



The never-ending problem of Miocene beaver taxonomy

ISAAC CASANOVAS-VILAR and DAVID M. ALBA

The finds of Miocene beavers are not rare at all. Nevertheless, in most localities these rodents are only represented by a few dental elements, so that large collections are only occasionally available to researchers. Hence, the description of sufficiently large samples, such as the recently published description of *Steneofiber depereti* from Hambach 6C (NW Germany, MN5) by Mörs and Stefen (2010), deserves the greatest attention. After a comprehensive description and comparison of the material, these authors conclude that previous citations of the beaver *Chalicomys jaegeri* from the MN4 to MN6 (early to middle Miocene) are misidentifications of the genus *Steneofiber*. Following Stefen (2009), these authors further question the validity of all the known *Chalicomys* species from the later middle Miocene (MN7+8). We agree with these authors that the occurrence of *C. jaegeri* in the middle Miocene is doubtful, but we disagree with their arguments for the synonymization of several species. Here we address this point and discuss the taxonomic criteria for distinguishing both genera, further reviewing the taxonomy of the genus *Chalicomys* at the species level.

On the distinction between *Steneofiber* and *Chalicomys*

Almost every author that has studied sufficiently complete material of *Steneofiber* or *Chalicomys* has proposed an emended diagnosis for these genera (e.g., Crusafont Pairó et al. 1948; Aldana Carrasco 1992; Huguency 1999; Casanovas-Vilar et al. 2008; Stefen 2009). Some of the older diagnoses refer simultaneously to *Steneofiber* and *Chalicomys* (= *Palaeomys*), which would largely explain the incorrect assignment of some MN4 to MN6 material to *Chalicomys jaegeri*. Both genera are no longer considered synonymous, and recent diagnoses have emphasized the higher hypsodonty, more abundant cement and longer striae/iids in *Chalicomys* as compared to *Steneofiber* (Huguency 1999; Casanovas-Vilar et al. 2008; Stefen 2009). In the most recent emended diagnosis Stefen (2009) considered the length of the p4 hypostrids as the main diagnostic character. According to this author, in *Steneofiber* the hypostrid closes before reaching the base of the crown, while in *Chalicomys* it remains open. Stefen (2009), however, disregards other diagnostic features, such as the more hypsodont cheek teeth in *Chalicomys*, or the abundant presence of cement infilling the synclines/iids. Cement may be present in *Steneofiber depereti* as a thin layer on the hypostridia and/or the mesostridia (as in IPB-HaH 6375; Mörs and Stefen 2010: fig. 6C). Nevertheless, in

Chalicomys, even in the earliest species such as *Chalicomys catalaunicus* and *Chalicomys batalleri*, cement occurs abundantly in all the synclines/iids (Casanovas-Vilar et al. 2008). Stefen (2009) reports two premolars from Eppelsheim, the type locality of *C. jaegeri*, that are devoid of cement and on this basis questions the taxonomic validity of this character. This, however, merely seems an exception to the general rule for this species, with the presence of abundant cement apparently being a synapomorphy of a *Chalicomys* + *Castor* clade. Casanovas-Vilar et al. (2008) further mentioned the presence of a tetralophodont pattern in the cheek teeth of *Chalicomys*, whereas *Steneofiber* would retain a pentalophodont one. As pointed out by Stefen (2009), this feature disappears with moderate wear, so that in many instances it is not useful for distinguishing both genera. Nevertheless, when discernible, it clearly separates the older species of *Steneofiber* from those of *Chalicomys*, although younger species such as *S. depereti* already display the derived tetralophodont pattern (even though an additional anterior fossa/id may be present in some molars). To sum up, the diagnosis of *Chalicomys* by Stefen (2009), which is the one followed by Mörs and Stefen (2010), ignores some important diagnostic characters. Accordingly, the synonymies suggested by these authors for certain Miocene *Chalicomys* species must be reconsidered.

Institutional abbreviations.—IPB-HaH, Steinmann Institut (Paläontologie), Rheinische Friedrich-Wilhelms Universität, Bonn, Germany; IPS, Institut Català de Paleontologia, Bellaterra (Cerdanyola del Vallès), Barcelona, Spain.

Species of *Chalicomys*

According to Stefen (2009) and Mörs and Stefen (2010), the genus *Chalicomys* would only include the type species, *C. jaegeri*, and the questionable *C. plassi*. Their criteria therefore differ from that of Casanovas-Vilar et al. (2008), who distinguished three additional species within this genus. In particular, Mörs and Stefen (2010) reassigned *C. catalaunicus* to ?*Eucastor* (*Schreuderia*), transferred *C. subpyrenaicus* to *Steneofiber*, and synonymized *C. batalleri* with *S. depereti*. In the following lines we will review the species included within the genus *Chalicomys*. See Table 1 for a list of the species discussed and their synonymies.

Huguency (1999) placed *C. catalaunicus* within the poorly known subgenus *Schreuderia*, which she considered a likely subgenus of the North American *Eucastor*. *Schreuderia* had been previously erected as a genus by Aldana Carrasco (1992) to accommodate *S. adroveri*, which strongly resembles *Chali-*



Fig. 1. IPS 31102, a left maxillary fragment with the upper incisor and P4–M2 of the castorid *Chalicomys catalaunicus* (Bataller, 1838) from Sant Quirze (MN7+8 from the Vallès-Penedès Basin, Catalonia, Spain). Note the abundant cement infilling all synclines.

comys but shows a markedly reduced M3. Huguency (1999) noted that some molars of *Schreuderia adroveri* and *Chalicomys catalaunicus* show a tendency to display an S-pattern, leading her to place them into the same subgenus, which she considered to be related to castoroidines. This was later disputed by Korth (2001), who considered *Schreuderia* to be a castorine, probably even a subgenus of *Chalicomys*. Certainly, a few molars of *C. catalaunicus* display a tendency towards an S-pattern at particular wear stages, but generally the occlusal pattern is castorine-like. Moreover, the cheek teeth are hypsodont and the striae/iids are longer than in *Steneofiber depereti*, further displaying abundant cement in all the synclines/iids (Fig. 1; see also Crusafont Pairó et al. 1948: pls. 5–8). These features strongly support the inclusion of this taxon in *Chalicomys* as a distinct and rather small-sized species, which partially overlaps with *S. depereti* but tends to be somewhat larger (Fig. 2). A revision of the type species is clearly needed in order to assess the validity of the (sub)genus *Schreuderia*.

Mörs and Stefen (2010) considered *Chalicomys batalleri* a junior subjective synonym of *S. depereti* because they overlap in dental size and the p4 hypostridium in *C. batalleri* supposedly does not reach the crown base. However, the only known p4 of the latter species is still implanted in the mandible (Casanovas-Vilar et al. 2008: figs. 2, 3) and the hypostridium continues into the alveolus, so that it is not possible to know whether it closed near the base of the tooth. Size is neither a distinguishing criterion, because *C. batalleri* overlaps with both *S. depereti* and *Chalicomys jaegeri* (Fig. 2). On the contrary, *C. batalleri* differs from *S. depereti* by numerous features, namely: the occurrence of abundant cement in all the fossettes/iids (as in *C. jaegeri*); the more well-developed hypostridia and mesostria in the upper cheek teeth; and the presence of three moderately developed striae on the lingual side of the P4, while only a rather short mesostria is present in *S. depereti* (cf. Mörs and Stefen 2010: fig. 5W; Casanovas-Vilar et al. 2008: fig. 4E, K). Both Stefen (2009) and Mörs and Stefen (2010) further question the taxonomic value of enamel crenulations, which were considered to be diagnostic of *C. batalleri*. The latter authors argued that the holotype (a right hemimandible) belongs to a juvenile individual, because of the presence of crenulations. Nevertheless, the holotype shows the complete definitive dentition and the cheek teeth already display a moderate degree of wear, indicating

that it belongs to an adult. Histological sections of extant beaver molars have shown that crenulations do in fact occur in old specimens at advanced wear stages (Hünemann 1966; Kotsakis 1989), indicating that this feature cannot be solely indicative of a juvenile ontogenetic stage. Given all the reasons outlined above, we consider that *C. batalleri* is a valid species that should be retained in *Chalicomys*.

Concerning *Chalicomys subpyrenaicus*, Mörs and Stefen (2010) do not question the validity of this species, even though available specimens overlap in size with *S. depereti*. Nevertheless, given the fact that the hypostridia close above the crown base and that only mesostriae are well expressed on the lingual side, these authors transfer this species to *Steneofiber*. In spite of the correctness of the assertions above, it must be emphasized that, in *C. subpyrenaicus*, cement is present in all the fossettes/iids. Accordingly, we consider that it should be retained in *Chalicomys*.

Finally, *C. plassi* is known by only two teeth (the holotype, which is a p4, and a m3) from Dorn-Dürkheim (MN11, SW Ger-

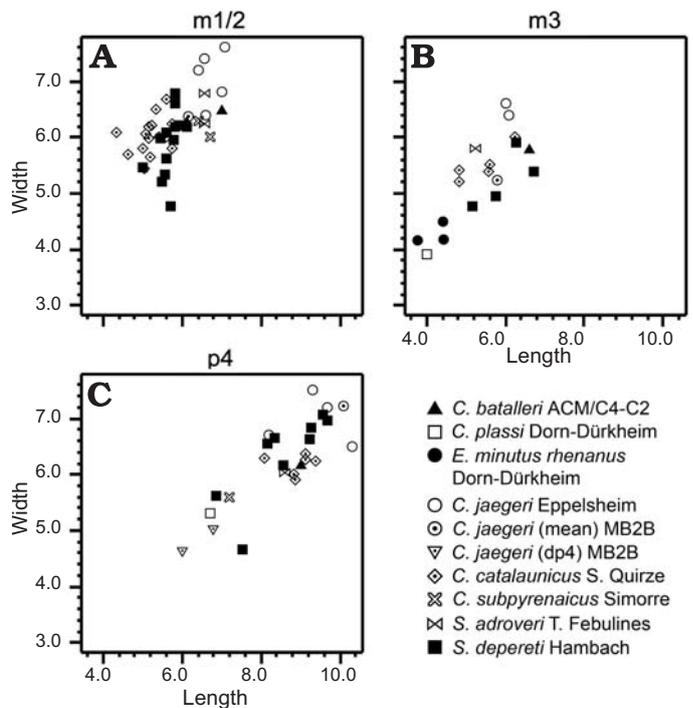


Fig. 2. Scatterplot for the lower cheek teeth of all the *Chalicomys* species as compared to *Steneofiber depereti*. *Schreuderia adroveri* and *Euroxonomys minutus rhenanus* comb. nov. are also included for discussion (see text for details). A. m 1/2. B. m3 C. p4. The measurements for *S. depereti* from Hambach were taken from Mörs and Stefen (2010); for *Chalicomys jaegeri* from Eppelsheim from Stefen (2009) and from MB2B from Van de Weerd (1976); for *Chalicomys plassi* and *E. minutus rhenanus* from Dorn-Dürkheim from Franzen and Storch (1975); for *S. adroveri* from Torrent de Febulines from Aldana Carrasco (1992); for *Chalicomys batalleri* from ACM/C4–C2 and *Chalicomys subpyrenaicus* from Simorre from Casanovas-Vilar et al. (2008); and for *Chalicomys catalaunicus* from Sant Quirze from Crusafont Pairó et al. (1948) and Casanovas-Vilar et al. (2008). Acronyms for locality names are as follows: ACM/C4–C2, Abocador de Can Mata locality C4–C2; MB2B, Masía del Barbo 2B. All the measurements are in millimetres.

Table 1. Species included within the genus *Chalicomys* Kaup, 1832. For each species an abridged synonymy list is provided.

<p>Genus <i>Chalicomys</i> Kaup, 1832</p> <p><i>Chalicomys jaegeri</i> Kaup, 1832 (type species)</p> <p><i>Palaeomys castoroides</i> Kaup, 1832 (original description)</p> <p><i>Chelodus typus</i> Kaup, 1832 (original description)</p> <p><i>Steneofiber jaegeri</i> (Kaup, 1832): Stehlin and Helbing (1925)</p> <p><i>Castor vidali</i> Crusafont, Villalta, and Bataller, 1948</p> <p><i>Palaeomys plassi</i> Franzen and Storch, 1975</p> <p><i>Chalicomys subpyrenaicus</i> (Lartet, 1851)</p> <p><i>Castor subpyrenaicus</i> Lartet, 1851 (original description)</p> <p><i>Steneofiber jaegeri</i> (Kaup, 1832): Stehlin and Helbing (1925)</p> <p><i>Steneofiber depereti carnutense</i> Ginsburg, 1971</p> <p><i>Steneofiber subpyrenaicus</i> (Lartet, 1851): Mörs and Stefen (2009)</p> <p><i>Chalicomys catalaunicus</i> (Bataller, 1838)</p> <p><i>Steneofiber jaegeri</i> (Kaup, 1832): Bataller (1924)</p> <p><i>Steneofiber minutus</i> var. <i>catalaunica</i> (Bataller, 1938) (original description)</p> <p><i>Steneofiber depereti</i> Mayet, 1908: Crusafont et al. (1948)</p> <p><i>Steneofiber hesperus</i> Douglass, 1901: Xu (1994)</p> <p>?<i>Eucastor</i> (<i>Schreuderia</i>) <i>catalaunicus</i> (Bataller, 1938): Huguency (1999)</p> <p><i>Chalicomys adroveri</i> (Aldana Carrasco, 1992)</p> <p><i>Chalicomys jaegeri</i> Kaup, 1832: Agustí et al. (1984)</p> <p><i>Schreuderia adroveri</i> Aldana Carrasco, 1992 (original description)</p> <p>?<i>Eucastor</i> (<i>Schreuderia</i>) <i>adroveri</i> (Aldana Carrasco, 1992): Huguency (1999)</p>

many). This species stands out because of its small size as compared to the other known *Chalicomys* and *Steneofiber* species (Fig. 2). Mörs and Stefen (2010) did not mention this material, but Stefen (2009) considered that it could be probably assigned to *Chalicomys*, because the hypostriid extends until the crown base. Rekovets et al. (2009) consider the specimens of Dorn-Dürkheim to be juveniles of *Chalicomys jaegeri* (= *Palaeomys castoroides* in Rekovets et al. 2009) and in accordance synonymise *Chalicomys plassi* with this species. Nevertheless, these authors do not discuss this issue further. Interestingly, the p4 of *C. plassi* overlaps in size with the dp4 of *C. jaegeri*, which is also present in Dorn-Dürkheim (Fig. 2). Franzen and Storch (1975) argued that this specimen could be clearly distinguished from the dp4 of *C. jaegeri* by the presence of three well-defined roots. Nevertheless, the dp4 of *C. jaegeri* does indeed show three roots exactly in the same position (see Van de Weerd 1976: pls. 15, 4a). Accordingly, we consider that this tooth is most likely a dp4 of *C. jaegeri*, and that *C. plassi* is a junior subjective synonym of the latter. Regarding the supposed m3 of *C. plassi*, it corresponds in size (Fig. 2) and morphology to the m3 of *Euroxenomys minutus rhenanus* comb. nov. from Dorn-Dürkheim. Furthermore, as in *E. minutus rhenanus*, the “m3” of *C. plassi* is devoid of cement. We therefore agree with Rekovets et al. (2009) and conclude that *C. plassi* is not a valid species, resulting from unfortunate misidentification of the cheek teeth of other beaver species present at Dorn-Dürkheim.

Final remarks

The genera *Steneofiber* and *Chalicomys* are not easy to distinguish from one another. The type species *C. jaegeri* is clearly different from *Steneofiber*, but in the case of earlier *Chalicomys* species the distinction is not so clear. Hence, a differential generic diagnosis that only considers the characters present in *C. jaegeri*, such as that by Stefen (2009), inevitably results in a re-assignment of the remaining species to *Steneofiber*. Here we propose to distinguish both genera on the basis of the occurrence of abundant cement in the fossettes/ids, which is a derived character shared between *Chalicomys* and the extant *Castor*.

Acknowledgements.—We sincerely acknowledge the comments by the reviewers of this paper Marguerite Huguency (Université Claude-Bernard, Lyon, France), Gudrun Daxner-Höck (Naturhistorisches Museum Wien, Austria), and Jérôme Prieto (Ludwig-Maximilians Universität München, Germany) which surely improved the final result. This study has been possible thanks to the support of the Generalitat de Catalunya (Grup de Recerca Consolidat 2009 SGR 754 of the AGAUR) and the Spanish Ministerio de Ciencia e Innovación (CGL2010-21672/BTE, CGL2008-00325/BTE, and RYC-2009-04533 to DMA).

References

- Agustí, J., Moyà-Solà, S., and Gibert, L. 1984. Mammal distribution dynamics in the eastern margin of the Iberian Peninsula during the Miocene. *Paleobiologie Continentale* 14: 33–46.
- Aldana Carrasco, E. 1992. Los Castoridae (Rodentia, Mammalia) del Neógeno de Cataluña (España). *Treballs del Museu de Geologia de Barcelona* 2: 99–141.
- Bataller, J.R. 1924. Contribució a l'estudi de nous mamífers fòssils de Catalunya. *Arxius de l'Institut de Ciències* 12: 36–41.
- Bataller, J.R. 1938. *Els ratadors fòssils de Catalunya*. 64 pp. Impremta de la Casa d'Assistència President Macià, Barcelona.
- Casanovas-Vilar, I., Alba, D.M., Almécija, S., Robles, J.M., Galindo, J., and Moyà-Solà, S. 2008. Taxonomy and paleobiology of the genus *Chalicomys* Kaup, 1832 (Rodentia, Castoridae), with the description of a new species from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain). *Journal of Vertebrate Paleontology* 28: 851–862. [CrossRef]
- Crusafont Pairó, M., Villalta, J.F. de, and Bataller, J.R. 1948. Los castores fósiles de España. *Boletín del Instituto Geológico y Minero de España* 61: 321–423.
- Franzen, J.L. and Storch, G. 1975. Die unterpliozäne (turolische) Wirbeltierfauna von Dorn-Dürkheim, Rheinhessen (SW-Deutschland). 1. Entdeckung, Geologie, Mammalia: Carnivora, Proboscidea, Rodentia. Grabungsergebnisse 1972–1973. *Senckenbergiana lethaea* 56: 233–303.
- Ginsburg, L. 1971. Sur l'évolution des *Steneofiber* (Mammalia, Rodentia) en France. *Comptes Rendus Académie des Sciences, Paris, Série D* 273: 2159–2161.
- Huguency, M. 1999. Family Castoridae. In: G.E. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*, 281–300. Verlag Friedrich Pfeil, Munich.
- Hünnerman, K.A. 1966. Der Bau des Biber-Prämolaren und seine Verwendbarkeit für die Systematic der Castoridae (Rodentia, Mammalia). *Neues Jahrbuch für Geologie und Palaöontologie-Abhandlungen* 125: 227–234.
- Kaup, J. 1832. Beschreibung dreier Gattungen urweltlicher Nager des Zoologischen Museums zu Darmstadt, welche von den jetzt lebenden Genera verschieden sind. *Isis von Oken* 9: 992–996.

- Korth, W.W. 2001. Comments on the systematics and classification of the beavers (Castoridae, Rodentia). *Journal of Mammalian Evolution* 8: 279–296. [CrossRef]
- Kotsakis, T. 1989. Quelques observations sur les Castoridae du Turolien et du Ruscinién. *Bolletino della Società Paleontologica Italiana* 28: 271–276.
- Lartet, E. 1851. *Notice sur la colline de Sansan, suivie d'une récapitulation des diverses espèces d'animaux vertébrés fossiles, trouvés soit à Sansan, soit dans d'autres gisements du terrain tertiaire miocène dans le Bassin Sous-Pyrénéen*. 41 pp. J. A. Portes, Auch.
- Mörs, T. and Stefen, C. 2010. The castorid *Steneofiber* from NW Germany and its implications for the taxonomy of Miocene beavers. *Acta Palaeontologica Polonica* 55: 189–198. [CrossRef]
- Rekovets, L., Kopij, G., and Nowakowski, D. 2009. Taxonomic diversity and spatio-temporal distribution of late Cenozoic beavers (Castoridae, Rodentia) of Ukraine. *Acta Zoologica Cracoviensia* 52A: 95–105.
- Stefen, C. 2009. The European Tertiary beaver *Chalicomys jaegeri* (Rodentia, Castoridae) revisited. *Kaupia* 16: 161–175.
- Stehlin, H.G. and Helbing, H. 1925. Catalogue des Ossements de Mammifères Tertiaires de la Collection Bourgeois à l'Ecole de Pont-Levoy (Loir et Cher, France). *Bulletin de la Société d'Histoire Naturelle et d'Anthropologie du Loir-et-Cher* 18: 77–277.
- Van de Weerd, A. 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins* (4): 1–185.
- Xu, X. 1994. Evolution of Chinese Castoridae. In: C.K. Li, Y. Tomida, and T. Setoguchi (eds.), *Rodent and Lagomorph families of Asian origin and Diversification*. *Natural Science Museum Monographs* 8: 77–97.

Isaac Casanovas-Vilar [isaac.casanovas@icp.cat] and David M. Alba [david.alba@icp.cat], Institut Català de Paleontologia (ICP), Mòdul ICP, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

Received 27 May 2010, accepted 14 September 2010, available online 20 September 2010.