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MORPHOMETRIC CONSIDERATIONS OF THE TEETH OF THE PALAEOCASTORINE BEAVERS *CAPACIKALA*, *PALAEOCASTOR* AND "*CAPATANKA*"

Clara Stefen

ABSTRACT

A morphologic and morphometric study of teeth of some beavers of the group of Palaeocastorinae is presented in order to demonstrate that statistic analyses of tooth parameters could contribute to a better understanding of this group of beavers. The focus was laid on larger samples of *Capacikala gradatus*, *Palaeocastor nebrascensis* and "*Capatanka*" *cankpeopi*. Additionally, some cranial measurements are briefly considered. Overall morphology of the teeth is very similar in the three genera and can hardly be used to differentiate the considered taxa. Except for hypo- and mesostriae, striae in general are rare in the available material. Whether their rarity is due to how few unworn or little worn teeth are available, or due to the lack of these structures is unclear. Striae thus cannot be considered of taxonomic value in this group. Likewiese, neither the presence of anterior or posterior fossettes, nor their shape and orientation are taxonomically diagnostic.

The discriminant analysis of wear-independent residuals showed some separation of *Capacikala gradatus*, "*Capatanka*" *cankpeopi* and *Palaeocastor nebrascensis* with reasonable sized samples, but not all statistically significantly. The separation of all studied taxa on the basis of the wear-independent residuals of teeth showed some power to separate groups, but here the influence of the differences in sample seizes might be too strong to make clear statements. Also the comparison of tooth row length did not give a clear size separation between all taxa. Size data on skulls are limited and may not represent the real variation.

The data of tooth morphometry indicate similarities between *C. cankpeopi* and *C. magnus* thus their taxonomic status should be reviewed. Also the differentiation between *Capacikala parvus*, *Capacikala gradatus* and *Capatanka minor* should be reviewed as well as the species assignments in *Palaeocastor*. Material assigned to *Palaeocastor* sp. could be separated into three size forms. *P. fossor* is clearly separated.

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INTRODUCTION

Castoridae are known from the late Eocene or early Oligocene to modern times with varying numbers of genera; one today and over 23 described from the Tertiary (McKenna and Bell 1997). The earliest radiation of beavers was the one of palaeocastorine beavers (Subfamily Palaeocastorinae Martin 1987) known from North America only. Xu (1996) saw *Agnotocastor* (Stirton 1935) as sister taxon to this subfamily of beavers, Rybczynski (2007, figure 3) indicated Castorinae and Castoroidinae as sister groups to *Agnotocastor* sp. and Palaeocastorinae. The phylogenetic relationship within this subfamily is still little resolved. Korth (2001) included *Palaeocastor* (Leidy 1869), *Euhapsis* (Peterson 1905), *Capacikala* (MacDonald 1963), *Fossorcastor* (Martin 1987) and *Pseudopalaeocastor* (Martin 1987) (Xu 1996 assigned this to *Nannasfber* Xu 1996) in this subfamily. A review of the group was given by Martin (1987). In more recent reviews of Castoridae, *Capacikala* and *Palaeocastor* were retained as separate genera by McKenna and Bell (1997). The synonymization of *Capatanka* (McDonald 1963) to *Palaeocator* suggested by McKenna and Bell (1997) has been followed by Korth (2001) and Rybczynski (2007).

Geographically these Palaeocastorinae come from Oregon, South and North Dakota, Wyoming and some from Nebraska. Stratigraphically the earliest occurrence of this group is in the Whitneyan, Latest Oligocene: *Palaeocastor nebrascensis* (Leidy 1869) from the Mauvaises Terres of White River, represented by fragmented skulls and jaw material and teeth (Leidy 1869:338, pl 26, figures 7, 8); now not numbered at the Academy of Natural Sciences in Philadelphia (Xu 1996). The Palaeocastorinae are known to be fossorial, and some species are directly associated with the burrows *Daimonelix* Barbour 1892 (Martin and Bennett 1977; Martin 1994).

The genus *Capacikala* was nominated about 40 years ago by MacDonald (1963) and has been included in the revision of palaeocastorine beavers by Martin (1987) and in the analysis of Castoridae by Xu (1996) but it still seems poorly understood. There is ample material from the Wounded Knee, Sharps Formation (Martin 1987) and some from Muddy Creek Wyoming (Xu 1996) and the John Day Formation. "*Capatanka,*" also nominated by McDonald, has been synonymized to *Palaeocastor*, and other species have been assigned to different genera by different authors indicating difficulties in understanding this group of beavers. A good understanding is further complicated by the nomination of several new species that are scarcely illustrated and documented only with little material and few measurements, but some details on the infraorbital foramen and lower jaws are explained in Martin (1987) and Xu (1996).

I discuss the subject of teeth in this report because it is not discussed in great detail anywhere. More specifically, morphology and morphometry of larger samples of teeth are focused on here. Discriminant analyses of several measurements can help to reveal taxonomic differences. The goal of this study is to better understand the systematics of palaeocastorine beavers, especially those assigned to *Palaeocastor*, *Capacikala* and "*Capatanka*" mainly on the basis of tooth morphology and morphometry under consideration of wear stages of the material. Some aspects of skull morphometry will also be considered and discussed to hopefully contribute some new aspects to the discussion of the taxonomic status of these beavers.

MATERIAL AND METHODS

A detailed revision of the Palaeocastorinae has not been attempted in this report because the study of much more material than was feasible would be required. Taxonomy of this group of beavers has not been uniformly treated in recent literature and here I follow the classification of Martin 1987 and McKenna and Bell (1997). Only "*Capatanka*" – synonymised to *Palaeocastor* – is retained written in quotations marks here for clarity. The following taxa have been used, particularly *Capacikala gradatus* (Cope 1879), *Palaeocastor nebrascensis* and "*Capatanka*" *cankpeopi* McDonald (1963) with larger samples. Less material could be studied of *Capacikala parvus* (Xu 1996), "*Capatanka*" *minor* (Xu 1996), "*Capatanka*" *magnus* (Romer and Cormack 1928), "*C*". *minor* Xu 1996, *Palaeocastor peninsulatus* (Cope 1881), *Palaeocastor fossor* (Peterson 1905) (assigned to *Fossorcastor* Martin 1987 by Xu (1996)), *Pseudopalaeocastor barbouri* (Peterson 1905) (assigned to *Nannasfiber* (Xu 1996) by Xu (1996)).

Material of *Palaeocastor*, *Capacikala* and "*Capatanka"* was studied in the collections of the South Dakota School of Mines and Technology (SDSM), Los Angeles County Museum (LACM), Museum of Palaeontology, University of California Berkeley (UCMP), American Museum of Natural History (AMNH) and Frick Collection of Mammals in the AMNH (F:AM) and the collection of the University of California in Riverside. Material from SDSM and LACM were assigned to the taxa according to MacDonald (1963) and Xu (1996) where possible. Data for some species (not included in all statistical analyses) were taken from Martin (1987) and Xu (1996). Material of Recent *Castor fiber* Linné 1758, sometimes referred to in comparisons, was studied in the Museum of Zoology Dresden (MTD) and Zoological collection of the University of Halle-Wittenberg, Germany.

Teeth were measured to the nearest 0.01 mm using a digital calliper at the occlusal surface and – where possible – at the base of the tooth. As nearly all of the studied teeth were still in the alevoles, the height of the teeth was not considered. The nomenclature of teeth follows Stirton (1935). Notes were taken on the number of flexi/fossettes in the anterior and posterior part of the teeth (the paraflexus/fossette or flexid/fossetid, respectively, represents 1 anterior "fossette" and the metaflexus/fossette or metaflexid/fossetid, respectively, represents 1 posterior "fossette") and the presence of striae/striids in unworn or few worn teeth. To avoid lengthy descriptions, the term "fossette" in quotation marks is used in generalized way to include flexus, fossette, flexid and fossettetid respectively, referring to the enamel island in a certain position of the tooth irrespectively of its closure or whether an upper or lower tooth is considered. Uppercase letters represent maxillary teeth, and lower case letters represent mandibular teeth.

Beaver teeth are known to change in the pattern of enamel islands on the occlusal surface and size from the tip to the base (Stirton 1935; Crusafont Pairo 1948; Stefen 1997). To make interspecific comparisons, using specimens of the same age would be ideal. In fossils, determination of the individual age is generally difficult, but a scheme to determine age is desirable. Therefore, the studied teeth were grouped according to tooth wear and thus ages into four age or wear classes. The studied species all have brachydont to subhypsodont teeth so that it is assumed that similar wear stages determined on the basis of morphology of the teeth could represent similar ages, and a similar time span can be assumed to elapse between these stages. That would be more difficult if beaver species with subhypsodont and hypsodont teeth were compared. These wear stages used here to group the material are: unworn – no wear can be observed; tooth crown usually not of full height; if these teeth are in the jaw they have not reached occlusion yet; slightly worn – little wear can be observed and the chewing surface is flat showing the typical pattern of flexids; medium worn – mesoflexus/id is closing or just closed; heavily or strongly worn – hypoflexus/id is closing or closed (Stefen 2001; Stefen and Mörs 2008). Comparative data of other taxa from the literature without given wear stages could not be used in the statistical analyses.

The general change of beaver teeth with wear indicates strong correlation of the measured parameters with wear and age. Therefore, a method was searched to eliminate or at least minimize the influence of wear from the data and make teeth of different wear stages easily comparable. It should also help to make it easier to compare species better represented by teeth of different wear stages. Thus, linear regressions of all the length and width measurements against age (the four wear stages) were performed and the resulting unstandardized residuals were saved and used in further tests. For teeth of undetermined wear stages, no unstandardized residuals were saved. Discriminant analyses (DFAs) of different sets of taxa and unstandardized residuals were used to see how well taxa could be differentiated. The DFAs were completed using Wilk's lambda statistics, entry of all variables at once not stepwise, with equal prior probabilities of groups and covariance within groups. A χ^2 test in cross tables (including all studied taxa) testing the significance of the number of anterior or posterior "fossettes" against wear stage was performed.

All statistical analyses were performed using SPSS 13.

RESULTS

Morphology of the teeth

The cheek teeth of the studied taxa are all brachydont to subhypsodont and relatively low crowned. Lots of the studied teeth are medium to strongly worn and only for some taxa unworn or little worn teeth were observed. The available teeth of the different taxa were not of similar wear stage (e.g. Figure 1).

Some representative dentitions of *Capacikala*, "*Capatanka*" and *Palaeocastor* arranged with increasing wear are illustrated in Figures 2-5. The premolars are the largest teeth in the tooth rows, but especially, with little wear, the size difference to molars is small. Whereas germs of all mandibular cheek teeth are slightly rectangular, slightly longer than wide, with wear the lower molars m1/2 become more and more square, m3 more or less rounded. The same can be observed in the maxillary cheek teeth, but here molars M1/2 are more square in the beginning and become more oval (broader than long) with wear and M3 more trian-

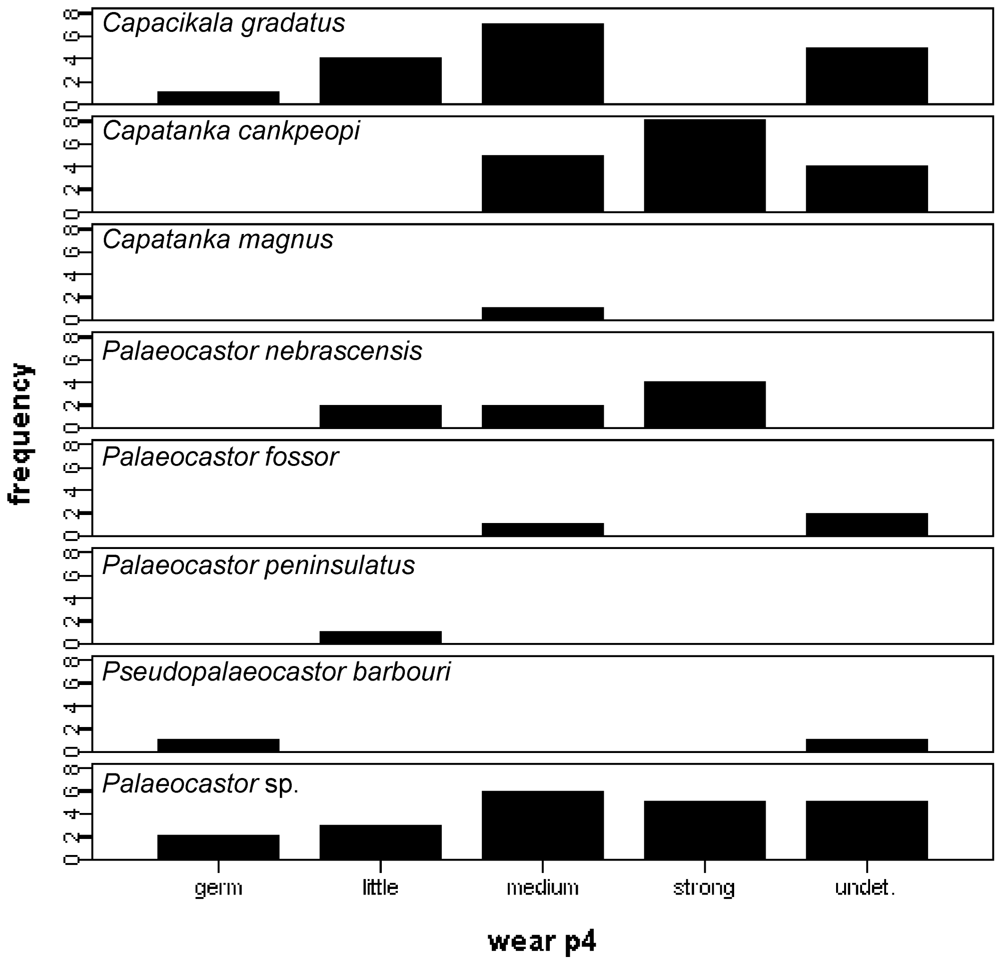


FIGURE 1. Frequency distribution of wear stages of p4 of the studied taxa. The determined wear stages are 0 to 3, 9 is of undetermined wear.

gular or rounded. The tendency to develop oval M1/2 with wear seems to be strongest in *Palaeocastor* and here also the M3 seem to be more oval than in the other taxa.

Overall, the morphology of the cheek teeth appears quite similar and comparatively simple with para-“fossette”, meso-“fossette”, meta-“fossette” and hypoflexus/id when little to strongly worn. The meta-“fossette” tends to be lost in strongly worn teeth, especially in maxillary teeth. Tooth germs and teeth with little wear are slightly more complex in the occulsal pattern, (e.g. *Capacikala gradatus* SDSM 53343), sometimes with irregular mesoflexids and connections between “fossettes.” The parafossettes are more variable in form, often hook-shaped, in p4 than in m1-3, where they are straighter and more or less rectangular to the lingual side of the tooth. They are long, nearly extending from side to side of the tooth in little to medium worn lower cheek teeth, but become shorter in medium to strongly worn teeth.

In maxillary tooth rows P4 is the largest tooth. This becomes more pronounced with wear. Most medium to strongly worn upper molars show only hypoflexus/fossette and mesofossette, strongly diagonally oriented and sometimes curved.

The number of fossettes in the anterior and posterior part of the teeth is given in Table 1. Due to little material in some cases it was not attempted to differentiate according to wear stage here. The Chi^2 test including all studied taxa indicates no significant correlation between wear stage and number of anterior fossettes in p4 and P4 and to posterior fossettes in p4, m3, P4, and M1/2. Overall more variability in the number of fossettes can be observed in teeth of no or little wear.

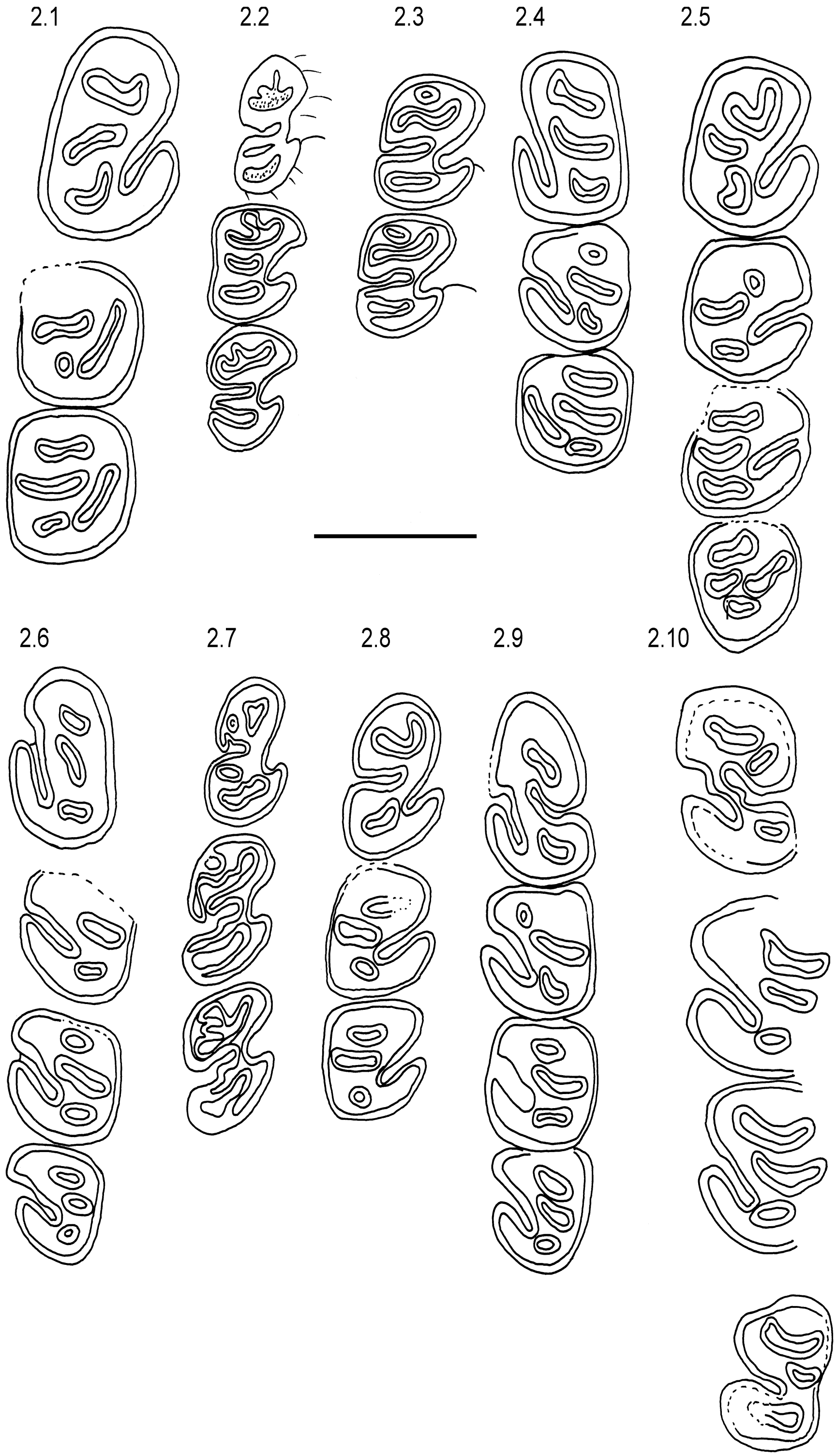


FIGURE 2. Drawings of mandibular dentitions of representatives of *Palaeocastor* or *Capacikala* and *Capatanka*. 2.1) *Palaeocastor* UCMP 65195; 2.2) *Palaeocastor* or *Capacikala* SDSM 5437; 2.3) *Palaeocastor* or *Capacikala* SDSM 5438; 2.4) *Palaeocastor* sp. SDSM 5475; 2.5) *Palaeocastor* sp. SDSM 55115; 2.6) *Palaeocastor* sp. SDSM 62431; 2.7) *Palaeocastor nebrascensis* UCMP 114451; 2.8) *Palaeocastor nebrascensis* UCMP 114461; 2.9) *Palaeocastor* sp. SDSM 54235; 2.10) *Capatanka* sp. SDSM 5672. Scale bar = 5 mm.

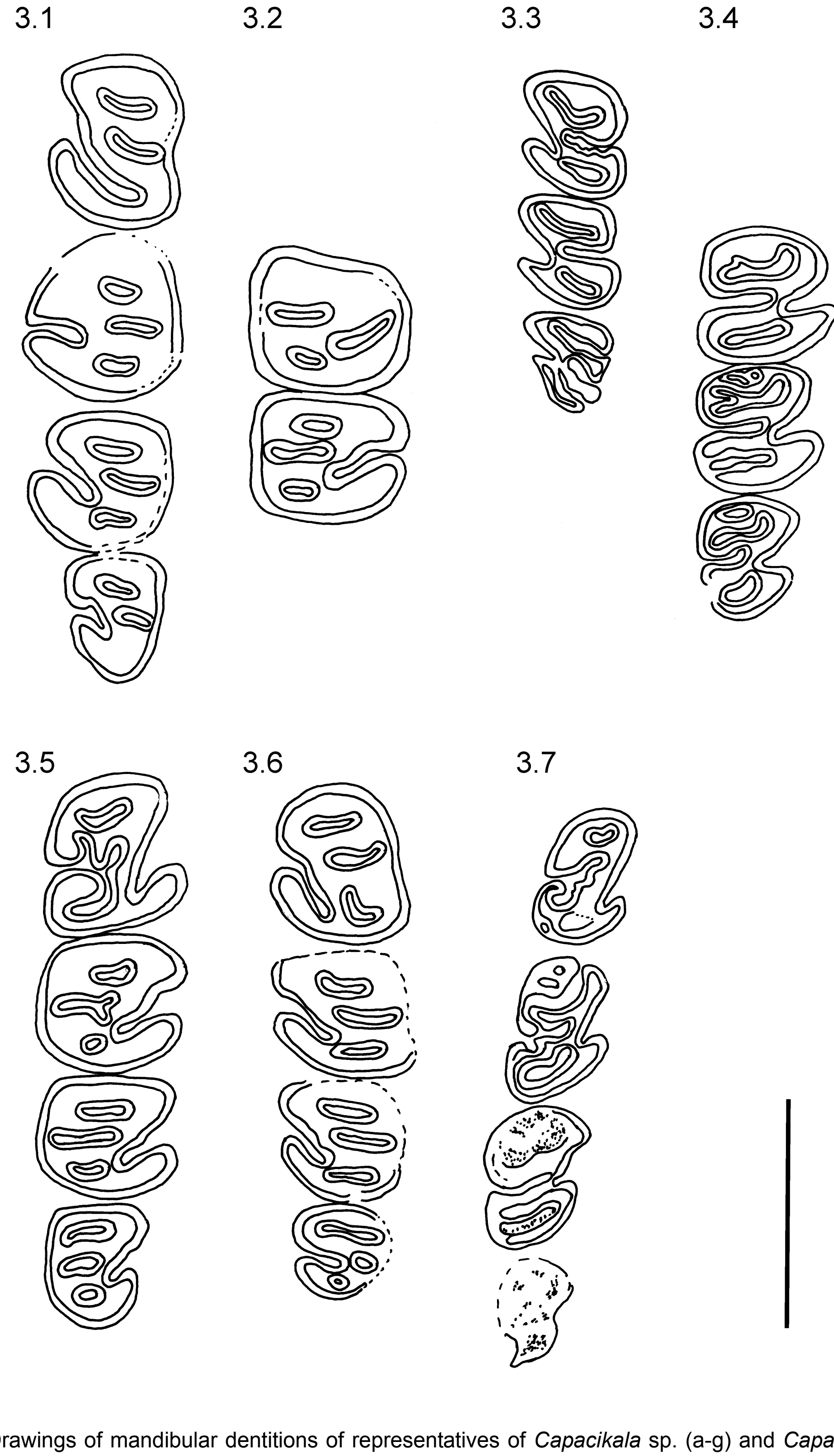


FIGURE 3. Drawings of mandibular dentitions of representatives of *Capacikala* sp. (a-g) and *Capatanka* (h-i). 3.1) SDSM 55109; 3.2) SDSM 53375; 3.3) SDSM 53339; 3.4) SDSM 5455; 3.5) SDSM 5448; 3.6) SDSM 5695; 3.7) SDSM 53343. Scale bar = 5 mm.

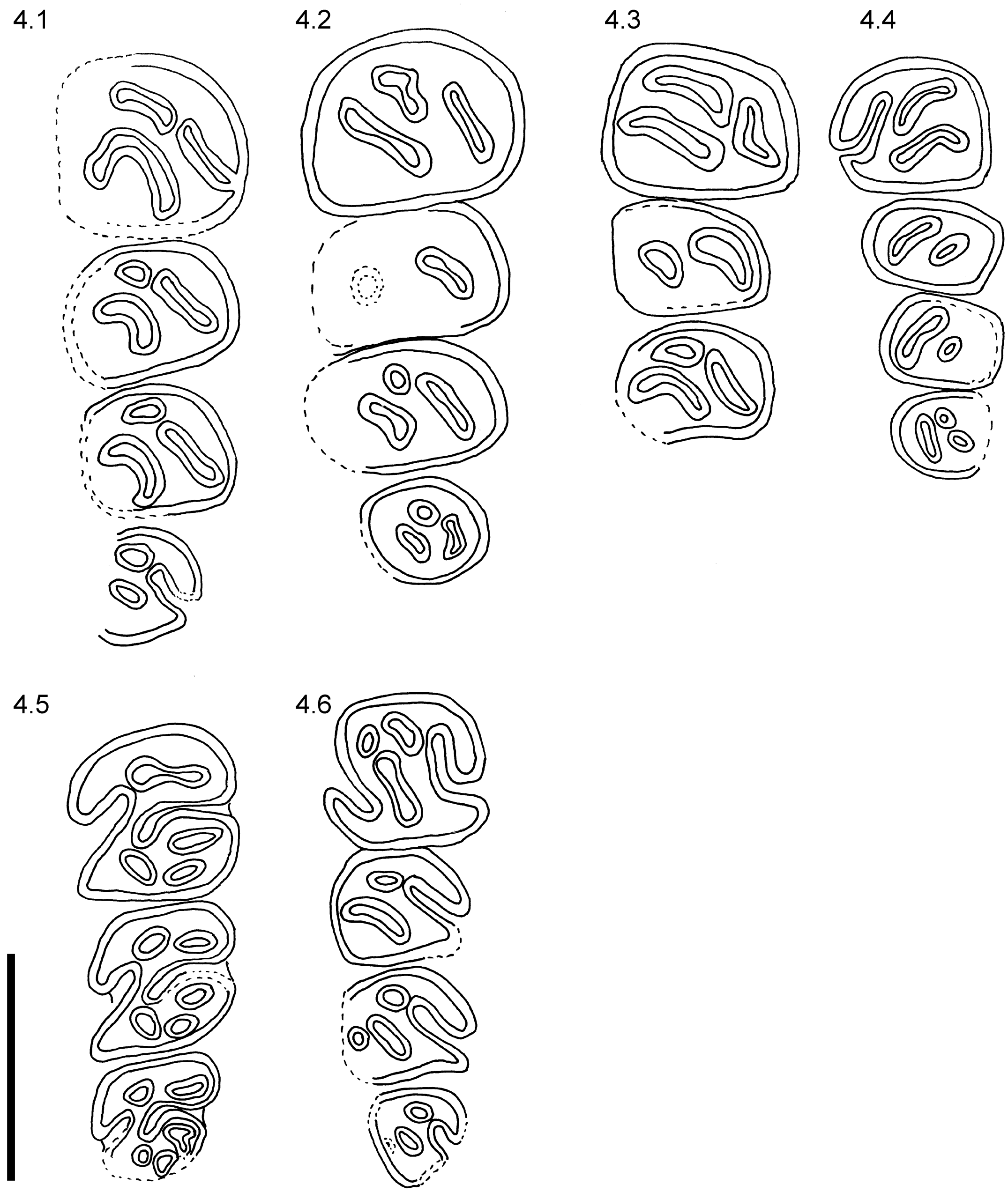


FIGURE 4. Drawings of maxillary tooth rows of *Capacikala* sp. 4.1) SDSM 55108; 4.2) SDSM 53344; 4.3) SDSM 5483; 4.4) F:AM 64552; 4.5) SDSM 5426; 4.6) SDSM 5489. Scale 5mm.

Besides hypostiae/iids and mesostriae/iids, short notches were observed in only a few cases: a metastriid was found on the m3 of *Capacikala gradatus* (SDSM 5982); a parafossette with an anterior opening was found on the p4 of *Palaeocastor nebrascensis* (UCMP 114452) and *P. fossor* (F:AM 64188); a short parastriid or a lateral opening of a paraflexid was found on p4 of *Capacikala gradatus* (LACM 9595); a parastriid and metastriid was found on m3 of the same species (LACM 9405); and a probable metastriid was found on m3 of *Palaeocastor* sp. (LACM 9494). No such notches were observed in *"Capatanka" cankpeopi.*

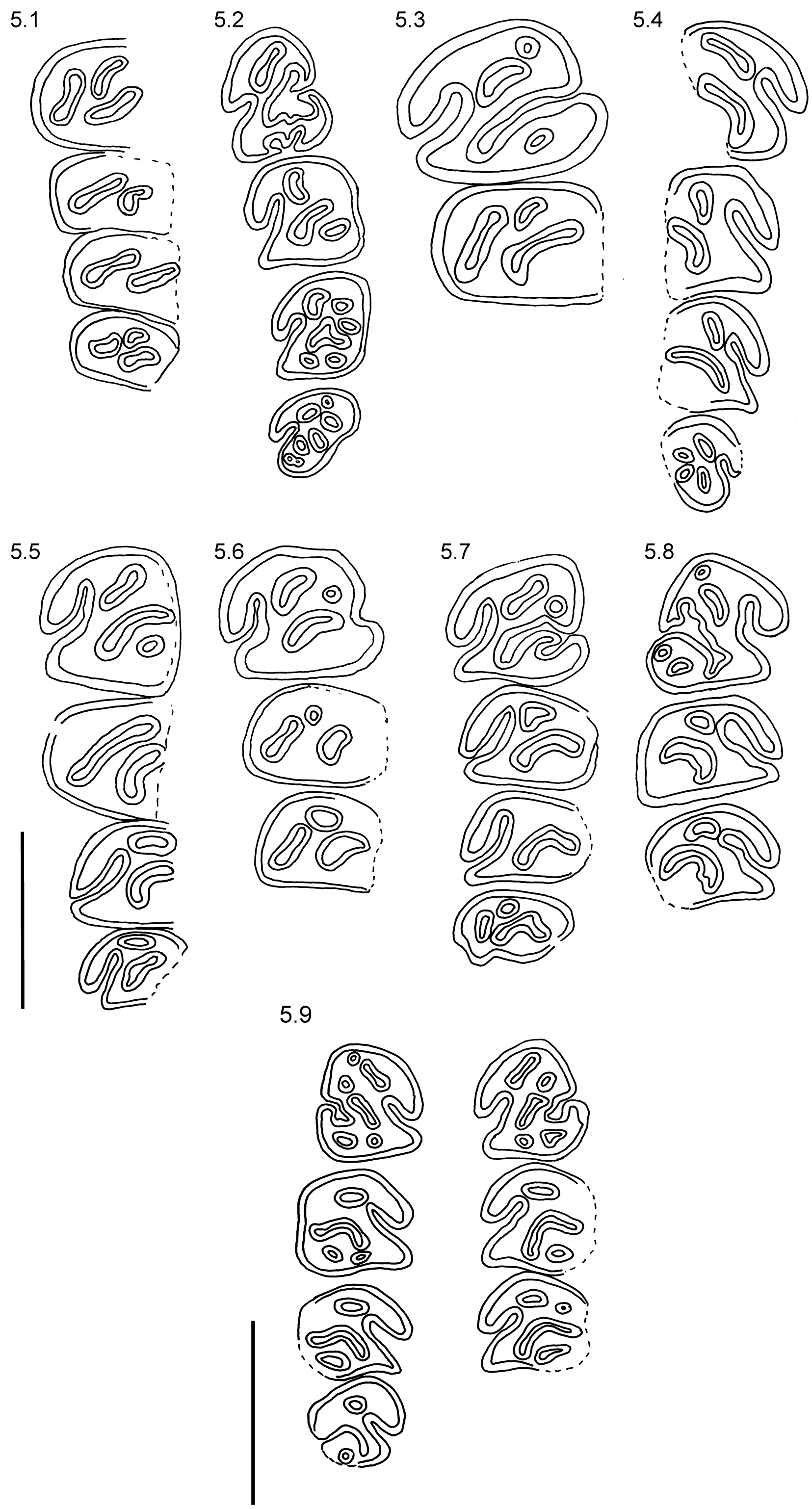


FIGURE 5. Drawings of maxillary tooth rows of *Capatanka* sp. (5.1-5.4) and *Palaeocastor* (5.5-5.9). 5.1) *Capatanka* sp. SDSM 53421; 5.2) *Capatanka* sp. SDSM 53512; 5.3) *Capatanka* sp. SDSM 5440; 5.4) *Capatanka* sp. SDSM 5672; 5.5) *Palaeocastor* sp. SDSM 55115; 5.6) *Palaeocastor* sp. UCMP 114785; 5.7) *Palaeocastor* sp. SDSM 53378; 5.8) *Palaeocastor* sp. SDSM 54235; 5.9) *Palaeocastor nebrascensis* UCMP 114635 right and left dentition. Scale bar = 5 mm.

TABLE 1. Frequency of anterior and posterior "fossettes" in taxa with more material in absolute numbers and percentages. No separate counting was performed differentiated to wear stage. w. s. – wear stage of teeth as far as determined; undet. – teeth of undetermined wear stage.

				Anterior fossettes						Posterior fossettes					
Taxon	**w.s.**	**tooth**	**n**	**0**	**1**	**2**	**3**	**>3**	**undet.**	**0**	**1**	**2**	**3**	**>3**	**undet.**
Capacikala gradatus	0-2	m1,2	31		17	9	3		2		28	1			2
Capacikala gradatus		m1,2	100%		54.8	29	9.6		6.5		90.3	3.2			6.5
Capacikala gradatus	0-2	p4	19		9	3		1	4		10	2	1	1	4
Capacikala gradatus		p4	100%		47.4	15.8		5.3	21.1		52.63	10.5	5.3	5.3	21.1
Capacikala gradatus	0-2	m3	23		12	9			2		20				3
Capacikala gradatus		m3	100%		52.17	39.1			8.7		86.9				13
Capacikala gradatus	2-3	M1,2	16	1	12				3	10	3				3
Capacikala gradatus		M1,2	100%	6.2	75				18.75		18.75				18.75
Capacikala gradatus	1, 3	M3	6	1	2		2		1	3			2		1
Capacikala gradatus		M3	100%	16.6	33.3		33.3		16.6	50			33.3		16.6
Capacikala gradatus	2, 3	P4	8	2	5				1	6	1				1
Capacikala gradatus		P4	100%	25	62.5				12.5	75	12.5				12.5
Captanka cankpeopi	2-3	m1,2	38	10	16			1	9	3	25			1	9
Captanka cankpeopi		m1,2	100%	26.3	42.1			2.7	25	7.9	65.7			2.7	25
Captanka cankpeopi	2-3	p4	17	2	8	4			2		14	1			1
Captanka cankpeopi		p4	100%	11.76	47.1	25			12.5		87.5	6.25			6.25
Captanka cankpeopi	2-3	m3	14	2	9				3	1	10				3
Captanka cankpeopi		m3	100%	14.3	64.3				21.4	7.1	71.4				21.4
Captanka cankpeopi	1-3	M1,2	13	1	6	4			1	1	4	3	3		2
Captanka cankpeopi		M1,2	100%	7.7	46.2	30.8			7.7	7.7	30.8	23.1	23.1		15.4
Captanka cankpeopi	2-3	M3	6		1	2	3				2	2	2		
Captanka cankpeopi		M3	100%		16.6	33.3	50				33.3	33.3	33.3		
Captanka cankpeopi	2-3	P4	7		2	3	1		1		3	3			1
Captanka cankpeopi		P4	100%		28.6	42.9	14.3		14.3		42.9	42.9			14.3
Palaeocastor nebrascensis	1-3	m1,2	23	3	13	6					23				
Palaeocastor nebrascensis		m1,2	100%	13	56.5	26					100				
Palaeocastor nebrascensis	1-3	p4	8		7		1				8				
Palaeocastor nebrascensis		p4	100%		87.5		14.3				100				
Palaeocastor nebrascensis	0-2	m3	4		4						4				
Palaeocastor nebrascensis		m3	100%		100						100				
Palaeocastor nebrascensis	2-3	M1,2	21	1	17	2	1			10	5	2	2		1
Palaeocastor nebrascensis		M1,2	100%	4.8	80.9	9.5	4.8			47.6	23.8	9.5	9.5		4.8
Palaeocastor nebrascensis	2-3	M3	6		6					5	1				
Palaeocastor nebrascensis		M3	100%		100					83.3	16.6				
Palaeocastor nebrascensis	2-3	P4	13		9	1	1			5	3	2	2		1
Palaeocastor nebrascensis		P4	100%		69.2	7.7	7.7			38.46	23.1	15.4	15.4		7.7

Morphometrics of the Teeth

The length x width diagrams (Figures 6 and 7) illustrate the size of cheek teeth of the studied material. All teeth and teeth of different wear stages have been compared separately. All p4 of *Capacikala gradatus,* "*Capatanka*" *cankpeopei*, *Palaeocastor* sp. and *P. nebrascensis* form one group, with no clear-cut subdivisions, *Capacikala* being the smallest (shorter and less wide) and "*Capatanka*" the largest (Figure 6.1). Teeth of *Palaeocastor* sp. overlap with both other taxa. The one measurement for "*Capatanka*" *magnus* falls well within the size range of "*C*". *cankpeopi*. All length x width data of p4 are parallel to the 45° line, indicating p4s are only slightly longer than wide. The p4 of all taxa increase in length and width with wear. Mandibular p4 of different species of *Palaeocastor* are difficult to differentiate on the basis of the size of teeth (Figure 6.2); even *Pseudopalaeocastor barbouri* falls within this group. Just one strongly worn tooth of *Palaeocastor* sp. is markedly broader (LACM 9305).

The lower molars, separated as m1,2 and m3, also fall within one group parallel but slightly above the 45° degree line, indicating a general near square outline being slightly wider than long with wear. More lower molars than premolars are available, but not of similar wear stages. Therefore, medium to strongly worn m1/2 were compared (Figure 6.3). Teeth of "*Capatanka*" *cankpeoi* and *Capacikala gradatus* fall in separate groups, but teeth of *Palaeocastor* sp. overlap with both (for clarity not shown in the diagram). Even though in general medium worn teeth of *Capacikala gradatus* are larger than little worn ones, there is considerable overlap of small medium worn teeth and little worn ones, which should not occur in one species. According to size of m1/2 (irrespectively of wear) *Palaeocastor* sp., *P. nebrascensis, P. peninsulatus, P. fossor* and *Pseudopalaeocastor barbouri* cannot be separated (Figure 6.4). Looking at m3 of these taxa there seem to be three size groups, two of *Palaeocastor* sp. and *P. nebrascensis* and *P. fossor* together with larger teeth, but less material of these is available (Figure 6.5). In all studied taxa m3 are slightly smaller than m1/2, and morphometric changes in the molars with wear are small. They increase slightly in length and width in *Capacikala*, increase slightly more in width than in length in "*Capatanka*" and *Palaeocastor*.

The upper premolars, mostly medium to strongly worn ones, are generally slightly wider than long. Especially those of "*Capatanka*" *cankpeopi* vary considerably in width (Figure 7.1). The one measurement for "C." *magnus* is larger than for "C". *cankpeopi. Capacikala parvus* falls well within the size range of *C. gradatus* here. Length x width data for M1/2 indicate a large variation in size for *Capacikala gradatus*.

M3 is slightly shorter and less wide than M1/2. Looking at all M1/2 irrespective of wear stage, "*Capatanka*" *cankpeopi* is slightly larger, than *Capacikala gradatus, C. parvus* falls below the range of *C. gradatus* considering the two data overlapping directly with "*Capatanka*" *minor* are not really *Capacikala* (Figure 7.2). M3 of "*Capatanka*" *minor* is clearly smaller than the M3 of *Capacikala parvus*.

Looking at the upper molars on the basis of wear stages, "*Capatanka*" *minor* is smaller than "*C*". *cankpeopi, Capacikala gradatus* and *Palaeocastor nebrascensis* in strongly worn teeth (Figure 7.3), but the medium worn M1/2 fall well within *P. nebrascensis*. Medium worn teeth of *Capacikala parvus* are smaller than little worn teeth of *C. gradatus* but the samples are small.

Discriminant Analysis with Wear Independent Residuals

The descriptive statistics of the unstandardized residuals based on the tooth measurements are given in the Appendix. Using these age-independent residuals either for upper or lower teeth in DFAs shows that separation of the taxa is possible – to some degree.

In a DFA based on the maxillary cheek teeth of the taxa with larger samples, *Capacikala_gradatus*, "*Capatanka*" *cankpeopi* and *Palaeocastor nebrascensis* these seem to separate well, but there is no statistical significance for the functions (Figure 8). Using mandibular teeth in the DFA (Figure 9) the means of these three taxa are well separated along function 1 (mainly influenced by the residual based on length of p4), is statistically significant, but there are lots of non-grouped cases, including all available taxa (quite different in sample sizes) in the DFA with residuals of maxillary teeth (Figure 10). *Pseudopalaeocastor barbouri* and *Capacikala gradatus* separate well from the others. Using residuals based on lower teeth (Figure 11) *P. nebrascensis* separates strongly from the others along function 2 mainly based on the residual of m1, 2 width.

A DFA with different species originally assigned to *Palaeocastor* and residuals based on mandibular tooth measurements (not shown) indicates separation of *P. nebrascnesis*, and closeness of *P. peninsulatus, P. fossor* and *Pseudopalaeo-*

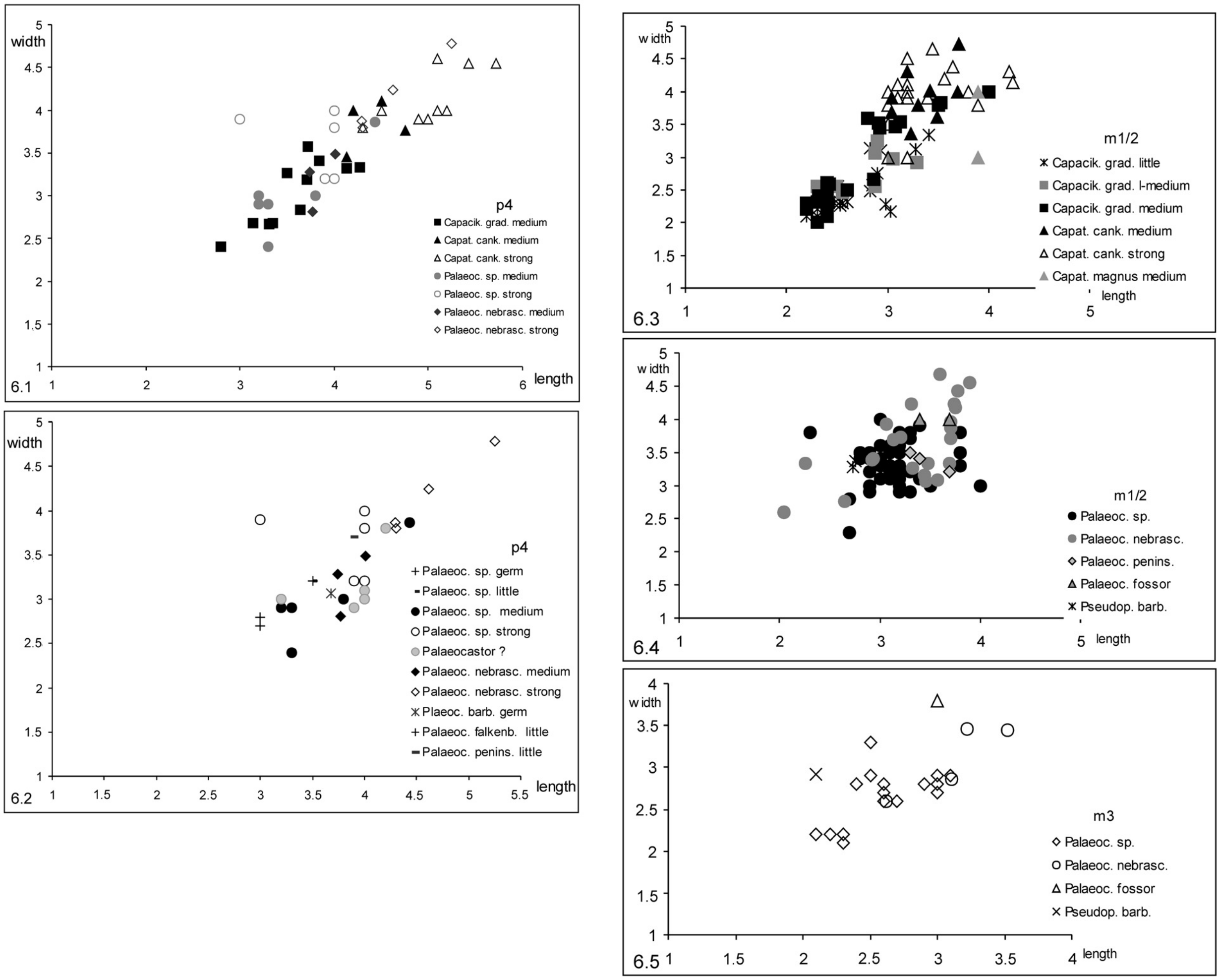


FIGURE 6. Length x width scatter diagrams (in mm) of different teeth of representatives of *Capacikala*, *Capatanka* and *Palaeocastor*. Teeth are differentiated to wear stages. Capacik. – *Capacikala*, grad – *gradatus*, Capat. – *Capatanka*, cank. – *cankpeopi*, Palaeoc. – *Palaeocastor*, nebrasc. – *nebrascensis*, penins. – *peninsulatus*; Pseudop. – *Pseudopalaeocastor*, barb. – *barbouri*, l-m – little to medium worn, m - medium worn, m-s – medium to strongly worn, s – strongly worn. 6.1 and 6.2) lower premolars; 6.3 and 6.4) lower molars 1, 2; 6.5) lower third molars.

castor barbouri based on mandibular teeth. But there is no statistical significance for the functions. A DFA based on maxillary teeth for the same taxa indicates stronger separation, here of *P. nebrascensis* along function 2 based mainly on the residual of length of M3 and *Pseudopalaeocastor barbouri* along function 1 mainly based on the residual of width of P4. In this case functions 1-4 are statistically significant.

Tooth Rows

Few data of tooth row lengths were available and are illustrated comparatively in Figure 12.2. As with individual teeth "*Capatanka*" *cankpeopi* is clearly larger than *Capacikala gradatus*. The size range for the lower dentitions of the larger samples are about 4 mm, still smaller than in the subhypsodont European Early Miocene beaver *Steneofiber eseri* von Meyer 1846. The range for the hypsodont and considerably larger Recent *Castor fiber* is about 10 mm. *Palaeocastor* sp. shows the largest range in size of lower dentitions, *P. nebrascensis* overlaps with "*Capatanka*" *cankpeopi*. The picture for maxillary dentitions is similar, but fewer data were available. The large size range indicated for *Palaeocastor fossor* is based on two measurements only.

Skulls

The morphology of skull material of the considered taxa has been discussed elsewhere (Martin 1987; Xu 1996), and a relevant description in all

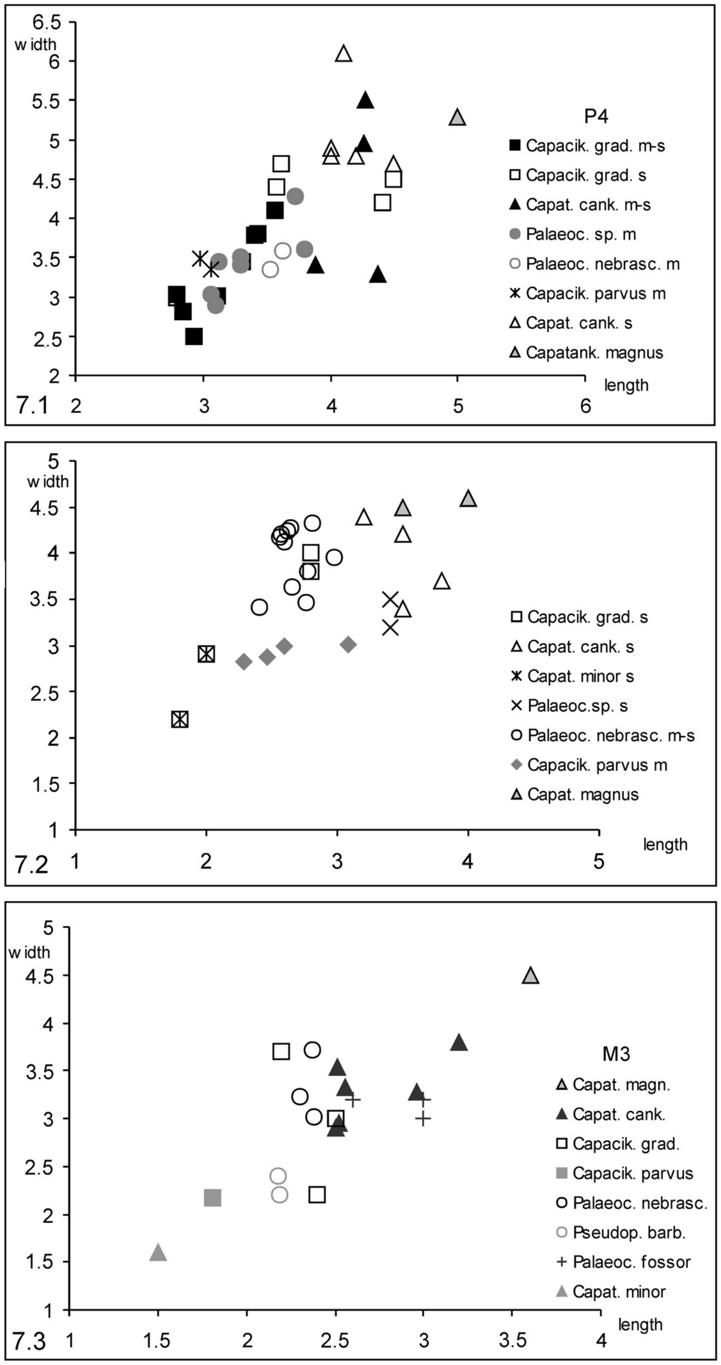
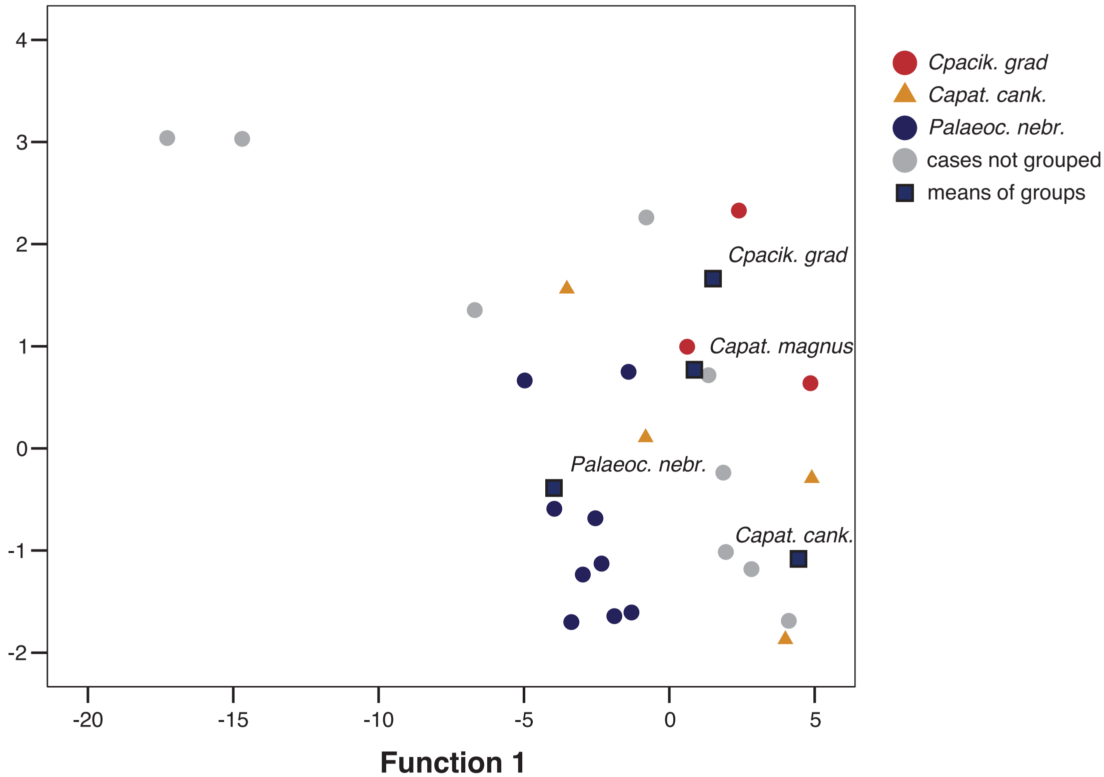


FIGURE 7. Length x width scatter diagrams (in mm) of maxillary teeth of representatives of *Capacikala*, "*Capatanka"* and *Palaeocastor*. Abbreviations as in Figure 6. Data for "*Capatanka*" *magnus* from Martin (1987), therefore without determined wear stage. 7.1. upper premolar; 7.2) upper molar 1,2; 7.3) upper third molar.

detail is beyond the scope of this paper. However, the available data for skull length and zygomatic width are briefly considered in the context of the morphometrics discussion here. Comparing the skull length x width data for some taxa shows that all skulls are nearly as broad at the zygomatic arch as long; this is particularly strong for *Euhapsis* (Figure 13.1). "*Capatanka*" *magnus* is clearly larger than the others. Considering the potential range indicated by two measurements of *Capacikala gradatus* considerable overlap between the nominated species in the length x width ratios of skulls can be assumed. For comparison, the range of the larger

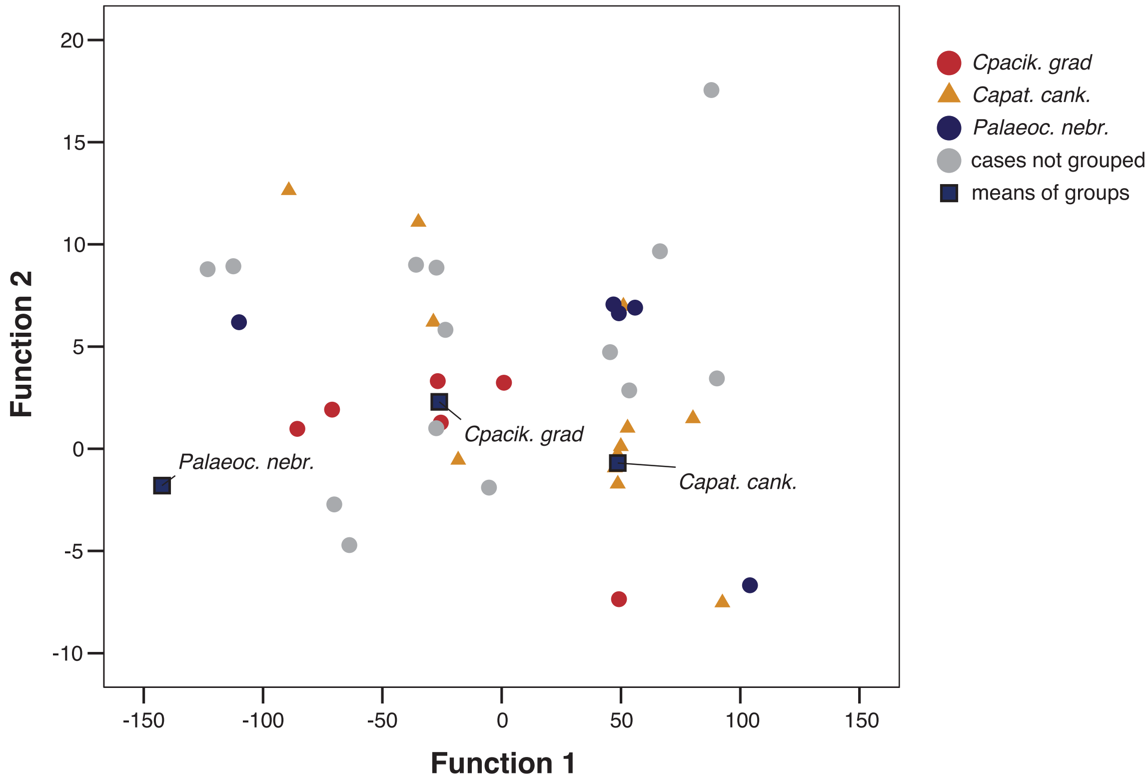


Structure-Matrix

	Function	
	1	2
Res_BM3s†	.581(*)	.234
Res_LMs	.111	.861(*)
Res_LM3s†	.294	.811(*)
Res_BMs	.073	.771(*)
Res_LP4s	.039	.566(*)
Res_BP4s	.137	.444(*)

Common correlation within the groups between discriminant variables
and canonical discriminant functions.
Variables are ordered according to their absolute correlations within the functions
* greatest absolute correlation between each variable and a discriminant function
† Variable not used in analysis.

FIGURE 8. Discriminant analysis using wear-independent residuals based on maxillary teeth of *Capacikala gradatus* (Capacik. gad.), *Capatanka cankpeoi* (Capat. cank.) and *Palaeocastor nebrascensis* (Palaeoc. nebr.) with relatively large samples (see Appendix for details on residuals). Structure Matrix is given, there is no statistical significance for function 1-2 (significance function 1 to 2 0.217, function 2 0.422).

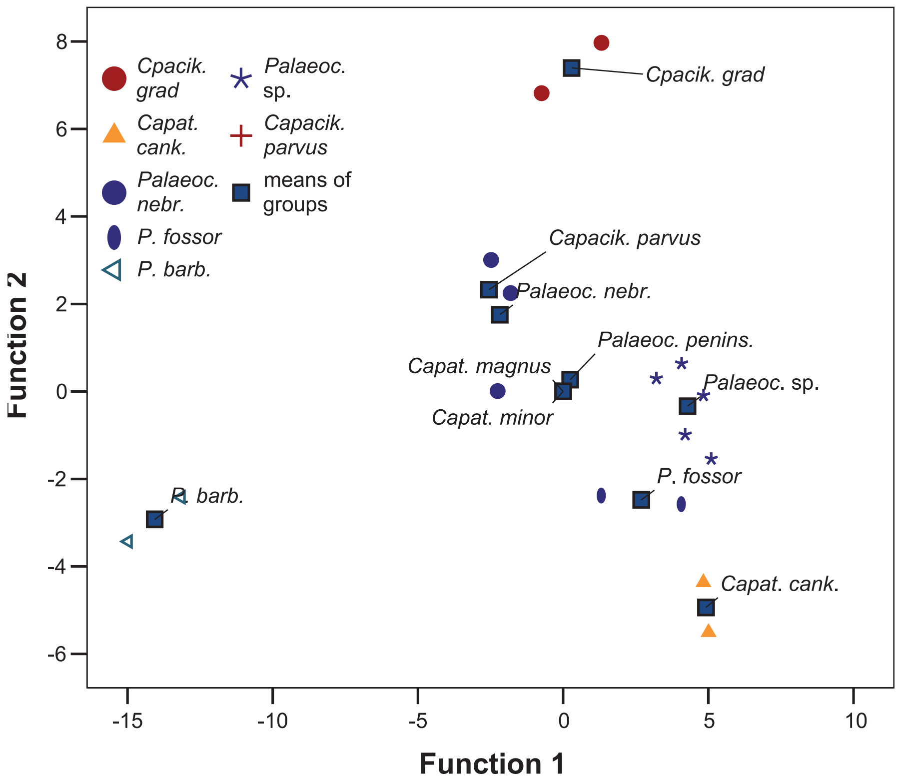


Structure-Matrix

	Function	
	1	2
Res_Bm3i†	.797(*)	-.106
Res_Lm3i†	-.492	-.795(*)
Res_Lp4i	.056	.672(*)
Res_Bminf	.121	.389(*)
Res_Bp4i	.023	.305(*)
Res_Lmi	.063	.110(*)

Common correlation within the groups between discriminant variables
and canonical discriminant functions.
Variables are ordered according to their absolute correlations within the functions
* greatest absolute correlation between each variable and a discriminant function
† Variable not used in analysis.

FIGURE 9. Discriminant analysis based on residuals of measurements of mandibular cheek teeth of the same taxa as in Fig. 8. Structure matrix for function 1 to 2 is given; Statistical significance of function 1 to 2 (significance function 1 to 2 0.001, function 2 0.263). Abbreviations as in Fig. 8.

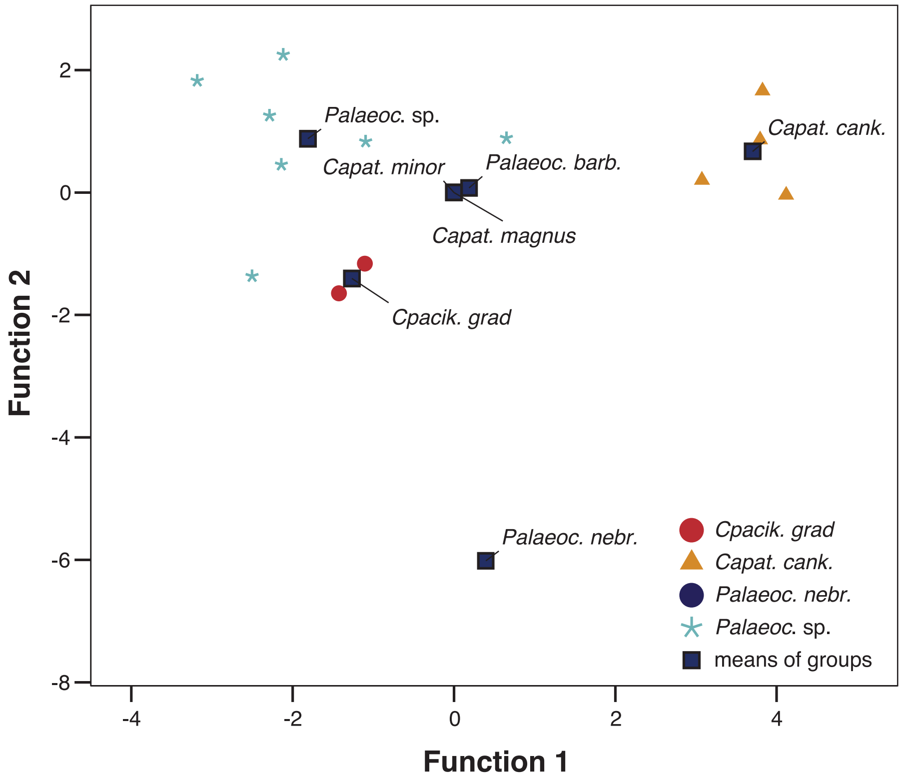


Strukcure-Matrix

	Function					
	1	2	3	4	5	6
Res_LxBM3s	-.037	.672(*)	.086	.589	.423	.113
Res_BM3s	-.015	.670(*)	.502	.140	.381	.366
Res_BMs	-.059	,223	.267	.741(*)	.342	.457
Res_LMs	.084	.272	.243	.661(*)	-.263	.594
Res_LP4s	.098	.224	.090	.270	.135	.917(*)
Res_BP4s	.216	.205	.181	.195	.429	.810(*)

Common correlation within the groups between discriminant variables and canonical discriminant functions.
Variables are ordered according to their absolute correlations within the functions
* greatest absolute correlation between each variable and a discriminant function

FIGURE 10. *Capacikala gradatus* (Capacik. gad.), *Capatanka cankpeoi* (Capat. cank.) and *Palaeocastor nebrascensis* (Palaeoc. nebr.) with relatively large samples, *Palaeocastor* sp. (Palaeoc. sp.), *P. fossor, Pseudopalaeocastor barbouri* (P. barbouri) and *Capacikala parvus* (Capacik. parvus) with smaller samples (see Appendix for details on residuals). The structure matrix for all fucntions 1 to 6 is given, illustrated are function 1 to 2; statistical significance for function 1 to 6 (significance function 1 to 2 0.000, function 2 to 6 0.000, function 3 to 6 0.52, function 4 to 6 0.513, function 5 to 6 0.669 and function 6 0.887).



Structure-Matrix

	Function		
	1	2	3
Res_Lm3i	.291(*)	.279	.193
Res_Bminf	.066	.378(*)	.074
Res_Bm3i	.174	.346(*)	.242
Res_Lmi	.157	.295(*)	.187
Res_Lp4i	-.007	.252(*)	.072
Res_Bp4i	.014	.158(*)	.089

Common correlation within the groups between discriminant variables and canonical discriminant functions.
Variables are ordered according to their absolute correlations within the functions
* greatest absolute correlation between each variable and a discriminant function

FIGURE 11. Discriminant analysis based on residual of measurements of mandibular teeth of the same taxa as in Fig. 10. Structure matrix for all 4 functions are given, illustrated are functions 1-2; statistical significance for function 1 to 4 (significance function 1 to 3 0.004, function 2 to 3 0.25 and function 3 0.164).

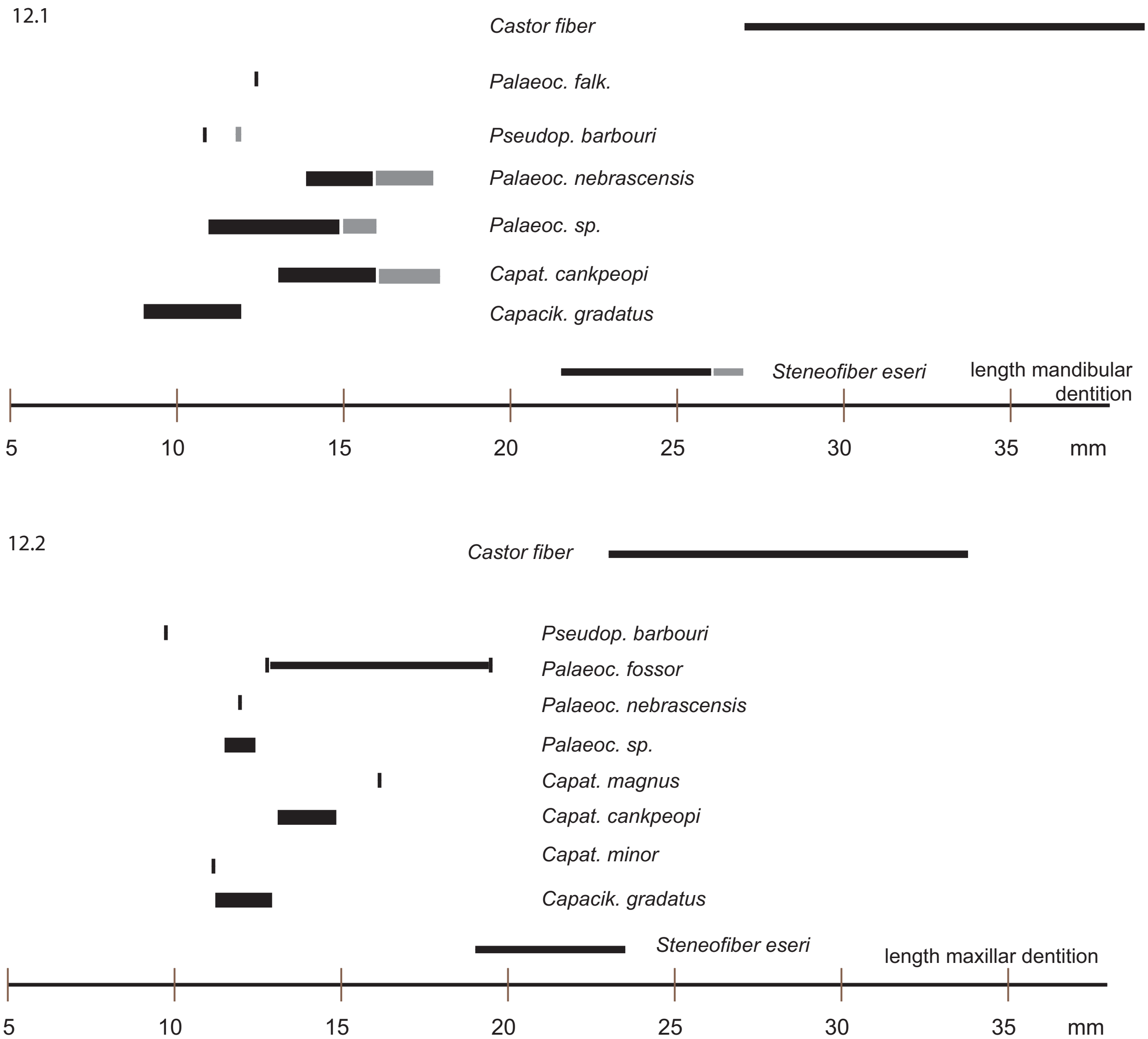


FIGURE 12. Lengths of mandibular (a) and maxillary (b) tooth rows of representatives of *Capacikala* (Capacik.), "*Capatanka*" (Capat.), *Palaeocastor* (Palaeoc.) and *Pseudopalaeocastor* (Pseudop.) (in mm). Black bars represent measurements of tooth rows, grey bars of alveoles. Short vertical lines represent measurements of individual specimens. For comparison ranges of the European Early Miocene *Steneofiber eseri* from Ulm Westtangente, Germany, Earl Miocene and Recent *Castor fiber* are given (data from Stefen 1997, 2009). Data are by the author and some taken from Martin (1987).

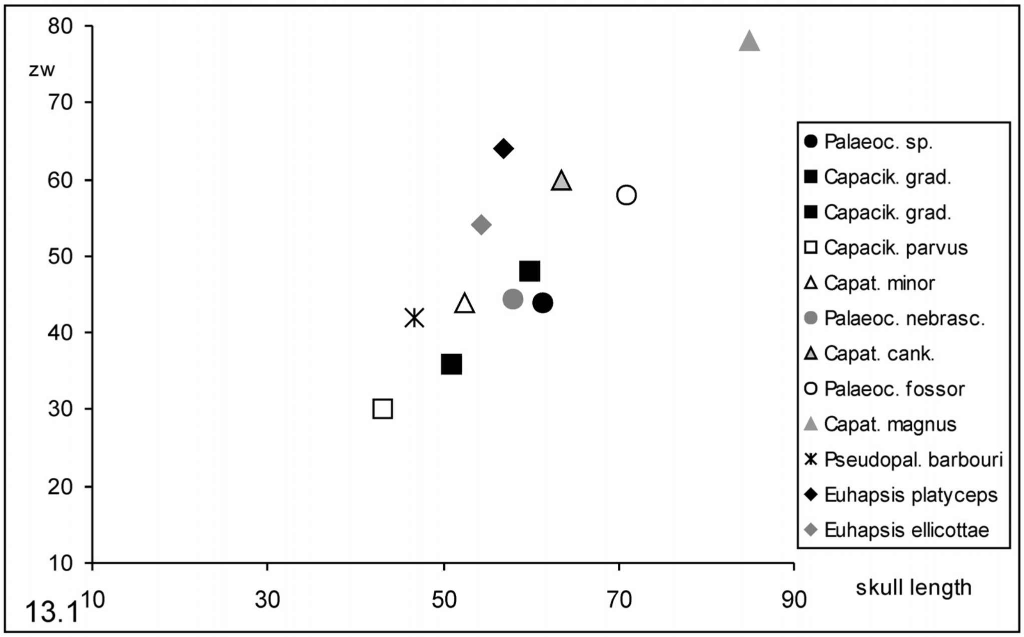
Castor fiber and *C. canadensis* (Kuhl 1820) are given.

DISCUSSION AND TAXONOMY

Even though Martin (1987) noted that dental characters are probably not the best tool for understanding beaver taxonomy, they are considered in particular here in this study, because beaver teeth or fragmentary mandibular and maxillary material with few teeth are generally found more often than complete skulls or fragmented ones with many taxonomically relevant features preserved.

The flattened incisors have been noted as characteristic for fossorial beavers by Stirton (1935). *Euhapsis* and *Palaeocastor* clearly show flat incisors, but *Capacikala* has semi-flat ones, and species assigned to "*Capatanka*" vary between flat and semi-flat (SDSM 53421, LACM 17692). Even the semiaquatic Recent *Castor* is somewhat difficult to classify; lower incisors are more flat-faced than upper ones which are semi-flat, and there are some changes with ontogeny.

The observed para- and metastriae/iids or rather notches are very few. The presence of



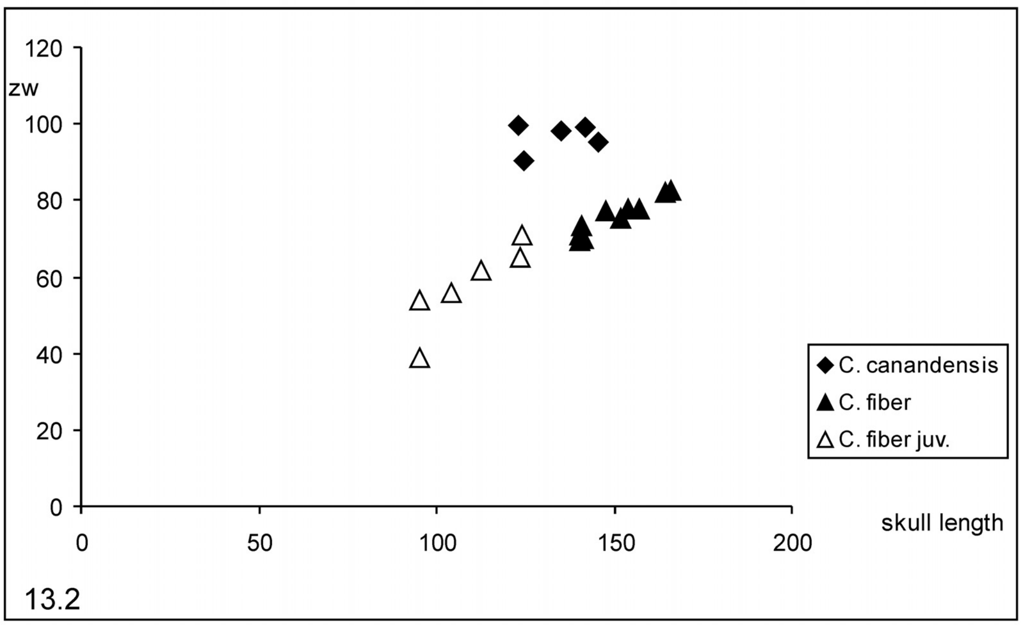


FIGURE 13. Length of skull (maximal length) x zygomatic width (zw) of skulls of some fossil taxa (13.1) and Recent *Castor* (13.2). *Palaeocastor* (Palaeoc.) sp. SDSM 4209, *Capacikala_gradatus* (Capacik. grad.) JODA 621 (black square) and SDSM 5489 (grey square), *Capacikala* (Capacik.) *parvus* and "*Capatanka*" (Capat.) *minor* from Xu 1996 (partially calculated from figure), *Palaeocastor* (Palaeoc.) *nebrascensis* UCMP 114635 and "*Capatanka*" *cankpeopi* (Capat. cank..) LACM 22443., *Palaeocastor fossor*, "*Capatanka*" *magnus*, *Pseudopalaeocastor* (Pseudopal.) *barbouri*, *Euhapsis platyceps* and *E. ellicottae* from Martin (1987). *Castor canadenis* (C. can), *C. fiber* (C. fib) of adults and juveniles (juv) are illustrated; data from Stefen (2009).

striae/iids has been used as a characteristic feature for beavers by Stirton (1935). However, in his diagnosis for *Palaeocastor* he did not include other striae/iids besides hypostria/striid and mesostria/striid, and later authors (Martin 1987; Xu 1996) did not comment on the presence of striae/striids. As they only appear in very early stages of wear, in most material it is difficult to comment on. For *"Capatanka",* which is mainly represented by worn teeth, it is unclear whether short striae/ids or notches other than the hypostriae/iids and mesostriae/iids occur. The lack of extra notches is comparable to Miocene beavers where *Steneofiber eseri* and *S. castorinus* show few very short striae in early stages of wear, and the later *S. depereti* shows longer striae (Stefen 1997).

Comparisons in size of the teeth assigned to *Capacikala*, "*Capatanka*" and *Palaeocastor* respectively show that those of "*Capatanka*" *cankpeopi* are generally larger and those of *Capacikala* smaller. However, a detailed interpretation of length x width data of teeth is complicated by the different sized samples and wear stages present. The length x width data of m1, 2 (Figure 6.3) indicate that probably not all teeth assigned to *Capacikala gradatus* belong to this species as some little and medium worn teeth overlap in small size. But a clear- cut differentiation in two groups is also difficult as some little-medium worn teeth overlap with both possible size groups. For upper P4 *Capacikala parvus*, generally distinguished by smaller size (Xu 1996), falls well within the size range of *C. gradatus*. The size differences are only slightly clearer when teeth of the different wear stages are considered. *"Capatanka"* minor overlaps in size with *Capacikala gradatus* and, to some degree, with *C. parvus.* Whether this size difference alone can be considered a taxonomic distinction is uncertain because M1/2 vary markedly in size in *Capacikala gradatus,* which completely overlap with measurements of teeth assigned to C. gradatus and *"Capatanka" minor.*

The larger samples of *Capacikala gradatus* and *Palaeocastor* sp. show a variability in size comparable to other beavers of different radiations like *Steneofiber eseri* (Stefen 1997). Unfortunately, however, not all taxa could be compared with similar numbers of teeth in the same wear stages. Differentiation between different species of *Palaeocastor* is nearly impossible on the basis of tooth morphometry alone.

The DFAs indicate: *Pseudopalaeocastor barbouri*, "*Capatanka*" *cankpeopi* and *Capacikala gradatus* or rather *Palaeocastor nebrascensis* and "*Capatanka*" *cankpeopi* using maxillary or mandibular teeth separate well, but the other studied species are difficult to differentiate.

Comparison of the lengths of lower and upper dentitions of the studied taxa do not give a clear picture mainly due to small and different sample sizes. For lower dentitions the samples of "*Capatanka*" *cankpeopi*, *Capacikala gradatus* and *Palaeocastor nebrascensis* and *Palaeocastor* sp. seem to give a fairly realistic picture of the natural variation compared to the also subphysodont *Steneofiber eseri*. The larger size range of Recent *Castor fiber* is certainly due to its larger size and hypsodonty, and therefore not a proxi for the fossil palaeocastorine beavers. The few data for *Pseudopalaeocastor barbouri* are at the lower size range, even smaller than "*Capatanka*" *minor* mainly differentiated by its smaller size. Overall the available data on tooth row length do not contribute much to the better understanding of the studied taxa. Not much further clarity can be found concerning the taxa, but that "*Capatanka*" *minor* is similar to *Capacikala gradatus*, several taxa assigned to *Palaeocastor* overlap and "*Capatanka*" *cankpeopi* is the largest.

The few available data on skull width and length of palaeocastorine beavers (Figure 13.1) probably do not represent the natural range of variation in size. Only for *Capacikala gradatus* some variation is indicated. Data for Recent *Castor* indicate a possible range of variation (Figure 13.2), however, certainly larger than for the smaller palaeocastorine beavers. *Capacikala gradatus*, *C. parvus*, *Palaeocastor nebrascensis* and *Pseudopalaeocastor barbouri* are very close. "*Capatanka*" *cankpeopi*, *Palaeocastor fossor* and *Euhapis platyceps* are very close, but larger than the other taxa. All these taxa have a nearly square skull only slightly longer than broad.

McKenna and Bell (1997) included "*Capatanka*" in *Palaeocastor*. The morphometrics of teeth do not contribute well to the systematic status on genus level, but the slight differences on their own would not necessitate a generic differentiation of "*Capatanka*", *Capacikala* and *Palaeocastor*.

Judging from these discussed data alone it seems likely that *C. cankpeopi* and *C. magnus* belong to the same species, "*Capatanka" minor* is more likely to belong to *Capacikala* with slightly smaller and relatively longer skulls. Only *Capacikala parvus* seems clearly smaller than other taxa. The differentiation between *Capacikala parvus*, *Capacikala gradatus* and "*Capatanka" minor* should be reviewed as well as the species assignments in *Palaeocastor*. Judging from the data considered herein it seems that *P. peninsulatus* is smaller than *P. nebrascensis.* Material assigned to *Palaeocastor* sp. includes three size forms, and *P. fossor* needs to be clearly separated.

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APPENDIX

Descriptive statistics of the measurements and the wear-stage independent residuals based on these measurements against the four wear stages; rounded where appropriate. For all taxa residuals were only calculated against the four determined wear stages. Abbreviations in all tables: st.-dev. – standard deviation, L – length, B width, mesF – number of "fossettes" in anterior part of tooth, distF – "fossettes" in distal part of tooth, res - residual; lower case letters indicate mandibular teeth, upper case letter maxillar teeth.

Descriptive statistics *Capacikala gradatus*.

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	67	1.80	2.20	4.00	179.17	2.674	.0453	.3711	.138
B m1/2	62	2.00	2.00	4.00	163.62	2.639	.0630	.4961	.246
mesF m1/2	64	4	0	4	109	1.70	.108	.867	.752
distF m1/2	64	1	1	2	66	1.03	.022	.175	.031
L p4	17	2.33	2.60	4.93	57.80	3.400	.1598	.6588	.434
B p4	16	2.40	2.00	4.40	47.28	2.955	.1567	.6268	.393
mesF p4	12	5	1	6	20	1.67	.414	1.435	2.061
distF p4	12	5	1	6	18	1.50	.417	1.446	2.091
L m3	23	1.61	1.60	3.21	52.23	2.271	.0860	.4125	.170
B m3	21	1.64	1.50	3.14	45.04	2.145	.0945	.4329	.187
mesF m3	21	1	1	2	30	1.43	.111	.507	.257
distF m3	21	0	1	1	21	1.00	.000	.000	.000
L M1/2	18	1.77	1.80	3.57	51.14	2.841	.1059	.4491	.202
B M1/2	15	2.70	2.20	4.90	57.77	3.851	.1788	.6924	.479
mesF M1/2	15	1	0	1	14	.93	.067	.258	.067
distF M1/2	15	1	0	1	3	.20	.107	.414	.171
L P4	8	2.10	2.40	4.50	25.56	3.195	.2922	.8263	.683
B P4	8	1.90	3.00	4.90	33.26	4.158	.2310	.6534	.427
mesF P4	7	1	0	1	5	.71	.184	.488	.238
distF P4	7	1	0	1	1	.14	.143	.378	.143
L M3	7	2.00	1.50	3.50	17.07	2.439	.2198	.5815	.338
B M3	6	1.40	1.60	3.00	14.75	2.458	.2083	.5103	.260
mesF M3	6	3	0	3	9	1.50	.500	1.225	1.500
distF M3	6	3	0	3	6	1.00	.632	1.549	2.400
Res_Lmi	65	1.4519	-1.6437	-.191986	-66.0254	-1.0161	.06122	.49353	.244
Res_Bm1/2	60	1.8508	-1.6061	.24472	-47.0417	-.7840	.06491	.50279	.253
Res_mesFm1/2	62	2.0007	-2.0776	-.07692	-56.7937	-.9160	.05488	.43212	.187
Res_distFm1/2	62	1.0000	-1.4647	-.46471	-70.3118	-1.1341	.05941	.46776	.219
Res_Lp4	12	2.0000	-3.1438	-1.14378	-23.8589	-1.9882	.15763	.54604	.298
Res_Bp4	11	1.2570	-2.2202	-.96324	-19.1173	-1.7379	.12771	.42358	.179
Res_mesFp4	10	1.0000	-2.3244	-1.32436	-16.2532	-1.6253	.15116	.47801	.228
Res_distFp4	10	2.8132	-2.4005	.41275	-13.6286	-1.3629	.24922	.78812	.621
Res_Lm3	23	2.3543	-2.4677	-.11344	-28.0040	-1.2176	.15690	.75246	.566
Res_Bm3	21	2.3740	-2.0077	.36627	-17.9100	-.8529	.17171	.78688	.619

Res_mesFm3	21	1.6947	-1.5420	.15267	-14.1652	-.6745	.13290	.60901	.371
Res_distFm3	21	2.0000	-2.2466	-.24658	-23.3962	-1.1141	.15617	.71564	.512
Res_LM1/2	18	3.2076	-1.4291	1.77844	2.6391	.1466	.19542	.82912	.687
Res_BM1/2	15	4.3964	-2.3474	2.04896	-5.4245	-.3616	.26450	1.02441	1.049
Res_mesFM1/2	15	1.0000	-.4239	.57615	3.4862	.2324	.12444	.48196	.232
Res_distFM1/2	15	1.2394	-.5062	.73320	3.1252	.2083	.12856	.49792	.248
Res_LP4	8	1.6841	-.5618	1.12235	2.8783	.3598	.23125	.65408	.428
Res_BP4	8	1.6548	-.9472	.70756	-.75312	-.0941399	.18188	.51444	.265
Res_mesFP4	7	1.1555	-.5756	.57983	2.7479	.3926	.16284	.43084	.186
Res_distFP4	7	1.3846	-.7275	.65714	1.2923	.1846	.16138	.42697	.182
Res_LM3	7	3.6973	-2.0662	1.63163	-4.3164	-.6166	.52152	1.37981	1.904
Res_BM3	6	3.2353	-1.6536	1.58177	-1.2062	-.2010	.52372	1.28285	1.646
Res_mesFM3	6	2.7907	-2.0103	.78036	-1.6899	-.2817	.54824	1.34291	1.803
Res_distFM3	6	2.7196	-2.1244	.59526	-1.8677	-.3113	.57335	1.40442	1.972
Gültige Werte (Listenweise)	0								

Descriptive statistics *Capacikala parvus*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L M1/2	4	.80	2.28	3.08	10.42	2.6050	.17071	.34142	.117
B M1/2	4	.19	2.82	3.01	11.69	2.9225	.04608	.09215	.008
L P4	2	.09	2.98	3.07	6.05	3.0250	.04500	.06364	.004
B P4	2	.14	3.34	3.48	6.82	3.4100	.07000	.09899	.010
L M3	1	.00	1.81	1.81	1.81	1.8100	.	.	.
B M3	1	.00	2.17	2.17	2.17	2.1700	.	.	.
mesF M3	1	0	1	1	1	1.00	.	.	.
Res_LM1/2	4	.99777	-.81799	.17978	-.90227	-.22557	.21291	.42582	.181
Res_BM1/2	4	.23901	.03004	.26905	.56044	.14011	.05796	.11592	.013
Res_LP4	2	.07218	-.41497	-.34279	-.75776	-.37888	.03609	.05104	.003
Res_BP4	2	.08185	-.57306	-.49121	-1.06427	-.53214	.04092	.05788	.003
Res_LM3	1	.00000	.07779	.07779	.07779	.07779	.	.	.
Res_BM3	1	.00000	-.15943	-.15943	-.15943	-.15943	.	.	.
Res_mesFM3	1	.00000	-.48320	-.48320	-.48320	-.48320	.	.	.

Descriptive statistics of *Capatanka cankpeopi*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	38	1.50	3.00	4.50	130.07	3.4229	.0662	.40798	.166
B m1/2	37	1.73	3.00	4.73	146.69	3.9646	.0622	.37759	.143
mesF m1/2	29	5	0	5	25	.86	.184	.990	.980
distF m1/2	29	4	0	4	29	1.00	.122	.655	.429
L p4	17	1.97	3.75	5.72	80.93	4.7606	.1323	.54562	.298
B p4	16	1.35	3.45	4.80	65.34	4.0838	.0938	.37504	.141
mesF p4	14	2	0	2	16	1.14	.177	.663	.440
distF p4	15	1	1	2	16	1.07	.067	.258	.067
L m3	14	.55	2.80	3.35	42.33	3.0236	.0430	.16089	.026
B m3	13	1.12	2.38	3.50	40.65	3.1269	.0861	.31033	.096
mesF m3	11	1	0	1	9	.82	.122	.405	.164
distF m3	11	1	0	1	10	.91	.091	.302	.091
L M1/2	12	1.08	2.72	3.80	38.60	3.2167	.1140	.39500	.156
B M1/2	11	1.55	2.85	4.40	40.34	3.6673	.1608	.53322	.284
mesF M1/2	12	2	0	2	16	1.33	.188	.651	.424
distF M1/2	11	3	0	3	19	1.73	.304	1.009	1.018
L P4	7	.62	3.88	4.50	29.59	4.2271	.0750	.19839	.039
B P4	7	2.81	3.29	6.10	32.76	4.6800	.3885	1.02778	1.056
mesF P4	6	2	1	3	11	1.83	.307	.753	.567
distF P4	6	1	1	2	9	1.50	.224	.548	.300
L M3	6	.70	2.50	3.20	16.25	2.7083	.1218	.29842	.089
B M3	6	.90	2.90	3.80	19.78	3.2967	.1398	.34238	.117
mesF M3	6	2	1	3	14	2.33	.333	.816	.667
distF M3	6	2	1	3	12	2.00	.365	.894	.800
Res_Lm1/2	36	1.2988	-.7894	.50938	1.00860	.02802	.08141	.48847	.239
Res_Bm1/2	35	2.1067	-1.5017	.60500	-12.0572	-.34449	.09064	.53621	.288
Res_mesFm1/2	29	3.0007	-.5774	2.42326	1.2537	.04323	.12071	.65005	.423
Res_distFm1/2	29	1.7500	-.4647	1.28529	6.5235	.22495	.09256	.49846	.248
Res_Lp4	13	1.2669	-2.3002	-1.03334	-22.0984	-1.69988	.09542	.34405	.118
Res_Bp4	12	1.2569	-2.4191	-1.16218	-20.5239	-1.71032	.12724	.44077	.194
Res_mesFp4	10	1.0048	-1.3292	-.32436	-6.2916	-.62916	.15241	.48195	.232
Res_distFp4	13	7.0000	-1.4005	5.59955	3.3568	.25822	.67310	2.42688	5.890
Res_Lm3	14	1.0285	-.3965	.63196	2.6277	.18770	.13584	.50828	.258
Res_Bm3	13	1.1054	-.6083	.49709	-.09216	-.00709	.11738	.42323	.179
Res_mesFm3	11	1.6947	-1.2366	.45802	-2.3512	-.21374	.20846	.69137	.478
Res_distFm3	11	1.0000	-.2466	.75342	3.3699	.30635	.15503	.51417	.264
Res_LM1/2	12	7.2143	-1.9302	5.28402	-1.8613	-.15511	.53626	1.85767	3.451
Res_BM1/2	11	7.4214	-1.2593	6.16207	1.2356	.11233	.62339	2.06755	4.275
Res_mesFM1/2	12	8.1562	-1.4239	6.73231	4.5385	.37821	.63545	2.20125	4.846
Res_distFM1/2	11	2.4788	-1.2668	1.21202	.9805	.08914	.27906	.92552	.857

Res_LP4	7	1.2165	-1.4575	-.24099	-6.4007	-.91438	.19976	.52852	.279
Res_BP4	7	1.4735	-1.7598	-.28630	-5.9222	-.84603	.22128	.58545	.343
Res_mesFP4	6	1.1555	-.4202	.73529	.2563	.04272	.22401	.54872	.301
Res_distFP4	6	1.0000	-.3429	.65714	1.0967	.18278	.16186	.39648	.157
Res_LM3	6	1.8218	-1.9768	-.15495	-7.1629	-1.19382	.24099	.59029	.348
Res_BM3	6	1.8192	-1.9279	-.10868	-7.7469	-1.29115	.26123	.63985	.409
Res_mesFM3	6	1.5271	-1.0103	.51680	-3.0078	-.50129	.25274	.61908	.383
Res_distFM3	6	1.2399	-1.1244	.11550	-3.3070	-.55117	.19007	.46556	.217

Descriptive statistics *Capatanka minor*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L M1/2	7	.97	1.80	2.77	17.20	2.4571	.14764	.39063	.153
B M1/2	5	2.00	2.20	4.20	16.74	3.3480	.35619	.79647	.634
mesF M1/2	7	1	0	1	6	.86	.143	.378	.143
distF M1/2	7	0	0	0	0	.00	.000	.000	.000
L P4	2	.10	3.31	3.41	6.72	3.3600	.05000	.07071	.005
B P4	2	.34	3.45	3.79	7.24	3.6200	.17000	.24042	.058
distF P4	2	0	2	2	4	2.00	.000	.000	.000
L M3	2	.86	1.50	2.36	3.86	1.9300	.43000	.60811	.370
B M3	1	.00	1.60	1.60	1.60	1.6000	.	.	.
mesF M3	2	1	0	1	1	.50	.500	.707	.500
distF M3	2	1	0	1	1	.50	.500	.707	.500
Res_LM1/2	7	1.20979	.56864	1.77844	6.71189	.95884	.18414	.48720	.237
Res_BM1/2	5	2.51586	-.46689	2.04896	3.02430	.60486	.44807	1.00191	1.004
Res_mesFM1/2	7	.15615	.42000	.57615	3.87692	.55385	.02231	.05902	.003
Res_distFM1/2	7	.00000	.49380	.49380	3.45657	.49380	.00000	.00000	.000
Res_LP4	2	.08020	-.68764	-.60744	-1.29508	-.64754	.04010	.05671	.003
Res_BP4	2	.19877	-.75429	-.55552	-1.30981	-.65491	.09939	.14055	.020
Res_distFP4	2	.00000	.04176	.04176	.08352	.04176	.00000	.00000	.000
Res_LM3	2	2.53646	-.90483	1.63163	.72680	.36340	1.26823	1.79355	3.217
Res_BM3	1	.00000	1.58177	1.58177	1.58177	1.58177	.	.	.
Res_mesFM3	2	1.26357	-.48320	.78036	.29716	.14858	.63178	.89348	.798
Res_distFM3	2	1.23988	-.64462	.59526	-.04936	-.02468	.61994	.87673	.769

Descriptive statistics *Capatanka magnus*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	2	.00	3.90	3.90	7.80	3.9000	.00000	.00000	.000
B m1/2	2	1.00	3.00	4.00	7.00	3.5000	.50000	.70711	.500
mesF m1/2	1	0	1	1	1	1.00	.	.	.
dist F m1/2	1	0	1	1	1	1.00	.	.	.
L p4	2	.60	4.20	4.80	9.00	4.5000	.30000	.42426	.180
B p4	2	1.10	4.00	5.10	9.10	4.5500	.55000	.77782	.605
mesF p4	1	0	1	1	1	1.00	.	.	.
distF p4	1	0	1	1	1	1.00	.	.	.
L M1/2	4	.50	3.50	4.00	15.00	3.7500	.14434	.28868	.083
B M1/2	4	.10	4.50	4.60	18.20	4.5500	.02887	.05774	.003
L P4	2	.00	5.00	5.00	10.00	5.0000	.00000	.00000	.000
B P4	2	.00	5.30	5.30	10.60	5.3000	.00000	.00000	.000
L M3	2	.00	3.60	3.60	7.20	3.6000	.00000	.00000	.000
B M3	2	.00	4.50	4.50	9.00	4.5000	.00000	.00000	.000
Res_Lm1/2	2	.00000	-.8267	-.82672	-1.6535	-.82672	.00000	.00000	.000
Res_Bm1/2	2	.63972	-1.0347	-.3950	-1.4297	-.71486	.31986	.45235	.205
Res_mesF1/2	1	.00000	-.5774	-.5774	-.5774	-.57743	.	.	.
Res_distF1/2	1	.00000	-.4647	-.4647	-.4647	-.46471	.	.	.
Res_Lp4	2	6.64418	-1.9740	4.6701	2.6961	1.34805	3.32209	4.69814	22.073
Res_Bp4	2	6.05797	-2.3335	3.7245	1.3912	.69553	3.02899	4.28363	18.350
Res_mesFp4	1	.00000	-1.3292	-1.3292	-1.3292	-1.32916	.	.	.
Res_distFp4	1	.00000	-1.4005	-1.4005	-1.4005	-1.40045	.	.	.

Descriptive statistics *Palaeocastor fossor*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	2	.30	3.40	3.70	7.10	3.5500	.15000	.21213	.045
B m1/2	2	.00	4.00	4.00	8.00	4.0000	.00000	.00000	.000
mesF m1/2	2	0	1	1	2	1.00	.000	.000	.000
distF m1/2	2	0	1	1	2	1.00	.000	.000	.000
L p4	2	.50	4.00	4.50	8.50	4.2500	.25000	.35355	.125
B p4	2	.50	3.70	4.20	7.90	3.9500	.25000	.35355	.125
mesF p4	1	0	1	1	1	1.00	.	.	.
distF p4	1	0	1	1	1	1.00	.	.	.
L M1/2	6	.70	2.80	3.50	19.80	3.3000	.11832	.28983	.084
B M1/2	6	.70	3.80	4.50	24.40	4.0667	.10220	.25033	.063
mesF M1/2	4	1	1	2	5	1.25	.250	.500	.250
distF M1/2	4	0	1	1	4	1.00	.000	.000	.000
L P4	3	.75	3.35	4.10	11.45	3.8167	.23511	.40723	.166
B P4	3	.20	3.90	4.10	11.90	3.9667	.06667	.11547	.013
mesF P4	2	0	1	1	2	1.00	.000	.000	.000
distF P4	2	0	1	1	2	1.00	.000	.000	.000
L M3	3	.40	2.60	3.00	8.60	2.8667	.13333	.23094	.053
B M3	3	.20	3.00	3.20	9.40	3.1333	.06667	.11547	.013
mesF M3	2	0	1	1	2	1.00	.000	.000	.000
distF M3	2	0	1	1	2	1.00	.000	.000	.000
Res_Lm1/2	2	.11203	-.75203	-.64000	-1.39203	-.69602	.05602	.07922	.006
Res_Bm1/2	2	.00000	-1.03472	-1.03472	-2.06943	-1.03472	.00000	.00000	.000
Res_mesFm1/2	2	.00000	-.57743	-.57743	-1.15487	-.57743	.00000	.00000	.000
Res_distFm1/2	2	.00000	-.46471	-.46471	-.92941	-.46471	.00000	.00000	.000
Res_Lp4	1	.00000	-1.85543	-1.85543	-1.85543	-1.85543	.	.	.
Res_Bp4	1	.00000	-2.07654	-2.07654	-2.07654	-2.07654	.	.	.
Res_mesFp4	1	.00000	-1.32916	-1.32916	-1.32916	-1.32916	.	.	.
Res_distFp4	1	.00000	-1.40045	-1.40045	-1.40045	-1.40045	.	.	.
Res_LM1/2	4	.12472	-1.34182	-1.21710	-5.24256	-1.31064	.03118	.06236	.004
Res_BM1/2	4	.62896	-1.84427	-1.21531	-5.74178	-1.43545	.14862	.29724	.088
Res_mesFM1/2	4	.15615	-.42385	-.26769	-1.53923	-.38481	.03904	.07808	.006
Res_distFM1/2	4	.00000	-.26680	-.26680	-1.06718	-.26679	.00000	.00000	.000
Res_LP4	3	7.60147	-1.24099	6.36048	3.95869	1.31957	2.52057	4.36575	19.060
Res_BP4	2	.00000	-.81860	-.81860	-1.63720	-.81860	.00000	.00000	.000
Res_mesFP4	2	.00000	-.42017	-.42017	-.84034	-.42017	.00000	.00000	.000
Res_distFP4	2	.00000	-.34286	-.34286	-.68571	-.34286	.00000	.00000	.000
Res_LM3	2	.00000	-2.04824	-2.04824	-4.09648	-2.04824	.00000	.00000	.000
Res_BM3	2	.26007	-1.49878	-1.23871	-2.73749	-1.36875	.13003	.18391	.034
Res_mesFM3	2	.00000	-.48320	-.48320	-.96641	-.48320	.00000	.00000	.000
Res_distFM3	2	.00000	-.64462	-.64462	-1.28924	-.64462	.00000	.00000	.000

Descriptive statistics *Palaeocastor nebrascensis*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	22	1.86	2.04	3.90	74.98	3.4082	.08848	.41500	.172
B m1/2	22	2.08	2.60	4.68	80.81	3.6732	.11829	.55483	.308
mesF m1/2	22	3	0	3	27	1.23	.160	.752	.565
distF m1/2	22	1	0	1	21	.95	.045	.213	.045
L p4	8	1.51	3.74	5.25	34.74	4.3425	.18326	.51834	.269
B p4	8	1.97	2.81	4.78	29.50	3.6875	.22076	.62440	.390
mesF p4	8	2	1	3	10	1.25	.250	.707	.500
distF p4	8	0	1	1	8	1.00	.000	.000	.000
L m3	4	.90	2.62	3.52	12.47	3.1175	.18710	.37420	.140
B m3	4	.86	2.60	3.46	12.36	3.0900	.21455	.42911	.184
mesF m3	4	0	1	1	4	1.00	.000	.000	.000
distF m3	4	0	1	1	4	1.00	.000	.000	.000
L M1/2	21	1.45	2.28	3.73	64.32	3.0629	.08173	.37453	.140
B M1/2	15	1.35	2.82	4.17	52.63	3.5087	.11599	.44922	.202
mesF M1/2	21	3	0	3	24	1.14	.125	.573	.329
distF M1/2	20	4	0	4	19	.95	.276	1.234	1.524
L P4	13	1.33	3.07	4.40	48.57	3.7365	.11040	.39804	.158
B P4	11	1.74	3.04	4.78	44.85	4.0773	.18331	.60798	.370
mesF P4	12	3	1	4	18	1.50	.289	1.000	1.000
distF P4	12	3	0	3	13	1.08	.336	1.165	1.356
L M3	6	.25	2.30	2.55	14.35	2.3917	.03458	.08472	.007
B M3	3	.70	3.02	3.72	9.97	3.3233	.20739	.35921	.129
mesF M3	6	0	1	1	6	1.00	.000	.000	.000
distF M3	6	1	0	1	1	.17	.167	.408	.167
Res_Lm1/2	21	2.29502	-1.75577	.53926	-19.01508	-.90548	.21181	.97062	.942
Res_Bm1/2	21	2.36464	-2.00913	.35551	-23.02507	-1.0964	.17322	.79381	.630
Res_mesFm1/2	21	2.00000	-1.57743	.42257	-14.12509	-.67262	.16768	.76839	.590
Res_distFm1/2	21	2.00000	-1.46471	.53529	-14.75882	-.702801	.20592	.94365	.890
Res_Lp4	8	2.27873	-3.30614	-1.02741	-14.46836	-1.80855	.29789	.84257	.710
Res_Bp4	8	1.73452	-2.89670	-1.16218	-14.52667	-1.81583	.23364	.66083	.437
Res_mesFp4	8	2.00958	-2.32916	-.31957	-8.62366	-1.07796	.31380	.88757	.788
Res_distFp4	8	2.00000	-2.40045	-.40045	-9.20358	-1.15045	.31339	.88641	.786
Res_Lm3	4	2.05339	-2.41964	-.36626	-5.50151	-1.37538	.41934	.83867	.703
Res_Bm3	4	1.54689	-2.34485	-.79796	-6.41208	-1.60302	.32238	.64475	.416
Res_mesFm3	4	2.00000	-2.54198	-.54198	-6.16794	-1.54199	.40825	.81650	.667
Res_distFm3	4	2.00000	-2.24658	-.24658	-4.98630	-1.24658	.40825	.81650	.667
Res_LM1/2	21	2.80845	-1.62868	1.17978	-9.72884	-.46328	.19405	.88925	.791
Res_BM1/2	15	2.61015	-1.34110	1.26905	-1.95869	-.13058	.23326	.90340	.816
Res_mesFM1/2	21	1.00000	-.42385	.57615	-1.43231	-.06821	.10003	.45838	.210
Res_distFM1/2	20	1.23941	-.50620	.73320	1.42469	.07124	.10836	.48459	.235
Res_LP4	13	1.51326	-1.33723	.17603	-6.34282	-.48791	.14488	.52236	.273
Res_BP4	11	1.16369	-1.15768	.00601	-5.14461	-.46770	.11005	.36500	.133
Res_mesFP4	12	1.00000	-.42017	.57983	.89076	.07423	.13499	.46761	.219

Res_distFP4	12	.76923	-.34286	.42637	1.27033	.10586	.08513	.29490	.087
Res_LM3s	6	1.44665	-1.24428	.20237	-.76842	-.12807	.22462	.5502	.303
Res_BM3s	3	.91024	-1.17496	-.26472	-1.97747	-.65916	.26968	.46710	.218
Res_mesFM3	6	1.00000	-.48320	.51680	2.10078	.35013	.16667	.40825	.167
Res_distFM3	6	1.23988	-.64462	.59526	2.33169	.38862	.20665	.50618	.256

Descriptive statistics *Palaeocastor peninsulatus*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	3	.40	3.30	3.70	10.40	3.4667	.12019	.20817	.043
B m1/2	3	.30	3.20	3.50	10.10	3.3667	.08819	.15275	.023
mesF m1/2	2	1	1	2	3	1.50	.500	.707	.500
distF m1/2	2	0	1	1	2	1.00	.000	.000	.000
L p4	1	.00	3.90	3.90	3.90	3.9000	.	.	.
B p4	1	.00	3.70	3.70	3.70	3.7000	.	.	.
L m3	1	.00	3.00	3.00	3.00	3.0000	.	.	.
Res_Lm1/2	3	.14938	-1.75203	-1.60265	-4.99469	-1.66490	.04488	.07774	.006
Res_Bm1/2	3	.19192	-1.71486	-1.52294	-4.88868	-1.62956	.05642	.09772	.010
Res_mesFm1/2	2	.50017	-1.57743	-1.07726	-2.65470	-1.32735	.25009	.35368	.125
Res_distFm1/2	2	.00000	-1.46471	-1.46471	-2.92941	-1.46471	.00000	.00000	.000
Res_Lp4	1	.00000	-2.79613	-2.79613	-2.79613	-2.79613	.	.	.
Res_Bp4	1	.00000	-3.07654	-3.07654	-3.07654	-3.07654	.	.	.
Res_Lm3	1	.00000	-.38583	-.38583	-.38583	-.38583	.	.	.

Descriptive statistics *Palaeocastor* sp.

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	49	1.70	2.30	4.00	152.90	3.1204	.04305	.30137	.091
B m1/2	49	1.70	2.30	4.00	160.80	3.2816	.04744	.33209	.110
mesF m1/2	42	5	0	5	47	1.12	.137	.889	.790
distF m1/2	44	1	0	1	42	.95	.032	.211	.044
L p4	21	1.43	3.00	4.43	75.33	3.5871	.09923	.45472	.207
B p4	21	1.60	2.40	4.00	66.46	3.1648	.09673	.44326	.196
mesF p4	18	3	1	4	23	1.28	.177	.752	.565
distF p4	18	0	1	1	18	1.00	.000	.000	.000
L m3	19	1.00	2.10	3.10	49.90	2.6263	.06747	.29409	.086
B m3	18	1.20	2.10	3.30	47.80	2.6556	.07286	.30912	.096
mesF m3	13	1	1	2	15	1.15	.104	.376	.141
distF m3	13	2	0	2	13	1.00	.113	.408	.167
L M1/2	14	1.40	2.00	3.40	39.90	2.8500	.08880	.33224	.110
B M1/2	13	1.30	2.70	4.00	44.70	3.4385	.10224	.36864	.136
mesF M1/2	8	3	0	3	11	1.38	.375	1.061	1.125
distF M1/2	8	3	0	3	11	1.38	.460	1.302	1.696
L P4	7	.70	3.10	3.80	23.20	3.3143	.09110	.24103	.058
B P4	7	1.40	2.90	4.30	23.50	3.3571	.19501	.51594	.266
mesF P4	3	1	1	2	5	1.67	.333	.577	.333
distF P4	3	0	1	1	3	1.00	.000	.000	.000
L M3	6	.70	2.00	2.70	13.80	2.3000	.11547	.28284	.080
B M3	6	.40	2.70	3.10	17.50	2.9167	.06009	.14720	.022
mesF M3	3	3	1	4	8	2.67	.882	1.528	2.333
distF M3	3	4	0	4	5	1.67	1.202	2.082	4.333
Res_Lm1/2	35	2.44814	-1.86407	.58407	-20.22563	-.57788	.14955	.88473	.783
Res_Bm1/2	34	2.44780	-1.90677	.54103	-19.37927	-.56998	.13221	.77093	.594
Res_mesFm1/2	30	2.00069	-1.57743	.42326	-15.32234	-.51075	.10095	.55293	.306
Res_distFm1/2	32	8.00000	-1.46471	6.53529	-7.37059	-.23033	.25670	1.45210	2.109
Res_Lp4	20	8.88139	-3.26239	5.61900	-5.96694	-.29835	.66115	2.95675	8.742
Res_Bp4	20	8.91436	-3.30579	5.60857	-6.50445	-.32522	.67308	3.01008	9.061
Res_mesFp4	17	9.00958	-3.32436	5.68522	.42831	.02520	.80891	3.33523	11.124
Res_distFp4	17	9.00000	-3.40045	5.59955	-.80761	-.04751	.80869	3.33431	11.118
Res_Lm3	13	7.97331	-1.42142	6.55189	.58380	.04491	.58132	2.095982	4.393
Res_Bm3	13	8.36881	-1.45023	6.91859	1.20082	.09237	.60496	2.181214	4.758
Res_mesFm3	10	8.00000	-1.54198	6.45802	10.27481	1.02748	.92406	2.92214	8.539
Res_distFm3	11	8.00000	-1.24658	6.75342	18.28767	1.66252	.99509	3.30034	10.892
Res_LM1/2	12	1.12249	-.59349	.52899	-4.24889	-.35407	.09147	.31685	.100
Res_BM1/2	12	2.00634	-1.21531	.79103	-4.40717	-.36726	.18859	.65330	.427
Res_mesFM1/2	6	1.00000	-.42385	.57615	-.69923	-.11654	.19540	.47863	.229
Res_distFM1/2	6	1.00000	-.50620	.49380	.15982	.02664	.16455	.40307	.162
Res_LP4	6	1.32079	-1.00040	.32038	-2.75692	-.45949	.17709	.43377	.188

Res_BP4	6	.59077	-.64321	-.05245	-2.27467	-.37911	.09705	.23771	.057
Res_mesFP4	3	1.15546	-.42017	.73529	.05042	.01681	.36204	.62707	.393
Res_distFP4	3	1.00000	-.34286	.65714	-.02857	-.00952	.33333	.57735	.333
Res_LM3	5	1.25061	-1.51227	-.26166	-3.80951	-.76190	.24884	.55643	.310
Res_BM3	5	.52014	-1.36875	-.84861	-5.80345	-1.16069	.08819	.19721	.039
Res_mesFM3	2	.52713	-1.01034	-.48320	-1.49354	-.74677	.26357	.37274	.139
Res_distFM3	2	.23988	-.64462	-.40474	-1.04936	-.52468	.11994	.16962	.029

Descriptive statistics *Pseudopalaeocastor barbouri*

variable	N	range	min	max	sum	mean	standard error	st.- dev	variance
L m1/2	2	.03	2.73	2.76	5.49	2.7450	.01500	.02121	.000
B m1/2	2	.09	3.28	3.37	6.65	3.3250	.04500	.06364	.004
L p4	2	.58	3.10	3.68	6.78	3.3900	.29000	.41012	.168
B p4	2	.16	2.90	3.06	5.96	2.9800	.08000	.11314	.013
L m3	1	.00	2.10	2.10	2.10	2.1000	.	.	.
B m3	1	.00	2.91	2.91	2.91	2.9100	.	.	.
L M1/2	5	.68	2.41	3.09	13.43	2.6860	.12917	.28884	.083
B M1/2	5	.50	2.50	3.00	13.46	2.6920	.08399	.18780	.035
L P4	3	.17	2.53	2.70	7.76	2.5867	.05667	.09815	.010
B P4	3	.72	2.40	3.12	8.50	2.8333	.22040	.38175	.146
L M3	3	.02	2.18	2.20	6.57	2.1900	.00577	.01000	.000
B M3	3	.35	2.05	2.40	6.65	2.2167	.10138	.17559	.031
Res_Lm1/2	2	.01120	-1.40099	-1.38979	-2.79078	-1.39539	.00560	.00792	.000
Res_Bm1/2	2	.05757	-1.63169	-1.57412	-3.20581	-1.60291	.02879	.04071	.002
Res_Lp4	1	.00000	-3.66566	-3.66566	-3.66566	-3.66566	.	.	.
Res_Bp4	1	.00000	-3.52845	-3.52845	-3.52845	-3.52845	.	.	.
Res_Lm3	1	.00000	-1.46591	-1.46591	-1.46591	-1.46591	.	.	.
Res_Bm3	1	.00000	-1.50818	-1.50818	-1.50818	-1.50818	.	.	.
Res_LM1/2	4	.84810	-1.83046	-.98236	-5.28891	-1.3223	.20791	.41583	.173
Res_BM1/2	4	.47801	-.95738	-.47937	-2.52127	-.63032	.11193	.22385	.050
Res_LP4	2	.00000	-1.98191	-1.98191	-3.96381	-1.98191	.00000	.00000	.000
Res_BP4	2	.08185	-2.36260	-2.28075	-4.64335	-2.32167	.04092	.05788	.003
Res_LM3	2	.01787	-1.60111	-1.58324	-3.18435	-1.59218	.00893	.01263	.000
Res_BM3	2	.26007	-1.45851	-1.19844	-2.65694	-1.32847	.13003	.18390	.034