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# The castorid *Steneofiber* from NW Germany and its implications for the taxonomy of Miocene beavers

THOMAS MÖRS and CLARA STEFEN



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Craniodental remains of a medium-sized beaver from the early middle Miocene of Hambach (MN 5) in the Lower Rhine Basin of northwestern Germany are described and assigned to *Steneofiber depereti*. The relatively rich material (6 mandibles and 56 isolated teeth) was collected from a single locality, Hambach 6C, and comprises specimens representing juvenile to very old individuals. This makes it possible to assess the morphologic and metric variability of a single population of *Steneofiber depereti*. Metrically, the mandibular tooth rows compare favorably in size to those of three subspecies described from the Loire Basin in France: *Steneofiber depereti janvieri*, *Steneofiber d. caliodorensis*, and *Steneofiber d. depereti*. Therefore in our opinion, division into subspecies cannot be applied to *S. depereti* in general. The difference in size between the smaller beaver from Hambach and the contemporaneous larger *S. d. carnutense* from the Loire Basin is remarkable. The taxonomy of early middle Miocene medium-sized castorids, referred to *Steneofiber depereti*, *Steneofiber subpyrenaicus*, and *Chalicomys jaegeri* is discussed. The presence of the derived beaver *C. jaegeri* in MN 4 to MN 6 is questioned and assignment to *Steneofiber* suggested. The occasional appearance of single *C. jaegeri* features in *S. depereti* supports the existence of a European lineage from the Orleanian *S. depereti* to the Vallesian *C. jaegeri*. The taxonomic status of *S. subpyrenaicus* remains unresolved.

Key words: Mammalia, Rodentia, Castoridae, morphology, systematics, Neogene, Hambach, Lower Rhine Basin.

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## Introduction

Whereas today beavers are represented by the genus *Castor* only, in the European Miocene the group had a higher diversity of up to six different genera (Hugueney 1999). The most common beaver genus in Miocene faunas is *Steneofiber*, which is a European evolutionary lineage (Schreuder 1929). There is a general consensus regarding the tendency in this lineage to increase size and hypsodonty with time. In connection with this, striae/striids were elongated and more persistent with wear (Schreuder 1931; Stirton 1935; Ginsburg 1971; Stefen 1997). Less clear, however, is the taxonomic status of material referred to the lineage.

Although common, *Steneofiber* is generally not abundant in Miocene faunas (e.g., Stefen 2009a). It has been found in several localities in Europe (Hugueney 1999), but larger samples are thus far only described in detail from the lower Miocene of St. Gérard in France (Pomel 1847; Filhol 1879; Viret 1925; Stefen 2005) and Ulm-Westtangente in Germany (Stefen 1997). Both localities have yielded a small-sized beaver: *Steneofiber castorinus* Pomel, 1853 in France and the slightly larger *Steneofiber eseri* (von Meyer, 1846) in Germany. Abundant material is also known from the lower and

middle Miocene of the Loire Basin in France (e.g., Artenay and Baigneaux, Faluns de la Touraine and Anjou, Pontlevoy-Thenay; Mayet 1908; Ginsburg 1971, 1988). This material of a medium-sized beaver is referred to *Steneofiber depereti* Mayet, 1908, but the material has not been described in comprehensive detail. *S. depereti* from the Loire Basin has been subdivided into several chronosubspecies of slightly different size by Ginsburg (1971, 1988).

Recently, the middle Miocene locality Hambach 6C yielded numerous teeth and mandibular fragments of a medium-sized *Steneofiber*. This makes it possible to assess the morphologic and metric variability of this beaver and to evaluate the validity of Ginsburg's subspecies concept. In this respect, Hambach 6C is particularly interesting, since it is contemporaneous with the middle Miocene sites in the Loire Basin (Faluns de la Touraine and Anjou, Pontlevoy-Thenay).

The castorid fossils were recovered from the Hambach opencast lignite mine, about 35 km west of Cologne (Fig. 1). They are part of a rich vertebrate assemblage that accumulated in channel deposits of a meandering stream that intersect the Miocene lignite beds (Mörs et al. 2000; Mörs 2002). The Hambach mine is within the Lower Rhine Embayment, which



Fig. 1. Location of the Hambach opencast lignite mine in northwestern Germany.

is a graben structure active since the Oligocene and filled with interlocking marine and terrestrial sediments (Schäfer et al. 2004). Hambach 6C is the northwesternmost Miocene vertebrate locality thus far known from Europe. It has produced thousands of vertebrate remains, representing marine sharks and rays, marine and freshwater teleosts, amphibians, reptiles, birds, and mammals. Among the mammals, one artiodactyl (Rössner and Mörs 2001) and several small mammals have been described (Ziegler and Mörs 2000; Nemetschek and Mörs 2003; Mörs and Kalthoff 2004; Mörs 2006, 2008). Besides the castorid described here, Hambach 6C has also produced material of the rare beaver *Anchitheriomys suevicus* which has been analysed separately (Stefen and Mörs 2008). The enamel microstructure of both taxa has been studied by Koenigswald and Mörs (2001). Based on its diverse rodent fauna, Hambach 6C can be placed within the younger part of Neogene mammal unit MN 5. This corresponds to the earliest middle Miocene, estimated to span 15.2 to 16.0 Mya (Mörs et al. 2000; Mörs 2002).

**Institutional abbreviations.**—IPB-HaH, Steinmann Institut (Paläontologie), Rheinische Friedrich-Wilhelms Universität, Bonn, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

**Conventions.**—The morphological description of the teeth follows Stirton (1935). Measurements (Table 1) were taken with calipers at the occlusal surface and where possible at the base of the teeth to the closest 0.01 mm.

## Systematic paleontology

Order Rodentia Bowdich, 1821

Family Castoridae Hemprich, 1820

Genus *Steneofiber* Geoffroy, 1833

*Type species:* *Steneofiber castorinus* Pomel, 1847, lower Miocene, France.

*Steneofiber depereti* Mayet, 1908

Figs. 2–6.

*Assigned subspecies:* *Steneofiber depereti depereti* Mayet, 1908, subspecies assignment Ginsburg, 1971; *Steneofiber depereti caliodorensis* Ginsburg, 1971; *Steneofiber depereti janvieri* Ginsburg, 1988.

**Material.**—Left I: IPB-HaH 6415, 6416 (frag.), 6417 (frag.); right I: IPB-HaH 6418 (frag. juv.), 6429 (frag.); left DP4: IPB-HaH 5166; left P4: IPB-HaH 5088, 6374, 6375, 6378, 6380; right P4: IPB-HaH 6376; left M1/2: IPB-HaH 5102, 5086, 6382, 6383 (germ), 6384 (germ), 6385 (germ), 6387, 6388, 6401, 6442; right M1/2: IPB-HaH 5107, 5109, 6377, 6386; left M3: IPB-HaH 5165, 6389, 6390; right M3: IPB-HaH 5101, 6391; left mandible with i (frag.), p4–m3: IPB-HaH 5149; right mandible with i, m1–m3: IPB-HaH 5150; left mandible with i, p4–m2: IPB-HaH 5167; left mandible with i (frag.), p4–m3: IPB-HaH 6408; right mandible with i, p4–m3: IPB-HaH 6409; left mandible (frag.) with i: IPB-HaH 6422; left i: IPB-HaH 6415, 6419 (frag.), 6420 (frag.), 6421 (frag.), 6423 (frag.), 6425 (frag. juv.); right i: IPB-HaH 5103 (frag.),

Table 1. Dimensions of the teeth of *Steneofiber depereti* from the middle Miocene of Hambach 6C (in mm). L, width across enamel band for incisors, anterior-posteriorly at occlusal surface for cheek teeth; pos, tooth position; m, measurement; W, depth mesio-distally.

pos	m	N	min	max	mean	standard deviation	variance
i	L	17	4.93	6.85	6.13	0.45	0.2
	W	13	3.67	6.68	6.07	0.81	0.66
I	L	5	4.48	7.14	5.94	0.98	0.96
	W	5	5.23	6.80	6.07	0.56	0.31
p4	L	9	6.91	9.66	8.61	0.96	0.92
	W	9	4.63	7.05	6.33	0.78	0.61
m	L	21	4.99	6.71	5.77	0.42	0.18
	W	18	3.94	6.73	5.62	0.72	0.51
P4	L	5	6.69	9.60	7.65	1.13	1.28
	W	5	5.47	8.03	6.93	0.98	0.97
M1/2	L	13	4.13	5.55	4.91	0.39	0.16
	W	13	3.53	6.02	4.67	0.84	0.71
M3	L	4	4.69	5.64	5.12	0.47	0.25
	W	4	4.85	5.91	5.29	0.51	0.26

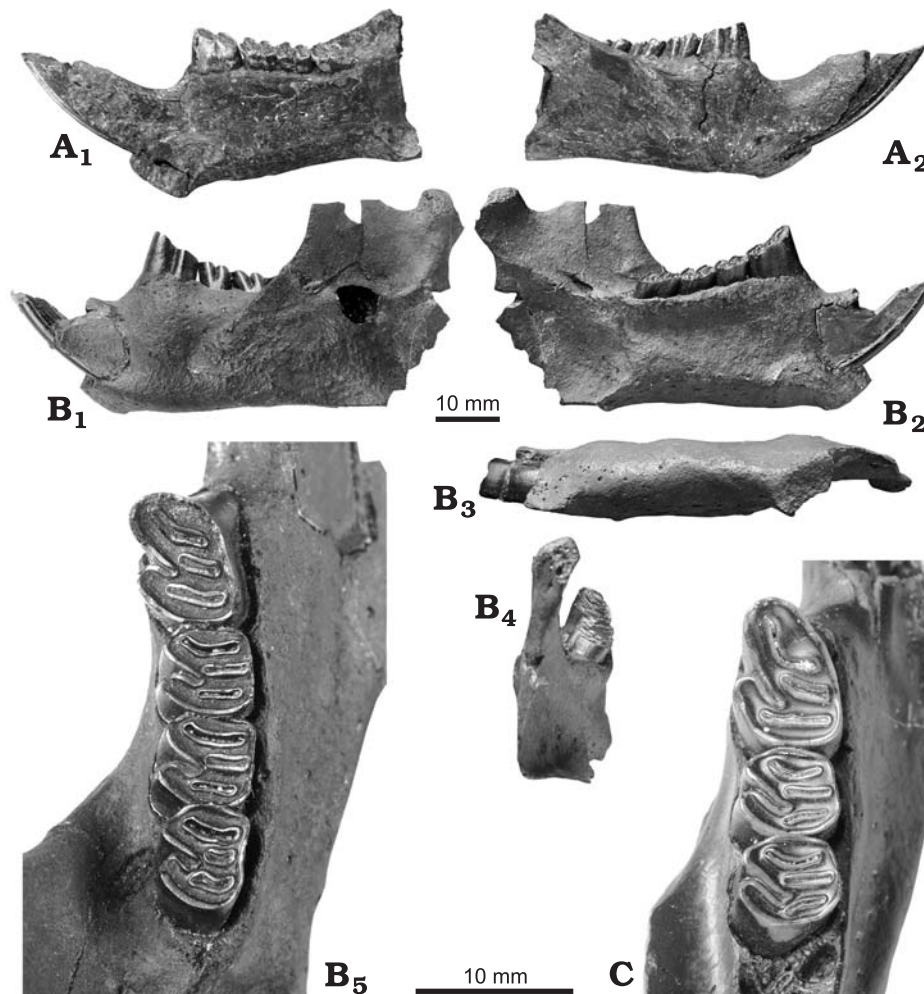


Fig. 2. Mandibles of the castorid *Steneofiber depereti* from the middle Miocene of Hambach 6C, northwestern Germany. A. IPB-HaH 6409 in lingual (A<sub>1</sub>) and labial (A<sub>2</sub>) views. B. IPB-HaH 5149 in labial (B<sub>1</sub>), lingual (B<sub>2</sub>), ventral (B<sub>3</sub>), and posterior (B<sub>4</sub>) views; B<sub>5</sub>, tooth row in occlusal view. C. IPB-HaH 5167, tooth row in occlusal view.

5104 (frag.); left dp4: IPB-HaH 6392, 6394; right dp4: IPB-HaH 6393; left p4: IPB-HaH 6397, 6440; right p4: IPB-HaH 5105, 6395, 6396; left m1/2: IPB-HaH 6443 (germ), 6399; right m1/2: IPB-HaH 5043, 5100, 5106, 6400; left m3: IPB-HaH 6404; right m3: IPB-HaH 5110, 6402; for measurements see Table 1.

## Description

**Mandibles.**—The mandibular material consists of three fragments with complete dentition (HaH 5149, 6408, 6409), one fragment (HaH 5150) lacking the p4 (which is most likely HaH 5105, found close to the mandible at the site Ho SFH 6), and one fragment (HaH 5167) lacking the m3. These mandibles represent individuals of different age, from the youngest (HaH 6408) with a nearly unworn p4 to the oldest (HaH 5167) in which the mesofossetids of p4–m2 are closed.

The most complete of the three is HaH 5149, which lacks only the uppermost part of the coronoid process and most of the angular process. It exhibits a prominent chin process an-

terior to p4 and a relatively straight ventral rim of the ramus between the chin process and the angular shelf. In lateral view, the m3 is hidden by the anterior rim of the coronoid process. The superior masseter crest ends in a marked tuberculum mandibulae in the ventral half of the mandible. Dorsal to the posterior end of the incisor, the base of the coronoid and condylar processes forms a distinct depression. The condyle is situated high above the tooth row. The mental foramen is situated in the middle of the ramus, anterior to p4 and dorsal to the chin process (best visible in HaH 5149). From the preserved part of the angular shelf (crista pterygoidea) which starts posterior to m3, it can be deduced that it is horizontal, as an extension of the ventral rim of the mandibular ramus (Fig. 2B<sub>3</sub>). A deep fossa for the pterygoid muscle is present. The mandibular foramen is elongated and situated on the crest continuing from the lingual alveolar rim to the condylar process. The occlusal surface of the tooth row is convex (Fig. 2B<sub>2</sub>).

**Incisors.**—There are 22 incisor fragments, 11 upper ones and 11 lower ones, including six in mandibular fragments. Fifteen of these have a preserved tip. The wear facets of the up-



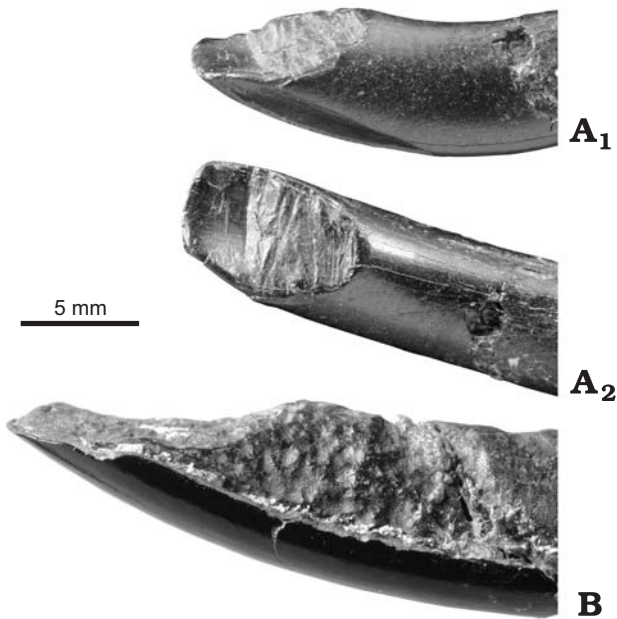


Fig. 3. Incisors of the castorid *Steneofiber depereti* from the middle Miocene of Hambach 6C, northwestern Germany. **A**. Tip of right I (IPB-HaH 6418) in oblique-lateral (**A<sub>1</sub>**) and lingual (**A<sub>2</sub>**) views. **B**. Tip of left I (IPB-HaH 6419) in lateral view.

per and lower incisors differ in shape. The facet of the lower incisors is longer and extends in a constant angle from the tip to the lingual side. The facet of the upper ones is shorter and consists of two parts: a very steep part at the very tip with nearly only the enamel band, and a posterior, more angled part. All incisors have a slightly skewed triangular cross section; the medial tip of the triangle is closer to the midline of the jaw. The enamel face is very slightly convex and the enamel surface is smooth.

**Lower dentition.**—The description is based on three isolated dp4, five isolated p4, four p4 still in the mandibles and 23 lower molars, 14 of them still in situ. Overall, the cheek teeth are subhypsodont, developing complete roots with age. The hypostriid never extends to the base of the cheek teeth. The premolar is the largest of the cheek teeth.

Two of the dp4 are strongly worn, with the mesoflexid almost closed (Figs. 4F, G, 5O, P). The third (HaH 6394) shows meso- and metaflexid, both associated with short striids; the mesostriid is clearly longer than the meta-striid (Fig. 5X).

The p4 are shaped like a figure eight when slightly to moderately worn. With increasing wear, lower premolars show a slender, elongated anterior and a shorter, broader posterior part. The anteriormost edge is oriented anterolaterally and is the least worn and highest area of the convex occlusal surface. The hypostriid generally ends well above the base of the tooth. However, in one p4 (HaH 6397) the hypostriid does not show the typical closure, but narrows and continues as a well-expressed notch to the base of the tooth (Fig. 5AA). Whether the hypoflexid continues to the base of the premolar cannot be assessed. In a second specimen (HaH 6440) the hypostriid closes, but a marked groove extends to the base.

On the lingual side even the least worn p4 (HaH 6408) shows only a mesostriid. Some premolars have an additional groove in the anterior third of the lingual side (HaH 5167, 6408). The parafofsettid, mesoflexid/fofsettid and metafofsettid are all straight and diagonally oriented on the chewing surface. Exceptions are HaH 6395 and 6397, which have a transverse metafofsettid. The para- and metafofsettid are generally long and extend almost from the lingual to the labial side. In moderately to heavily worn p4 the parafofsettid is hook-like. A single premolar has an additional fofsettid posterior to the mesoflexid.

The lower molars (19 m1/2, 7 m3) are rectangular in outline. There are a few germs and only slightly worn molars differing in the presence and development of lingual striids. An

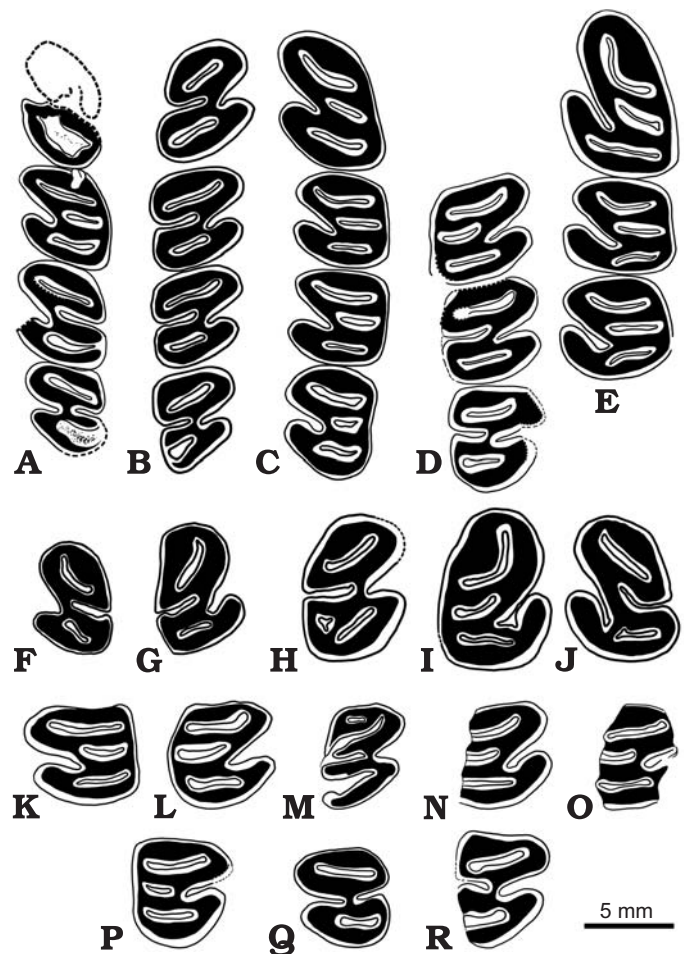


Fig. 4. Occlusal pattern of lower cheek teeth of the castorid *Steneofiber depereti* from the middle Miocene of Hambach 6C, northwestern Germany. Mandibular tooth rows (**A–E**), deciduous teeth (**F, G**), premolars (**H–J**), molars (**K–R**); left p4–m3, IPB-HaH 6408 (**A**); right p4–m3, IPB-HaH 6409 (**B**); left p4–m3, IPB-HaH 5149 (**C**); right m1–m3, IPB-HaH 5150 (**D**); left p4–m2, IPB-HaH 5167 (**E**); left dp4, IPB-HaH 6392 (**F**); right dp4, IPB-HaH 6393 (**G**); right p4, IPB-HaH 6396 (**H**); right p4, IPB-HaH 6395 (**I**); left p4, IPB-HaH 6397 (**J**); left m1/2, IPB-HaH 6399 (**K**); right m1/2, IPB-HaH 5100 (**L**); right m1/2, slightly worn with a lingually open metaflexid, IPB-HaH 5043 (**M**); right m1/2, IPB-HaH 5106 (**N**); right m1/2, IPB-HaH 6400 (**O**); right m3, IPB-HaH 5110 (**P**); left m3, IPB-HaH 6404 (**Q**); right m3, IPB-HaH 6402 (**R**).

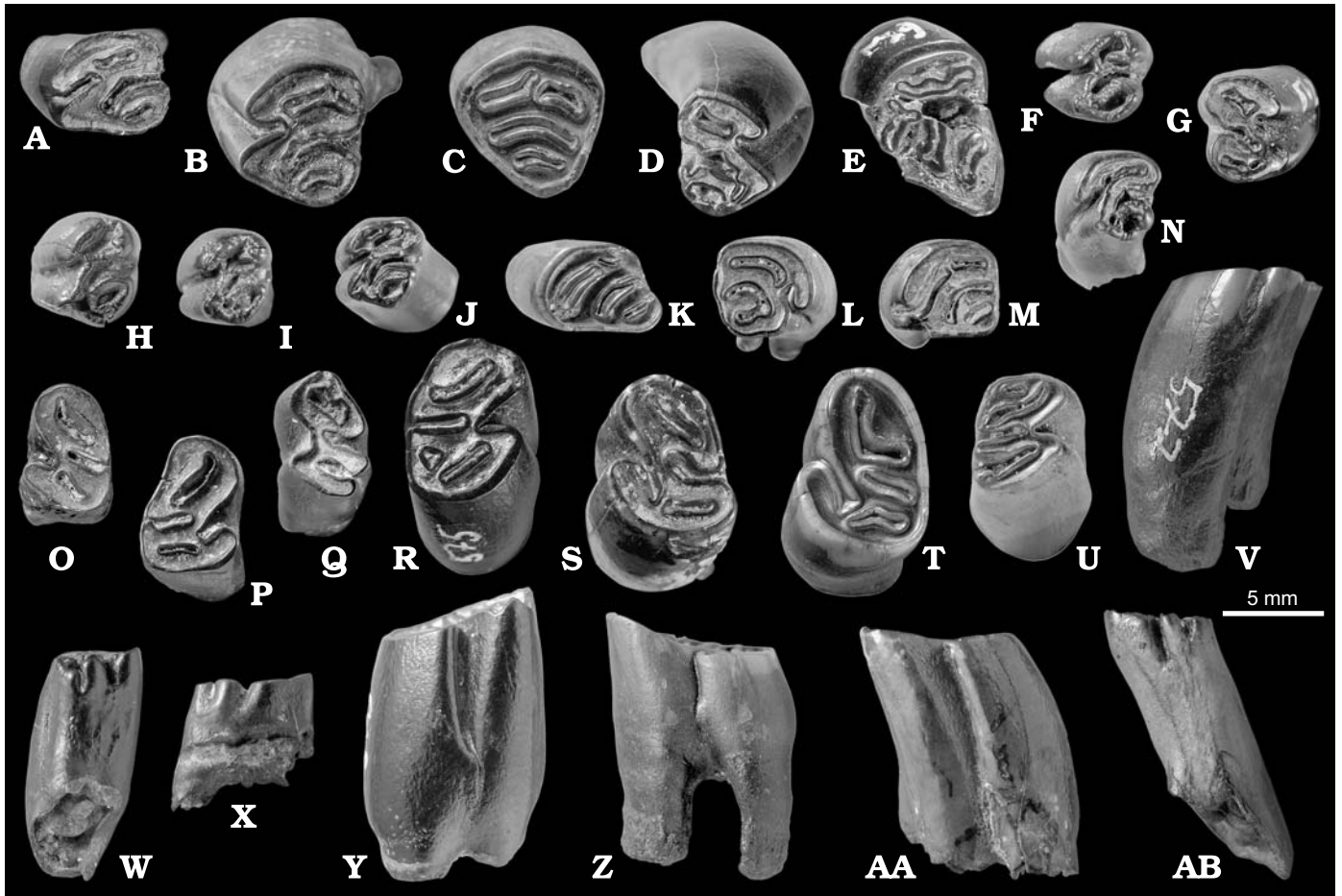


Fig. 5. Cheek teeth of the castorid *Steneofiber depereti* from the middle Miocene of Hambach 6C, northwestern Germany. DP4 in occlusal view: IPB-HaH 5166 (A); P4 in occlusal view: IPB-HaH 5088 (B), IPB-HaH 6374 (C), IPB-HaH 6376 (D), IPB-HaH 6380 (E); M1/2 in occlusal view: IPB-HaH 5102 (F), IPB-HaH 6377 (G), IPB-HaH 6383 (H), IPB-HaH 6384 (I), IPB-HaH 6385 (J), IPB-HaH 6401 (K); M3 in occlusal view: IPB-HaH 5101 (L), IPB-HaH 6390 (M), IPB-HaH 5165 (N); dp4 in occlusal view: IPB-HaH 6392 (O), IPB-HaH 6393 (P), IPB-HaH 6394 (Q); p4 in occlusal view: IPB-HaH 6396 (R), IPB-HaH 6397 (S), IPB-HaH 6440 (T); m1/2 in occlusal view: IPB-HaH 5043 (U); P4 in lingual view: IPB-HaH 6375 (V); M3 in labial view: IPB-HaH 5165 (W); dp4 in lingual view: IPB-HaH 6394 (X); p4 in labial view: IPB-HaH 6396 (Y), IPB-HaH 6440 (Z), IPB-HaH 6397 (AA); m1/2 in lingual view: IPB-HaH 5043 (AB).

isolated molar germ (HaH 6443) has a mesostriid only. In contrast, a slightly worn m1/2 (HaH 5043) exhibits a distinct metastriid, which is half the length of the mesostriid. The more worn m2 and m3 show no metastriid, but the metaflexid is still open (HaH 6408). Generally, parafossettid, mesoflexid/fossettid and metafossettid are straight and transversely oriented on the chewing surface. A single molar (HaH 5043) shows two unique features: the paraflexid opens into the mesoflexid at the lingual wall and an additional preparafossettid is present. As for the p4, the size of the lower molars is homogeneous and indicates a single species (Fig. 7).

*Upper dentition.*—In contrast to the lower dentition, the upper is represented by isolated teeth only: one DP4, six P4, 14 M1/2, and five M3. Many of them are not or only slightly worn. The premolar is the largest of the upper cheek teeth, while all the molars are similar in size.

The worn DP4 shows a closing mesoflexus and a still open hypoflexus. The shape and orientation of the flexi and fossettes are like in P4. The outline of the premolars changes

with wear from rectangular to square to triangular to elongated triangular. The anteromedial side is rounded in all stages. The hypostria closes well above the tooth base, and is filled with cement in one specimen (HaH 6375). Even the least worn P4 shows only a mesostria on the labial side. Hypoflexus/fossette and parafossette are in line and are of nearly equal length on the occlusal surface. The mesoflexus/fossette is always bent and extends almost to the posterior side of the tooth. The metafossette is usually the smallest element. In the least worn P4 (HaH 6376) the mesoflexus shows an irregular outline with a small enamel island pinching off at the posterior end. In the slightly more worn HaH 5088 this small island is isolated.

The outline of the M1/2 changes with wear from rectangular (longer than wide) to square to rectangular (wider than long). When strongly worn the tooth is posterolabially elongated and thus appears triangular (HaH 6401). The M3 is more rounded and slightly elongated posteriorly. Most molars show only a mesostria on the labial side but two M3



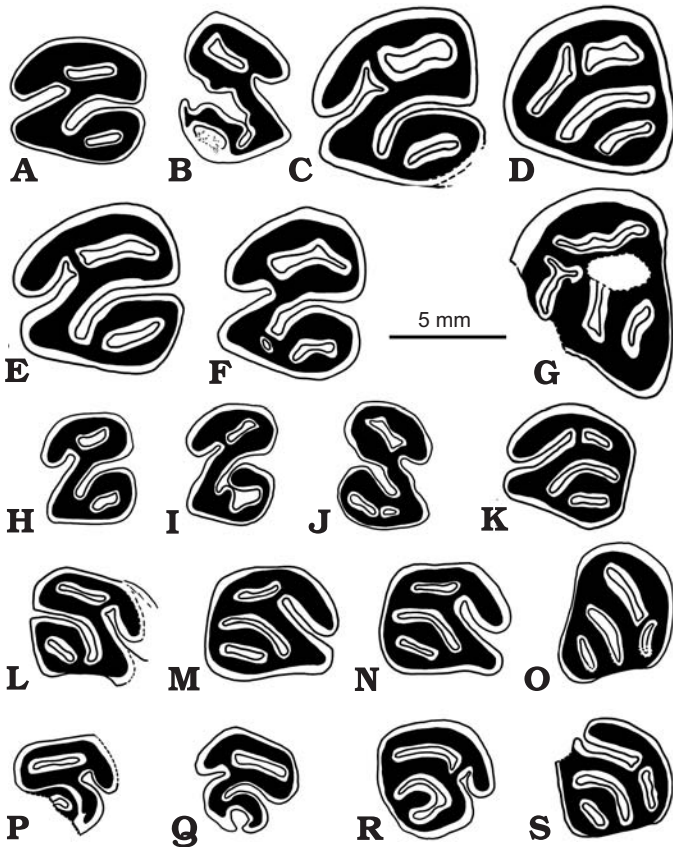


Fig. 6. Occlusal pattern of upper cheek teeth of the castorid *Steneofiber depereti* from the middle Miocene of Hambach 6C, northwestern Germany. Deciduous tooth (A), premolars (B–G), molars (H–S); left DP4, IPB-HaH 5166 (A); right P4, IPB-HaH 6376 (B); left P4, IPB-HaH 6375 (C); left P4, IPB-HaH 6374 (D); left P4, IPB-HaH 6378 (E); left P4, IPB-HaH 5088 (F); left P4, IPB-HaH 6380 (G); left M1/2, IPB-HaH 6388 (H); left M1/2, IPB-HaH 6387 (I); right M1/2, IPB-HaH 6377 (J); left M1/2, IPB-HaH 6382 (K); right M1/2, IPB-HaH 5109 (L); right M1/2, IPB-HaH 5107 (M); right M1/2, IPB-HaH 6386 (N); left M1/2, IPB-HaH 6401 (O); right M3, IPB-HaH 6391 (P); left M3, IPB-HaH 6389 (Q); right M3, IPB-HaH 5101 (R); left M3, IPB-HaH 6390 (S).

(HaH 5165, 6389) possess a metastrria nearly as long as the mesostrria. The shape and orientation of the flexi and fossettes is like in P4, but hypoflexus/fossette and parafossette may differ in size. Three M1/2 show an additional, small island in the posterior part of the tooth, and one M3 (HaH 5101) shows a fusion between meso- and metafossette. Unworn to very slightly worn teeth show some peculiarities: a connection between the hypoflexus and parafossette in two teeth (HaH 5086, 5165) and a posterior opening of the metafossette in HaH 5102.

## Discussion

**Assignment of the described material.**—The material from Hambach 6C is comparable to other medium-sized beavers from the late lower to middle Miocene of France and Germany (Fig. 7). The Hambach beaver is significantly larger

than the contemporaneous small-sized beaver species, which is assigned either to *Trogotherium minutum* or *Steneofiber minutus*. It can also be distinguished from the slightly smaller early Miocene (MN 2) *Steneofiber eseri* and *Steneofiber castorinus* (Fig. 8). Three medium-sized beaver species have been recorded from the late lower to middle Miocene: *Steneofiber depereti* Mayet, 1908, *Steneofiber subpyrenaicus* (Lartet, 1851), and *Chalicomys jaegeri* Kaup, 1832.

Mandibles of medium-sized castorids have rarely been described in detail. Judging from the few figured specimens, the gross morphology of the Hambach mandibles is comparable to that of *S. depereti* from Chevilly (Huguency 1999: text-fig. 28.4C) and Pontlevoy (*S. subpyrenaicus* in Mayet 1908: pl. 12: 8, 9). They are similar in having a prominent chin process and a relatively straight ventral rim of the ramus, the position and angle of the anterior rim of the coronoid process, and the height of the mandibular ramus. The better preserved mandible from Pontlevoy shows a similar position of the condyle and an angular shelf comparable to those of the Hambach specimens.

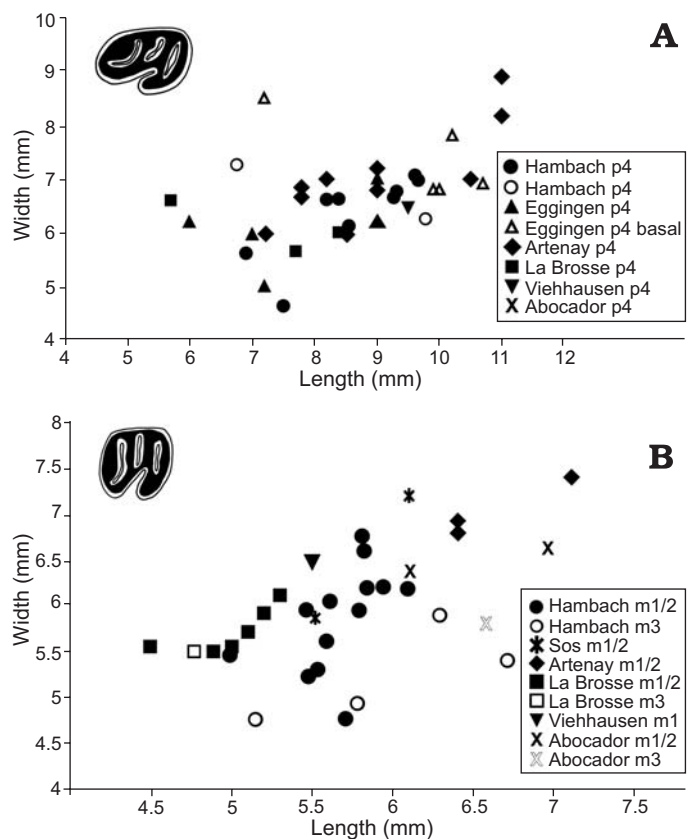


Fig. 7. Dimensions of lower cheek teeth of the castorid *Steneofiber depereti* from the middle Miocene of Hambach 6C, northwestern Germany, in comparison to material from early and middle Miocene localities in France and Germany. Data for Eggingen-Mittelhart (MN 4) (CS unpublished data) and Sach and Heizmann (2001), for Artenay (MN 4) (CS unpublished data), for La Brosse (MN 3) from Ginsburg et al. (2000), for Viehhausen (MN 5) from Seemann (1938), and for Sos (MN 5) from Ginsburg (1967). "*Chalicomys*" *batalleri* from Abocador de Can Mata, Spain, MN 7/8 (Casanovas-Vilar et al. 2008) is included. Lower premolars (A) and lower molars (B).

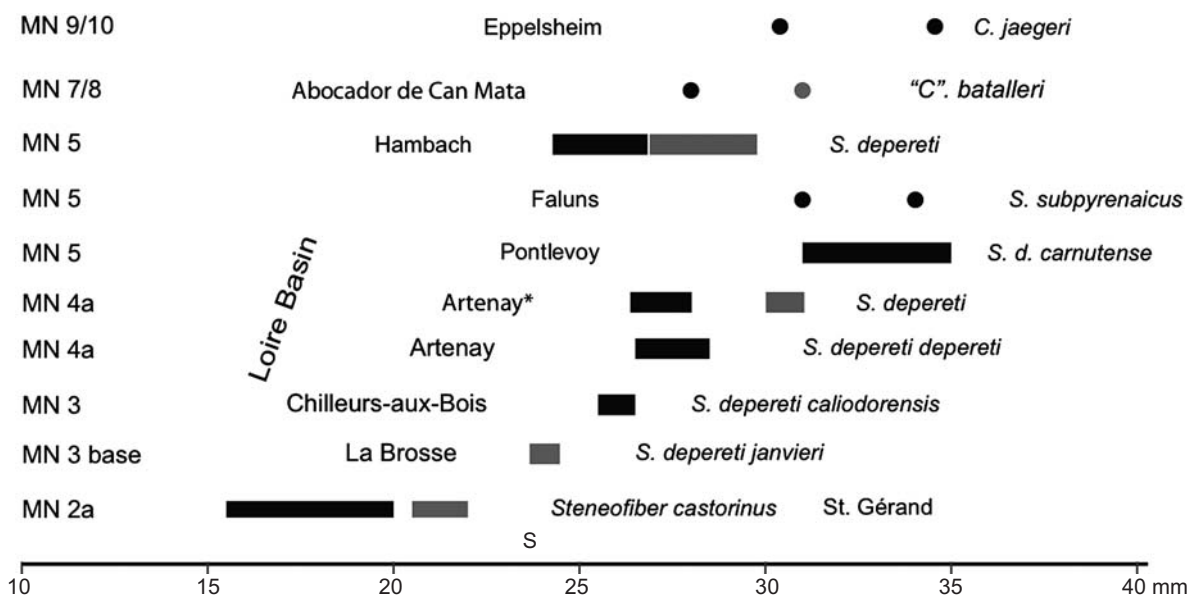


Fig. 8. Lengths of mandibular tooth rows of *Steneofiber depereti* from the middle Miocene of Hambach 6C, in comparison to other representatives of the genus from early and middle Miocene localities in France, and in comparison to representatives of *Chalicomys*. For St. Gérard and Hambach are both given the lengths of occlusal surfaces and the alveole lengths. Data for *Steneofiber castorinus* and *S. depereti* from Artenay (marked with \*) from Stefen (2005), for subspecies of *S. depereti* in the Loire Basin from Hugueney (1999), for "*Chalicomys*" *batalleri* from Casanovas-Vilar et al. (2008), and for *Chalicomys jaegeri* from Kaup (1833) and Ünay (1976).

The cheek teeth of the Hambach beaver are characterized by closed hypostria/iids, the lack of labial stria/iids except mesostria/iids, and the absence of substantial cement. These dental features are in agreement with descriptions of *Steneofiber depereti* (Mayet 1908; Ginsburg 1971; Stefen 1997; Hugueney 1999; Sach and Heizmann 2001). In contrast, *Chalicomys jaegeri* from the type locality Eppelsheim has hypostriids extending to the base of the teeth, three well expressed striids on the lingual side, and synclines filled with cement. Therefore, the Hambach castorid cannot be assigned to *C. jaegeri*. The third species, *Steneofiber subpyrenaicus*, is poorly described (Lartet 1851; Mayet 1908; Hugueney 1999) and can hardly be distinguished from *S. depereti* (see discussion below). The dimensions of the cheek teeth and mandibular tooth rows from Hambach fit well within the size range given for *S. depereti* (Mayet 1908; Ginsburg 1971, 1988; Hugueney 1999; Ginsburg et al. 2000; Sach and Heizmann 2001). Since the Hambach castorid corresponds in morphology and size to *S. depereti*, we assign it to this species.

**Subspecies of *Steneofiber depereti*.**—Ginsburg (1971, 1988) observed an increase in size without substantial morphological changes in *S. depereti* from progressively younger localities in the Loire Basin, and suggested a sequence chronosubspecies of increasing size, representing an evolutionary lineage (Fig. 8). This has been recently accepted as valid in an overview of European Miocene beavers by Hugueney (1999). Ginsburg (1971) distinguished three subspecies on the basis of the length of the mandibular tooth row: *S. depereti caliodorensis* from Chilleurs (MN 3) and possibly Chitenay (MN 3), *S. depereti depereti* from Artenay (MN 4a) only, and *S.*

*depereti carnutense* from Chevilly (MN 4) and several other localities (MN 4/5 to MN 5). Later Ginsburg (1988) included a fourth subspecies: *S. depereti janvieri* from La Brosse (early MN 3) and numerous other localities.

The tooth row lengths from Hambach overlap the values of *S. depereti janvieri*, *S. depereti caliodorensis*, and *S. depereti depereti* (according to the values given by Ginsburg 1971, 1988 and Hugueney 1999). If the alveolar length of the Hambach mandibles is considered, they are even beyond the given maximum for *S. depereti depereti* (Fig. 8). These three subspecies are known from the Loire Basin from MN 3 to MN 4a only. However, Hambach is referred to late MN 5 and thus its beaver is contemporaneous with the significantly larger form *S. depereti carnutense* from, e.g., Pontlevoy-Thenay. This shows clearly that the sequence of increasingly larger subspecies is a local phenomenon within the Loire Basin. In different geographic regions, populations of *S. depereti* can be of different size at the same time, as demonstrated here for the Lower Rhine Basin versus the Loire and Aquitaine (Sos) Basin in MN 5. Thus, the division into progressively larger subspecies in the Loire Basin cannot be applied to European *S. depereti* in general. There may have been several isolated populations within Europe undergoing a similar increase in size during the Miocene. Therefore, subspecies differentiations may only make sense in one limited area, whereas in a European perspective one should refer to *S. depereti*, with a rather wide range of metric variability.

***Steneofiber subpyrenaicus*.**—The second and least known species of medium-sized beavers was named, without illustration, *Castor subpyrenaicus* by Lartet (1851) on the basis of



three cheek teeth from the middle Miocene of the Aquitaine Basin. Two teeth were recovered from Villefranche-d'Astarac near Simorre (Gers; Astaracian, MN 7/8) and one from Bonrepos (Haute-Garonne). Later, Gervais (1859: pl. 48: 5) figured one of the teeth (a p4) from the middle Miocene of Villefranche-d'Astarac as *Steneofiber subpyrenaicus*. This specimen, from Suèvres (Orleanian, MN 5), was referred to his new species *S. depereti* by Mayet (1908). Nevertheless, Mayet (1908) lists *S. subpyrenaicus* as present in the Loire Basin. He refers only material from the Faluns, e.g., several mandibles from Pontlevoy, to *S. subpyrenaicus*, and none from the terrestrial deposits of the Orléanais. Finally, Ginsburg (1967) assigned all Miocene castorids from the Loire Basin to *S. depereti*, and developed the idea of progressively larger subspecies (Ginsburg 1971, 1988). The largest subspecies, *S. depereti carnutense*, includes the beavers from Pontlevoy, originally assigned to *S. subpyrenaicus* by Mayet (1908).

Whereas Ginsburg (1967, 1971) includes at least the Loire Basin material of *S. subpyrenaicus* in *S. depereti*, Mayet (1908) had already pointed to a similarity to *S. jaegeri*, which is now generally included in the genus *Chalicomys*. Schlosser (1884) proposed synonymy between *S. subpyrenaicus* and *C. jaegeri*. However, Hugueney (1999) argues that sufficient distinction between *S. subpyrenaicus* and *C. jaegeri* might be possible with more material. She refers to a left mandible of *S. subpyrenaicus* from Simorre, which represents the same stratigraphic level as the type locality Villefranche-d'Astarac. However, in this dentition the hypostrids close above the base and only mesostrids are well expressed on the lingual side (Hugueney 1999: text-fig. 28.6D), like in *S. depereti*. Taking into account the characteristic features of *Chalicomys* given below, this mandible can in our opinion not be referred to *Chalicomys*, but represents a species of *Steneofiber*.

Whether *S. subpyrenaicus* represents a species that can be distinguished from *S. depereti* by size and morphology can only be assessed with a detailed study of all the relevant material, and is beyond the scope of this paper. Two possible outcomes of such a study seem probable to us, both of which would have implications for the taxonomy of *Steneofiber*. It might turn out that *S. subpyrenaicus* from the Astaracian of the Aquitaine Basin can be distinguished as a separate species from *S. depereti*. In that case, *S. depereti carnutense*, which has tooth rows that are clearly larger than those of the other three subspecies, as well as those of *S. depereti* from Hambach, could represent *S. subpyrenaicus* in Orleanian strata. Thus, Mayet's (1908) recognition of two species in the Loire Basin would be supported. If it turns out that *S. subpyrenaicus* cannot be distinguished from *S. depereti*, the latter should be regarded as junior synonym of *S. subpyrenaicus*.

Casanovas-Vilar et al. (2008) accept *S. subpyrenaicus* as a separate species, but assign it to *Chalicomys* as Schlosser (1884) did. Like in the specimen from Simorre (Hugueney 1999: text-fig. 28.6D), the hypostrid closes before the base of the crown. Therefore, it should not be attributed to *Chalicomys*, even if there is cement in the striids.

*Chalicomys jaegeri*.—The third representative of medium-sized beavers is generally considered as the successor of *S. depereti* (Ginsburg 1971; Stefen 1997). A possible Asian origin for *C. jaegeri* has been suggested by Hugueney (1999). In size, *C. jaegeri* is at the lower end of the range of *S. depereti* from Chevilly and Pontlevoy (Fig. 8). Kaup (1833) gives 35 mm, Ünay (1976) 31 mm for a mandibular tooth row of *C. jaegeri* from type locality Eppelsheim (MN 9). *C. jaegeri* from Eppelsheim, recently revised by Stefen (2009b), is characterized by three features: hypostrids extending to the base of the cheek teeth, three well expressed striids on the lingual side, and marked cement filling the synclines (Kaup 1832: pl. 26: 1–4; reproduced in Stefen 2009b: fig. 1). Already in beaver populations of MN 5 age there are individual teeth that show an elongated hypostrid (e.g., HaH 6397, Fig. 5AA, this paper, and SMNS 42989 from Eggingen-Mittelhart: Stefen 1997: text-fig. 39b). A cement filling of synclines may occur in more worn specimens (Hugueney 1999: 285; HaH 6375, Fig. 5V, this paper). Even though individual teeth may show one of these features, they cannot be singled out from the rest of the population of *S. depereti*, since the combination of all three characters is diagnostic for *C. jaegeri*, and three well expressed lingual striids have not been observed in any of these teeth. The occasional occurrence of single *C. jaegeri* features in MN 5 populations of *S. depereti* supports the European lineage from *S. depereti* to *C. jaegeri*, as had been suggested previously (Schreuder 1931; Stefen 1997). The lack of records from MN 6 to MN 7/8 in the Loire Basin is not contradictory, as already proposed by Ginsburg (1971).

Recently, a new species of *Chalicomys*, *C. batalleri*, has been described from Abocador de Can Mata (MN 7/8) in Spain (Casanovas-Vilar et al. 2008). The holotype, a right mandible with complete dentition (Casanovas-Vilar et al. 2008: figs. 2A–C, 3A–C) represents a juvenile specimen, as the crenulations and the latero-anteriorly open paraflexid of the p4 indicate. Crenulations are juvenile features, which becomes very clear when rich material from one locality is studied, as from Ulm-Westtangente (Stefen 1997) or as here from Hambach 6C. Crenulations should not be used in taxonomic diagnoses (e.g., Hugueney 2004; Barisone et al. 2006). Because in *C. batalleri* the hypostrid of the p4 does not reach the base of the crown and the teeth are less hypsodont than in *C. jaegeri*, Stefen (2009b) suggests that the specimen should rather be referred to *Steneofiber* than *Chalicomys*. The length of the lower tooth row of "*C. batalleri*" falls within the range of alveolar length of *S. depereti* from Hambach 6C and its alveolar length reaches the smallest size of *S. d. carnutense* from the Loire Basin. Therefore, it can be assumed that it most likely represents *S. depereti*.

It is striking that in the time interval from MN 4 to MN 6 only the material from France is referred to *S. depereti*, whereas contemporaneous material from other countries (Germany, Switzerland, Austria, Poland) is mostly labelled as *C. jaegeri* (see Hugueney 1999: table 28.1). However, despite the referral of these materials to *C. jaegeri*, we question

the occurrence of this derived beaver in this time period. Most likely all these beavers from MN 4 to MN 6 represent *Steneofiber depereti* or *S. subpyrenaicus*.

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