

Equus (Sussemionus) ovodovi Eisenmann et Vasiliev, 2011 from the Late Pleistocene of Western Siberia

Natalya A. Plasteeva*, Sergey K. Vasiliev & Pavel A. Kosintsev

ABSTRACT. Small equid remains are frequent in the Late Pleistocene deposits in the southern part of Western Siberia. Re-examination of fossil material previously attributed to *E. hydruntinus* or *E. hemionus* revealed its attribution to *E. ovodovi*. Morphologically it is characterized by slender third metapodials, short protocone on the upper teeth, V-shaped lingual valley, and occurrence of isolated stylids on the lower teeth. In Late Pleistocene *E. ovodovi* was widespread in the southern part of Western Siberia. Its remains are reported from Priobskoye Plateau, Altai, and Kuznetsk Alatau. To the east the range reached at least the Yenisei River. Radiocarbon dates suggest *E. ovodovi* inhabited the area until the end of the Kargin interstadial (MIS 3).

KEY WORDS. *Equus ovodovi*, Equidae, Pleistocene, Western Siberia, morphology.

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***Equus (Sussemionus) ovodovi Eisenmann, Vasiliev, 2011* в позднем плейстоцене Западной Сибири**

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РЕЗЮМЕ. Костные остатки мелкой формы лошади часто встречаются в позднеплейстоценовых отложениях юга Западной Сибири. Повторное изучение ископаемого материала, ранее относимого к *E. hydruntinus* или *E. hemionus*, показало их принадлежность к *E. ovodovi*. Морфологически этот вид характеризуется стройными метакарпальными и метатарзальными костями, коротким протоконом на верхних зубах, V-образной лингвальной долинкой и присутствием изолированных столбиков на нижних зубах. В позднем плейстоцене вид был широко представлен на юге Западной Сибири. Найдены *E. ovodovi* происходят с территории Приобского плато, Алтая и Кузнецкого Алатау. На восток ареал доходил, по меньшей мере, до Енисея. Радиоуглеродные даты свидетельствуют о том, что *E. ovodovi* обитала на рассматриваемой территории вплоть до конца каргинского интерстадиала.

КЛЮЧЕВЫЕ СЛОВА. *Equus ovodovi*, Equidae, плейстоцен, Западная Сибирь, морфология.

Introduction

During the Late Pleistocene, southwestern Siberia was inhabited by two coexisting equids: the large-sized caballoid *Equus ferus* Boddaert, 1785 and a small-sized horse. Remains of small-sized horse have been attributed to *Equus hemionus* Pallas, 1775 (Galkina & Ovodov, 1975; Foronova, 1990) or *Equus hydruntinus* Regalia, 1907 (Derevianko *et al.*, 1990; Foronova, 1990; Derevianko *et al.*, 2003; Vasiliev *et al.*, 2006a; Vasiliev *et al.*, 2006b). Fossil material obtained from several caves in the Altai Mountains (Vasiliev *et al.*, 2008) and alluvial sites of the Pre-Altai Plain (Vasiliev & Orlova, 2006) indicate that in the Late Pleistocene this small horse was broadly distributed in the area and commonly served as prey for animal predators and ancient humans.

Recent DNA study of horse remains from Proskuriakova Cave (Khakassia) revealed that it does not belong, as

was previously thought, to *E. hydruntinus* or true horses but represents a separate monophyletic group of equids (Orlando *et al.*, 2009). On the basis of skeletal remains from the cave a new species was described *Equus ovodovi* Eisenmann, Vasiliev, 2011 (Eisenmann & Vasiliev, 2011). The name honors N.D. Ovodov who excavated faunal remains from Altai caves, including Proskuriakova Cave.

Radiocarbon age of *E. ovodovi* bones from Proskuriakova Cave corresponds to 42.4–45.7 kyr BP. Detailed examination of tooth and skeletal morphology of the new species showed that *E. ovodovi* belongs to the subgenus *Sussemionus*, supposedly extinct in the Middle Pleistocene (Eisenmann, 2010). These equids were widespread in the first half of the Pleistocene from Western Europe through eastern Siberia and Alaska (Eisenmann *et al.*, 2008). The discovery of *E. ovodovi* in Khakassia suggests that sussemiones survived in western Siberia until the end of the Late Pleistocene.

Table 1. List of localities and number of examined specimens (small equid / large equid).

| Locality | Lat; Long | Teeth | Mc III | Mt III |
|------------------|------------------|--------|--------|--------|
| Hyena's Den Cave | 51,3; 83,1 | 329/68 | 11/14 | 12/4 |
| Okladnikova cave | 51,4; 84,0 | — | 3/3 | 2/1 |
| Taradanovo | 53,5; 81,5 | — | 4/76 | 4/64 |
| Chik | 54,5; 82,5 | — | 1/48 | —/35 |
| Kurtak | 55; 91 | — | 17/36 | 14/27 |
| Irtysh river | 57,4–58,4; 68–71 | 12/50 | 37 | — |
| Merimy | 58,0; 68,0 | 2/4 | 28 | — |
| Abatskoe | 56,2; 70,3 | — | 6 | — |
| Blinnikovo | 57,5; 68,0 | — | 4 | — |
| Epanchino | 58,1; 68,4 | — | 4 | — |

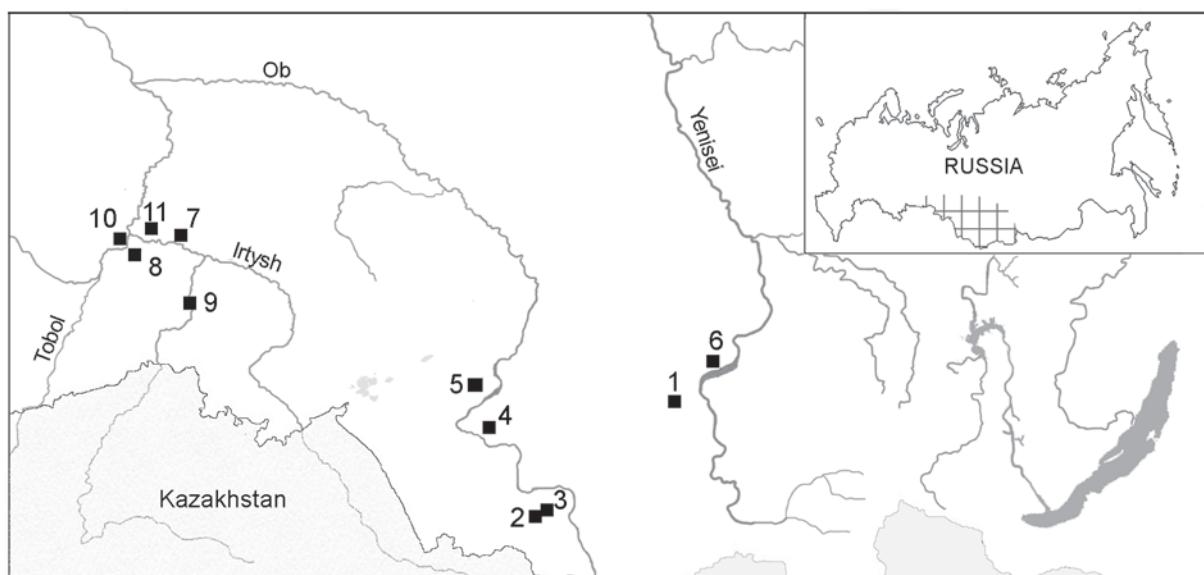


Fig. 1. Map of the Pleistocene localities with equid remains.

1 — Proskuriakova Cave, 2 — Hyena's Den Cave, 3 — Okladnikova cave, 4 — Taradanovo, 5 — Chik, 6 — Kurtak, 7 — Irtysh, 8 — Merimy, 9 — Abatskoe, 10 — Blinnikovo, 11 — Epanchino.

In this paper we present a description and re-examination of the small horse remains from several additional sites, located in the southern part of western Siberia.

Materials and methods

Small equid remains were found in alluvial sites in the Ob River basin (Chik, Taradanovo) and cave sites in Altai (Denisova, Kaminnaya, Strashnaya, Chagyrskaya, Hyena's Den, Okladnikova) in association with caballoid horses. These two groups of equids differ from each other in size and proportions of skeletal elements. Most of the bones, except small fragments, vertebrae, ribs and bones from juvenile specimens can be attributed to each size group visually. Horse remains from cave deposits accumulated by predators or ancient humans are highly fragmented so fossil material from Denisova, Kaminnaya, Strashnaya and Chagyrskaya

caves (Vasiliev, 2009; Vasiliev & Zenin 2009; Lobachev *et al.*, 2012) is not presented in this paper.

The current study focuses on horse teeth, metacarpal and metatarsal bones from Hyena's Den and Okladnikova caves, Taradanovo and Chik alluvial sites (Tab. 1, Fig. 1). Small equid remains from these sites were initially identified as *E. hydruntinus* (Vasiliev, 2004; Vasiliev *et al.*, 2006b). Only permanent teeth (P2–M3, p2–m3), metacarpal (mc III) and metatarsal (mt III) bones with fully fused epiphyses from adult individuals were included in the analysis.

In order to clarify the distribution of small equid in southwestern Siberia we used additional unpublished data on fossil horses from the rivers Irtysh (Epanchino, Irtysh), Ishym (Abatskoe), Tobol (Merimy, Blinnikovo) and Yenisei (Kurtak). All materials originated from alluvial sites and most of the bones can be dated to MIS 3 (Krivonogov, 1988; Vasiliev *et al.*, 2008).

Data on *E. ovodovi* from Proskuriakova Cave are cited according to Eisenmann & Vasiliev (2011).

Table 2. Radiocarbon dates for bones of small equid remains from Western Siberia (noncalibrated values).

| Locality | Sample | Lab.No. | ¹⁴ C BP | Source |
|--------------------|-------------------|------------|--------------------|------------------------------|
| Proskuriakova Cave | <i>E. ovodovi</i> | CURL-10275 | 42480±1500 | Orlando <i>et al.</i> , 2009 |
| Proskuriakova Cave | <i>E. ovodovi</i> | CURL-10284 | 45770±2250 | Orlando <i>et al.</i> , 2009 |
| Chik | small equid | SPb-1343 | 23200±800 | this paper |
| Taradanovo | small equid | SPb-1340 | 28340±800 | this paper |

The radiocarbon age of the cave deposits (Proskuriakova, Okladnikova, and Hyena's Den caves) and Chik alluvial site corresponds to the Karginian Interstadial, MIS 3 (Krause *et al.*, 2007; Vasiliev *et al.*, 2008; Orlando *et al.*, 2009; Lobachev *et al.*, 2012). Series of radiocarbon dates from Taradanovo, except several infinite dates, correspond to MIS 3 (Vasiliev & Orlova, 2006) and most of the mammal remains belong to Late Pleistocene faunal complex (Vasiliev *et al.*, 2008). Radiocarbon dates on *E. ovodovi* from Proskuriakova Cave and small horse remains from Chik and Taradanovo provide an age range between 45 and 23 kyr BP (Tab. 2).

For comparative purposes we used data on fossil caballoid horses, *E. hemionus* and *E. hydruntinus*. Holocene occurrence of *E. hemionus* in western Siberia has been reported (Ermolova, 1978; Devyashin & Kosintsev, 2013), but there is no secure evidence of this species from Pleistocene deposits. The presence of *E. hemionus* in southwestern Siberia during the Late Pleistocene is still debatable, that is why for morphological comparison we used data on modern Mongolian wild ass (V. Eisenmann, online data). The sample of *E. hydruntinus* comes from several Crimean sites (Eisenmann & Baryshnikov, 1994; Kuzmina, 1997; van Asperen *et al.*, 2011).

Teeth were measured following Eisenmann *et al.* (1988) with author's designations. On each tooth occlusal length (L) and width (W), length of the protocone (LP) and postflexid (LPF) were measured. For each sample the protocone ($IP=LP\times 100/L$) and postflexid ($IF=LPF\times 100/L$) indexes were also calculated. Size and shape of horse teeth vary with stage of wear (Plasteeva, 2013) and their size variation is especially noticeable in highly worn and unworn specimens. In this work dental measurements were taken from samples with a crown height of 30–50 mm. Absolute crown height was measured on the buccal side from the division of the roots to the occlusal surface. From metacarpal and metatarsal bone 12 dimensions proposed by Eisenmann & Beckouche (1986) were taken. The slenderness index ($3\times 100/1$) and distal sagittal keel index ($14\times 100/12$) were used to compare absolute size and relative proportions of third metapodials. All measurements were taken with a digital caliper to the nearest 0.1 mm.

Size and shape differences of dental elements, metacarpal and metatarsal bones were analyzed using log ratio diagrams, descriptive, nonparametric (Mann-Whitney *U* test) and multivariate statistics (principal component analysis performed on raw data). Data were checked for normality by the Shapiro-Wilk test. The data from

Kurtak is not normally distributed (measurements 1, 4 and 5 on metacarpal bone), so differences in size between two groups of equids were analyzed using Mann-Whitney *U* test. In order to analyze overall size differences in the equid sample from southwestern Siberia we used principal component analysis. All statistical analyses were performed using Statistica 5.0 (Statsoft Inc., www.statsoft.com).

Histogram and scatter plot are presented for metacarpal bone; results for the metatarsal bone are only discussed in the text.

All examined material is stored in the Institute of archaeology and ethnography (Novosibirsk) and Institute of plant and animal ecology (Ekaterinburg).

Systematic paleontology

Order Perissodactyla Owen, 1848
 Family Equidae Linnaeus, 1758
 Genus *Equus* Linnaeus, 1758
 Subgenus *Sussemionus* Eisenmann, 2010

Equus (Sussemionus) ovodovi Eisenmann & Vasiliev, 2011

Type locality. Proskuriakova Cave, Khakassia, Russia.

Material. Hyena's Den Cave: upper cheek teeth: P2 — 34, P3—4 — 52, M1-2 — 77, M3 — 37; lower cheek teeth: p2 — 21, p3—4 — 49, m1—2 — 41, m3 — 20; third metacarpal bone — 11; third metatarsal bone — 12. Chik: third metacarpal bone — 1. Okladnikova cave: third metacarpal bone — 2; third metatarsal bone — 2. Taradanovo: third metacarpal bone — 4; third metatarsal bone — 4 (collections IAET RAS).

Description and comparison. Absolute sizes of the upper and lower cheek teeth are given in Appendix I, II. The size of the cheek teeth of small horse from Hyena's Den Cave is similar to *E. ovodovi* from Proskuriakova Cave and *E. h. hemionus*, but larger than size of the teeth of *E. hydruntinus*. The protocone is short on the premolars; on the molars it can be elongated (Fig. 2). The anterior half of the protocone is smaller than the posterior. The base of the protocone can be hollow or flat. The size of the pli caballine varies greatly. The enamel on the teeth is plicated, sometimes — highly plicated. *E. hydruntinus* and *E. hemionus*, on the other hand, characterized by the simple enamel pattern and short, reduced pli caballine (Eisenmann, 1980; van Asperen *et al.*, 2011).

The double knot on the lower teeth is asymmetrical, with an elongated metaconid. The enamel pattern on

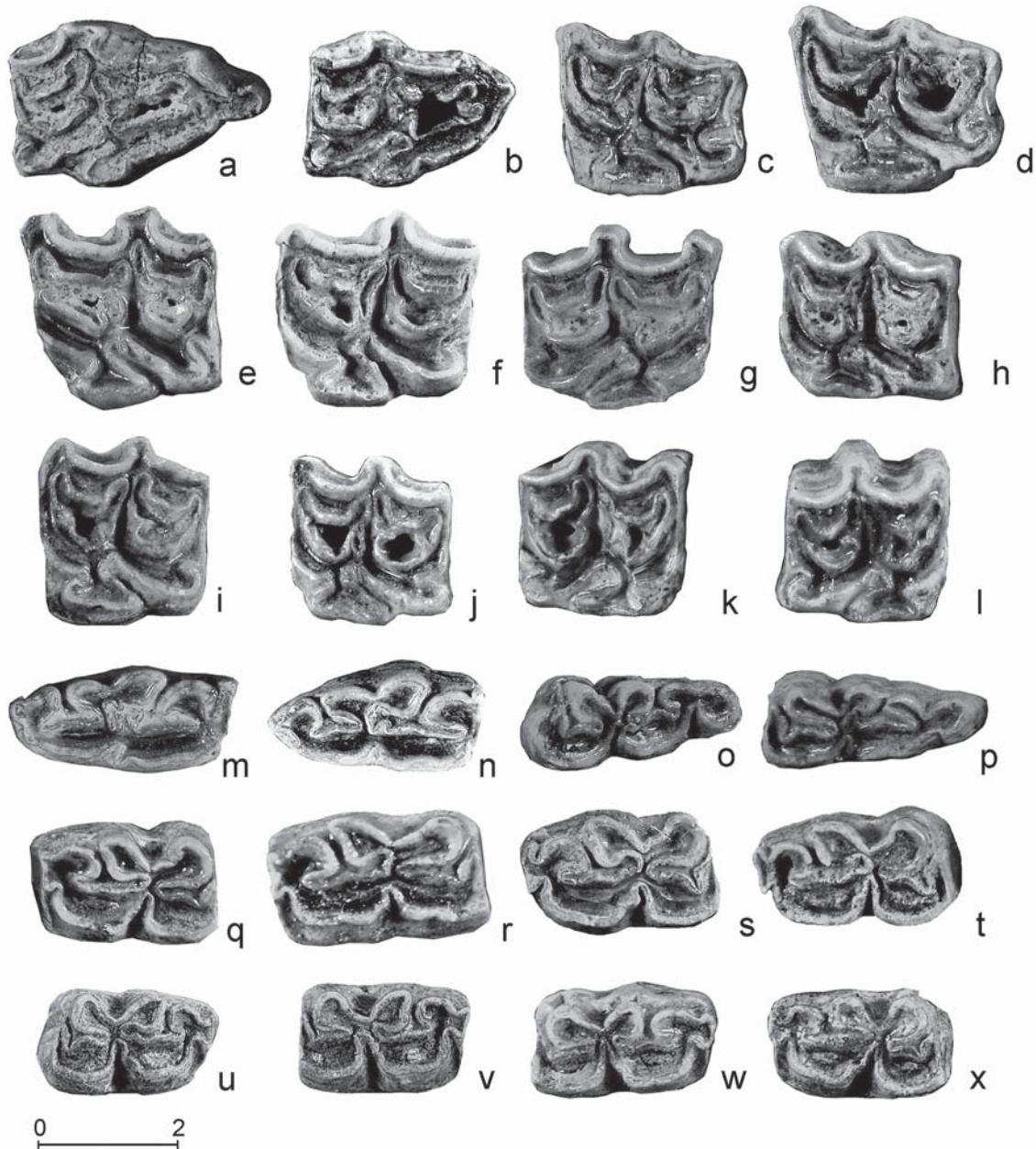


Fig. 2. Upper and lower cheek teeth of small equid from Hyena's Den Cave: a, b — P2 dex; c, d — M3 sin; e, f — P3—4 sin; g — P3—4 dex; h, i, j — M1—2 sin; k, l — M1—2 dex; m, n — p2 sin; o, p — m3 sin; q, r, s, t — p3—4 dex; u, v, w — m1—2 sin; x — m1—2 dex.

the lower dentition can include isolated stylids. The inner (lingual) valley is shallow. The ectoflexid is deep on the molars and sometimes penetrate the neck of the double knot as in *E. hydruntinus*. The ectoflexid on the lower teeth of extant Mongolian wild ass only reaches the neck of the double knot. Buccal wall of the proto- and hypoconids on the molars can be flat or rounded and differs in that from *E. hydruntinus* (Davis, 1980). These morphological traits are similar to *E. ovodovi* from Proskuriakova Cave. Protocone indices of small equid teeth are greater than those of *E. hydruntinus* but

can overlap in their values with extant *E. h. hemionus*; postflexid indices shows the opposite (Fig. 3).

The metacarpal and metatarsal bones are more slender than in *E. ferus* (Eisenmann, 1979), with a small developed sagittal crest on the distal end (Appendix III—IV). The posterio-external process on the proximal end of metatarsal bone is small (Fig. 4). Distal articular breadth is nearly equal or smaller than supra-articular breadth, in contrast to caballoid horses.

As compared to extant Mongolian wild ass and *E. hydruntinus* the metacarpals and metatarsals of *E.*

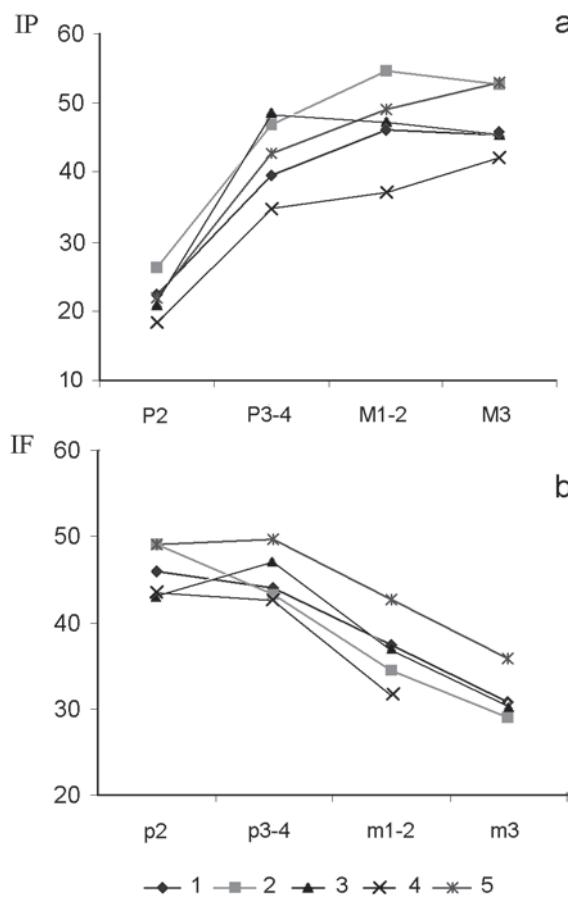


Fig. 3. Ratio diagrams of upper (a) and lower (b) dental proportions: 1 — small equid Hyena's Den Cave; 2 — *E. ferus* Hyena's Den Cave; 3 — *E. ovodovi* Proskuriakova Cave (Eisenmann & Vasiliev, 2011); 4 — *E. hydruntinus* Prolokom 2 (Eisenmann & Baryshnikov, 1994); 5 — *E. h. hemionus*.

Table 3. Relative proportions (n; Mean / Min–Max) of metacarpal and metatarsal bones of fossil equids from Proskuriakova Cave (Eisenmann & Vasiliev, 2011), Hyena's Den Cave, Chik, Taradanovo, Kurtak and modern *E. h. hemionus* (V. Eisenmann, online data).

| Species | Metacarpal bone | | Metatarsal bone | |
|-----------------------|----------------------|----------------------------|----------------------|----------------------------|
| | slenderness index | distal sagittal keel index | slenderness index | distal sagittal keel index |
| Proskuriakova Cave | | | | |
| <i>E. ovodovi</i> | 1; 13.3 | — | 6; 11.0 / 10.5–11.5 | 4; 86.2 / 81.8–90.0 |
| <i>E. ferus</i> | — | — | 3; 13.5 / 13.0–13.7 | 3; 83.3 / 80.9–86.0 |
| Hyena's Den cave | | | | |
| small equid | 10; 13.9 / 12.8–14.9 | 11; 89.1 / 86.3–92.8 | 7; 11.8 / 10.8–12.5 | 11; 87.0 / 84.9–90.6 |
| <i>E. ferus</i> | 5; 17.8 / 17.2–18.7 | 11; 83.0 / 79.2–86.1 | 4; 14.4 / 13.6–15.7 | 3; 84.2 / 81.5–87.2 |
| Taradanovo | | | | |
| small equid | 3; 14.0 / 13.6–14.4 | 4; 88.3 / 84.7–92.3 | 2; 11.2; 11.5 | 5; 85.5 / 84.4–86.9 |
| <i>E. ferus</i> | 62; 16.4 / 14.7–18.1 | 72; 82.7 / 77.4–90.9 | 63; 13.0 / 11.0–14.9 | 64; 83.2 / 77.3–87.3 |
| Chik | | | | |
| small equid | — | — | 1; 14.4 | 1; 89.4 |
| Kurtak | | | | |
| small equid | 15; 12.9 / 11.9–13.6 | 17; 88.5 / 83.3–92.4 | 14; 10.6 / 9.6–12.2 | 12; 88.9 / 85.0–95.5 |
| <i>E. ferus</i> | 36; 16.4 / 14.9–17.9 | 34; 82.8 / 79.8–88.6 | 27; 13.3 / 11.9–14.8 | 27; 83.4 / 79.6–86.9 |
| <i>E. h. hemionus</i> | 10; 11.8 / 10.9–12.7 | 10; 89.8 / 87.1–93.5 | 10; 9.7 / 8.8–10.4 | 10; 87.8 / 84.5–90.3 |

ovodovi are larger and more robust with a deep diaphysis (Tab. 3).

Mean values and variation limits of relative breadth of the diaphysis in *E. h. hemionus* lower than in fossil horses from southwestern Siberia. Modern wild asses and *E. hydruntinus* are similar to *E. ovodovi* in small developed sagittal crest on the distal end on the third metapodials.

Morphological differences between three equid species reflect log ratio diagrams (Fig. 5). Log ratio diagrams of small equid metacarpals from Okladnikova cave, Taradanovo, and Hyena's Den Cave are similar to *E. ovodovi* from the type locality and distinguish from those of caballoid horses, *E. hydruntinus* and *E. h. hemionus*. For the metatarsal bone, log ratio diagrams follow the same pattern and show differences in absolute size and relative proportions between *E. ovodovi*, *E. ferus*, *E. h. hemionus* and *E. hydruntinus*.

Based on size and morphology of skeletal elements the small equid from Hyena's den and Okladnikova caves, Taradanovo and Chik determined as *E. ovodovi*.

Results and discussion

Distribution of *E. ovodovi* in Western Siberia. To clarify the distribution of *E. ovodovi* in southwestern Siberia we examined multiple data on horse remains from different alluvial sites to the west and east from Altai and Khakassia. There are several alluvial sites from the Tobol, Irtysh, Ishym and Yenisei river valleys (Fig. 1) with large number of equid remains which dates to MIS III.

Morphological study of 68 dental specimens (13 upper and lower dental rows and six isolated teeth) showed no evidence of *E. ovodovi* in alluvial samples from Irtysh river. All specimens belong to *E. ferus*. The



Fig. 4. Metacarpal (a, b) and metatarsal (c, d) bones of small equid from Hyena's Den Cave.

protocone on the upper teeth is elongated. The double knot on the lower teeth is asymmetrical, with U-shaped lingual valley. Isolated stylids are absent. Principal component analysis of complete metacarpal bones ($n=139$) from southwestern Siberia indicates significant variation in shape but little variation in size. The first two principal components explain 85% of the total sample variance. First principal component (PC1) with negative factor loadings is strongly correlated with most of the original values (measurements 3–14) and PC2 reflects the length of the metacarpal bone (Appendix V).

A scatter plot of PC scores (Fig. 6) illustrates a clear separation between *E. ferus* and *E. ovodovi* material from Altai and Khakassia on PC1. This separation reflects a difference in metacarpal proportions: *E. ovodovi* has more slender, gracile bones than caballoid horses.

So we can assume that to the west of Priobskoye Plateau up to the Urals (Kuzmina, 2000) there is no

evidence of small equid remains. PC analysis also revealed that the sample from Kurtak (eastern Sayan Mountains) falls into two groups and 17 specimens fall within the distribution of *E. ovodovi* from Altai and Khakassia. Mann-Whitney test on metacarpal ($N_{\text{small equid}}=17$, $N_{E. ferus}=36$) and metatarsal ($N_{\text{small equid}}=14$, $N_{E. ferus}=27$) bones between the two groups of equids from Kurtak produce a significant result for original measurements (Appendix VI).

Small equid remains from Kurtak were previously attributed to *E. hemionus* (Ovodov, 1992; Kuzmin, 2011). The lack of horse teeth in the sample makes it difficult to determine the taxonomic position of the small equid from Kurtak. Based on skeletal morphology the small horse from Kurtak resembles *E. ovodovi* from Altai and Khakassia. Despite the difference in size, metacarpal and metatarsal proportions from Kurtak (Tab. 3) are similar to *E. ovodovi*. Differences in absolute size of the bones can reflect regional variabil-

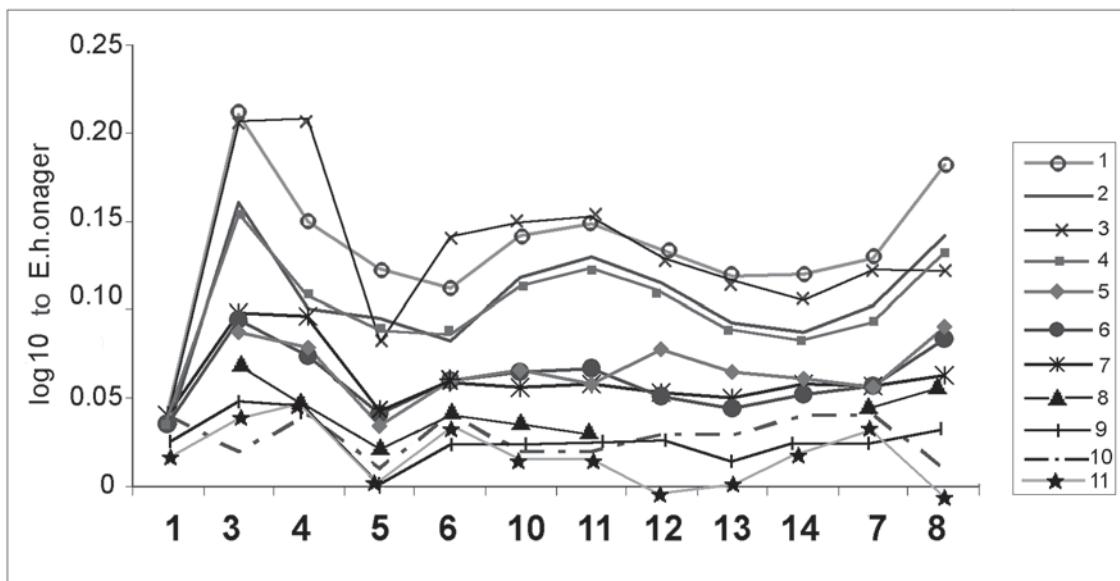


Fig. 5. Log ratio diagrams of measurements on equid metacarpals.

E. ferus: 1 — Okladnikova cave (n=3), 2 — Taradanovo (n=76), 3 — Hyena's Den Cave (n=14); 4. Kurtak (n=36); small equid: 5 — Okladnikova cave (n=3), 6 — Taradanovo (n=4), 7 — Hyena's Den Cave (n=11), 8 — *E. ovodovi* Proskuriakova Cave (n=4); 9 — Kurtak (n=17); 10 — *E. h. hemionus* (n=10); 11 — *E. hydruntinus* (van Asperen *et al.*, 2011).

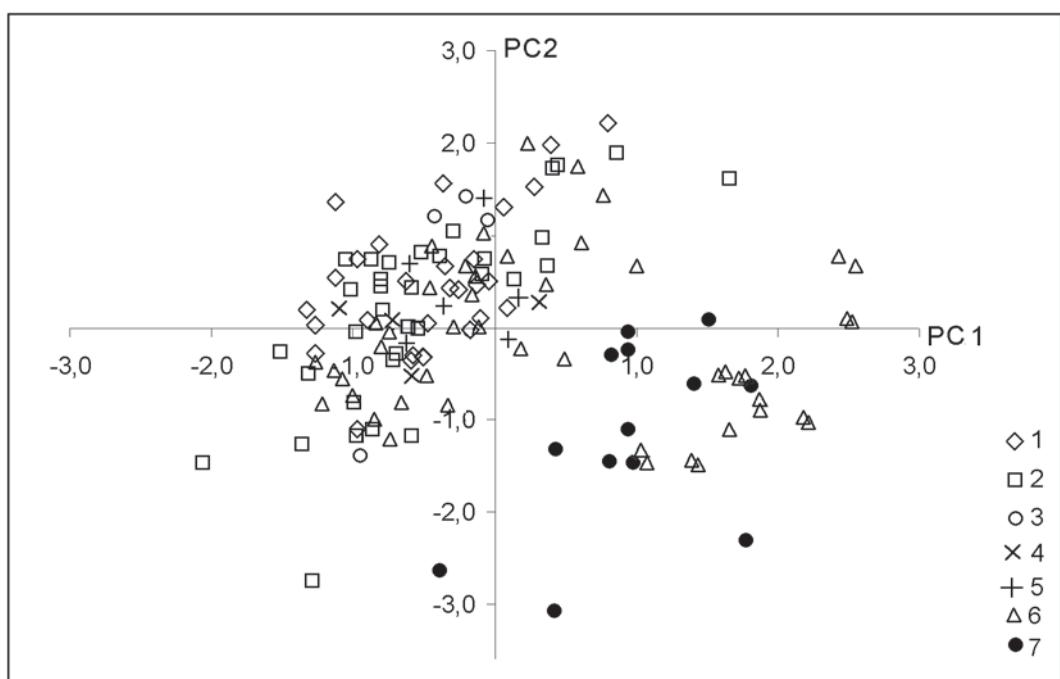


Fig. 6. Results of PC analysis of horse metacarpals.

1 — Merimy (n=28), 2 — Irtysh (n=37), 3 — Epanchino (n=4), 4 — Blinnikovo (n=4), 5 — Abatskoe (n=6), 6 — Kurtak (n=47), 7 — *E. ovodovi* from Chik, Taradanovo, Hyena's Den Cave (n=13).

ity of horses in the Late Pleistocene or chronological heterogeneity of fossil material.

The geographical distribution of *E. ovodovi* in the Late Pleistocene was probably restricted to Northern Asia. In Eastern Europe *E. ovodovi* is replaced by *E. hydruntinus*. In the Late Pleistocene it was widespread in the south of the Russian Plain, Crimea, and Caucasus

(Gromova, 1949; David, 1982). The presence of *E. hydruntinus* in Northern Asia during the Pleistocene is not confirmed (Orlando *et al.*, 2006; Eisenmann *et al.*, 2008).

The number of *E. ovodovi* remains considerably increases from the north southward. In Priobskoye Plateau (Chik and Taradanovo) the number of bones is low (0.1–1.6% from large mammals fauna), in the cave

deposits from Altai and Kuznetsk Alatau it increases to 0.2–3.2% and even reaches 33% in the Hyena's Den Cave. Though the northern limit of range is unclear, we can assume that *E. ovodovi* inhabited the south of Western Siberia and its range did not expand far to the north.

The eastern part of the range reached the Yenisei River and apparently extended further east. *E. ovodovi* was identified from the south cis-Baikalian region (Klementiev *et al.*, 2011). Small and slender equid remains referred to *E. hemionus* (Ravskii *et al.*, 1964; Konstantinov & Nemerov, 1978; Kasparov, 1986; Klementiev, 2008; Vasiliev, 2003) are reported from the Pleistocene deposits up to the Transbaikalia. After the discovery of Sussemione horses these materials should be re-examined. Species identification of equid remains is rather difficult because of their marked size overlap. The size of the skeletal elements places *E. ovodovi* between *E. ferus* and hemione-like equids.

Recent study of mitochondrial DNA shows that *E. ovodovi* is more closely related to asses and zebras, than caballoid horses (Orlando *et al.*, 2009; Vilstrup *et al.*, 2013). It shares dental and postcranial characters such as shape of the protocone and the double knot, slender third metapodials with a small developed sagittal crest with both *E. hydruntinus* and *E. hemionus*. *E. ovodovi* also have some primitive features like highly plicated enamel and isolated stylids on their teeth; and primitive *Equus* characters like isolated stylids on the lower teeth. In the most part of their range Sussemiones went extinct at about 0.5 Ma (Eisenmann *et al.*, 2008), while *E. ovodovi* inhabited southern Siberia till the end of the Kargin interstadial (MIS 3).

Conclusions

Two equid species, *E. ovodovi* and caballoid horse *E. ferus*, co-occurred in Late Pleistocene of Western Siberia. The two species can be differentiated by dental morphology, size and proportions of skeletal elements. In the Late Pleistocene, *E. ovodovi* inhabited the southern part of Western Siberia. To the east its range reached at least the Yenisei River. Radiocarbon dates obtained from Proskuriakova, Chik, and Taradanovo sites suggest *E. ovodovi* survived in the area till the end of the Kargin interstadial (MIS 3).

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Appendix I. Measurements of the upper cheek teeth of equid specimens from Hyena's Den Cave (n; Mean ± st. dev. / Min–Max) and comparative material (n; Mean / Min–Max), mm.

| Species | P2 | P3–4 | M1–2 | M3 |
|--|------------------------------------|------------------------------------|------------------------------------|------------------------------------|
| Length | | | | |
| small equid, Hyena's Den Cave | <u>26</u> ; 36.0±2.06 32.5–40.8 | <u>51</u> ; 27.2±1.08 25.0–29.6 | <u>75</u> ; 24.2±1.20 21.5–26.5 | <u>37</u> ; 27.9±1.57 24.8–32.0 |
| <i>E. ferus</i> , Hyena's Den Cave | 1; 40.0 | <u>18</u> ; 28.8±1.77 26.2–32.1 | <u>8</u> ; 27.7±0.9 27.0–29.5 | <u>12</u> ; 30.8±1.94 28.3–34.7 |
| <i>E. ovodovi</i> , Proskuriakova Cave (Eisenmann & Vasiliev, 2011) | 2; 32.0–35.5 | <u>7</u> ; 26.3 24.4–26.8 | <u>7</u> ; 24.1 22.0–26.1 | 1; 28.2 |
| <i>E. hydruntinus</i> , Prolom 2 (Eisenmann & Baryshnikov, 1994) | <u>8</u> ; 30.5 27.3–32.8 | <u>13</u> ; 24.4 22.3–26.2 | <u>26</u> ; 21.1 19.0–23.6 | <u>13</u> ; 22.1 19.5–24.5 |
| <i>E. hydruntinus</i> , Crimea (Kuzmina, 1997) | <u>11</u> ; 31.4 29.3–32.5 | <u>38</u> ; – 21.6–27.3 | <u>55</u> ; – 19.5–27.5 | <u>30</u> ; 22.6 19.5–25.5 |
| <i>E. hydruntinus</i> , Emine-Bair-Khosar (van Asperen et al., 2011) | <u>8</u> ; 32.5 31.8–33.7 | <u>17</u> ; 25.2 23.5–27.4 | <u>17</u> ; 22.3 20.9–24.0 | <u>10</u> ; 24.3 20.1–27.3 |
| <i>E. h. hemionus</i> (V. Eisenmann, online data) | <u>16</u> ; 36.6 33.0–39.0 | <u>36</u> ; 27.0 23.5–29.0 | <u>36</u> ; 23.8 21.5–27.0 | <u>16</u> ; 25.1 20.0–30.0 |
| Width | | | | |
| small equid, Hyena's Den Cave | <u>33</u> ; 24.7±1.34 20.4–27.7 | <u>47</u> ; 26.8±1.32 24.0–29.5 | <u>74</u> ; 26.3±1.24 23.8–29.7 | <u>35</u> ; 23.6±1.0 21.7–25.9 |
| <i>E. ferus</i> , Hyena's Den Cave | 1; 27.8 | <u>17</u> ; 29.7±1.71 27.0–32.5 | <u>7</u> ; 29.6±1.4 27.3–31.2 | <u>10</u> ; 25.5±1.76 23.4–28.8 |
| <i>E. ovodovi</i> , Proskuriakova Cave (Eisenmann & Vasiliev, 2011) | 2; 20.7–24.7 | <u>7</u> ; 26.6 24.8–28.3 | <u>7</u> ; 26.2 23.2–28.7 | 1; 23.0 |
| <i>E. hydruntinus</i> , Prolom 2 (Eisenmann & Baryshnikov, 1994) | <u>7</u> ; 20.6 17.2–22.5 | <u>13</u> ; 23.7 21.9–25.9 | <u>26</u> ; 21.3 19.2–22.9 | <u>13</u> ; 19.0 16.4–21.4 |
| <i>E. hydruntinus</i> , Crimea (Kuzmina, 1997) | <u>11</u> ; 21.3 19.8–22.5 | <u>38</u> ; – 21.2–25.0 | <u>55</u> ; – 20.0–25.0 | <u>30</u> ; 19.2 16.0–21.2 |
| <i>E. hydruntinus</i> , Emine-Bair-Khosar (van Asperen et al., 2011) | <u>8</u> ; 21.8 20.1–24.5 | <u>17</u> ; 24.2 21.9–25.6 | <u>17</u> ; 23.3 21.7–24.9 | <u>10</u> ; 20.9 19.6–23.1 |
| <i>E. h. hemionus</i> (V. Eisenmann, online data) | <u>16</u> ; 24.3 22.5–27.5 | <u>36</u> ; 26.4 25.0–28.0 | <u>36</u> ; 24.4 22.5–26.5 | <u>16</u> ; 20.4 17.2–24.0 |
| Length of the protocone | | | | |
| small equid, Hyena's Den Cave | <u>34</u> ; 8.0±1.11 6.2–9.8 | <u>50</u> ; 10.8±0.99 8.5–13.3 | <u>76</u> ; 11.1±1.07 8.5–13.3 | <u>37</u> ; 12.7±1.16 10.4–15.0 |
| <i>E. ferus</i> , Hyena's Den Cave | 1; 10.5 | <u>18</u> ; 13.1±2.13 10.0–16.3 | <u>9</u> ; 14.9±1.5 13.2–17.0 | <u>12</u> ; 16.2±1.09 15.0–18.0 |
| <i>E. ovodovi</i> , Proskuriakova Cave (Eisenmann & Vasiliev, 2011) | 2; 7.0–7.4 | <u>7</u> ; 12.8±1.63 10.2–14.1 | <u>7</u> ; 11.4±1.05 10.3–13.3 | 1; 12.8 |
| <i>E. hydruntinus</i> , Prolom 2 (Eisenmann & Baryshnikov, 1994) | <u>8</u> ; 5.6 4.7–7.0 | <u>13</u> ; 8.5 6.0–10.0 | <u>26</u> ; 7.8 5.8–11.3 | <u>13</u> ; 9.3 8.0–11.1 |
| <i>E. hydruntinus</i> , Crimea (Kuzmina, 1997) | <u>10</u> ; 6.5 5.5–7.5 | <u>38</u> ; – 7.5–11.2 | <u>55</u> ; – 6.0–11.5 | <u>30</u> ; 10.2 8.0–12.0 |
| <i>E. hydruntinus</i> , Emine-Bair-Khosar (van Asperen et al., 2011) | – | <u>17</u> ; 8.4 7.0–10.2 | <u>17</u> ; 8.6 7.4–9.9 | – |
| <i>E. h. hemionus</i> (V. Eisenmann, online data) | <u>16</u> ; 8.0 6.0–9.0 | <u>36</u> ; 11.6 9.0–14.0 | <u>36</u> ; 11.7 10.0–14.5 | <u>16</u> ; 13.2 11.0–15.5 |

Appendix II. Measurements of the lower cheek teeth of equid specimens from Hyena's Den Cave (n; Mean ± st. dev. / Min–Max) and comparative material (n; Mean / Min–Max), mm

| Species | p2 | p3–4 | m1–2 | m3 |
|--|------------------------------------|------------------------------------|------------------------------------|------------------------------------|
| Length | | | | |
| small equid, Hyena's Den Cave | <u>19</u> ; 32.5±1.64 30.0–36.2 | <u>48</u> ; 26.4±1.22 23.3–29.1 | <u>41</u> ; 25.1±1.43 23.0–28.7 | <u>20</u> ; 31.5±1.23 29.0–32.9 |
| <i>E. ferus</i> , Hyena's Den Cave | <u>3</u> ; 33.7±0.35 33.5–34.1 | <u>11</u> ; 28.6±1.81 25.9–31.8 | <u>6</u> ; 26.6±1.32 24.8–28.4 | <u>7</u> ; 36.1±1.18 35.0–37.9 |
| <i>E. ovodovi</i> , Proskuriakova Cave (Eisenmann & Vasiliev, 2011) | <u>5</u> ; 31.6 28.8–34.5 | <u>12</u> ; 26.2 24.0–28.4 | <u>12</u> ; 24.0 21.4–24.7 | <u>6</u> ; 30.3 28.2–31.7 |
| <i>E. hydruntinus</i> , Prolom 2 (Eisenmann & Baryshnikov, 1994) | <u>19</u> ; 26.6 22.1–28.8 | <u>22</u> ; 23.4 20.9–25.7 | <u>21</u> ; 21.6 18.3–24.0 | <u>10</u> ; 25.8 22.0–28.2 |
| <i>E. hydruntinus</i> , Crimea (Kuzmina, 1997) | <u>25</u> ; 27.2 25.0–30.0 | <u>55</u> ; – 21.6–25.6 | <u>64</u> ; – 18.6–29.5 | <u>20</u> ; 25.4 22.0–27.5 |
| <i>E. hydruntinus</i> , Emine-Bair-Khosar (van Asperen et al., 2011) | <u>5</u> ; 27.4 24.5–28.7 | <u>12</u> ; 24.5 21.1–26.1 | <u>11</u> ; 22.6 20.9–24.0 | <u>9</u> ; 25.9 20.9–28.6 |
| <i>E. h. hemionus</i> (V. Eisenmann, online data) | <u>17</u> ; 31.2 28.0–33.0 | <u>34</u> ; 27.5 25.0–30.0 | <u>34</u> ; 24.7 22.5–28.0 | <u>15</u> ; 29.2 27.0–31.5 |
| Width | | | | |
| small equid, Hyena's Den Cave | <u>21</u> ; 15.8±0.90 13.6–17.4 | <u>47</u> ; 17.2±0.99 14.7–19.0 | <u>37</u> ; 15.1±1.39 12.0–18.0 | <u>19</u> ; 12.9±1.10 11.4–14.8 |
| <i>E. ferus</i> , Hyena's Den Cave | <u>3</u> ; 18.5±0.50 18.0–19.0 | <u>11</u> ; 20.3±0.91 19.0–22.0 | <u>6</u> ; 18.9±0.46 18.3–19.4 | <u>7</u> ; 16.6±0.74 15.7–17.5 |
| <i>E. ovodovi</i> , Proskuriakova Cave (Eisenmann & Vasiliev, 2011) | <u>5</u> ; 15.7 13.6–17.0 | <u>12</u> ; 17.4 16.1–18.4 | <u>12</u> ; 16.4 14.0–18.3 | <u>6</u> ; 13.5 11.0–14.5 |
| <i>E. hydruntinus</i> , Prolom 2 (Eisenmann & Baryshnikov, 1994) | <u>19</u> ; 12.5 9.7–14.2 | <u>22</u> ; 13.8 12.0–15.7 | <u>21</u> ; 12.3 10.7–13.6 | <u>10</u> ; 11.1 8.5–13.0 |
| <i>E. hydruntinus</i> , Crimea (Kuzmina, 1997) | <u>25</u> ; 15.3 13.5–18.0 | <u>55</u> ; – 14.2–18.2 | <u>64</u> ; – 12.5–16.8 | –* |
| <i>E. hydruntinus</i> , Emine-Bair-Khosar (van Asperen et al., 2011) | <u>5</u> ; 14.2 13.2–15.6 | <u>12</u> ; 14.9 13.2–17.2 | <u>11</u> ; 13.6 12.2–16.0 | <u>9</u> ; 12.5 10.8–13.5 |
| <i>E. h. hemionus</i> (V. Eisenmann, online data) | <u>16</u> ; 14.6 13.0–16.0 | <u>34</u> ; 16.1 15.0–17.7 | <u>34</u> ; 14.3 12.0–16.0 | <u>15</u> ; 12.6 11.0–14.0 |
| Length of the postflexide | | | | |
| small equid, Hyena's Den Cave | <u>21</u> ; 15.0±1.15 13.0–17.0 | <u>49</u> ; 11.7±1.42 8.0–14.0 | <u>39</u> ; 9.4±1.19 6.5–12.3 | <u>20</u> ; 9.7±1.52 7.2–13.4 |
| <i>E. ferus</i> , Hyena's Den Cave | <u>3</u> ; 16.5±0.87 15.5–17.0 | <u>11</u> ; 12.4±1.84 9.2–15.0 | <u>6</u> ; 9.1±1.1 8.2–11.0 | <u>7</u> ; 10.5±0.96 9.3–12.1 |
| <i>E. ovodovi</i> , Proskuriakova Cave (Eisenmann & Vasiliev, 2011) | <u>5</u> ; 13.8 8.8–16.2 | <u>12</u> ; 12.4 7.2–16.1 | <u>12</u> ; 8.8 6.4–11.5 | <u>6</u> ; 9.2 7.3–12.0 |
| <i>E. hydruntinus</i> , Prolom 2 (Eisenmann & Baryshnikov, 1994) | <u>19</u> ; 11.6 6.8–14.7 | <u>22</u> ; 10.0 6.9–13.5 | <u>21</u> ; 6.8 5.2–9.2 | – |
| <i>E. hydruntinus</i> , Crimea (Kuzmina, 1997) | <u>25</u> ; 12.8 10.5–15.5 | <u>55</u> ; – 8.2–14.0 | <u>64</u> ; – 5.0–11.0 | <u>20</u> ; 6.8 5.3–8.0 |
| <i>E. hydruntinus</i> , Emine-Bair-Khosar (van Asperen et al., 2011) | <u>5</u> ; 12.4 11.6–13.7 | <u>12</u> ; 12.4 10.7–15.5 | <u>11</u> ; 9.4 6.4–12.1 | <u>9</u> ; 10.6 8.3–11.7 |
| <i>E. h. hemionus</i> (V. Eisenmann, online data) | <u>17</u> ; 15.3 11.8–17.0 | <u>34</u> ; 13.7 11.5–16.9 | <u>34</u> ; 10.5 8.5–13.0 | <u>7</u> ; 10.3 9.0–11.0 |

* In the original paper presented incorrect values

Appendix III. Measurements (mm) of third metacarpal bones of small equid from western Siberia (n; Mean ± st. dev. / Min–Max) and comparative material on *E. hyduntinus* from Crimea and *E. h. hemionus* (n; Mean / Min–Max or n; Mean)

| Measurement | Small equid | | | | <i>E. hyduntinus</i> | | <i>E. h. hemionus</i> (V. Eisenmann, online data) |
|--|--------------------------------------|-----------------------|----------|-------------------------------------|---------------------------------|--|---|
| | Hyena's Den Cave | Okladni- kova cave | Chik | Taradanovo | Crimea (Kuzmina, 1997) | Emine- Bair- Khosar (van Asperen <i>et al.</i> , 2011) | |
| 1. Maximal length | <u>11; 232.8±9.80</u> 219.0–250.3 | – | 1; 221.6 | <u>3; 230.3±6.41</u> 225.3–237.5 | <u>33; 211.8</u> 196.0–228.0 | 5; 221.9 | <u>10; 229.9</u> 220.0–240.0 |
| 3. Minimal breadth of the diaphysis | <u>10; 32.5±2.12</u> 28.8–36.0 | 1; 31.7 | 1; 31.8 | <u>3; 32.2±0.40</u> 31.7–32.4 | <u>32; 26.1</u> 22.2–27.8 | 5; 28.8 | <u>10; 27.1</u> 24.2–29.0 |
| 4. Depth of the diaphysis | <u>10; 26.3±1.25</u> 24.9–28.2 | 1; 25.3 | 1; 23.2 | <u>3; 25.0±0.42</u> 24.7–25.5 | <u>34; 21.7</u> 18.2–23.5 | 5; 23.5 | <u>9; 23.2</u> 22.0–25.0 |
| 5. Proximal articular breadth | <u>11; 47.2±2.46</u> 43.6–51.7 | 2; 45.2; 48.3 | 1; 44.9 | <u>3; 47.5±0.46</u> 47.2–48.0 | <u>50; 41.0</u> 36.5–43.8 | 5; 43.2 | <u>10; 44.4</u> 42.5–46.0 |
| 6. Proximal articular depth | <u>10; 31.1±1.66</u> 28.5–33.5 | 2; 30.2; 32.0 | 1; 29.9 | <u>3; 31.1±0.10</u> 31.0–31.2 | <u>53; 29.3</u> 26.0–32.0 | 5; 29.4 | <u>10; 29.7</u> 28.6–31.0 |
| 7. Maximal diameter of the articular facet for the third carpal bone | <u>11; 39.0±2.16</u> 36.0–42.9 | 2; 38.0; 39.8 | 1; 37.4 | <u>3; 39.0±0.53</u> 38.4–39.4 | – | 5; 36.7 | <u>10; 37.2</u> 36.0–39.0 |
| 8. Diameter of the articular facet for the second carpal bone | <u>11; 14.2±0.92</u> 39.3–47.9 | 2; 14.8; 15.5 | 1; 12.5 | <u>3; 14.9±0.85</u> 14.0–15.7 | – | 5; 12.0 | <u>10; 12.7</u> 11.0–14.0 |
| 10. Distal maximal supra-articular breadth | <u>11; 44.1±2.46</u> 39.3–47.9 | 1; 45.0 | 1; 44.1 | <u>4; 44.9±0.65</u> 44.1–45.6 | – | 5; 40.1 | <u>10; 40.3</u> 37.7–42.0 |
| 11. Distal maximal articular breadth | <u>11; 44.0±2.13</u> 30.2–36.6 | 1; 44.0 | 1; 43.2 | <u>4; 44.9±1.29</u> 43.3–46.4 | <u>46; 36.9</u> 32.6–39.5 | 5; 40.0 | <u>10; 40.7</u> 38.0–44.0 |
| 12. Distal maximal depth of the keel | <u>11; 33.2±1.61</u> 30.2–36.6 | 1; 35.3 | 1; 31.0 | <u>4; 33.1±0.71</u> 32.5–34.1 | <u>47; 28.2</u> 24.5–31.0 | 5; 29.2 | <u>10; 31.4</u> 30.0–33.5 |
| 13. Distal minimal depth of the lateral condyle | <u>11; 27.1±1.34</u> 25.3–30.3 | 1; 28.0 | 1; 25.4 | <u>4; 26.7±0.59</u> 26.0–27.4 | – | 5; 24.2 | <u>4; 24.5</u> 23.5–25.0 |
| 14. Distal maximal depth of medial condyle | <u>11; 29.6±1.57</u> 27.2–33.3 | 1; 29.8 | 1; 27.7 | <u>4; 29.2±1.12</u> 27.7–30.1 | – | 5; 26.9 | <u>10; 28.2</u> 27.0–30.5 |

Appendix IV. Measurements of third metatarsal bones of small equid from Western Siberia (n; Mean ± st. dev. / Min–Max) and comparative material on *E. hydruntinus* from Crimea and *E. h. hemionus* (n; Mean / Min–Max or n; Mean), mm

| Measurement | Small equid | | | <i>E. hydruntinus</i> | | <i>E. h. hemionus</i> (V. Eisenmann, online data) |
|--|-------------------------------------|-----------------------|----------------------------------|---------------------------------|---|---|
| | Hyena's Den Cave | Oklad- nikova cave | Taradanovo | Crimea (Kuzmina, 1997) | Emine- Bair- Khosar (van Asperen <i>et al.</i> , 2011) | |
| 1. Maximal length | <u>7; 270.8±3.28</u> 265.4–275.2 | – | 2; 267.0. 275.4 | <u>12; 251.2</u> 236.7–258.5 | 8; 253.5 | <u>10; 266.8</u> 253.0–277.0 |
| 3. Minimal breadth of the diaphysis | <u>7; 31.8±1.56</u> 29.0–33.2 | – | 2; 30.8. 30.9 | <u>19; 25.5</u> 23.6–27.5 | 8; 27.1 | <u>10; 26.0</u> 22.9–28.0 |
| 4. Depth of the diaphysis | <u>7; 32.0±1.64</u> 29.3–34.0 | – | 2; 31.4. 33.2 | <u>19; 25.7</u> 23.0–27.0 | 8; 27.2 | <u>9; 26.1</u> 25.0–28.0 |
| 5. Proximal articular breadth | <u>7; 45.0±1.19</u> 42.8–46.2 | – | 2; 46.9. 49.4 | <u>37; 40.5</u> 38.0–43.2 | 8; 41.9 | <u>10; 41.9</u> 39.0–45.0 |
| 6. Proximal articular depth | <u>7; 40.1±1.63</u> 37.1–42.5 | – | 2; 40.2. 43.7 | 34; 36.1 33.0–40.3 | 8; 37.1 | <u>10; 37.0</u> 36.0–39.0 |
| 7. Maximal diameter of the articular facet for the third tarsal bone | <u>7; 41.6±1.19</u> 39.4–43.0 | – | 2; 43.7. 44.0 | – | 8; 37.6 | <u>10; 38.0</u> 35.0–40.0 |
| 8. Diameter of the articular facet for the fourth tarsal bone | <u>5; 11.6±1.15</u> 10.2–12.8 | – | 2; 12.1. 12.8 | – | 8; 9.6 | <u>10; 9.7</u> 7.5–11.0 |
| 10. Distal maximal supra-articular breadth | <u>12; 44.2±1.54</u> 41.0–46.5 | – | <u>4; 43.4±1.11</u> 39.5–45.5 | – | 8; 39.2 | <u>10; 38.2</u> 35.0–40.0 |
| 11. Distal maximal articular breadth | <u>11; 44.2±1.33</u> 42.8–47.4 | 2; 42.5; 46.3 | <u>4; 44.3±0.85</u> 42.0–46.3 | <u>21; 37.6</u> 34.0–41.3 | 8; 38.1 | <u>10; 38.9</u> 35.1–41.1 |
| 12. Distal maximal depth of the keel | <u>12; 34.1±0.94</u> 32.8–36.0 | 2; 34.0; 34.0 | <u>4; 33.5±0.97</u> 31.4–36.6 | <u>21; 29.0</u> 25.0–32.0 | 8; 29.9 | <u>10; 31.7</u> 30.0–34.0 |
| 13. Distal minimal depth of the lateral condyle | <u>11; 26.7±0.98</u> 25.2–28.7 | 2; 25.5; 25.8 | <u>4; 26.1±0.67</u> 24.4–28.4 | – | 8; 23.8 | <u>4; 23.9</u> 23.1–24.5 |
| 14. Distal maximal depth of medial condyle | <u>11; 29.8±1.04</u> 28.2–31.3 | 2; 26.6; 29.0 | <u>4; 28.7±0.93</u> 26.6–31.8 | – | 8; 26.1 | <u>10; 27.8</u> 26.5–30.0 |

Appendix V. Factor loadings for the variables in principal component analysis on metacarpal bones

| Variable | PC1 | PC2 |
|--------------|-------|----------|
| 1 | -0.42 | -0.87 |
| 3 | -0.95 | 0.08 |
| 4 | -0.81 | -0.21 |
| 5 | -0.82 | 0.19 |
| 6 | -0.93 | -0.06 |
| 7 | -0.92 | 0.04 |
| 8 | -0.80 | 0.24 |
| 10 | -0.96 | 0.16 |
| 11 | -0.95 | 0.18 |
| 12 | -0.95 | 0.03 |
| 13 | -0.93 | -0.09 |
| 14 | -0.94 | -0.15 |
| Expl.Var., % | 77.1 | 08.03.15 |

Appendix VI. Results for Mann-Whitney test on metacarpal and metatarsal bones between small (mean¹) and large (mean²) equids from Kurtak

| Measurement | metacarpal III | | | metatarsal III | | |
|-------------|-------------------|-------------------|-------|-------------------|-------------------|-------|
| | mean ¹ | mean ² | p | mean ¹ | mean ² | p |
| 1 | 226.4 | 228.1 | 0.567 | 261.3 | 272.6 | 0.01 |
| 3 | 29.1 | 37.4 | <0.01 | 27.7 | 36.2 | <0.01 |
| 4 | 23.6 | 26.9 | <0.01 | 28.9 | 33.7 | <0.01 |
| 5 | 42.9 | 52.7 | <0.01 | 41.3 | 54.3 | <0.01 |
| 6 | 28.6 | 32.9 | <0.01 | 35.9 | 45.4 | <0.01 |
| 7 | 36.1 | 42.0 | <0.01 | 38.1 | 47.6 | <0.01 |
| 8 | 13.0 | 16.7 | <0.01 | 10.0 | 13.1 | <0.01 |
| 10 | 40.6 | 50.3 | <0.01 | 39.8 | 52.0 | <0.01 |
| 11 | 40.2 | 51.0 | <0.01 | 40.0 | 52.9 | <0.01 |
| 12 | 30.8 | 37.8 | <0.01 | 30.8 | 40.0 | <0.01 |
| 13 | 24.8 | 29.5 | <0.01 | 24.1 | 30.8 | <0.01 |
| 14 | 27.2 | 31.4 | <0.01 | 27.5 | 33.4 | <0.01 |