

# Intraspecific variability of beaver teeth (Castoridae: Rodentia)

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Received 31 May 2007; accepted for publication 14 March 2008

The metric variability of the teeth of *Castor fiber* Linné, 1758 and *Castor canadensis* Kuhl, 1820 with age are assessed. The ages of the studied specimens of *C. fiber* range from about 2 months to 16–17 years. Measurements of all teeth are given, and show a large range of size variation over all ages. The greatest size ranges can be observed for incisors, premolars, and third molars. Size variations of the fossil beavers *Steneofiber eseri* v. Meyer, 1846, *Steneofiber castorinus* Pomel, 1847, *Anchitheriomys suevicus* Schlosser, 1884, and *Trogontherium cuvieri* Fischer de Waldheim, 1809 are compared with those of *C. fiber*, and are of the same range and magnitude. It seems that it is nearly impossible to age beavers exactly with non-invasive methods on the basis of tooth morphology, namely by the form and pattern of enamel islands on the chewing surface of the cheek teeth. Therefore, in conclusion, it is suggested that the observed variability in the size of fossil beaver teeth should be interpreted as changes with age in accordance with the overall size range in *C. fiber*. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **155**, 926–936.

**ADDITIONAL KEYWORDS:** *Anchitheriomys* – *Castor* – *Hydrochoerus hydrochaeris* – postnatal growth – *Steneofiber* – tooth morphology – *Trogontherium*.

## INTRODUCTION

Size differences are one criterion that can be used to distinguish between species, particularly between small mammals, in the fossil record. Besides the diagnostic interspecific differences, the existence of intraspecific size variation is well known. It is often difficult to assess the intraspecific variability between adults, especially if fossil material is rare. Assessing size differences attributable to ontogeny is often even more difficult in fossil species. Comparative data on ontogenetic changes in size and overall morphology of recent mammals are sometimes hard to obtain. Thus, for fossil species, the question often remains of how much an observed variability in a sample reflects postnatal growth, and how much can be considered sufficient to distinguish between species?

In several studies, only adult specimens are considered to reduce the influence of age on the parameter(s) of interest (e.g. Macholán, 1996a; Mora, Olivares & Vassallo, 2003). In some cases, mathematical tools are used to eliminate age-related size differences or size differences in general, in order to be able to compare data (e.g. Macholán, 1996b). Another approach is to compare specimens within different age groups. This requires a prior assessment of the individual age of the specimens, which has been discussed for several mammals, and often includes tooth replacement, to render the young of the year identifiable, and general tooth wear or specific wear patterns.

The most prominent example where teeth, and in particular tooth replacement and wear of the incisors, are used in age determination are horses (e.g. Habermehl, 1961; Richardson, Lane & Waldron, 1994; Richardson, Cripps & Lane, 1995; Muylle, Simoens & Lauwers, 1996; Muylle *et al.*, 1997). Also, for some other economically important species, age

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determinations on the basis of teeth have been given, e.g. for domestic cattle, *Capra hircus* Linné, 1758, *Ovis ammon* Linné, 1758, *Cervus elaphus* Linné, 1758, and *Myocastor cypus* (Molina, 1782) (Habermehl, 1961). Age classification schemes on the basis of teeth are also available for some other species, e.g. for *Crocidura russula* Herman, 1780 (Saint Girons, 1973; Yalden, Morris & Harper, 1973), *Mus musculus* Linné, 1758 (Becker, 1952; Lidicker, 1966), and for domestic dogs (Silver, 1969). Tooth replacement patterns were used to identify the young of the year in e.g. beavers (Novak, 1987) or *Hystrix* Linné, 1758 (Corbet & Jones, 1965). For *Hystrix*, the morphology of enamel folds of the cheek teeth has not turned out to be useful for age determinations (Habermehl, 1961). For the coypu (*Myocastor coypus* (Molina, 1782)), the growth across the enamel face of the incisors is used for age determinations (Habermehl, 1961).

The Castoridae are a family of rodents represented by two species in the recent fauna, but with a much more diverse fossil record known from the late Eocene to recent times (Korth, 2001). Recent beavers are characterized by hypsodont teeth; Tertiary beavers had mesodont to subhypsodont teeth, and during the evolutionary history of the Castoridae the hypsodonty of the teeth increased (Stirton, 1935). This trend is even visible in pleistocene material of *Castor* (Hünemann, 1966; Heinrich, 1989).

The size variation of teeth within samples of fossil beavers from several localities seems large, and has been explained by different wear (e.g. Stefen, 1997), and by postnatal growth for *Anchitheriomys suevicus* Schlosser, 1884 (Stefen & Mörs, 2008), but this has been questioned. The overall variability of recent beavers has previously been addressed by Lönnberg (1909), and, in particular, the morphological changes with wear of teeth has been addressed by Hünemann (1966), and was also investigated by Lavrov (1949). Other authors have presented data on skulls of recent *Castor* Linné, 1758, and indirectly show some of the metric variability (e.g. Hinze, 1950; Véron, 1992). Changes in skull morphology and the associated allometric relationships during ontogeny have been addressed, for example, by Hinze (1950), Frahnert & Heidecke (1992), and Frahnert (2000). Methods to determine the age of *Castor fiber* Linné, 1758 have been developed on the basis of the formation of the frontoparietal crest, the eruption of teeth, and the cementum deposition at the roots of the teeth (Hinze, 1950; Freye, 1959; Piechocki & Stiefel, 1977; Stiefel & Piechocki, 1986; Lux, 1990; Moll, 1999). Nevertheless, metric and morphological variability of teeth were not considered in great detail. But these data in particular are important for comparison with fossil material, which in the most part consists of isolated teeth and jaw fragments.

In this paper, the intraspecific metric variation and postnatal changes of teeth in recent beavers are assessed. The observed size ranges are compared with some known substantial samples of Tertiary fossil beavers. In this way the study shall be a contribution to the understanding of the variability of recent beaver teeth, in order to be better prepared to assess the ontogenetic relevance of size differences in samples of fossil species.

## MATERIAL AND METHODS

Material of the European beaver was studied in the Institute of Biology, Zoological Collection of the Martin-Luther-University Halle-Wittenberg, Germany, and of the Canadian beaver in the Museum of Vertebrate Zoology, University of California Berkeley, USA (MVZ). In total, 36 specimens of *C. fiber* from the catchment area of the middle Elbe in the greater vicinity of Halle/Saale, Sachsen-Anhalt, eastern Germany, of different ages were studied. The age of these specimens had been determined in Halle according to the methods based on sections of the teeth described by Stiefel & Piechocki (1986) and Moll (1999). In total, 41 specimens of *Castor canadensis* Kuhl, 1820 of different subspecies assignment, and from different regions in North America, were measured in the MVZ. The subspecies differentiation was not further considered in this study. I estimated the age of the specimens of *C. canadensis* using the method of Hinze (1950) and Freye (1959), based on the course and fusion of the frontoparietal crests on the skull. The age of younger individuals was determined after Piechocki & Stiefel (1977), using the successive eruption of teeth. This gives an age range for the studied *C. fiber* from of about 3 months to 18 years, and from about 4 months to 3–4 years of age for *C. canadensis*. Specimens determined to be e.g. more than 2-years old are plotted in the graphs as 25-months old.

Measurements were taken with digital calipers to the nearest 0.01 mm. Teeth measurements of the cheek teeth were taken at the occlusal surface, at a right angle to the plane of the occlusal surface. Where possible, the teeth were also measured at the base of (the enamel covered) crown, at right angles to the long axis of the tooth: these are called the basal lengths or widths, respectively. Measurements of the incisors were taken just below the worn tip. The nomenclature for the measurements of incisors is as follows: length, in the mesiodistal direction across the enamel band; width, in the linguolabial direction across the incisor. The mandibular tooth rows are measured at the occlusal surface. The morphological description of cheek teeth follows the nomenclature of Stirton (1935).

Additionally, classical measurements of the skull were taken, such as condylobasal length, diastema (in upper and lower tooth row), length of nasal, length of incisive foramen, mastoid width, width of snout, and interorbital breadth, as in Frahnert (2000). A list of the abbreviations used is provided in the Appendix.

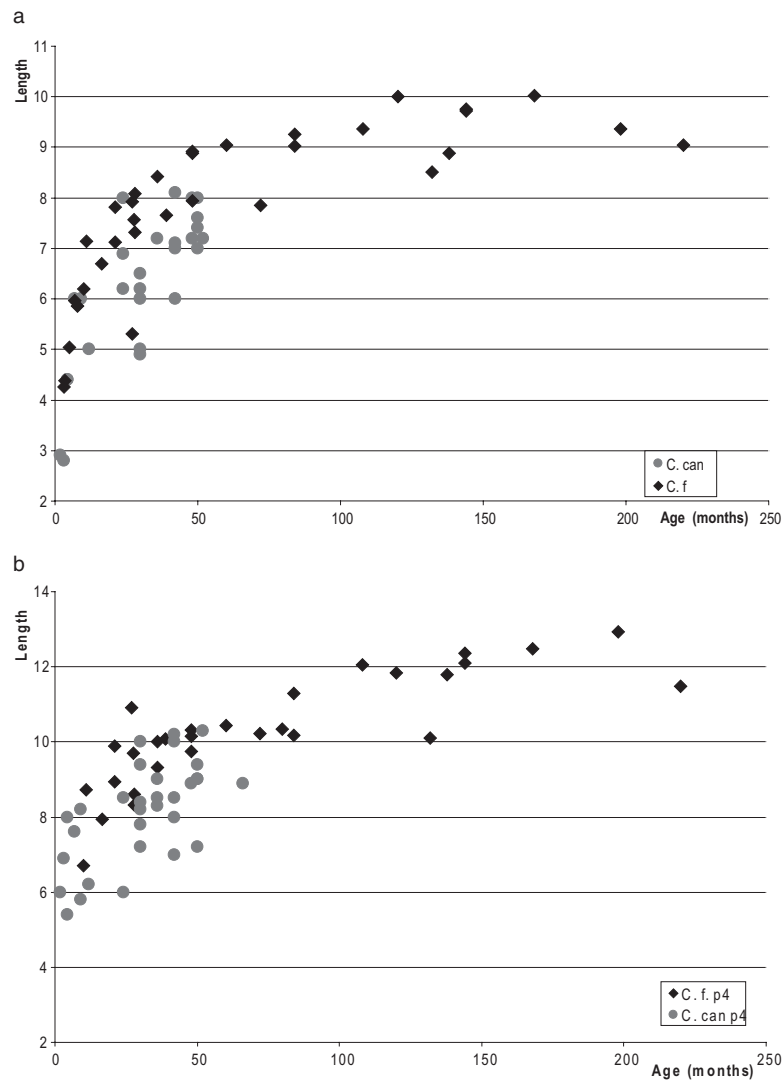
Data on comparative material of Tertiary beavers include those for *Steneofiber eseri* v. Meyer, 1846 from Ulm Westtangente (Lower Miocene, mammal biozone age MN2a; Stefen, 1997), *Steneofiber castorinus* Pomel, 1847 from St. Gérard MN2a (Filhol, 1879; Stefen, 2005), *A. suevicus* from Hambach 6C (early middle Miocene, MN5; Stefen & Mörs, 2008). *Trogontherium cuvieri* was studied in the collections

of the Museum in Maastricht and Leiden (C. Stefen, unpubl. data).

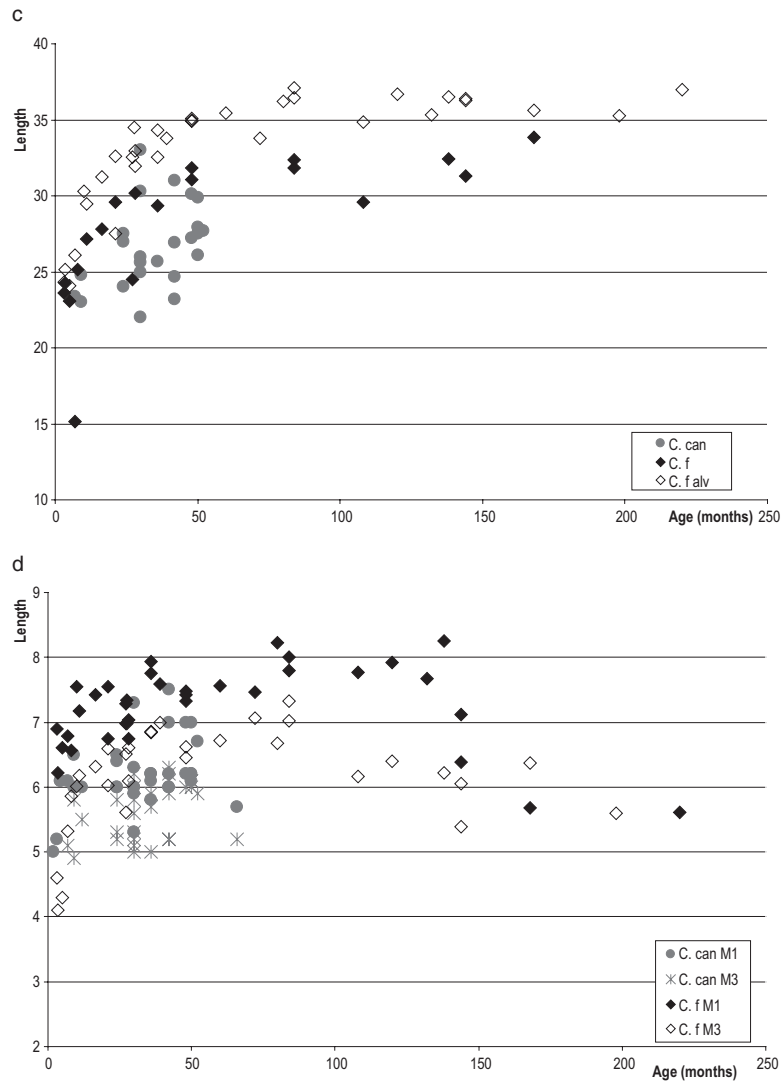
Comparisons were also made to the capybara, *Hydrochoerus hydrochaeris* Linné, 1766, which is the largest living rodent. This should indicate how much of an effect could be attributed to sheer size. Material in the Museum für Tierkunde, Dresden (MTD) was used: B18786 and B17860, both juveniles; and B4976 and B7095, both adults; exact ages unknown.

## RESULTS

The size variation with age for some individual teeth and the tooth row in both *C. fiber* and *C. canadensis* is illustrated in Figure 1 and Table 1. The lengths



**Figure 1.** Scatter plots showing changes in the length of teeth and mandibular tooth row with age for *Castor fiber* (C. f) and for *Castor canadensis* (C. can). A, lower incisor (i inf); B, lower premolar; C, upper tooth row (C. f alv length measured at alveoles of tooth row); D, upper molars, M1 and M3, respectively.



**Figure 1.** *Continued*

and widths of individual teeth, as well as the length of the tooth rows, show a similar pattern of exponential growth. Thus, a nearly linear increase in size can be seen within the first 45–50 months (up to 4.2 years) of age, which levels off with only a little size increase with age thereafter. The size is nearly constant from the age of about 6–7 years, and reaches the absolute maximum around an age of about 120 months (about 10 years). Within the first 50 months, the length of the incisors in *C. fiber* nearly doubles, from about 4 to nearly 8 mm, the length of the lower premolar increases by about 4 mm, and the length of the tooth row increases by nearly 10 mm. The overall range of variation in lower incisor length over all studied ages is about 6 mm (equal to about 58% of the maximal length, maxl, of the incisor) in *C. fiber* (Table 1). The highest

ranges in size over all studied ages are visible in the width of M3, width of P4, and width and length of the lower incisor. The lowest ranges were observed in the length of m1, M1, and M2, width of m1, and length of m1.

The length of the second lower molar of *C. fiber* can increase by up to 4 mm (from 6 to 10 mm) during postnatal growth, and this is equivalent to about 40% maxl of m2.

The few cranial measurements studied here show a similar growth pattern, with a nearly linear growth at young ages and less growth in older age. For interorbital width, mastoid breadth, condylobasal length, and mandibular diastema, it seems that the growth plateau is reached at about 37–40 months (3–3.5-years old), i.e. is reached earlier than in tooth growth.

**Table 1.** Measurements for some isolated teeth and tooth rows for the species studied

| Taxon                            | Tooth   | <i>n</i> | min (mm) | max (mm) | Range (mm) | Range in % of max. length of tooth |
|----------------------------------|---------|----------|----------|----------|------------|------------------------------------|
| <i>Castor fiber</i>              | i l     | 34       | 4.26     | 10.02    | 5.76       | 57.48                              |
| <i>Castor fiber</i>              | i b     | 34       | 4.26     | 10.63    | 6.37       | 59.92                              |
| <i>Castor fiber</i>              | P4 l    | 30       | 6.70     | 12.93    | 6.23       | 48.18                              |
| <i>Castor fiber</i>              | P4 b    | 30       | 6.22     | 9.30     | 3.08       | 33.11                              |
| <i>Castor fiber</i>              | M1 l    | 34       | 6.62     | 9.51     | 2.89       | 30.38                              |
| <i>Castor fiber</i>              | M1 b    | 34       | 5.90     | 0.94     | 4.04       | 40.64                              |
| <i>Castor fiber</i>              | M2 l    | 35       | 5.88     | 10.11    | 4.23       | 41.84                              |
| <i>Castor fiber</i>              | M2 b    | 35       | 4.52     | 9.17     | 4.65       | 40.71                              |
| <i>Castor fiber</i>              | M3 l    | 29       | 4.85     | 8.85     | 3.99       | 45.08                              |
| <i>Castor fiber</i>              | M3 b    | 29       | 4.00     | 8.00     | 4.00       | 50.00                              |
| <i>Castor fiber</i>              | P4–m3 l | 21       | 27.81    | 39.49    | 11.68      | 29.58                              |
| <i>Castor fiber</i>              | I l     | 29       | 4.47     | 9.97     | 5.50       | 55.17                              |
| <i>Castor fiber</i>              | I b     | 29       | 4.44     | 9.80     | 5.36       | 54.69                              |
| <i>Castor fiber</i>              | P4 l    | 30       | 6.97     | 13.65    | 6.68       | 48.94                              |
| <i>Castor fiber</i>              | P4 b    | 30       | 4.34     | 11.12    | 6.78       | 60.97                              |
| <i>Castor fiber</i>              | M1 l    | 35       | 5.61     | 8.25     | 2.64       | 32.00                              |
| <i>Castor fiber</i>              | M1 b    | 35       | 5.37     | 10.06    | 4.69       | 46.62                              |
| <i>Castor fiber</i>              | M2 l    | 34       | 5.37     | 7.74     | 2.37       | 30.62                              |
| <i>Castor fiber</i>              | M2 b    | 34       | 4.43     | 9.26     | 4.83       | 52.16                              |
| <i>Castor fiber</i>              | M3 l    | 33       | 4.10     | 7.32     | 3.22       | 43.99                              |
| <i>Castor fiber</i>              | M3 b    | 33       | 3.22     | 9.62     | 6.40       | 66.53                              |
| <i>Castor fiber</i>              | P4–M3 l | 18       | 23.10    | 33.87    | 10.77      | 31.79                              |
| <i>Hydrochoerus hydrochaeris</i> | i l     | 4        | 2.00     | 11.40    | 9.40       | 82.46                              |
| <i>Hydrochoerus hydrochaeris</i> | i b     | 4        | 2.00     | 8.60     | 6.60       | 76.74                              |
| <i>Hydrochoerus hydrochaeris</i> | I l     | 4        | 1.80     | 11.90    | 10.10      | 84.87                              |
| <i>Hydrochoerus hydrochaeris</i> | I b     | 4        | 2.00     | 9.00     | 7.00       | 77.78                              |
| <i>Hydrochoerus hydrochaeris</i> | P4 l    | 4        | 5.30     | 23.50    | 18.20      | 77.40                              |
| <i>Hydrochoerus hydrochaeris</i> | P4 b    | 4        | 3.00     | 9.80     | 6.80       | 69.39                              |
| <i>Hydrochoerus hydrochaeris</i> | P4–m3 l | 4        | 24.35    | 84.17    | 59.82      | 71.07                              |
| † <i>Steneofiber eseri</i>       | i & I l | 38       | 2.30     | 6.00     | 3.70       | 61.67                              |
| † <i>Steneofiber eseri</i>       | i & I b | 36       | 3.00     | 7.00     | 4.00       | 57.14                              |
| † <i>Steneofiber eseri</i>       | P4 l    | 38       | 5.18     | 8.00     | 2.82       | 35.25                              |
| † <i>Steneofiber eseri</i>       | P4 b    | 36       | 3.82     | 7.20     | 3.38       | 46.94                              |
| † <i>Steneofiber eseri</i>       | M1/2 l  | 64       | 3.20     | 6.00     | 2.80       | 46.67                              |
| † <i>Steneofiber eseri</i>       | M1/2 b  | 64       | 3.00     | 6.80     | 3.80       | 55.88                              |
| † <i>Steneofiber eseri</i>       | M3 l    | 7        | 4.66     | 5.19     | 0.53       | 10.21                              |
| † <i>Steneofiber eseri</i>       | M3 b    | 7        | 3.80     | 4.80     | 1.00       | 20.83                              |
| † <i>Steneofiber eseri</i>       | P4 l    | 24       | 5.30     | 7.77     | 2.47       | 31.78                              |
| † <i>Steneofiber eseri</i>       | P4 b    | 23       | 3.42     | 7.00     | 3.58       | 51.14                              |
| † <i>Steneofiber eseri</i>       | M1/2 l  | 14       | 4.00     | 5.80     | 1.80       | 31.03                              |
| † <i>Steneofiber eseri</i>       | M1/2 b  | 15       | 3.70     | 6.20     | 2.50       | 40.32                              |
| † <i>Steneofiber eseri</i>       | M3 l    | 20       | 3.25     | 4.90     | 1.65       | 33.67                              |
| † <i>Steneofiber eseri</i>       | M3 b    | 18       | 3.31     | 5.04     | 1.73       | 34.33                              |
| † <i>Steneofiber eseri</i>       | P4–m3 l | 5        | 21.50    | 26.00    | 4.50       | 17.30                              |
| † <i>Trogonthierium cuvieri</i>  | i l     | 17       | 6.85     | 10.61    | 3.76       | 35.38                              |
| † <i>Trogonthierium cuvieri</i>  | i b     | 17       | 8.66     | 14.00    | 5.34       | 38.14                              |
| † <i>Trogonthierium cuvieri</i>  | I l     | 18       | 8.55     | 10.88    | 2.33       | 21.41                              |
| † <i>Trogonthierium cuvieri</i>  | I b     | 18       | 9.44     | 13.85    | 4.41       | 31.84                              |
| † <i>Trogonthierium cuvieri</i>  | P4–m3 l | 8        | 31.62    | 38.81    | 7.19       | 18.52                              |
| † <i>Anchitheriomys suevicus</i> | i l     | 8        | ca. 6    | 13.90    | ca. 7.90   | ca. 56.83                          |
| † <i>Anchitheriomys suevicus</i> | i b     | 9        | 7.00     | 13.60    | 6.60       | 48.53                              |
| † <i>Anchitheriomys suevicus</i> | I l     | 6        | 6.00     | 10.00    | 4.00       | 44.44                              |



Table 1. Continued

| Taxon                            | Tooth   | n  | min (mm) | max (mm) | Range (mm) | Range in % of max. length of tooth |
|----------------------------------|---------|----|----------|----------|------------|------------------------------------|
| † <i>Anchitheriomys suevicus</i> | M1/2 l  | 16 | 7.40     | 8.80     | 1.40       | 15.91                              |
| † <i>Anchitheriomys suevicus</i> | M1/2 b  | 16 | 6.70     | 9.40     | 2.70       | 28.72                              |
| † <i>Anchitheriomys suevicus</i> | M3 l    | 4  | 6.20     | 7.60     | 1.40       | 18.42                              |
| † <i>Anchitheriomys suevicus</i> | M3 b    | 5  | 5.90     | 7.40     | 1.50       | 20.27                              |
| † <i>Anchitheriomys suevicus</i> | M1/2 l  | 7  | 7.10     | 8.30     | 1.20       | 14.46                              |
| † <i>Anchitheriomys suevicus</i> | M1/2 b  | 6  | 5.20     | 7.00     | 1.80       | 25.71                              |
| † <i>Anchitheriomys suevicus</i> | P4-m3 l | 7  | 27.20    | 39.00    | 11.80      | 30.25                              |
| † <i>Monosaulax pansus</i>       | i & I l | 50 | 2.20     | 4.20     | 2.00       | 47.62                              |
| † <i>Monosaulax pansus</i>       | i & I l | 50 | 2.20     | 4.30     | 2.10       | 48.80                              |
| † <i>Monosaulax pansus</i>       | P4 l    | 43 | 3.20     | 8.00     | 4.80       | 60.00                              |
| † <i>Monosaulax pansus</i>       | P4 b    | 43 | 2.95     | 4.90     | 1.95       | 39.79                              |
| † <i>Monosaulax pansus</i>       | P4 l    | 22 | 3.60     | 5.00     | 1.40       | 28.00                              |
| † <i>Monosaulax pansus</i>       | P4 b    | 22 | 3.80     | 6.20     | 2.40       | 38.70                              |
| † <i>Monosaulax pansus</i>       | M1/2 l  | 57 | 2.80     | 3.60     | 0.80       | 22.22                              |
| † <i>Monosaulax pansus</i>       | M1/2 b  | 57 | 2.60     | 4.50     | 1.90       | 42.22                              |
| † <i>Monosaulax pansus</i>       | M3 l    | 19 | 2.60     | 3.50     | 0.90       | 25.71                              |
| † <i>Monosaulax pansus</i>       | M3 b    | 18 | 2.70     | 3.70     | 1.00       | 27.03                              |

Data on *Monosaulax pansus* from Stefen (2001).

Abbreviations: b, width of tooth; I/i, upper or lower incisors, respectively; l, length of tooth; max, maximum; min, minimum; P4–M3/p4–m3, upper or lower tooth row, respectively.

The differences observed in the size ranges for the teeth of both species in this study, however, are a result of the different age structure of the samples, with no *C. canadensis* older than about 66 months. Therefore, no comparison between the two recent castorid species is attempted herein. Overall, *C. canadensis* is slightly smaller than *C. fiber*.

#### COMPARISON OF CASTOR WITH FOSSIL BEAVERS

The size range from juvenile to fully grown individuals is about 5.7 mm for incisor length in recent *Castor*: this is equivalent to about 57% of the maxl of the incisor (Table 1). For the length of the upper incisor of *A. suevicus*, the range is 7.9 mm, which is equivalent to nearly 57% of the maxl of the tooth. This is very similar to modern *Castor*, and thus the observed size differences in the small sample of fossil teeth of *A. suevicus* can well be attributed to postnatal growth, as suggested by Stefen & Mörs (2008).

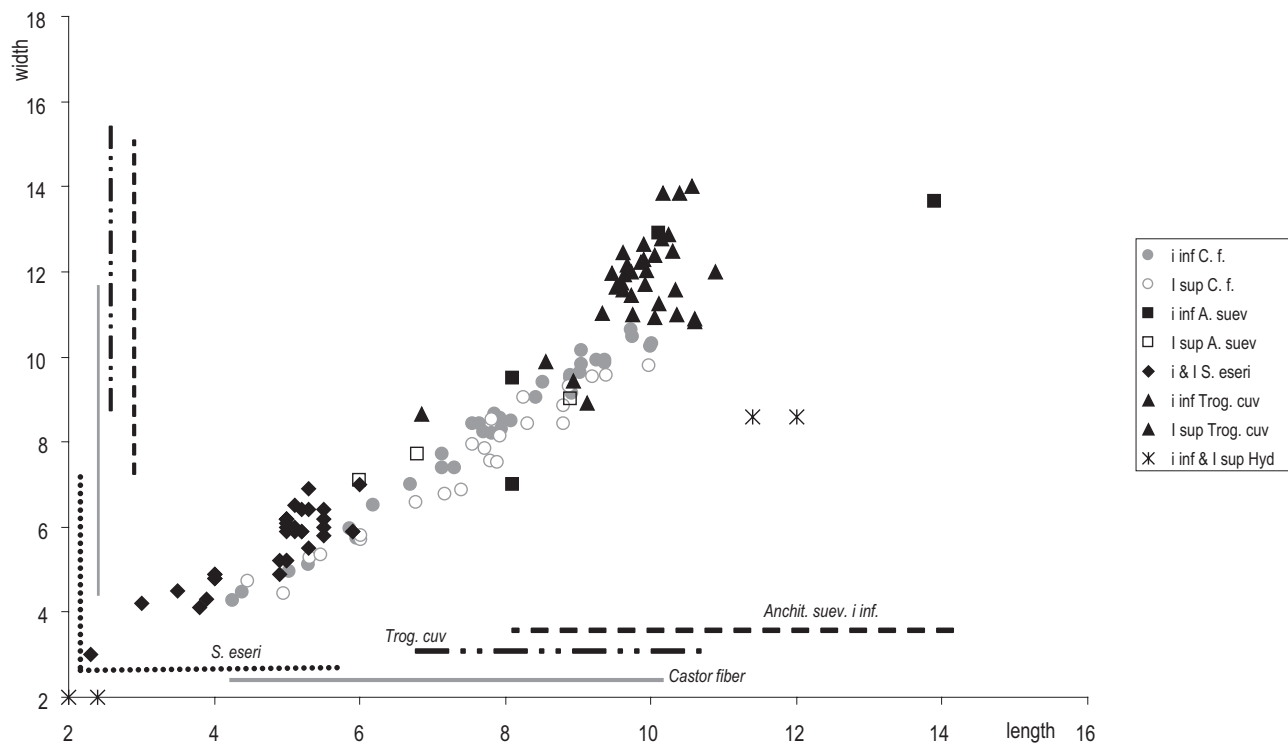
The range of the length of upper incisors differs between these two species: about 55% maxl in *Castor*, and about 44% in *Anchitheriomys* (Fig. 2, Table 1). The range in length of upper and lower incisors together is 62% maxl of the incisor in *S. eseri*, which is even larger than in modern *Castor*. The few studied specimens of the larger capybara (*H. hydrochaeris*) show a range in the length of upper and lower incisors of over 80% of maxl.

The size ranges of mandibular tooth rows for different fossil beavers and *C. fiber* are illustrated in Figure 3. For all of the species studied, a noticeable variation in tooth row length can be observed: about 11 mm (30% maxl) in *C. fiber*, 11.8 mm (30% maxl) in *A. suevicus*, and 60 mm (71% maxl) in *H. hydrochaeris*. For the samples of the early Miocene *S. eseri* and *S. castorinus* studied, the range of the mandibular tooth row is around 4 mm and 17% of maxl. In all species, the low size ranges were observed in m1/2 and M1/2 lengths and widths, respectively.

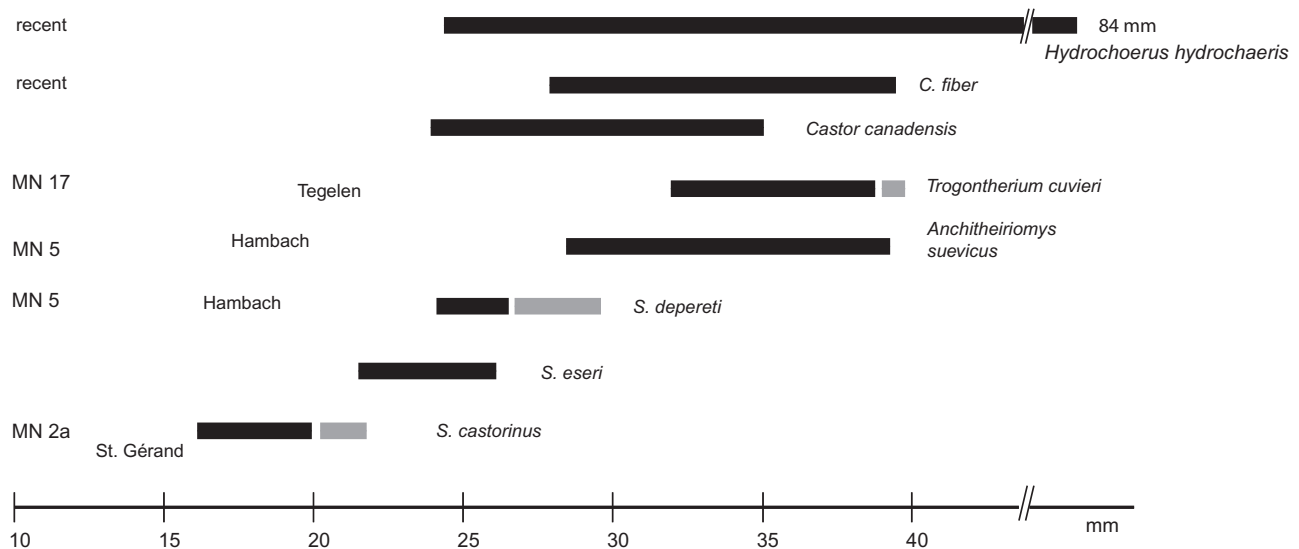
In recent *Castor*, no pattern in the form and distribution of enamel folds and islands on the chewing surface, which could be used as clear age indicators, were recognizable (Fig. 4). There are only a few features, like the closing of the para-, meso-, or metafossette, and, at the latest, hypofossette, that can be easily determined.

#### DISCUSSION

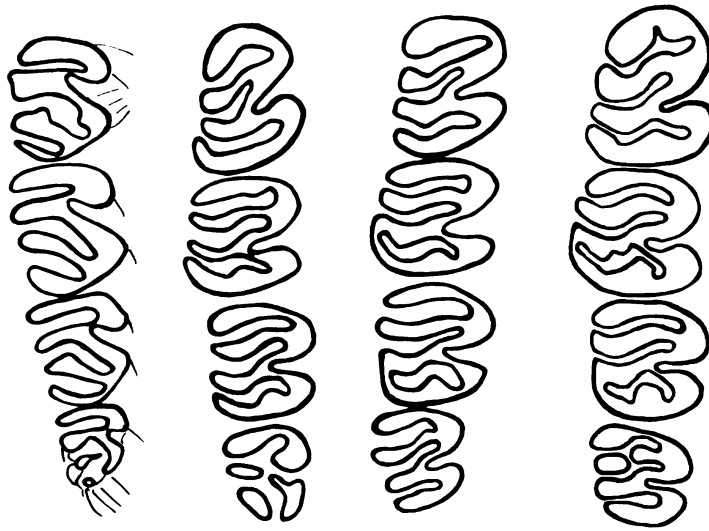
The data show a large, intraspecific size variation of the teeth that is attributable to changes with age in the Castoridae. For *C. fiber*, the data indicate large size ranges with age in lower and upper incisors, the length of lower premolars, the length and width of upper premolars, and the width of upper M3. Smaller ranges were observed for molar lengths. However, tests to see whether the differences in the observed ranges in length and width of the individual teeth are



**Figure 2.** Length–width plot of incisors (i inf, lower incisor; I sup, upper incisor) over different ages for recent *Castor fiber* (C. f.) in comparison with the fossils *Steneofiber eseri* (S. eseri), *Anchitheriomys suevicus* (A. suev), and *Trogontherium cuvieri* (Trog. cuv), and with recent *Hydrochoerus hydrochaeris* (Hyd). Ranges of lengths and widths for the castorid species are indicated close to the axes.



**Figure 3.** Lengths of mandibular tooth rows of recent *Castor fiber* of different ages in comparison with the fossils *Steneofiber eseri*, *S. castorinus*, *S. depereti*, *Anchitheriomys suevicus*, and *Trogontherium cuvieri*, and with recent *Hydrochoerus hydrochaeris*. The MN scale shows the European Mammal Neogene biozones for the fossil material. MN2a is early Miocene. Hambach, Tegelien, St. Gérard are the localities from where the represented fossil samples were studied. Data for *S. eseri* are from Stefen (1997), data for *A. suevicus* are from Stefen & Mörs (2008), data for *T. cuvieri* are the author's unpublished data, and data for *C. fiber* and *H. hydrochaeris* are from this paper.



**Figure 4.** Mandibular tooth rows of *Castor fiber* at different ages. A, 94/104, 5-months old; B, 94/190, 39-months old; C, 94/107, 48-months old; and D, 94/65, 80-months old. All are from the Zoological Collection University Halle-Wittenberg. Scale bar: 5 mm.

statistically significant, and indicate underlying substantial differences in the growth regime of individual teeth, were not performed. More detailed developmental and statistical studies would be necessary to test this, but are beyond the scope of this paper. The overall picture, with greater variation in incisors, length of p4 and P4, and width of P4, m2, m3, M2, and M3, seems reasonable. Incisors and, to a lesser degree, p4/P4 are the 'freest' teeth, with either no or only one adjacent tooth in the dentition, and thus have space to increase in size. The m3s are probably less free to increase in length because of the limited size of the jaw and their caudal position in it. The m1, m2 or M1, M2, have less space to increase in length with age. At a very old age, from 150 months onwards, the lengths of M1 and M3 even decrease slightly in *C. fiber*. This can also be observed in other fossil beavers, where the upper molars get shorter but broader as a result of use (Crusafont Pairó, 1948; Stefen, 1997).

The size ranges for the teeth and tooth rows of *H. hydrochaeris* are even larger: up to 84% maxl for upper incisors, and 71% maxl for mandibular tooth rows (Table 1). No data to determine the age of specimens in collections could be found for the capybara. In this species, even the overall shape of the incisor changes during postnatal growth: in juveniles, the upper incisors are round with nearly equal length and width, but they become more flattened labiolingually, and a depression in the middle of the labial side develops with increasing age. Such a difference in the shape of incisors of young and old individuals cannot be observed in *Castor*.

The difference in the magnitude in the size range of individual teeth between *Castor* and *Hydrochoeris* could be attributed to the different size of the species: *Castor*, with a weight of 12–25 kg, on average 22 kg, exhibits no sexual dimorphism in size, and has a lifespan of maybe 24 years in the wild, and 35–50 years in zoos (Nowak, 1999); *H. hydrochaeris*, with a weight of 27–79 kg, on average 50 kg in males and 61 kg in females, has a lifespan of 8–10 years in the wild, and over 12 years in captivity (Nowak, 1999). Both species are not closely related, but belong to different families of rodents. Differences in the evolutionary history, and thus inherited developmental constraints, may explain differences in the observed size ranges. The data for capybara support the general assumption that larger animals show a larger size range because of the larger size increase with age. Capybara and beaver are the largest living rodents, and share hypsodont teeth. Most fossil beavers were smaller, and had subhypsodont teeth, and are not directly comparable with modern *Castor* in this respect. Nothing is known about their lifespan or the timing of their postnatal development. Nevertheless, *S. eseri* from the early Miocene and *A. suevicus* from the middle Miocene show a size range over all ages represented in the fossil sample that is comparable in magnitude with modern *Castor* (Table 1). Crusafont Pairó (1948) noted smaller ranges for *Steneofiber depereti* Mayet, 1909. The large Pliocene–Pleistocene European beaver *Trogotherium cuvieri* Fischer de Waldheim, 1809 shows size ranges for the teeth that are noticeably smaller than in *Castor*, e.g. about 35% maxl for lower incisor length compared



with about 57% maxl in recent *Castor*. On first sight this seems surprising, because this species was hypsodont like *Castor*, and the teeth were of similar size. However, the size range determined in this study may not be representative of the overall size variation with age, because of a lack of very young or very old individuals in the random fossil sample.

The methods used to age beavers described by Piechocki & Stiefel (1977), Stiefel & Piechocki (1986), and Moll (1999) work well for recent *Castor*, but a direct transferral to Tertiary beavers is difficult. To transfer the sequence of tooth eruption to fossil beavers might work, and had been used to assess the population structure of the sample of *S. eseri* from Ulm Westtangente (Stefen, 1997), but one might object to that, because we do not know if this smaller species had similar developmental times to *Castor*. Whether the method of studying the cementum attachment to roots would work has not yet been tested, and as it is destructive, it might not be feasible for fossil teeth.

It is impossible to find visible morphological traits of the teeth of modern beavers without using intrusive methods to determine the age of the individual, or even to conclude if the specimen was at least 50 months of age or older (Fig. 4). For the subhypsodont teeth of fossil beavers it is even more difficult, and with the current knowledge of tooth morphology, it is impossible to accurately assess the individual age. Changes with wear in the occlusal pattern have been demonstrated (e.g. Stirton, 1935; Crusafont Pairó, Villalta Comella & Bataller Calatayud, 1948; Stefen, 1997). A scheme to use the successive closing of flexioids (or synclines) to determine the wear stage cannot be correlated directly to individual age, only to vague categories like very young and very old, and to a big field in the middle (Stefen, 2005).

Also, other methods to assign subhypsodont and hypsodont teeth to age groups have been proposed, like the index of hypsodonty (Van Valen, 1960) that has been modified and applied to several groups, mainly ungulates. Heinrich (1989) modified an age classification used by Kretzoi (1977), and distinguished six age classes in the studied Pleistocene *Castor*, based on pulpa closure and tooth wear. These methods using crown height are helpful to compare samples and to explain size variation with changes in age, but the age classes can not – so far – be clearly correlated to exact individual ages. Therefore, hypsodonty indices will not be discussed further here.

So far, it is near to impossible to develop a clear correlation between tooth wear, and/or morphology, and individual age that applies to all castorids alike. That is to both non- and subhypsodont teeth of most Miocene beavers, as well as to hypsodont teeth of the modern *Castor*, and also to some upper Tertiary

beavers (e.g. *Trogotherium* Fischer de Waldheim, 1809; *Castoroides* Foster, 1838; *Dipoides* Jaeger 1835). Therefore, up to now it only seems possible to assess the variability of fossil beaver samples using the entire size variation of *Castor* that is known to be attributable to age and postnatal growth. In this way, for samples of fossil beavers, at least ranges in size (length or width) of individual teeth, or tooth rows of up to 60% maxl, should be considered as intraspecific, because of ontogenetic differences, unless there are substantial and consistent morphological differences between smaller and larger teeth, that are of another magnitude than those occurring generally with wear in beavers, as documented for several species (e.g. Stirton, 1935, Crusafont Pairó *et al.*, 1948; Hünemann, 1966; Heinrich, 1989; Stefen, 1997).

Castorids might be special within the rodents in this respect, as they are very large and have a long lifespan (of over 16 years), compared with most holarctic rodents, such as voles, and even with other medium-sized rodents (e.g. nutria with a normal lifespan in the wild of 2–3 years, but which can live for up to 7 and even 10 years in captivity; Nowak, 1999). The larger capybara shows even larger intraspecific size variation with age, of up to over 80% maxl for teeth (Fig. 2, Table 1). As indicated in this study, the intraspecific size variation attributable to increasing age is even larger in this species. It also has hypsodont teeth and is comparable with the recent beaver in its life expectancy of about 8–10 years in the wild (Nowak, 1999).

Another point that sometimes renders studies on castorids and comparison of data difficult, is the fact that the angle of measuring the length and width changes with wear, as indicated by Heinrich (1989). This is a result of the angled position of the teeth in the jaws (upper and lower likewise), resulting in eruption of the teeth and wear that is not at a right angle to the long axis of the tooth. Therefore, the size increases reflected in the measurements are not the full size increases, but are to some degree caused by the slightly different angles at which the measurements are taken on differently worn teeth. The resulting error increases with hypsodonty in castorids.

## CONCLUSION

For both of the recent beavers *C. fiber* and *C. canadensis*, the variation in size of the teeth is large over all ages and is of similar magnitude. The teeth increase in size nearly linearly up to the age of about 50 months, and show little size increase afterwards. Thus, 50 months seems to be the cut-off point between individuals with teeth that are still growing and individuals with fully grown teeth. The intraspecific variability between fully grown individuals is

relatively small: most of the intraspecific variability derives from ontogenetic changes within the first 50 months. No morphological feature of the teeth that can be studied with non-invasive methods can clearly indicate this age. To use these data for comparison with samples of fossil beavers, it is suggested that the overall size variation must be used, because in fossil samples a good age determination is not possible. The range of some samples of Tertiary fossil beavers, e.g. of *S. eseri*, *A. suveicus*, and *T. cuvieri* compare well with the variability of recent *Castor* with age. The larger recent rodent *H. hydrochaeris* shows an even larger range of intraspecific variation in the size of its teeth and tooth rows.

### ACKNOWLEDGEMENTS

I want to thank Dr D. Heidecke, curator of the Zoological Collection of the Martin-Luther-Universität Halle-Wittenberg, for allowing me to study and to borrow material, and for the hospitality that I received while there. Similarly, I thank Dr B. Stein, formerly at the Museum of Vertebrate Zoology, University of California, Berkeley. The work at MVZ was supported by the DFG (grant ST 798/1-1). Dr D. Heidecke and the reviewers made helpful comments on the manuscript, and Dana Jones, Dresden, corrected the English.

### REFERENCES

- Becker K. 1952.** Die Hausratte (*Rattus rattus* L.) in Berlin und im Fläming. *Zoologischer Anzeiger* **148**: 259–269.
- Corbet GB, Jones LA. 1965.** The specific characters of the crested porcupines, *Hystrix*. *Proceedings of the Zoological Society London* **44**: 285–300.
- Crusafont Pairó M. 1948.** La castores fósiles de España. II. Biometría. *Boletín del Instituto Geológico y Minero de España* **61**: 425–449.
- Crusafont Pairó M, Villalta Comella JF, Bataller Calatayud JR. 1948.** Los castores fósiles de España. I. Parte general y descriptiva. *Boletín del Instituto Geológico y Minero de España* **61**: 321–423.
- Filhol MH. 1879.** Étude des mammifères fossiles de Saint-Gérard le Puy (Allier). *Annales des Sciences Géologiques* **2**: 1–252.
- Frahnert S. 2000.** Wachstumsbedingte Proportionsveränderungen am Schädel des Bibers, *Castor fiber* L., 1758 (Rodentia, Castoridae): Taxonomische Bedeutung und Diskussion funktioneller Aspekte. *Bonner Zoologische Beiträge* **49**: 131–153.
- Frahnert S, Heidecke D. 1992.** Kranimetrische Analyse europäischer Biber, *Castor Fiber* L. (Rodentia, Castoridae), erste Ergebnisse. *Semiaquatische Säugetiere, Wissenschaftliche Beiträge der Universität Halle* 175–189.
- Freye HA. 1959.** Descriptive Anatomie des Craniums vom Elbe Biber (*Castor fiber albicus* Matschie 1907). *Wissenschaftliche Zeitschrift der Universität Halle, Mathematisch Naturwissenschaftliche Reihe* **8**: 913–962.
- Habermehl KH. 1961.** Altersbestimmung bei Haustieren, Pelztieren und beim jagbaren Wild. Berlin: Paul Parey.
- Heinrich WD. 1989.** Biometrische Untersuchungen an Fossilresten des Bibers (*Castor fiber* L.) aus thüringischen Travertinen. *Ethnographisch-Archäologische Zeitschrift EAZ* **30**: 394–403.
- Hinze G. 1950.** Der Biber. Körperbau und Lebensweise Verbreitung und Geschichte. Berlin: Akademie Verlag.
- Hünemann KA. 1966.** Der Bau des Biber-Praemolaren und seine Verwendbarkeit für die Systematik der Castoridae (Rodentia, Mammalia). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **125**: 227–234.
- Korth WW. 2001.** Comments on the systematics and classification of the beaver. *Journal of Mammalian Evolution* **8**: 279–296.
- Kretzoi M. 1977.** Die *Castor*-Reste aus den Travertinen von Taubach bei Weimar. *Quartärpaläontologie* **2**: 389–400.
- Lidicker W, Jr. 1966.** Ecological observations on a feral house mouse population declining to extinction. *Ecological Monographs* **36**: 27–50.
- Lavrov LS. 1949.** [Ergebnisse und weitere perspektivische Entwicklung der Flußbiber in der Farmhaltung.]. *Wissenschaftliche-Methodische Beiträge (Moskau)* **13**: 174–194. (in russian).
- Lönnberg E. 1909.** A study of the variation of European Beavers. *Arkiv för Zoologi* **5**: 1–16.
- Lux K. 1990.** Altersbestimmung des Elbe-Bibers nach einem Molarenindex. Unpublished Diplomthesis Martin-Luther-University Halle-Wittenberg.
- Macholán M. 1996a.** Morphometric analysis of European house mice. *Acta Theriologica* **41**: 255–275.
- Macholán M. 1996b.** Multivariate morphometric analysis of European species of the genus *Mus* (Mammalia, Muridae). *Zeitschrift für Säugetierkunde* **61**: 304–319.
- Moll S. 1999.** Altersbestimmung nach Zahnzement-Zuwachslinien, Altersstruktur und Todesursachen beim Biber (*Castor fiber albicus* Matschie, 1907) der Mittelbe-Bevölkerung. Unpublished Diplomthesis Martin-Luther-University Halle-Wittenberg.
- Mora M, Olivares AI, Vassallo AI. 2003.** Size, shape and structural versatility of the skull of the subterranean rodent *Ctenomys* (Rodentia, Caviomorpha): functional and morphological analysis. *Biological Journal of the Linnean Society* **78**: 85–96.
- Muyllé S, Simoens P, Lauwers H. 1996.** Ageing horses by an examination of their incisor teeth: an (im)possible task? *Veterinary Record* **138**: 295–301.
- Muyllé S, Simoens P, Lauwers H, Van Loon G. 1997.** Ageing draft and trotter horses by their dentition. *The Veterinary Record* **141**: 17–20.
- Novak M. 1987.** Beaver. In: Novak M, Baker JA, Obbard ME, Malloch B, eds. *Wild furbearer management and conservation in North America*. Ontario: Ministry of Natural Resources, 283–312.
- Nowak RM. 1999.** *Walker's Mammals of the world*. Baltimore and London: The Johns Hopkins University Press.

- Piechocki R, Stiefel A. 1977.** Zahndurchbruch und Zahnwechsel beim Elbebiber, *Castor fiber albicus*. *Anatomischer Anzeiger* **142**: 374–384.
- Richardson JD, Lane JG, Waldron KR. 1994.** Is dentition an accurate indication of the age of a horse? *Veterinary Record* **135**: 31–34.
- Richardson JD, Cripps PJ, Lane JG. 1995.** An evaluation of the accuracy of ageing horses by their dentition: changes of dental morphology with age. *Veterinary Record* **137**: 117–121.
- Saint Girons MC. 1973.** L'âge des micromammifères. *Mammalia* **37**: 439–456.
- Silver IA. 1969.** The ageing of domestic animals. In: Brothwell D, Higgs E, eds. *Science in archaeology*. London: Thames and Hudson, 283–302.
- Stefen C. 1997.** *Steneofiber eseri* (Castoridae, Mammalia) von der Westtangente bei Ulm im Vergleich zu anderen Biberpopulationen. *Stuttgarter Beiträge zur Naturkunde B* **255**: 1–78.
- Stefen C. 2001.** The Barstovian (Miocene) beavers from Stewart Valley, Nevada, and a preliminary discussion of the genus *Monosaulax* mainly on the basis of tooth morphology. *PaleoBios* **21**: 1–15.
- Stefen C. 2005.** Description of the cranial morphology of the Early Miocene beaver *Steneofiber castorinus*. *Neues Jahrbuch für Mineralogie und Paläontologie* **2005**: 577–596.
- Stefen C, Mörs T. 2008.** The beaver *Anchitheriomys* from the Miocene of Central Europe. *Journal of Paleontology* **82**: 1009–1020.
- Stiefel A, Piechocki R. 1986.** Circanuelle Zuwachslinien im Molarenzement des Bibers (*Castor fiber*) als Hilfsmittel für exakte Altersbestimmungen. *Zoologische Abhandlungen Museum für Tierkunde Dresden* **41**: 165–175.
- Stirton RA. 1935.** A review of Tertiary beavers. *University of California Publications in Geological Sciences* **23**: 391–458.
- Van Valen L. 1960.** A functional index of hypsodonty. *Evolution* **14**: 531–532.
- Véron G. 1992.** Étude morphométrique et taxonomique du genre *Castor*. *Bulletin du Muséum d'Histoire Naturelle Paris 4e Séries* **14**: 829–853.
- Yalden DW, Morris A, Harper J. 1973.** Studies on the comparative ecology of some French small mammals. *Mammalia* **37**: 257–276.

## APPENDIX

Abbreviations: i, lower incisor; I, upper incisor; m1–m3, lower molars from one to three; M1–M3, upper molars from one to three; maxl, maximal length; p4, lower p4; P4, upper P4.