Unexpected finding of a new *Equus* species (Mammalia, Perissodactyla) belonging to a supposedly extinct subgenus in late Pleistocene deposits of Khakassia (southwestern Siberia)

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ABSTRACT
A new species of *Equus*, *E.* (*Sussemionus*) *ovodovi* n. sp., was excavated in Proskuriakova Cave (Khakassia, Southwestern Siberia) in deposits carbon dated at 40 000 BP. This slender, middle-sized equid was first considered as related to *E. hydruntinus* Stehlin & Graziosi, 1935 but biomolecular analyses showed that it actually belonged to a group hitherto unknown of *Equus*. Indeed, a more detailed study of the fossils evidenced features characteristic of the subgenus *Sussemionus* Eisenmann, 2010, common during the middle Pleistocene but supposed extinct after. The current article describes this new species.

KEY WORDS
Mammalia,
Perissodactyla,
Equus (*Sussemionus*)
ovodovi n. sp.,
late Pleistocene,
Proskuriakova,
southwestern Siberia,
new species.

RÉSUMÉ
*Découverte inattendue dans le Pléistocène Supérieur de Khakassie (sud-ouest Sibérien) d'une nouvelle espèce d'*Equus *(Mammalia, Perissodactyla) appartenant à un sous-genre supposé éteint.*
Une nouvelle espèce, *Equus* (*Sussemionus*) *ovodovi* n. sp., découverte dans les dépôts datés de 40 000 ans BP (par le ^{14}C) de la grotte Proskuriakova en Khakassie (sud-ouest de la Sibérie) est décrite. Il s'agit d'un équidé gracile, de taille moyenne, et qui fut d'abord considéré comme une forme d'*E. hydruntinus* Stehlin & Graziosi, 1935. C'est à ce titre que ses restes furent soumis à des analyses biomoléculaires. De façon surprenante, les analyses ont révélé que ces fossiles n'appartenaient ni à *E. hydruntinus*, ni à aucun groupe actuel connu (Orlando *et al.* 2009). Un examen plus détaillé du matériel a montré des traits caractéristiques du sous-genre *Sussemionus* Eisenmann, 2010, commun durant le Pléistocène moyen mais supposé éteint depuis.

MOTS CLÉS
Mammalia,
Perissodactyla,
Equus (*Sussemionus*)
ovodovi n. sp.,
Pléistocène supérieur,
Proskuriakova,
sud-ouest sibérien,
espèce nouvelle.

INTRODUCTION

In a previous article (Eisenmann 2006) a group of *Equus* Linnaeus, 1758 was unformally described under the name of "Sussemiones" in reference to the exhibited mosaic of "hemione-like" characters coexisting with features observed in equids from Süssenborn. Sussemiones were very successful, including slender as well as robust species, ranging from North America to Eurasia and Africa, but all seemed restricted to early and middle Pleistocene.

Thus it came as a surprise to find "Sussemione-like" characters on the material excavated in the late Pleistocene of Proskuriakova cave (Khakassia, Russia, southeastern part of Western Siberia) and dated to 40 000 BP (40 690 ± 1150 years, COAH 1517, bison; 40 595 ± 875 years, COAN 1518, bison; 40770 ± 1075 years, COAH 1519, bison). The equids from this cave have been first tentatively referred to *E.* cf. *hydruntinus* Stehlin & Graziosi, 1935 and it was in that frame that samples have been subjected to biomolecular analyses in order to be compared to *E. hydruntinus* from other geographical areas. A subsequent osteological more detailed study of the fossils showed that they did not belong to *E. hydruntinus* nor to any other extant or recently extinct species, thus confirming the results of the biomolecular analyses (Orlando *et al.* 2009) and warranting the formal description of the subgenus *Sussemionus* Eisenmann, 2010 (Eisenmann in press).

The purpose of the current paper is to fully describe the new species from Proskuriakova and discuss its affinities with "hemione-like" recent equids (extant and late Pleistocene) and some much older ones (middle and early Pleistocene).

The Proskuriakova cave (54°26'43"N, 89°28'05"E) is situated on the right bank of the river Belyj Ius, in Khakassia (Okladnikov *et al.* 1975). The excavated material comprises a minimum of 47 mammalian species including *c.* 1000 identifiable bones belonging to 20 species of macromammals. Equids represent 14% of them and include a caballine and a slender species described in this article. Stone artefacts and broken bones evidence the occasional occupation of the cave by paleolithic humans.

MATERIAL AND METHODS

The material is preserved in the collection of the Institute of Archeology and Ethnography of the Siberian branch of the Academy of Sciences (IAES), at Novosibirsk. It is not very rich:

– a palatal fragment, with P3/-M1/ of both sides (IAES 21);
– 15 isolated upper cheek teeth;
– 6 lower cheek teeth rows;
– 4 fragments of MC;
– 7 MT including two fragments.

The material looks rather variable in size and shape, possibly reflecting some mixing from different ages. There is no doubt, however, that it belongs to a single species.

A conventional biometrical study was performed according to the methods described in the web site

TABLE 1. — Measurements in mm of third metatarsals length, distal articular breadth and diaphysis depth, of occlusal size (occlusal length + occlusal breadth)/2 of upper premolars and molars, and protocone length of upper premolars and molars of the extant *Equus hemionus onager* Moorcroft, 1841, *E. hydruntinus* Stehlin & Graziosi, 1935 from various localities, *E.* (*S.*) *ovodovi* n. sp. from Proskuriakova cave (Khakassia, Southwestern Siberia) and *E.* (*S.*) *altidens* Reichenau, 1915 from Süssenborn. Abbreviations: **M**, molars; **Mprot.**: protocone length of upper molars; **MT(1)**, third metatarsals length; **MT(4)**, diaphysis depth; **MT(11)**, distal articular breadth; **n**, number of specimens; **P**, premolars; **Pprot.**: protocone length of upper premolars; **brackets**, approximate values.

	n	MT (1)	n	MT(11)	n	MT(4)	n	P (L+w)/2	n	M (L+w)/2	n	P prot.	n	M prot.
E. hemionus onager	16	247.5	16	37.4	16	25.3	47	25.6	48	23	47	11.4	48	11
E. hydruntinus Dorog	3	267.7	4	39.3	7	28.9	2	23.6	3	21.9	2	7	3	7.4
E. hydruntinus Staroselie	12	255.1	20	37.1	12	26.8	7	23.3	17	21.4	7	7.5	17	8.4
E. hydruntinus Lunel-Viel	14	228.7	15	33.6	14	24.8	11	23.4	14	22.2	11	8	14	8.3
E. (*S.*) *ovodovi* n. sp. large	1	276.8	1	[44.5]	1	30.7	6	26.9	3	26.2	6	13.5	3	12.2
E. (*S.*) *ovodovi* n. sp. small	5	165.3	6	41	4	29.1	5	25.3	4	23.6	5	10.6	4	10.7
E. (*S.*) *altidens* Süssenborn	1	282	5	44.8	4	33.5	25	29.1	19	26.3	24	11.7	19	12.1

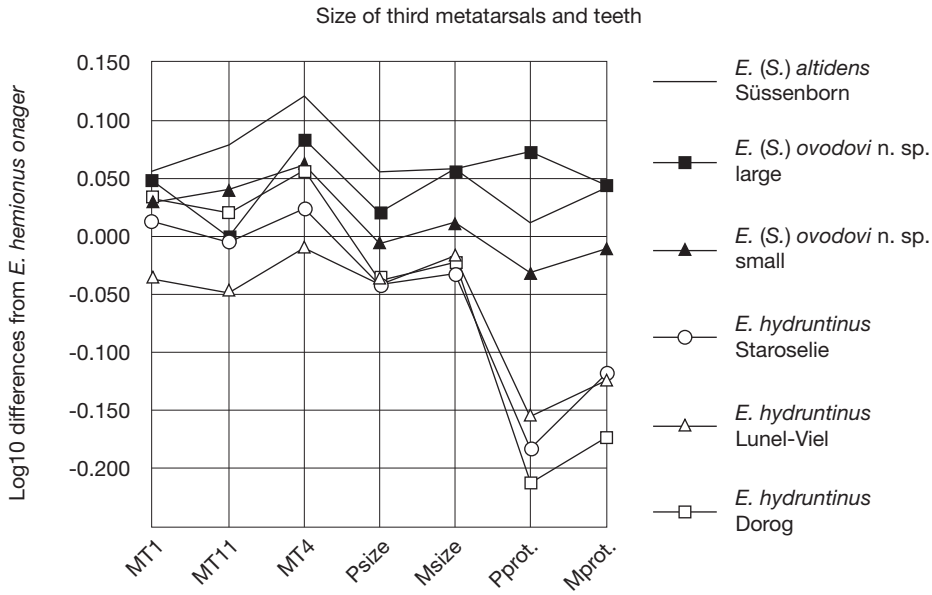

FIG. 1. — Simpson's ratio diagram comparing third metatarsals length (**MT1**), distal articular breadth (**MT11**), and diaphysis depth (**MT4**); size [size = (length + width)/2] of upper premolars (**P**) and molars (**M**); and protocone length of upper premolars (**Pprot**.) and molars (**Mprot**.) in *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia) to extant *E. hemionus onager,* Moorcroft, 1841, *E.* (*S.*) *altidens* Reichenau, 1915 (Süssenborn) and *E. hydruntinus* Stehlin & Graziosi, 1935 (Staroselie, Lunel-Viel, Dorog).

www.vera-eisenmann.com. It comprises Simpson's ratio diagrams allowing simultaneous comparisons of size and proportions of the studied specimens or groups of specimens. If two specimens are isometric, they will be represented by parallel lines. The reference basis (line zero of the diagrams) is given by the corresponding measurements in the extant *E. hemionus onager* Moorcroft, 1841. In the first ratio diagram (Fig. 1), the size of P3 or P4 and M1 or M2 is the mean of length and width of the tooth ([L+w]/2); it allows to compensate for the effect of wear since at the first stages the length is longer and the width smaller than at mid-wear, the reverse being true for the last stages of wear. For the ratio diagrams of the metapodials (Figs 8; 11), the chosen measurements give a good representation of the size and the proportions of the bone; for example, the slope of the line between 1 and 3 expresses the robustness or slenderness of the diaphysis (relative to *E. h. onager*).

The choice of measurements compared in ratio diagrams is arbitrary in the sense that any combination useful to distinguish (or find similarities between) specimens or species may be used; for example the size of M1 or M2 is similar in *E. hydruntinus* Stehlin & Graziosi, 1935 from Staroselie and Lunel-Viel but the metatarsals of the former are larger.

ABBREVIATIONS

P	premolar;
PIN	Paleontological Institute, russian academy of science, Moscow;
P2/, P3/, P4/	upper premolars;
P/2, P/3, P/4	lower premolars;
M	molar;
MC	third metacarpal;
MT	third metatarsal;
M1/, M2/, M3/	upper molars;
M/1, M/2, M/3	lower molars;
sin.	left;
dex.	right.

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Linnaeus, 1758
Genus *Equus* Linnaeus, 1758

FIG. 2. — Palatal fragment with P3/-M1/ of both sides (IAES 21), holotype of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova Cave (Khakassia, Southwestern Siberia). Scale bar: 3 cm.

Subgenus *Sussemionus* Eisenmann, 2010

***Equus* (*S.*) *ovodovi* n. sp.**

HOLOTYPE. — Palatal fragment, with P3/-M1/ of both sides (IAES 21).

ETYMOLOGY. — In honour of Professor N. D. Ovodov, of the Institute of Archeology and Ethnography (Novosibirsk) who excavated the Proskuriakova cave in 1973-1974.

MATERIAL EXAMINED. — Enumerated above and described below. Besides Proskuriakova cave, fossils possibly belonging to the same species were found in late Pleistocene alluvial deposits of "Pred-Altai plain" (Upper Ob) and in Altai caves where they can be traced up to the end of Pleistocene (Vasiliev *et al.* 2006).

TYPE LEVEL. — Late Pleistocene.

TYPE LOCALITY. — Proskuriakova cave, Khakassia, western Siberia.

DIAGNOSIS

Slender *Equus* slightly larger than the extant *E. hemionus onager*; cheek teeth relatively small; shallow postprotoconal grooves on the upper cheek teeth; shallow lingual grooves, elongated double knots and metaconids on the lower cheek teeth; deep vestibular grooves on the lower molars; occasional presence of a pli protostylid on P/2; deep diaphyses on the MC and MT.

GENERAL DESCRIPTION

The Simpson's ratio diagram (Fig. 1) where *E. hemionus onager* is the reference zero line, compares MT length, distal articular breadth, depth of the diaphysis (respectively MT1, MT11, MT4), size of P3/-P4/ (Psize), size of M1/-M2/ (Msize), protocone length of P3/-P4/ and of M1/-M2/ (Pprot.; Mprot.), in *E.* (*S.*) *ovodovi* n. sp. of Proskuriakova to the same dimensions in *E. hemionus onager* (zero line), in *E.* (*S.*) *altidens* Reichenau, 1915 (Süssenborn), and in three forms of *E. hydruntinus*.

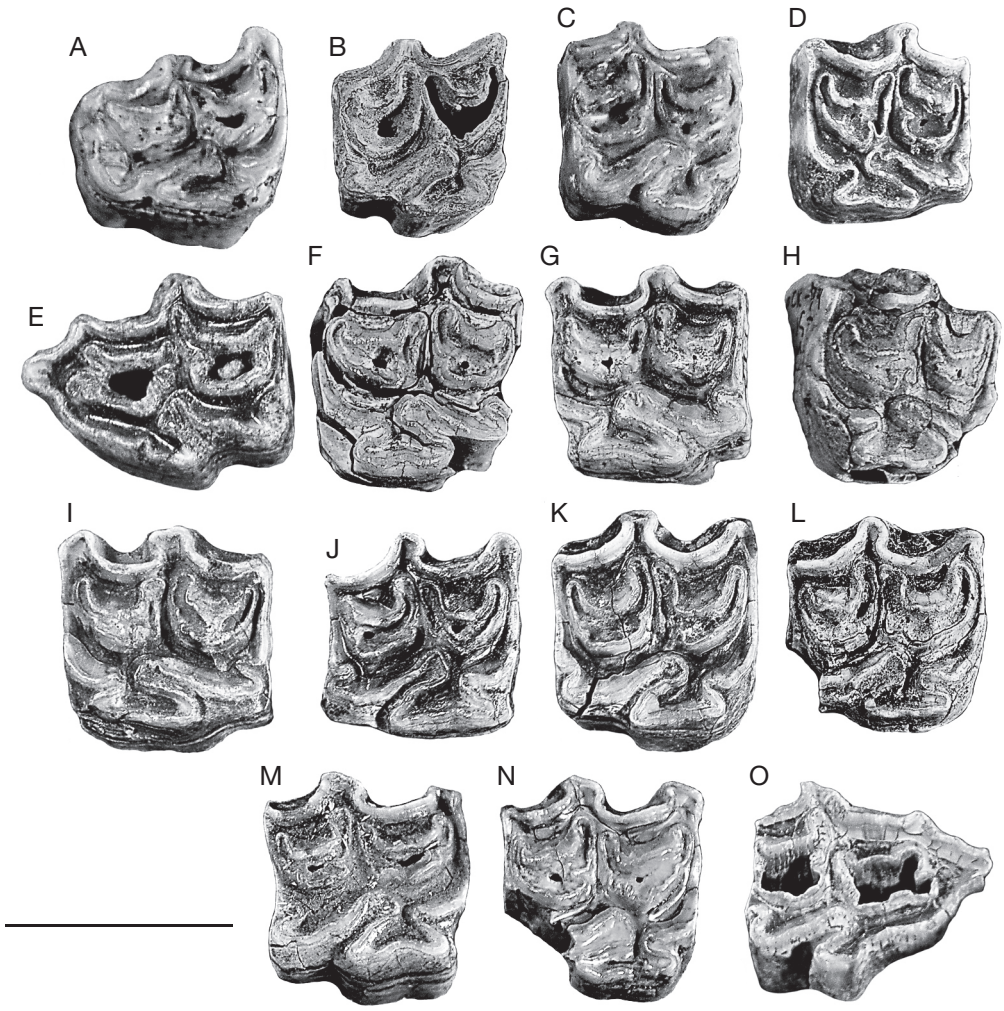

FIG. 3. — Upper cheek teeth of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova Cave (Khakassia, Southwestern Siberia): **A**, M3/ (no. 15); **B**, M (no. 12); **C**, P (no. 11); **D**, M (no. 13); **E**, P2/ (no. 1); **F**, P (no. 5); **G**, P (no. 4); **H**, P (no. 14); **I**, P (no. 3); **J**, M (no. 8); **K**, M (no. 9); **L**, M (no. 10); **M**, P (no. 6); **N**, P (no. 7); **O**, P2/ (no. 2). Scale bar: 3 cm.

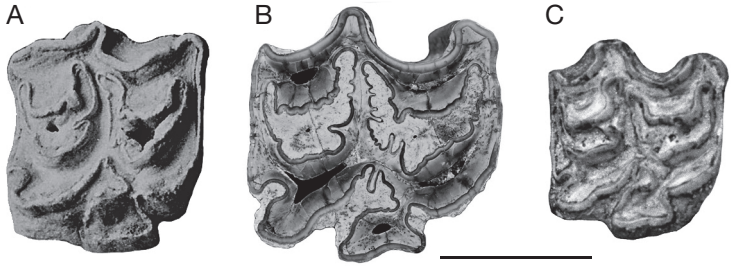

FIG. 4. — Upper cheek teeth: **A**, M of *E*. (*S.*) cf. *suessenbornensis* Reicheau, 1915 from Akhalkalaki (Vekua 1962) (AKHA 1290); **B**, P of *E.* (*S.*) *suessenbornensis* from Süssenborn (S 876); **C**, P3/ of *E*. (*Amerhippus*) *andium* Wagner-Branco, 1883, Punin, Ecuador (FAM 11). Scale bar: 3 cm.

TABLE 2. — Measurements (in mm) of upper cheek teeth of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia). Abbreviations: **Ht**, height of the crown; **L**, occlusal length; **LPT**, length of protocone; **W**, occlusal width.

Type	L	LPT	W	Ht
P3/				
IAES 21 sin.	*c.* 26.2	9.9	*c.* 24.4	32
IAES 21 dex.	*c.* 26.5	10.2	24.8	31
P4/				
IAES 21 sin.	25	11.7	*c.* 25.3	
IAES 21 dex.	24.4	10.7	25.6	
M1/				
IAES 21 sin.	22.4	10.7	25.5	28
IAES 21 dex.	*c.* 22.9	10.9	25.8	28
P2/				
IAES 1 sin.	35.5	7.4	24.7	53
IAES 2 dex.	32	7	20.7	27
M3/				
IAES 15 sin.	28.2	12.8	23	51
P3/-P4/				
IAES 3 sin.	26.8	13.8	27.2	38
IAES 4 sin.	26.2	14	27.5	38
IAES 5 sin.	26.8	13	28.3	35
IAES 6 dex.	26.8	14.1	26.2	37
IAES 7 dex.	26.5	13.6	26.6	34
M1/-M2/				
IAES 8 dex.	24.8	13.3	25.5	43
IAES 9 dex.	26.1	12	28.7	31
IAES 10 dex.	25.3	11.4	27	30
IAES 11 dex.	24.3	10.3	26.3	23
IAES 12 dex.	22.3	10.4	23.2	24
IAES 13 sin.	22	10.8	24.7	36
IAES 14 sin.	25.2	12.2	28.4	33

It shows slight size differences inside the Proskuriakova material, particularly in the length of the premolar's protocones (Fig. 1 [Pprot.]; Table 1). There is also a difference between the MT1-MT4-MT11 proportions between the "large" and "small" forms but since there is only one large MT (no. 6, with a damaged distal end), this does not seem very reliable).

More important are the differences between *E.* (*S.*) *ovodovi* n. sp. and both *E. hemionus* and *E. hydruntinus*:

– unlike *E. hemionus onager* teeth are relatively small and diaphyses are deep on the metatarsals;

– unlike *E. hydruntinus* protocones are relatively long.

The smaller form has proportions close to *E.* (*S.*) *altidens* from Süssenborn, Germany, a species *c.* 0.6 Ma old (Maul *et al.* 2000).

Upper cheek teeth (Table 2)

The enamel is simple, the plis caballin – when present – are small; the postprotoconal grooves are shallow. Size and shape of the protocones are very variable: short, pointed, and humped (Figs 2; 3C) like in some Sussemiones and *E. andium* Branco, 1883 (Fig. 4) or flat and long (Fig. 3I).

Lower cheek teeth (Tables 3; 4)

Small or large, the lower cheek teeth (Fig. 5) differ from hemiones by deep vestibular grooves on the molars, and from *E. hydruntinus*, by assymetric double knots. Some resemble to middle Pleistocene species (Fig. 6) found at Süssenborn and Akhalkalaki (Georgia), or to some *E.* (*Amerhippus*) *santaeelenae* Spillmann, 1938 of Tarija, Bolivia.

Third metacarpals

The material is very poor (Table 5) but it is possible to reconstruct the approximal length (Fig. 7).

Size and proportions look similar (Fig. 8) to the MC fragments found in the Mousterian of Tsopi, Georgia (Gabunia & Vekua 1989; Vekua pers. com. 1995).

Tsopi yielded also a deciduous upper series, a fragment of M3/, and several associated lower cheek teeth (Gabunia & Vekua 1989). One of these, a lower molar, is very interesting: it bears an ectostylid, and has a very deep vestibular groove reminding of some Sussemiones (Fig. 9). No other photographs are available.

Third metatarsals

MT no. 6 is more robust than the others and has a very developed keel (Table 6; Fig. 10).

The size of MT no. 6 is close to the mean of *E. hipparionoides* Vekua, 1962 MT from Akhalkalaki (Fig. 11) but the latter is closer by proportions to the smaller MT from Proskuriakova: deep diaphysis like MT no. 6 and 7 (measurement 4), and probably large distal articular breadth (distal end damaged) like MT no. 9 (measurement 11).

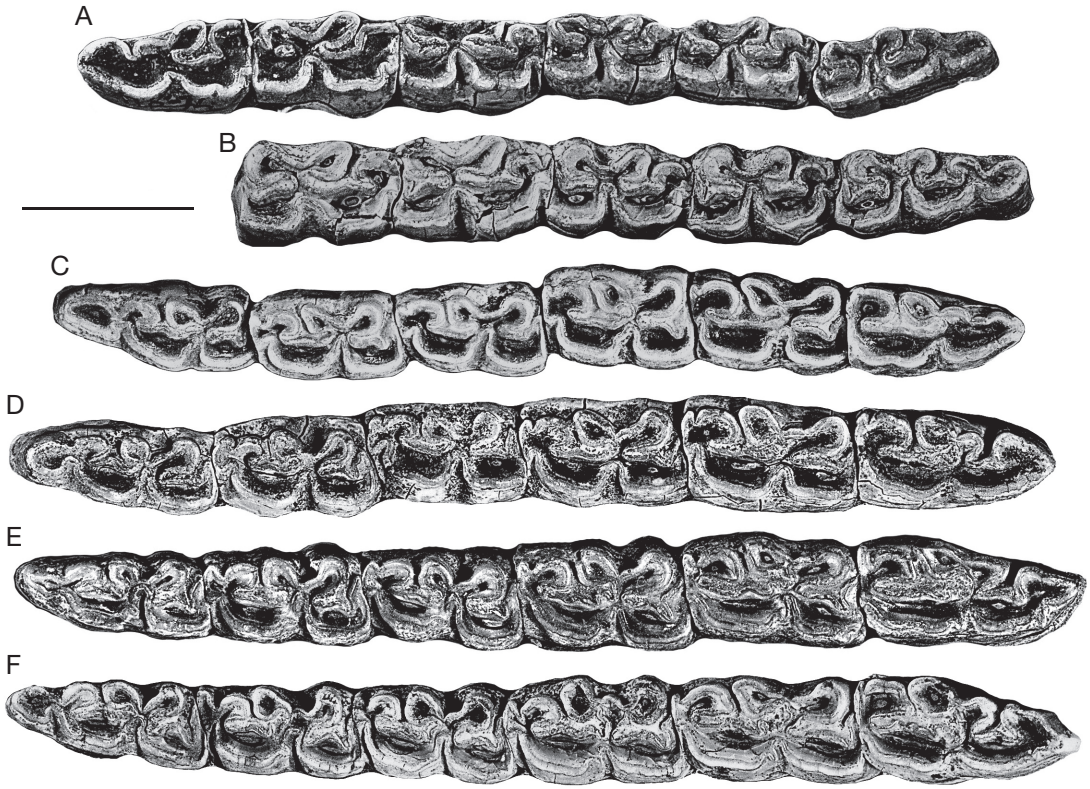

FIG. 5. — Lower cheek teeth series of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia): **A**, no. 1; **B**, no. 2; **C**, no. 3; **D**, no. 4; **E**, no. 5; **F**, no. 6. Scale bar: 3 cm.

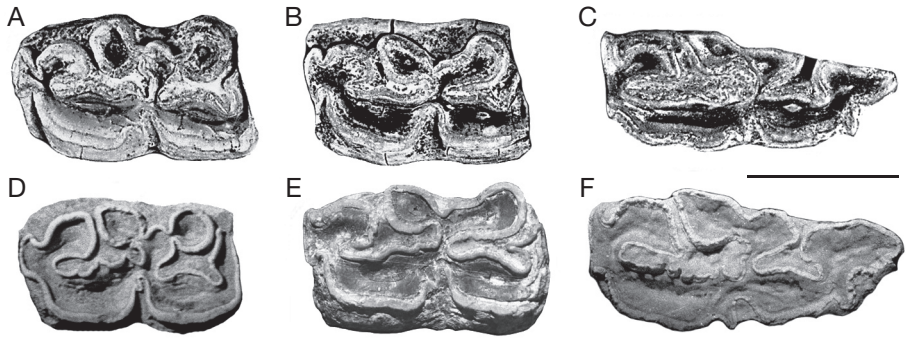

FIG. 6. — Lower cheek teeth of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia): **A**, P/4 (no. 6); **B**, P/4 (no. 4); **C**, P/2 (no. 6); **D**, P/4 of *E.* (*Amerhippus*) *santaeelenae* Spillmann, 1938 (V 689), Tarija, Bolivia; **E**, P S 3362 of *E. marxi* Reichenau, 1915 from Süssenborn; **F**, P/2 of *E.* cf. *sussenbornensis* from Akhalkalaki (Vekua 1962), no number. Scale bar: 3 cm.

TABLE 3. — Measurements (in mm) of lower cheek teeth of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia). Abbreviations: **L**, occlusal length; **LPF**, length of postflexid; **W**, occlusal width.

	P/2			P/3			P/4			M/1			M/2			M/3		
IAES no.	L	LPF	W	L	LPF	W	L	LPF	W	L	LPF	W	L	LPF	W	L	LPF	W
1 dex	34.1	16	16	28.4	16.1	17.1	28	12.9	17.3	24.1	11.5	16	24.7	10.7	15.2	31	11.1	13.5
2 dex	34.5	16.2	17	27.2	16	18	26.5	12.7	18	24.5	9.2	17	24.5	9	16.2	28.2	7.9	13.9
3 dex	31.6	13.8	16.1	27.7	12.7	18.4	26.7	11	18.4	24	8.5	18.3	24.5	9	17.5	30.6	8.6	14.4
4 dex	28.8	14	15.7	24.8	14	16.8	24.4	11.9	17.5	24	8.6	16.9	24	9.5	16.3	31.7	12	13.9
5 sin				26.3	12.8	17.1	25.5	11.5	17.9	23.8	7.9	16.8	23.8	8.3	16.9	30.3	8.5	14.5
6 sin	29	8.8	13.6	24.5	7.2	16.2	24	9.6	16.1	21.4	6.4	15.3	24.5	7.3	14	29.8	7.3	11

FIG. 7. — Anterior view of MC of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia): **A**, no. 3; **B**, no. 4; **C**, no.2. Scale bar: 3 cm.

TABLE 4. — Measurements (in mm) of lower cheek series from of *E.* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia).

	L P3-P4	L M1-M3	L P2-M3
1 dex	88.7	78	175.8
2 dex	87.5	77.3	169.5
3 dex	85	78.5	168.5
4 dex	79	80	162
5 sin		78.5	
6 sin	77.8	74.8	154

TABLE 5. — Measurements (in mm) of MC of *E.* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia). **1**, maximal length; **3**, breadth at the middle of diaphysis; **4**, depth at the same level; **5**, proximal articular breadth; **6**, proximal depth; **7**, diameter of articular facet for Os carpale III; **8**, diameter of articular facet for Os carpale IV; **10**, distal supra-articular breadth; **11**, distal articular breadth.

	MC no. 2	MC no. 3	MC no. 4	MC no. 5
1	*c.* 230			
3	30.5	*c.* 29.6	*c.* 29.1	30.1
4	23.8			23.3
5	46	*c.* 44.8		
6	31.2	28.8		
7	38.5	37.5		
8	13.7	14.5		
10			42	
11			*c.* 41.5	

REMARKS

Note that molecular analyses were performed on samples ACAD2302 (MT no. 9), ACAD2303 (MT no. 12), and ACAD2305 (fragment of juvenile MT no. 14) belonging to the smaller form.

DISCUSSION AND CONCLUSION

It may happen that a poor, relatively recent, and specifically uncertain material is at the origin of

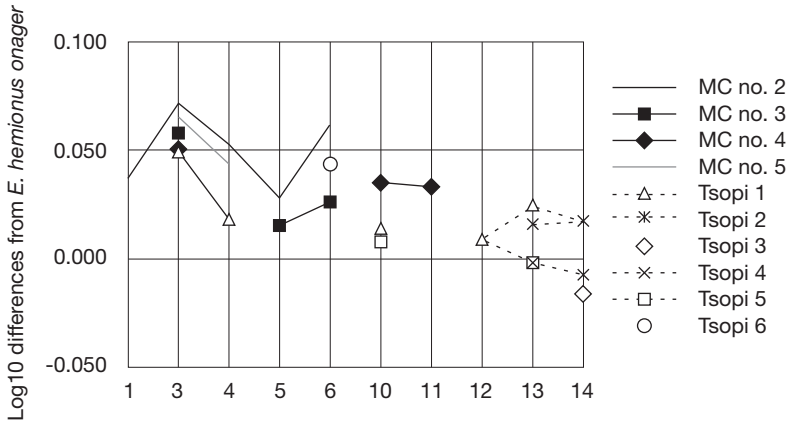

FIG. 8. — Ratio diagram comparing fragmentary MC of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia) and from Tsopi (Tbilisi Laboratory collections): numbers (1, 3, 4, etc.) refer to the measurements of Table 2. Collection numbers: **Tsopi 1**, 58-950; **Tsopi 2**, 57-24-899; **Tsopi 3**, 58-1490; **Tsopi 4**, 13; **Tsopi 5**, 57-436-28; **Tsopi 6**, 58-335.

FIG. 9. — Lower cheek teeth of Sussemiones: **A**, *Equus verae* Sher, 1971, M/1 (PIN 3100-333), Chukochya; **B**, *Equus* sp., M/2 (58-1031), Tsopi; **C**, *E.* (*S.*) cf. *suessenbornensis* Reichenau, 1915 from Akhalkalaki (Vekua 1962), M/2, no. 4. Scale bar: 2 cm.

TABLE 6. — Measurements (in mm) of MT of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia): **1**, maximal length; **2**, lateral length; **3**, breadth at the middle of diaphysis; **4**, depth at the same level; **5**, proximal articular breadth; **6**, proximal depth; **7**, diameter of articular facet for Os tarsale III; **8**, diameter of articular facet for Os tarsale IV; **10**, distal supra-articular breadth; **11**, distal articular breadth; **12**, depth of the keel; **13**, least depth of the medial condyle; **14**, greatest depth of the medial condyle. Samples for molecuar studies were taken on MT no. 9 and 12.

	MT no. 6	MT no. 7	MT no. 8	MT no. 9	MT no. 10	MT no. 11	MT no. 12
1	276.8	276.5	269.6	257.2	261.1		262
2	265.5	269.1	261.7	250.5	255		254.5
3	31.7	29	28.7	29.6	28.7		28.2
4	30.7	30.4	30	28.5			27.5
5	48.3	44.2	43	41.5			42
6	43	38.8	38.2	37.3			36.5
7	44.6	39	39.4	39			38.2
8	10.7	11.2	9.4	9.7			9.6
10	46.8	41.7	40.3	41.7	43.1	41.7	37.8
11	*c.* 44.5	40.6	39	41.9	41.6		37.5
12	38	31.8	32.1	32.1		32	
13	28.5	25	25	24.9	26.1		
14	31.1	27.8	27.5	28.3	30.1	27	25.5

FIG. 10. — MT of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova Cave (Khakassia, Southwestern Siberia): **A**, no. 6, ventral view; **B**, no. 7, ventral view; **C**, no. 8, dorsal view. Scale bar: 3 cm.

very exciting discoveries. Such is the case of the Proskuriakova equids which appear to be survivors of Sussemiones, a group of fossils believed extinct since *c.* 0.5 Ma, and not just a form of *E. hydruntinus*, a species widely represented during late Pleistocene.

The belonging of *E.* (*S.*) *ovodovi* n. sp. to such an old fossil group, were it based on osteological characters alone, could look doubtful. Fortunately, molecular biology studies point in a similar direction. Samples from hemiones, *E. hydruntinus,* and *E.* cf. *hydruntinus* from Proskuriakova were analysed to clarify the taxonomic relationships and geographic range of these groups (Orlando *et al.* 2009). Surprisingly, all three *E.* cf. *hydruntinus* samples from Proskuriakova did not cluster with *E. hydruntinus* or hemiones but formed a new monophyletic group with strong support, and no specific affinity with other non caballines *Equus*. Cyt *b* sequences supported this arrangement. Moreover, this new clade is separated from *E. hydruntinus* specimens, and Asian and Middle Eastern hemiones by not possessing the 28-bp deletion in the first HVR-1 PCR fragment, deletion shared by hemiones and *E. hydruntinus* in contrast to other equids. The genetic distances separating the three Russian specimens from hemiones are of a similar magnitude to other species (for instance those separating donkey and hemione), suggesting that this clade should be considered a distinct taxonomic group, representing a new species, distinct from *E. hydruntinus*, and with no extant relative.

We have remarked above that another late Pleistocene equid (from the Mousterian of Tsopi, Georgia), also refered to a sort of *E. hydruntinus*, shows dental features (Fig. 6) characteristic of early or middle Pleistocene *Equus*. All things put together, it is justified to accept the survival of Sussemiones into late Pleistocene but this survival is probably restricted to endemic levels. Indeed usually, from the middle Pleistocene and on, fossil *Equus* are easily classified inside extant groups: osteological characters show that the European *E. mosbachensis* Reichenau, 1901 (*c.* 0.5 Ma; Maul *et al.* 2000) is a modern horse; the North African *E. mauritanicus* Pomel, 1897 (*c.* 0.7 Ma; Geraads *et al.* 1986) belongs inside plain zebras, as well as the South African *E. capensis* Broom, 1909 (for which this belonging was confirmed by molecular biology, see Orlando *et al.* 2009). There are, however, exceptions like the enigmatic *E. valeriani* Gromova, 1946 described by Gromova (1946) from Uzbekistan, on the basis of very large cheek teeth. It was excavated in 1938 in the Upper Paleolithic site of Samarkand, in association with a cervid (close to *C. elaphus* Linnaeus, 1758) and badly preserved remains of some bovid. At that time, and in that place, only true (caballine) horses and hemiones are usually found. But *E. valeriani* cannot be a horse or a hemione: its lower cheek teeth have a primitive, "stenonine" double knot (although the ectoflexids are not very deep). The upper cheek teeth have a very thin and

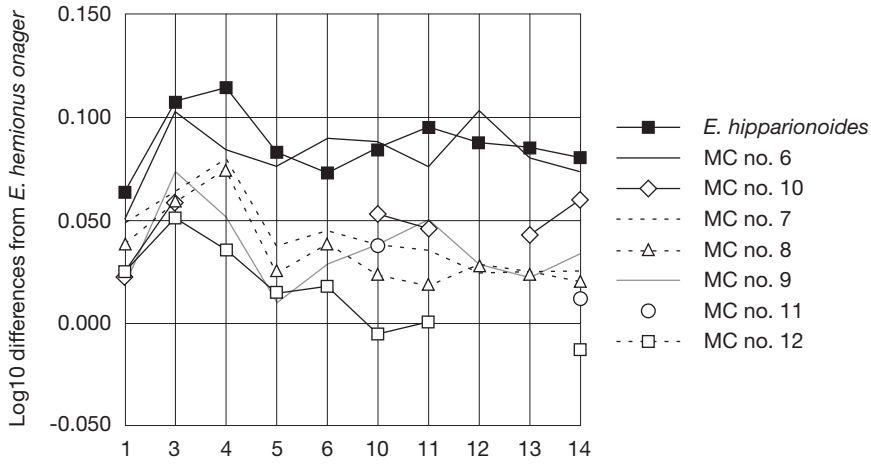

FIG. 11. — Ratio diagram comparing MT of *Equus* (*S.*) *ovodovi* n. sp., Proskuriakova cave (Khakassia, southwestern Siberia) to the mean (n = 6-9) of MT of *E. hipparionoides* Vekua, 1962 from Akhalkalaki. Numbers (1, 3, 4, etc.) refer to the measurements listed in the caption of Table 6.

plicated enamel and a long protocone. Nothing is known about the rest of the skeleton.

In this context of finding supposedly extinct groups in relatively recent deposits, another recent discovery is very interesting. Fossils belonging to the bovid genus *Soergelia* have never been found later than early Pleistocene except at Taradanov Iar, on the right bank of the river Ob (south-east of Western Siberia). Various bones from Taradanov Iar have been dated at > 45 000 BP to 80 000-100 000 BP (Vasiliev & Orlova 2006).

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