FIGURE 18. *Stephanorhinus kirchbergensis*; Chumysh River at Kytmanovo (Kytmanovo District, Altay Territory, southeast Western Siberia). The left Mc II, NSMLL-102. 1, dorsal view. 2, lateral view. 3, volar view. 4, proximal view. Ob River at Taradanovo Village (Suzun District, Novosibirsk Province, southeast Western Siberia). The left Mc IV, IAE TRD-17. 5, dorsal view. 6, medial view. 7, volar view. 8, proximal view. Scale bar ruled in centimeters.

(Guérin, 1980). In *C. antiquitatis,* if both facets are present, the dorsal one is semicircular, with its width little larger than its height, and the plantar facet is circular. When the facets are united, the common facet is L-shaped (Guérin, 1980). In *S. kirchbergensis*, just as in NSMLL-105 and IAE TRD-2, the cross-section of the diaphysis is oval and stretched in the dorso-plantar direction without sharp inflections in the contour. In *C. antiquitatis*, the diaphysis has a round cross-section with sharp bends due to the frequent presence of sharp longitudinal ridges on the surface of the diaphysis (Guérin, 1980).

ODONTOLOGICAL ANALYSIS

Adaptation of some animal groups to a food base that included a high proportion of abrasive food (grass) led to significant physiological and morphological differences from those who preferred a diet with a small percentage of rough food (Clauss et al., 2008). Recent and Pleistocene rhi-

noceroses are one of the most prominent representatives that demonstrate a high degree of specialization of adaptation to different ecological environments. Therefore, considering the morphological features of the fossil material represented by *Stephanorhinus kirchbergensis*, we focused on the morphological characteristics that reflected food preferences. For greater clarity, the study was carried out by comparing *S. kirchbergensis* with the morphology of *Coelodonta antiquitatis* that lived in West Siberia. We used the methods presented in Fortelius (1982) and Clauss et al. (2008) to study the morphological differences of typical browsers and grazers based on the recent African rhinoceroses *Diceros bicornis* and *Ceratotherium simum.*

First of all, let us consider the adaptations associated with increased resistance of the teeth to abrasion caused by different dietary requirements. The considerable amount of silica in the grass and its cover of dust in the Pleistocene landscapes under arid climate significantly affected the rate of dental wear. Therefore, the appearance of hypsod-

FIGURE 19. *Stephanorhinus kirchbergensis*; Bijsk (Altay Territori, southeast Western Siberia). The left Mc II, GR PC-203. 1, dorsal view. 2, lateral view. 3, volar view. 4, proximal view. The right Mc II, GR PC-214, 5. dorsal view. 6, lateral view. 7, volar view. 8, proximal view. Scale bar ruled in centimeters.

TABLE 8. Measurements of McII of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from southeastern Western Siberia and Europe. All measurements are in mm. Sample sizes are given in parentheses. The following measurements were used: maximum length in the sagittal plane (ML); antero-posterior diameter of the proximal epiphysis (APD); transverse diameter of the proximal epiphysis (TD); antero-posterior diameter of the distal epiphysis (APDde); transverse diameter of the distal epiphysis (TDde); transverse diameter of the diaphysis in the middle (mTDd).

	S. kirchbergensis					C. antiquitatis			
Dimensions	**Altay Territory NSMLL-102**	**Altay Territory GR PC-203**	**Altay Territory GR PC-214**	**Europe (Guérin, 1980 tab. 139)**		**Europe (Guérin, 1980 tab. 139)**		**Altay Territory and Novosibirsk Province, IAE: Krasniy Yar, Taradanovo, Chumysh**	
				Range	**Mean**	**Range**	**Mean**	**Range**	**Mean**
ML	187.5	186	c194	179 – 212	195.4(13)	148 - 180	164.2(60)	144.7 - 180.4	164.3(26)
APD	46	62.5	59	42.5 – 60	48.2(12)	40 - 58	47(57)	35 – 52	44.7(26)
TD	48	58.5	61	41 – 57	48.0(12)	41 - 66.5	52.9(61)	47 – 63	54.8(26)
APDde	44	51.5		37.5 - 53.7	45.0(12)	35 - 52.5	43.1(58)	35 – 49	42.8(26)
TDde	52	52	57	45 – 56	48.9(12)	37.5 - 57	48.8(55)	41.4 - 56.5	47.7(26)
mTDd	40	40	44	33.5 - 41.5	38.6(13)	31.5 - 50	42.4(60)	37 - 48.7	42(26)
Indexes, %									
TD/ML	25.6	31.5	31.4		24.6(12)		32.2(60)	29.6 - 36.2	33.4(26)
mTDd/ML	21.3	21.5	22.7		19.7(13)		25.8(60)	23.8 - 28.7	25.5(26)
TDde/ML	27.7	28	29.4		25(12)		29.7(55)	26.2 – 32	29(26)

FIGURE 20. *Stephanorhinus kirchbergensis*; Ob River at Taradanovo village (Suzun District, Novosibirsk Province, southeast Western Siberia). The left Mc IV, IAE TRD-18. 1, dorsal view. 2, medial view. 3, volar view. 4, proximal view. The left Mt IV, IAE TRD-2. 5, dorsal view. 6, medial view. 7, plantar view. 8, proximal view. Scale bar ruled in centimeters.

TABLE 9. Measurements of McIV of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from southeastern Western Siberia and Europe. All measurements are in mm. Sample sizes are given in parentheses. The following measurements were used: maximum length in the sagittal plane (ML); antero-posterior diameter of the proximal epiphysis (APD); transverse diameter of the proximal epiphysis (TD); antero-posterior diameter of the distal epiphysis (APDde); transverse diameter of the distal epiphysis (TDde); transverse diameter of the diaphysis in the middle (mTDd).

| Dimensions | *S. kirchbergensis* | | | | *C. antiquitatis* | | | |
| | Novosibirsk Province, IAE TRD-17 | Novosibirsk Province, IAE TRD-18 | Europe (Guérin, 1980 tab. 141) | | Europe (Guérin, 1980 tab. 141) | | Altay Territory and Novosibirsk Province, IAE: Krasniy Yar, Taradanovo, Chumysh | |
			Range	Mean	Range	Mean	Range	Mean
ML	199	188.5	172.5 - 193	182.1(9)	126.5 - 176.5	151.1(59)	136 - 163.5	151.3(25)
APD	52	51.5	39 - 51	43.3(12)	39 – 52	45(52)	35 – 49	44.9(25)
TD	55.5	51	48 - 62	51.6(12)	41 - 62.5	53.3(57)	47 – 61	55.4(25)
APDde	51	0	41 - 50	44.9(9)	34 – 48	42.3(50)	37 – 45	41.5(25)
TDde	56	52.5	43 - 51	47.3(8)	42 - 62.5	47.9(58)	43 – 55	49.6(25)
mTDd	44.5	40	34 - 42	38.1(10)	32 – 46	37.6(59)	30.5 – 48	38.6(25)
Indexes, %								
TD/ML	27.9	27		28.3(9)		35.3(57)	34.6 – 38.4	36.6(25)
mTDd/ML	22.4	21.2		20.9(9)		24.9(59)	22.4 - 29.4	25.5(25)
TDde/ML	28.1	27.9		26(8)		31.7(58)	31.2 - 35.6	32.8(25)

FIGURE 21. *Stephanorhinus kirchbergensis*; Tobol Horizon level (Middle Pleistocene), Ob River at Krasniy Yar (Tomsk Province, southeast Western Siberia). The right Mc III, PM TSU 5/5197. 1, lateral view. 2, dorsal view. The left Mc III, PM TSU 5/2723. 3, lateral view. 4, dorsal view. Scale bar ruled in centimeters.

onty, as a result of adaptation to increased wear of the teeth, is observed in many groups of animals. We use the description of the morphological differences between hypsodont and brachyodont types of teeth in rhinos (Fortelius, 1982). The upper teeth described here show the main features of the brachyodont type, different from the characteristics of the hypsodont type observed in *Coelodonta antiquitatis*.

The occlusal surface of the upper teeth of *S. kirchbergensis* is concave (Figure 24.3); in *Coelodonta antiquitatis,* the occlusal surface is flat (Figure 24.4). Up to STU7, the buccal side of the upper teeth of *S. kirchbergensis* is higher than the lingual and highly inclined to the lingual side, i.e., there is a bucco-lingual constriction in the occlusal area of the crown in slightly worn teeth (Figure 12.1-2; mesial view). Teeth of this type are characterized by uneven wear of the occlusal surface. After STU7, the crown height on the buccal and lingual sides becomes equal (Figure 14.1), and the buccal side becomes shorter than the lingual in the following stages (Figures 13.1-2, 14.2, 15.1). In *C. antiquitatis*, almost vertical buccal and lingual walls have nearly equal height, and wear is equal. In *S. kirchbergensis,* the ectoloph of all upper teeth is serrated. In *C. antiquitatis*, the ectoloph is straight. In *S. kirchbergensis*, secondary folds of all upper premolars and molars do not merge with each other until the very last stages of wear and do not form closed inner valleys. In *C. antiquitatis,* the secondary folds usually merge in the very first stages of wear, forming the closed inner valleys. In some specimens of *S. kirchbergensis*, styles are

TABLE 10. Measurements of McIII of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from southeastern Western Siberia and Europe. All measurements are in mm. Sample sizes are given in parentheses. The following measurements were used: maximum length in the sagittal plane (ML); antero-posterior diameter of the proximal epiphysis (APD); transverse diameter of the proximal epiphysis (TD); antero-posterior diameter of the distal epiphysis (APDde); transverse diameter of the distal epiphysis (TDde); transverse diameter of the diaphysis in the middle (mTDd); transverse diameter of the distal joint (TDdj).

| | *S. kirchbergensis* | | | | | | *C .antiquitatis* | | |
| | | | | | **Western Europe: (Guérin, 1980, tab. 140)** | | **Tomsk Province, Krasniy Yar (QIII) PM TSU** | **Western Europe: (Guérin, 1980, tab. 140)** | |
Dimensions	**Tomsk Province, Krasniy Yar, PM TSU 5/ 5197**	**Krasniy Yar (Shpansky and Billia, 2012) PM TSU 5/ 2723**	**Rybinsk (Beljaev a, 1939)**	**Taubach (Kalke, 1977)**	**Range**	**Mean**	**n=7**	**Range**	**Mean**
ML	C186	229	225	204.2	206-250.5	225.2(13)	164-198	162-213	189(79)
APD	C50	56.6	64	63.7-67.8	50-59	54.2(13)	42-58	42.5-61.5	52.2(80)
TD	70	63	80	63.7-67.8	58-71	63.9(17)	58.2-79	59.5-79	68.2(90)
APDde	–	56	64		48-58.5	52.8(14)	41.8-55	44-57.5	50.8(68)
TDde	–	80.4	90	73.9	64.5-83	73.8(14)	55-71	57.5-74	65.8(77)
TDdj	–	64	70	59.1	52-64.5	59.6(13)	–	49-65	56.1(77)
mTDd	67.5	60.5	72	53.5-55.7	54-70.5	61.4(16)	48-58	46-66	56.4(86)
Indexes, %									
TD/ ML	–	27.5	35.6	31.2		28.4	33-39.9		36.1(79)
TDde/ ML	–	35.1	40	36.2		32.8	31.9-36.2		34.8(77)
mTDd/ ML	–	26.4	31.1	26.2		27.3	28.2-30.1		29.9(79)

TABLE 11. Measurements of tibia of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from southeastern Western Siberia and Europe. All measurements are in mm. Sample sizes are given in parentheses. The following measurements were used: maximum length in the sagittal plane (ML); antero-posterior diameter of the proximal epiphysis (APD); transverse diameter of the proximal epiphysis (TD); antero-posterior diameter of the distal epiphysis (APDde); transverse diameter of the distal epiphysis (TDde); transverse diameter of the diaphysis in the middle (mTDd); transverse diameter of the diaphysis in the middle (mTDd); antero-posterior diameter of the diaphysis in the middle (mAPDd); transverse diameter of the tuberositas tibia (TDtt).

| Dimensions | S. kirchbergensis | | | C. antiquitatis | | | |
| | Altay Territory, NSMLL-110 | Europe (Guérin, 1980 tab. 144) | | Europe (Guérin, 1980 tab. 144) | | Altay Territory and Novosibirsk Province IAE: Krasniy Yar, Taradanovo, Chumysh | |
		Range	Mean	Range	Mean	Range	Mean
ML	444	404 - 457	429(3)	323.5 - 433	381.1(67)	364 - 424	394.5(4)
APD	133		137.5(1)	87 - 157.5	136.8(42)	125 - 156	141.3(4)
TD	149		136(1)	111 - 163	133.4(50)	119 - 147	134.4(4)
APDde	90	75.5 - 92	85.6(12)	70 - 98	82.3(88)	77 - 91.5	85.3(4)
TDde	122.5	105 - 128	111.8(12)	92 - 127	106.8(88)	101 - 120	109.4(4)
mAPDd	62	60.5 - 69.5	64.4(5)	51 - 77	63.2(82)	57 - 67	64(4)
mTDd	69	63.5 - 80	70.5(5)	59 - 82.5	70.1(85)	65 - 73	69.3(4)
TDtt	54					60 - 74	66.8(4)
Indexes, %							
TD/ML	33.6		31.7(1)		35(50)	32.3 - 36.5	34(4)
mTDd/ML	14		16.4(3)		18.4(67)	15.3 - 17.3	16.2(4)
TDde/ML	27.6		26(3)		28(67)	26.2 - 28.6	27.7(4)
APD/ML	30		32.1(1)		35.9(42)	34.1 - 37.9	35.8(4)
mAPDd/ML	15.5		15(3)		16.6(67)	17.2 - 17.9	17.6(4)
APDde/ML	20.3		20(3)		21.6(67)	20.2 - 23.6	21.6(4)
TDtt/TD	36.2					43.8 - 54.6	49.8(4)

TABLE 12. Measurements of the astragalus of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from southeastern Western Siberia and Europe. All measurements are in mm. Sample sizes are given in parentheses. The following measurements were used: maximum transverse diameter measured perpendicularly to the vertical axis of the astragalus (ATD); maximum height, measured perpendicularly to the first diameter of the astragalus (AH); transverse diameter of distal joint of the astragalus (ATD artic. dist.); transverse diameter of distal part of the astragalus below the collar (ATD max dist.).

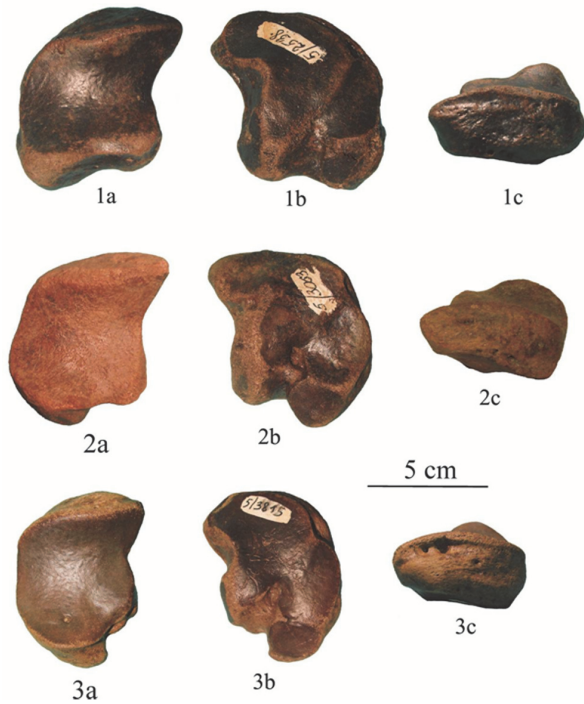| Dimensions | S. kirchbergensis | | | | C. antiquitatis | | |
| | AltayTerritory, | Tomsk Province, Krasniy Yar (Shpansky and Billia, 2012) | Europe (Guérin, 1980 tab. 145) | | Tomsk Province, Krasniy Yar (Shpansky and Billia, 2012) | Europe (Guérin, 1980 tab. 145) | |
	NSMLL-107	PM TSU 5/740	Range	Mean	n=39	Range	Mean
ATD	112	113	93 – 113	101.7(31)	82-111	84 - 112	95.7(112)
AH	104.5	104	85 – 105	95.8(29)	79-98	77 - 102	87(112)
ATD artic. dist.	93	93	74 – 93	84.7(29)		68 – 91	80.9(107)
ATD maxi dist.	97.5	96	79 – 99	89(30)	85-98	75 – 97	85.1(108)

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FIGURE 22. The navicular: *Stephanorhinus kirchbergensis*, Tobol Horizon level (Middle Pleistocene), Ob River at Krasniy Yar (Tomsk Province, southeast Western Siberia). 1, PM TSU 5/2538. 2. PM TSU 5/3063. *Coelodonta antiquitatis*, Karginian Horizon, Ob River at Krasniy Yar (Tomsk Province, southeast Western Siberia), 3. PM TSU 5/3815. a, proximal view. b, distal view. c, dorsal-medial view.

the thickness of enamel is uneven along the perimeter of the tooth. It is thicker on the buccal and lingual sides. In *C. antiquitatis*, the thickness of the enamel is even along the tooth perimeter. In *S. kirchbergensis*, the shape of M3 in the dorsal plane is close to triangular, with merged ecto- and metalophs (Figure 15.2-4). In *C. antiquitatis*, the M3 cross-section is quadrate in shape, and the metaloph is often separated from the ectoloph. In all lower teeth of *S. kirchbergensis*, the lophids are convex on the occlusal side. In *C. antiquitatis*, lophids are flattened on the occlusal side. All lower teeth of *S. kirchbergensis* are convex on the buccal side, i.e., there is a smooth expansion from the occlusal part of the crown and a smooth constriction to the root. In *C. antiquitatis*, the walls on the buccal and lingual sides are almost vertical and flattened. All of the upper and lower teeth of *S. kirchbergensis* are characterized by relatively smooth enamel without a clear pattern of enamel prisms, by the absence of rugosity, and by the rare presence of cementum. In *C. antiquitatis*, the enamel surface is rough, generally with a distinct pattern of enamel prisms or wrinkling. Cementum is retained and often covers a large portion of the tooth crown in *C. antiquitatis*.

Further, it is necessary to review the results of adaptations associated with different ways of grinding the food for brachyodont and hypsodont types of teeth. The chewing process of brachyodont teeth is in two phases (Fortelius, 1982; Popowics and Fortelius, 1997; Steuer et al., 2010). In the first phase (the cutting phase), the sharp edge of the ectoloph interacts only with the dorsal buccal edge of the lower teeth, producing the primary tearing of

isolated. For example, isolation of the protocone is observed (Figure 12.1; occlusal view). In *C. antiquitatis*, styles are not isolated. In *S. kirchbergensis*,

TABLE 13. Morphological comparison of the navicular bone of *Stephanorhinus kirchbergensis* versus *Coelodonta antiquitatis*.

	Stephanorhinus kirchbergensis	*Coelodonta antiquitatis*
1.	The proximal articular surface has a wide notch in the latero-plantar side.	The notch is either very weak or absent.
2.	The dorso-lateral angle is not very acute and only slightly elongated. Correlatively with this, the width of the proximal articular surface is approximately the same as the length.	The dorso-lateral angle always well pronounced and markedly elongated in the lateral direction. The proximal articular surface is more extended latero-medially.
3.	The process talocaudalis (which is used for connection with a cubic bone) is displaced to the plantar edge of the lateral side.	The process talocaudalis is placed at the middle of the lateral side.
4.	The dorso-medial angle has a convex shape.	The dorso-medial angle is oblique.
5.	The joint, on the distal side, has a well pronounced indentation in the proximal direction between facets for connection with III cuneiform and I cuneiform.	This indentation is no such pronounced.
6.	The III cuneiform facet has a well pronounced gap from the dorso-lateral edge of the bone.	This gap is no such pronounced.

FIGURE 23. *Stephanorhinus kirchbergensis*; Chumysh River at Kytmanovo (Kytmanovo District, Altay Territory, southeast Western Siberia). The left Mt II, NSMLL-101. 1, dorsal view. 2, lateral view. 3, plantar view. 4, proximal view. The left Mt IV, NSMLL-105. 5, dorsal view. 6, medial view. 7, plantar view. 8, proximal view. Scale bar ruled in centimeters.

the plant tissues. In this stage, a brief but intense stress concentrated on a small area of surface is produced. Only the serrated edge of the ectoloph participates in this phase. The shape of the ectoloph curves follows the shape of curves in lophids of the lower teeth and the dorsal buccal edge of lophids in the lower teeth. This leads to the occurrence of polished facets on the buccal edge of lophids, which are at an acute angle to the occlusal surface (Figure 24.1). In the second phase (the crushing phase), there is an interaction of the main part of the occlusal surface for both upper and lower teeth, with a translocation in the oral-aboral direction (Figure 24.5). The features of this masticatory apparatus in *Stephanorhinus kirchbergensis* were developed from a juvenile age. A characteristic facet is observed on the milk teeth of the juvenile mandible NSMLL-12 (Figure 2). In brachyodont teeth, both phases are well developed, while in hypsodont teeth, the first phase is rudimentary and the second phase proves to be the main one, representing the crushing under high pressure and large side amplitude. As a result, the

occlusal surface of the upper and lower teeth of *Coelodonta antiquitatis* is flat (Figure 24.2, 24.4, 24.6).

The next adaptations are caused by different chewing forces for brachyodont and hypsodont types of teeth. A large proportion of herbaceous plants in the diet of *Coelodonta antiquitatis* increases the force required for its milling. Mandibles of large herbivores are forced to move laterally with a large amplitude, when the animal is required to create a maximum force to break the plant tissue, which has in its structure long, longitudinal, durable, and elastic fibers (as in grass). If the feeding objects have a mosaic structure, as does the leaf of a shrub or young tree, movements back and forth are enough to break it (Sanson, 2006). The increase in forces in herbivores is reached by relevant morphological adaptations of the mandible. In this case, the relative height and thickness of the horizontal corpus and the relative height of the mandibular condyle above the level of the tooth row are increased. All of the mandibles studied appear more slender than *C. antiquitatis* according

TABLE 14. Measurements of MtII of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from southeastern Western Siberia and Europe. All measurements are in mm. Sample sizes are given in parentheses. The following measurements were used: maximum length in the sagittal plane (ML); antero-posterior diameter of the proximal epiphysis (APD); transverse diameter of the proximal epiphysis (TD); antero-posterior diameter of the distal epiphysis (APDde); transverse diameter of the distal epiphysis (TDde); transverse diameter of the diaphysis in the middle (mTDd).

| Dimensions | *S. kirchbergensis* | | | *C. antiquitatis* | | | |
| | Altay Territory, NSMLL-101 | Europe (Guérin, 1980 tab. 152) | | Europe (Guérin, 1980 tab. 152) | | Altay Territory and Novosibirsk Province, IAE: Krasniy Yar, Taradanovo, Chumysh | |
		Range	Mean	Range	Mean	Range	Mean
ML	188	173.5 - 195	180.7(7)	140 - 157.5	148.5(37)	130.5 - 176.8	146.9(16)
APD	43.5	44 - 51	47.1(9)	36.5 - 51	41.8(34)	37 - 51.6	43(16)
TD	34	31 - 39	34.8(9)	27.5 - 38	32.6(36)	25.6 – 39.3	32.6(16)
APDde	46	41 - 48.5	43.2(7)	33.5 - 43	38.1(33)	34.7 – 46.7	37.7(16)
TDde	41	38 - 44	41(6)	31.5 - 44.5	37.6(36)	30 - 47.5	36.4(16)
mTDd	31	26.5 - 33.5	29.1(7)	23.5 - 37	31.1(37)	25.5 – 33.8	29.3(16)
Indexes, %							
TD/ML	18.1		19.2(7)		21.8(36)	17.7 – 27.1	22.3(16)
mTDd/ML	16.5		16.1(7)		20.9(37)	18.6 – 22.5	20(16)
TDde/ML	21.8		22.7(6)		25.3(36)	22.4 – 27.7	24.8(16)

TABLE 15. Measurements of MtIV of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from southeastern Western Siberia and Europe. All measurements are in mm. Sample sizes are given in parentheses. The following measurements were used: maximum length in the sagittal plane (ML); antero-posterior diameter of the proximal epiphysis (APD); transverse diameter of the proximal epiphysis (TD); antero-posterior diameter of the distal epiphysis (APDde); transverse diameter of the distal epiphysis (TDde); transverse diameter of the diaphysis in the middle (mTDd).

| Dimensions | *S. kirchbergensis* | | | | *C. antiquitatis* | | | |
| | Altay Territory, NSMLL-105 | Novosibirsk Province, IAE TRD-2 | Europe (Guérin, 1980 tab. 154) | | Europe (Guérin, 1980 tab. 154) | | Altay Territory and Novosibirsk Province, IAE: Krasniy Yar, Taradanovo, Chumysh | |
			Range	Mean	Range	Mean	Range	Mean
ML	188.5	176	170 - 182.5	178.2(3)	127 - 155	144.9(40)	122.2 – 163	146.8(15)
APD	54.5	51.5	44 - 53	47.2(6)	37 - 51.5	44.3(39)	37.1 - 51.5	46.3(15)
TD	54	53	47 - 53.5	50.1(6)	41 - 57	46.5(37)	36.7 - 52.5	46.4(15)
APDde	52	46.5	44.5 - 51.5	48.8(3)	36 - 46	40.8(35)	36.3 – 47	42.5(15)
TDde	43	40	37 - 43	40.3(4)	31 - 41	36.1(36)	29.1 – 45	36.1(15)
mTDd	35	28.5	33.5 - 36.5	34.8(4)	24 - 40	30.5(40)	22.2 – 41	30.6(15)
Indexes, %								
TD/ML	28.6	30.1		28.1(3)		32.1(37)	27.1 - 37.5	31.7(15)
mTDd/ML	18.6	16.2		19.5(3)		21.1(40)	16.1 - 26.4	20.8(15)
TDde/ML	22.8	22.7		22.6(3)		24.9(36)	22.2 - 27.6	24.6(15)

to characteristics listed above. It can be seen on Figure 25, where indices of molars relative length (Figure 25; Ind. 1), horizontal corpus relative height (Figure 25; Ind. 2-7) and thickness (Figure 25; Ind. 8-12) for *S. kirchbergensis* are lower than those for *C. antiquitatis*.

The adaptation to a more selective manner of feeding is presented by a very narrow, spoon-like mandibular symphysis area and shortened viscerocranium, because of the reduced diastema (Table 4, Figure 3, Figure 8.1, occlusal view). In *Coelodonta antiquitatis,* the area of mandibular sym-
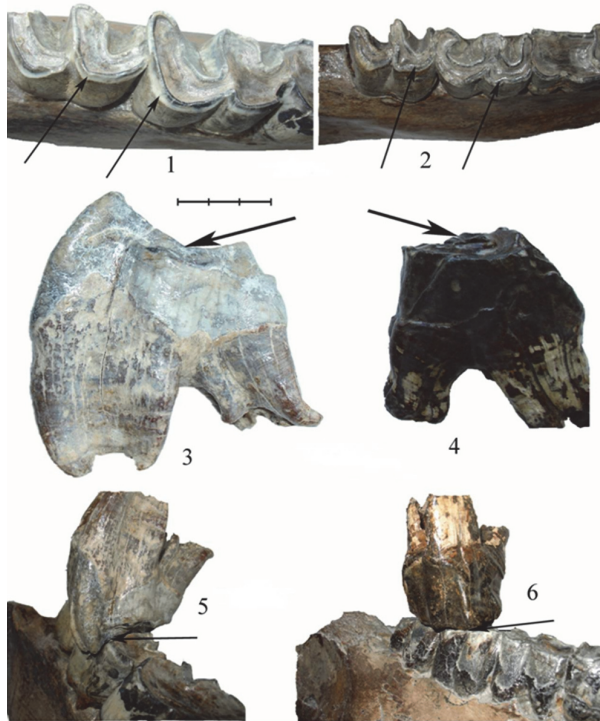
FIGURE 24. The specifics of the wear of the occlusal surfaces of the lower and upper teeth of *Stephanorhinus kirchbergensis* (1,3,5) and *Coelodonta antiquitatis* (2,4,6). Arrows indicate the morphological differences associated with a different biomechanical masticatory system for the browser and the grazer. Scale bar ruled in centimeters.

physis is flat, wide, and relatively long (Table 4). Another result of this adaptation may be a less wide opening of the mouth. In *Stephanorhinus kirchbergensis*, this is caused by the more acute angle of rise in the vertical ramus of the mandible (Figures 7, 10). In *C. antiquitatis*, the vertical ramus rises slightly, which allows the mouth to open wider. Another adaptation to a more selective manner of feeding could be the high body position and slender structure of the *S. kirchbergensis* postcraniun. This is well illustrated by the morphometric data of the material presented (Tables 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, Figures 16, 17, 18, 19, 20, 21, 22, 23). The structure of the occipital region of the cranium allowed feeding on the vegetation at a higher level. Distinctive features of *C. antiquitatis* are the adaptations for gathering food from the ground: shortened limbs, a strongly overhanging occipital crest that prevents lifting the head high, and an elongated viscerocranium caused by the shifting of orbits in the caudal direction.

MESOWEAR ANALYSIS

Characteristics of 12 teeth of *Stephanorhinus kirchbergensis* were used as an input data for mesowear analysis. Ten of them were characterized in the present work, and data about two teeth (P4 and M1) were taken from the article of Shpansky and Billia (2012) (Table 16).

All of the studied upper molars of *Stephanorhinus kirchbergensis* from West Siberia had a high occlusal relief. A high percentage of teeth
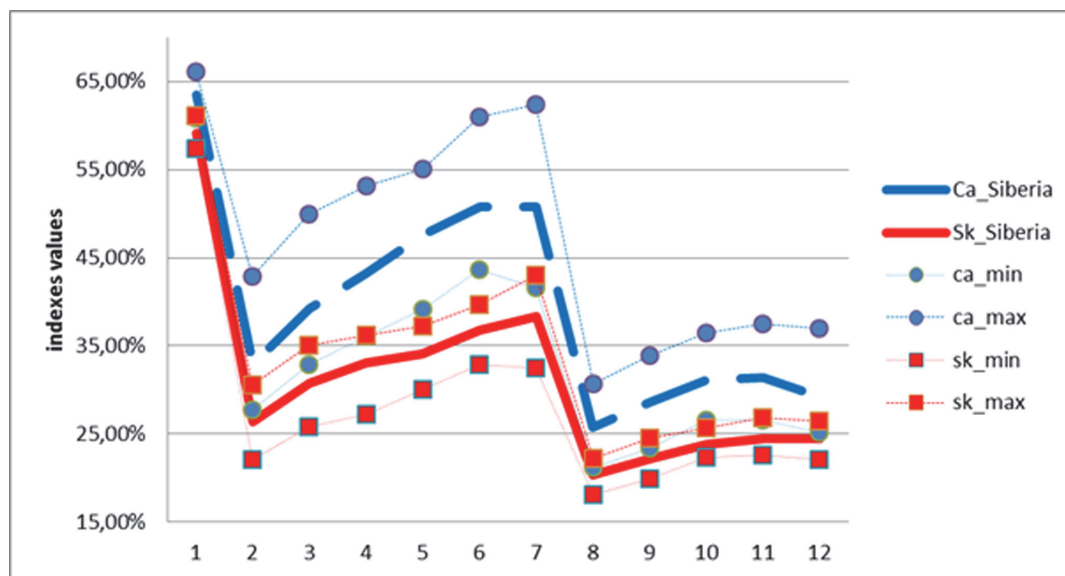

FIGURE 25. Indexes of the mandible of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis*.

TABLE 16. Mesowear scores for occlusal relief and cusp shape for maxillary teeth of fossils *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis*.

Species	locality	Specimen identification number	Upper tooth	occlusal relief (high=h, low=l)	cusp shape (sharp=s, round=r, blunt=b)
Stephanorhinus kirchbergensis	fossils from the southeast of Western Siberia	IAE CHU-1	M2	h	R
		IAE CHU-5	M2	h	S
		IAE CHU-2	P4	h	S
		IAE CHU-6	P4	h	S
		IAE CHU-7	P4	h	S
		IAE CHU-8	P4	h	R
		IAE BB-1	M3	h	R
		IAE CHU-4	M3	h	R
		PM TSU 5/3495	M1	h	R
		PM TSU 5/2878	P4	h	R
		PM TSU 5/396	M1	h	R
		NSMLL 21052	M2	h	S
Coelodonta antiquitatis		IAE CHU 51	P4	l	B
		IAE CHU 52	P4	l	R
		IAE CHU 53	P4	l	R
		IAE CHU 54	P4	l	B
		IAE CHU 55	P4	l	R
		IAE CHU 56	M1	l	B
		IAE CHU 57	M1	l	R
		IAE CHU 58	M1	l	B
		IAE CHU 59	M1	l	B
		IAE CHU 60	M1	l	B
		IAE CHU 61	M1	l	R
		IAE CHU 62	M2	l	R
		IAE CHU 63	M2	l	R
		IAE CHU 64	M2	h	R
		IAE CHU 65	M2	h	R
		IAE CHU 66	M2	l	R
		IAE CHU 67	M2	h	R
		IAE CHU 68	M2	l	B
		IAE CHU 69	M2	l	R
		IAE CHU 70	M2	l	R
		IAE CHU 71	M3	l	B
		IAE CHU 72	M3	h	R
		IAE CHU 73	M3	h	R
		IAE CHU 74	M3	h	R
		IAE CHU 75	M3	h	R

have sharp apices (41.6%). The rest of the teeth have rounded apices, none of them have blunt apices (Table 17). In *C. antiquitatis* from the same region, only 28% had a high occlusal relief, 64% of specimens had rounded cusps, and 36% had blunt cusps; no specimen displayed sharp cusps (Table 17).

Even the conservative assessment of hypsodont index (on lower third molars from the material presented) gives values close to 1.7 for *Stepha-*

TABLE 17. Mesowear scores for the set of 27 typical extant species and for the fossil assemblages. (Continued on next page.)

Species	Locality	Sources	label	% high	% sharp	% round	% blunt	N
Stephanorhinus kirchbergensis	fossils from the southeastern Western Siberia		SK_SWS	100	41,6	58,4	0	12
Coelodonta antiquitatis			CA_SWS	28	0	64	36	25
Stephanorhinus hundsheimensis	fossils from the Sussenborn	(Kahlke and Kaiser, 2011)	SH_SUESS	91.9	5.7	94.3	0	36
Stephanorhinus hundsheimensis	fossils from the Voigtstedt		SH_VOI	100	100	0	0	6
Stephanorhinus hemitoechus	fossils from the Bilzingsleben II	(Asperen and Kahlke, 2014)	SHM_B	80	12	88	0	25
Stephanorhinus kirchbergensis			SK_B	82.6	8.7	87	4.3	23
Stephanorhinus kirchbergensis	fossils from the Weimar-Ehringsdorf		SK_WE	89.5	28.9	71.1	0	76
Stephanorhinus kirchbergensis	fossils from the Weimar-Taubach		SK_WT	82.6	39.1	60.9	0	23
Stephanorhinus hemitoechus	fossils from the UK MIS 7		SHM_U7	36.4	30	60	10	11
Stephanorhinus kirchbergensis			SK_U7	83.3	16.7	66.7	16.6	6
Stephanorhinus hemitoechus	fossils from the UK MIS 5e upland		SHM_U5u	85.7	9.5	90.5	0	21
Stephanorhinus hemitoechus	fossils from the UK MIS 5e lowland		SHM_U5l	63.6	9.1	81.8	9.1	11

norhinus kirchbergensis from West Siberia and 2 or a little larger for *Coelodonta antiquitatis*. Thus, *S. kirchbergensis* can be classified as brachyodont type, while *C. antiquitatis* belongs to the mesodont type. But, as shown in by Fortelius and Solounias (2000), using only the hypsodont index does not allow classifying definitely the individuals. In addition, this characteristic affects slightly the results of mesowear analysis.

Two groups of attributes of dental specimens were used as an input for a Mann-Whitney U-test: one for *Stephanorhinus kirchbergensis* and the other for *Coelodonta antiquitatis*. The values of attributes were formed based on two mesowear variables (relief of the occlusal surface and the shape of cusps) listed in Table 16, as follows: 1 = high and sharp; 2 = high and rounded; 3 = low and sharp; 4 = low and rounded; and 5 = low and blunt. The test result showed the expected high degree of difference between *S. kirchbergensis* and *C. antiquitatis* in dietary mesowear signals, i.e., the probability of the coincidence of these two groups was negligible ($p < 0.001$).

The diagram summarizing the cluster analysis (Figure 26) reflects the distribution of the fossil rhi-

noceroses of Europe and Siberia according to dietary preferences, against the reference data set of 27 species of extant ungulate mammals selected by Fortelius and Solounias (2000) on the basis of information about their dietary preferences (Janis, 1988). The distribution of these 27 extant ungulates in the diagram completely coincides with other lines of paleodietary evidence (Fortelius and Solounias 2000; Kaiser and Solounias, 2003; Kahlke and Kaiser, 2011). The distribution of European *S. hundsheimensis* in the diagram is congruent with data from Kahlke and Kaiser (2011), and distributions of *Stephanorhinus kirchbergensis* and *S. hemitoechus* are congruent with data from van Asperen and Kahlke (2014). The diagram illustrates the partition of the set of the animals examined into four groups. The extreme groups are grazers and browsers. The browsers group includes animals whose diet comprises no more than 10% of grass. The grazers group includes animals whose diet is more than 90% of grass. Animals with a mixed diet are placed in the central part of the diagram. The group that is closer to the grazers consists of the mixed grazer feeders with prevailing consumption of grass, compared to another

TABLE 17 (continued).

Species	Locality	Sources	label	% high	% sharp	% round	% blunt	N
Alces alces	extant species	(Fortelius and Solounias, 2000)	AA	100	100	0	0	30
Diceros bicornis			DB	100	94.1	5.9	0	34
Dicerorhinus sumatrensis			DS	100	80	20	0	5
Giraffa camelopardalis			GC	94	73.7	26.3	0	61
Odocoileus hemionus			OH	100	72.7	27.3	0	33
Odocoileus virginianus			OV	100	88.8	11.2	0	18
Okapia johnstoni			OJ	100	87.5	12.5	0	8
Rhinoceros sondaicus			RS	100	100	0	0	5
Ceratotherium simum			cs	0	0	72	28	26
Alcelaphus buselaphus			ab	57	4.4	67.6	28	76
Bison bison			bb	0	0	26.7	73.3	15
Connochaetes taurinus			ct	55	15.3	55.7	29	52
Damaliscus lunatus			dl	20	20	60	20	5
Equus burchelli			eb	0	27	39.4	33.6	122
Equus grevyi			eg	0	34.4	41.4	24.2	29
Hippotragus equinus			he	85	3.9	96.1	0	26
Hippotragus niger			hn	85	0	85	15	20
Kobus ellipsiprymnus			ke	96	0	100	0	22
Redunca redunca			rr	91	6.4	91	2.6	77
Aepyceros melampus			Me	100	35.3	64.7	0	17
Capricornis sumatraensis			Ca	100	45.5	50	4.5	22
Cervus elaphus canadensis			Cc	100	47.4	52.6	0	19
Gazella granti			Gg	88	50	50	0	18
Gazella thomsoni			Gt	88	55.5	43.2	1.3	146
Ovibos moschatus			Om	81	57.6	42.4	0	52
Taurotragus oryx			To	100	50	50	0	14
Tragelaphus scriptus			Ts	100	51	49	0	47

central group that is closer to the browsers, which is mixed browser feeders.

The position of West Siberian *Coelodonta antiquitatis* in the diagram lies adjacent to the typical extant grazer *Ceratotherium simum.* This is due to very similar values of mesowear signals of these two species of rhino, indicating the same high level of adaptation to the rough abrasive food base. *Stephanorhinus kirchbergensis* of West Siberia appears in the same group with extant mammals such as the impala *(Aepyceros melampus),* suma-tran serow *(Capricornis sumatraensis),* wapiti *(Cervus elaphus canadensis),* Grant's gazelle *(Gazella granti),* Thomson's gazelle *(Gazella thomsoni),* *(Ovibos moschatus),* common eland *(Taurotragus oryx),* and bushbuck *(Tragelaphus scriptus).* This group of animals belongs to mixed browser feeders. It is caused by a small Euclidean distance between the mesowear signals of animals from this group. Also, specimens of *S. kirchbergensis* from the beginning of the Late Pleistocene in the European areas of Weimar-Ehringsdorf and Weimar-
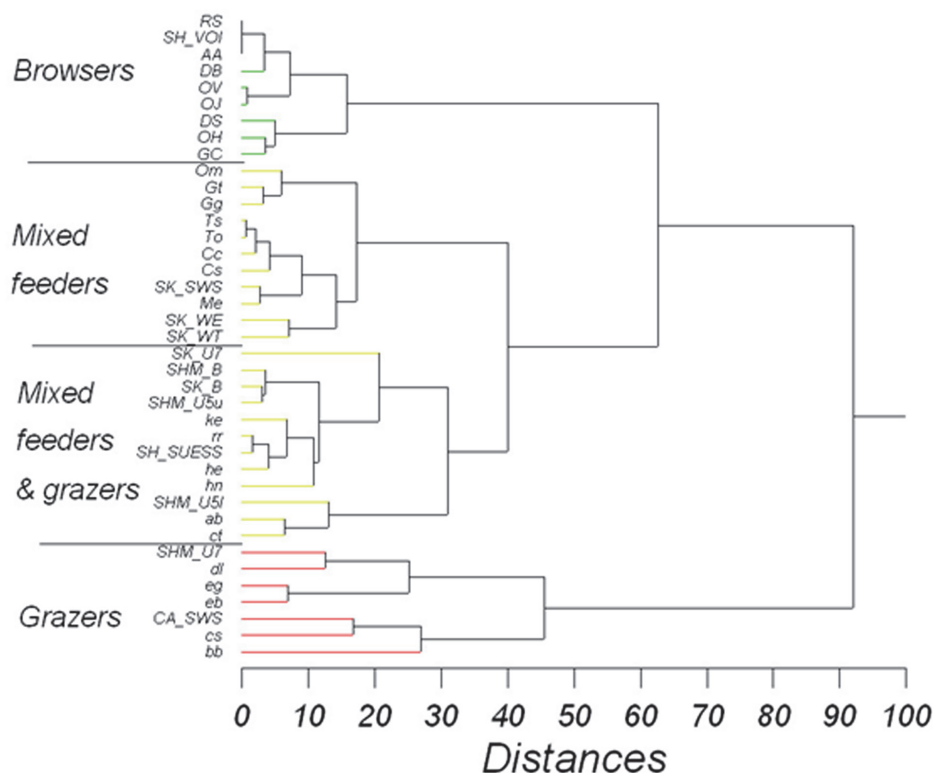
Cluster Tree

FIGURE 26. Hierarchical cluster diagram based on the reference tooth positions of upper P4-M3 according to the extended mesowear method (Kaiser and Solounias, 2003). Distances = Euclidean distance (root-mean-squared difference). Clusters are based on a set of 27 typical extant species model. Classification follows the conservative (CONS) scheme of Fortelius and Solounias (2000): Browsers (CONS): AA = *Alces alces*, DB = *Diceros bicornis*, DS = *Dicerorhinus sumatrensis*, GC = *Giraffa camelopardalis*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus*, Grazers (CONS): ab = *Alcelaphus buselaphus*, bb = *Bison bison*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, dl = *Damaliscus lunatus*, eb = *Equus burchelli*, eg = *Equus grevyi*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, rr = *Redunca redunca*; Mixed feeders (CONS): Cc = *Cervus elaphus canadensis*, Ca = *Capricornis sumatraensis*, Gg = *Gazella granti*, Gt = *Gazella thomsoni*, Me = *Aepyceros melampus*, Om = *Ovibos moschatus*, To = *Taurotragus oryx*, Ts = *Tragelaphus scriptus*. European fossil populations of *Stephanorhinus hundsheimensis* (Kahlke and Kaiser, 2011): SH_SUESS = Su ̈ßenborn, SH_VOI = Voigtstedt; S. *kirchbergensis* (van Asperen and Kahlke, 2014): SK_B = Bilzingsleben II, SK_WE = Weimar-Ehringsdorf, SK_WT = Weimar-Taubach, SK_U7 = UK MIS 7; *S. hemitoechus* (van Asperen and Kahlke, 2014): SHM_B = Bilzingsleben II, SHM_U7 = UK MIS 7, SHM_U5u = UK MIS 5e upland, SHM_U5l = UK MIS 5e lowland. Southeast Western Siberia fossil populations: SK_SWS = *S. kirchbergensis,* CA_SWS = *Coelodonta antiquitatis.*

Taubach also belong to this group (van Asperen and Kahlke, 2014).

BIOGEOCHEMICAL ANALYSES

To date, a great deal of information is known about the biogeochemistry of Quaternary mammal remains and particularly about rhinos. But research on the *Stephanorhinus* genus is rare (Palmqvist et al., 2003), and even less information is presented specifically on *S. kirchbergensis* (Pushkina et al., 2014). Comparative study of the biogeochemical composition (including stable isotopes) of bone tissue was made for the Sk_ui1 sample and a number of samples of Late and Middle Pleistocene mammals from Middle Irtysh and other regions because of uncertainty about the findings' age (probably Middle Pleistocene). We have estab-

lished that the amount of trace elements in the Sk_ui1 tissue sample from the Ust-Ishim area (0.2 mass %) falls into the same group with suspected or known Late Pleistocene remnants (0.1-0.25 mass %) and is significantly different from those of the Middle Pleistocene (0.35–0.4 mass %).The Sk_ui1 sample also displayed a quite large organic carbon content (11.42 mass %), typical for Late Pleistocene samples. The stable isotopic analysis of Sk_ui1 gave the following results: 1) for bone bioapatite, $\delta^{13}C_{PDB}$ = −11.30‰; and 2) for bone collagen, $\delta^{13}C_{PDB}$ = −19.66‰, $\delta^{15}N_{air}$ = 2.84‰. The stable isotopic composition of the bone sample of a woolly rhinoceros from Ust-Ishim region was: 1) for bone bioapatite, $\delta^{13}C_{PDB}$ = −9.40‰; and 2) for bone collagen, $\delta^{13}C_{PDB}$ = −19.33‰, $\delta^{15}N_{air}$ = 5.40‰. Parameters of mammalian tissues' stable isotopic composition are determined by isotope fractionation in the food and water, which changes naturally through the food chains from the producers with a different type of photosynthesis and preferred habitats to consumers of higher trophic levels (Bocherens and Drucker, 2013). Interpreting the stable isotopic composition of the tissues is more effective when there is complex evidence for several species and many specimens of each species, because individual values vary, and the total ensemble of data may be shifted in isotopic valuesdepending on the geochemical and climatic conditions of the region (Bocherens, 2003). However, the interpretation of individual measurements is also possible by using the accumulated information. The degree of enrichment of collagen by $\delta^{15}N$ isotope is very informative. Low values of $\delta^{15}N$ in collagen of herbivores can be explained by several factors: the use of food that is pioneer vegetation, increased acidity of soils, and the predominance of shrubs and trees in the diet spectrum (Bocherens, 2003). This is in agreement with the traditional view about the browsing feeding strategy of *S. kirchbergensis* and the mesowear analysis results for Siberian specimens. For instance, significantly reduced $\delta^{15}N$ relative values are characteristic of browsers such as *Alces alces*, *Cervus elaphus*, and *Rangifer tarandus*. The value of $\delta^{15}N$ for Sk_ui1 is smaller than that for the woolly rhinoceros from Belgium, France, and Yakutia (Bocherens, 2015), while the comparative sample of woolly rhinoceros from the Irtysh Valley corresponds to the values for European representatives of this species. This discrepancy may reflect different nutritional adaptation of two species of Siberian rhinoceroses. High $\delta^{13}C$ value (as in both

test samples) is characteristic for inhabitants of open ecosystems where there are dominant plants with C_3 type of photosynthesis and/or an abundance of lichens in the vegetation cover. The stable isotopic composition of bioapatite of both *S. kirchbergensis* and *C. antiquitatis* suggests that they consumed very fresh, probably largely melt, water.

MORPHOMETRIC ANALYSIS OF THE JUVENILE MANDIBLE

At present, juvenile mandibles of *Stephanorhinus kirchbergensis* are known in several localities in Europe, China (Shennongjia) (Kahlke, 1975, 1977; Guérin, 1980; Lacombat, 2006; Tong and Wu, 2010), and Altai (Russia) (NSMLL-12). The largest number of juvenile mandibles is known in the localities of Weimar-Taubach and Weimar-Ehringsdorf in Europe. A representative collection of *Coelodonta antiquitatis* juvenile mandibles of different individual ages from the following localities was used as comparative material: Krasniy Yar of Tomsk Province (Shpansky, 2014), Novosibirsk Province, and Altai Territory.

The main differences between juvenile mandibles of *S. kirchbergensis* and those of *Coelodonta antiquitatis* are the absence of thickening in the ventral part of the horizontal corpus and more massive teeth (Table 2).

The change in the average indices of lower deciduous teeth (relation of tooth width to its length) from dp1 to dp4 is not linear in *Stephanorhinus kirchbergensis* or in *Coelodonta antiquitatis* (Figure 27). At the same time, the main trend in *C. antiquitatis* from West Siberia is that the greatest width index is observed on dp2, while dp4 has less width index than dp2, and it has often the minimal value of width index with respect to the other teeth of the same jaw (Figure 28). Dynamics of changes in the average values of the width indices of the deciduous teeth from dp1 to dp4 in *C. antiquitatis* from West Siberia, as well as from European regions, reflects this general trend. The exception is the value for dp1 in the European plot, which was obtained from the only specimen, and therefore may not reflect the value of the population (Figure 27). For the mandible of *S. kirchbergensis* (NSMLL-12), another index distribution is observed. The width index of dp4 is the highest. It is much greater than the width index of dp2 (Figure 29). The same may be observed for four mandibles from Weimar-Taubach (MIS 5e) (Kahlke, 1977), where the width index of all dp4 is at least the same as that of dp2 (Figure 29). For the older locality of Weimar-Ehringsdorf (MIS 7) (Kahlke,
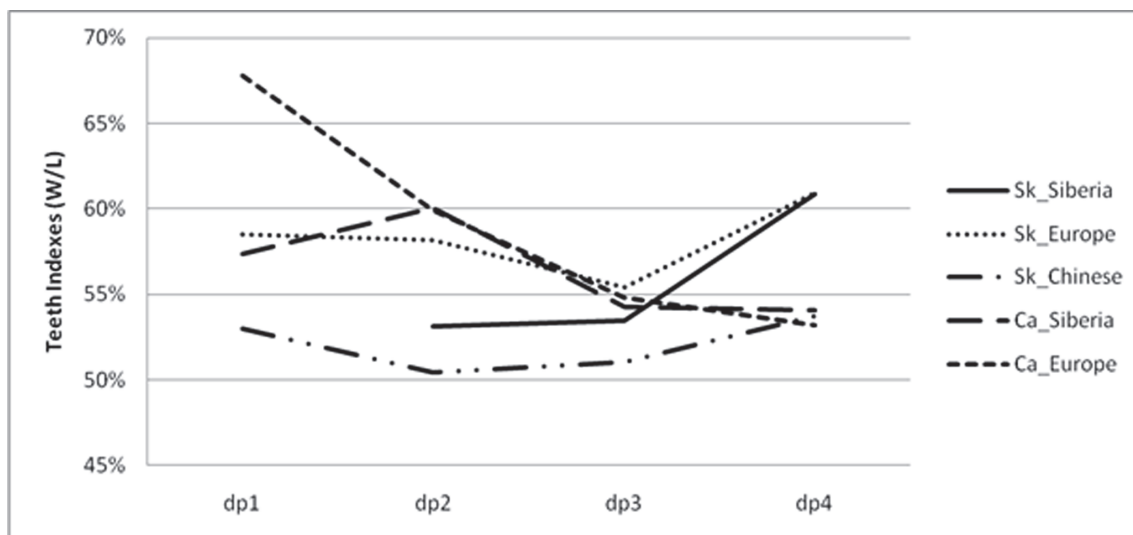
FIGURE 27. Indexes of the lower deciduous teeth of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from Siberian, European, and Chinese regions.

1975), the width index of dp4 compared to dp2 is more variable. The maximal value of the width index is observed on dp1, but the main trend in the width index of dp4 and dp2 remains the same, i.e., for three of five jaws that we present here, the width index of dp4 is lower than that of dp2. In the other two jaws, the width index between dp4 and dp2 is close to that in *C. antiquitatis* (Figure 29). Considering that mesowear signals of adults from the locality of Weimar-Ehringsdorf (MIS 7) on the hierarchical graph (Figure 26) also shift towards grazers, the slight shift of teeth proportions in juveniles towards the *C. antiquitatis* condition appears quite explainable. The trend of changes in deciduous teeth indices from dp1 to dp4 in NSMLL-12 is similar with the trend of change in the indices of *S. kirchbergensis* average indices from Europe (Figure 27). For localities in China, we can only observe the general dynamics of the average indices of the deciduous teeth from dp1 to dp4 for *S. kirchbergensis* (Figure 27), because Tong and Wu (2010) provided information only on isolated teeth and there is no full information on mandibles of juveniles.

To determine the age of the juvenile NSMLL-12, a juvenile individuals of extant African black rhinos (*Diceros bicornis*) and white rhinos (*Ceratotherium simum*) were used as comparative material (Schaurte, 1966; Dittrich, 1974), and the method of age determination proposed by Hillman-Smith et al. (1986) was used. Based on the assumption that the order of deciduous teeth eruption, functioning, and replacement were close to those of extant rhinoceroses, we applied the method introduced by

Hillman-Smith et al. (1986) in order to estimate the age of NSMLL-12. In NSMLL-12, only the deciduous teeth dp2 (STL5), dp3 (STL5), and dp4 (STL4) were erupted and functioned in the initial stage. The degree of wear of preserved deciduous teeth of NSMLL-12 is closest to the specimen IQW 1968/9761 of the juvenile mandible of *S. kirchbergensis* from Taubach (Kahlke, 1977). Therefore, dp1 in NSMLL-12 was not used, or dp1 was used in the earliest stage (STL2 or STL3), just as in IQW 1968/9761. Because alveolar pockets for permanent teeth P2 and P3 were not found after apertum of the NSMLL-12 textus, it is likely that m1 had not yet started erupting from the bone tissue. It corresponds to stages STL1 or STL2. Information about stages of wear of dp1-m1 from NSMLL-12 completely corresponds to information on the expected state of mandibular teeth in Hillman-Smith et al. (1986: table IV). This corresponds to the age of a juvenile rhinoceros, 12–18 months.

DISCUSSION

Sizes and morphological features of lower dentitions and mandibles from different locations in Siberia correspond to specimens known from Europe. The adult mandibles studied may be separated into two groups, which differ considerably by the length of their tooth rows. The first group, including the specimens IAE KY-4323, IRM 2436, and GR PC 1165, is characterized by the length of p2-m3 varying from 263 mm to 265 mm. The second group of specimens, NSMLL-10, Sk_ui1, NSMLL 22090, GR PC 1164, and KB MAN K-397, has a length of tooth row that varies from 278 mm
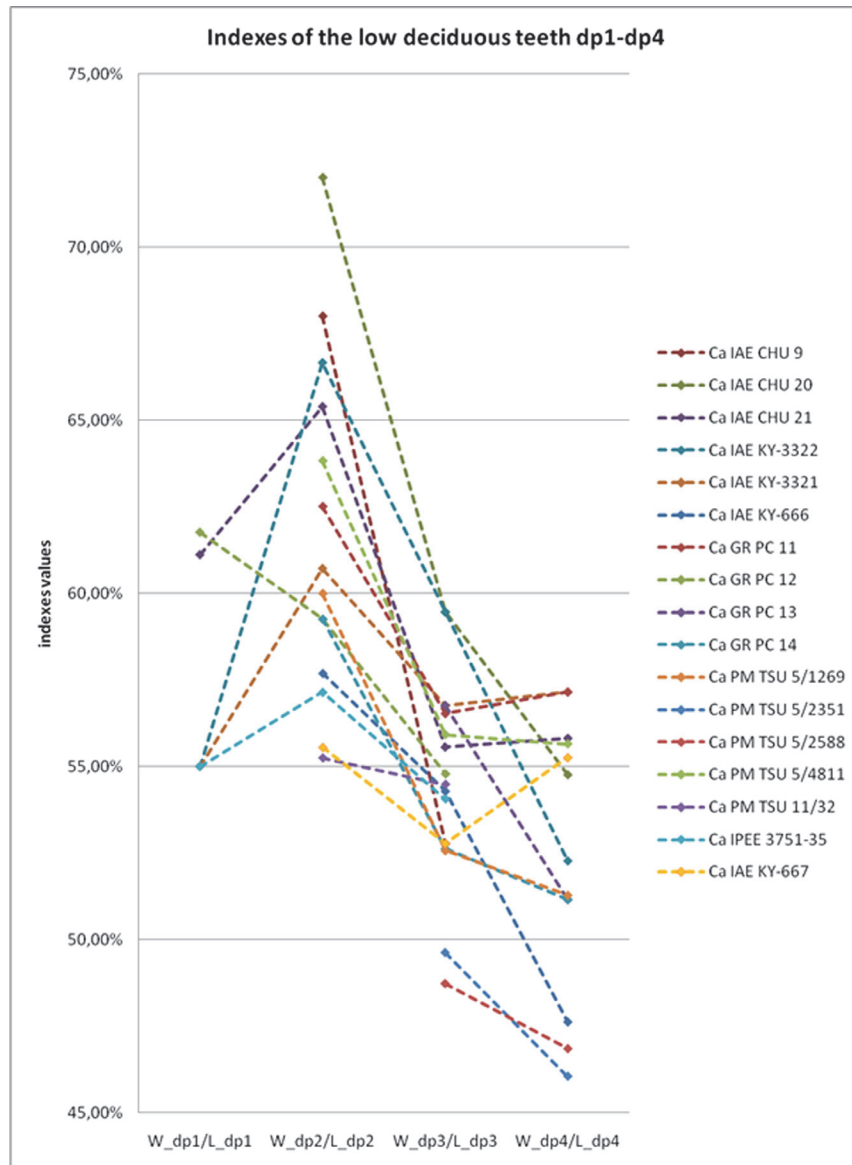
FIGURE 28. Indexes of the lower deciduous teeth dp1-dp4 of *Coelodonta antiquitatis* (Ca).

to 289 mm. Premolar tooth row p2-4 length for all mandibles varies from 108 mm to 118 mm (Table 4). Differences are more visible in the length of m1-3. For the first group, the length of m1-3 varies from 152 mm to 155 mm, while for the second it varies from 163 mm to 171 mm. It may be assumed that these differences are a consequence of expressed sexual dimorphism of body size for *Stephanorhinus kirchbergensis*, by analogy with sexual dimorphism of body size in extant species: *Rhinoceros unicornis* (Dinerstein, 1991) and *Ceratotherium simum* (Owen-Smith, 1975). Thus, of the total number of jaws considered, 30% are jaws with short dentition (presumably female), 20% are

young individuals (less than 10 years old), and 50% are jaws with a long dentition (presumably male). All jaws with a short tooth row belong to adult animals older than 20 years, while there are two groups for the jaws with a long dentition: young animals aged 15–20 years and individuals over 20 years old. To a certain extent this distribution agrees with the general model of sexual dimorphism of extant rhinos that reflects the hierarchy of dominance (Mihlbachler, 2003, 2005, 2007). This model explains the resurgence in mortality among young rhino males because of the severe dominance of older individuals. Such a surge in mortality is not observed among females. A more detailed
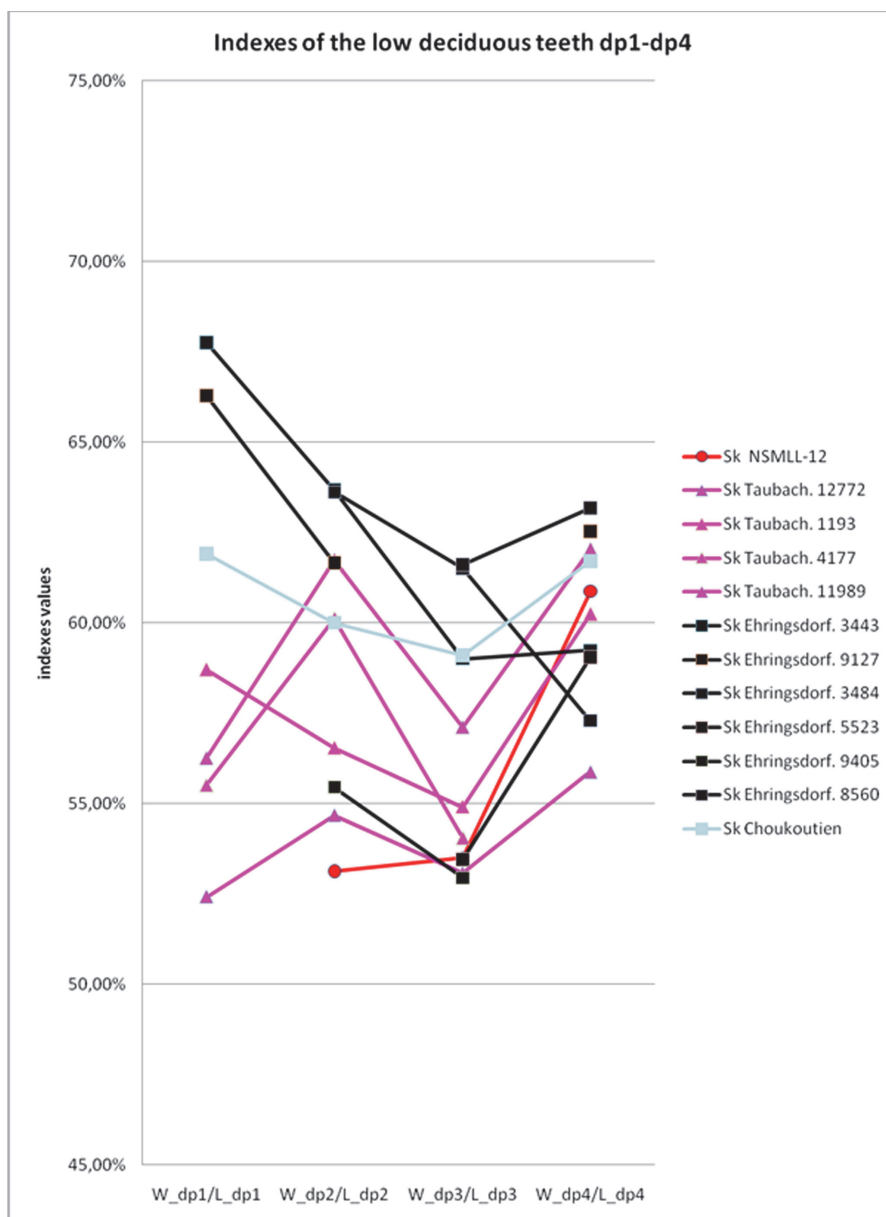
FIGURE 29. Indexes of the lower deciduous teeth dp1-dp4 of *Stephanorhinus kirchbergensis* (Sk).

study of the model of sexual dimorphism of *S. kirchbergensis* using the capabilities of statistical systems is currently impossible because of the insufficient amount of material. For the same reason, it has been impossible to study the morphology of sexual dimorphism, because for definitive studies it is necessary to have complete skeletons of *S. kirchbergensis* individuals of both sexes, or at least complete skulls with mandibles, which to date have not been found.

Comparative analysis of the postcranium from the localities of West Siberia showed their morpho-logical similarity and closeness in size to remains of *Stephanorhinus kirchbergensis* from Europe.

Morphological analysis of the dental features presented and comparison with extant typical browsers and grazers (Fortelius, 1982; Clauss et al., 2008) show the shift towards the browsers in the material studied. On the other hand, it would be an oversimplification to assume that *Stephanorhinus kirchbergensis* was exclusively a forest dweller. The diet of *S. kirchbergensis* contained a high percentage of abrasive food, as is observed from mesowear analysis of European remains (Hernesniemi et al., 2011; Kahlke and Kaiser, 2011;
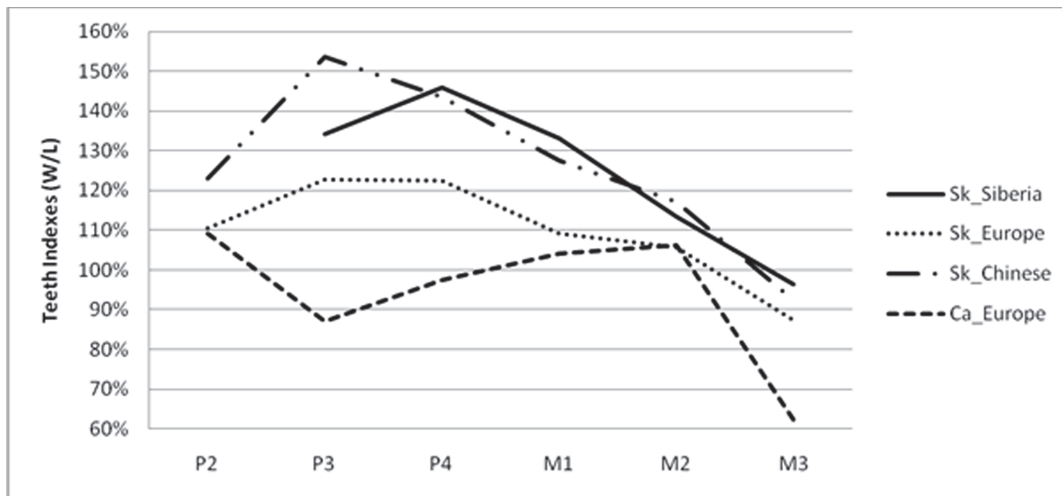
FIGURE 30. Indexes of the upper permanent teeth of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from Siberian, European, and Chinese regions.

van Asperen and Kahlke, 2014); these analyses showed significant dietary flexibility that depended on the quality of the ecological environment. At the same time, morphological features and mesowear signals of *S. kirchbergensis* inhabiting Europe in the Late Pleistocene indicate a higher dietary specialization shifted to browsers, compared with the early and Middle Pleistocene. Mesowear analysis of the dietary preferences of Siberian *S. kirchbergensis* also shows their higher dietary specialization, comparable to mesowear signals of *S. kirchbergensis* from the beginning of the Late Pleistocene in Europe from Weimar-Taubach (van Asperen and Kahlke, 2014). However, the heavy continental climate of Siberian regions and the poorer food base contributed to the process of *S. kirchbergensis* adaptation to the local environment. In addition to the increased molar row length, characteristic of *S. kirchbergensis* in all regions of their habitat, representatives of the Siberian region tend to increase the relative width of the upper and lower molars (Figures 30, 31). Thus, the increase in the occlusal surface area is observed. It allowed increasing the volume of the processed food per unit of time and adapting to the poor food base. According to the results of mesowear analysis, unlike *Coelodonta antiquitatis, S. kirchbergensis* could not inhabit West Siberia in the periods of tundra–steppe habitat conditions. The structure and relief of the occlusal surface of teeth show that *S. kirchbergensis* had not adapted to using strongly abrasive vegetation. Even in the interglacial periods, it probably had to disperse to the more southerly areas, for the same reasons. The results of the

stable isotopic study of the single sample of the Siberian *S. kirchbergensis* indicate that it was a browser-type that fed presumably in predominantly open landscapes.

Despite overall similar mesowear signals for *Stephanorhinus kirchbergensis* in the Siberian region and in Europe at the beginning of Late Pleistocene (MIS 5e), it cannot be stated with certainty that *S. kirchbergensis* existed contemporaneously in Siberia and Europe. A variety of landscape and climatic conditions and interspecies competition had led to significant variability of Pleistocene rhinoceroses' feeding behavior (van Asperen and Kahlke, 2014). This circumstance does not allow extrapolating the paleoecological assessments gained from the European materials to Siberian representatives of *S. kirchbergensis.* On one hand, all the remains of *S. kirchbergensis* previously found in southeastern West Siberia (Kemerovo and Tomsk Provinces) (Alekseeva, 1980; Shpansky and Billia, 2012) and on Vilyuy River (Dubrovo, 1957) were assigned to the Middle Pleistocene, based on accompanying fauna, including *Mammuthus* ex gr. *trogontherii-chosaricus, Megaloceros giganteus ruffi,* and *Equus* ex gr. *mosbachensis-germanicus.* In addition, it can be noted that the degree of fossilization of the existing Middle Pleistocene residues agrees to a certain extent with the degree of fossilization of new remains of *S. kirchbergensis* from the Altai Territory and Novosibirsk Province. On the other hand, although the latest findings of *S. kirchbergensis* on the beaches from Altay Territory and Novosibirsk Province do not have a stratigraphic linkage, it is
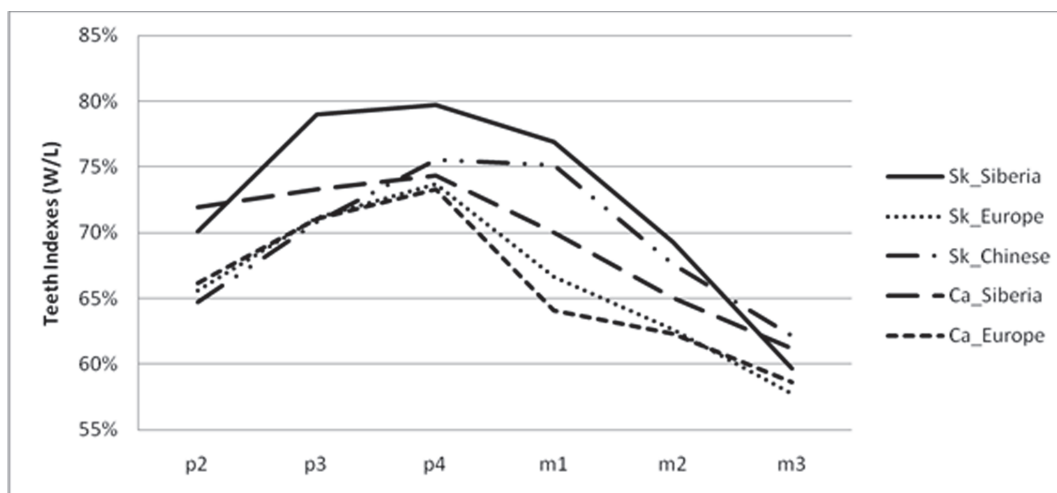
FIGURE 31. Indexes of the lower permanent teeth of *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* from Siberian, European, and Chinese regions.

characteristic that the accompanying fauna of all these locations is mainly from the Late Pleistocene, and there are very few remains of the Middle Pleistocene megafauna.

However, until now, none of the finds related to *Stephanorhinus kirchbergensis* discovered in Siberia has been unequivocally attributed to the Late Pleistocene. Quantitative data on the chemical composition of the sample from the Middle Irtysh give an indirect indication that individual specimens of *S. kirchbergensis* could have existed in West Siberia in the Late Pleistocene. To date, we can assert that despite its small number, the population of *S. kirchbergensis* was distributed fairly widely in Siberia in the places most favorable to their dietary preferences—river valleys with rich bush vegetation.

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