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Véra EISENMANN & Sergei K. VASILIEV

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Discovery of two crania of *Equus* (*Sussemionus*) *ovodovi* Eisenmann & Vasiliev, 2011 (Mammalia, Perissodactyla) from the Late Pleistocene of Khakassia, Russia

Véra EISENMANN
Centre de recherche en paléontologie — Paris (CR2P), CNRS, MNHN, Sorbonne Université, Département Origines et Évolution, Muséum national d'Histoire naturelle, case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
vera.eisenmann@orange.fr

Sergei K. VASILIEV
Institute of Archaeology and Ethnography, Siberian Branch of the Russian Academy of Sciences, 630090 Novosibirsk (Russia)
sergei.vasiliev.iaet@gmail.com

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ABSTRACT
Two crania, 40 000 years old, collected inside the Fanatics Cave in Khakassia (Southern Siberia) have improved our knowledge of *Equus ovodovi* Eisenmann & Vasiliev, 2011 anatomy. *Equus ovodovi* belongs to the subgenus *Sussemionus* Eisenmann, 2010 all other members of which went extinct during the Middle Pleistocene. By cranial morphology as well as by other anatomical and molecular characters, *E. ovodovi* differs from all other *Equus* species and in particular from *E. hydruntinus* Regàlia, 1907 to which it was initially referred. *E. ovodovi* has narrower choanae and supra-occipital crest and a longer muzzle. By these features it resembles *E. vekuae* Eisenmann, 2022 from the Early Pleistocene of Dmanisi, Georgia, another species belonging or closely related to the subgenus *Sussemionus*. It differs from it, however, by the position of hormion relative to basion and staphylion.

KEY WORDS
Late Pleistocene, Mammalia, Perissodactyla, *Equus*, Siberia, Khakassia, craniometry.

RÉSUMÉ
*Découverte de deux crânes d'*Equus *(*Sussemionus*)* ovodovi *Eisenmann & Vasiliev, 2011 (Mammalia, Perissodactyla) du Pléistocène supérieur de Khakassie, Russie.*
Deux crânes, vieux de 40 000 ans, provenant de la Grotte des Fanatiques, en Khakassie (Sibérie méridionale, Russie), sont venus améliorer notre connaissance de l'anatomie d'*Equus ovodovi* Eisenmann & Vasiliev, 2011. Cette espèce appartient au sous-genre *Sussemionus* Eisenmann, 2010 dont tous les autres membres ont disparu depuis le Pléistocène moyen. Par la morphologie crânienne comme par d'autres caractères anatomiques et moléculaires, *E. ovodovi* diffère de tous les autres *Equus*, en particulier d'*E. hydruntinus* Regàlia, 1907 avec lequel il fut initialement confondu : *E. ovodovi* présente une protubérance occipitale externe et des choanes plus étroites et un museau plus long. Par ces caractères, *E. ovodovi* ressemble à *E. vekuae* Eisenmann, 2022 (Pléistocène inférieur de Dmanisi en Géorgie) – une autre espèce appartenant ou apparentée aux sussemiones – mais en diffère par la position de l'hormion par rapport au basion et au staphylion. *Equus vekuae* est une autre espèce appartenant ou apparentée aux sussemiones.

MOTS CLÉS
Pléistocène supérieur, Mammalia, Perissodactyla, *Equus*, Sibérie, Khakassie, craniométrie.

Fig. 1. — *Equus* (*Sussemionus*) *ovodovi* Eisenmann & Vasiliev, 2011 cranium IAET-1: **A**, profile; **B**, dorsal view; **C**, ventral view. Scale bar: 10 cm. Photos: S. K. Vasiliev.

INTRODUCTION

Equus ovodovi Eisenmann & Vasiliev, 2011 was a paleontological surprise. DNA analyses of supposed *E. hydruntinus* Regàlia, 1907 fossils from southern Siberia led instead to the discovery of a new clade of *Equus* Linnaeus, 1758, with no extant relative, and distinct from *E. hydruntinus* (Orlando *et al.* 2009). Reexamination of the teeth and metapodials confirmed that they did not belong to *E. hydruntinus*, instead its characters pointing to a relationship with members of the subgenus *Sussemionus* Eisenmann 2010 (Eisenmann & Vasiliev 2011). The species referred to *Sussemionus* were supposed extinct since the

FIG. 2. — *Equus* (*Sussemionus*) *ovodovi* Eisenmann & Vasiliev, 2011 cranium IAET-2: **A**, ventral view; **B**, dorsal view; **C**, profile. Scale bar: 10 cm. Photos: S. K. Vasiliev.

Middle Pleistocene, while the studied Siberian fossils belong to a new species, *E.* (*Sussemionus*) *ovodovi* Eisenmann & Vasiliev, 2011 are dated *c.* 40 000 year old. The material included only upper and lower cheek teeth and some limb bones.

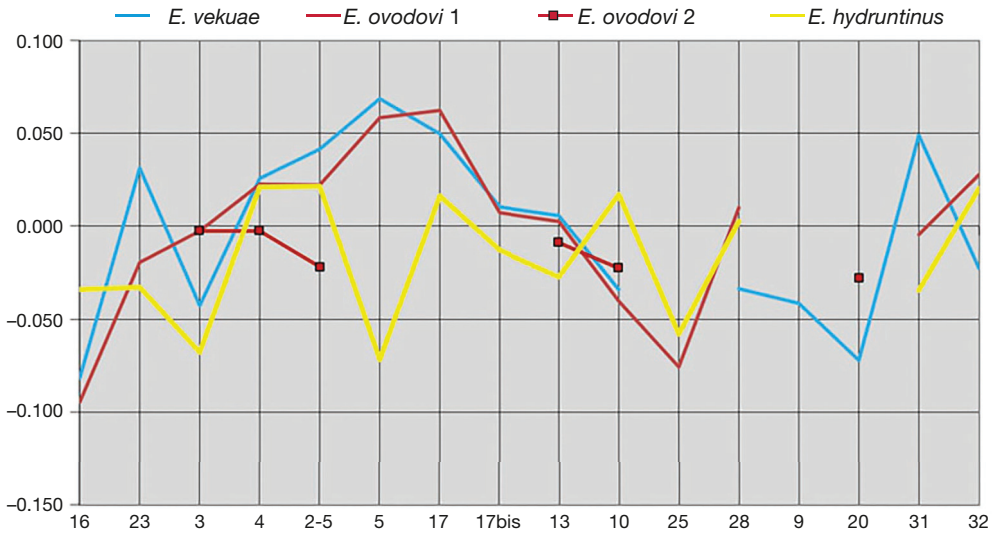
Two crania recently found in another close locality of Khakassia – the vertical Fanatics trap-Cave – by paleozoologist N.D. Ovodov in 1983 allow us to better understand the anatomy of this species and its differences compared to other species included in the subgenus *Sussemionus*. The trap-cave is located in the south-east of Western Siberia, in the central part of Khakassia (53°19'N, 90°20'E). The bones of Holocene mammals (mainly hares, rodents, and martens) were collected from the surface layer, while the remains of Pleistocene-aged animals lay below. They include:

– Five skeletons of cave hyenas (*Crocuta spelaea* Goldfuss, 1823) (Vasiliev & Ovodov 2024).

– Incomplete skeletons of a wolf (*Canis lupus* Linnaeus, 1758) and a wolverine (*Gulo gulo* Linnaeus, 1758), as well as individual bones and skulls from three and two individuals, respectively,

TABLE 1. — Measurements (in mm) of *Equus* (*Sussemionus*) *ovodovi* Eisenmann & Vasiliev, 2011 crania (Table) and Simpson's ratio diagrams (Figure). Measures: **2**-**5**, palatal length *sensu stricto*; **3**, vomerine length; **4**, postvomerine length; **5**, muzzle length; **9**, length of choanae; **10**, greatest choanal breadth; **13**, frontal breadth; **16**, breadth of the supra-occipital (lambdoidal) crest; **17**, muzzle breadth at the posterior borders of I3; **17bis**, least muzzle breadth between the crests; **20**, height of the external auditive meatus; **23**, anterior ocular line; **25**, facial height in front of P2; **28**, cranial height; **31**, length of the naso-incisival notch; **32**, cheek length.

		Dm53/59.B1gl192			EBK Ba2 C1(B) 384
		Dmanisi	Fanatics	Fanatics	Emine Bair Khosar
	Measure number	*E. vekuae*	*E. ovodovi* 1	*E. ovodovi* 2	*E. hydruntinus*
Measurements					
57.2	16	47.4	46	–	52.9
345.1	23	371	330	–	320
118.7	3	107.6	118	118	101.5
101.8	4	108	107.2	101.2	106.8
113.6	2-5	125	119.6	108	119.3
103.8	5	121.6	118.7	–	88
55.3	17	62	63.8	–	57.4
41.5	17bis	42.5	42.2	–	40.3
195.9	13	198.4	197	192	184
47.6	10	44	43.4	45.2	49.5
101.5	25	–	85.3	–	88.8
89.5	28	82.8	91.6	–	90
62.5	9	56.8	–	–	–
14.4	20	12.2	–	13.5	–
143.0	31	160	141.5	–	132.1
162.3	32	154	173	–	170
433.4	1	–	459	–	409
Log10 E.h.o.					
1.757	16	–0.082	–0.095	–	–0.034
2.538	23	0.031	–0.019	–	–0.033
2.074	3	–0.043	–0.003	–0.003	–0.068
2.008	4	0.026	0.022	–0.003	0.021
2.055	2-5	0.042	0.022	–0.022	0.021
2.016	5	0.069	0.058	–	–0.072
1.743	17	0.050	0.062	–	0.016
1.618	17bis	0.010	0.007	–	–0.013
2.292	13	0.006	0.002	–0.009	–0.027
1.678	10	–0.034	–0.040	–0.022	0.017
2.006	25	–	–0.076	–	–0.058
1.952	28	–0.034	0.010	–	0.002
1.796	9	–0.042	–	–	–
1.158	20	–0.072	–	–0.028	–
2.155	31	0.049	–0.005	–	–0.034
2.210	32	–0.023	0.028	–	0.020



– Remains of *Martes zibellina* (Linnaeus, 1758), *Putorius eversmanni* (Lesson, 1827), *Vulpes vulpes* (Linnaeus, 1758) and *Vulpes corsac* (Linnaeus, 1768),

– Remains from three individuals of *Bison priscus* (Bojanus, 1827), including a lower jaws, a skull fragment, and several limb bones.

Three radiocarbon dates have been obtained from bone remains of Fanatics Cave. For two individuals of cave hyenas, they were 42 140 ± 330 and 37 350 ± 448 BP, and an exorbitant dating (> 50 000 years old) was obtained for a humerus of the Baikal yak *Poehagus mutus baicalensis* Verestchagin, 1954 (Vasiliev *et al.* 2020).

MATERIAL AND METHODS

Each of the *E. ovodovi* crania disintegrated into several dozen fragments during their extraction but in three places on cranium IAET-1 and in two places on cranium IAET-2, the connecting areas between the occipital and anterior parts of the skull were preserved, which allowed them to be anatomically reliably connected. After a long and minutious reconstruction, it was possible to restore both (Figs 1; 2). They were measured according to the method described by Eisenmann (1986).

Their size and proportions (Tables 1; 2) were compared by Simpson's diagrams with *E. hemionus onager* Boddaert, 1785 as reference to other crania, in particular to the perfectly preserved cranium of *E. hydruntinus* from Ukraine published by Van Asperen *et al.* (2012).

Dimensions of the upper cheek teeth were compared to another sample of *E. ovodovi* teeth found in the Logovo hyenae Cave, Altai (Appendix 1).

ABBREVIATIONS

I	incisor;
M	molar;
MIS	Marine Isotopic Stage;
P	premolar;
x	mean;
min	minimum;
max	maximum;
s	standard deviation;
v	coefficient of variation.

RESULTS

As expected, *E. ovodovi* crania do not resemble *E. hydruntinus* nor any extant species (Eisenmann 2022: figs 28, 42) though such narrow supra-occipital crests occur in extant and fossil horses (Eisenmann 2022: figs 58, 62).

From *E. hydruntinus* they differ mainly (Table 1) by the smaller breadth of their supra-occipital crest (measure 16), their longer muzzle (measure 5) and their relatively narrow choanae (measure 10).

Surprisingly, they are rather similar to the Early Pleistocene *E. vekuae* Eisenmann, 2022 from Dmanisi (Eisenmann 2022: 57) apart from their relatively shorter post-vomerine length (measure 4) and their relatively deeper naso-incisival notch (measure 32).

The teeth are similar to that of the *E. ovodovi* type and other specimens from Proskuriakova, and differ from *E. hydruntinus* by longer protocones (Eisenmann & Vasiliev 2011).

TABLE 2. — Measurements in mm of upper cheek teeth of *Equus* (*Sussemionus*) *ovodovi* Eisenmann & Vasiliev, 2011 from Fanatics Cave, Khakassiaw (Institute of Archaeology and Ethnography, Novosibirsk).

Measure description	Measure number	IAET-1	IAET-2
Basilar length	1	459	452
Palatal length	2	235	231
Palatal length sensu stricto	2-5	119	106.7
Vomerine length	3	118	118
Postvomerine length	4	107.2	101.2
Muzzle length	5	116	–
Diastema length	6	92	–
Length of premalers (P2-P43)	7	88.3	85.1
Length of molars (M1-M3)	7 bis	72.5	72
Length of cheek teeth (P2-M3)	8	159	155
Length of choanae	9	–	–
Greatest choanal breadth	10	43.4	45.2
Frontal breadth	13	197	192
Bizygomatic breadth	14	168.2	–
Cranial breadth	15	109	–
Breadth of the supra-occipital (lambdoidal) crest	16	46	–
Muzzle breadth at the posterior borders of I3	17	63.8	–
Least muzzle breadth between the crests	17bis	42.2	–
Vertex length	18	508	–
Infra-orbital height	19	9	9.2
Height of the external auditive meatus	20	–	13.5
Antero-posterior diameter of the orbit	21	58.5	63
Dorso-ventral diameter of the orbit	22	55.5	–
Anterior ocular line	23	330	–
Posterior ocular line	24	175.3	–
Facial height in front of P2	25	85.3	–
Facial height between P4 and M1	26	132.8	–
Cranial height	28	91.6	89.5
Breadth of the occipital condyles	29	81	73
Breadth of the foramen magnum	30	34	32
Length of the naso-incisival notch	31	141.5	–
Cheek length	32	173	–

DISCUSSION

The fossils from the Fanatics Cave have the same localization (Khakassia) as those of Proskuriakova holotype and are about the same age (*c.* 40 000 years). But the range of *E. ovodovi* was larger both in space and time. Several fossils have been found in the Middle Pleistocene (MIS-7-8) slightly north of Novosibirsk and in the Late Pleistocene (MIS-3 and MIS-5). The range of *E. ovodovi* included not only the south of Western and Central Siberia (Plasteeva *et al.* 2019), but extended up to northeastern China (Yuan *et al.* 2019). It was in this region that during the excavations of several monuments of the Shan culture, the most recent (3.5-4 thousand years ago) remains of *E. ovodovi* were found. In addition to the morphology of the remains themselves, this was also confirmed by the results of biomolecular studies (Cai *et al.* 2022).

In the Old World, the subgenus *Sussemionus* is documented by robust species at least from the middle Olyorian (*c.* 600 000 year) in Northeastern Siberia by *E. verae*, and slightly later by *E. coliemensis* Lazarev, 1980. Slender "pseudo-hydruntines" species originally comprised in the subgenus

may perhaps be a distinct group (Eisenmann 2022) to which belongs the Early Pleistocene *E. vekuae.* Granted that resemblances between *E. vekuae* and *E. ovodovi* are limited to a few cranial proportions, it seems yet worth to mention them.

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APPENDIX 1. — Measures in mm of upper cheek teeth of *Equus* (*Sussemionus*) *ovodovi* Eisenmann & Vasiliev, 2011.

		***E. ovodovi*, Fanatic Cave**			
		IAET-1		**IAET-2**	
		sin	**dex**	**sin**	**dex**
P2/-M3/ alveloar length		160	159.7	157.5	157
P2/-M3/ occlusal length		159.2	159	154.6	155
P2/	occlusal length	35	36	34.3	33.5
	protocone length	8.2	7.8	7.1	7.1
	occlusal breadth	23.3	24.2	23.7	23.1
	crown height		33	45	46
	protocone index	23.43	21.67	20.7	21.19
P3/	occlusal length	27	26.8	26.2	26.9
	protocone length	10.4	10.5	8.7	9
	occlusal breadth	25.1	25.8	24.5	24.5
	crown height		34		53
	protocone index	38.52	39.18	33.21	33.46
P4/	occlusal length	26	26	26	25.3
	protocone length	11.3	11.4	9.9	9.2
	occlusal breadth	25.9	26.5	25.1	25.4
	crown height				
	protocone index	43.46	43.85	38.08	36.36
M1/	occlusal length	23	24	22.8	22.5
	protocone length	12.1	11.9	8.6	8.2
	occlusal breadth	25.6	25.5	25	24.8
	crown height		45		54
	protocone index	52.61	49.58	37.72	36.44
M2/	occlusal length	23.7	23.3	23	23.6
	protocone length	13	12.6	10	9.8
	occlusal breadth	25.5	25.4	24.6	24.7
	crown height		46		56
	protocone index	54.85	54.1	43.48	41.53
M3/	occlusal length	27	26.7	26.6	26
	protocone length	12	12.3	10.8	10.4
	occlusal breadth	23	23.7	22.2	22.2
	crown height		49		60
	protocone index	44.44	46.07	40.6	40

	P2, Fanatic Cave					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	4	34.7	33.5	36	1.06	3.05
protocone length	4	7.55	7.1	8.2	0.54	7.15
occlusal breadth	4	23.58	23.1	24.2	0.49	2.08
crown height	3	41.33	33	46	7.23	17.49
protocone index	4	21.75	20.7	23.43	1.19	5.47

	P2, Logovo hyaeny Cave, mid-wear					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	20	36.14	32.5	40.8	2.23	0.5
protocone length	28	7.84	6.3	9.8	1.04	0.2
occlusal breadth	27	24.52	20.4	27.7	1.36	0.26
crown height	28	35.61	26	48	6.05	1.14
protocone index	20	21.68	15.9	26.6	2.81	0.63

	P3-P4, Fanatic Cave					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	8	26.28	25.3	27	0.58	2.21
protocone length	8	10.05	8.7	11.4	1.03	10.25
occlusal breadth	8	25.35	24.5	26.5	0.7	2.76
crown height	2	43.5	34	53	13.44	30.90
protocone index	8	38.27	33.21	43.85	3.99	10.43

	P3-P4, Logovo hyaeny Cave, mid-wear					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	73	27.3	25	29.6	1	0.12
protocone length	74	10.71	8	13.3	1.02	0.12
occlusal breadth	67	26.74	24	29.5	1.33	0.16
crown height	74	45.08	26	61	7.99	0.93
protocone index	72	39.49	30.5	51.2	3.56	0.42

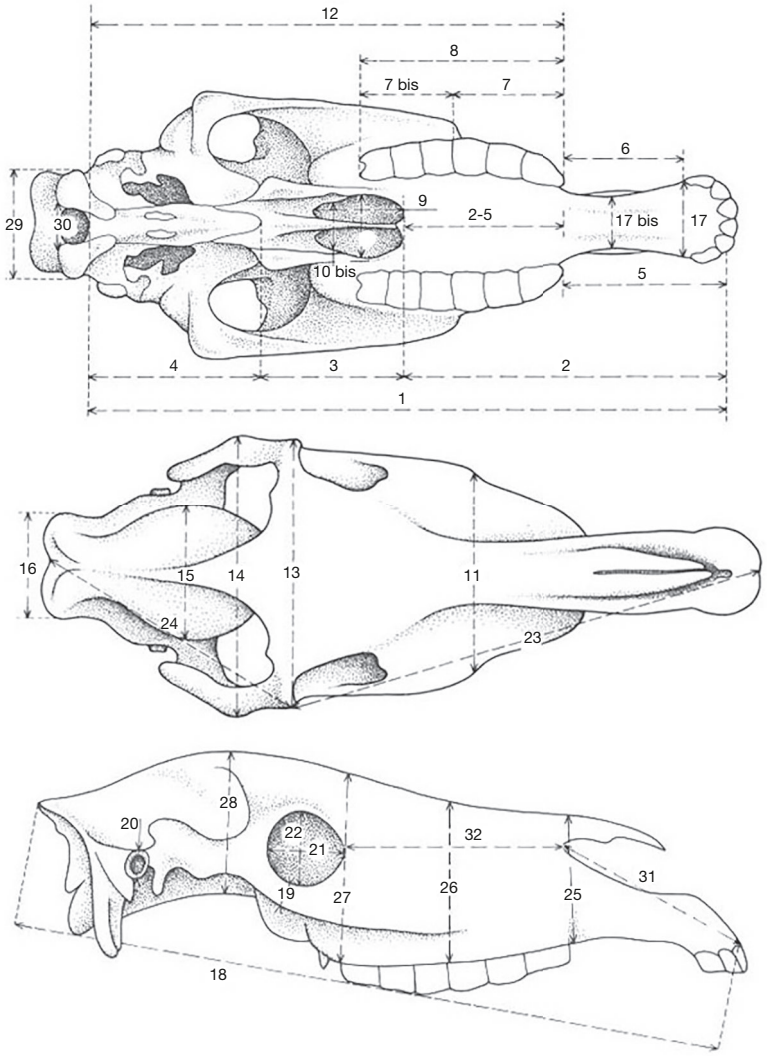
	M1-M2, Fanatic Cave					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	8	23.24	22.5	24	0.5	2.15
protocone length	8	10.78	8.2	13	1.86	17.25
occlusal breadth	8	25.14	24.6	25.6	0.41	1.63
crown height	4	50.25	45	56	5.56	11.06
protocone index	8	46.29	36.44	54.85	7.42	16.03

	M1-M2, Logovo hyaeny Cave, mid-wear					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	112	24.3	21.5	26.7	1.14	0.11
protocone length	120	11.19	8.5	13.5	1.06	0.1
occlusal breadth	115	26.36	23.6	29.7	1.21	0.11
crown height	120	45.07	29	62	8.91	0.81
protocone index	111	46.16	33.9	57.5	4.3	0.41

	M3, Fanatic Cave					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	4	26.58	26	27	0.42	1.58
protocone length	4	11.38	10.4	12.3	0.92	8.08
occlusal breadth	4	22.78	22.2	23.7	0.72	3.16
crown height	2	54.5	49	60	7.78	14.28
protocone index	4	42.78	40	46.07	2.95	6.90

	M3, Logovo hyaeny Cave, mid-wear					
Equus ovodovi	**n**	**x**	**min**	**max**	**s**	**v**
occlusal length	52	27.68	24.5	32	1.51	0.21
protocone length	56	12.8	10.4	15	1.17	0.16
occlusal breadth	55	23.47	21.2	25.9	0.97	0.13
crown height	58	45.02	28	63	9.53	1.25
protocone index	52	46.55	39	59.2	4.71	0.65

Appendix 2. — System of measurements of *Equus* Linnaeus, 1758 crania, occlusal, dorsal and profile views (from top to bottom).



1, Basilar length;
2, Overall palatal length;
2-**5**, Palatal length *sensu stricto*;
3, Vomerine length;
4, Post-vomerine length;
5, Muzzle length;
6, Diastema;
7, Premolar length (P2-P4);
7 bis, Molar length (M1M3);
8, Length of cheek teeth (P2M3);
9, Length of choanae;
10, Greatest choanal breadth;
10 bis, Least choanal breadth;
12, Length from Basion to anterior borders of P2;
17, Muzzle breadth at the posterior borders of I3;
17 bis, Least muzzle breadth (between the crests);
29, Breadth at the occipital condyles;
30, Breadth of foramen magnum.

11, Facial breadth;
13, Frontal breadth;
14, Bizygomatic breadth;
15, Cranial breadth;
16, Breadth of the supra-occipital crest;
23, Anterior ocular line;
24, Posterior ocular line.

18, Greatest length;
19, Height of the infra-orbital bar;
20, Height of the external auditive meatus;
21, Antero-posterior orbital diameter;
22, Dorso-ventral orbital diameter;
25, Facial height in front of P2;
26, Facial height between P4 and M1;
27, Facial height behind M3;
28, Cranial height;
31, Length of the naso-incisival notch;
32, Cheek length.