

REVIEW PAPER

A Brief Overview of the Evolution of European Tertiary Beavers

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Abstract

Beavers are a well defined group of rodents that are known from the late Eocene to recent times. Today only one genus with two species, *Castor fiber* and *Castor canadensis* – both with several described subspecies – occur in Eurasia and North America respectively. During the Tertiary beavers were much more diverse in North America, Europe and Asia ranging in size from about a mouse to a capybara. In Europe there is one major radiation starting in the Late Oligocene or Early Miocene with *Propalaeocastor* (= *Astenofiber*) or *Steneofiber*, with several subsequent species of *Steneofiber*, leading to *Chalicomys*, and *Trogotherium*. Some generic distinctions are still not quite clear here. Probable immigrants to Europe include *Anchitheriomys* and *Dipoides*. One difficulty in understanding castorid evolution is posed by the fact, that especially European beavers are often found in low numbers and the bulk of the fossil material consists of isolated teeth and mandibular or small maxillary fragments. Skulls and even substantial skull fragments are generally rare. As recent *Castor* and larger samples of fossil beavers show great morphometric variability, it is strongly suggested to discuss beaver taxonomy on the basis of populations or representative statistical samples, not based on individual teeth or extremely fragmentary material. More names and descriptions will not help our understanding of this group of rodents. Particularly the differentiation of *Steneofiber* and *Chalicomys* as well as the taxonomic position of the small species assigned to *Trogotherium* or/and *Steneofiber* still need further discussion.

Key words: European Castoridae, phylogeny, *Steneofiber*, *Trogotherium*, *Chalicomys*

Introduction

Today, beavers are represented by the genus *Castor* only, occurring in the Holarctic. *Castor canadensis* and *C. fiber* are generally accepted species but subspecies differentiation (e.g. Taylor 1916, Gabryś and Ważna. 2003, Rosell and Steifetten 2004, Peterson et al. 2005, Babik et al. 2005, Ducroz et al. 2005, Durka et al. 2005) and within genus evolution (Barisone et al. 2006, Durka et al. 2005) are less clear. During the Tertiary a much higher diversity of Castoridae with up to 30 described genera existed (Korth 2001a, McKenna and Bell 1997), the distribution has also been restricted to North America and Eurasia. The southernmost record in Europe is assumed to come from the Granada Basin in southern Spain (Mio-Pliocene *Dipoides problematicus*, (García-Alix et al. 2007). The earliest forms assigned to *Agnotocastor* occur in North America and Asia nearly simultaneously (Korth and Emry 1997, Korth 2001a). Several radiations can be distinguished, one in the upper Oligocene and Miocene of palaeocastorid beavers in North America without any further descendants, the European one originating from the Early Miocene *Steneofiber* or

even late Oligocene *Propalaeocastor* (= *Astenofiber*) and a probable radiation in North America originating in *Monosaulax* leading to *Eucastor*, *Dipoides* and possibly also *Castoroides* (Stirton 1935, Schreuder 1929, Mayhew 1978). The palaeocastorid beavers are fossorial and associated with the burrows originally described as *Daemonelix* (Barbour 1892). Wood cutting is known for recent *Castor* and *Dipoides* (Rybczynski 2007), a semiaquatic lifestyle for recent *Castor* and assumed for *Steneofiber* (Hugueny and Escuil-lé 1995), *Trogotherium cuvieri* (Schreuder 1929) and *Castoroides* (Moore 1890).

During the European Miocene up to six different genera (*Steneofiber*, *Trogotherium*, *Chalicomys*, *Anchitheriomys*, *Dipoides*, *Eucastor* (*Schreuderia*)?) have been recorded (Hugueny 1999). The most common beaver genus in early to middle Miocene faunas is *Steneofiber* which has been considered at the base of an European evolutionary lineage *Steneofiber* – *Chalicomys* – *Castor* (Schreuder 1931). The other lineage which can be seen in Europe is the *Steneofiber*–*Trogotherium* lineage (Mayhew 1978, Stefen 1997).

Recent *Castor*, as well as *Chalicomys*, *Steneofiber*, *Schreuderia*, *Romanofiber* and *Zamolxifiber* (the

two latter synonymized to *Trogontherium* by Mayhew 1978 and this is followed herein) have been grouped as Castorinae by Korth (2001 a), and *Castor*, *Hystri-cops*, *Sinocastor*, *Steneofiber* have been grouped as Castorinae by Rybczynski (2007).

Anchitheriomys as well as *Dipoides* have to be considered immigrants to Europe and will not be dealt with in detail here (see for *Anchitheriomys*: Roger 1898, Heizmann 1982, Korth and Emry 1997, Korth 2001b, 2004, Stefen and Mörs 2008; for *Dipoides* Schlosser 1885, Shothwell 1955). *Eucastor* (*Schreuderia*)? needs further detailed evaluation as *Eucastor* is defined on North American beaver material (Stirton 1935) and *Schreuderia* has been named by Aldana Carrasco (1992) based on material from Spain which metrically fits well within the range of *Chalicomys* (Stefen 2009a).

In this paper, some aspects of the phylogeny of European Tertiary beavers are summarized and discussed.

Probable European evolutionary lineage *Steneofiber* – *Chalicomys*

The genus *Steneofiber* from the lower Miocene can be seen as basis of the European radiation of Tertiary beavers (Fig. 1; Schreuder 1931, Mayhew 1978, Stefen 1997). Probably it derived from the Oligocene forms of *Asteneofiber* (Hugueny 1999). The Oligocene forms had originally been referred to *Steneofiber* (e.g. Misonne 1957) then to *Asteneofiber* by Kretzoi (1974) and more recently to *Propalaeocastor* by Wu et al. (2004). These Oligocene forms are known from a few teeth only and will not be considered further herein.

Steneofiber castorinus from the locality St. Gérard in France, assigned to the European Mammalian Neogene biozone MN 2a is known from cranial material (Fig. 2; e.g. Gervais 1852, Taf. 48, Abb 9, 9a, b Viret 1929, plate II Fig 1a and b) revised by Stefen (2005). *Steneofiber eseri* is known from several sites in Southern Germany from isolated teeth and from a good sample also including fairly crushed cranial and postcranial material from Ulm-Westtangente, Southern Germany, also from MN 2a (Stefen 1997). *S. castorinus* and *S. eseri* can be considered two species as there are statistically significant differences in the size of the teeth (Stefen 2001). Thus a split in two – or potentially even more – lineages might have occurred already in the late Oligocene; due to the little preserved material it will be difficult to pinpoint. Based on the geographical regions where fossils of the subsequent taxa are found the possible lineages are illustrated in Fig 1. The line from *Steneofiber* to *Chalicomys jaegeri* (= *Palaeomys*) and to *Castor* had been proposed by Schreuder (1931) and others, a line from *Steneofiber* to *Trogontherium* e.g. by Mayhew (1978).

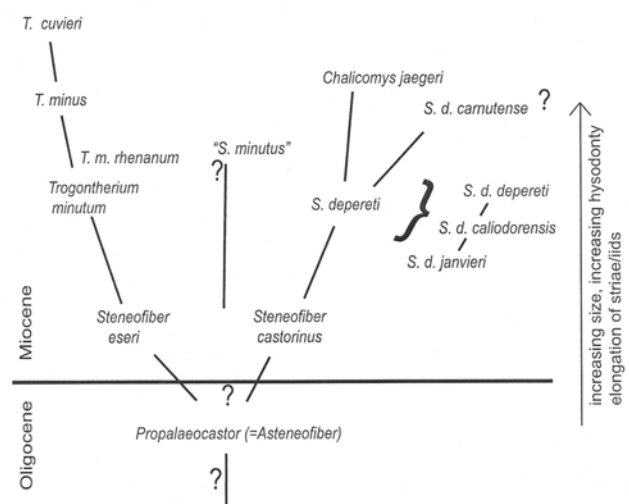


Figure 1. Proposed evolutionary History of the European beaver lineage originating in *Steneofiber* (e.g. Schreuder 1929, Stirton 1935, Mayhew 1978, Stefen 1997). The subspecies division and sequence of *Steneofiber depereti* has been suggested by Ginsburg (1971, 1988). The separation between *Steneofiber castorinus* and *S. eseri* is based on statistical differences in tooth size (Stefen 2001) and putting these at the base of two different subsequent lineages is arbitrary based on geographic occurrences. The taxonomic position of *S. minutus* remains unclear (see text)

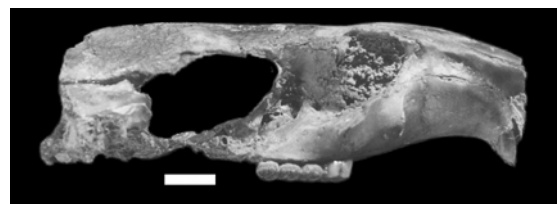
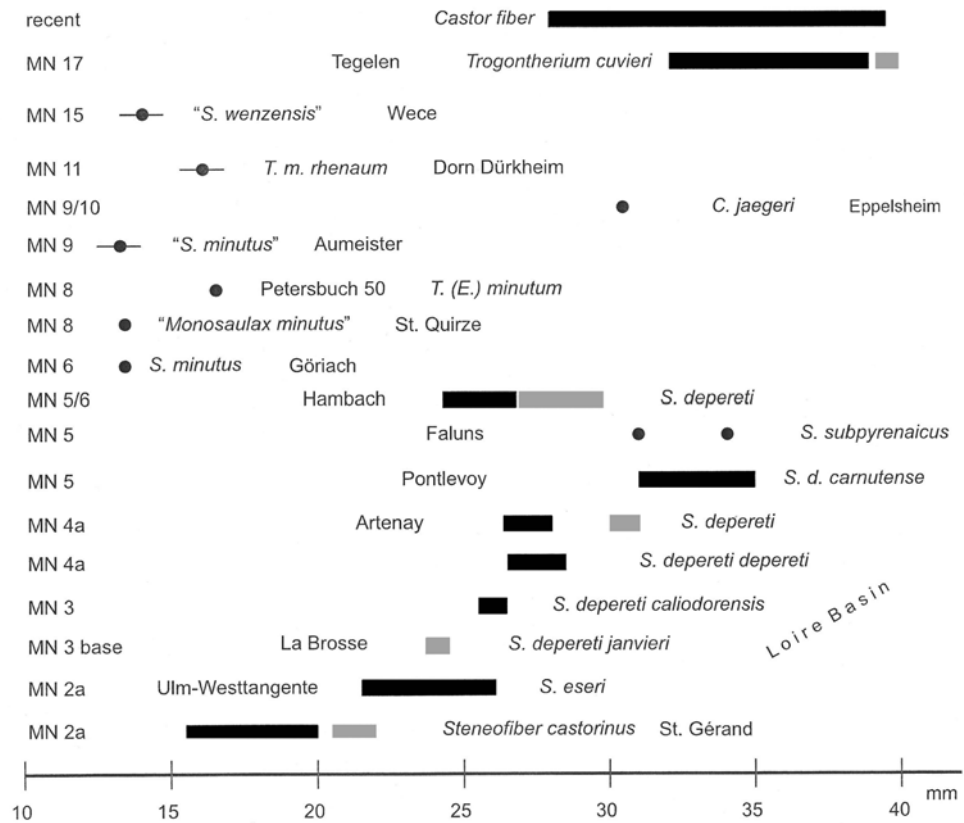


Figure 2. Skull *Steneofiber castorinus* from Saint Gérard, (Musée national d'Histoire naturelle Paris SG3654) which is the one studied by Geoffroy Saint-Hillaire (1833) to introduce the genus *Steneofiber* in lateral view from Stefen 2005. Scale = 1 cm

There is a general consensus about the tendency in both lineages to increase size and hypsodonty; also striae/striads were elongated and more persistent with wear (Schreuder 1931, Stirton 1935, Ginsburg 1971, Stefen 1997, 2009a). Therefore the transition and specific differentiation between the genera (or species) in both lineages remains difficult, even more so as not all named species are represented by cranial material or even large samples of teeth. No cranial material has yet been described of *S. depereti* nor of *Chalicomys jaegeri*.

Recently, a new species of *Chalicomys*, *C. batalleri* has been described from MN 7/8 in Spain (Casanovas-Vilar et al. 2008). The crenulations indicated as specific for this species are interpreted as juvenile features by Mörs and Stefen (2010) and as the specimen falls within the size range of *Steneofiber*

Figure 3. Length of mandibular tooth rows of some European beaver species in comparison to recent Castor fiber adopted from Stefen (2009a) and Mörs and Stefen (2010). Black bars represent measurements of tooth crowns or literature, grey bars represent measurements at the alveols. If not otherwise stated, data are from own measurements. *Monosaulax minutus* from Aldana Carrasco (1992), *T. minutum rhenanum* estimated after Franzen and Stroch (1975), subspecies of *S. depereti* from Ginsburg (1971, 1988) and Hugueney (1999), "*S. wenzensis*" estimated after Sulimski (1964), *S. minutus* from Aumeister estimated after Stromer (1928), from Göriach from Hofmann (1893)



depereti from Hambach these authors argue that it rather represents *S. depereti*.

For *Steneofiber depereti*, an intraspecific evolution of increasingly larger subspecies has been suggested based on material from the Loire basin by Ginsburg (1971, 1988; Fig. 3). However, Mörs and Stefen (2010) studied material of *Steneofiber depereti* from Hambach 6C and showed that the size range of the species from this one locality overlapped with several of the suggested subspecies. Thus, the subspecies differentiation seems to be local phenomena of the Loire Basin and not a generally valid. Problems with the largest subspecies *S. d. carnutense* remain, as this subspecies is larger than *S. depereti* from Hambach. It is similar in size to the named *Steneofiber subpyrenaicus*. As little material is known this has not been further addressed and would need further study. Here, *S. depereti* is tentatively depicted in the *Steneofiber – Chalicomys* lineage as the size increase fits well in this picture but *Chalicomys jaegeri* and *S. depereti* might represent separate evolutionary lineages of increasing size both based on earlier representatives of *Steneofiber*.

Probable European evolutionary lineage *Steneofiber – Trogontherium*

In the other probable European castorid lineage from *Steneofiber* to *Trogontherium*, the large Plio-Pleis-

tocene species *Trogontherium cuvieri* is fairly well known from cranial material (Fischer de Waldheim 1809, Newton 1892, Schreuder 1929, 1931, Dechaseaux 1967, Mayhew 1978). Its geographical distribution in Europe has been reviewed recently by Fostovicz-Frelik (2008). Unfortunately, the other species assigned to this genus are less well known and often based on little material. Therefore, even the differentiation of and transition from *Steneofiber* to *Trogontherium* remains not well defined. Major features generally used to characterize *Trogontherium* as based on *T. cuvieri* are: subhypsodont teeth with little or no crown cement, relative large premolars, long, cone shaped upper M3 with a number of additional flexids and incisors with wrinkled enamel (Mayhew 1978). Within Castoridae striated enamel on incisors also occur independently in *Anchitheriomys* and *Castoroides* (also in *Propalaeocastor*) and an elongated M3 also in *Castoroides*. In *Trogontherium*, however, the striation is much weaker.

The smaller species of *Trogontherium* are less well known and no agreement on the taxonomy of small species exist. Mayhew (1978) accepted *T. minutum* (von Meyer 1838) and *T. minus* Newton 1890 (from Hajnacka, Slatina, Weze the specimen of "*S. wenzensis*" see below, Red Crag Nodule Beds) and discussed the proposed evolutionary lineage from *Trogontherium minutum* (occurring from MN 11 to MN 15) to *T. mi-*

nus (occurring from the MN 14 to MN 16) to *T. cuvieri* (occurring from the upper Pliocene onwards). *T. minus* was described by Newton (1890) on the basis of a right maxilla fragment with P4 to M2 thus lacking the usually diagnostic elongated M3 in the type specimen. Mayhew (1978: 433) indicted that *T. minus* is larger than *T. minutum* and separated the species pointing to the fact that a division in his proposed phylogenetic line was arbitrary.

The subspecies *Trogotherium minutum rhenanum* is known from teeth from Dorn Dürkheim (MN 11) named and described by Storch in Franzen and Storch (1975). A skull assigned to *T. (Euroxenomys) minutus* unfortunately lacking some taxonomically important characters had been described from the fissure filling Petersbuch 50 according to the fauna referred to MN 8 (Stefen and Rummel 2003). It has been referred to the subgenus *Euroxenomys* as it lacks striation of the enamel in the upper incisors.

Huguency (1999) referred small beaver species from the middle Miocene upwards to *Trogotherium (Euroxenomys) minutum* (referring to *Chalicomys minutus* von Meyer 1838 as type), separating them on the subspecies level in *T. m. minutum* and *T. m. rhenanum*. Thus the overall geological range for *T. (Euroxenomys) minutus* would be MN 4 to MN 13 (Huguency 1999). Small beavers originally described as *Chalicomys minutus* by von Meyer (1838) have been referred to *Steneofiber* and *Monosaulax* as well. Only a few teeth have been described e.g. from Göriach (Hofmann 1893), from near Munich (Stromer 1928) and from Spain (Crusafont et al. 1948, Aldana Carrasco 1992). The question whether any European beaver specimen should be referred to *Monosaulax* will not be discussed here but seems unlikely.

As the increasing size, particularly the elongation to a cone-like shape of the M3, is considered characteristic of *Trogotherium*, the available data for teeth assigned to *Trogotherium* and *Steneofiber* have been analysed (Fig. 4, 5). A comparison with "*Steneofiber wenzensis*" (Sulimski 1964, assigned to *Trogotherium* by Mayhew 1978 and to *T. (Euroxenomys) minutum* by Huguency 1999 herein kept as representative of *Steneofiber* due to the lack of elongation of M3 but some other difficulties remain with the generic assignment) indicated that two lineages might have coexisted for longer during the Miocene: one of *Steneofiber* indicated by "*S. wenzensis*" in MN 15 with non elongated M3 and one of *Trogotherium* with already elongated M3 in specimen of the subgenus *Euroxenomys* in MN 8 (Petersbuch 50) but lacking the striated enamel in upper incisors (Stefen and Rummel 2003). As so little material of these forms is available from Central Europe an evaluation remains difficult.

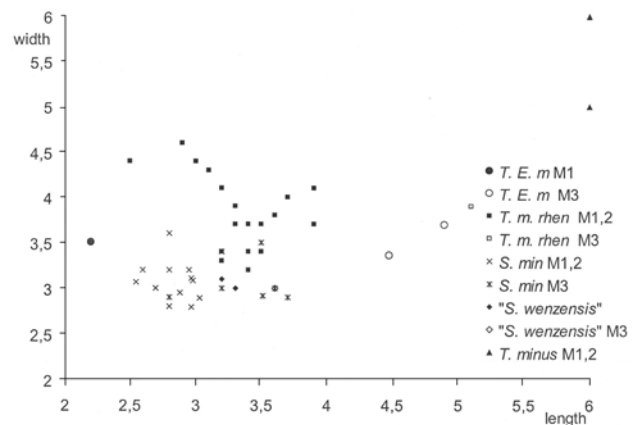


Figure 4. Length and width scatter diagram for *Trogotherium (Euroxenomys) minutum* from Petersbuch 50 (*T. E. min Pb50*) in comparison to other beavers from Stefen and Rummel (2003). *T. m. rhen* - *Trogotherium minutum rhenanum*; *S. min* - small beavers referred to *Steneofiber minutus* (Stromer 1928; Hofmann 1893); *S. wenzensis* - beaver from Weze (MN 15) originally described as *Steneofiber wenzensis* (Sulimski 1964, here separated on purpose from *Trogotherium* for clarity although referred to *T. (Euroxenomys) minutum* by Huguency 1999); *T. minus* from Mayhew (1978)

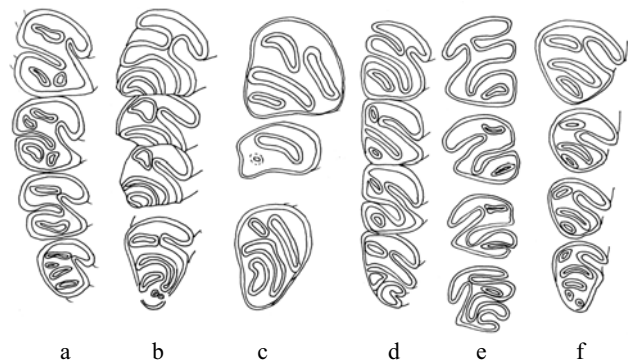


Figure 5. Comparative drawing of maxillary tooth rows of maxillary dentitions of some castorids: a) *Steneofiber eseri* from Ulm-Westtangente after Stefen (1997), b) *Trogotherium minutum rhenanum* from Dorn Dürkheim after Storch in Franzen and Storch (1975), M3 not associated with P4-M2, c) *Trogotherium (Euroxenomys) minutum* from Petersbuch 50 preserved in situ from Stefen and Rummel (2003), d) "*Steneofiber*" *wenzensis* after the skull from Sulimski (1964), e) *Chalicomys jaegeri* from Eppelsheim after Stefen (2009a), the teeth are preserved in situ with the gaps, f) *Trogotherium cuvieri* the Type of Fischer de Waldheim from Azof as in Newton (1893). Dentitions are not to scale but brought to the same size for comparison, approximate length of the tooth rows are: a) 19 mm, b) 17 mm (from measurements given in Franzen and Storch 1975), c) 11 mm, 14 mm (after Sulimski 1964), e) 27 mm (sum of the measurements of the individual teeth), and f) between 35 and 38 mm typical for *Trogotherium cuvieri* from Tegelen (own measurements)

The time span of the mammalian biozones MN 6 to MN8 seems to be the time of transition in both the *Steneofiber* – *Trogontherium* and *Steneofiber* – *Chalicomys* lineage which might need ecological consideration. From this time relatively few isolated teeth from different localities are described but no substantial samples allowing statistical analysis (see Hugueny 1999 for list of localities). Larger samples including juvenile, adult, and very worn teeth from one locality are important if not necessary to understand morphometrics of fossil beavers. The variability in size and changes with wear are particularly large in this family of rodents (see Stefen 2009b for recent *Castor* and e.g. Stirton 1935, Crusafont Pairó 1948, Crusafont Pairó et al. 1948, and Stefen 1997 for fossil beavers). Therefore, it seems important to base taxonomic comparisons on larger samples.

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