

New data on the Miocene dormouse *Simplomys* García-Paredes, 2009 from the peri-alpin basins of Switzerland and Germany: palaeodiversity of a rare genus in Central Europe

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Abstract

Simplomys, a dormouse with a simple dental morphology compared to other glirids, shows a continuous evolution in Spain during the end of the Ramblian and up to the middle Aragonian, the stratigraphic frame considered in this work. In contrast, the record of the genus in Central Europe is reduced to a few localities spanning from the early to the middle Miocene. We review the record from the Burdigalian to Langhian equivalent to the deposition of the uppermost Upper Marine Molasse (OMM) to the lower part of the Upper Freshwater Molasse (OSM) and conclude the occurrence of three distinct species. The youngest species, *Simplomys simplicidens*, is recognised in Schönenberg (Germany, MN5) and Courendlin-Solé (Switzerland; MN4). Material from a fissure filling near Glovelier (Switzerland, MN4) supplied the new species, *Simplomys hugi*, whereas the localities Petersbuch 2 and Erkersthofen 2 (both fissure fillings from Germany, MN4) contain species closely related to it. Finally, and pending further advances in the taxonomy of the Iberian *Simplomys*, the oldest population from the fissure filling of Schnaitheim (Germany; MN3) remains in open nomenclature (*Simplomys* sp.). The genus *Simplomys* has not been recorded eastwards from the Swabian and Franconian Jura Plateaus from Germany and its youngest occurrence in Schönenberg is correlated to the South German local scale OSM C+D, at around 15.5 Ma.

Keywords Rodentia · Gliridae · Burdigalian · Langhian · North Alpine Foreland Basin · Jura Plateau

Abbreviations

FJP	Franconian Jura Plateau
GLS	German local scale
M/m	Upper/lower molar

M1/2 and m1/2	Refer to either first or second molars when the differentiation is not possible
MJSN	JURASSICA Museum (former Musée jurassien des Sciences Naturelles)
MN	Mammal Neogene
NAFB	North Alpine Foreland Basin
OMM	Obere Meeresmolasse (Upper Marine Molasse)
OSM	Obere Süßwassermolasse (Upper Freshwater Molasse)
P/p	Upper/lower premolar
SJP	Swabian Jura Plateau
SLS	Swiss local scale

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Introduction

The distal area of the North Alpine Foreland basin (NAFB) and the surrounding Swabian and Franconian Jura Plateaus

in southern Germany are now seen as one of the key areas in Europe for the understanding of mammal evolution during the early and middle Miocene. Indeed, due to decades of investigations, numerous and rich fossil localities have been discovered and taxonomically studied (Prieto and Rummel 2016, and references therein). This allows to recognise small-mammal successions whose stratigraphic resolution has little equivalent in Europe, especially for the period from the terminal Upper Marine Molasse (abbreviated OMM) to the Brackwater Molasse and Upper Freshwater Molasse (the latter being abbreviated OSM; ~ 17.5 to ~ 11.3 Ma). Some of the taxa command the attention due to their rarity and commonly contribute to the biostratigraphic correlation or even the biogeographic affinity of a given assemblage. For instance, the cricetid rodent *Megacricetodon* cf. *gregarius* is a key species for the recognition of the very short biozone Helsinghausen of Kálin and Kempf (2009) in Switzerland (see also Prieto and Rummel 2016, and references therein) and demonstrates short migration of western origin in the NAFB. Similarly, one single tooth of *Mirabella* in both Rembach (Germany; Ziegler and Fahlbusch 1986) and Reiden-Sertel (Switzerland; de Bruijn and Saraç 1992) summarises the record of the genus outside of Greece, Turkey and Bosnia and Herzegovina. Amongst the diverse glirid record, *Seorsumuscardinus* is only recorded in two localities from the NAFB (Tägernastrasse, Canton of St. Gallen, Switzerland, Bolliger 1992a; de Bruijn 1998; Affalterbach, Bavaria, Germany, Prieto and Böhme 2007; Prieto 2009), but represents a common element of the Karpatian and early Badenian from Austria (Daxner-Höck and Höck 2015; Prieto et al. 2016), and is also documented in Serbia (Marković et al. 2016) and Greece (Doukas 2003). Another glirid taxon that is rare in Central Europe is of special interest due to its very common and diversified occurrence in the Iberian Peninsula: the genus *Simplomys*. This dormouse with a simple dental morphology shows a continuous evolution in Spain during the early Miocene and especially, for what concerns this paper, during the end of the Ramblian and up to the middle Aragonian (García-Paredes et al. 2009, 2016). The genus is also well known in France (e.g. Aguilar et al. 1999; Bulot et al. 2009; García-Paredes et al. 2009). In sharp contrast, *Simplomys* only occurs in a handful of localities in Switzerland and Germany. The few fossils have either (1) never been described in detail (Glovelier; Switzerland; Hug et al. 1997) or (2) never re-investigated at the species level in the view of the latest state of taxonomic knowledge (Schnaitheim, Petersbuch 2, Erkersthofen 2, Schönenberg; Germany; Mayr 1979; Wu 1993), or (3) are new to science (Courrendlin-Solé; Switzerland; Prieto et al. 2017). The aim of this work is thus to provide new and complementary information and comment on the implications of the presence of *Simplomys* in Central Europe.

Material and methods

The measurements are given in mm (length × width) and follow the method presented by Prieto et al. (2016: fig. 3). In addition, the m3 have been measured following Freudenthal (2004), meaning length perpendicular to the anterior border. Although using a slightly different baseline for the two first lower molars, the method of Freudenthal (2004) and Prieto et al. (2016) led to identical results. In contrast, García-Paredes et al. (2009, 2010) use either the posterior contact facet (baseline premolars and m1) or the anterior one (baseline m2 and m3). The variations resulting from these orientations do not differ significantly from the measurement provided herein. It is worth to notice that no indication regarding the method is provided by Mayr (1979) and Wu (1993). The nomenclature of the teeth follows Freudenthal and Martín-Suárez (2006). The referred specimens from Glovelier and Courrendlin-Solé belong to the JURASSICA Museum in Porrentruy (Canton of Jura, Switzerland). The fossils from Schnaitheim, Petersbuch 2, Erkersthofen 2 and Schönenberg are stored in the Bavarian state collections for Paleontology and Geology in Munich (Germany).

Biochronostratigraphic notes

The stratigraphic range of the Swiss and German localities follows Prieto and Rummel (2016; adapted and adjusted from Kálin and Kempf 2009; Abdul Aziz et al. 2010; Reichenbacher et al. 2013; Sant et al. 2017; Prieto et al. 2018). We refer to Kálin and Kempf (2009) for the correlation of the corresponding local biozonation to the MN system, but we do not divide biozone MN4 into two subunits. The Iberian record of *Simplomys* in its chronostratigraphic context was presented in García-Paredes et al. (2009, 2016) and Van der Meulen et al. (2012). Recent advances regarding the Aragonian in the Calatayud-Montalbán Basin were published by García-Paredes et al. (2016). We restrict the analysis to the time roughly covering the end of the OMM (early MN4) to the beginning of the OSM (late MN4–MN5), but we also include the MN3 fissure filling of Schnaitheim (Germany) previously described by Mayr (1979) for comparative reasons. In addition to the geographic interest of this latter site (close to the localities Petersbuch 2 and Erkersthofen 2), the fossils deserve a revision in the light of recent studies.

The studied localities and their stratigraphic context

Switzerland

Glovelier (NAFB; Burdigalian; SLS: *Glovelier*; GLS: *not named*; MN4)

The fossil-rich stratified fissure fillings in the Oxfordian limestones at “la Petite Morée” are located 2 km WSW from

Glovelier (Canton of Jura; Fig. 1). The fossil material is common in the sandy clay of the first fissure and consists of both reworked terrestrial and marine remains contemporaneous to the infilling (Hug et al. 1997). All fossils come from the top layer of the fissure filling, constituted of thin-laminated sand with small mud clasts at its base. Despite the stratigraphic and faunal significance of the fossil mammals, only a faunal list was provided by Kälin and Kempf (2009). The assemblage is characterised by the presence of *Democricetodon* and two species of *Ligerimys*, and represents the reference and unique fauna of the *Democricetodon franconicus*–*Megacricetodon collongensis* interval zone of Kälin and Kempf (2009). What regards *Simplomys*, these authors previously recognised the presence of *Pseudodryomys simplicidens*.

Courrendlin-Solé (NAFB; Burdigalian; SLS: Tägermaustrasse; GLS: OSM A; MN4)

The composite fauna has been described from the Montchaibeux Member in the Delémont Basin west of the Birse river (Prieto et al. 2018; Fig. 1), as a result of the geological surveys during the construction of the highway A16. The association of *Megacricetodon* aff. *collongensis* and *Melissiodon* correlates the fauna to the *Megacricetodon collongensis*–*Keramidomys* interval zone. The locality stands out by the relative high abundance of *Simplomys* aff. *simplicidens* (20% of the total number of small mammal teeth).

Germany

Schnaitheim (SJP; Burdigalian; SLS: Trub-Sältenbach; GLS: not named; MN3)

This fissure filling was excavated in 1938 in an abandoned White Jura quarry situated west of Heidenheim a. d. Brenz (Dehm 1939; Bavaria; Fig. 1c). The fossil-enriched part of the infill derives from a few centimetres thick layer. Dehm (1939) correlated the fauna to the early Burdigalian. Fahlbusch (1970) proposed a younger age for Schnaitheim than Wintershof-West (MN3) based on the evolutionary state of the eomyid rodent *Ligerimys antiquus*.

Petersbuch 2 (FJP; Burdigalian; SLS: Glovelier; GLS: not named; MN4)

A NW/SE-directed fossil-enriched fissure connecting several NS-directed fissures from a karst system of the White Jura δ near Petersbuch (Bavaria; Fig. 1) was presented by Heissig (1978). The association *Democricetodon*/*Melissiodon*/*Ligerimys* correlates the fauna to MN4 correspondingly to the Swiss biozone of Glovelier. Notably, Ziegler and Fahlbusch (1986, p. 40) reported the presence of few

Megacricetodon teeth in Petersbuch 2. The species is clearly larger than *M.* aff. *collongensis* (the expected *Megacricetodon* species in MN4; see Courrendlin-Solé), having similar size to its descendant *M. bavaricus*. Ziegler and Fahlbusch (1986) refrained to conclude about the phylogenetic position of these *Megacricetodon* teeth. These fossils possibly indicate the presence of mixed faunal elements of younger origin. The proportion of *Simplomys* in the glirid fauna is very low (0.78% for *S. simplicidens*–herein *S. hugi* n. sp.–after Wu 1993).

Erkersthofen 2 (FJP; Burdigalian; SLS: Glovelier; GLS: not named; MN4)

The fauna was obtained from a yellow-brown clay filling the main fissure of a karst system (White Jura δ , quarry on the street Erkersthofen-Petersbuch; Bavaria; Fig. 1; Heissig 1978). Based on the lineage *Pseudotheridomys-Ligerimys*, Ziegler and Fahlbusch (1986) proposed that Erkersthofen 2 is very close in age to Petersbuch 2, but somewhat younger.

Schönenberg (NAFB; Langhian; SLS: Vermes 1; GLS: OSM C+D-SCH; MN5)

The fossils were derived from a 1-m-thick reworked deposit (Fahlbusch 1975) in a sand pit situated 400 m north of Schönenberg, 8 km south of Burgau (Bavaria; Fig. 1). The size of *Megacricetodon* aff. *bavaricus* from Schönenberg (mean m1: 1.83×1.10 ; see Wu 1982) correlates the fauna to the OSM C+D-SCH. Mayr (1979) observed that *Simplomys simplicidens* represents 3% of the rich and diverse glirid assemblage (more than 200 teeth belonging to 9 species).

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Gliridae Muirhead, 1819

Genus *Simplomys* García-Paredes, in García-Paredes et al. (2009)

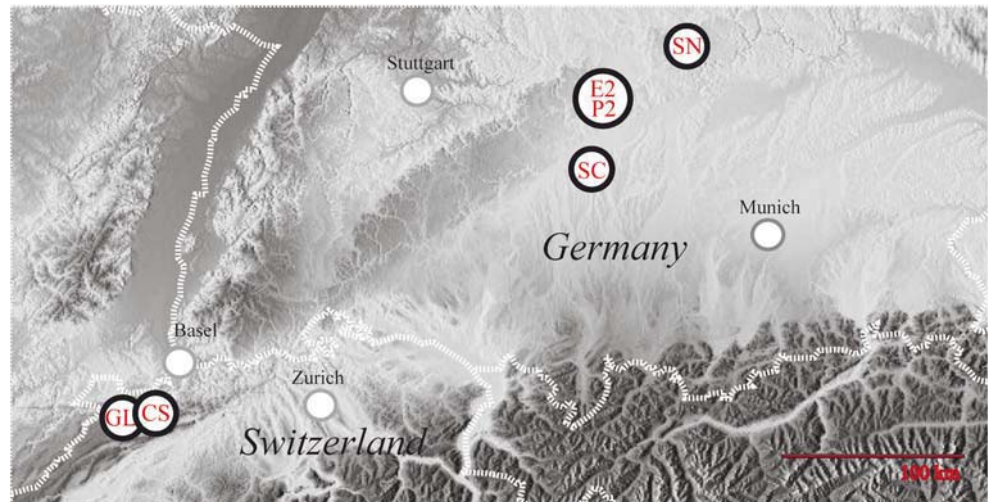
Species previously included in the genus: *Simplomys simplicidens* (de Bruijn 1966) (type species), *S. robustus* (de Bruijn, 1967), *S. aljaphi* (Hugueney et al., 1978), *S. julii* (Daams, 1989), *S. meulenorum* García-Paredes, in García-Paredes et al. (2009).

Simplomys hugi n. sp.

Figs. 2, 3, 4

1997 *Pseudodryomys simplicidens* Kälin, Table 2 (continued)
2009 *Pseudodryomys simplicidens* Kälin and Kempf, pp. 196, 225

Fig. 1 Geographic position of the studied localities (background image from <https://maps-for-free.com/>). CS Courendlin-Solé, GL Glovelier, E2 Erkersthofen 2, P2 Petersbuch 2, SC Schnaitheim, SN Schönenberg



2009 *Pseudodryomys simplicidens* García-Paredes et al., Appendix S1 p. 7

Diagnosis: Medium-sized *Simplomys* species with weakly developed centrolophids: absent to weak in m1 and m2; somewhat longer and interrupted in a few m2, reaching then one fourth of the molar width. Lower third molars with variable morphology, either simple with only three main ridges, or with the presence of a well-developed centrolophid (longer than in m1) and a distinct mesolophid that connects the posterolophid in the midline of the tooth. All crests end freely in the labial part of the upper molars and centrolophs are absent. The longitudinal connection between anteroloph and protoloph is missing on the first two upper molars. A weak precingulum is always present on M1.

Differential diagnosis: *Simplomys hugi* n. sp. mainly differs:

- from *Simplomys aljaphi* in having less complicated dental pattern, less developed centrolophids, and a more simplified m3.
- from *Simplomys julii* in having larger teeth, less straight anteroloph and anterior valley of M1, longer centrolophids and the presence of some m3 with five ridges.
- from *Simplomys simplicidens* from the type locality Valdemoros 3B in having smaller first two molars, lacking the longitudinal connection between anteroloph and protoloph, less developed centrolophids and the presence of some very simple m3 with three ridges. García-Paredes et al. (2009) included in *S. simplicidens* older Spanish populations with notable size and morphologic differences. *S. hugi* n. sp. differs from these populations in lacking centrolophs and in the less developed centrolophids.
- from *Simplomys robustus* in being clearly smaller, having less developed centrolophids.
- from *Simplomys meulenorum* in being smaller (except for some m3 of the older populations assigned to the species by García-Paredes et al. 2009), lacking the longitudinal

connection between anteroloph and protoloph, as well as the interruption of the anteroloph of the M1, having less developed centrolophids and having some m3 with three ridges.

Derivatio nominis: Named after Wolfgang A. Hug who first discovered the fossil locality “la Petite Morée” during a geological prospection.

Type material: Holotype: left fragmentary maxillary with unerupted P4 and D4 in situ (MJSN-GLM017-001; Fig. 2). Paratypes: MJSN-GLM017-002 to MJSN-GLM017-095: one right maxillary fragment with M2 (MJSN-GLM017-002), one left maxillary fragment with M1 (MJSN-GLM017-003), two right maxillary fragments with M1 (MJSN-GLM017-004 and 005), one fragment of mandible without teeth (MJSN-GLM017-006), the rest of the specimens (MJSN-GLM017-007 to 095) are isolated teeth: 1 D4, 8 P4, 16 M1, 14 M2, 5 M3, 2 d4, 2 p4, 14 m1, 18 m2 and 11 m3 (Fig. 3). Measurements: see Table 1.

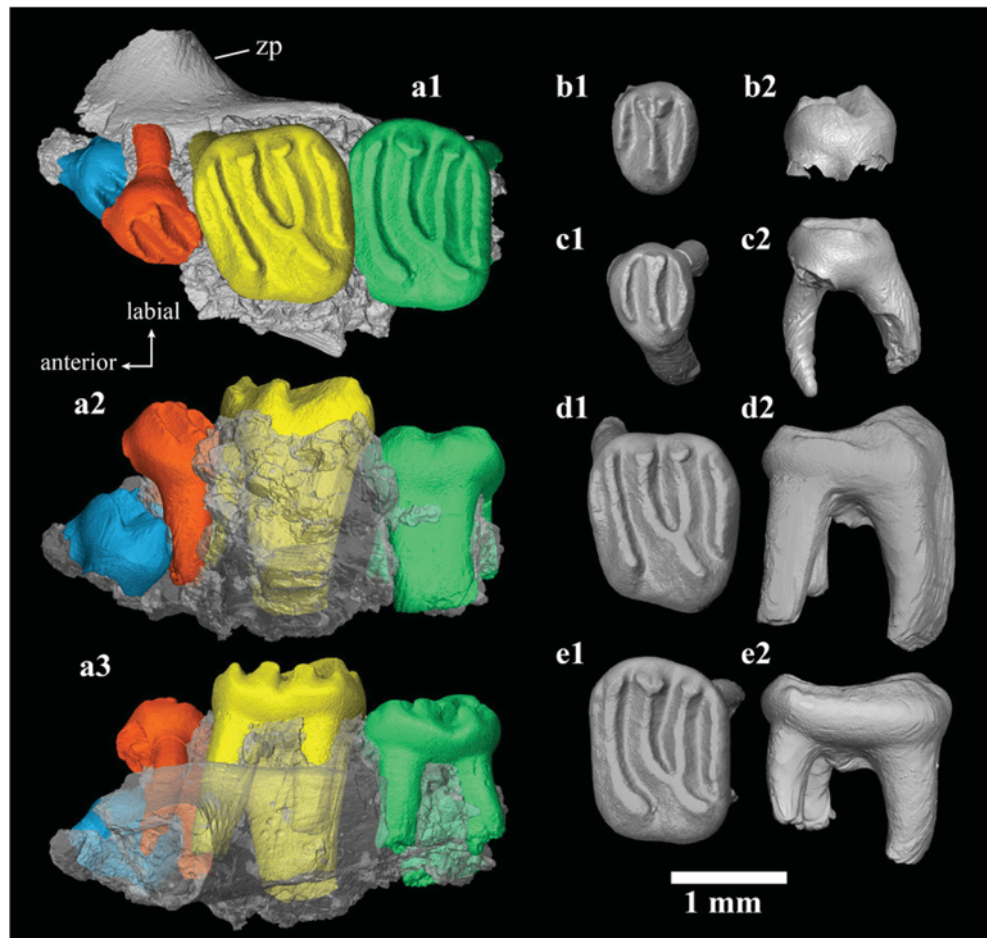
Type horizon: Glovelier is a sandy and marly stratified karstic filling located in an Oxfordian limestone quarry at “la Petite Morée”, European Mammal Neogene Biozonation MN4, SLS: Glovelier, *Democricetodon franconicus*–*Megacricetodon collongensis* interval zone.

Type locality: Glovelier (at “la Petite Morée” quarry), 2 km WSW from the town of Glovelier

Occurrences: Beside Glovelier, *Simplomys* aff. *hugi* n. sp. is recognised in Petersbuch 2. In addition, a few teeth from Erkersthofen 2 are suspected to also belong to the new species.

Description of the holotype: The holotype of *Simplomys hugi* nov. sp. is a fragment of maxillary with complete DP4, P4, M1 and M2 (see below for the description of the teeth). It preserves a small part of the zygomatic arch which starts lateral to the M1. The unerupted P4 is located slightly anterolabially to DP4. All roots of P4 are broken. Only the anterolabial root of DP4 is broken. Both roots of M1 and M2 are full.

Fig. 2 Holotype of *Simplomys hugi* n. sp. from Glovelier. **a1–3** Different views of the holotype (MJSN-GLM017-0001): left upper mandible fragment with P4 (blue), DP4 (red), M1 (yellow) and M2 (green), including part of the zygomatic process (zp). **a1** Occlusal view. **a2** Lingual view. **a3** Labial view (reversed). **b–e** Details of the teeth belonging to the holotype (b1–e1: occlusal views; b2–e2) anterior views). (b) P4 (MJSN-GLM017-0001-1). (c) DP4 (MJSN-GLM017-0001-2). (d) M1 (MJSN-GLM017-0001-3). (e) M2 MJSN-GLM017-0001-4



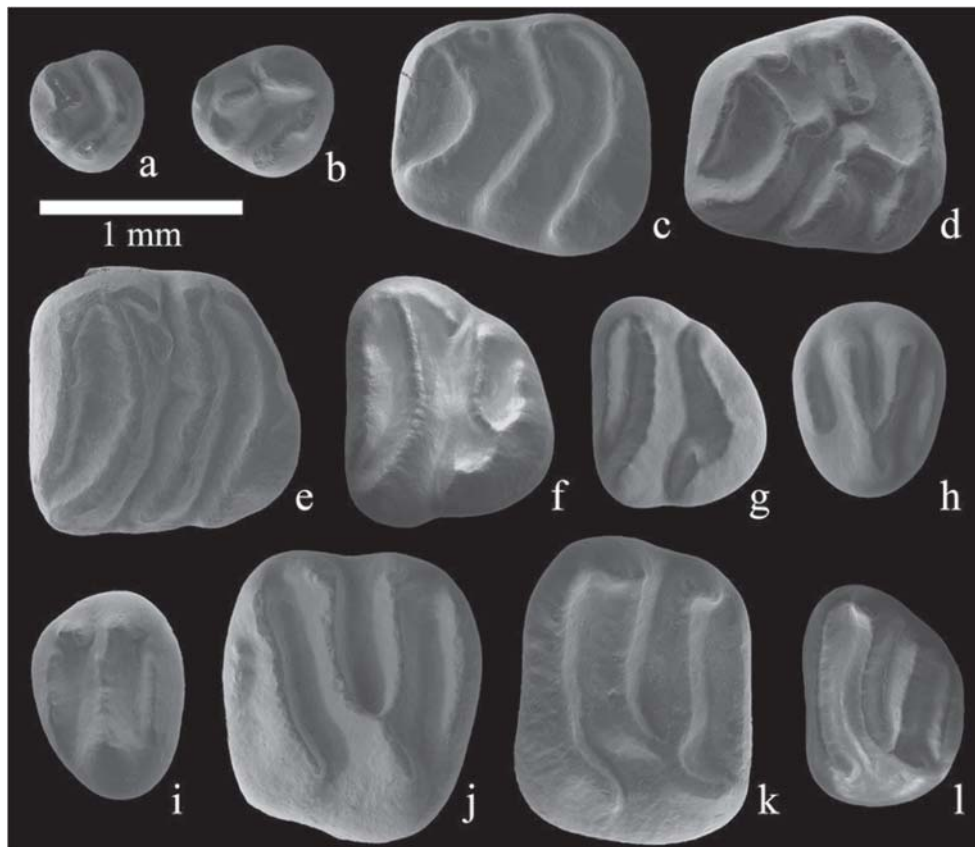
Description of the type series

DP4 and P4: The DP4 from the holotype is similar to the simplified pattern in P4. The anteroloph is long and curved, connected to the paracone. The paracone and metacone are not separated completely, which is the main difference to the P4. The other isolated DP4 shows pronounced wear. The tooth is rounded with some slight folds on the occlusal surface, and it is hard to distinguish the crests and cusps. All P4 have a similar slight wear stage with the oval occlusal surface; however, two different morphologic types can be observed amongst the nine P4. Six of them have a relative short and free anteroloph, with the three crest-like main cusps, and the protoloph connects to the metaloph near the protocone forming a Y-shape in the centre. These six teeth also display a posteroloph longer than the anteroloph (Fig. 3h). The other morphologic types show a longer and slender anteroloph; all cusps are coniform and the protocone is stronger and higher than the two other cusps; the protoloph is either interrupted by a small notch or connects to the metaloph close to the labial side (Fig. 3i). The occlusal surface of the DP4 is flat in lateral view whereas it is concave in the centre in P4. Both DP4 and P4 have three roots, with one robust root in the lingual side and two thinner ones in the labial side.

M1: The tooth usually displays a squared outline with a simple morphologic pattern: only four main crests remain without any centrolophs (Fig. 3j). There is a weak but distinct precingulum on the anterior side of anteroloph. The anteroloph is long and almost straight with a little curve which might be caused by the precingulum; it is free and extended posterolingually. An anterior arm of paracone and a posterior arm of metacone are present and weak in all upper molars. The protoloph is the longest crest, and it connects to the metaloph with a backward bend; its lingual part is parallel to the anteroloph. The posteroloph is shorter than anteroloph, and both its lingual and labial parts are free. M1 has three roots like P4, with a slightly concave occlusal surface in lateral view.

M2: It can be easily distinguished from the M1 by the lack of a precingulum and the rectangular shape due to a proportionally greater width (Fig. 3k). The anteroloph is transverse in the middle and oblique lingually. It either connects to the anterior arm of paracone (but the connection is weak and lower than the crest) or ends freely. Both protoloph and metaloph are less oblique than in M1. The lingual part of protoloph is bent

Fig. 3 *Simplomys hugi* n. sp. from Glovelier. **a** dp4 (MJSN-GLM017-0049). **b** p4 (MJSN-GLM017-0050). **c** m1 (MJSN-GLM017-0059). **d** m1 (MJSN-GLM017-0064). **e** m2 (MJSN-GLM017-0074). **f** m3 (MJSN-GLM017-0085). **g** m3 (MJSN-GLM017-0090). **h** P4 (MJSN-GLM017-0007). **i** P4 (MJSN-GLM017-0008). **j** M1 (MJSN-GLM017-0024). **k** M2 (MJSN-GLM017-0042). **l** M3 (MJSN-GLM017-0044). All teeth are presented in the left orientation (e, g, j and k reversed)



backward and reaches the posterolingual corner of the tooth. The posteroloph is straighter than in M1. The roots and the occlusal surface in lateral view are similar to that of M1.

M3: It has a trapezoid outline with the labial side more reduced posteriorly than the lingual side (Fig. 3l). The anteroloph is straight and almost transverse, connected labially to the anterior arm of paracone and being lingually free. The posteroloph is the shortest ridge, connected lingually to the protocone and labially to the posterior arm of the metacone

(the connection is weak and lower than the crests). No root is preserved. The occlusal surface in lateral view is almost flat.

Mandible: One slender mandible without teeth has been found with a shallow, weakly curved diastema (MJSN-GLM017-006). The cavities of the roots indicate one root for the dp4 or p4, two roots for the m1 and three roots for the m2 and m3. The coronoid process is not preserved, but its base shows an origin lateral to the posterior part of m2 (based on the position of the roots). The masseter crests are ‘U’-shaped; both the dorsal and the ventral crests are weak. The

Table 1 Measurements (mm) of the teeth of *Simplomys hugi* n. sp. from Glovelier

	N	Length					Width				
		Min	Mean	Max	StD	CV	Min	Mean	Max	StD	CV
DP4	2	0.62	0.65	0.67	–	–	0.79	0.81	0.82	–	–
P4	9	0.68	0.73	0.78	0.032	4.31	0.89	0.96	1.02	0.041	4.30
M1	19	1.12	1.24	1.31	0.046	3.76	1.30	1.42	1.53	0.056	3.96
M2	15	0.06	1.17	1.30	0.059	5.01	1.29	1.51	1.62	0.083	5.53
M3	5	0.68	0.78	0.83	0.063	8.10	0.98	1.11	1.25	0.098	8.83
dp4	2	0.53	0.58	0.63	–	–	0.53	0.55	0.57	–	–
p4	2	0.63	0.65	0.66	–	–	0.66	0.68	0.70	–	–
m1	14	1.14	1.30	1.40	0.073	5.60	1.07	1.21	1.34	0.077	6.37
m2	18	1.24	1.33	1.44	0.045	3.36	1.24	1.35	1.46	0.058	4.29
m3	11	0.88	1.00	1.10	0.075	7.57	1.07	1.18	1.30	0.083	7.08

dorsal masseter crest joins the ventral one at a point below the posterior part of m1. The ventral masseter crest extends even further, to a point below the anterior edge of m1. The position of the mental foramen is high but not visible in occlusal view. Mesioposteriorly, the mental foramen is near the distal end of the diastema.

dp4 and p4: The outlines of dp4 and p4 are almost oval with the anterior part narrower than the posterior one. The dp4 is relatively smaller than p4 and with a simpler morphology (Fig. 3a). The anterolophid is absent in two dp4 but present in two other p4 as a small tuber which is either connected to other ridges or isolated. The anterior part of both teeth is occupied by one curved and highest ridge, with occasionally a notch inside. The curved posterolophid is continuous in dp4 and separated to two ridges in p4 (Fig. 3b). Both dp4 and p4 have only one root. In both dp4 and p4, the lateral view of occlusal surface is curved by the highest ridge in the anterior part.

m1: The anterior part of m1 is narrower than the posterior one. The four main lophids are labially free. The anterolophid is oblique posterolabially to the metaconid. The metalophid has a right-angle-like bend backward in the middle, connected to the protoconid which is slightly anterior to the metaconid. The mesolophid bend is weaker than that of the metalophid, with the turning point closer to the labial side. The posterolophid is the longest lophid and curves posteriorly, being connected to the mesolophid through a weak entoconid. The hypoconid is elongated and included in the posterolophid. All m1 present an either weak or absent centrolophid in the lingual edge, connected to the metaconid (Fig. 3c, d). Three out of 14 specimens display a variable pattern with two extra crests (Fig. 3d). One crest starts at the turning point of metalophid and extends posteriorly but ends free. The other connects the mesolophid to the hypoconid and separates the mesolophid into two parts: the lingual part with a slight notch and the labial one with a deep notch. Otherwise, the metalophid is more oblique in the lingual side. There are two roots in the m1, with the anterior root thinner than the posterior one. The occlusal surface in lateral view is flat.

m2: It differs from m1 in having a more rectangular surface and the posterolophid is more enlarged at its posterolingual part (Fig. 3e). The four main lophids are similar to that of m1, but less curved. The anterolophid is almost transverse and the metalophid is the longest lophid. The posterolophid almost contacts the entoconid but is separated from it by a small notch. The centrolophid is either more developed than in m1 (3/18) and reaching up to one fourth of the molar width (but in this case always interrupted), or as weak as in m1 (15/18). The m2 has three roots, with two of them in the anterior side. The occlusal surface in lateral view is similar to m1.

m3: It has a subtriangular outline with a strong reduction in the posterolabial side. The anterolophid is transverse and labially free. The metalophid is the longest lophid with a slight

curve and connects with the anterolophid in the lingual edge. The lateral part of the tooth displays two different morphologic types. One type (7/11) shows a well-developed centrolophid (longer than in the m1) which extends posterolingually; a weak but distinct mesoconid is present and connects to the hypoconid by the anterior arm of hypoconid in the labial side; the mesolophid is transverse in the lingual side and bends towards the hypoconid in the midline of the tooth, then connects to it directly; the posterolophid is weak and shorter than the mesolophid and free lingually (Fig. 3f). The other morphologic type (4/11) lacks the centrolophid and mesolophid; thus, it is relatively smaller than the former type in size, but the posterolophid is more developed and extends anterolingually to contact the entoconid (Fig. 3g). In both types, the roots and occlusal surface in lateral view are similar to as described in the m2.

Remarks: Never described the teeth from Glovelier have been previously assigned to *Pseudodryomys simplicidens* (Kälin 1997; Kälin and Kempf 2009) and finally included in *Simplomys* by García-Paredes et al. (2009). First, due to the morphologic variability of the m3 and P4, the taxonomic homogeneity of the population has to be discussed. Two m3 morphotypes are observed: one “*S. simplicidens*-like” with well-developed mesolophid and one “*S. meulenorum*-like” with reduced m3. This could indicate the presence of two species in Glovelier. Two different morphotypes are also observed on P4. On the other hand, no differences are observed on the remaining teeth and their size range does not exceed the variability observed in other species. These observations confirm the systematic homogeneity of the population, although these morphotypes of m3 and P4 could suggest an ongoing speciation process.

All upper molars lack the centrolophs, which is clearly less frequent for *S. simplicidens* of the zone B and Ca from the Spanish Calatayud-Montalbán Basin, but typical for *S. meulenorum* and *S. julii*, the latter being too small to be considered herein. The centrolophids are less developed than in *S. simplicidens* and *S. robustus* populations from the Aragonian in Spain, but somewhat exceed in length what is expected in typical *S. meulenorum* molars, especially in the m1. Similarly, the size of the molars does not reach *S. meulenorum*, but is similar to that of *S. simplicidens*. On the whole, the molars correspond in size to *S. simplicidens* from the local biozone B-Da in the Aragonian type area (García-Paredes et al. 2009: fig. 10), but morphologically are clearly distinguishable from the latter species (see above, § Differential diagnosis) and therefore we propose that the material from Glovelier belongs to a new species named *Simplomys hugi* herein.

Other populations close to *Simplomys hugi* n. sp.: Wu (1993) recognised strong similitudes between one of the two *Pseudodryomys* species of Petersbuch 2 (assigned to *P. simplicidens* in her work) and the species of Erkersthofer 2. She also noticed that the German molars differ from the type

Simplomys simplicidens collection from Valdemoros 3B in being smaller and more delicate, as well as in lower molars having shorter centrolophids. In addition, the m3 is reduced in Petersbuch 2, showing only three transversal crests as well as a very short centrolophid, and a weak precingulum on M1. These features fit *S. hugi* n. sp., but the molars are also close to *S. simplicidens* from Spanish localities similar in age, except for the centrolophids which are longer in these populations. The small longitudinal extension at the anterior part of the protoloph (Fig. 4k) is absent in the species from Glovelier; this morphologic characteristic is however highly variable in *S. simplicidens* and *S. meulenorum*. Thus, the teeth from Petersbuch 2 are assigned to *S. aff. hugi* n. sp. (Fig. 4a–k, for measurements and descriptions see Wu 1993 and Fig. 5). The three teeth from Erkersthofen 2, all less diagnostic upper molars, lack all the centrolophids and fit the size range of *S. hugi* with the M1 featuring a weak precingulum. Their size and

morphology do not definitively negate an assignment to *S. simplicidens*, but considering the geographic proximity of Petersbuch and Erkersthofen (around 3 km), as well as the close temporal frame of both faunas, the teeth from Erkersthofen 2 are more likely to belong to a form close to the new species due to the differences listed above. Thus, they are assigned to *S. cf. hugi* n. sp. (Fig. 4l–n). In addition, an interesting material from Béon 2 (France, MN4) was described as *Pseudodryomys* aff. *simplicidens* by Bulot et al. (2009). The fossils from Béon 2 belong to the lower size range of *S. hugi* n. sp. and feature M2 that lack centrolophs as in *S. hugi* n. sp. In contrast, the lower molars with poorly developed centrolophids are morphologically closer to *S. meulenorum*, and the anterolophids and metalophids are clearly interrupted, a morphology also not recognised in Glovelier. Consequently, until more material is available, we maintain these two populations as taxonomically different.

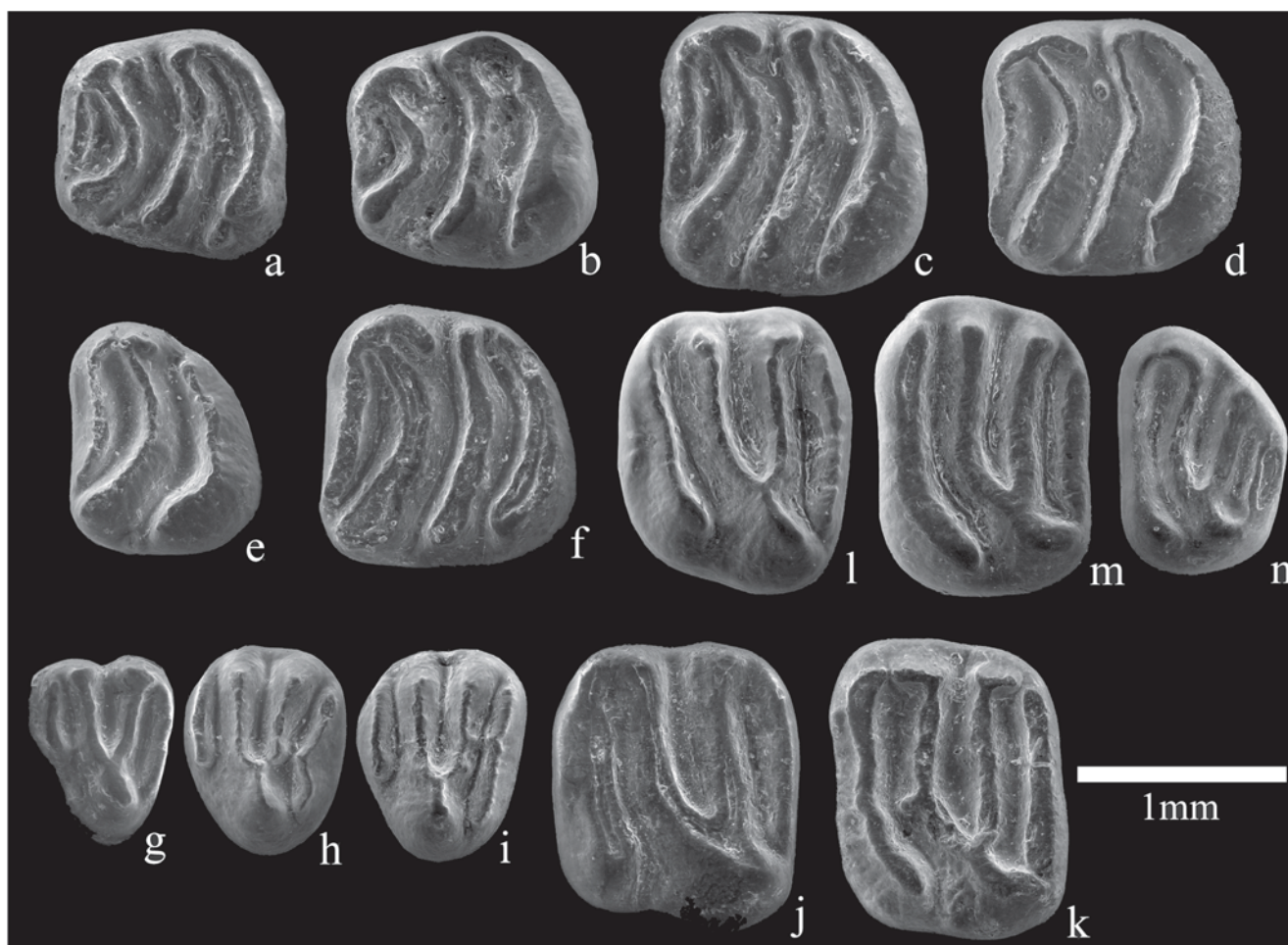
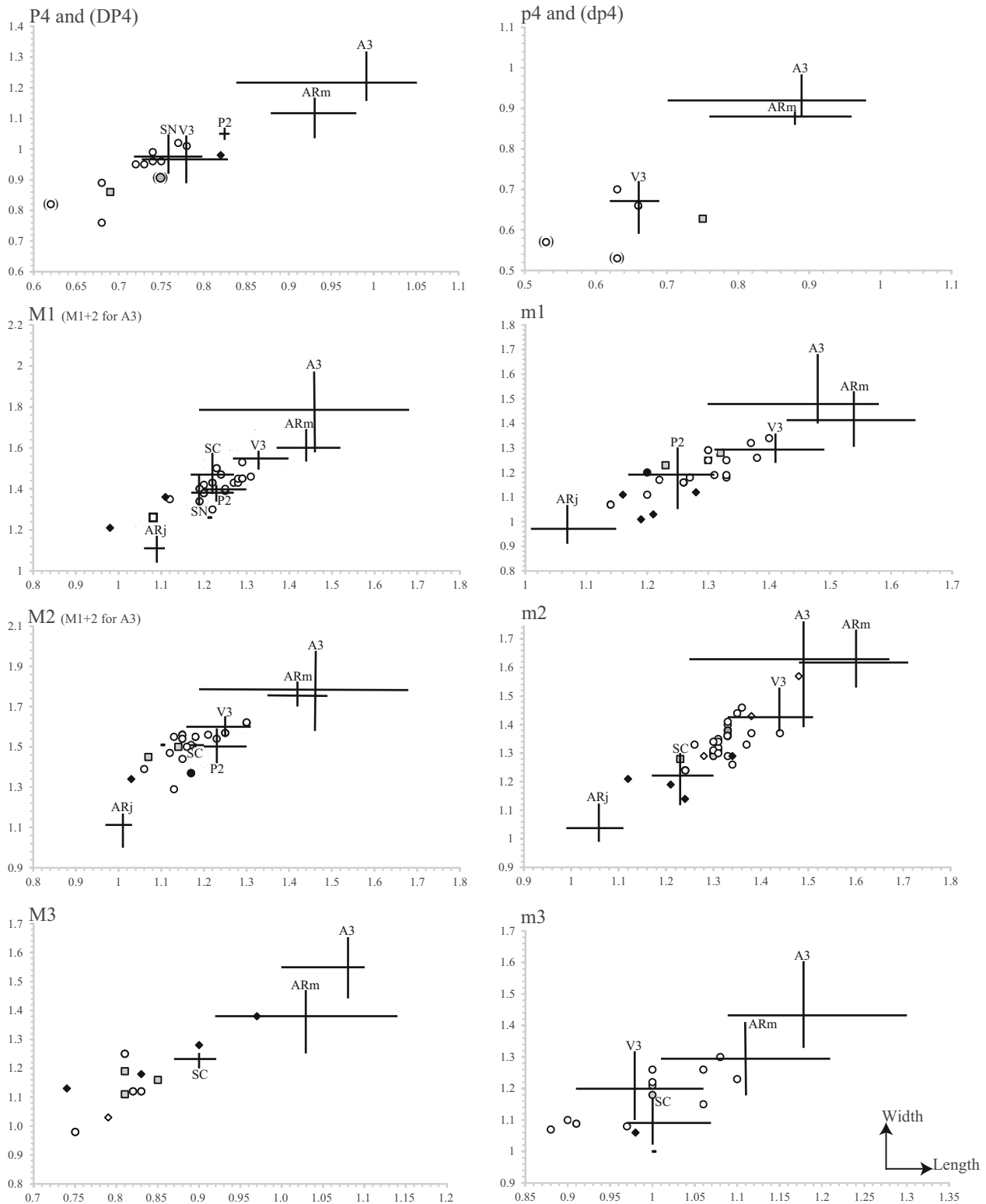


Fig. 4 *Simplomys* from Petersbuch 2 (*S. aff. hugi* n. sp.; a–k) and Erkersthofen 2 (*S. cf. hugi* n. sp.; l–n). a m1 (BSPG-1976-XXII-5835). b m1 (BSPG-1976-XXII-5834). c m2 (BSPG-1976-XXII-5836). d m2 (BSPG-1976-XXII-5837). e m3 (BSPG-1976-XXII-5839). f m2 (BSPG-1976-XXII-5838b). g PD4 (BSPG-1976-XXII-5829). h P4 (BSPG-1976-

XXII-5830). i P4 (BSPG-1976-XXII-5831). j M1 (BSPG-1976-XXII-5832). k M2 (BSPG-1976-XXII-5833). l M1 (BSPG-1974-XIV-1497). m M2 (BSPG-1974-XIV-1498). n M3 (BSPG-1974-XIV-1499). All teeth are presented in the left orientation (a, d–g, i, l and m reversed)



◆ Ateca III: *S. robustus* (A3) ◆ Artesilla: *S. julii* (ARj) ● Artesilla: *S. meulenorum* (ARm) ◆ Béon2: *S. sp.* (B2) □ Courrendlin-Solè: *S. simplicidens*
 ○ Glovelier: *S. hugi* ○ Petersbuch 2: *S. meulenorum* (P2) ● Schnaitheim: *S. sp.* (SN) ■ Schönenberg: *S. cf. simplicidens* (SC) Δ Valdemoros 3B: *S. simplicidens*
Fig. 5 Bivariate diagrams comparing the size of *Simptomys* populations. Data from: this paper, de Bruijn (1966), Adrover (1978), Mayr (1979), Daams (1989), Wu (1993), García-Paredes (2006), García-Paredes et al. (2009), and Bulot et al. (2009). Note that the M1 and M2 are not discriminated for Ateca 3

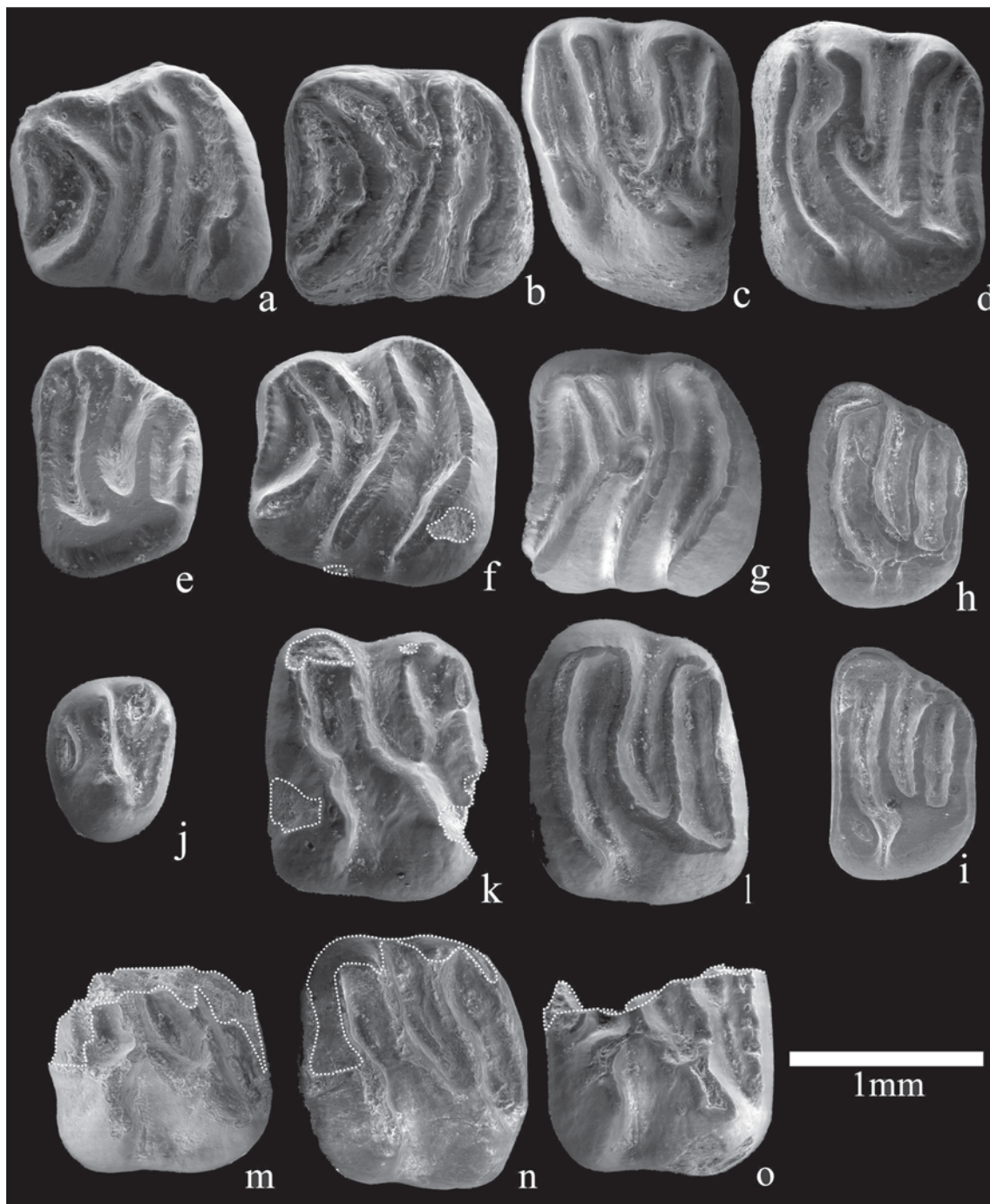


Fig. 6 *Simplomys* from Schönenberg (*S. cf. simplicidens*; **a–e**) and Courrendlin-Solé (*S. simplicidens*; **f–o**). **a** m1 (BSPG-1966-IX-18). **b** m2 (BSPG-1966-IX-75). **c** M1 (BSPG-1966-IX-76). **d** M2 (BSPG-1966-IX-77). **e** M3 (BSPG-1966-IX-78c). **f** m1 (MJSN-SOL006-323). **g** m2 (MJSN-SOL006-267). **h** M3 (MJSN-SOL008-138). **i** M3 (MJSN-

SOL008-125). **j** P4 (MJSN-SOL006-312). **k** M1? (MJSN-SOL008-145). **l** M2 (MJSN-SOL006-326). **m** M1? (MJSN-SOL005-177). **n** M1? (MJSN-SOL006-334). **o** M1? (MJSN-SOL006-305). All teeth are presented in the left orientation (**b**, **j–l** and **o** reversed)

Simplomys simplicidens (de Bruijn 1966)
Fig. 6f–o, Fig. 7

Referred material from Courrendlin-Solé: One m3 (MJSN-SOL006-330) originally referred to *Simplomys* aff.

simplicidens by Prieto et al. (2018) is assigned herein to *Pseudodryomys ibericus*. The other specimens, also initially assigned to *S. aff. simplicidens* by Prieto et al. (2018), are now attributed to *S. simplicidens* and comprise 19 isolated teeth (MJSN-SOL005-177, -006-120, 267, 284, 305, 307, 312,

323, 324, 326, 327, 329, 330, 334, 336, -008-125, 138, 145, 154 and 155); 2 P4 ($0.73 \times -$, 0.78×0.60), 8 M1/2 ($1.2 \times -$, $- \times 1.43$, 1.14×1.50 (M2), 1.07×1.45 (M2), ca. $1.14 \times -$), 4 M3 (0.81×1.19 , 0.85×1.16 , 0.81×1.11), 1 p4 (0.68×0.63), 2 m1 (1.32×1.28 , 1.23×1.23), 2 m2 ($- \times$ ca. 1.29 , 1.23×1.28), 1 m3. Measurements: see also Fig. 5.

Description

P4: One of the two premolars is lingually damaged. The complete tooth displays an almost oval outline and a simple dental pattern with four ridges. The anteroloph is short, somewhat oval, and is situated in the middle part of the anterior border. In the damaged tooth, this crest is longer. The protoloph runs almost parallel to the width axis of the P4 and ends lingually in a poorly developed protocone. The oblique, oval and short metaloph does not reach the protocone. The posteroloph is a low crest that connects to the protocone posterolingually in one P4, whereas, in the damaged one, this connection is achieved much more labially, resulting in the interruption of the posteroloph in its labial part. All crests end labially free. Probably three roots.

M1 and M2: The distinction between the two first upper molars can normally be achieved in *Simplomys*. Unfortunately, numerous molars are damaged in Courrendlin-Solé, and such discrimination might be hazardous for some specimens. As a result, first and second molars are described together. The molars show four main ridges, with the metaloph connected to the protoloph in all teeth but one (Fig. 6k) in which the metaloph is then interrupted shortly before of its contact with the protoloph. The anteroloph is interrupted in one damaged M1/2 (Fig. 6o). The same specimen, as well as a second one, shows a connection between the two anterior ridges through a small oblique crest. This connection is at the draft stage in a third molar. Four molars have a posteroloph that ends lingually free. In two other teeth, both M2, this crest connects to the protocone. The labial connections are variable and often hardly observable due to the conservation of the specimens. Otherwise, most of them show the connection anteroloph-protoloph and a small notch splits metaloph and posteroloph. In one specimen, these connections are interrupted, whereas both are present in one other specimen. First and second molars have four roots.

M3: One molar is strongly damaged. The other two teeth show a slightly rounded posterior part which is narrower than the anterior one. All M3 develop four ridges. The anteroloph connects to the metaloph at the labial border of the teeth, but ends lingually free or very close to the protocone. The three other crests join the protocone. The labial connection of the two posterior ridges is variable: either connected, disconnected or even interrupted with the posteroloph curved forwards. Three roots are present.

p4: The outline is oval with the posterior part wider than the anterior one. They are morphologically simpler than the molars. The anterolophid-metalophid complex is reduced to a structure having three lobes. A crest starting at the anterolabial corner runs labially towards the entoconid without reaching it. The latter structure is small, bean-shaped and isolated from the posteroloph. The posteroloph is long and strongly curved.

m1: The anterior part is narrower than the posterior one. The teeth have five ridges. The slightly curved and short anterolophid ends free in the anterolingual part of the tooth, above the protoconid. It connects labially to the metalophid and centrolophid. The metalophid is strongly curved. The centrolophid runs parallel to the metalophid and its length is almost half of the width of the molar. The two posterior ridges are strong and labially connected in one m1, whereas a notch discriminates superficially the crest in a second molar. Other superficial notches occur in the latter specimen, three at the posterolophid and one at the mesolophid. The protoconid is the lowest structure of the molar.

m2: The m2 is morphologically very close to the m1. It differs in the outline, the anterior part being wider than the posterior one, and resulting in somewhat less curved ridges. The centrolophid is equally long as in the m1 but the enlargement of the anterior part of the m2 induces that the length of the crest represents only about a quarter of the molar width. One tooth shows an additional and small ridge close to the middle part of the metalophid as an extension of the centrolophid (Fig. 6g).

Remarks: Unfortunately, a high proportion of teeth from Courrendlin-Solé is partly damaged, and, although they represent the most abundant dormouse of the locality, it is not possible to evaluate the morphometric variation of the species. Based on the available fossil material, the lower molars do not show the presence of more than one taxon. In contrast, the M1/2 show notable differences in robustness and pattern of the main crests. The more robust morphotype reminds of *Praearmantomys* and *Armantomys* in some characters. Nevertheless, important characteristics differentiating *Simplomys* from these genera are the following: the still less robust ridges, the lower degree of hypsodonty (especially regarding *Armantomys*) and the relatively more lingual and constant connection of the protoloph and the metaloph in M1 and M2. They also differ in the position of the posteroloph having the same height in *Armantomys* and *Praearmantomys*, whereas it is lower in *Simplomys*. This arrangement of crests is present in the molars from Courrendlin-Solé, with the exception of one, on which the metaloph is not connected to the protoloph, although the posteroloph is not at the level of the protoloph and the ridges are not ending free at the labial side (like it is the case in *Praearmantomys* and *Armantomys*). However, this strong morphological variation does not preclude us from referring all specimens to *Simplomys* since this strong variability has been pointed out by García-Paredes

(2006) in larger samples from the Iberian Calatayud-Montalbán Basin.

Compared to the Spanish record, the teeth from Courrendlin-Solé are on average smaller than *Simplomys meulenorum* (see García-Paredes et al. 2009) and larger than *S. julii* (see Daams 1989). In contrast, *Simplomys robustus* is much larger, but some morphological characteristics seen in Courrendlin-Solé recall the species. *Simplomys aljaphi* differs in its more complicated dental pattern. All lower molars show a well-developed centrolophid, connecting the species from Courrendlin-Solé to *S. simplicidens* or *S. robustus*. In the upper molars, the anteroloph is often not isolated at the labial side of the molars. This characteristic is not observed in the other Swiss and German material studied herein. García-Paredes (2006) showed that these connections are variable in *S. simplicidens*, rarer in M1 than in M2. The anterior and double connections are known during the zones B-Da from the Calatayud-Montalbán Basin for the M1, common for the M2 for the same period, but also present in the younger fauna. As far as the molar collection is representative, the lack of centroloph in M1-2 is a derived character that is more frequent in fauna younger than Courrendlin-Solé. Considering the geographical position of Courrendlin-Solé, the French fossil record is important, especially in the Rhône-Alpes region and the Massif Central. *Simplomys* cf. *simplicidens* and *S. aff. robustus* are recognised in Vieux-Collonges (e.g. Maridet 2003) and *S. aljaphi* in Montaigu-le-Blin (*Pseudodryomys aljaphi* nov. sp. in Hugueney et al. 1978). Although the Aquitanian species can be excluded, the forms from Vieux-Collonges were not sufficiently described and therefore cannot be discussed herein. The material from Courrendlin-Solé shows a size similar to the smaller assemblages of *S. simplicidens* amongst all the material described from the Calatayud-Montalbán Basin (García-Paredes 2006; García-Paredes et al. 2009). The latter authors demonstrate a trend towards larger size in this species, that is especially evident between approximately 16 and 15.5 Ma. The Courrendlin-Solé material shows a size comparable to the lower Aragonian assemblages in Spain older than 16 Ma, which is compatible with the biochronological position of Courrendlin-Solé within the Tägeraustasse zone of Kálin and Kempf (2009).

Summing up, we consider the *Simplomys* teeth assemblage of Courrendlin-Solé as monospecific. Although the teeth are a bit smaller than those from the type locality, we follow the taxonomy used by García-Paredes et al. (2009) in assigning the fossils to *S. simplicidens*.

Simplomys cf. *simplicidens*

Fig. 6a–e

Referred material from Schönenberg: Mayr (1979) reported 10 isolated teeth from this locality; we actually only studied 5 molars out of 10. These fossils are the ones figured by Mayr

(1979: Plate IX; figs. 18–22). Measurements: see Mayr (1979) and Fig. 5.

Description: see Mayr (1979).

Remarks: The centrolophids of the lower molars are relatively long, and the species from Schönenberg belongs thus either to *S. simplicidens* or *S. robustus*. Both species are discriminated mostly based on the relative size and the simplicity of the morphology of the premolars and m3. These dental elements have not been found in Schönenberg. However, *S. robustus* is not expected due to stratigraphic reasons, and the teeth from Schönenberg are clearly smaller. In addition, the teeth fit best in size with *S. simplicidens* populations comprised between the local biozones A and Da in the Aragonian type area, except the m2 which rather fit to the lower range of Db (García-Paredes et al. 2009: fig. 10). We consequently refer the molars to *S. cf. simplicidens*. Mayr (1979) used the morphotypes defined by Daams (1974) for describing the molars. As a result, the information provided by Mayr (1979) implies that all M1 and M2 lack a centroloph. In contrast, the figured M2 (Fig. 6d) shows a small and interrupted crest which is situated posteriorly to the labial part of the curved protoloph. This crest may be seen such as a remnant centroloph, but is most probably the result of an aberrant morphology. As mentioned earlier in the text, the absence of these crests is frequent in the biozones Da and Db from the Calatayud-Montalbán Basin and almost the rule in younger biozones. In M2, both centrolophs are frequent in samples from zone B and early C (being the posterior centroloph more frequent), and rare in the remaining C and in younger biozones.

Simplomys sp.

Fig. 8

Referred material from Schnaitheim: Mayr (1979) studied 25 teeth, but we only observe 9 specimens stored in the BSPG. Measurements: see Mayr (1979) and Fig. 5. Note that some doubtful molars are included in the figure (see discussion below).

Description: see Mayr (1979).

Remarks: Mayr (1979) referred the specimens to *Pseudodryomys simplicidens*. However, the reduced centrolophids of the figured lower molars also relate to *S. meulenorum*, *S. julii* or *S. hugi* n. sp. However, *S. julii* is too small to be considered herein. Similarly, *S. meulenorum* is too large. In addition, the m3 from Schnaitheim is reduced. García-Paredes et al. (2009, p. 644) observed that “the m3 of *S. meulenorum* sp. nov. and *S. simplicidens* have the mesolophid and posterolophid fused into a single ridge, but this union is achieved in different ways in both species”. Whereas in *S. meulenorum* “the mesolophid [...] is mainly composed of the posterolophid”, this ridge is in *S. simplicidens* “equally composed of the lingual part of the mesolophid and the labial part of the posterolophid separated by an inflexion”; this results in a medially situated inflexion in *S. simplicidens*, whereas it is near the lingual border in the second species. Regarding this morphologic character, the m3 from Schnaitheim fits with *S.*

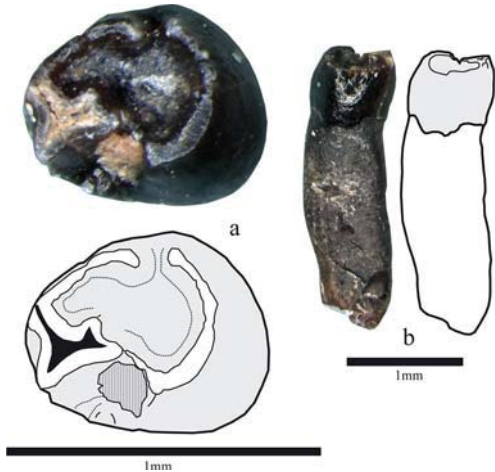


Fig. 7 *Simplomys simplicidens* (de Bruijn, 1966) from Courrendlin-Solé. p4 (MJSN-SOL006-336). a Occlusal view. b Labial view

meulenorum, and also with the simplified m3 morphotype of *S. hugi* n. sp. from Glovelier.

After Mayr (1979), 5 out of 6 M1 and all M2 lack the centrolophs (morphotype F of Daams 1974). In contrast, one M1 shows the posterior centroloph (morphotype D of Daams 1974; not figured by Mayr 1979). The first two upper molars studied herein show indeed that either both centrolophs are short but present in one molar (Fig. 8i), or the drafts of the crests occur. The presence of these crests allow to exclude *S. hugi* n. sp. Basically, Mayr (1979) linked the two first lower molars to the morphotype M of Daams (1974), in which the centrolophid is relatively short, but without clear indication about the real length of the crest. We partially disagree with this interpretation based on the observation of the m1 (Fig. 8a), and the length of the centrolophids cannot be evaluated using this method for the entire sample, because we could not access all material. Mayr (1979) also recognised an m2 with posterotropid which excludes its adscription to *Simplomys*.

Based on the material available for this study and figured in Fig. 8, the population from Schnaitheim presents its own morphologic characteristics. Interestingly, the trend of losing centrolophs has been observed in *S. simplicidens* (García-Paredes et al. 2009), and it is tempting to consider the remains of these crests in Schnaitheim as a primitive configuration of *S. hugi* n. sp. upper molars. Unfortunately, we lack detailed information regarding the *Simplomys* record in the Ramblian succession of the Iberian Peninsula for further comparisons, as well as regarding other MN3 Central European forms.

Consequently, awaiting further advances in the taxonomy, the species from Schnaitheim remains in open nomenclature.

Discussion and conclusions

The genus *Simplomys* was erected by García-Paredes in García-Paredes et al. (2009) and now includes the six

species listed above, of which all but *S. meulenorum* were defined previously under the genus *Pseudodryomys*. *Simplomys* is characterised mainly by cheek teeth with moderately high crown and relatively simple morphology. The premolars and third molars are simplified and small. Hordijk et al. (2015; see also García-Paredes et al. 2009) note that species belonging to *Simplomys* mainly differ in size, or, in the case of *S. meulenorum*, by the degree reduction of p4/P4-m3/M3. In the case of *S. simplicidens*, significant differences in size are observed through its long stratigraphic range (García-Paredes et al. 2009). Moreover, several species can occur in a single assemblage and poorly represented species in one given assemblage could well be misidentified, as belonging to the more frequent one. This problematic has been underlined by the continuous evolution of *Simplomys* in Spain during the end of the Ramblian and up to the Middle Aragonian (García-Paredes et al. 2009, 2016; Fig. 9).

In the localities from Central Europe considered herein, only one site, namely Petersbuch 2, was considered to contain two *Pseudodryomys* species (*P. simplicidens* and *Pseudodryomys* sp.). Indeed, Wu (1993) segregated two teeth from Petersbuch 2 from the BSPG (named *Pseudodryomys* sp.), a P4 and a m3, based on specific morphologic characteristics: the P4 has equally long anteroloph and posteroloph; the main ridges of the m3 are less inclined, the centrolophid medium sized and the posterior part of the tooth less reduced. It is worth to mention that the m3 has been figured (Wu 1993: Plate 5, fig. 16) and does not fit morphologically within the concept of *Simplomys*. Wu (1993) noticed that all M1 (Stuttgart collection) feature two centrolophs that tend towards connection, a characteristic indeed known in *S. aljaphi*, but also present in other genera. Considering these facts, we cannot confirm the presence of a second *Simplomys* species in Petersbuch 2.

Simplomys in Central Europe first occurs at La Chaux 7 (Kälin 1997; Engesser and Mödden 1997; Weidmann et al. 2003; García-Paredes et al. 2009; *Simplomys* aff. *aljaphi*; Switzerland). In the same locality, *Pseudodryomys* sp. was also reported. A study of the specimen(s) however was not possible; hence, we refrain from an evaluation of the taxonomical accuracy of this identification. Anyway, this occurrence is anyway outside the stratigraphic range considered herein (Aquitanian; MN 2). In contrast, the Aquitanian localities of the German part of the Lower Freshwater Molasse did not yield any *Simplomys* so far (e.g. Werner 1994).

Kälin and Kempf (2009) still assigned the *Simplomys* species to the genus *Pseudodryomys*. It is thus difficult to interpret the records that are not assigned to a distinct species, as is the case of *Pseudodryomys* sp. from Trub-Sältenbach (Switzerland; MN3b). These authors noticed that the dormice are diverse, including species

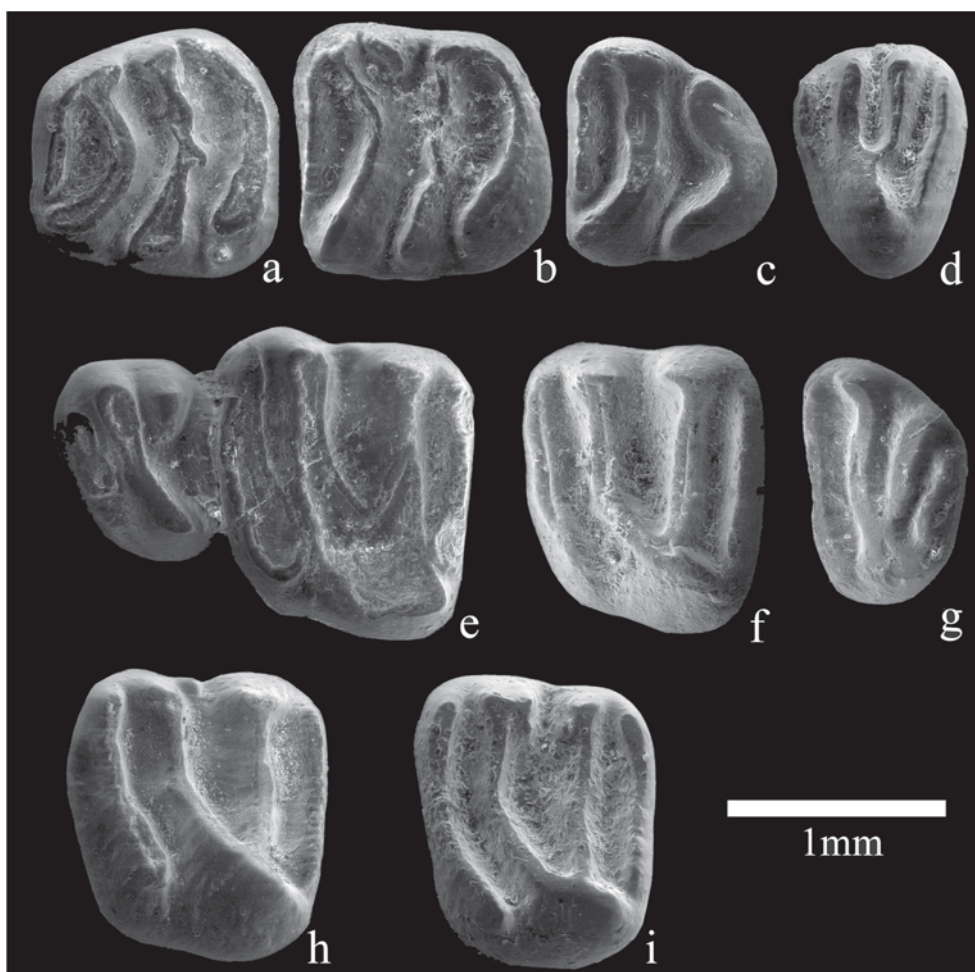


Fig. 8 *Simplomys* sp. from Schnaitheim. **a** m1 (BSPG-1940-VI-1422). **b** m2 (BSPG-1940-VI-1423). **c** m3 (BSPG-1940-VI-1423). **d** P4 (BSPG-1940-VI-1427). **e** Maxillary fragment with P4-M1 (BSPG-1940-VI-

1425). **f** M1 (BSPG-1940-VI-1428). **g** M3 (BSPG-1940-VI-1420). **h** M1 (BSPG-1940-VI-1426). **i** M1 (BSPG-1940-VI-1429b). All teeth are presented in the left orientation (**a**, **c**, **f** and **g** reversed)

showing close affinities to the Spanish bioprovince, such as *Nievella* sp.. *Simplomys* is not recorded in Goldinger Tobel 8 (Bolliger 1996), even if this locality is similar in its composition to Trub-Sältenbach and even if the occurrence of *Simplomys* is now proved further eastward in Schnaitheim. Also, *Pseudodryomys* sp. was mentioned in Goldinger Tobel 1 (Bolliger 1992b), but the material has not been reviewed. Indeed, the lower molars discovered in Goldinger Tobel 8 are not much different from *S. hugi* n. sp. described in the younger fissure fillings from Germany and Switzerland, but the presence of reduced centrolophs in the upper ones precludes any assignment to this new species (which lacks these crests), without completely excluding a phylogenetic relationship between the populations. Pending a revision of the Ramblian *Simplomys* succession in the Iberian Peninsula, the phylogenetic relationships between the species of Central Europe and other European species

remain uncertain. The new species recorded in Glovelier recalls in some points *S. meulenorum* and *S. julii*. Glovelier is the only fauna that documents the *Democricetodon franconicus*–*Megacricetodon collongensis* interval zone of Kälin and Kempf (2009) in Switzerland. The German counterparts of Glovelier (Petersbuch 2 and Erkersthofen 2) contain also species close to *S. hugi* n. sp.. The faunas at the beginning of the deposition of the Brackwater Molasse and OSM lack *Simplomys* at present, although rich localities have been studied in the NAFB (e.g. Ziegler and Fahlbusch 1986; Kälin and Kempf 2009), with the notable exception of Courrendlin-Solé which according to Prieto et al. (2018) contains *S. simplicidens*. *Pseudodryomys* sp. from Eiboden (biozone Tägemaustrasse) reported by Kälin and Kempf (2009) is not taxonomically clear, and we did not recognise *Simplomys* in the fossils of the locality stored in the Natural History Museum in Basel. Finally, Schönenberg represents the youngest occurrence of *Simplomys* outside Western Europe. The fossil site belongs to the OSM C+

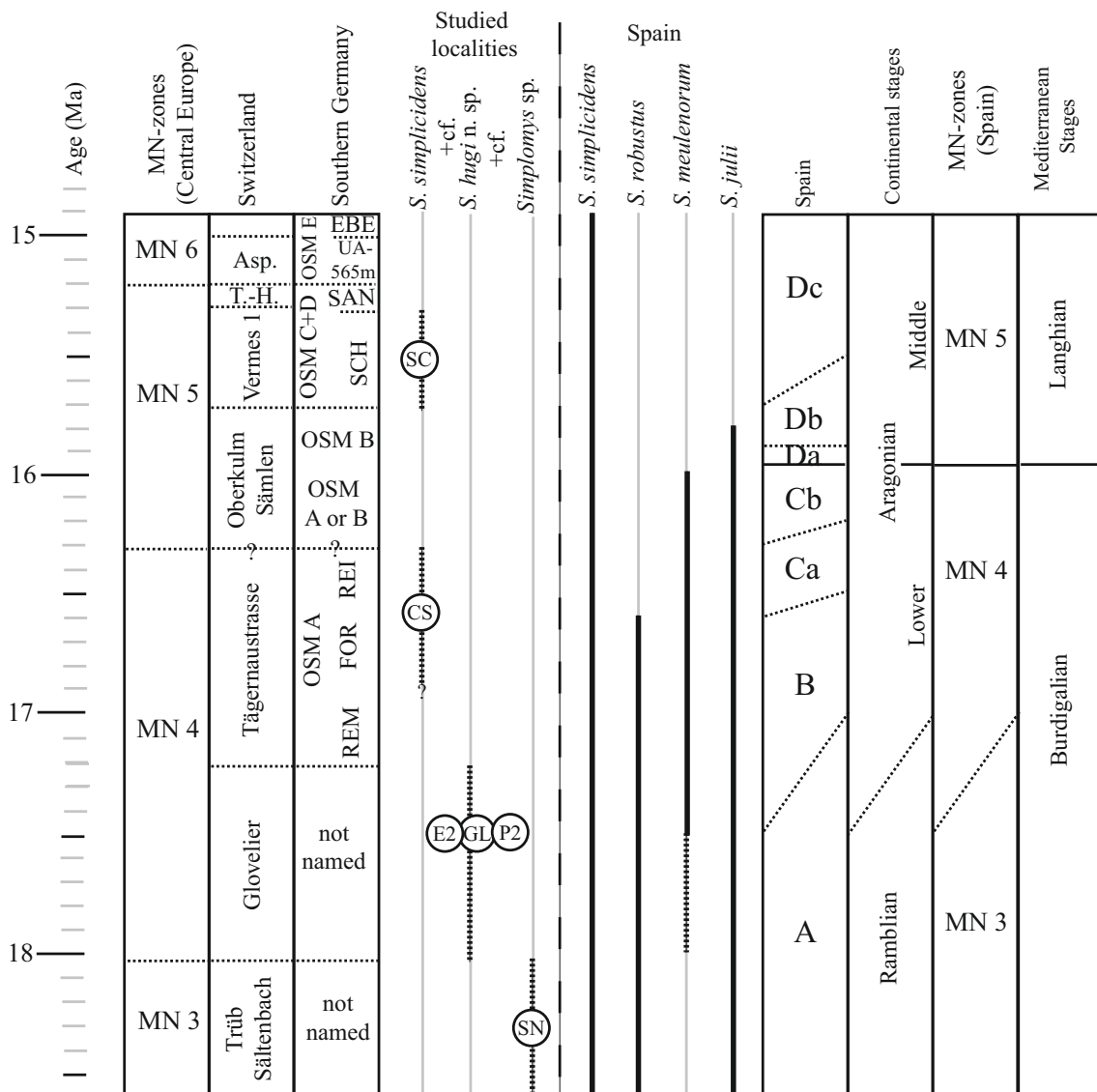


Fig. 9 Stratigraphical distribution of the species of *Simptomys* from Central Europe compared to the record from the Iberian Peninsula. SC Schnaitheim, E2 Erkersthofen 2, GL Glovelier, P2 Petersbuch 2, CS Courrendlin-Solé, SN Schönenberg

D, a biozone which has provided numerous and rich localities in the whole NAFB. Surprisingly, the presence of the genus has not been demonstrated elsewhere in Germany and Switzerland for this biozone. The evolutionary state (size and absence of centrolophs in the M1 and M2) of *S. simplicidens* from Schönenberg and Courrendlin-Solé are in accordance with their stratigraphic position, but the material is not rich enough to clearly unravel the evolutionary trends in Central Europe. Interestingly, Schönenberg is stratigraphically close to the middle Aragonian biozone Db which includes in Spain taxa of central European affinities (García-Paredes et al. 2016, and references therein). At present, *Simptomys* has not been recorded eastward from the Franconian plateau (e.g. Daxner-Höck and Höck 2015; Hír et al. 2016). Pending a detailed revision of the *Simptomys* from France (often only cited in faunal lists), as well as of those from the Ramblian from Spain, the evaluation of the

biostratigraphic/palaeobiogeographic values of the German and Swiss *Simptomys* record at the European scale stays evasive, but the presence of a new species at around 17 Ma in the peri-alpin area indicates that speciation already occurred at this time.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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