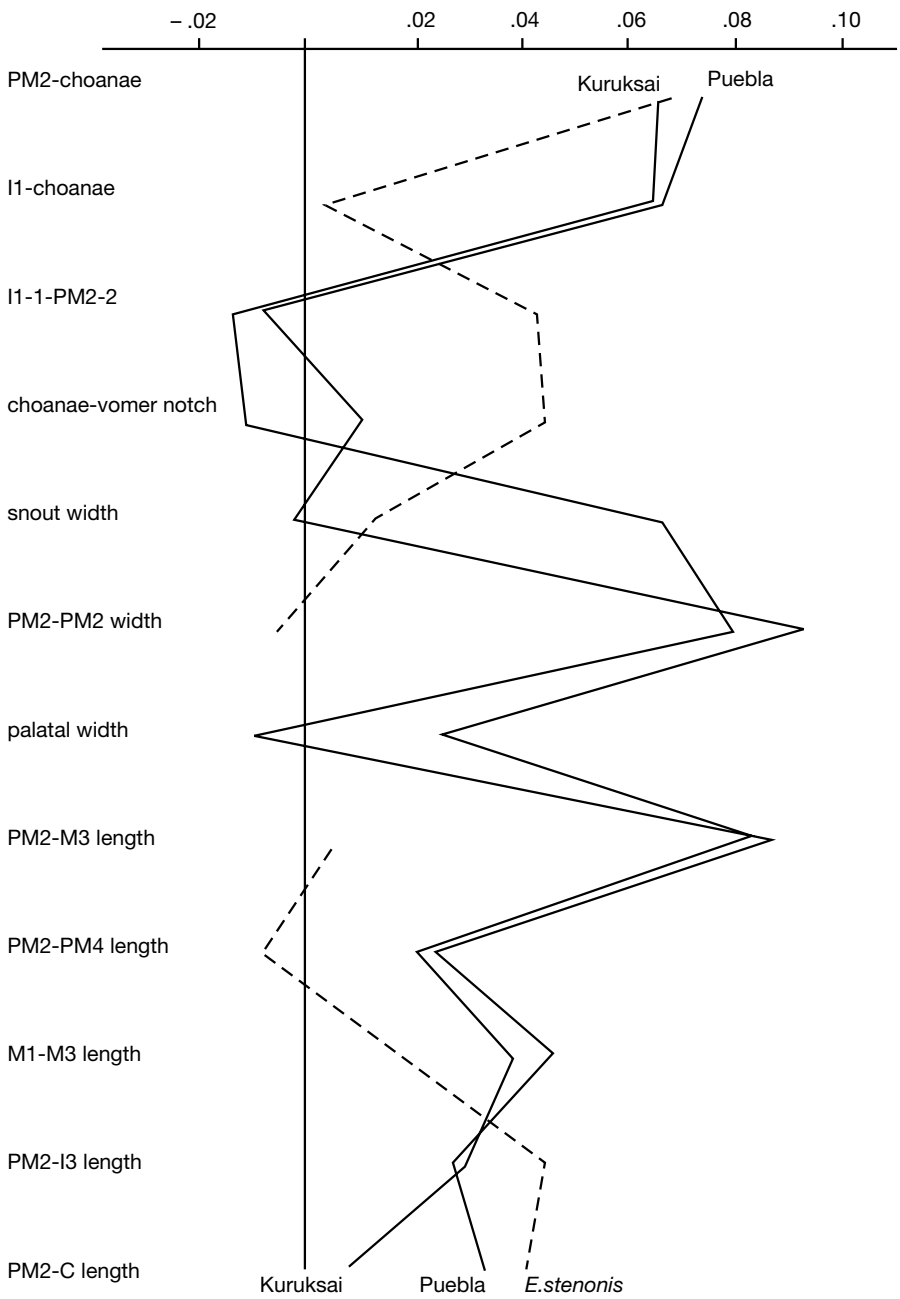

FIG. 8. — Simpson's ratiodiagram on the skull, comparing *E. stenonis* (type IGF 560, stippled line), *E. stenonis* from Puebla de Valverde and Kuruksai. Arbitrary standard (in logs): distance I1-choanae 2.14, distance PM2-choanae 2.13, snout length I1-1- PM2-2 2.15, distance choanae-vomer notch 2.10, snout width I3-I3 1.85, PM2-PM2 width 1.80, palatal width outside tooth row 2.10, alveolar tooth row length PM2-M3 2.20, premolar row length PM2-PM4 2.00, molar row length M1-M3 1.90, diastemal length PM2-I3 2.00, diastemal length PM2-C 1.80. Note the short snout (I1-PM2) in the skulls from Puebla and Kuruksai.

TABLE 6. — Measurements on the limb-bones of *Equus*, Tadzhikistan (in mm). Loc. Lakhuti 2 (IZP collections).

Mc, Mt	total l.	prx. br.	a.-p. prx.	dist. br.	protub. br.	keel diam.	midshaft br.
2-889/L-2	232	49.6	35.1	47.5	49.5	35.1	35.0
2-xxx/L-2	218+	50.6	35.7	49.2	51.2	33.3	36.0
2-887/L-2	267	50.0	42.8	46.1	47.8	35.7	32.0
2-288/L-2	271	49.6	42.2	46.6	47.5	38.0	33.9
2-899/L-2	267+	–	–	46.6	47.8	34.4	32.3

Astragalus	dist.art.br.	a.-p. dist.	height
2-893/L-2	51.7	35.8	60.9
2-901/L-2	54.7	40.0	67.8
2-894/L-2	–	–	66.5

Phal. I	total l.	dors. l	midshaft br.
2-892/L-2	83.0	76.0	32.0

Freudenberg, 1914 (Vangengeim *et al.* 1988; Sharapov 1988).

The horse from Lakhuti 2 was referred to *E.* aff. *namadicus* by Zhegallo (*in* Vangengeim *et al.* 1988), mainly on the basis of the little worn upper cheek teeth (GIN 3848/281-67, Vangengeim *et al.* 1988: 4, plate X), believed to have an unusually short molar row. In the uppers the protocone is heeled, which in the equids is considered an advanced character (protoconal mean length PM3-PM4 14.5 mm, M1-M2 16.2 mm). Primitive characters are the deep post-protoconal groove in PM4 and the premolar styles lacking grooving (for terminology, see Fig. 9). The pli caballin is weak, especially in the molars. The lower cheek teeth (IZP 2-881/L-2) have a shallow ectoflexid in m1-m3. There is a pli caballinid, but no visible protostylid. The metaconid-metastylid double knot of the lower premolars is flattened, with a long-oval metaconid and sharply triangular metastylid separated by a V-shaped inner groove, typical of the stenonid horses (Fig. 12F). In the molars these cuspids are smaller and less angular. Both the upper and lower cheek teeth are very large, the upper tooth row measures 217 mm (premolar row 124.7 mm, molar row 96.4 mm) and the lower molar row 92.7 mm.

The limb bone sample comprises six Mt and McIII (GIN 3848, IZP /L-2), four proximal phalanges, one fragmentary phalanx II, one third phalanx, eight astragali and two calcanea (Table 6). The bones indicate a medium-sized horse: plotted on their breadth to length the bones fall in the lower range of the corresponding bones of typical *E. stenonis* from Valdarno but resemble those of *E. sivalensis* from the Indian subcontinent (Figs 4-6; 11, Lakhuti 2, Ind) (see Discussion). There is a discrepancy between large dental size and medium-sized limb bones, as is also the case with the other horses from this part of Asia (see Discussion).

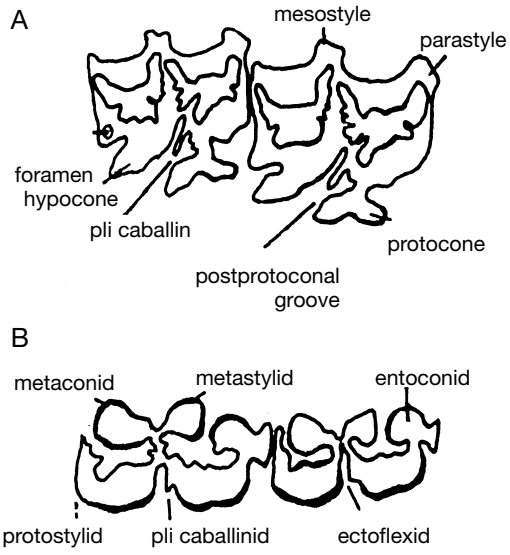

FIG. 9. — Upper and lower cheek teeth of a stenonid *Equus* with dental terminology used here. Protostylid and ectostylid not visible. **A**, upper cheek teeth; **B**, lower cheek teeth.

Late Pleistocene

Locality Ogzi-Kichik. This Upper Paleolithic (Fig. 2) living site is in front of a cave situated 20 km north-east of the village Dangara in the southeastern part of the Afghan-Tadzhik Depression. Excavations just outside the cave mouth were begun in 1971 by the archeologist V. A. Ranov.

Radiocarbon dating on coal from the cultural layer gave an age of 15 000 BP, which contradicts the type of the artefacts, considered Mousterian. Renewed datings have given dates of 30-40 000 BP (Ranov *et al.* 1973). The deposits are believed to be mixed.

Excavations have yielded a fauna of 26 mammals, birds and reptiles dated to post-Khosar time. The small mammals are represented by modern species, e.g. *Hemiechinus auritus* (Gmelin, 1770), *Hystrix* sp., *Marmota* cf. *himalayana* (Hodgson, 1841), *Ellobius talpinus* (Pallas, 1770), *Cricetulus migratorius* (Pallas, 1773), *Meriones tamariscinus* (Pallas, 1773), *Blanfordimys afghanus* (Thomas, 1912), *Pitymys juldaschi* (Severtzov, 1879), *Nesokia indica* (Gray & Hardwicke, 1830) and *Rattus turkestanicus* (Satunin, 1903). Among the large mammals there is *Canis lupus* Linnaeus, 1758, *Martes foina* (Erxleben, 1777), *Ursus* cf. *arctos* Linnaeus, 1758, *Stephanorhinus* cf. *kirchbergensis* (Jäger 1835), *Equus hydruntinus, E. hemionus* Pallas, 1775, *E. caballus* (from the uppermost levels), *Cervus elaphus* Linnaeus, 1758 and *Capra hircus* Linnaeus, 1758 (Ranov *et al.* 1973, emended). Shells of *Testudo* sp. are very common.

The material of *E. hemionus* comprises the left and right upper tooth rows of one individual (IZP 6-1084/OK) and isolated upper and lower, permanent and deciduous cheek teeth. The tooth rows measure 165.4 and 164.5 mm.

Equus hydruntinus is represented in the IZP collections by seven isolated permanent cheek teeth. A small sample in GIN (without No.) comprises three additional specimens.

In the uppers of *E. hydruntinus* the protocone has a heel, thus it is fairly long; the range in PM3-M2 is 8.6-10.1 mm (N 5), with a mean of 9.3 mm. This is slightly longer than in most local samples of this species, but corresponds to the mean protoconal length in *E. hydruntinus* from Pégourié, France (Guadelli 1995). The plication count is 5-9 (N 5), with a mean of six plications, which is within the range of other samples.

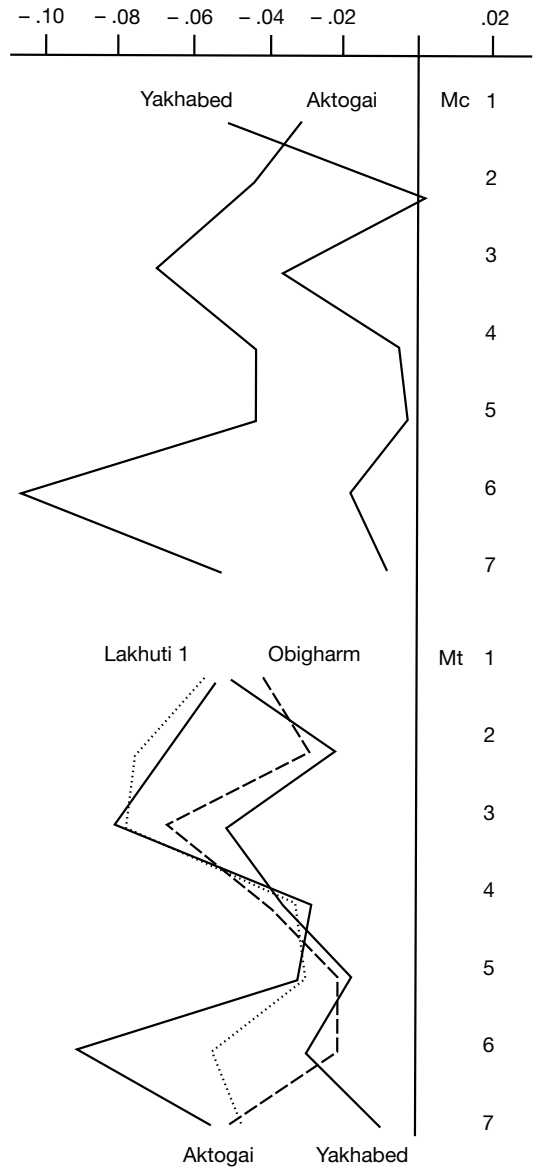

FIG. 10. — Simpson's ratiodiagram, comparing the metapodials (Mc top; Mt bottom) of the small horses from Aktogai, Yakhabed, Lakhuti 1 and Obigharm, using means of samples. Standard and measurements as in Fig. 7. Note flattening of proximal (measure 3) and distal (measure 6) diameters of the bones.

The horse is rare; there are nine permanent and deciduous cheek teeth in IZP, one in GIN. This is a large form, unfortunately the teeth are very fragmentary and partly burned. The protocone is long, from 14 to more than 15 mm.

This locality has yielded three species of equids, although probably from different levels in the cave. Three species of equids also occur from Tabun Cave and questionably from Shkul Cave, Palestine (BMNH collections). In the sample from Tabun *E. hydruntinus* and *E. caballus* occur together in level Eb, while *E. hydruntinus* and *E. hemionus* (as defined on the basis of the long protocone and shallow molar ectoflexid, thus contesting the identification with *E.* cf. *tabeti* Arambourg, 1970 by Eisenmann [1992]) occur in level C; the species thus possibly replace one another pairwise. Two sympatric equid species in one locality is common in the late Pleistocene of Eurasia, e.g. the ubiquitous *E. caballus* together with *E. hydruntinus* in Europe and with *E. hemionus* in Asia. At the periphery of the geographic range of the more localized species *E. hydruntinus* and *E. hemionus* in southeastern Europe and southwestern Asia, all three species may meet.

Locality Khudji. This late Pleistocene (Fig. 2) open air living site is situated at an elevation of 1200 m, 70 km north-east of the capital Dushanbe in the Afghan-Tadzhik Depression. The cultural layer, which covers 105 square metres, is 15-30 cm thick. It consists of loess in which the remains of ancient fireplaces are visible as blackened areas. The loess is basally in contact with ancient spring deposits and inclined loessic clay loams. In the lower part of the deposits there is a poorly fossilized soil. Here have been found Mousterian stone implements and mammalian bones, belonging to *Hystrix* sp., *Canis lupus, Equus hemionus, Sus scrofa* Linnaeus, 1758, *Cervus elaphus, Megaceroides* indet., *Bos* sp., and *Ovis/Capra* sp. (Sharapov 1994).

A number of isolated equid cheek teeth (Coll. IZP 7-/Kh) partly belong to *E. hemionus* (e.g. IZP 7-1122/Kh, upper M1-2, and 7-1128/Kh, lower pm3-4) (Fig. 12D), partly to a medium-sized caballoid horse (IZP 7-1127/Kh, lower pm3-4) (Fig. 12C), but mainly this small sample is taxonomically uncertain because fragmentary. In all the upper molars the pli caballin is either barely visible or lacking in spite of little or moderate dental wear, which could indicate their belonging to *E. hemionus*. Three lower m1-2 (IZP 7-1127/Kh (Fig. 12B) and -1129), possibly from one individual, have a deep ectoflexid reaching almost to the metaconid-metastylid commissure, a character rare in the hemiones (Eisenmann 1981). Because of wear, the morphology of their double knot is not clear, but for their size they correspond to the uppers in the sample.

COMPARISON AND DISCUSSION

The dental characters of the Tadzhik fossil *Equus,* e.g. relatively long protocone of the uppers and shallow molar ectoflexid of the lowers (hemionine dental characters), have caused local samples to be identified as *E. sivalensis* and *E. namadicus*, originally of the Siwalik Hills and Narbada Valley, the Indian subcontinent. These two species were described by Falconer & Cautley (1849) in the classical *Fauna Antiqua Siwalensis* (*FAS*). The lectotype specimens of the two species, skulls BMNH 16160 and 2683, respectively, are in the Natural History Museum, London, together with other skull and jaw fragments, isolated teeth and limb bones from the same areas. The limb bones clearly fall into two size groups. The smaller, more common bones, in *FAS* generally referred to as *Hipparion antelopinum* (Falconer & Cautley, 1849), are white in a reddish matrix. The larger bones are greyish-white in a brown matrix.

We believe that the smaller bones belong to *E. hemionus*, the kulan. Their measurements correspond to those on the bones of recent *E. hemionus* (own data and Eisenmann 1975: table 1; Dive & Eisenmann 1991). Among the Siwaliks equid teeth in BMNH, those pertaining to a hemione are not as readily distinguished from those of the larger equid as are the bones since there are no clear morphological differences.

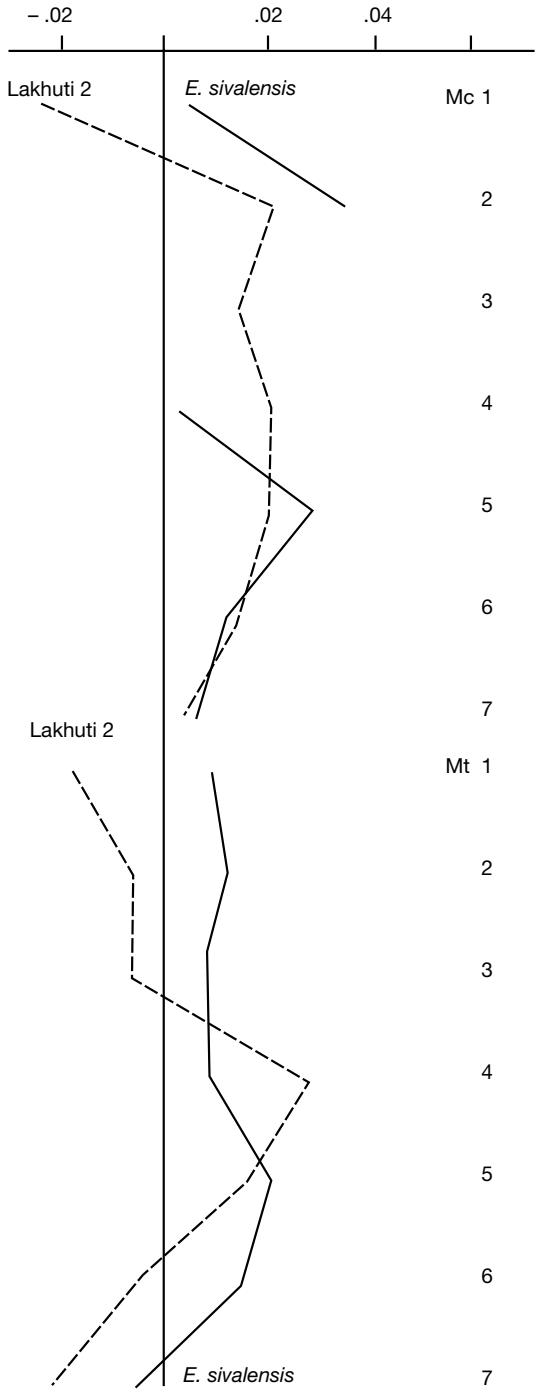

FIG. 11. — Simpson's ratiodiagram, comparing the metapodials (Mc top; Mt bottom) of *Equus sivalensis* from the Indian subcontinent with those from Lakhuti 2, using means of samples. Standard as in Fig. 7.

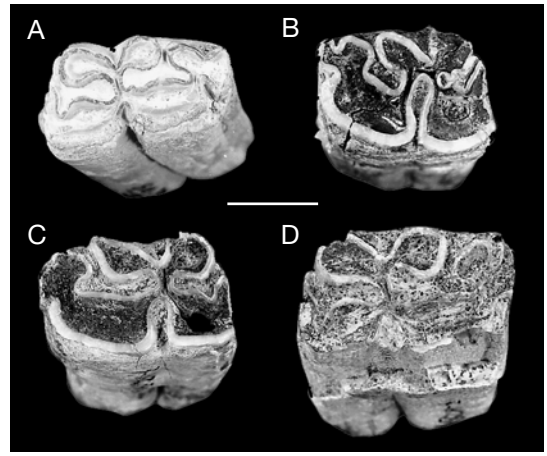

FIG. 12. — **A**, left lower m1-2 (IZP 4-762/D) of *E*. sp. from Obigharm; **B**, right lower m1-2 (IZP 7-1127/Kh) of *E*. sp. from Khudji; **C**, right lower pm3-4 (IZP 7-1127/Kh) of a caballoid horse from Khudji; **D**, left lower pm3-4 (IZP 7-1128/Kh) of ?*E. hemionus* from Khudji. Scale bar: A, 1.18 cm; B, 1.15 cm; C, 1.19 cm; D, 1.1 cm.

Some specimens, mainly from the Narbada Valley (e.g. several isolated teeth and tooth rows without a number; BMNH 256, 259, 2685 and 2689 called *E. palaeonus* Falconer & Cautley, 1849, and BMNH 18439), stand out for their small size, however, and resemble the teeth of the kulan (Eisenmann 1980, 1981: tables). In the Siwaliks collections the kulan may be stratigraphically younger than the large equid, since the hemiones are believed to have appeared only in the middle Pleistocene (Vangengeim & Zhegallo 1982).

The larger bones probably belong with the larger dental material. Of the two named species, *E. namadicus* is believed to be stratigraphically younger, to be larger and to have a longer protocone of its uppers than *E. sivalensis*. The teeth of the lectotype skulls, BMNH 2683 and 16160, are almost identical in size, but the protocones of BMNH 2683, the type of *E. namadicus*, are longer. However, there are intermediate specimens in the collections, e.g. BMNH 2666 and specimen 2 in Lydekker (1882 *in* Hooijer 1949: table II). Hooijer (1949; see also Matthew 1929; Colbert 1935) regarded *E. namadicus* a younger synonym of *E. sivalensis* and described a skull

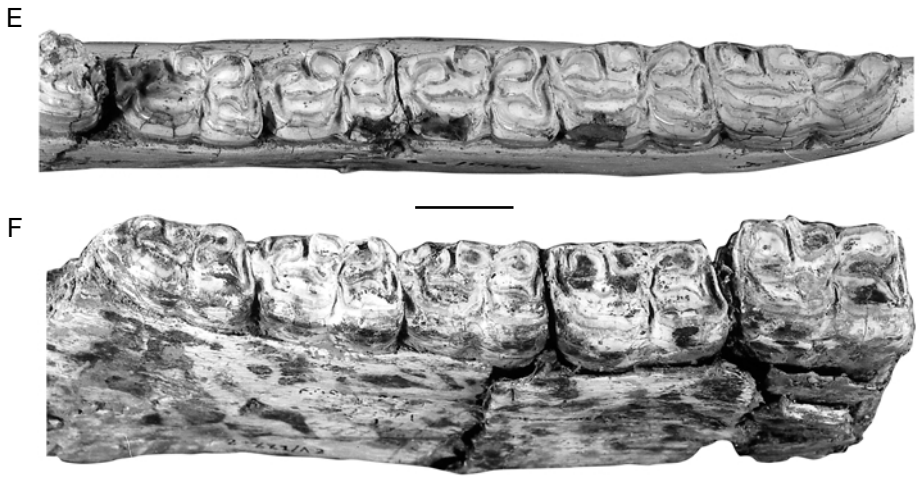

FIG. 12. — **E**, right lower pm2-m3 (IZP 3-1013/Ya) of *Equus* sp. from Yakhabed; **F**, right lower pm3-m3 (IZP 2-881/L-2) of *E.* aff. *sivalensis* from Lakhuti 2. Scale bar: E, 0.78 cm; F, 0.8 cm.

from Jhil, India, with a long protocone in its teeth, as *E. sivalensis*. We will follow Hooijer (1949) here and refer the large teeth and bones in the BMNH Siwaliks collections to *E. sivalensis*.

Compared with the Tadzhik fossil horses, *E.* sivalensis has slightly smaller teeth. Maximal length of upper PM2-M3 in the latter is 196 mm (the Jhil skull and one specimen in BMNH listed by Hooijer 1949, table II); lower pm2-m3 measure maximally 198 mm and 202 mm (BMNH 23107 called *E. cautleyi* Hopwood, 1936, and BMNH 2687). The protoconal length, when plotted to occlusal length of the tooth, covers almost the whole range observed in the Tadzhik horses: for their protoconal lengths the specimens from Kuruksai generally fall beneath or at the bottom of the range of the Siwaliks-Narbada horse, while the tooth row (GIN 3848/281-67) from Lakhuti 2 falls in the upper range of the latter. The protocones in the tooth rows from Karamaidan and Yakhabed are intermediate in length.

The few metapodials (two MtIII BMNH 16681 and 17828, proximal fragment BMNH 203, and single McIII BMNH 2671) of *E. sivalensis* seem to be longer and more gracile than those from Tadzhikistan, but all samples are unfortunately small (Figs 4; 5, Ind). The metapodials from Lakhuti 2 come closest in size and general proportions (Fig. 11, Lakhuti, *E. sivalensis*). The proximal phalanx (BMNH 2646) resembles those from Lakhuti 2 in length, but barely overlaps them in mid-shaft width (Fig. 6, Lak, Ind). The astragali and calcanea resemble those from Lakhuti 2.

Thus the horse from Lakhuti 2 referred to *E.* aff. *namadicus* on its dental morphology (Zhegallo *in* Vangengeim *et al.* 1988; Sharapov 1988), does resemble *E. sivalensis* (including *E. namadicus*) also for its limb bones, as represented in the Siwaliks collections in the BMNH.

Compared with typical *E. stenonis* from Valdarno, the Tadzhik horses have larger teeth with a longer protocone, particularly in the upper molars. The upper tooth row in *E. stenonis* measures 177 mm (IGF 583 from Tasso) to 191 mm (IGF 11023 from Olivola) and lower row 160 mm (IGF 14313 from Selvella) to 193 mm (IGF 11024 from Olivola); the protoconal range in P3-M2 is 6.2-11.1 mm (mean P3-4 8.6 mm, M1-2 9.4 mm). Although in *E. stenonis* the lower molars may have a shallow ectoflexid, e.g. in m1-m3 (IGF 560, the type jaw from Terranova), m2-m3 (IGF 11024), and m2 (IGF 14166), the two latter from Olivola, a shallow molar ectoflexid does not appear to be as general as in the Tadzhik

horses and the ectoflexid may even end flat at the metaconid-metastylid commissure (IGF 14312 from Selvella). However, if only the type skull and jaw of *stenonis* were known, a shallow molar ectoflexid would be considered typical of that species. The snout in the skull (GIN 3120-320) from Kuruksai is shorter and broader than in the skulls of typical *E. stenonis* (IGF 560 and 11023 from Terranova and Olivola), but resembles that in the skull of *E. stenonis* from Puebla de Valverde, Spain (Fig. 8). The limb bones from Kuruksai and Karamaidan closely resemble those from Valdarno in size and general proportions (Figs 4-7, Kur, K).

The teeth of *E. stehlini* are almost identical to those of *E. stenonis* and among the isolated teeth from Valdarno the two species cannot be differentiated. The tooth rows are slightly shorter in *stehlini*, e.g. upper PM2-M3 measure 149 mm (IGF 563, the type from Terranova) to 167 mm (IGF 582 from Le Ville) and the lower row 166 mm (IGF 582 from Le Ville), but the protocones are almost identical in length: range in P3-M2 7.2-10.4 mm, mean P3-4 8.6 mm, M1-2 9.0 mm, a shallow ectoflexid appears to be rare. The limb bones are clearly smaller and the metapodials relatively slightly narrower than those of *stenonis* (Figs 4; 5). Although the metapodials of the small Tadzhik horses from ?Kuruksai, Lakhuti 1, Yakhabed, and Obigharm resemble those of *E. stehlini* in their breadth/length proportions, they differ in being proximally and distally flat. The teeth of the small Tadzhik horses differ from those of *stehlini* in their large size and longer protocone, and in having shallow molar ectoflexids.

Kochenov & Kozhamkulova (1988) described a small horse as *E.* (*Allohippus*) ex gr. *stenonis* from Aktogai, Kazakhstan. They dated their find to the Ilii Complex or middle Villafranchian. Although the limb bones are small and slender, the teeth are relatively large: the lower pm2-m3 measure 183.5 and 189.3 mm. The protocone is medium long, range in pm3-m2 10-13.2 mm, the molar ectoflexid is said to be deep (Kochenov & Kozhamkulova 1988: tables 1, 2). The limb bones resemble those of the small Tadzhik horses in size and proportions and in being proximally and distally flat, the protocone of the uppers is long in relation to tooth size, but in the lower molars a shallow ectoflexid may be less frequent. The small horse from Aktogai, although a stenonid, does not belong in *E. stenonis*; for its size and proportions it falls beneath the hypodigm of that species. It rather resembles *E. stehlini,* although the protocones of its upper cheek teeth are longer than in the latter.

The Tadzhik horses tend to have large teeth in relation to their limb bones; this is also true for the small horse from Aktogai. If *E. stenonis* and *E. stehlini* are taken to represent "normal" dental/limb bone proportions, the Tadzhik horses have up to 15% larger teeth in relation to their limb bone size (upper M1 occlusal surface area: Mt proximal articular surface area). Limb bone massivity reflects body mass, as does dental area. However, dental area may also reflect ecological conditions, such as resource availability and quality. Poor vegetation due to high fiber/nutrient ratio, high silica content, or contamination with grit may demand particularly effective chewing for nutrient extraction and wear resistant, thus large teeth. The longer protocone, if not simply correlated with tooth occlusal length, may be part of the same ecological parcel. A long protocone perpendicular to chewing direction increases shear during mastication (Rensberger *et al*. 1984). A shallow ectoflexid in the lower molars is considered advanced in the equids, but its ecological significance is unknown. Gromova (1952) suggested that a shallow ectoflexid prevents breaking of the tooth by tieing the trigonid and talonid more closely together, but there is no evidence that breaking is more common in earlier equids with a deep ectoflexid in both premolars and molars.

CONCLUSION

While the hipparions from Tadzhikistan, as far as can be judged on the basis of the scant material, are related to hipparions both in Europe and in China (Forsten 1997), the stenonid horses from

this area seem dentally to have their closest relatives in Asia. While the large teeth and relatively long protocone of the Tadzhik horses may be adaptations to ecological conditions, i.e. to food demanding effective chewing and wear resistant teeth, the shallow molar ectoflexid and its varying frequency in local populations both within and outside Tadzhikistan is of unknown functional significance. In the stenonid *Equus* of Tadzhikistan, of the Indian subcontinent, and of parts of western China (Xinjiang, Qinghai and Yunnan, but also Beijing Municipality in the north; Forsten 1986) a shallow molar ectoflexid, believed to be an advanced character in the equids, is relatively common in finds of different stratigraphic age. Interestingly, a molar shallow ectoflexid characterizes recent *E. hemionus*, still an inhabitant of central Asia.

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