



Original article

The equids from Liventsovka and other localities of the Khaprovskii Faunal Complex, Russia: A revision [☆]

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ABSTRACT

The age and homogeneity of the Khaprovskii Faunal Complex have been a matter of debate for a long time. This work provides the most complete information (photographs and numerical data) ever published on the equid remains of this Complex. Evidence is given for the presence of no less than three, possibly six taxa of Equids. Most fossils are referred to *Equus (Allohippus) aff. major* and to *Equus (Allohippus) livenzovensis*, both redefined on the basis of correlations between cranial and metapodial dimensions. Comparisons with Chinese fossils bring evidence for their age approximating 2.5 Ma. A third very large species is represented by a few teeth and metapodials which may have been intrusive. It is referred to *E. (Sussemionus) aff. verae* because of similarities with the NE Siberian species believed to be about 1 myr old. Accumulation of fossils during a long period is probably responsible for the large intraspecific variation observed in *E. (A.) major* and *E. (A.) livenzovensis* and for the occurrence of several other equid forms. Possible intrusions may also explain the abnormal number of observed taxa. Resemblances with Chinese and NE Siberian fossils indicate Asian influences on the composition of the Khaprovskii Faunal Complex.

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1. Introduction

Ann Forsten, one of the few paleontologists who *did* examine the fossil horses of Liventsovka, published an article on the subject (Forsten, 1998). In her Abstract she writes: “[...] their diversity may indicate faunal age heterogeneity, their taxonomic status indicates that the age of the fauna (or a part of it) is rather late than middle Villafranchian, and the references to *Equus livenzovensis* Baigusheva, from Italy and Spain are erroneous”. Unfortunately, her work was largely ignored. Authors went on to refer to *E. livenzovensis* or *E. cf. livenzovensis* (Palombo and Alberdi, 2017; Bernor et al., 2018, 2019; Cirilli et al., 2021) any early pleistocene large bone and to consider the Khaprovskii Complex of which Liventsovka is the richest in *Equus* fossils as a very old homogeneous assemblage. The present article further documents Forsten’s work by all the information at my disposal (photographs and measurement tables) and offer additional personal observations.

Abbreviations: **AMZ:** Azov Museum Reserve; **FAM:** Frick Collection of the American Museum of Natural History; **GIN:** Geological Institute, Moscow, Russia; **IGF:** Institute of Geology,

Florence, Italy; **IVPP:** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **L:** Liventsovka; **M:** Molar; **MC:** Third Metacarpal; **MT:** Third Metatarsal; **P:** Premolar; **Ph1 A:** First Anterior Phalanx; **Ph1 P:** First Posterior Phalanx; **Ph2 A:** Second Anterior Phalanx; **Ph2 P:** Second Posterior Phalanx; **RGU:** State University of Rostov, Rostov-on-Don, Russia; **ROMK:** Regional Museum of Rostov, Rostov-on-Don, Russia; **VSI:** Variation Size Index; **ZIN:** Zoological Institute, Petersburg, Russia.

2. Paleontological and biochronological setting

2.1. The Khaprovskii Faunal Complex

The Khapry sands were discovered and excavated by Gromov between 1934 and 1939. Many equid remains were described by Gromova (1949). Liventsovka was discovered later and studied in detail by Baigusheva (1964, 1968, 1971, 1978) and correlated by her to Khapry.

All the following geographical, geological, faunal lists and general information on the Khaprovskii Faunal Complex come from Titov (2008). The Khapry Sands extend for more than 120 km and up to 2 km width on the banks of Azov Sea (Fig. 1). The stratotype is near Khapry and the parastratotype at Liventsovka near

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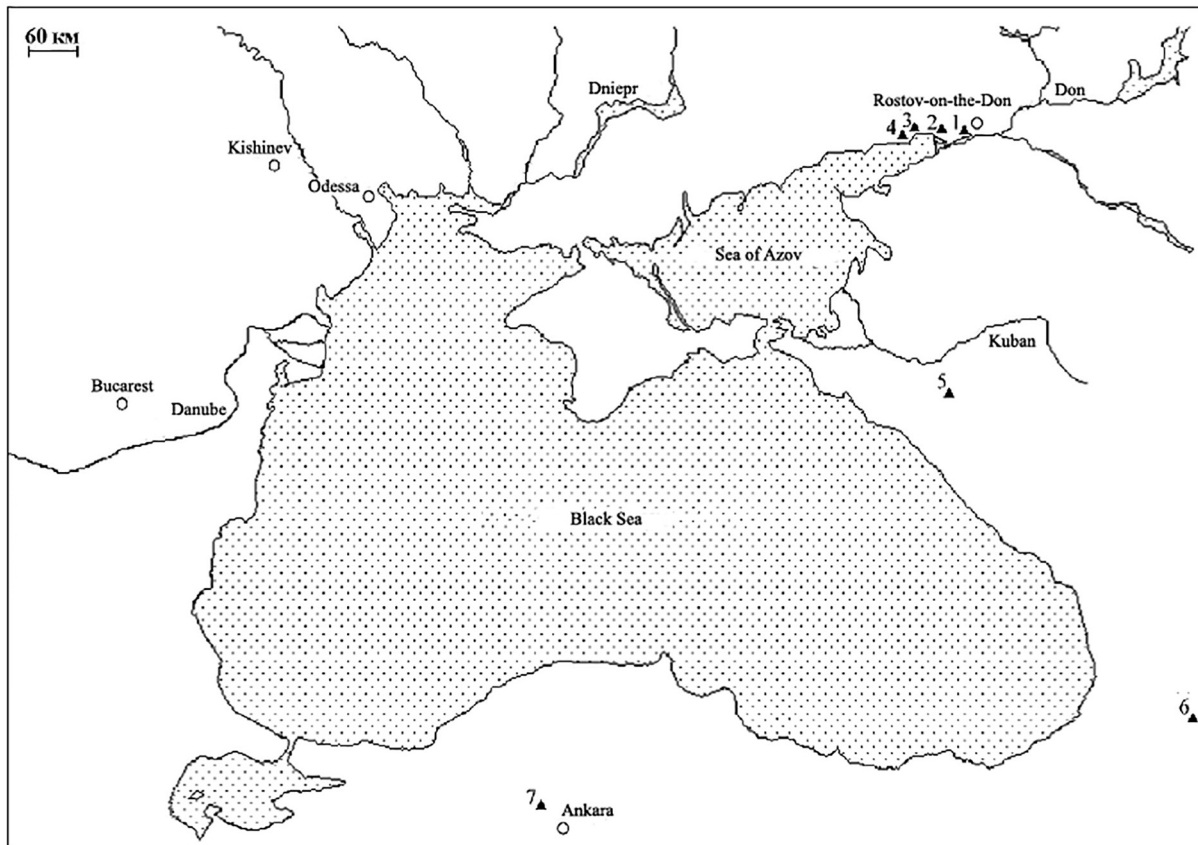


Fig. 1. Map modified from Titov (2008: fig. 2) showing the location of the Khaprovskii Complex fossil findings and of some other famous fossil localities around the Black Sea. 1: Liventsovka; 2: Khapry; 3: Morskaya; 4: Volovaya Balka; 5: Psekups; 6: Dmanisi; 7: Sarikol Tepe.

Rostov-on-Don. At the Liventsovka section the deposits range from 28 to 20 m in thickness; Titov (2008) estimates that the fossils could have accumulated for as long as 400,000 years. The strata show a reversed negatively magnetic polarity and, given the composition and stage of evolution of the Khapry fauna, are correlated with the pre-Olduvai part of the Matuyama chronozone. According to Titov's (2008) table 1, the localities containing equid fossils are mainly Khapry and Liventsovka (Fig. S1; Appendix A); less important are Mokryi Chaltyr, Merjanovka, and Morskaya. Although Titov does not mention *Equus* from Volovaya Balka, I have also studied a very interesting equine fossil from that locality which will be discussed later in this article.

2.2. Dealing with the long time of fossil accumulation of the Khaprovskii Complex

The assignment of fossil bones to two or more species is based first on considerations of dimensions: what is a normal intraspecific variation, and what are the correlations between various dimensions of various bones inside a skeleton? In the case of a fossil accumulation during a moderate period of time, the coefficients of variation are similar to those observed in extant species. If, however, the time of accumulation has allowed the species to evolve and change in size, it becomes necessary to rely on shape as well as dimensions: if size increases or decreases, the coefficients of variation may be abnormally large while bone proportions may stay constant. An accumulation time of nearly 500 kyr in the Khaprovskii Complex was long enough to allow changes in fossil species at least in size. A preliminary assessment of the size variation

is, however, essential even if shape observations may modify size-based deductions.

After presenting the material and describing the methods applied to its study, I will first address the question of the size of limb bones. Then I will describe and compare skulls and dental remains before limb bones, and finally I will tentatively assign all the fossils to species according to both size and shape.

3. Material and methods

3.1. Material

- From **Khapry Sands**: damaged cranium of a very large equid and other equid fossils housed in Moscow;
- From **Liventsovka**: fragments of a cranium and numerous other equid fossils housed at Rostov-on-Don and a few in Moscow. There are no precise stratigraphic provenances except those provided in Titov (2008: table 3): Remains of large vertebrates and mollusks, which were found *in situ* in fluvial facies of Liventsovka sand pit in 1953–1977 by Bajgusheva. These specimens are noted in Tables S5, S13, S14, S16, S20, S22, S23, S24 (Appendix A). Lower cheek teeth and radius found in the same layer as fragments of a *Canis cf. senezensis* cranium may be referred to *E. (Allohippus) liventzovensis*;
- From **Morskaya** there are only one upper molar, one MC, a radius, and a tibia;
- From **Volovaya Balka** come an inferior P2-P4 series, one upper lacteal tooth and one fragmentary metatarsal housed in Moscow;
- From **Mokryi Chaltyr**, several upper and lower cheek teeth;

- From **Merjanovka**, a fragment of MT housed at Rostov-on-Don.

There are many juvenile, fragmentary, and waterworn bones difficult to assign. The accession codes are GIN, RGU, ROMK L, and AMZ.

In all, there are two crania, one premaxillary, ten (mostly fragmentary) mandibles, seven upper series and 71 isolated upper cheek teeth, 17 lower series and 52 lower cheek teeth, 31 MC, 53 MT, 12 Ph1, 17 Ph2, and some other limb bones. I have seen all these fossils and measured most of them. Tatiana Kuznetsova who accompanied me on the trip to Rostov-on-Don measured some metapodials (noted in corresponding tables). I have not seen the tibia ROMK L 899, the talus ROMK L 1268 and the first phalanx ROMK L 1319 mentioned by Forsten (1998). Some of the phalanges noted without numbers are probably the same as mentioned by Forsten (1998). Claudio De Giuli gave me his photographs of limb bones. I took from Titov (2008: pl. V) photographs of metatarsals AMZ OP 1571(=RGU 490) and 1580 (= RGU 188), and I took from Azzaroli (2000) the profile views of the Liventsovka cranium fragments which I have arranged in a new way. All other photographs are mine.

3.2. Methods

3.2.1. System of measurements

The fossils were measured according to the system detailed and illustrated at: <https://vera-eisenmann.com/-system-of-measurements-for-equus-bones-and-teeth-english> (click on the element for which measurement details are needed).

3.2.2. Simpson's ratio diagrams

Simpson's ratio diagrams (Simpson, 1941) offer rapid and easy comparisons, both of size and shape, for a single bone or a group of bones. The reference is provided by a single bone (or a group of bones), or means of a bone sample, the dimensions of which are converted into decimal logarithms. By convention, logarithms of these dimensions are placed on the "0" line of the graph. I use the extant *E. hemionus onager* as reference. Dimensions of the material under study are also converted into decimal logarithms. Arithmetic differences between the reference logarithms and the logarithms of the studied dimensions are placed above the "0" line if they are positive (larger dimensions), or below if they are negative (smaller dimensions). In such a logarithmic diagram, proportions remain unchanged whatever the absolute dimensions: diagrams of two bones differing by their size but identical by their proportions will appear one above the other on parallel lines. Details and examples are given at: <https://vera-eisenmann.com/simpson-ratio-diagrams>.

3.2.3. Variability Size Index

A general view of the size of all bones inside the sample was provided by the Variability Size Index, a scaling technique used by archeozoologists (Uerpman 1982; Meadow 1999; <https://vera-eisenmann.com/variability-size-index-vsi>). A sample including all the bones of one taxon is chosen as the reference. Mean and standard deviation are calculated for each measurement of this sample. The comparisons are made using the following formula: $VSI = 25 \times (x - m)/s$ where s is the standard deviation of the mean (m) of the reference measurements 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 reference. As phrased by Meadow (1986), "Using this formula, the standard dimension is set at zero; a measurement one standard deviation larger than the standard (reference) dimension will be plotted at 25, one standard deviation smaller at -25, etc."

The chosen reference in this article is a sample of 546 bone breadths of *E. (Allohippus) vireti* from Saint-Vallier, France (Table S1; Appendix A). The 230 bones breadths from the Khaprovskii Complex were compared to this reference (Table S2; Appendix A) and to 279 bone breadths of *E. (Allohippus) senezensis* from Senèze, France (Table S3; Appendix A).

4. Results

4.1. Limb bones size

Detailed measurements are given in Tables S4-S18 (Appendix A). Fig. 2 shows the size differences and distribution between the limb bone breadths from Senèze (Fig. 2(A)) and Khaprovskii Complex (Fig. 2(B)) compared to the reference series from Saint-Vallier. Although the span is nearly the same for Senèze and the Khaprovskii Complex, the distribution of sizes is very different. The majority of Senèze limb bones cluster in normal way and span for a single species slenderer than the reference series from Saint-Vallier (centered on 0), while some much wider bones referred to *E. (Allohippus) major* (Eisenmann and Delson, ongoing work) are clearly apart. The distribution of Khaprovskii Complex bones shows that a majority of bones have breadths similar to Saint-Vallier but the distribution is too wide for a single species. The largest bones from Khaprovskii Complex are about the size or larger than those of *E. (Allohippus) major* from Senèze. The following diagram (Fig. 3) was drawn to assess whether clusters of similar-sized bones could be referred to one or more species. The accession numbers (and the references to photographs) show how any individual bone fits in the general picture.

4.1.1. Metacarpals size

Numerical data for 31 MC III (more or less damaged by erosion) are given in Table S4 (Appendix A). Claudio De Giuli provided photographs of four specimens (Fig. 4). When placed on the previous histogram, RGU 326 (Fig. 4(B)) and RGU 931 (Fig. 4(D)) appear inside the 125–150 column, i.e., four standard deviations from the reference average (*Allohippus vireti* of Saint-Vallier). No number (Fig. 4(A)) and RGU 576 (Fig. 4(C)) appear within the "–25 to 0" and "0 to +25" columns, respectively, i.e., one standard deviation of the reference average. The general distribution is too wide for a single species, consistent with overlaps of two or more taxa.

4.1.2. Metatarsals size

Measurements of 53 MT are presented in Tables S5 and S6 (Appendix A). Photographs of five specimens (ROMK L 233, ROMK L 165?, ROMK L 1220, no number, and ROMK L 1829, corresponding to Fig. 5(A, B, D, E, G), respectively) were taken by Claudio De Giuli; photographs of RGU 188 and RGU 490 (Fig. 5(C, F)) come from Titov (2008: pl. V). From the photographs of the MT (Fig. 5) it appears that there are four taxa of different size: A-B, C-D, E, and G. RGU 490 (F) may be matched to E or G. The general distribution of the MT on Fig. 3 is extremely wide even if RGU 483 and ROMK L 1220 may be dismissed for being immature or weathered. There may be two clusters: around 0 to –75 and around 0 to +75.

4.1.3. First phalanges (Ph1) and second phalanges (Ph2) size

Measurements are given in Tables S7-S10 (Appendix A). Ph1 plot at the same level as the medium to large metapodials. The Ph2 breadths, however, are generally smaller. There is a small overlap between the sizes of Ph1 and Ph2.

4.1.4. Other limb bones

The talus ROMK L 536 is very large. The smallest bone is the waterworn calcaneum RGU 254. The largest is the Tibia RGU 1707.

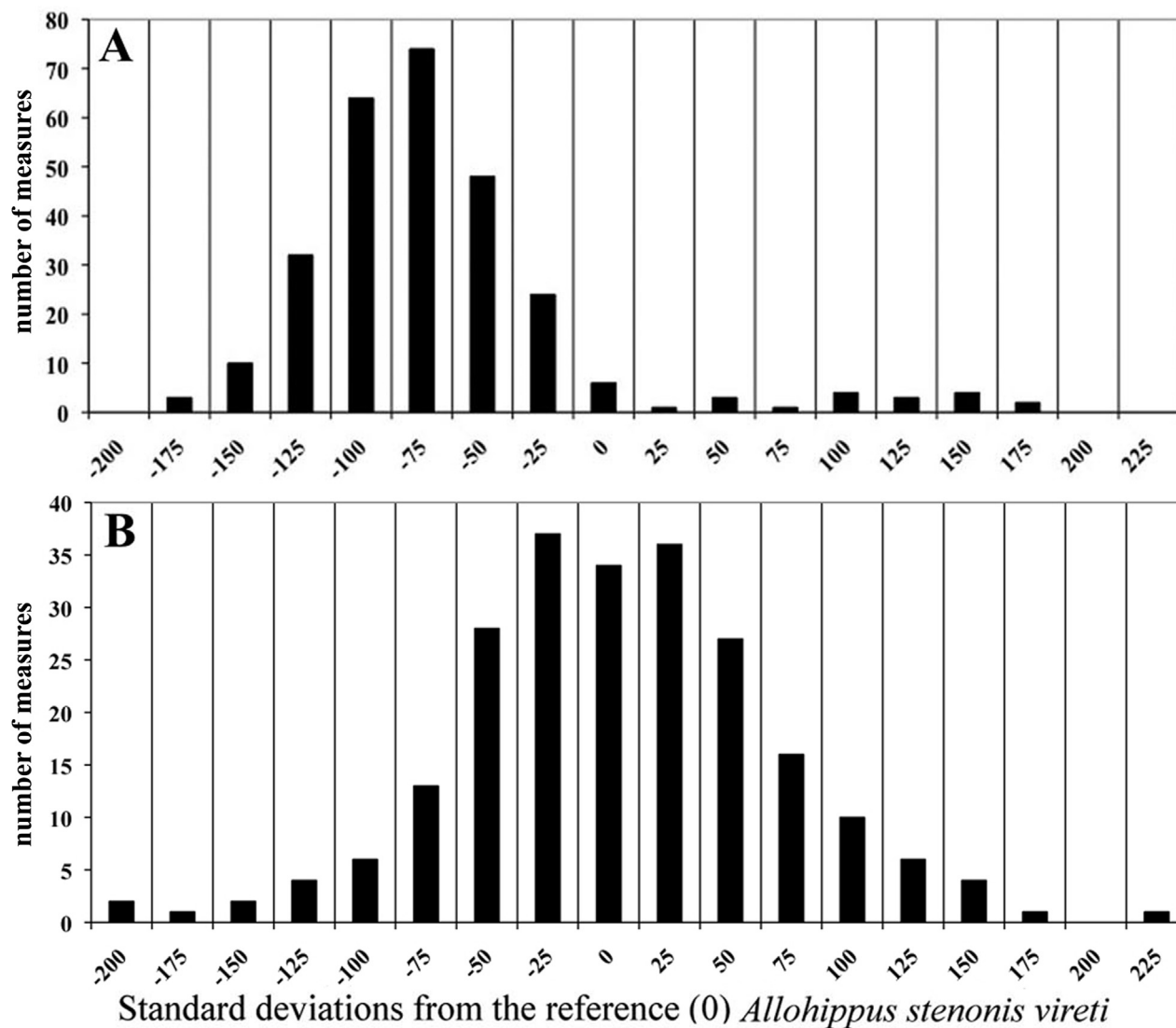


Fig. 2. Comparison of Variation Size Indices for 279 limb bone breadths from Senèze (A) and 230 breadths from Khaprovskii Complex (B). Graduations in abscissa correspond to one, two, three, etc. standard deviations from the reference *Allohippus vireti* of Saint-Vallier.

4.2. Description and comparisons of crania, mandibles and cheek teeth

4.2.1. Crania

The cranium ZIN 31078 was discovered at Khapry and studied by Gromova (1949) who referred it to *E. stenonis major*. Baigusheva (1978) referred it to *E. livenzovensis* and Titov (2008) to *E. (Allohippus) stenonis livenzovensis*. The muzzle is broken apart from the rest of the cranium without visible point of contact, and the nasal and occipital parts are badly damaged (Fig. 6, adapted from Gromova), but the specimen still affords valuable information (Table S19; Appendix A). In particular, the relative post-vomerine and palatal lengths and the cheek length leave no doubt as to its belonging to an *Allohippus*. I refer it to *E. (Allohippus) aff. major*. Basilar length is estimated at ca. 580 mm by Gromova (1949) and ca. 600 mm by Titov (2008) and by me. Although the M3 shows that it belonged to a young animal, the muzzle is remarkably narrow.

The cranium ROMKL 4 was discovered at Liventsovka, studied by Baigusheva (1978) who made it the new and only valid type for *E. (Allohippus) livenzovensis*. [In a previous study, Baigusheva (1971) proposed as type a very large MT (RGU 778) but did not

describe it.] Basilar length is estimated at ca. 570–580 mm by Titov (2008) and ca. 550 mm by me. On Fig. 7 I have arranged photographs of the fragments of the type cranium with the muzzle RGU 11 (better preserved than the fragment belonging to the cranium) and with the upper P2 ROMKL 911 (the upper P2 of the type cranium is missing). I used my own photographs and the dorsal view of the palate and the profile views published by Azzaroli (2000) which I have positioned in a different way.

In spite of trying various rearrangements and taking every possible care and caution in all tentative reconstructions, the result remains unsatisfying. The main problem is that there is no cranio-logical evidence to assign this cranium to *Allohippus*: no measurable cheek length nor naso-incisival notch, and no information on the Basion-Vomer nor Vomer-Palate distances. Therefore, it is with some doubt that I refer to it as *E. (Allohippus) livenzovensis*.

The Simpson's diagram (Fig. 8) compares the crania ZIN 31078 from Khapry, FAM 60-B 719 (*E. (Allohippus) sp.*) from Fan Tsun (Taigu District, SE Shansi, China), ROMKL 4 from Liventsovka, and the premaxillary RGU 11. ZIN 31078 is larger than the Chinese specimen but both have similar proportions although the muzzle is relatively longer in the latter (measures 2–5 and 5). ROMKL 4 is

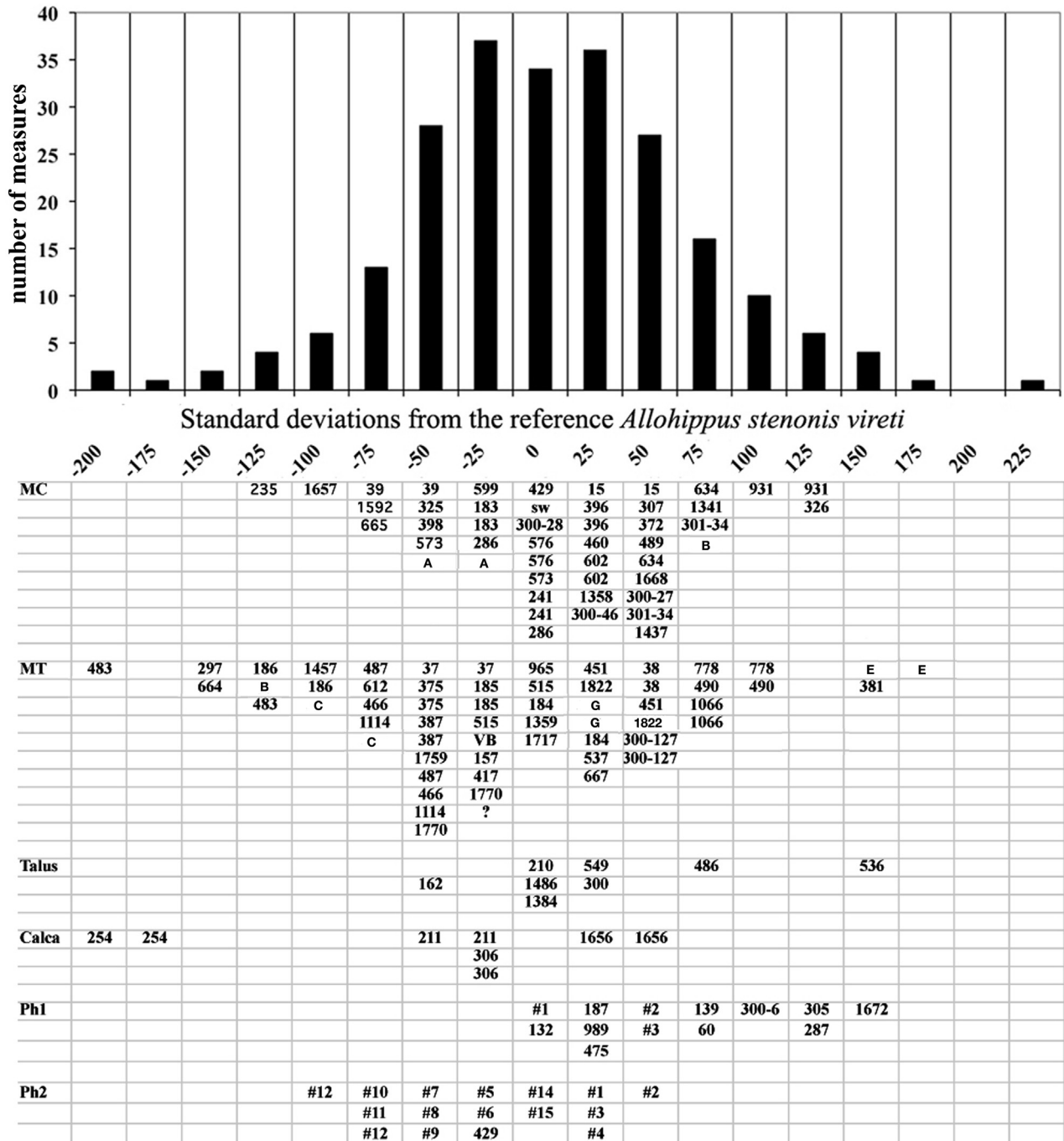


Fig. 3. Distribution of Khaprovskii Complex equid's MC, MT, Talus, Calcaneum, Ph1, and Ph2 breadths according to the Variation Size Index. Each bone is referred by its accession number or by the letter marking it in the photographs (Fig. 4 for MC, Fig. 5 for MT).

notably smaller. If my reconstruction treating the premaxillary RGU 11 as a part of ROMK L 4 is correct, the muzzle was also relatively shorter and wider in the latter (measures 2–5, 5, and 17).

4.2.2. Mandibles

There are ten remains of mandibles (Table S20; Appendix A), most of which are too fragmentary to allow comparisons beyond stating that some are 'larger' (RGU 355, RGU 395, ROMK L 16, ROMK L 95, ROMK L 229, and ROMK L 264) and some 'smaller' (RGU 92, RGU 562, ROMK L 1322, and the juvenile ROMK L 1233). The inclination of the ascending ramus of RGU 355 (Fig. 9(A)) is nearly at a right angle with the horizontal ramus while it is inclined backward in ROMK L 229 (Fig. 9(B)), which makes it

doubtful that both belong to the same species. Both, however, are too large to match the type cranium of *E. (A.) livenzovensis*: according to the correlations existing between cranial and mandibular dimensions (see: <https://vera-eisenmann.com/correlations-between-skull-and-mandible-dimensions>), the mandible ROMK L 229 may match the cranium ZIN 31078. Smaller mandibles may belong to *E. (Allohippus) livenzovensis*.

4.2.3. Upper cheek teeth

Photographs of the specimens from Khapry, Liventsovka, Morskaya and Volovaya Balka are presented in Figs. S2-S4 (Appendix A). Measurements are provided in Tables S21 and S22 (Appendix A).

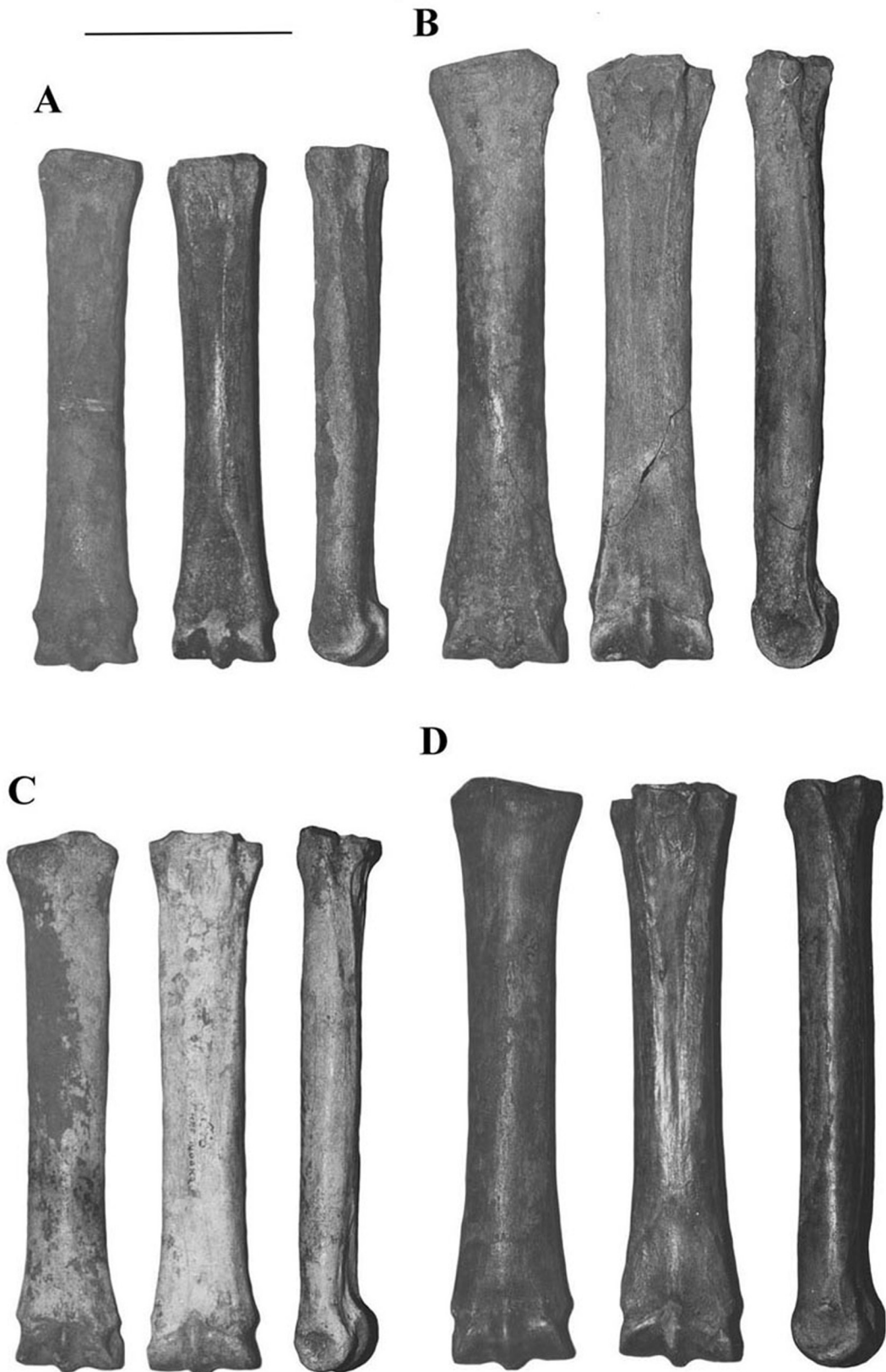


Fig. 4. Third metacarpals from Liventsovka in dorsal, ventral and profile views. **A.** no number. **B.** RGU 326. **C.** RGU 576. **D.** RGU 931. Scale bar: 5 cm.

Although size differences are large, the enamel pattern is remarkably similar in the majority of the teeth from Khaprovskii Complex: short protocones, narrow mesostyles, moderately pli-

cated fossettes; on premolars the plis caballin are often long and thin, and postprotoconal valleys are deep. There are several exceptions. Fig. 10 illustrates some of the following observations. The lit-

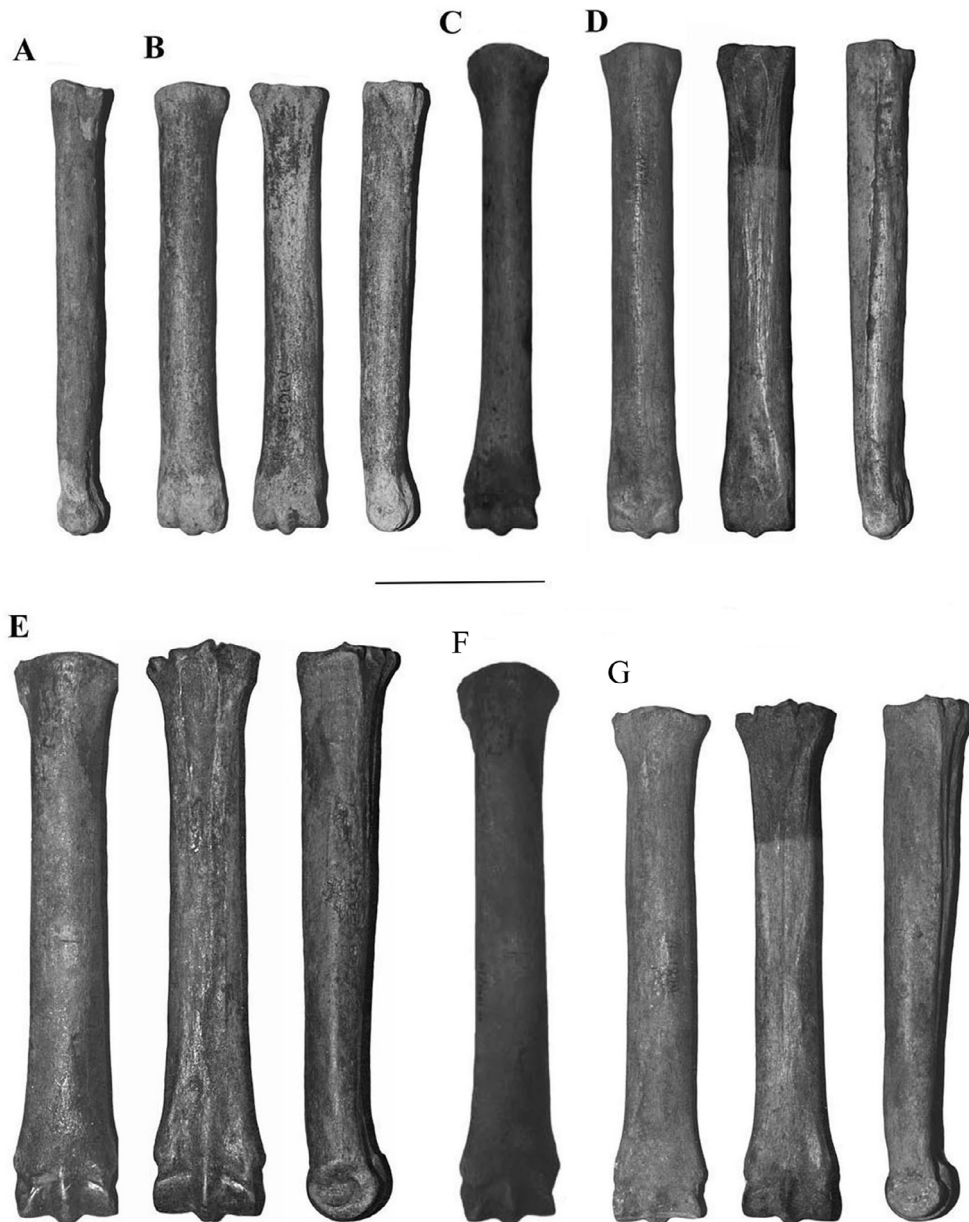


Fig. 5. Third metatarsals from Liventsovka. **A.** ROMK L 233, profile view. **B.** ROMK L 165? in dorsal, ventral and profile views. **C.** RGU 188, dorsal view. **D.** ROMK L 1220 in dorsal, ventral and profile views. **E.** specimen without number in dorsal, ventral and profile views. **F.** RGU 490, dorsal view. **G.** ROMK L 1829 in dorsal, ventral and profile views. Scale bar: 5 cm.

the worn dentition of *E. (Allohippus) major* (ZIN 31078; Fig. 10(C)) is very large (207 mm). The enamel of the fossettes does not appear very plicated. Plis caballin are well developed and additional plis are visible on the premolars. Protocones are short, asymmetrical, and tend to have convex vestibular and concave lingual borders. The premolar RGU 149 (Fig. 10(A)) probably belongs to the same species. According to their size, the premolar from Morskaya (Fig. 9(A)) and the lacteal from Volovaya Balka (Fig. 9(B)) could belong to *E. (Allohippus) major* from Khapry. The enamel pattern cannot be compared since the teeth of ZIN 31078 are very little worn. Premolar ROMK L 131 (Fig. 10(B)) is larger and has a longer, more symmetrical and grooved protocone. Its attribution will be discussed later.

Five moderately worn specimens (Fig. 10(A, C, D, G, H)) very probably belonged to the same animal. They are smaller than the

precedent but quite similar in their enamel pattern. Like in *E. (Allohippus) aff. major*, postprotoconal valleys are deep on premolars, plis caballin are long and thin, especially on the premolars, but there are no additional plis. Mesostyles are narrow. The molar RGU 387 (Fig. S2(F); Appendix A) is similar. Although quite smaller, the premolar ROMK L 1533 (Fig. 10(K)) has the same pattern as RGU 391 (Fig. 10(E)). According to their morphology, they should all be referred to *E. (Allohippus) aff. major* although their size is not 'major'. Premolars RGU 385 and ROMK L 1786 (Fig. 10(H, L)) have smaller plis caballin; the postprotoconal valleys are more shallow.

The teeth of *E. (Allohippus) livenzovensis* (ROMK L 4; Fig. 10(G)) are among the smallest of the whole sample. The postprotoconal valleys are shallow and the plis caballin small. I assign to the same species the molar ROMK L 1425 (Fig. 10(I)). The associated P4-M1

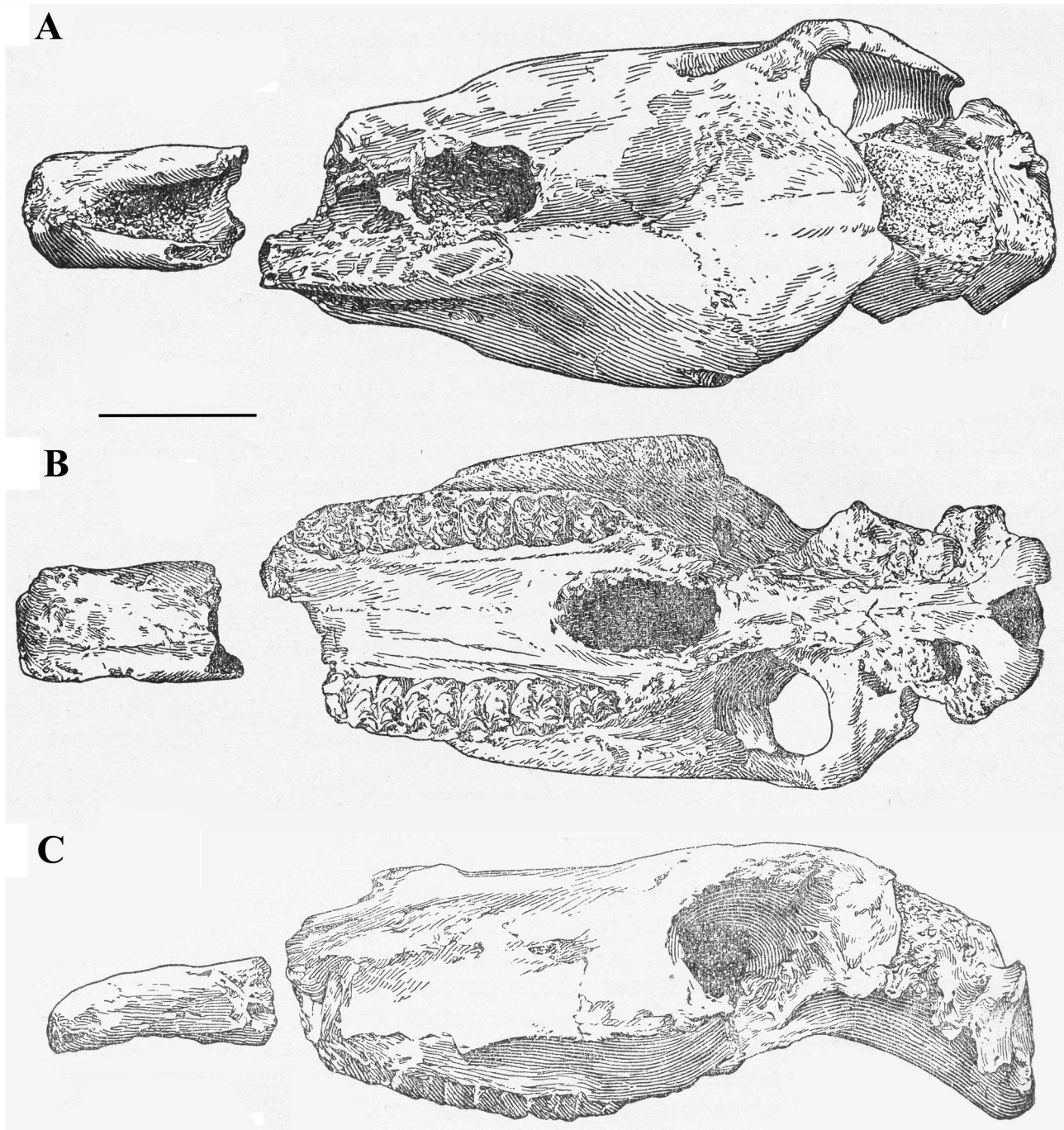


Fig. 6. Cranium of *E. (Allohippus) aff. major* ZIN 3178 from Khapry in dorsal (A), ventral (B) and profile (C) views (adapted from Gromova, 1949: figs. 7, 8). Scale bar: 10 cm.

(RGU 327; Fig. 10(J)) have extremely short, rounded protocones; these particularities may, however, be due to the advanced stage of wear.

Fig. S5 (Appendix A) compares the scatter diagrams of protocone length vs. mean of occlusal length and breadth of the P3P4 and M1M2 of *E. (Allohippus) vireti* from Saint-Vallier, France and the teeth of Khaprovskii Complex. On the whole, the latter are slightly larger and have shorter protocones, especially in the premolars.

4.2.4. Lower cheek teeth

Photographs of the right and left lower series are presented in Figs. S6 and S7 (Appendix A), respectively. Measurements are given in Tables S23 and S24 (Appendix A).

The most frequent pattern is that of ROMK L 395 (Fig. 11(A)): nearly rounded symmetrical double knots, shallow vestibular grooves on the premolars, deep on the molars, no pli protostylid on the P2, plicated enamel on postfossettes. Like for the upper cheek teeth, the pattern persists in more or less large teeth. ROMK L 395's size is compatible with *E. (Allohippus) aff. major*; ROMK L 92 (Fig. 11(B)) and RGU 2028 (Fig. S6(F); Appendix A) are compatible with *E. (Allohippus) livenzovensis*. In these two series the depth of the vestibular groove of molars is remarkable. The smallest teeth RGU 662 and ROMK L 1233 (Fig. 11(C, D)) could belong to a still smaller form.

In the large ROMK L 1278 (Fig. 11(E)) the enamel is very plicated on the P4 and the vestibular groove is very deep on the

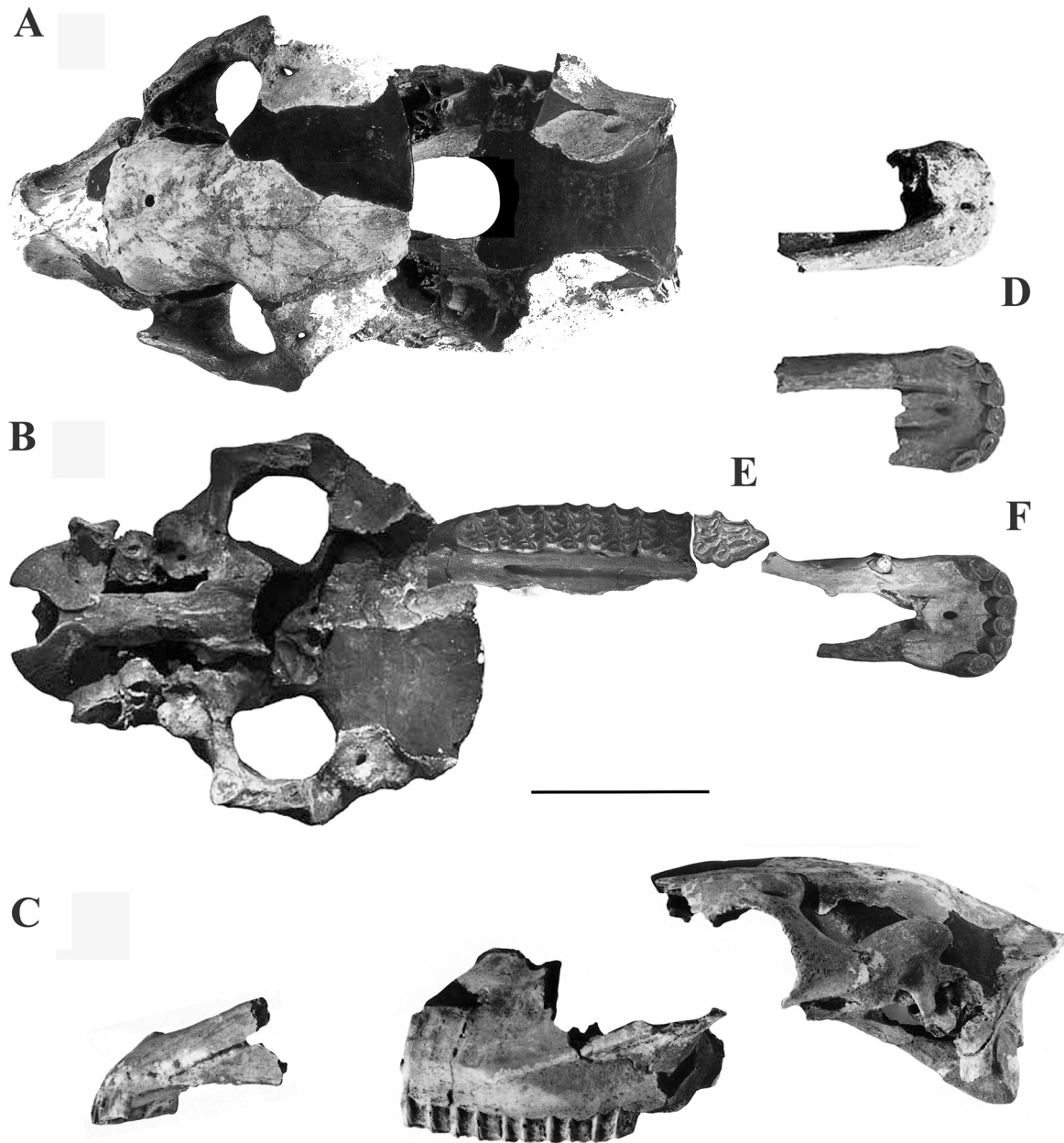


Fig. 7. A–D. Cranial fragments of *E. (Allohippus) livenzovensis* ROMK L 4. A: dorsal view; B: ventral view; C: profile view; D: dorsal and ventral views of muzzle. E. Occlusal view of the upper P2 ROMK L 911. F. Occlusal view of the muzzle RGU 11. Scale bar: 10 cm.

M1. The largest and most plicated specimen (GIN 302–10; Fig. 11 (F)) will be discussed later.

4.3. Metapodials referred to *E. (Allohippus) aff. major* and *E. (Allohippus) livenzovensis*

4.3.1. Metacarpals and metatarsals assignment to crania

Metapodial distal breadths are correlated to cranial Basilar lengths (see: <https://vera-eisenmann.com/skull-metapodials-ccor-relations>). Fig. 12 shows the scatter diagram of metapodials distal articular widths vs. basilar lengths in extant gracile *Equus* (Asses, Hemiones, and Grevy's zebras). Gracile extant species were chosen because of the relative gracility of the Khaprovskii equids. Additional points on the diagram are the cranium and associated MT of *E. (Allohippus) senezensis* from Senèze (Partial skeleton SEN 06-0137+), the cranium QSV 226 and means of MC and MT distal articular breadths of *E. (Allohippus) vireti* from Saint-Vallier,

and the cranium NIH 02 and means of MC and MT distal articular breadths of *E. (Allohippus) sanmeniensis* from Nihowan. A linear regression was calculated on these fossils and the extant gracile *Equus*. The distal articular breadths of the metatarsals ROMK L 1066 and of the not numbered specimen of Fig. 5(E) are 57 mm and ca. 63 mm, respectively. According to the regression, the corresponding Basilar lengths can be expected around 640 mm and 680 mm or more, respectively. Although the crania from Khapry and Liventsovka are damaged and incomplete, their Basilar lengths may be estimated at ca. 550 mm for ROMK L 4 and 600 mm for ZIN 31078. According to the regression, the metapodial distal breadths can be expected around 49 mm and 54 mm.

4.3.2. MC and MT assigned to *E. (Allohippus) aff. major*

I refer to *E. (Allohippus) aff. major* 19 more or less complete MC (Fig. S8(A); Appendix A) with average distal articular breadths of

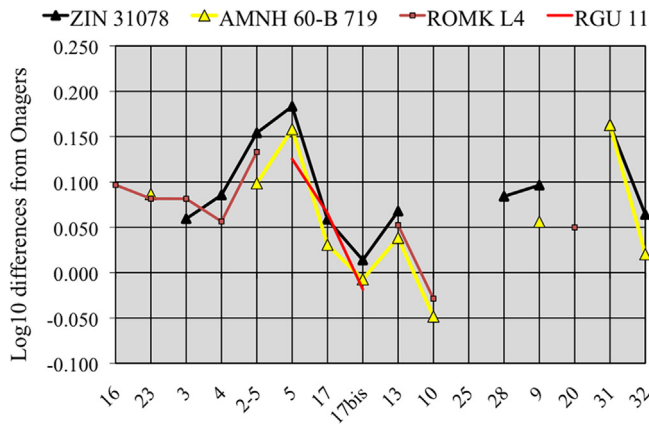


Fig. 8. Simpson's diagrams of *E. (Allohippus) aff. major*, *E. (Allohippus) sp.* from SE Shansi (China), *E. (Allohippus) livenzovensis* crania and of the muzzle RGU 11. 16: breadth of the supra-occipital crest; 23: anterior ocular line; 3: vomerine length; 4: post-vomerine length; 2–5: palatal length *sensu stricto*; 5: muzzle length; 17: muzzle breadth at the posterior borders of I3; 17bis: least muzzle breadth (between the crests); 13: frontal breadth; 10: greatest choanal breadth; 25: facial height in front of P2; 28: cranial height; 9: length of choanae; 20: height of the external auditive meatus; 31: length of the naso-incisival notch; 32: cheek length.

53.7 mm (ranging from 51 to 55 mm); the coefficient of variation is 2.52. They are marked by an asterisk in Table S4 (Appendix A). The average (Table S25; Appendix A) have slightly larger supra-articular (measure 10) than articular (measure 11) breadths (Fig. 13(A)). Most have relatively deep minimal depths of the medial condyle (measure 13).

I refer to *E. (Allohippus) aff. major* 11 more or less complete MT (Fig. 13(B)) marked by an asterisk in Tables S5 and S6 (Appendix

A). Most of them (Fig. S9(A); Appendix A) have very wide supra-articular distal breadths (measure 10) and very shallow minimal depths of the medial condyle (measure 13). The average distal breadth is only 50.6 mm (ranging from 46 to 55 mm); the coefficient of variation is large: 5.60 (Table S26; Appendix A). In my interpretation this reflects a change in size without change of proportions as can occur in bones of a taxon accumulated during a long period of time. Similar changes in size without changes in enamel pattern were observed for the cheek teeth.

4.3.3. MC and MT assigned to *E. (Allohippus) livenzovensis*

The referred 12 MC are clearly smaller than those of *E. (Allohippus) aff. major* (Table S25; Appendix A) and their proportions differ: they are slenderer, deeper in the diaphysis, and less deep at the medial condyle (Fig. 14(A)).

Some of the nine MT I referred to the same small species are juvenile and/or fragmentary (Fig. S9(B); Appendix A) and therefore their attribution is uncertain; the statistics of Table S26 (Appendix A) do not include too problematic dimensions. Average MT (Fig. 14 (B)) has wide proximal epiphyses (measure 5), shallow keels (measure 12), and relatively shallow medial condyles (measures 13 and 14).

The only similar metapodials I know of were found at Zdansky's Locality B (Henan, China) (Fig. 14). I have measured the MC in Beijing and used the data published by Zdansky (1935) on the MT.

4.4. Other limb bones referred to *E. (Allohippus) aff. major* and *E. (Allohippus) livenzovensis*

4.4.1. Attributions to *E. (Allohippus) aff. major*

Most large limb bones could belong to either this form or to large Sussemionas. Simpson's diagrams illustrate their sizes and proportions. There are not enough data on humeri (Fig. S10;

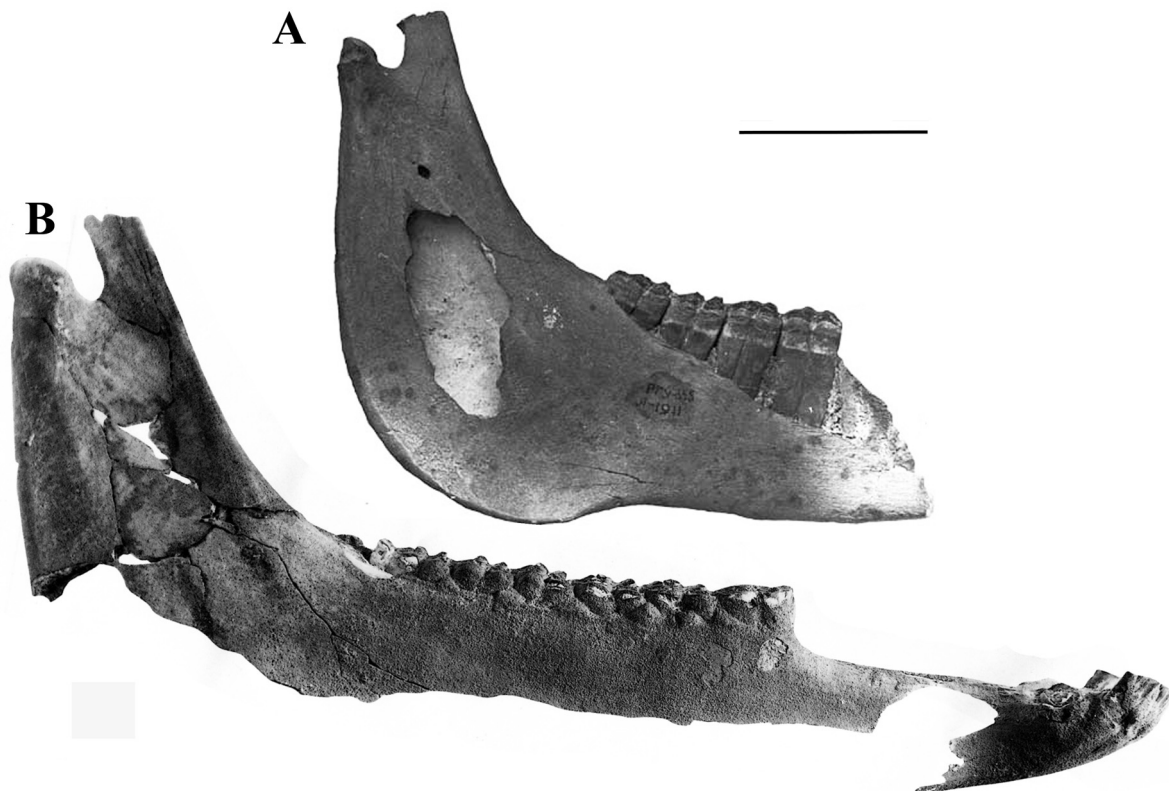


Fig. 9. Profile views of mandibles from Liventsovka. A. RGU 355. B. ROMK L 229. Scale bar: 10 cm.

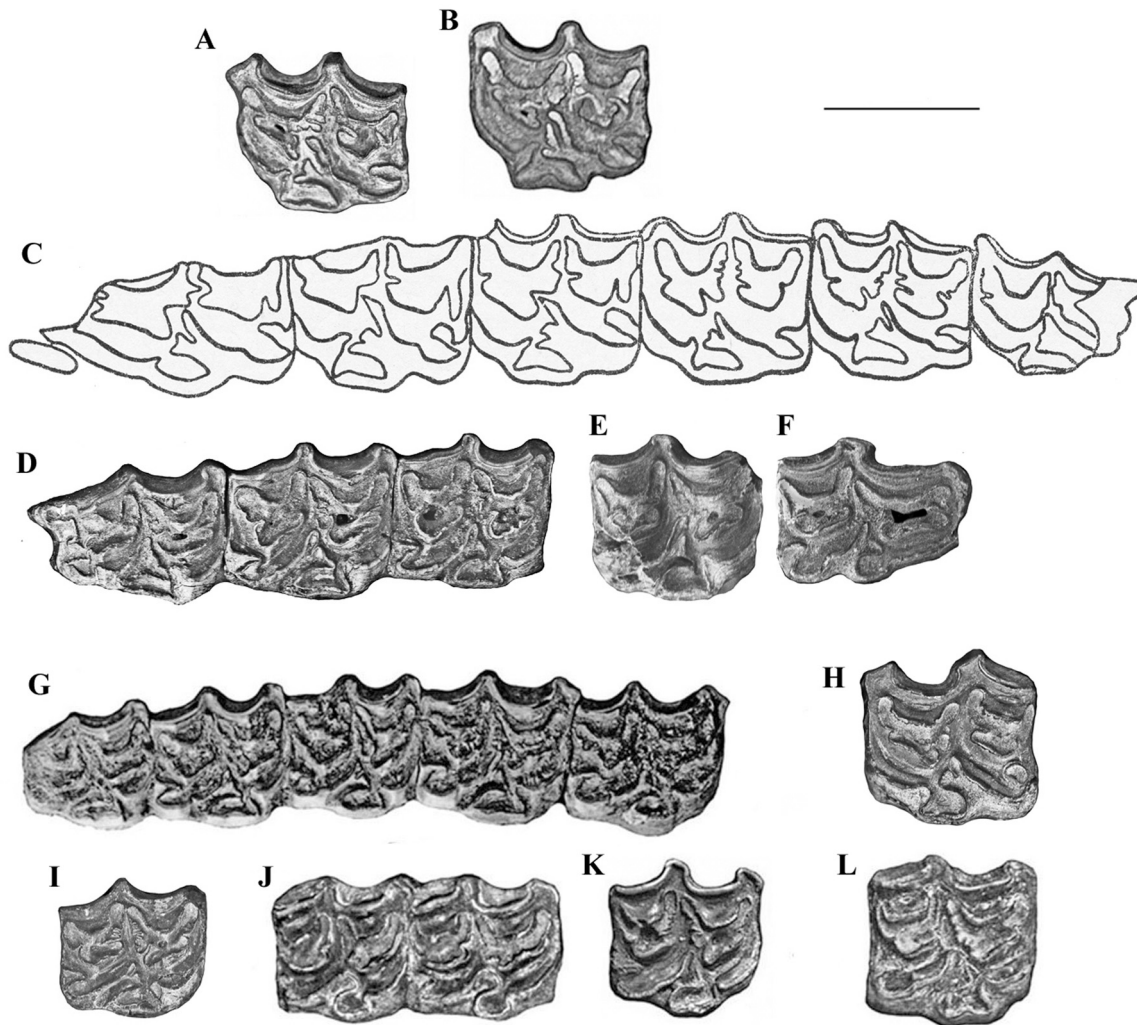


Fig. 10. Upper cheek teeth from Khaprovskii Complex in occlusal views. **A.** RGU 149, left P. **B.** ROMK L 131, sectioned P. **C.** ZIN 3178, left P2–M3 (after Gromova, 1949: fig. 4). **D.** RGU 391, right M1–M3. **E.** RGU 391, right P. **F.** RDU 389, right P2. **G.** ROMK L 4, right P3–M3. **H.** RGU 385, left P. **I.** ROMK L 1425, right M2. **J.** RGU 327, right P4–M1. **K.** ROMK L 1533, right P. **L.** ROMK L 1786, right P. Scale bar: 3 cm.

Appendix A). Size and proportions of radii are similar to *E. (Allohippus) major* from Senèze and to *E. (Sussemionus) sp.* from Untermassfeld, Germany (Fig. S11; Appendix A). Femora (Fig. S12; Appendix A) are larger but have proportions similar to *E. (Allohippus) vireti*. Tibiae are about the size of *E. (Allohippus) sp.* from Ceys-saguet, France (Fig. S13; Appendix A). I tentatively refer to *E. (Allohippus) aff. major* all Ph1 and nine Ph2 marked by asterisks in Tables S9 and S10 (Appendix A).

4.4.2. Attributions to *E. (Allohippus) livenzovensis*

Seven humeri referred to *E. (Allohippus) livenzovensis* are marked by asterisks in Table S13 (Appendix A). In size and proportions they resemble those of *E. (Allohippus) vireti* from Saint-Vallier (Fig. S14; Appendix A).

I refer 10 radii to *E. (Allohippus) livenzovensis*; they are marked by asterisks in Table S14 (Appendix A). They are about the size of *E. (Allohippus) vireti* but are slenderer (Fig. S15; Appendix A).

Four tibiae (marked by asterisks in Table S16; Appendix A) may belong to the same species and fall into the range of Saint-Vallier (Fig. S16; Appendix A). The calcanea ROMK L211 (Fig. 15(B)) and RGU 306 (Fig. 15(C)) probably also belong to this form.

I refer to *E. (A.) livenzovensis* one Ph1P (RGU 132), four Ph2A (#6 to #9) and five Ph2P (RGU 429 and #10 to #13).

4.5. Evidence for the presence of a third species: *Equus (Sussemionus) aff. verae*

A sectioned upper premolar from Liventsovka (ROMK L 131; Figs. 10(B), 16(B)) is very large, has a long protocone, a very long and narrow pli caballin and a small one in addition. Its enamel pattern is similar to RGU 149 (Fig. 10(A)) but ROMK L 131 is larger and has a longer and grooved protocone. It resembles more closely some teeth of the early Oloryan (*ca.* 1 Ma) *E. (Sussemionus) verae* from Chukochya (Fig. 16(D, E)), North Eastern Siberia (Sher, 1971, 1987) and/or the *Equus sp.* (Fig. 16(A, C)) from the early Early Pleistocene of Longgudong (Dragonbone Cave) in Jiashi County, Hubei Province, China (Zheng, 2004; Deng Tao, pers. comm.).

The P2–P4 GIN 302–10 from Volovaya Balka (Fig. 11(F)) stand completely apart from the rest of the Khaprovskii complex lower cheek teeth. The size is very large. The enamel is exceedingly plicated, even taking into account the little worn stage of the teeth. The plis caballinid are very long, a pli protostylid is present on the P2. There are similarities with the Early Pleistocene teeth of *E. (Sussemionus) verae* (Fig. 17(A, B)) and with the teeth (Fig. 17 (D, E)) of the early Early Pleistocene *Equus sp.* of Longgudong, although the enamel plication of Volovaya Balka is less pronounced.

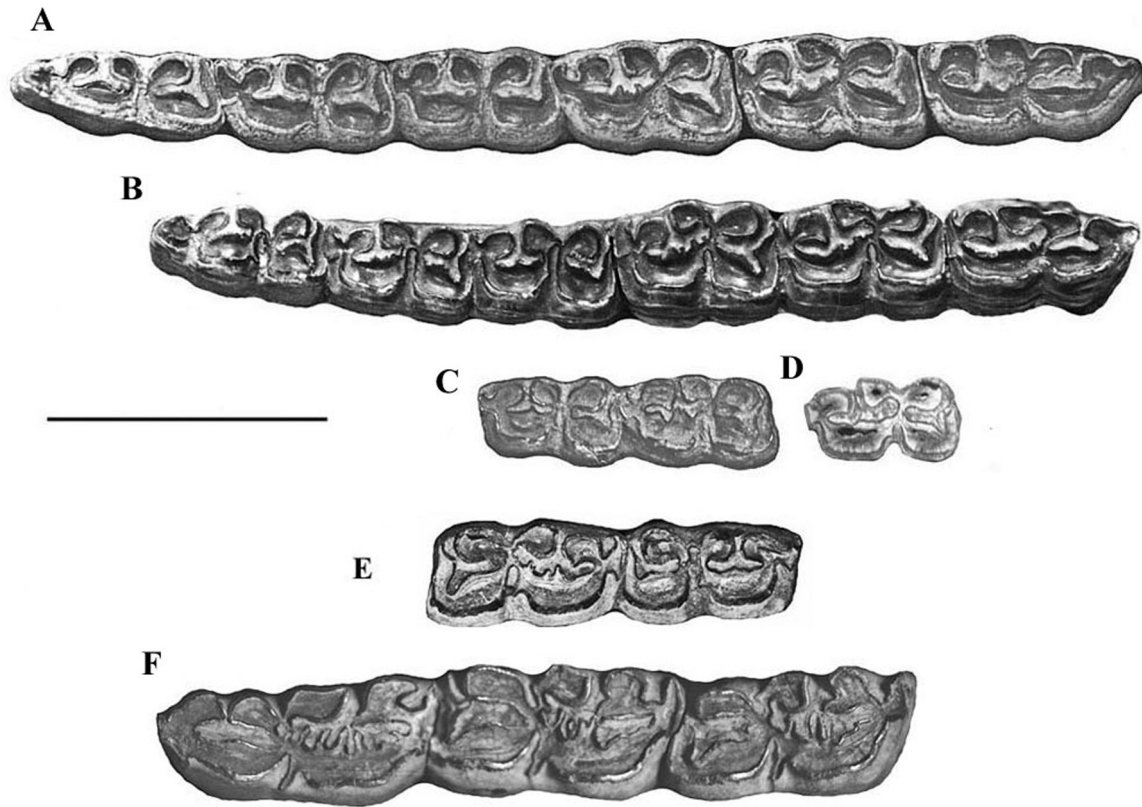


Fig. 11. Lower cheek teeth from Khaprovskii Complex in occlusal views. **A.** ROMK L 395, right P2-M3. **B.** ROMK L 92, right P2-M3. **C.** RGU 662, right P4-M1. **D.** ROMK L 1233, sectioned P. **E.** Liventsovka RGU 1278, left P4-M1. **F.** GIN 302-10, mirrored right P2-P4. Scale bar: 5 cm.

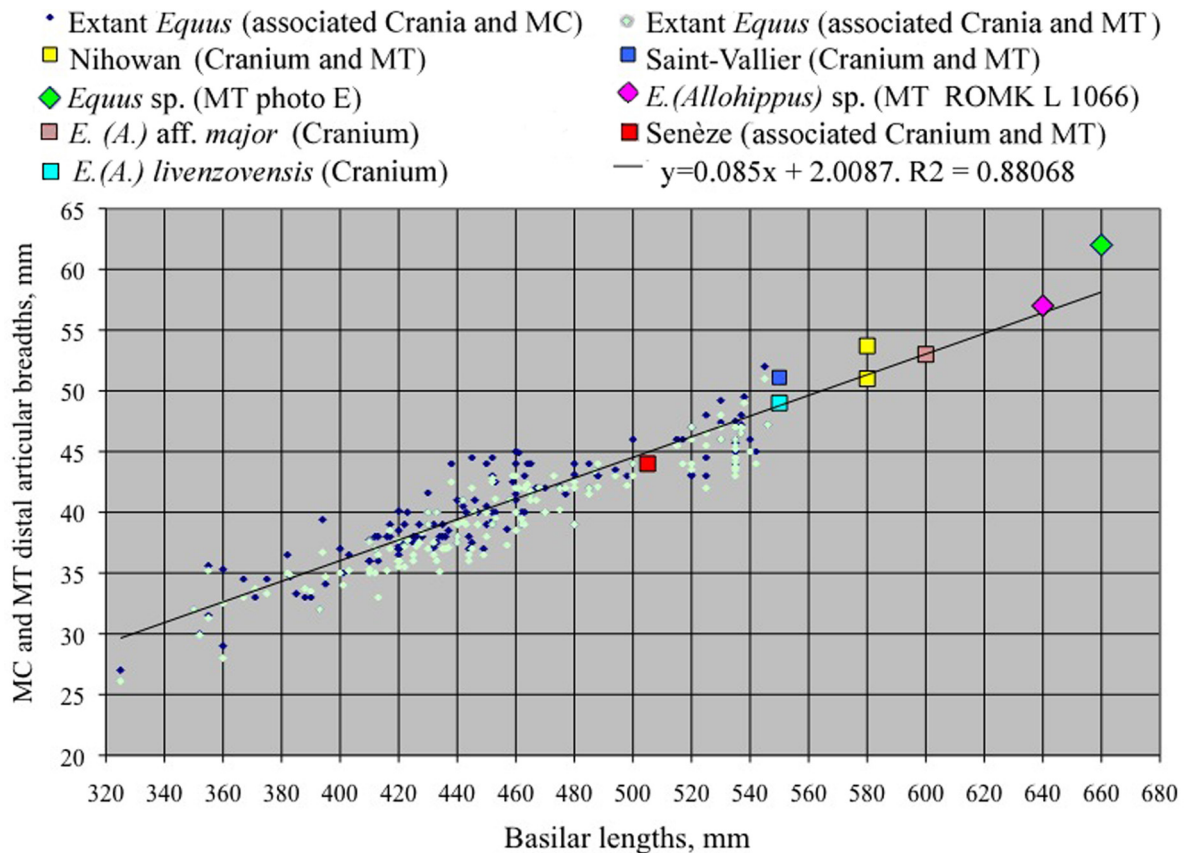


Fig. 12. Scatter diagram and linear regression of MC and MT distal articular breadths on cranial basilar lengths.

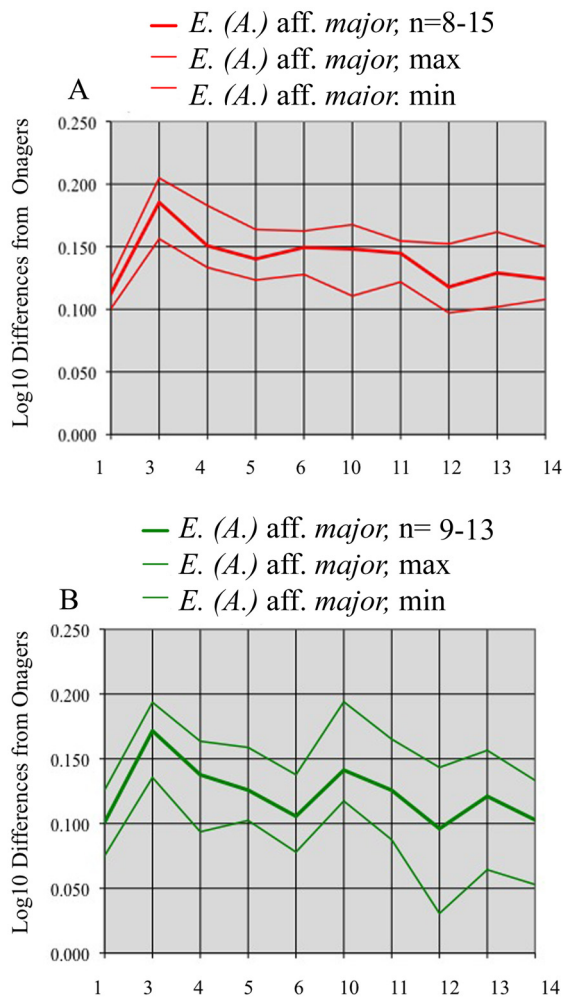


Fig. 13. Simpson's diagrams of *E. (Allohippus)* aff. *major* metapodials. **A.** Metacarpals. **B.** Metatarsals.

Two MC (RGU 326 and RGY 931; Fig. 4(B, D)) are larger but similar to MC of *E. (Sussemionus) verae* (Fig. 18(A)). Four MT (RGU 381, RGU 490, RGU 778, and RGU 1066) resemble the MT of *E. (Sussemionus) verae* and *E. (Sussemionus)* cf. *suessenbornensis* from Akhal-kalaki, Georgia (Fig. 18(B)).

4.6. Problematic fossils

Numerous bones are problematic, in part because of their fragmentary or waterworn state and/or their juvenile or very old age, but also because some do not resemble any fossil I know of.

4.6.1. Very large specimens

One of the largest MT I have ever studied is the specimen with no number shown in Fig. 5(E). Its size (Table S6; Appendix A) is close to the giant specimens from Adycha (NE Siberia) but its keel is much deeper (Fig. S17; Appendix A). The tibia RGU 1707 and the talus ROMK L 536 (Fig. 19) may also belong to this species.

4.6.2. Incertae sedis

Metacarpals. The metacarpals GIN 301–34 (Morskaya), GIN 300–27 (Khapry), RGU 372 and RGU 1437 (Liventsovka) show some resemblances with Pg 1958 from Tegelen (Fig. S18; Appendix A): they are large, rather slender and deep both at the diaphysis and at the epiphyses; they may, however, still belong to *E. (A.)*

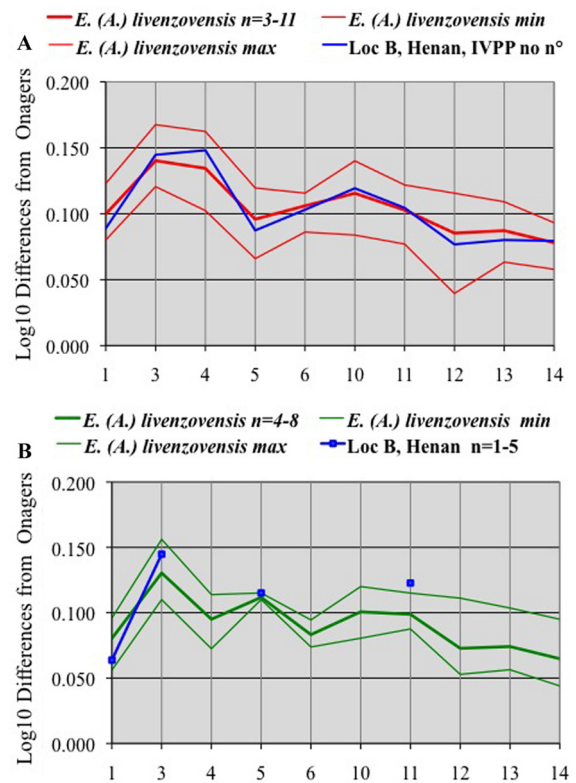


Fig. 14. Simpson's diagrams of *E. (Allohippus) livenzovensis* and *E. (Allohippus)* sp. (from Loc. B of Zdansky; Henan, China) metapodials. **A.** Metacarpals. **B.** Metatarsals.

aff. *major* to which they have been assigned. RGU 1769 is small and has a deep diaphysis, but seems to have similar proportions. RGU 235 is also small; since it is waterworn most of its dimensions are uncertain.

Metatarsals (Fig. S19; Appendix A). According to the VSI, the subadult specimen RGU 483 has one of the smallest breadths of the whole bone sample; even if the breadths are affected by its young age, the small maximal length should be reliable. All other MT are remarkable by their deep diaphyses. GIN 300–127 from Khapry resembles a MT from Kislang, Hungary. ROMK L 1770 is very slender. Usually, slenderness and depth of diaphysis occur in equids living in dry conditions.

Tibiae (Fig. S20; Appendix A). Among the tibiae, two are especially frustrating since both specimens are well preserved: RGU 1157 and RGU 1697. They have deeper diaphyses than usual, and so does the juvenile RGU 249. RGU 719, RGU 1033 and RGU 1789 are very small. Although no attribution can be proposed it is interesting to note that many of these bones have remarkably deep diaphyses.

5. Discussion

5.1. Comparison and discussion of various assignments and attributions

The main source of disagreements between the interpretations of Forsten (1998), Titov (2008) and mine (this article) is the different correlations assumed between crania and limb bones. According to the regression of metapodial distal breadths vs. basilar lengths (Fig. 12) the very large metapodials referred by Titov to *E. (A.) stenonis livenzovensis* and by Forsten to *Equus major* are too large to be associated with the cranium ZIN 31078. On the other hand, the metapodials referred by Forsten to *E. livenzovensis* are

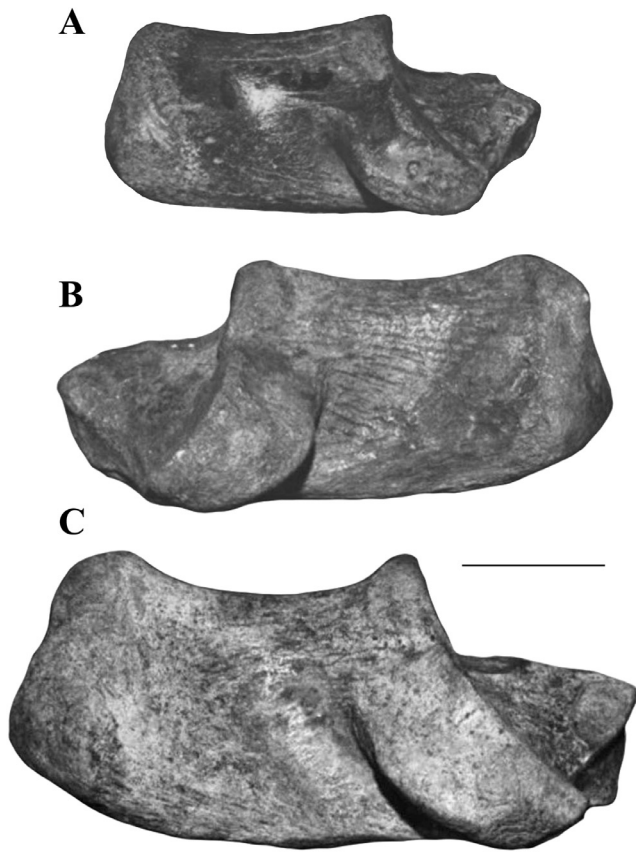


Fig. 15. Calcanea ROMK L 254 left (A), ROMK L 211 right (B) and RGU 306 left (C) in medial view. Scale bar: 3 cm.

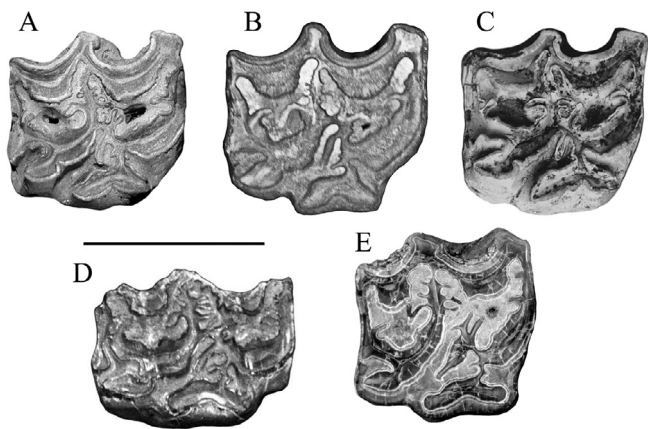


Fig. 16. A-C. Occlusal views of upper right premolars of *Equus* sp. A, C: V 13460-28 (A) and V 13460-10 (C) from Dragonbone Cave, China; B: sectioned ROMK L 131 from Liventsovka. D, E. Occlusal views of upper right premolars of *E. (Sussemionus) verae* from Chukochya. D: PIN 831-461.28; E: PIN 2998-243. Scale bar: 3 cm.

too large to be associated with the cranium ROMK L 4. In my interpretation, the first ones belong to *E. (Sussemionus) aff. verae* and the latter to *E. (A.) aff. major* (not Forsten's *E. major*). In consequence, I refer to *E. (A.) livenzovensis* most of the metapodials referred by Forsten to *Equus cf. altidens*. Of course, there are some other minor disagreements to be discussed later but the general pattern is summarized in Fig. 20.

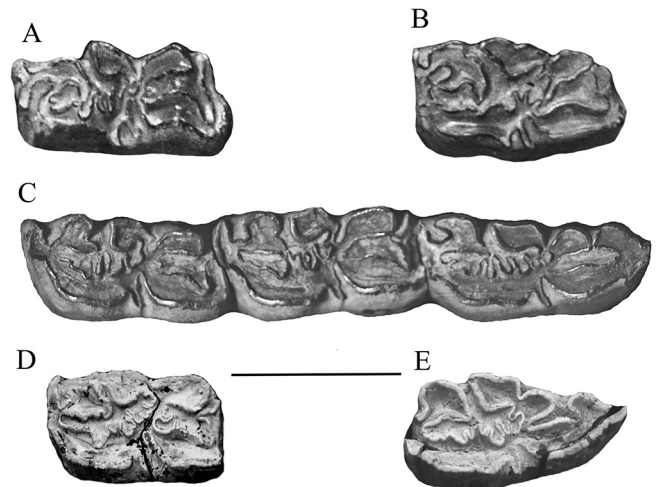


Fig. 17. Lower cheek teeth of *Equus* sp. in occlusal views. A, B. Right lower molar (A) and P2 (B) of PIN 3491-162 from Chukochya. C. Right lower P2-P4 from Volovaya Balka, GIN 302-10. D, E. Right lower P V 13460-55 (D) and lower P2 V 13460-51 (E) from Dragonbone Cave, China. Scale bar: 3 cm.

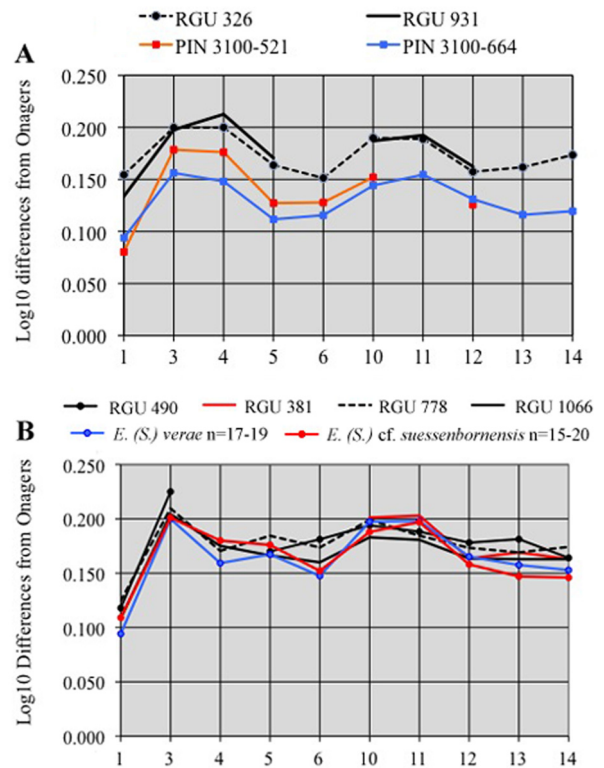


Fig. 18. A. Simpson's diagrams of *E. (Sussemionus) aff. verae* (RGU 326, RGU 391) and *E. (S.) verae* (PIN 3100-521, PIN 310-664) metacarpals. B. Simpson's diagrams of *E. (S.) aff. verae* (RGU 490, RGU 381, RGU 778, RGU 1066), *E. (S.) verae*, and *E. (S.) cf. suessenbornensis* (Akhalkalaki) metatarsals.

5.2. The question of the small species

As stated above, most limb bones referred by Forsten (1998) to *Equus cf. altidens* and by Titov (2008) to *Equus* sp. are referred here to *E. (A.) livenzovensis*. There are, however, some cheek teeth that may belong to a smaller form than *E. (A.) livenzovensis*: ROMK L 1233, section of one premolar (Fig. 11(D)) from a fragmen-



Fig. 19. Left Talus L 536 in anterior view. Scale bar: 5 cm.

tary juvenile ramus, and RGU 662, associated lower P4-M1 (Fig. 11 (C)). The other specimens are more problematic:

- Associated upper P4-M1 (RGU 327): They differ from the rest of small teeth by very short protocones (Fig. 10(J)); lowermost points in Fig. S5(B), Appendix A). However, the teeth are very worn;
- Juvenile talus (L 141), MT (RGU 483), first phalanx (L 475), and fragmentary and/or waterworn bones (Figs. S18-S20; Appendix A);
- The waterworn calcaneum RGU 254 (Fig. 18(A)) is indeed very small but Forsten (1998) suggested that it may belong to *Hipparion*. An upper M1 or M2 was mentioned in the list of equid remains from Khaprovskii Complex (Gromova, 1949; Baigusheva, 1971). Titov (2008) noted its strongly plicated enamel and its wide and deep protocone and its resemblance to *Hipparion* teeth from The Red Craggs (Great Britain). He referred it to *H. moritutum*.

5.3. Age and zoogeographical affinities of the Khaprovskii Faunal Complex

In his extensive publication on the large mammals of the Khaprovskii Faunal Complex, Titov (2008) comes to the conclusion that

it spanned a time from 2.6 to 2.2 Ma, corresponding to most of MN 17 (Saint-Vallier) biozone. He explains the occurrence of classically younger elements (*Canis*, *Coelodonta*, *Eucladoceros*, etc.) by the influence of Asian faunas which is evidenced by the presence of *Elasmotherium*, large *Paracamelus*, *Gazellospira*, and *Libralces* (Fig. S1 and related supplementary references; Appendix A).

My observations on the similarities between *E. (Allohippus) aff. major* cranium and the one from Fan Tsun, SE Shansi, as well as between the metapodials of the small *E. (A.) livenzovensis* and those from Loc. B of Henan support Titov’s conclusions about Asian influences and also about the age of the Khaprovskii Complex since both Fan Tsun and Loc. B are believed to be ca. 2.5 myr old (Deng Tao, pers. comm.). Titov (2008) admits the possibility of younger intrusive fossils inside the Khaprovskii sands. Thus, the specimens I refer to *E. (Sussemionus) aff. verae*, as well as the very large tibia, talus and metapodials may be younger than the rest of the fauna. Teeth and metapodials further confirm an Asian influence on the fauna since they resemble fossils from NE Siberia and China.

Resemblances with European equids are scarce: some metacarpals described above have some resemblances with Pg 1958 from Tegelen but are still compatible with *E. (A.) aff. major*. On the other hand, the metatarsal GIN 300-127 from Khapry is clearly different and very similar to a specimen from Kislang. Forsten (1998) denied the alleged resemblances to Montopoli, but she was and still remains ignored (Bernor et al. 2018, 2019; Cirilli et al., 2021). My observations confirm her opinion. The distal medial condyle depths (variables 13 and 14) of the MC from Montopoli are much smaller than those of the MC from Liventsovka (Fig. 21). The first anterior phalanx IGF 11074 and the posterior IGF 11124 from Montopoli (not the reverse as misidentified by Bernor et al., 2018) are

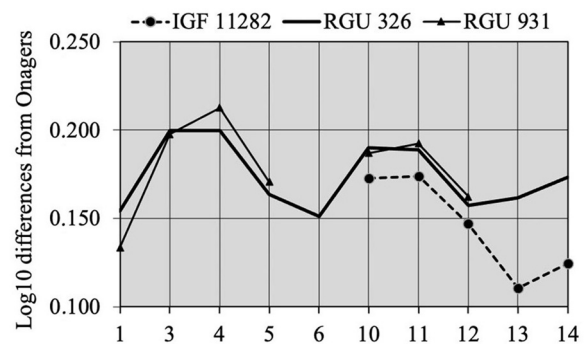


Fig. 21. Simpson's diagram comparing the proportions of a MC from Montopoli and of two MC from Liventsovka.

		CRANIA	Basilar Lengths	MC	MT
This article	<i>Incertae sedis</i>		ca 680 mm		Fig. 5(E)
Titov	<i>E. (A.) stenorion livenzovensis</i>	ZIN 31078 and ROMK L 4		Large	Large
Forsten	<i>Equus major</i>	ZIN 31078		Large	Large
This article	<i>E. (Sussemionus) aff. verae</i>		ca 640 mm	Large	Large
Forsten	<i>Equus livenzovensis</i>	ROMK L 4		Medium	Medium
This article	<i>E. (A.) aff. major</i>	ZIN 31078	ca 600 mm	Medium	Medium
Titov	<i>Equus sp.</i>			Small	Small
Forsten	<i>Equus cf. altidens</i>			Small	Small
This article	<i>E. (A.) livenzovensis</i>	ROMK L 4	ca 550 mm	Small	Small

Fig. 20. Comparison of the crania-metapodials assignments proposed in this article with those of Titov (2008) and Forsten (1998).

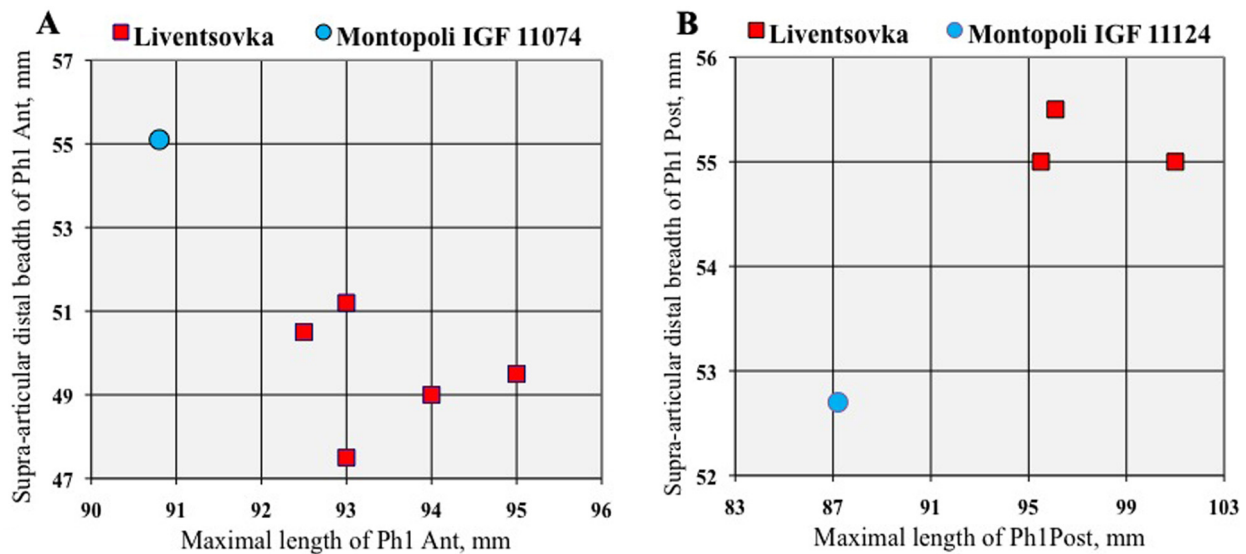


Fig. 22. Scatter diagrams comparing Montopoli and Liventsovka first anterior (A) and posterior (B) phalanges dimensions.

also different from those of the Khaprovskii Complex (Fig. 22(A, B)).

5.4. Concluding remarks

5.4.1. Specific heterogeneity and high intraspecific variation

The number of species represented inside the Khaprovskii Complex collections of equid fossils remains debatable. In addition to the two best represented species, *E. (A.) aff. major* and *E. (A.) livenzovensis*, and to *E. (Sussemionus) aff. verae* (represented by one upper premolar, one lower premolar series and six metapodials), there may be:

- an *Hipparion* species represented by a single tooth and possibly a very small waterworn calcaneum RGU 254;
- a small equid represented by lower cheek teeth RGU 662 and ROMK L 1233;
- a very large equid represented by the tibia RGU 1707, the talus ROMK L 536 and the MT illustrated in Fig. 5(E);
- some *incertae sedis* equids characterized by unusual metapodial and tibiae diaphysis depths (Fig. S18–S20; Appendix A).

The coefficients of variation are very high inside the MT sample referred to *E. (A.) aff. major*. The size is also very variable in teeth presenting the same enamel pattern.

5.4.2. Heterogeneity in age

Abnormally large intraspecific size variation is liable to occur if fossils accumulated during a timespan long enough to evolve larger or smaller dimensions. The occurrence of three and possibly six equid species also suggests an heterogeneity in age of the Khaprovskii Complex. Both large intraspecific variation and occurrence of numerous species may result from the long duration of the Khaprovskii's sands deposition and from the possible presence of intrusive fossils as noted by Titov (2008).

The ages of the cranium from Fan Tsun, SE Shansi and of the metapodials from Locality B of Zdansky, Henan are both believed to approximate 2.5 Ma (Deng Tao, pers. comm.). Their respective resemblances with *E. (A.) aff. major* and *E. (A.) livenzovensis* support such an age for most Liventsovka equid fossils. Given their similarities with the NE Siberian equids, the possibly intrusive *E. (Sussemionus) aff. verae* teeth and metapodials may be as young as 1 Ma.

5.4.3. Asian affinities of the Khaprovskii Complex Fauna

They were stressed by Titov (2008) and are supported by resemblances with Chinese cranium, upper and lower teeth, and metapodials.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data (including Tables S1–S26 and Figs. S1–S20) to this article can be found online at <https://doi.org/10.1016/j.geobios.2021.11.001>.

References

- Azzaroli, A., 2000. On *Equus livenzovensis* Bajgusheva 1978 and the "stenonid" lineage of Equids. *Paleontographia Italica* 87, 1–17.
- Baigusheva, V.S., 1964. Khaprovskaya fauna Liventsovskogo peschanogo kariera (Rostovskaya oblast). *Bulletin Komissii po izucheniyu chetvertichnogo perioda* 29, 44–50 [In Russian].
- Baigusheva, V.S., 1968. Paleontologicheskaya kharakteristika po faune mlekopitayushchikh osnovnykh verkhne pleistotsenovykh razrezov severo-vostochnogo Priazovya (Liventsovka, Port-Katon). *Avtoreferat dissertatsii kandidata geologo-mineralogicheskikh nauk, Rostovskii gosudarstvennii universitet, Rostov-na-Donu* [In Russian].
- Baigusheva, V.S., 1971. Iskopajemaja teriofauna Liventsovskogo kariera (Severo-Vostochnoje Priazovije). *Materialy po faunam Antropogena SSSR, Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* 49, 5–29 [In Russian].
- Baigusheva, V.S., 1978. Krupnaja loshad' khaprovskovo kompleksa iz alliuvia severo-vostochnovo priazovia. *Izvestia Severo-Kavkazkovo nauchnovo tsentra vysshej shkoly estestvennoj nauki* 1, 98–102 [In Russian].

- Bernor, R.L., Cirilli, O., Wang, S.Q., Rook, L., 2018. *Equus cf. livenzovenzis* from Montopoli, Italy (early Pleistocene; MN16b; ca. 2.6 Ma). *Bollettino della Società Paleontologica Italiana* 57, 203–216.
- Bernor, R.L., Cirilli, O., Jukar, A.M., Potts, R., Bukhsianidze, M., Rook, L., 2019. Evolution of early *Equus* in Italy, Georgia, the Indian Subcontinent, East Africa, and the origins of African zebras. *Frontiers in Ecology and Evolution* 7, 166.
- Cirilli, O., Bernor, R.L., Rook, L., 2021. New insights on the Early Pleistocene equids from Roca-Neyra (France, Central Europe): implications for the *Hipparion* LAD and the *Equus* FAD in Europe. *Journal of Paleontology* 95, 406–425.
- Forsten, A., 1998. The fossil horses (Equidae, Mammalia) from the Plio-Pleistocene of Liventsovka near Rostov-Don, Russia. *Geobios* 31, 645–657.
- Gromova, V.I., 1949. Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 1. Obzor i opisanie form. *Trudy Paleontologicheskii institut, Akademii a nauk SSSR, Moskva* 17, 373 p. [In Russian].
- Meadow, R., 1999. The use of size index scaling techniques for research on archaeozoological collections from the Middle East. *Festschrift für Angela von den Driesch zum 65, 285–300*.
- Palombo, M.R., Alberdi, M.T., 2017. Light and shadows in the evolution of South European stenooid horses. *Fossil Imprint* 73, 115–140.
- Sher, A.V., 1971. Mlekopitaiushchie i stratigrafia Pleistotsena krainego severo-vostoka SSSR i severnoi Ameriki. *Nauka, Moskva*, p. 310.
- Sher, A.V., 1987. Olyorian land mammal age of Northeastern Siberia. *Palaeontographia italica* 74, 97–112.
- Simpson, G.G., 1941. Large pleistocene felines of North America. *American Museum Novitates* 1136, 1–27.
- Titov, V.V., 2008. Late Pliocene large mammals from Northeastern Sea of Azov Region. Managing editor Acad. G.G. Matishov, Rostov-on-Don, SSC RAS Publishing, 264 p.
- Uerpmann, H.P., 1982. Faunal remains from Shams ed-din Tannira, a Halafian Site in Northern Syria. *Beyrutus* 30, 3–52.
- Zdansky, O., 1935. *Equus* und andere Perissodactyla. *Palaeontologia Sinica, Ser. C* 6 (5), 1–54.
- Zheng, S.H. (edit.), 2004. *Jishi Hominid Site*. Beijing Science Press, 412 p.