



Evolution / Évolution

**Sussemionus**, a new subgenus of *Equus* (Perissodactyla, Mammalia)*Sussemionus*, un nouveau sous-genre d'*Equus* (Perissodactyla, Mammalia)

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## ABSTRACT

The new subgenus of *Equus*, *Sussemionus*, is defined by peculiar dental characters so far unknown, or exceptional in late Pleistocene and extant *Equus*; it was in consequence assumed to be restricted to the early and middle Pleistocene. During that period, it was highly successful, ranging from North America to Ethiopia, and included dry-adapted (*E. granatensis*-like) and more humid-adapted (*E. colimensis*-like) species. Recent molecular and osteological analyses concurred to prove its survival until ca 45 KYBP in Khakassia, southwest Siberia, Russia.

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## R É S U M É

Le nouveau sous-genre d'*Equus*, *Sussemionus*, très répandu au cours du Pléistocène moyen, est défini par l'originalité de ses caractères dentaires : plis caballins à large base, parfois multiples ou renflés, protocones parfois très courts ; développement extraordinaire des stylides, métaconides très allongés et parfois bilobés, sillons linguaux à peine marqués, sillons vestibulaires parfois très profonds, même sur les prémolaires. De telles morphologies, rarissimes chez les *Equus* actuels, étaient jusqu'à présent inconnues au Pléistocène supérieur ; on supposait donc le groupe éteint depuis le Pléistocène moyen. De récentes études moléculaires et paléontologiques ont montré que ce n'était pas le cas : une espèce appartenant à ce sous-genre est en effet documentée dans une grotte du sud-ouest de la Sibérie ; le matériel date d'environ 45 000 ans.

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## 1. Description

The term “Sussemionus” was first used in an informal way to group early and middle Pleistocene equid species with characteristic teeth [1]. Discoveries of new data, both paleontological and molecular [2,3], recommend a formal description and extend the temporal range of this group.

*Sussemionus*, n. subgenus.

Derivatio nominis:

In reference to the mixture of osteological characters, some of which are observed (namely) in the fossil equids

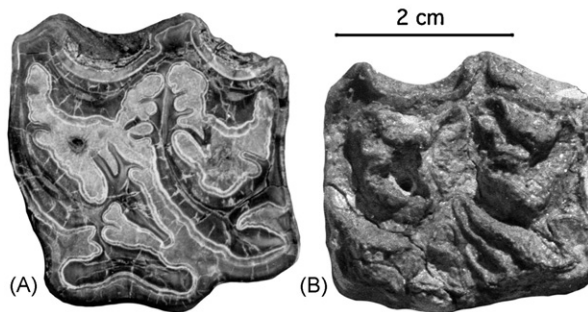
from Süssenborn, Germany, and some others in extant hemionus.

Diagnosis:

Upper cheek teeth (Fig. 1) with peculiar plis caballin: multiple and/or with a very large base (Fig. 1A, Fig. 4A, Fig. 6), sometimes club-shaped (Fig. 1B). Such morphologies are unknown in extant species of *Equus* and in *Allohippus*. The enamel is often very plicated and the postprotoconal valley may be very deep. Protocones may be extremely short.

On the lower cheek teeth (Fig. 2), the occurrence of stylids, sometimes isolated, is remarkable. Isolated ectostylids are characteristic of late African hipparions but exceptional in extant *Equus*. Plis protostylids on P/2

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**Fig. 1.** Upper premolars of *Sussemionus*. A. *E. cf. verae*, section of PIN 2998-243, Chukochya, loc. 26. B. *E. hipparionoides*, P4/ of Akha 100, Akhalkalaki. Illustrations of these teeth were also published in [1].

(characteristic of extant Grevy's zebras [4]) occur frequently (Fig. 2A). Plis protostylids on P/3-M/3 may be extremely developed (Fig. 2B) as well as plis hypostylids (Fig. 2C); the latter may even be isolated on M/3. The shape of the double knot of many lower premolars resembles extant hemiones, sometimes in an extreme, caricatural way: the metaconid is elongated, sometimes bilobated, the lingual valley is shallow, at times nearly absent (Fig. 2D and E). Unlike Hemiones, another particularity is the frequency of very deep vestibular valleys, on molars and even on some premolars (Fig. 2F). But the depth of the vestibular valley is very variable: associated teeth may have very deep and very shallow valleys (Fig. 2G). Both features are uncommon in extant species.

Type species: *E. coliemensis* Lazarev 1980 [5].

Origin: Kolyma, NE Siberia, Russia.

Age: late Early Pleistocene.

### 1.1. Description of the type material

Although not perfectly preserved, the skull IA 1741, type of *E. coliemensis* (Fig. 3, Table 1) belongs to *Equus*. The

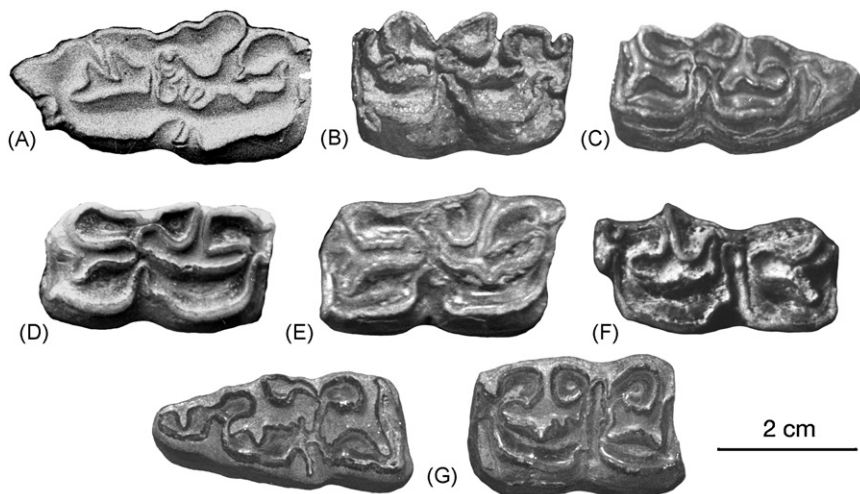
**Table 1**

Measurements in mm of *E. coliemensis* skull. The numerotation of the measurements refers to the system illustrated on the web site [www.vera-eisenmann.com](http://www.vera-eisenmann.com). Approximate dimensions between brackets.

		Chukochya <i>E. coliemensis</i> IA 1741
1	Basilar length	538
2	Overall palatal length	282
2–5	Palatal length s.s.	140
3	Vomerine length	[133]
4	Post-vomerine length	[123]
5	Muzzle length	[140]
6	Diastema	112
7	P2/-P4 length	[101]
7bis	M1/-M2/ length	82
8	P2/-M3/ length	[180]
10	Greatest choanal breadth	53
10bis	Least choanal breadth	42
11	Facial breadth	164
12	Length from Basion to anterior borders of P2/	[398]
13	Frontal breadth	230
14	Bizygomatic breadth	210
15	Cranial breadth	105
16	Breadth of supra-occipital crest	53
17	Muzzle breadth at posterior borders of I3/	70
17bis	Least muzzle breadth (between the crests)	55
18	Greatest length	590
19	Height of the infra-ocular bar	11
20	Height of the external auditory meatus	16.5
21	Antero-posterior orbital diameter	62
22	Dorso-ventral orbital diameter	58.5
23	Anterior ocular line	440
24	Posterior ocular line	225
29	Breadth at the occipital condyles	90
30	Breadth of foramen magnum	34

skull is as large as a Grevy's Zebra but with proportions more like Hemiones [6].

The upper cheek teeth of the type are plicated and have plis caballins wide at their base (Fig. 4A, Table 2). There are



**Fig. 2.** Lower cheek teeth of *Sussemionus*. A. P/2 of *E. verae*, Chukochya loc. 21, PIN 835-123. B. P/4 of *E. hipparionoides*, Akhalkalaki, no. 99. C. M/3 of *E. cf. verae*, Yukon, Old Crow loc. 9, NMC 32165. D. P/3 of *E. granatensis*, Venta Micena, VM 84/C3-B9-12. E. P/3 of *E. verae*, Krestovka, PIN 3020-47 (851-74/8). F. P/3 of *E. suessenbornensis*, Süssenborn, S 9281. G. Associated M/3 and M/1 of *E. verae*, Chukochya loc. 37, PIN 3100-333. Illustrations of B, C, D, E, and G were also published in [1].

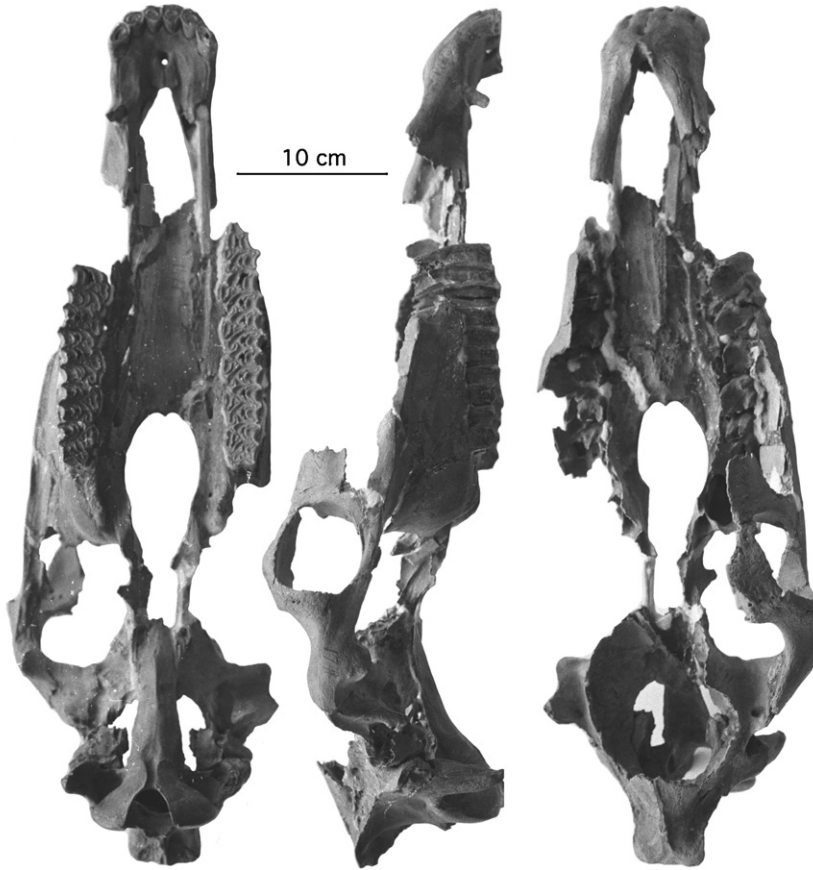


Fig. 3. *E. coliemensis* skull, IA 1741. From left to right: ventral view, profile, dorsal view.

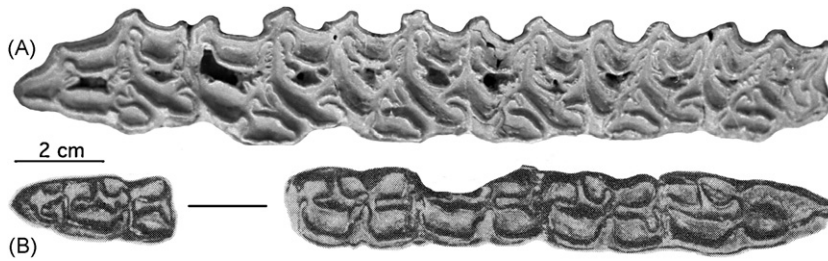


Fig. 4. *E. coliemensis*. A. Left P2/-M3/ of the type skull IA 1741. B. Right P2-M/1 and M/3 of IA 1721. Illustrations of these teeth were also published in [1].



Fig. 5. Lower cheek teeth series tentatively referred to *Sussemionus*. A. AMNH 116502, Dry Mountains, Arizona, adapted from Azzaroli and Voorhies 1993. B. Lost Chicken, Alaska. Illustrations of these teeth were also published in [1].

**Table 2**  
Measurements in mm of some upper cheek teeth dentitions of various *Sussemionus* species. L: occlusal length of the protocone. Prot L: occlusal length of the protocone. W: occlusal width. Ht: height of the crown. Additional data may be found on [www.vera-eisenmann.com](http://www.vera-eisenmann.com).

	P2/			P3/			P4/			Ht
	L	Prot L	W	L	Prot L	W	L	Prot L	W	
<i>E. süssenbornensis</i>	44.2	11.4	30	33.6	12.6	30	35.4	15	33	
<i>E. süssenbornensis</i>		8.5	29	31	13.5	33	31.5	15	33	
<i>E. cf. süssenbornensis</i>				36	14	32	30.4	12	32	26
<i>E. coliemensis</i>	39.7	8.3	27.2	32	12.7	30.5	29.6	12.2	29.6	
<i>E. granatensis</i>	38.5	8	27	29	9	27	28	11	28	
<i>E. hipparionoides</i>				29	[7.5]	28	25	6.0	26	
	M1/			M2/			M3/			Ht
	L	Prot L	W	L	Prot L	W	L	Prot L	W	
<i>E. süssenbornensis</i>	30.4	12.5	31.7	31	13.5	28.7	30	14.2	25.2	
<i>E. süssenbornensis</i>	28	14	30	29	13.1	30	33.9	16.6	27.2	
<i>E. cf. süssenbornensis</i>	27.3	11.7	30	29.5	14.5	30.5	34	15	26	27
<i>E. coliemensis</i>	26.6	11.4	27.9	26.2	12.3	26.1	28.4	12.4	24.8	
<i>E. granatensis</i>	26	8.5	27	27	11	27	26.5	8	22.5	
<i>E. hipparionoides</i>	26	7.0	24	26	10	23.5				43

no associated lower cheek teeth but some were referred to *E. coliemensis* by Lazarev (Fig. 4B, Table 3). On the lower cheek teeth, the enamel is plicated and the hypostylid very developed on M/3.

Other species already referred to *Sussemionus* – now the new subgenus (see description and illustrations in [1]):

- *E. süssenbornensis* (Süssenborn, Germany), *E. cf. süssenbornensis* (Akhalkalaki, Georgia; Cueva Victoria, Spain), *E. verae* (NE Siberia), *E. cf. verae* (Alaska, Yukon). The metapodials are large and robust;
- *E. granatensis* (Venta Micena, Spain), *E. hipparionoides* of Akhalkalaki, the very poorly defined *E. altidens* and the slightly better founded *E. marxi* of Süssenborn. Teeth and/or metapodials of this group are found in the British Forest Beds (Trimingham), and in Spain (Cueva Victoria, Cullar de Baza, Huescar). The metapodials are slender.

## 1.2. New data

Orlando et al. [2] analysed some late Pleistocene samples from Proskuriakova cave (Khakassia, southwest Siberia, Russia) believed to belong to a kind of *E. hydruntinus*. Unexpectedly, instead of an *E. hydruntinus* or some hemione, they found a new clade of *Equus* with no extant relative, and distinct from *E. hydruntinus*.

A more detailed osteological study of the fossils from Proskuriakova cave confirmed the biomolecular findings: the *Equus* from Proskuriakova is neither an hydruntine nor an hemione; it shows dental features of *Sussemionus* [3] (description in press). In the course of the same study, it was discovered that another late Pleistocene *Equus*, believed to belong to a hydruntine, should also be referred to *Sussemionus*. It was excavated at the Mousterian site of Tsopi, Georgia.

## 2. Discussion and conclusions

### 2.1. Origin of *Sussemionus*

In the late Blancan of Arizona, there is a very small species [7] reminding of *Sussemionus* (Fig. 5A). Another, much larger species, with marked *Sussemionus* characters (Fig. 5B) was found in Alaska inside probably Pliocene deposits (more than 2 Ma, A. Sher pers. comm.). It seems thus that, like most equids, *Sussemionus* originated in North America.

### 2.2. Geographical and chronological ranges

The subgenus *Sussemionus* was very successful, judging by its geographical distribution from Arizona to possibly Ethiopia (Fig. 6), and its chronological range from ca 2 Ma to about 45–50 ka (Proskuriakova cave).

### 2.3. Environments

Dental and skeletal morphologies of extant *Equus* allow one to make assumptions as to the environment of fossil equids. Usually, a simple enamel is observed in species feeding on hard vegetation, while a more complicated

**Table 3**

Measurements in mm of some lower cheek teeth dentitions of various *Sussemionus* species. L: occlusal length. L DN: occlusal length of the double knot. L postf: occlusal length of the postflexid. W: occlusal width. Ht: height of the crown. Approximate dimensions between brackets. Additional data may be found on [www.vera-eisenmann.com](http://www.vera-eisenmann.com).

			P/2					P/3				
			L	L DN	L postf	W	Ht	L	L DN	L postf	W	Ht
<i>E. süssenbornensis</i>	Süssenborn	S 9281	39	17.7	17	18	38	35	23	13	19.2	46
<i>E. cf. süssenbornensis</i>	Akhalkalaki	Akha 1	42	16.7	19	16	44	35	20	17.5	18	55
<i>E. verae</i>	Chukochya, loc. 21	PIN 835-123	41	20.5	18	18.7	[65]	34	20.5	17.5	22	70
<i>E. granatensis</i>	Venta Micena	VM 84 C3.B9.12	36.6	14.2	17.4	16		32.7	19.2	16.8	17.2	
<i>E. hipparionoides</i>	Akhalkalaki	Akha 99	37			17	23.5	33	18.3	14	17	21
			P/4					M/1				
			L	L DN	L postf	W	Ht	L	L DN	L postf	W	Ht
<i>E. süssenbornensis</i>	Süssenborn	S 9281	33	21	11.1	20	51	30	17.5	11	16	44
<i>E. cf. süssenbornensis</i>	Akhalkalaki	Akha 1	33	18.5	15.3	18	[67]	30	17	11	17	
<i>E. verae</i>	Chukochya, loc. 21	PIN 835-123	32.5	20	16	22	77	30	18.3	16	19	67
<i>E. granatensis</i>	Venta Micena	VM 84 C3.B9.12	29.5	18	13.2	16.8		28.4	16.8	10.2	14.5	
<i>E. hipparionoides</i>	Akhalkalaki	Akha 99	30.5	16.1	12.8	16.2	28	28.3	16.1	8.7	16.8	20
			M/2					M/3				
			L	L DN	L postf	W	Ht	L	L DN	L postf	W	Ht
<i>E. süssenbornensis</i>	Süssenborn	S 9281	30	17.2	11	16	48	35	14.5	16.2	50	
<i>E. cf. süssenbornensis</i>	Akhalkalaki	Akha 1	31.7	16.5	11	16	50	37	16		15	45
<i>E. verae</i>	Chukochya, loc. 21	PIN 835-123	29.5	17	14	20	67	35	15.5	14	17	69
<i>E. granatensis</i>	Venta Micena	VM 84 C3.B9.12	28	15.6	8.9	14.3		33	15.2	9.3	13.7	
<i>E. hipparionoides</i>	Akhalkalaki	Akha 99	29	14.2	9	14.7	25					

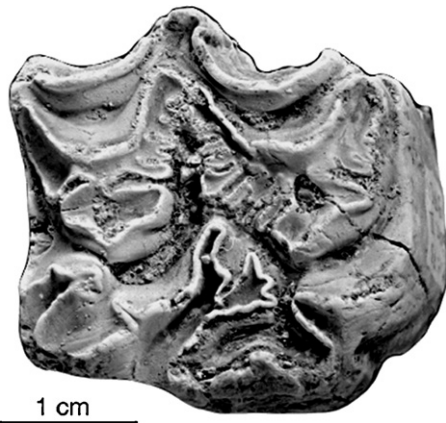


Fig. 6. Upper premolar from the Acheulean of Gomboré II (Melka Kunturé, Ethiopia), 73–1978. Illustration also published in [1].

enamel is found in species feeding on a softer one [8, p. 98]. Slenderness and cursorial proportions are linked to open landscapes, while robustness and 'graviportal' proportions are observed in opposite cases [9].

The extremely rich collection of equids from Venta Micena (Spain) include no other species than *E. granatensis*. This equid had a simple enamel, slender limb bones, and cursorial proportions [10]. On the other hand, in Chukochya, from where *E. coliemensis* and *E. verae* (possibly a junior synonym) were described, there is no evidence of a slender species. *E. coliemensis* had a very plicated enamel and robust limb bones.

Things are more complicated for the other findings where both slender and robust equids were excavated: the time encompassed by Süssenborn deposits is very long; Cueva Victoria may have been equally heterogeneous. It seems that Akhalkalaki is the only place where a robust form (*E. cf. suessenbornensis*) and a slender one

(*E. hipparionoides*) have coexisted, at least in a broad paleontological sense.

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