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Sexual dimorphism in Pleistocene *Bison priscus* (Mammalia, Bovidae) with a discussion on the position of *Bison schoetensacki*

With: 3 Text-figures, 3 Tables

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Abstract

The expression of sexual dimorphism in *Bison priscus*, as found in the metacarpal bone, is comparable to that of extant *Bison bonasus*. This is contradictory to the widely accepted view of Schertz (1936a, b) who found only a small expression of sexual dimorphism in *Bison priscus*. At sites where *Bison priscus* and *Bison schoetensacki* are found together (Chatillon-Saint-Jean, Mosbach, Mauer) it is considered likely that females of *Bison priscus* have been erroneously attributed to *Bison schoetensacki*. The validity of *Bison schoetensacki* is questioned.

K e y w o r d s : *Bison priscus*, *Bison schoetensacki*, Pleistocene, sexual dimorphism

Introduction

Sexual dimorphism is a common phenomenon in extant *Bison*. Because Recent species display sexual dimorphism it stands to reason to assume that extinct Pleistocene *Bison* species also showed (large) differences between the sexes.

In this paper I investigate how sexual dimorphism is expressed in the fossil record of *Bison priscus* on the basis of the metacarpus.

The metacarpal bone of bovids is chosen because of its strong expression of sexual dimorphism (SCHERTZ 1936a, b; BRUGAL, 1984Ð1985), its relative abundance in fossil assemblages and the fact that it is mostly intact, making it an ideal object for comparative study.

SHER (1997) found that the metacarpus is one of the most representative and informative sources in the taxonomic research of *Bison*; provided that a large enough sample is available.

First a framework is created through a short literature survey of accounts on sexual dimorphism in extant *Bison*, followed by a discussion of the results of multivariate analyses on metacarpal bone of Weichselian *Bison priscus*.

These results are compared with publications on sexual dimorphism in Pleistocene *Bison*.

Sexual dimorphism in extant *Bison*

In both *Bison bonasus* and *B. bison* sexual dimorphism is clearly visible, most prominently in the shoulder and front legs. While males have a massive head and shoulder region (used in dominance fights), females are comparatively slender in this part of the body. Consequently, a much larger weight acts on the front legs of males, calling for a heavier bone structure.

Sexual dimorphism is most strongly expressed in the metacarpal bone (BRUGAL, 1984–1985). This was already noted by SCHERTZ (1936a, b) who found a strong expression of sexual dimorphism in the mediolateral plane of the proximal joint and at midshaft.

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SCHERTZ (1936b) used the following formula to calculate the amount of difference between the two sexes for a particular measurement:

$$\frac{X_1 - X_2}{X_1 * 1\%} = \text{percentage difference}$$

X_1 = Average male value
X_2 = Average female value

In the present paper this formula is used to express sexual dimorphism in the metacarpal bone of present day *Bison bison* and *B. bonasus* (Table 1). Measurements are based on the research of SCHERTZ (1936b) and EMPEL & ROSKOSZ (1963).
Sexual dimorphism manifests itself strongly in the proximal transverse diameter and is even more pronounced at midshaft (see Table 1.). The differences are clearly present in *Bison bonasus* and even stronger in *B. bison*. Differences in metacarpal length are minor.

Sexual dimorphism in *Bison priscus*

Since the mid-seventies fishermen have dredged up large amounts of fossil material from the southern part of the North Sea. The bulk of the material belongs to a faunal assemblage of Weichselian age (VAN KOLFSCHOTEN & LABAN, 1995), consisting of *Mammuthus primigenius, Coelodonta antiquitatis, Equus caballus, Bison priscus, Ovibos moschatus, Rangifer tarandus, Megaceros giganteus, Crocuta crocuta* and *Panthera leo*, among others.

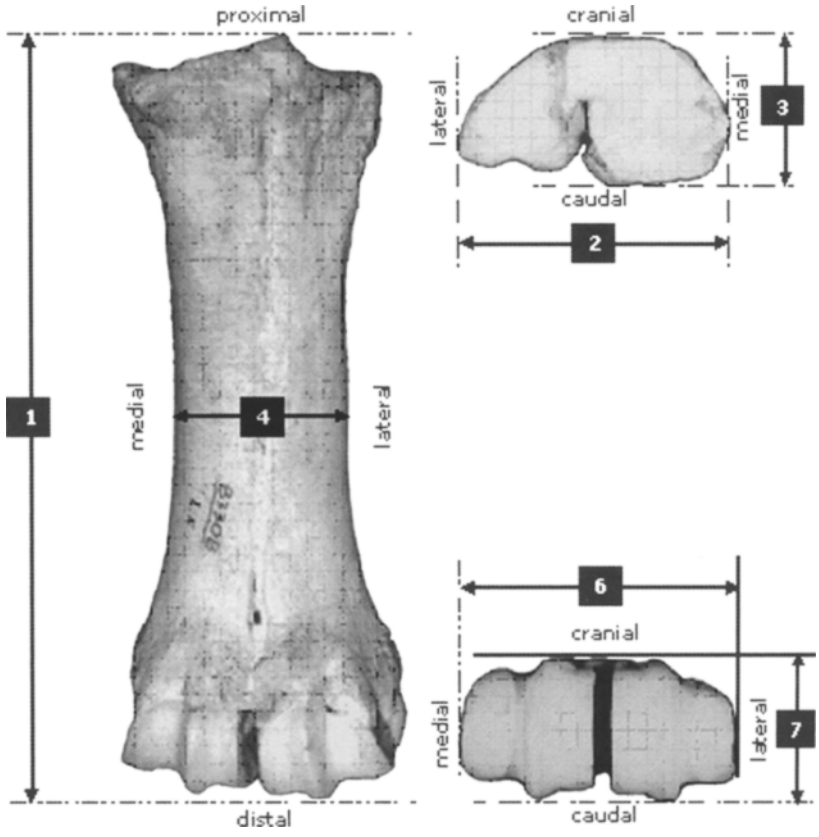

Figure 1. Measurements taken from metacarpal bone. Measurement 5 (not shown) is the anterio-posterior diameter at midshaft

Table 1. Sexual dimorphism in metacarpal bone of *Bison bonasus* and *B. bison*. Sizes in mm.

Greatest length				
SCHERTZ (1936b)	207,1	213,1	2,8	*Bison bonasus*
EMPEL & ROSKOSZ (1963)	209,5	217,5	3,7	*Bison bonasus*
SCHERTZ (1936b)	188,7	201,0	6,1	*Bison bison*
Proximal transverse diameter				
SCHERTZ (1936b)	65,3	74,8	12,7	*Bison bonasus*
EMPEL & ROSKOSZ (1963)	68,7	79,8	13,9	*Bison bonasus*
SCHERTZ (1936b)	59,0	74,1	20,4	*Bison bison*
Transverse diameter, mid-shaft				
SCHERTZ (1 936b)	35,4	43,4	18,4	*Bison bonasus*
EMPEL & ROSKOSZ (1963)	38,2	48,8	21,7	*Bison bonasus*
SCHERTZ (1936b)	34,3	47,0	27,0	*Bison bison*
No. of metacarpal bones				
SCHERTZ (1936b)	4	7		*Bison bonasus*
EMPEL & ROSKOSZ (1963)	13	16		*Bison bonasus*
SCHERTZ (1936b)	7	8		*Bison bison*

The abundance and quality of preservation of the metacarpus of *Bison priscus* made it an excellent subject for studying the expression of sexual dimorphism. Well-preserved, complete, adult metacarpals of *Bison priscus* (N = 18) were used for multivariate analysis. All metacarpi came from the collection of the Dutch Museum of Natural History, Naturalis, in Leiden.

From every metacarpal bone 7 measurements were taken (see fig. 1) to perform a cluster analysis and principal component analysis (PCA) using the Multivariate Statistical Package (MSVP, Kovach Computing, version 3.13f). The measurements are added in Appendix I.

The cluster analysis shows two distinct groups (fig. 2); the PCA (fig. 3) showed that these two groups are separated mainly through size differences (72% of total variation is explained by the eigenvalue of the first axis), strongly suggesting intraspecific variation.

Using the calculation of SCHERTZ (1936b) on the North Sea metacarpal bones I get results (Table 2) that agree very well with the values obtained for *Bison bonasus* (Table 1). Again, while differences in total length are limited, the transverse diameters show marked differences between the two groups. It is therefore concluded that the two groups from the North Sea represent male and female individuals of *Bison priscus*.

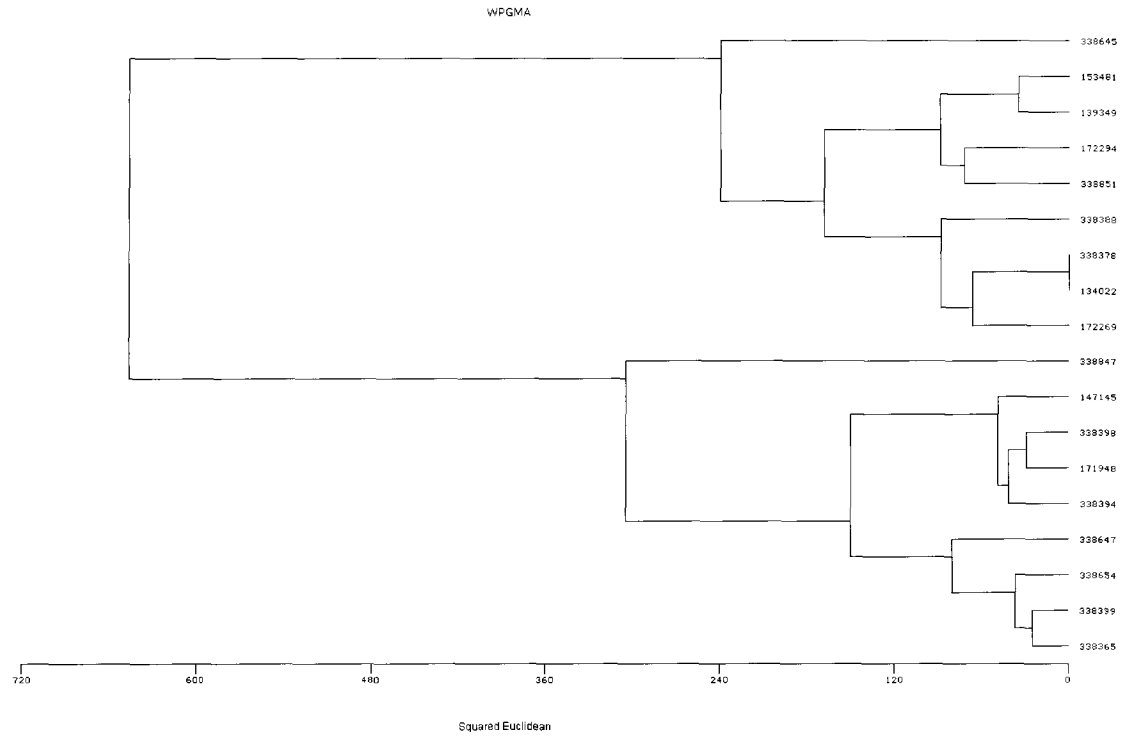

Figure 2. Cluster analysis of *Bison priscus* metacarpi from the North Sea

Discussion and conclusions

SCHERTZ (1936b) also found that sexual dimorphism in *Bison priscus* skulls is less obvious when compared to extant *Bison*. Since the impact of skull dimensions on the postcranial skeleton is clearly demonstrated in *Bison bonasus*, SCHERTZ postulated that a smaller difference in cranial features must result in less sexual dimorphism in the postcranial skeleton, again most clearly in the metacarpal bone. Indeed, based on measurements of metacarpals from Roter Berg near Saalfield, Mosbach and Mauer SCHERTZ (1936b) found a markedly smaller sexual dimorphism in *Bison priscus* when compared with *Bison bonasus*.

These results are contradictory to the results presented in Table 2. In contrast to the findings of SCHERTZ (1936b), the North Sea material shows a sexual dimorphism in *Bison priscus* that is comparable to that of extant *Bison bonasus*.

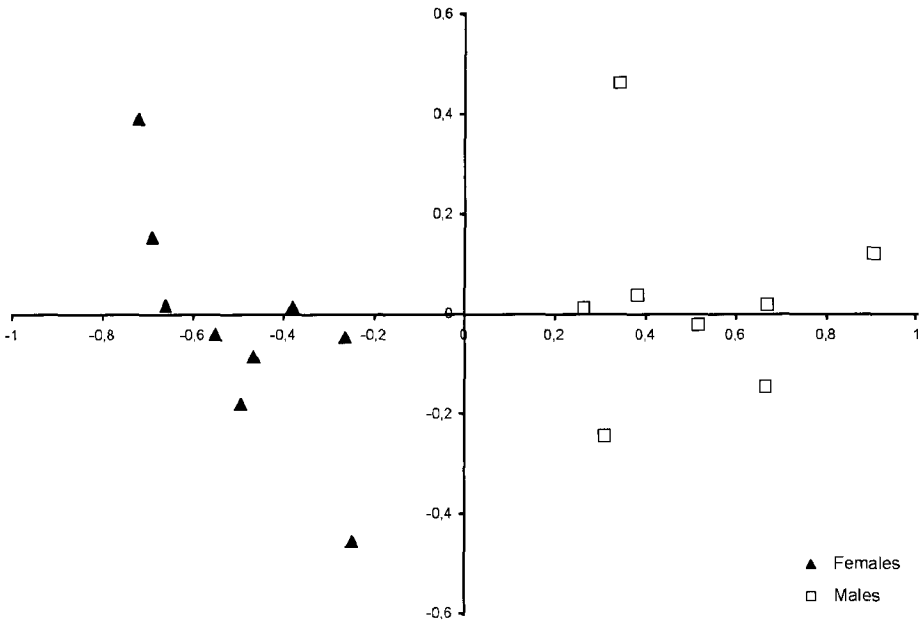

Figure 3. Plot of the first two principle axes of the PCA using the *Bison priscus* metacarpi from the North Sea.

However, SCHERTZ (1936a) also distinguishes metapodials of a second bovid in Mosbach and Mauer. Assuming that the size and slenderness of these metapodials lie beyond the intraspecific, age and sex related variation of *Bison priscus*, SCHERTZ attributes them to *Bison schoetensacki*.

SCHOETENSACK (1908) reports remains of a small *Bison* found in Mosbach and Mauer. On measurements he took from two skull fragments, three isolated horn cores and a lower jaw he concludes that this species is more similar to *Bison bonasus* than to *Bison*

Table 2. Sexual dimorphism in metacarpus of *Bison priscus*. Sizes in mm.

Measurement	Female	Male	%diff
Greatest length			
North Sea	235,2	241,9	2,8
Proximal transverse diameter			
North Sea	76,7	88,3	13,1
Transverse diameter, mid-shaft			
North Sea	45,6	56,7	19,6
No. of metacarpal bones			
North Sea	9		

priscus. He considers it to be a new species of *Bison* from the Pleistocene of Europe. Based on observed differences with *Bison bonasus*, FREUDENBERG (1914) suggests the name *Bison schoetensacki* for this small form.

CHAUVIRÉ (1962) interpreted the differences between two groups of bovid Mcc from Chatillon-Saint-Jean as sexual dimorphism of *Bison priscus*. Ten years later, MOURER-CHAUVIRÉ (1972) compared both *Bison* forms of Chatillon with data published by Schertz (1936b) on Mosbach and Mauer. The similarity between the two forms found in Chatillon with *Bison priscus* of Mosbach und Mauer on the one hand and *Bison schoetensacki* on the other hand led her to conclude that the small form of Chatillon is *Bison schoetensacki*.

However, using the formula of SCHERTZ (1936b) to calculate the amount of difference between the metacarpi of *Bison priscus* and *Bison schoetensacki* at Mosbach, Mauer and Chatillon-Saint-Jean, Table 3 shows a result that is very similar to the expression of sexual dimorphism in *Bison priscus* of the North Sea.

I therefore interpret the metacarpi from Mauer, Mosbach, and Chatillon-Saint Jean which SCHERTZ (1936 a, b), resp. MOURER-CHAUVIRÉ (1972) assigned to *B. schoetensacki*, as those of females of *B. priscus*.

This interpretation of the material is preferred over the presumed presence of two species in these localities since:

- It shows that fossil *Bison* had a similar sexual dimorphism as the Recent species, rather than assuming that two fossil species had next to no differences between the sexes.
- It does not require an explanation as to how two herd-living, similarly sized, large herbivores could survive without extreme side-by-side competition.
- There is no evidence to support a variation beyond intraspecific limits, as suggested by SCHERTZ (1936a).

Table 3. Difference between metacarpi of *Bison priscus* and *Bison schoetensacki* from Mosbach and Mauer, after SCHERTZ (1936a, 62) and Chatillon-Saint-Jean, after CHAUVIRÉ (1962) and MOURER-CHAUVIRÉ (1972). Sizes in mm.

Measurement	*Bison priscus*	*Bison schoeten-sacki*	%diff
SCHERTZ, 1936a	256,1	244,5	4,6
CHAUVIRÉ, 1962, 1972	245,1	252,4	2,9
Proximal transverse diameter			
SCHERTZ, 1936a	84,7	72,6	14,2
CHAUVIRÉ, 1962, 1972	79,4	93,9	15,4
Transverse diameter, mid-shaft			
SCHERTZ, 1936a	52,1	44,1	15,3
CHAUVIRE, 1962, 1972	48,8	61,0	20,0
No. of metacarpal bones			
SCHERTZ, 1936a	19	5	
CHAUVIRE, 1962, 1972	10	12	

In the opinion of SALA (1986) metapodials of *Bison schoetensacki* differ only in size from those of *Bison priscus*. Like SCHERTZ (1936a) no objective morphometric arguments are given to validate this opinion. However, if size instead of shape is the only difference, this clearly favours intraspecific variation over interspecific variation in which case shape differences are expected to be more dominant.

Interpreting SCHERTZ' data set as being the result of sexual dimorphism implies that *Bison schoetensacki* FREUDENBERG 1914 is a junior synonym to *B. priscus* (BOJANUS 1827), since these data include the type locality of *B. schoetensacki*, Mauer.

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Appendix I.

Measurements of Bison *priscus* metacarpi

This appendix contains the measurements of the metacarpi of *Bison priscus* from the collection of the National Museum of Natural History, Naturalis, in Leiden.

The first column (No.) refers to the collection number of Naturalis. The remaining columns contain the individual measurements.

Please refer to fig. 1 for the location and orientation of these measurements.

Bison priscus, females

No.	1	2	3	4	5	6	7
338647	226,0	72,0	48,0	45,0	34,0	75,0	40,0
338365	233,0	75,0	47,0	44,0	31,0	76,0	41,0
147145	235,0	77,0	43,0	49,0	32,0	78,0	44,0
338398	238,0	77,0	46,0	46,0	30,0	80,0	42,0
338654	230,0	77,0	45,0	47,0	31,0	78,0	40,0
171948	238,0	78,0	45,0	45,0	35,0	81,0	42,0
338394	238,0	78,0	45,0	50,0	33,0	84,0	43,0
338399	232,0	78,0	45,0	43,0	32,0	76,0	44,0
338847	247,0	78,0	47,0	41,0	33,0	78,0	45,0
Average	235,2	76,7	45,7	45,6	32,3	78,4	42,3

Bison priscus, males

No.	1	2	3	4	5	6	7
172294	245,0	82,0	50,0	58,0	32,0	88,0	46,0
338645	232,0	84,0	49,0	59,0	39,0	90,0	45,0
139349	247,0	87,0	52,0	55,0	38,0	87,0	45,0
153481	248,0	87,0	50,0	58,0	40,0	91,0	46,0
338851	242,0	87,0	51,0	55,0	35,0	84,0	44,0
172269	244,0	90,0	52,0	59,0	33,0	95,0	47,0
134022	239,0	91,0	50,0	55,0	34,0	91,0	45,0
338378	239,0	91,0	50,0	55,0	34,0	91,0	45,0
338388	241,0	96,0	55,0	56,0	38,0	93,0	48,0
Average	241,9	88,3	51,0	56,7	35,9	90,0	45,7