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Biochronology of European Miocene Tetraconodontinae (Suidae, Artiodactyla, Mammalia) flowing from recent revision of the Subfamily

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(With 35 figures and 20 tables)

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Abstract

The re-discovery of the type material of *Conohyus simorrensis* and *Parachleuastochoerus valentini* prompted a revision of European tetraconodonts which led to more precise definitions of these taxa, and revealed that there were two additional genera of the subfamily represented in the European fossil record, *Retroporcus* (type species *R. complutensis*) and *Versoporcus* (type species *V. steinheimensis*). Continued research on European tetraconodont fossils housed in various European museums has resulted in a certain amount of reallocation of specimens previously attributed to *Hyotherium*, *Propotamochoerus*, and *Conohyus*. This article reviews tetraconodont material from Switzerland, Germany, Austria, Slovakia and Turkey and includes some undescribed specimens from Spain, focussing on their biostratigraphic implications.

Keywords: Suidae, Tetraconodontinae, Miocene, Biostratigraphy, Europe

Introduction

A profound revision of the suid subfamily Tetraconodontinae was rendered necessary following the re-discovery of the original collections of the species *Sus simorrensis* Lartet, 1851 and *Sus valentini* Filhol, 1882 (Pickford 2013a, 2013b, 2014; Pickford & Laurent 2014) (See section on Systematic Palaeontology).

Firstly, Lartet's (1851) sample of fossils from Villefranche d'Astarac, the type locality of *Sus simorrensis*, contains two tetraconodont taxa, *Conohyus simorrensis* (Lartet, 1851) and *Retroporcus matritensis* (Golpe-Posse, 1972) (Pickford & Laurent 2014). Many descriptions of *Conohyus simorrensis* prior to 2010 include specimens of both of

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these taxa, but several authors have noticed that the species, as understood since Stehlin's (1899–1900) monograph, comprises a greater range of morphometric variation than is normally encountered in suids, and this was articulated as indicating the presence of two subspecies in the samples: *Conohyus simorrensis simorrensis* (Lartet, 1851) and *Conohyus simorrensis goeriachensis* Van der Made, 1998, the latter a junior synonym of *Hyotherium soemmeringi matritensis* Golpe-Posse, 1972 (Pickford & Laurent 2014).

Secondly, the recognition of the holotype of *Sus valentini* from St Gaudens, France (Pickford 2014) in the old collections of the Muséum National d'Histoire Naturelle, Paris, where it had been mis-labelled, led to a reappraisal of medium sized European tetraconodonts, and it was found that a substantial quantity of specimens of this species from France and Spain had been misattributed to other taxa, mainly *Propotamochoerus palaeochoerus* (Kaup, 1833) or *Conohyus simorrensis* (*e.g.,* Golpe-Posse 1972; Alba *et al*. 2006; Van der Made *et al*. 2014). The same applies to some fossils from Switzerland, Germany and Austria.

The aim of this contribution is to reassess Middle and Late Miocene suid material from Switzerland, Germany, Austria, Spain, Turkey and Slovakia and to discuss its biochronological implications. Other examples of misidentified fossils will undoubtedly be uncovered by continued research and there remain several samples that are inadequately represented which renders definitive identification difficult. The approach adopted in this paper is a site by site description and biostratigraphic analysis rather than a taxonomic revision which has already been done (Pickford 2013a, 2013b, 2014; Pickford & Laurent 2014). A summary taxonomy of European tetraconodonts is provided in the Systematic Palaeontology section.

Material and Methods

Fossils examined are from localities in Austria, Croatia, France, Germany, Hungary, Romania, Poland, Portugal, Serbia, Slovakia, Spain, Switzerland and Turkey (Fig. 1).

Tetraconodont fossils are housed in many institutions in Europe (see abbreviations below).

CCECL – Centre de Conservation et Etudes des Collections, Lyon

DPZ – Department of Palaeontology, University of Zaragosa

FSL – Faculty of Science, University of Lyon I

GBW – Geologische Bundesanstalt, Wien

GPIT – Geology and Palaeontology Institute, Tübingen

HLMD – Hessisches Landesmuseum, Darmstadt

IPS – Institut Català de Paleontologia Miquel Crusafont, Sabadell

IPUW – Institute of Palaeontology, University of Wien

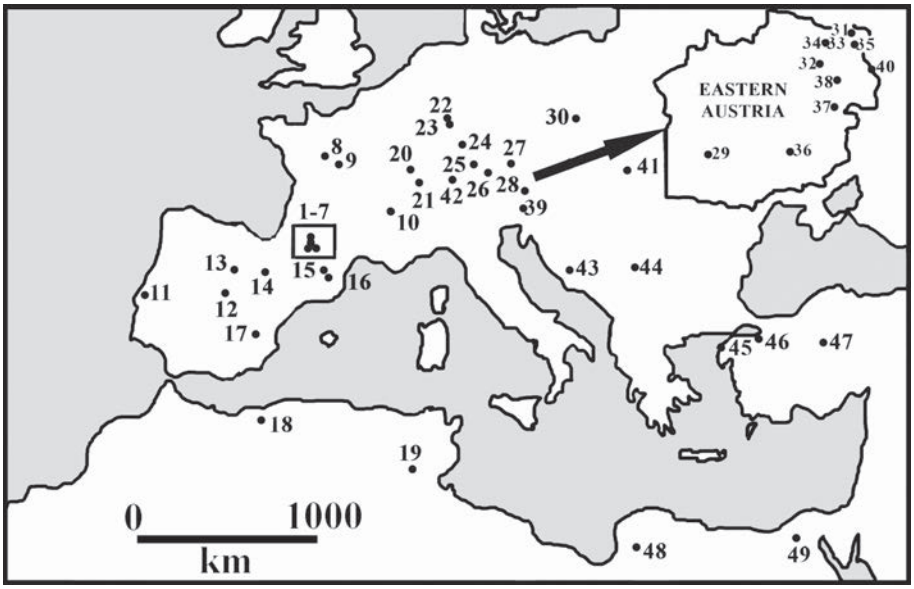

Fig. 1. Location of selected European and North African tetraconodont localities. 1) Malartic, 2: Sansan, 3: Simorre, 4: Villefranche d'Astarac, 5: Bonnefond, 6: Le Fousseret, 7: Saint Gaudens (Valentine), 8: Lublé, Hommes, 9: Channay, Pontlevoy, 10: La Grive-Saint-Alban, 11: Fonte do Pinheiro, Azambujeira, 12: Carpetana, Puente de Vallecas, Alhambra, Somosaguas, 13: Montejo de la Vega, 14: El Buste, La Ciesma, Molina de Aragon, 15: St Quirze, 16: Can Llobateres, Can Ponsic, Santiga, 17: Mira, 18: Bou Hanifia (Dublineau), 19: Beglia, 20: Charmoille, Aargau, 21: La Chaux-de-Fonds, 22: Gau-Weinheim (Wiesberg), 23: Esselborn, Eppelsheim, 24: Steinheim, Melchingen, Salmendingen, 25: Breitenbrunn, Kleineisenbach, Wartenberg, Hinterauerbach, 26: Urlau, Tutzing, 27: Pischelsberg, 28: Göriach, 29: Au, 30: Przeworno, 31: Klein Hadersdorf, 32: Atzelsdorf, 33: Mariathal, 34: Hollabrunn, 35: Gaiselberg, 36: Gratkorn, 37: Pitten, 38: Eichkogel, 39: Rosenthal, 40: Neudorf, 41: Rudabanya, 42: Elgg, 43: Lucane, 44: Mala Miliva, 45: Alçitepe (Nuri Yamut), 46: Paşalar, 47: Bâlâ, 48: Sahabi, 49: Wadi Natrun. (See also VAN DER MADE *et al*. 2014).

MAFI – Museum of the Hungarian Geological Institute, Budapest

MNCN – Museo Nacional de Ciencias Naturales, Madrid

MNHN – Muséum National d'Histoire Naturelle, Paris

MSIM – Museo San Isidro, Madrid

NMA – Naturmuseum Augsburg

NHMB – Natural History Museum, Basel

NHMUK – Natural History Museum of the United Kingdom, London

NHMM – Natural History Museum, Mainz (Naturhistorisches Museum Mainz / Landessammlung Fur Naturkunde Rheinland-Pfalz)

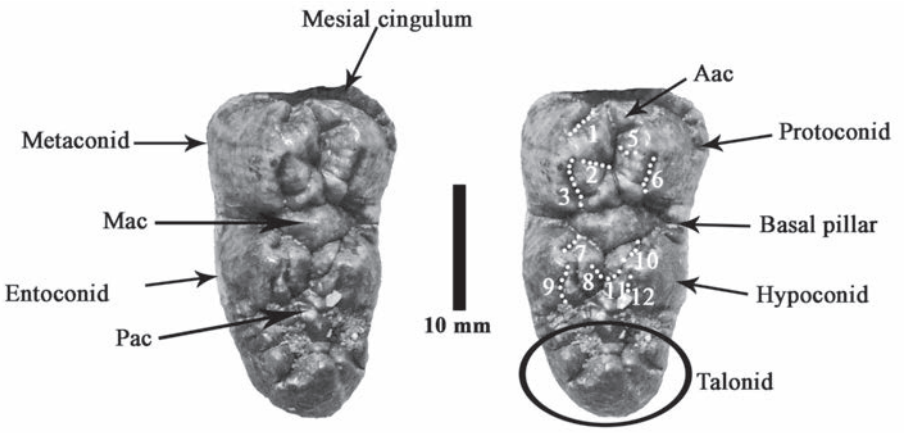

Fig. 2. Dental nomenclature of unworn right m/3 of *Parachleuastochoerus valentini* from Hinterauerbach, Germany. Dotted lines denote the Furchen which are numbered according to the scheme of HÜNERMANN (1968). These Furchen and the lesser wrinkles soon wear away with use, and are therefore usually only clearly visible on unworn specimens (Aac: Anterior accessory cusplet, Mac: Median accessory cusplet, Pac: Posterior accessory cusplet) (stereo occlusal views).

NHMW – Naturhistorisches Museum, Wien

PIMUZ – Palaeontology Institute of the Museum of the University of Zürich

SMF – Senckenberg Institute Frankfurt

SMNS – Staatliches Museum für Naturkunde, Stuttgart

SNMK – Staatliches Naturkundemuseum Karlsruhe (HKMS in HEISSIG 1989)

SNSB-BSPG – Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatsammlung für Paläontologie und Geologie, München

UMJGP (Universalmuseum Joanneum Graz Geologie und Paläontologie) (in previous literature: LMJG – Landesmuseum Joanneum, Graz)

Material studied and imagery

The fossils examined are listed in the tables of measurements. Images were captured with a Sony Cybershot, 18.2 megapixel camera and treated with Photoshop Elements 3 to remove unwanted background and to optimise contrast. Scales were added manually.

Measurements of teeth were made with sliding calipers to the nearest 0.1 mm. Cusp nomenclature is based on the tribosphenic system of OSBORN & GREGORY (1907), with the grooves (Furchen) numbered according to the scheme of HÜNERMANN (1968) and PICKFORD (1988). VAN DER MADE (1996) stressed the importance of crests on the main cusps.

Dental terminology

In this paper, lower case letters (c – canine, d – deciduous molar, i – incisor, p – premolar, m – molar) signify lower teeth, whereas upper case letters (C, D, I, P, M) signify upper teeth. The meristic position is given beneath the forward slash for lower teeth and above the forward slash for upper teeth (*i.e.,* the forward slash denotes the occlusal surface). The letters "m" or "f" associated with the canine, denote male and female respectively. Thus c/m signifies a lower male canine, D4/ signifies the upper 4th deciduous molar, p/3 signifies the lower third premolar; M1/ the first upper molar and so on. This system of presentation, even though somewhat redundant (because lower case or upper case letters denote the lower or upper tooth row, as does the forward slash relative to the meristic position), alerts the author and the reader about typographical errors (for example if a "c" is accidentally typed "C") because the meristic position relative to the forward slash provides sounder evidence about the tooth row from which the specimen came.

Systematic Palaeontology

Family Suidae GRAY, 1821

Subfamily Tetraconodontinae LYDEKKER, 1876

Genus *Conohyus* PILGRIM, 1925

Type species: *Sus simorrensis* LARTET, 1851 as designated by PILGRIM (1925, 1926)

Diagnosis: Tetraconodont suids in which the anterior premolars (p/1, p/2, P1/, P2/) are not vertically offset in the jaw with respect to the p/3 and P3/, crowns of anterior premolars slightly sectorial without marked mesial and distal buccal expansion and with pointed main cusp, anterior premolars markedly smaller than P3/ and P4/; occlusal surface of talonid of m/3 slightly twisted with respect to the surface of the anterior lophids, distal root of m/3 slightly inclined buccally, talonid cusp positioned slightly buccal of the midline of the tooth; M3/ with posterior accessory cusplet slightly to the lingual side of the midline of the crown, largely posterior to the hypocone; dentine-enamel junction of the molars have relatively low relief (dentine exposure occurs with medium wear); lower male canines scrofic in section with shallow lingual and buccal longitudinal gutters and a prominent longitudinal ridge of cementum on the enamel-free distal surface (from PICKFORD & LAURENT 2014).

Other species included: *Conohyus doati* (LARTET, 1851)

Occurrence of the genus: See Annex

Conohyus simorrensis (LARTET, 1851)

Diagnosis: Species of *Conohyus* in which the lower molar row (m/1–m/3) measures *c.* 60 mm and the p/2–p/4 row measures *c.* 56 mm. Anterior premolars somewhat

trenchant, distal root of m/3 slightly buccally tilted. Lower male canine possesses a ridge of cementum on the distal enamel-free surface of the crown (diagnosis from PICKFORD & LAURENT 2014).

It is shown herein that *Sus abnormis* KAUP, 1859, is a junior synonym of *Sus simorrensis* LARTET, 1851, the valid name being *Conohyus simorrensis* (LARTET, 1851).

Occurrence of the species: See Annex

Conohyus doati (LARTET, 1851)

Diagnosis: Large species of *Conohyus*; m/1–m/3 *c.* 68 mm (from PICKFORD & LAURENT, 2014).

Occurrence of the species: See Annex

Genus *Retroporcus* nov. gen.

NB The original publication (PICKFORD & LAURENT 2014) of the genus inadvertently omitted the diagnosis and other information such as included species, occurrence of the genus and the *derivatio nominis*. In order to rectify this omission and to make the name available, the missing data is printed here for the first time.

Type species: *Retroporcus complutensis* PICKFORD & LAURENT 2014

Other species included: *Retroporcus sindiensis* (LYDEKKER, 1884), *?Hyotherium soemmeringi matritensis* GOLPE-POSSE, 1972 (p. 122, 155–156, pl. 6, fig. 6b).

Diagnosis of the genus: Tetraconodont suids in which the anterior premolars are bunodont with low main cusp and are vertically offset in the jaw with respect to the p/3 and P3/; p/2 and P2/ with bucco-distal expansion but weak bucco-mesial expansion; occlusal surface of talonid of m/3 not or only very slightly twisted with respect to the surface of the two anterior lophids, talonid almost in midline of the tooth, distal root of the m/3 almost vertical in the jaw. M3/ with the posterior accessory cusplet shortened mesio-distally and located in the midline of the crown largely buccal to the hypocone, imparting a more rectangular outline to the occlusal surface of the tooth; lower male canines scrofic, shallow buccal and lingual longitudinal gutters and without longitudinal cementum ridge on the enamel-free distal surface.

Occurrence of the genus: Austria (Au bei Aufkenz, Göriach): France (Auverse, Doué-la-Fontaine, Faluns, Lasse, Malartic, Simorre (Rajegats), Villefranche d'Astarac): Germany (Eppelsheim, Gau Weinheim, Laichingen): India (Siwaliks); Pakistan (Siwaliks): Serbia (Mala Miliva): Spain (Puente de Vallecas, Somosaguas): Switzerland (Anwil): Turkey (Paşalar)

Derivatio nominis: *Retro* from the Latin in the sense of "going backward in time", *porcus*, Latin for pig.

Type species: *Retroporcus complutensis* PICKFORD & LAURENT, 2014.

Other species included: *Retroporcus sindiensis* (LYDEKKER, 1884), *Retroporcus matritensis* (GOLPE-POSSE, 1972)

Emended diagnosis of the genus: Tetraconodont suids in which the anterior premolars are bunodont with low main cusp and are vertically offset in the jaw with respect to the p/3 and P3/; p/2 and P2/ with disto-buccal expansion but weak mesio-buccal expansion; occlusal surface of talonid of m/3 not or only very slightly twisted with respect to the surface of the two anterior lophids, talonid almost in midline of the tooth, distal root of the m/3 almost vertical in the jaw. Lower p/2 with distal part of crown largely overhanging the distal root; apex of crown in anterior third of the tooth; M3/ with the posterior accessory cusplet shortened mesio-distally and located in the midline of the crown largely buccal to the hypocone, imparting a more rectangular outline to the occlusal surface of the tooth, tendency for talon root to be doubled; lower male canines scrofic, shallow buccal and lingual longitudinal gutters and without longitudinal cementum ridge on the enamel-free distal surface. Anterior root of the zygomatic arch leaves the face at a shallow angle at the level of the P4/.

Differential diagnosis: *Retroporcus* differs from *Conohyus* by its more bunodont anterior premolars which are vertically offset in the jaws with respect to the posterior premolars; by the more exaggerated overhang of the distal part of the crown over the distal root; by the absence of a longitudinal ridge of cementum on the posterior surface of the lower canines; by its more symmetrical m/3 talonid morphology and root orientation; by the tendency for the talon root to be doubled. *Retroporcus* differs from *Parachleuastochoerus* and *Lophochoerus* by its more bunodont anterior premolars, and its more bucco-lingually inflated posterior premolars and by the anterior position of the root of the zygomatic arch (squared off and located at the level of M2/ in *Parachleuastochoerus*). *Retroporcus* differs from *Sivachoerus* by the absence of accessory cusplets in the P4/ close to the paracone and metacone, by its more bucco-lingually inflated posterior premolars and by its anteriorly positioned root of the zygomatic arch (squared off and located at the level of the M2/ in *Sivachoerus*). *Retroporcus* differs from *Tetraconodon* by the lesser inflation of the posterior premolars. *Retroporcus* differs from *Nyanzachoerus* and *Gerontochoerus* by its more inflated posterior premolars and by the anterior position of the zygomatic arch and by the absence of any elongation of the third molars by addition of extra loph(id)s.

Occurrence of the genus: See Annex

Retroporcus complutensis PICKFORD & LAURENT, 2014

Diagnosis: Species of *Retroporcus* slightly smaller than *Retroporcus matritensis*, with shorter premolars, in particular p/1, m/1–m/3 about 55 mm and p/2–p/4 about 50 mm.

Occurrence of the species: Spain (Somosaguas, Montejo de la Vega), Serbia (Mala Miliva).

Retroporcus matritensis (Golpe-Posse, 1972)

Diagnosis of the species: Species of *Retroporcus* in which the lower molar row is *c.* 60 mm long, lower p/2–p/4 row measures *c.* 66 mm long; upper molar row measures *c.* 55 mm; upper premolar row (P2/-P4/) measures *c.* 50 mm. Anterior premolars bunodont, vertically offset with respect to the level of the p/3 and P3/. Distal root of m/3 not or only slightly buccally tilted. No signs of a ridge of cementum on the distal enamel-free surface of the lower male canine (from Pickford 2014).

Occurrence of the species: See Annex

Genus *Parachleuastochoerus* Golpe-Posse, 1972

Diagnosis: Posterior upper premolars are enlarged compared to the anterior ones, but not broader than the molars, posterior lower premolars enlarged, but not as broad as the molars. P3/ with weak lingual cingulum and small, low disto-lingual cusplet. P1/ and P2/ elongated with slightly swollen distal end. Lower anterior premolars low crowned but slightly trenchant. Zygomatic arches depart abruptly from face at the level of M2/. Posterior choanae positioned far behind the distal ends of M3/. Sagittal crest present on neurocranium. Upper male canine crown has strongly developed mesial and distal crests that end cervically as points overhanging the root. Section of lower male canine verrucosic (from Pickford 2014).

Type species: *Parachleuastochoerus crusafonti* Golpe-Posse, 1972.

Other species included: *Parachleuastochoerus valentini* (Filhol, 1882), *Parachleuastochoerus huenermanni* (Heissig, 1989), P*arachleuastochoerus kretzoii* Fortelius, Amour-Chelu, Bernor & Fessaha, 2005

Occurrence of the genus: See Annex

Parachleuastochoerus crusafonti Golpe-Posse, 1972

Diagnosis: Small species of *Parachleuastochoerus*. Lower molar (m/1–m/3) row *c.* 46 mm long. Length of upper molar (M1/–M3/) row *c.* 43 mm (from Pickford 2014).

Occurrence of the species: See Annex

Parachleuastochoerus valentini (Filhol, 1882)

Diagnosis: Large species of *Parachleuastochoerus*. Upper molar row (M1/–M3/) *c.* 63 – 64 mm. Lower molar (m/1–m/3) row *c.* 68 mm. Upper male canine with exceptionally well developed mesial and distal crista, and reduced root dimensions (from Pickford 2014).

Occurrence of the species: See Annex

Parachleuastochoerus huenermanni (HEISSIG, 1989)

Diagnosis: Medium sized species of *Parachleuastochoerus*. Lower molar row *c.* 55 mm (from PICKFORD, 2014).

Occurrence of the species: See Annex

Parachleuastochoerus kretzoii FORTELIUS, AMOUR-CHELU, BERNOR & FESSAHA, 2005

Diagnosis: Species of *Parachleuastochoerus* slightly larger than the type species *Parachleuastochoerus crusafonti*. Length of lower molar row (m/1–m/3) *c.* 48 mm. Length of upper molar row (M1/–M3/) *c.* 45–46 mm (from PICKFORD 2014).

Occurrence of the species: See Annex

Genus *Versoporcus* PICKFORD, 2014

Type species: *Versoporcus steinheimensis* (FRAAS, 1870)

Diagnosis: Tetraconodont suids in which the zygomatic arches depart from the facial surface of the maxilla at a shallow angle above the P4/; p/3 smaller than the p/4, anterior premolars elongated but narrow and bunodont with prominent anterior and posterior cusplets, with lower p/1 and p/2 endowed with vertical disto-buccal ridges; no vertical offset between the cervical levels of the second and third premolars. Upper P1/ and P2/ with lingual cingular swellings mesially and distally. Mesial and distal cusplets of P1/ and P2/ prominent and slightly buccally positioned. Posterior choanae open up in line with the distal end of the M3/. Lower male canine scrofic (from PICKFORD 2014).

Other species included: *Versoporcus grivensis* (GAILLARD, 1899)

Occurrence of the genus: See Annex

Versoporcus steinheimensis (FRAAS, 1870)

Diagnosis: Small species of *Versoporcus*. Length of M1/–M3/ *c.* 56 mm; length m/1–m/3 *c.* 63 mm (from PICKFORD 2014).

Occurrence of the species: See Annex

Versoporcus grivensis (GAILLARD, 1899)

Diagnosis: Large species of *Versoporcus* in which the anterior premolars and the third molars are larger than those in *Versoporcus steinheimensis* while the posterior premolars have similar dimensions. Length M1/–M3/ *c.* 62 mm, length m/1–m/3 *c.* 65 mm (from PICKFORD 2014).

Occurrence of the species: See Annex

Genus incertae sedis.

Gen. indet. *antediluvianus* (KAUP, 1833)

Occurrence of the species: Eppelsheim, Germany

Locality by locality analysis of fossil suids

AUSTRIA

Atzelsdorf

DAXNER-HÖCK & BERNOR (2009) identified several fossil suid specimens from Atzelsdorf as *Parachleuastochoerus kretzoii* FORTELIUS *et al*., 2005, a species defined at Rudabánya, Hungary. Other suid specimens were attributed to *Albanohyus* cf. *pygmaeus* and Suidae *incertae sedis*. Examination of the Atzelsdorf material at the Naturhistorisches Museum, Vienna, reveals that there are three canines (two lower, one upper) of *Listriodon splendens* previously classed as *incertae sedis*. The *Albanohyus* GINSBURG, 1974, fossils from Atzelsdorf are similar to fossils from La Grive-St-Alban. In addition, there is a tooth (NHMW 2008z0073/0001) labelled as Hyaenidae, which is an upper P3/ of *Parachleuastochoerus kretzoii*.

HARZHAUSER (2009) and DAXNER-HÖCK & GÖHLICH (2009) correlated Atzelsdorf to basal MN 9. The suids from the locality (*Albanohyus pygmaeus*, *Listriodon splendens* and *Parachleuastochoerus kretzoii*) plead for a correlation close to the base of the Vallesian because the two former species of suids are generally characteristic of zone MN 8 but are occasionally reported from MN 9, in Spain, for example (PICKFORD & MORALES 2003). The co-occurrence of the Hipparionine equid *Hippotherium* (WOODBURNE, 2009) and the anchithere *Anchitherium* (DAXNER-HÖCK & BERNOR 2009) support this correlation.

Au bei Aflenz

Three fossils from Au bei Aflenz (VAN DER MADE 1998) (Table 1) are attributed to *Retroporcus matritensis*. The deposits probably correlate to MN 6 although from the point of view of the suid specimens it could be as old as MN 05 or as young as MN 09

Table 1. Measurements (in mm) of suid teeth from Au bei Aflenz, Austria, attributed to *Retroporcus matritensis* (lt – left, rt – right) (Own measurements).

Catalogue	Tooth	Length	Breadth
UMJGP 56693	p/3 lt	23.8	18.8
UMJGP 56694	P3/ lt	19.7	18.8
UMJGP 56696	M2/ rt	19.0	18.4

Eichkogel (sandpit unit)

HELLMUND (1995) attributed an isolated upper molar (NHMW 1954/0102/0001) from Eichkogel (sandpit unit – this addition is to distinguish the mammal locality from the stratigraphically younger locality "Eichkogel top") to *Propotamochoerus palaeochoerus*. The tooth is compatible in dimensions and morphology with *Parachleuastochoerus valentini* and *Versoporcus grivensis*. The slight antero-posterior compression of the lophs suggests that the tooth more likely represents the former than the latter species. The same site yielded an upper third molar (NHMW 1954/0074/0001) and an upper central incisor (NHMW 1954/0074/0002) of *Listriodon splendens*, so it is likely that the locality correlates to the base of MN 9, but not later in the zone as proposed by HELLMUND (1995), HARZHAUSER & BINDER (2004) and DAXNER-HÖCK & BERNOR (2009) who correlated it to MN 11. The mollusc assemblage (on which the Pannonian Lake deposit stratigraphy is established) indicates that the mammal-bearing deposits at Eichkogel belong to the middle Pannonian "zone E", correlating with MN9.

Gaiselberg

The suid material from Gaiselberg was attributed to *Hyotherium palaeochoerus* by ZAPFE (1949) who provided measurements and succinct descriptions of a lower jaw and four isolated teeth. He erroneously reported that the mandible was from the right side. This identification was retained by VAN DER MADE *et al*. (2014), but our own inspection of the fossil reveals the presence of enlarged alveoli for the p/4, indicating tetraconodont affinities. The specimens from Gaiselberg are illustrated for the first time (Figs 3–4, Table 2).

The distal alveoli of the p/4 are partly preserved and reveal that the p/4 had two confluent distal roots and was broader than the m/1, features characteristic of the subfamily Tetraconodontinae. The distal root of m/3 is bucco-lingually broad, and is even subdivided into two moieties. The molar enamel is thick and the cusps are rather low and bulbous, also features found in tetraconodonts rather than suines.

Measurements of the molars and p/4 alveoli indicate affinities with the species *Conohyus doati* (LARTET, 1851) known from Bonnefond, France (the type locality) (PICKFORD & LAURENT 2014), Spain (El Buste, La Ciesma) (AZANZA 1986) and Portugal (Fonte de Pinheiro) (ROMAN 1907) (Fig. 5). Other material of the species has been reported from the Dinotheriensande (Gau-Weinheim) (PICKFORD 2014) and it is known to occur at other sites in Germany (Hammerschmiede) as well as Turkey (Bayraktepe, Alçitepe (Nuri Yamut)) (personal observations).

According to DAXNER-HÖCK & BERNOR (2009) Gaiselberg correlates to MN 9. In other localities, the species *Conohyus doati* is known from MN 8 and MN 9, which is in agreement with this estimate.

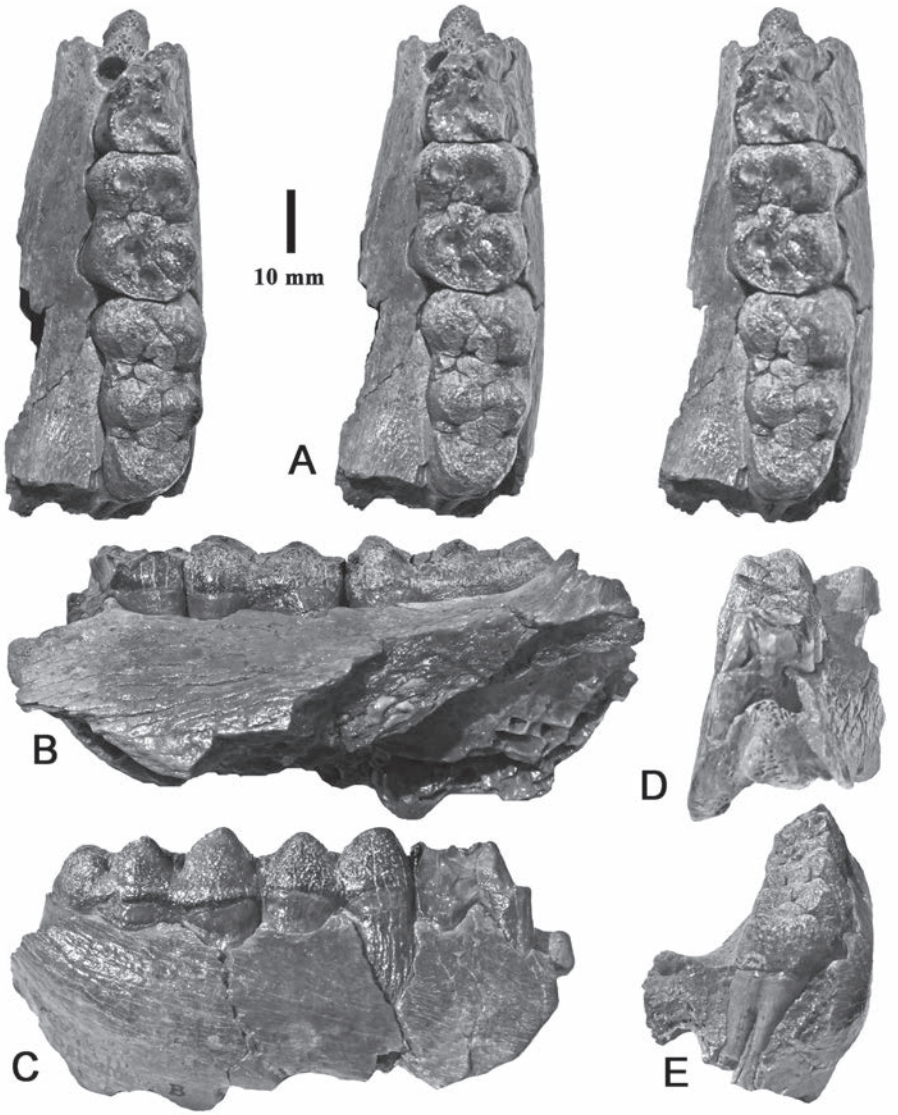

Fig. 3. NHMW 1977-1948, left mandible with m/1-m/3 and distal alveoli of p/4, *Conohyus doati* from Gaiselberg, Zistersdorf, Austria. **A**: stereo triplet occlusal view, **B**: buccal view, **C**: lingual view, **D**: anterior view to show the two posterior alveoli of the p/4 broader than the m/1, E: distal view to show bifurcate distal root of m/3.

Gratkorn

The recently described fauna from Gratkorn, Austria, contains several specimens belonging to the suids *Listriodon splendens* Von Meyer, 1846 and *Versoporcus grivensis*. The tetraconodont was previously attributed to *Conohyus* sp. by Gross *et al*.

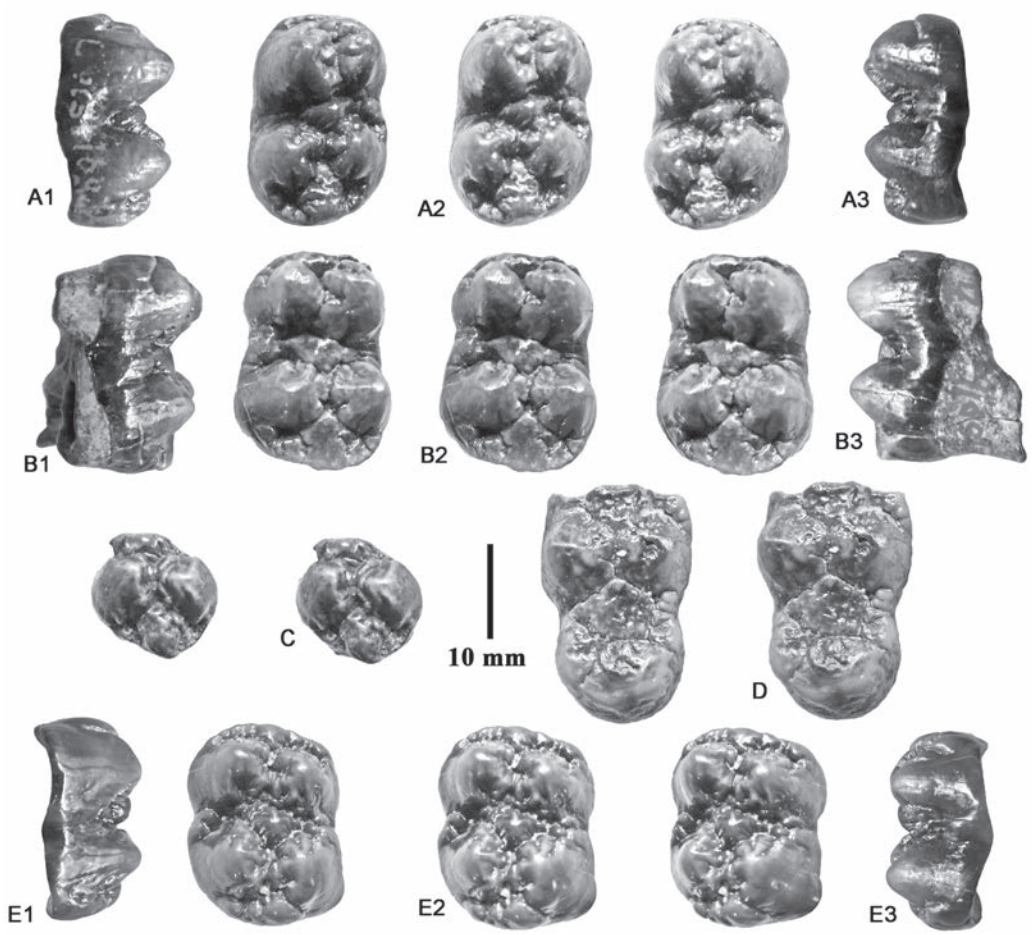

Fig. 4. NHMW 1977-1948, cheek teeth of *Conohyus doati* from Gaiselberg, Austria. **A**: right m/1, lingual, stereo triplet and buccal views, **B**: left m/1, buccal, stereo triplet and lingual views, **C**: lower molar fragment stereo occlusal view, **D**: right m/3 lacking the mesial lophid, stereo occlusal view, **E**: right M2/ buccal, stereo triplet and lingual views.

(2010), but the proportions of the premolars to molars and the morphology of the teeth indicate that the material belongs to *Versoporcus grivensis* (Fig. 6). VAN DER MADE *et al*. (2014) identified the Gratkorn tetraconodont as *Parachleuastochoerus steinheimensis*, but metric analysis indicates a closer agreement with the larger species *Versoporcus grivensis* concerning the dimensions of i/1 and i/2, p/2, p/3, m/2 and m/3 (no upper cheek teeth are known from Gratkorn) (Table 3). The fauna from Gratkorn thus correlates to MN 8 or the base of MN 9, in broad agreement with the assessment of GROSS *et al*. (2010) and VAN DER MADE *et al*. (2014) who placed Gratkorn in MN 7+8 (12–12.0 Ma).

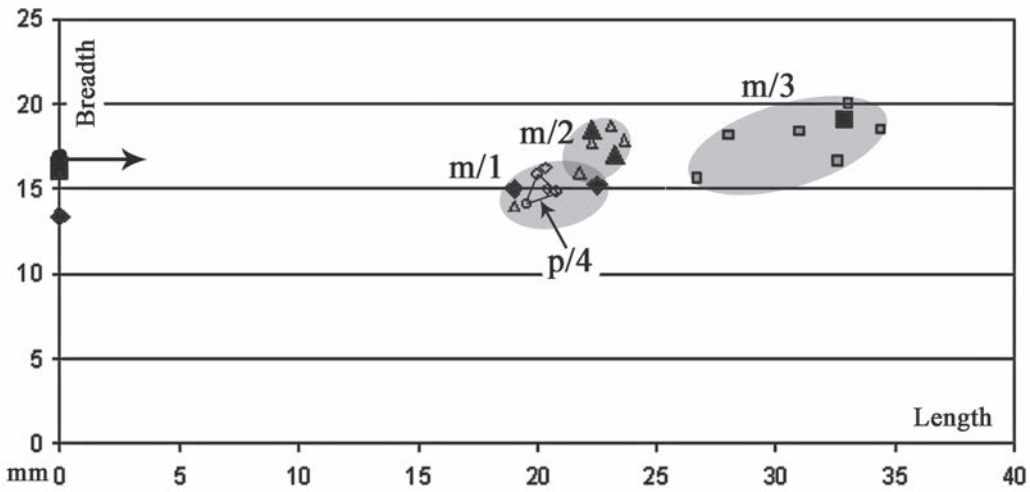

Fig. 5. Bivariate plot of the lower teeth of *Conohyus doati* from France, Spain, Portugal, Germany, Turkey (open symbols) and Gaiselberg, Austria (black symbols). Arrow on the vertical axis shows the estimated breadth of the p/4 in the Gaiselberg specimen of which only the distal alveoli are preserved. Note that it is broader than the m/1s.

Table 2. Measurements (in mm) of the teeth of *Conohyus doati* from Gaiselberg near Zistersdorf, Austria (L = Mesio-distal length, B = Bucco-lingual breadth, lt = left, rt = right, - measurement not possible, *P*. = *Propotamochoerus*) (Own followed by a year are the author's own measurements).

Catalogue		Tooth	L	B	Data source and comments
NHMW 1977/1948/0044	mandible	m/1 lt	19.0	15.0	Own 2014; Zapfe 1949 as rt m/1, *P. palaeochoerus*
NHMW 1977/1948/0045	Fig.4A	m/1 rt	22.5	15.2	Own 2014; Zapfe 1949 as lt m/2, 22.3 × 15 *P. palaeochoerus*
NHMW 1977/1948/0048	Fig. 4C	m/1 rt	-	13.4	Own 2014
NHMW 1977/1948/0044	mandible	m/2 lt	22.3	18.5	Own 2014; Zapfe 1949 as rt m/2, 22.5 × 19 *P. palaeochoerus*
NHMW 1977/1948/0046	Fig. 4B	m/2 rt	23.2	17.0	Own 2014; Zapfe 1949 as rt m/2, 23 × 17 *P. palaeochoerus*
NHMW 1977/1948/0044	mandible	m/3 lt	32.9	19.1	Own 2014; Zapfe 1949 as rt m/3, 31.5 × 19.5 *P. palaeochoerus*
NHMW 1977/1948/0047	Fig. 4D	m/3 rt	-	16.0	Own 2014
NHMW 1977/1948/0049	Fig. 4E	M2/ rt	22.3	19.2	Own 2014; Zapfe 1949 as 23.5 × 19 *P. palaeochoerus*
NHMW 1977/1948/0044	mandible	p/4 lt	-	16.6	Own 2014, estimated from alveolus

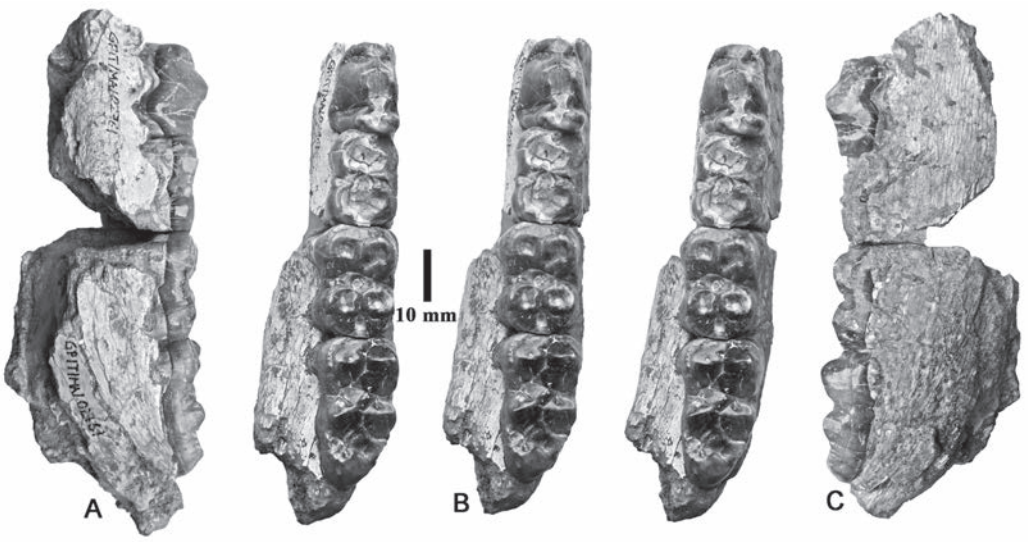

Fig. 6. GPIT MA 2761, left mandible of *Versoporcus grivensis* from Gratkorn, Austria, containing p/4-m/3, **A**: buccal, **B**: stereo triplet occlusal view, C: lingual view.

Table 3. Measurements (in mm) of suid teeth from Gratkorn, Austria (B = bucco-lingual breadth, L = mesio-distal length, lt = left, rt = right, *L. s.* = *Listriodon splendens*, *P. s.* = *Parachleuastochoerus steinheimensis*, *V. g.* = *Versoporcus grivensis*, - measurement not possible) (Own followed by a year are the author's own measurements).

Catalogue	Tooth	L	B	Taxon	Data source and comments
GPIT MA 2744	I1/ lt	30.0	12.6	*L. s.*	Own 2014; VAN DER MADE *et al.,* 2014 as ca. 30.2 × 0
GPIT MA 2735	I1/ rt	29.5	12.5	*L. s.*	Own 2014; VAN DER MADE *et al.,* 2014 as ca. 30.2 × 12,38
GPIT MA 2742	I3/ lt	-	7.0	*L. s.*	Own 2014
GPIT MA 2757	M1/ rt	18.4	17.5	*L. s.*	Own 2014
GPIT MA 2757	M2/ rt	23.0	21.5	*L. s.*	Own 2014
GPIT MA 2757	M3/ rt	26.0	-	*L. s.*	Own 2014
GPIT MA 2757	P4/ rt	15.2	17.0	*L. s.*	Own 2014
UMJGP 203426	p/3 rt	15.8	10.6	*L. s.*	VAN DER MADE *et al.,* 2014
UMJGP 203424	p/4 lt	16.9	12.8	*L. s.*	VAN DER MADE *et al.,* 2014
UMJGP 203425	p/4 rt	17.2	12.7	*L. s.*	VAN DER MADE *et al.,* 2014
UMJGP 203423	m/1 lt	16.3	13.4	*L. s.*	VAN DER MADE *et al.,* 2014
UMJGP 203427	m/3 rt	33.7	20.2	*L. s.*	VAN DER MADE *et al.,* 2014
UMJGP 204679	M1/ rt	17.9	16.5	*L. s.*	VAN DER MADE *et al.,* 2014
UMJGP 210906	P2/ lt	14.3	13.2	*L. s.*	VAN DER MADE *et al.,* 2014
UMJGP 210906	P3/ lt	-	15.3	*L. s.*	VAN DER MADE *et al.,* 2014

Table 3. Continued

Catalogue	Tooth	L	B	Taxon	Data source and comments
UMJGP 210906	P4/ lt	14.8	17.6	*L. s.*	Van der Made *et al.,* 2014
UMJGP 210911/1	M3/ rt	27.9	25.8	*L. s.*	Van der Made *et al.,* 2014
UMJGP 210911/2	M3/ lt	27.7	25.5	*L. s.*	Van der Made *et al.,* 2014
UMJGP 210904	I1/ lt	24.3	11.4	*L. s.*	Van der Made *et al.,* 2014
UMJGP 204651	i/1 rt	6.8	10.0	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204651	i/2 lt	7.5	11.2	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204651	i/2 rt	7.2	11.1	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204653	i/3 lt	9.8	6.2	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204656	i/3 rt	9.4	7.5	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 203651	I1/ rt	13.8	8.8	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204658	I2/ rt	13.2	6.4	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204659	I3/ rt	11.3	5.3	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
GPIT MA 2761	m/1 lt	18.7	14	*V.g.*	Own 2014; Van der Made *et al.*, 2014 as 18.2 × 0, *P. s.*
UMJGP 203698	m/1 lt	17.4	11.9	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204652	m/1 rt	16.6	11.9	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 26/13	m/1 rt	19.3	-	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
GPIT MA 2761	m/2 lt	21.2	17.0	*V.g.*	Own 2014; Van der Made *et al.,* 2014 as 21.9 × 16.5, *P. s.*
UMJGP 203698	m/2 lt	19.9	14.0	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204652	m/2 rt	19.3	13.9	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 26/13	m/2 rt	21.2	16.3	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
GPIT MA 2761	m/3 lt	28.5	16.6	*V.g.*	Own 2014; Van der Made *et al.,* 2014 as 27.3 × 15.9, *P. s.*
UMJGP 203698	m/3 lt	24.2	14.7	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204652	m/3 rt	24.9	14.7	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 26/13	m/3 rt	29.0	16.2	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 203698	p/1 lt	11.8	5.0	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 203698	p/2 lt	17.1	5.9	*V.g.*	Van der Made *et al.,* 2014 as 17.1 × 15.9 *P. s.*
UMJGP 204655	p/2 rt	17.2	6.4	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 26/13	p/2 rt	13.5	-	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204653+203713	p/3 lt	20.2	10.5	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204653	p/3 rt	20.5	10.5	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 26/13	p/3 rt	22.2	-	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
GPIT MA 2761	p/4 lt	18.6	14.0	*V.g.*	Own 2014; Van der Made *et al.,* 2014 as 18.9 × 14.5, *P. s.*
UMJGP 203698	p/4 lt	17.0	11.6	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 204652	p/4 rt	16.2	11.5	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*
UMJGP 26/13	p/4 rt	18.7	-	*V.g.*	Van der Made *et al.,* 2014 as *P. s.*

Göriach

The tetraconodont specimens from Göriach were well described and illustrated by HOFMANN (1893) who attributed them to *Hyotherium soemmeringi* (VON MEYER 1829, 1834). The material was revised by STEHLIN (1899–1900) and THENIUS (1956). More recently VAN DER MADE (1998) erected the subspecies *Conohyus simorrensis goeriachensis* on the grounds that the sample differed from material of *Conohyus simorrensis* (LARTET, 1851) from France and Spain. PICKFORD & LAURENT (2014) realised that the Göriach fossils are morphometrically similar to specimens called *Hyotherium soemmeringi matritensis* by GOLPE-POSSE (1972) and resurrected the name *matritensis* for this species. VAN DER MADE (1998) already noted the similarities between these Spanish and Austrian fossils.

PICKFORD & LAURENT (2014) studied the type series of *Conohyus simorrensis* from Villefranche d'Astarac, France, which had been lost for more than 150 years, and found that it contains remains of two genera of tetraconodont suids. They redefined the genus *Conohyus* (type species *Conohyus simorrensis*) and erected the genus *Retroporcus* for the second form, nominating the species *complutensis* from Somosaguas, Spain, as the type species. The Göriach fossils were transferred to this new genus as the combination *Retroporcus matritensis*. The specimens are similar to other European material from MN 6, being somewhat larger, but morphologically similar to *Retroporcus complutensis* which is known from localities correlated to MN 5 (PICKFORD & LAURENT 2014).

Hollabrunn

The suid fossils from Hollabrunn (NEHYBA & ROETZEL 2004) have been mentioned on three previous occasions but the specimens have never been described in detail. The two maxillae from the site are important because they reveal that the taxon represented is *Parachleuastochoerus valentini* and not *Hyotherium palaeochoerus* (SICKENBERG 1929) nor *Conohyus simorrensis* (PIA & SICKENBERG, 1934) nor *Parachleuastochoerus steinheimensis* (VAN DER MADE *et al*. 2014). The P3/s and P4/s are bucco-lingually more slender than the homologous teeth in *Conohyus* and *Retroporcus*, being compatible with *Parachleuastochoerus* and *Versoporcus* (Fig. 7). The premolar to molar proportions (P4/ broader than M1/) and the morphology of the P3/ and P4/ exclude appurtence of these maxillae to the similar sized suine *Propotamochoerus palaeochoerus*. The M3/s are elongated as in *Parachleuastochoerus*, not as foreshortened and broad as in *Versoporcus* (PICKFORD 2014) (Fig. 8, Table 4). A major difference between *Versoporcus* and *Parachleuastochoerus* concerns the point of departure of the zygomatic arch from the face of the maxilla. In *Versoporcus steinheimensis* the anterior root of the zygomatic arch (the facial crest) sweeps gently backwards from the maxilla starting at the level of the P3/ (CHEN 1984) whereas in *Parachleuastochoerus valentini* it departs from the face of the maxilla at a right angle opposite the front of M1/ (STEHLIN 1899–1900). The facial crests are not preserved on the Hollabrunn maxillae, but the surface of the maxilla above

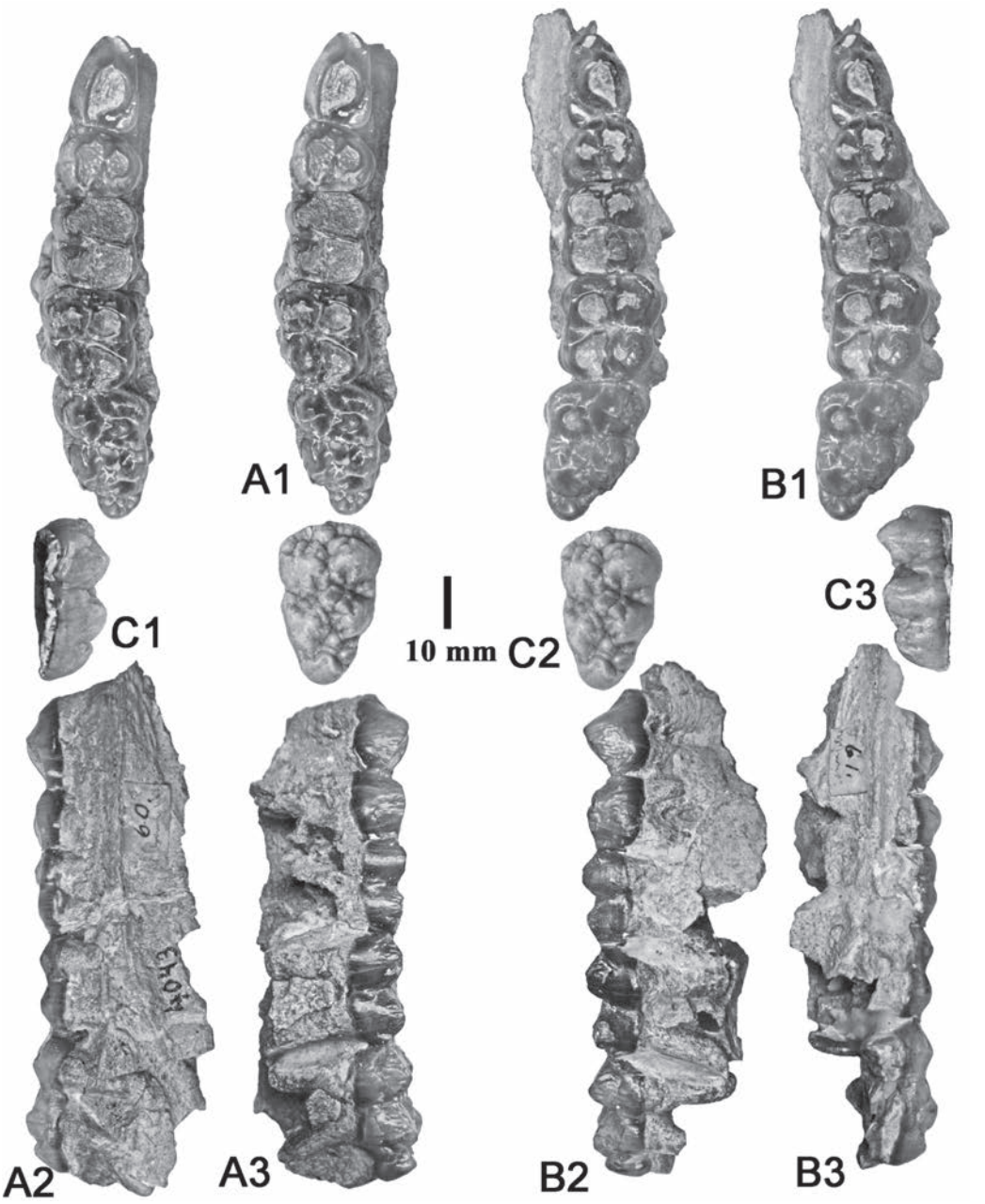

Fig. 7. *Parachleuastochoerus valentini* from Hollabrunn, Austria. **A**: IPUW 4043 (old n° 60) right maxilla containing P3/-M3/, A1: stereo occlusal view, A2: lingual view, A3: buccal view; **B**: IPUW 4043 (old n° 61) left maxilla with P3/-M3/, B1: stereo occlusal view, B2: buccal view, B3: lingual view; **C**: IPUW 168 left M3/, C1: lingual, C2: stereo occlusal, C3: buccal view.

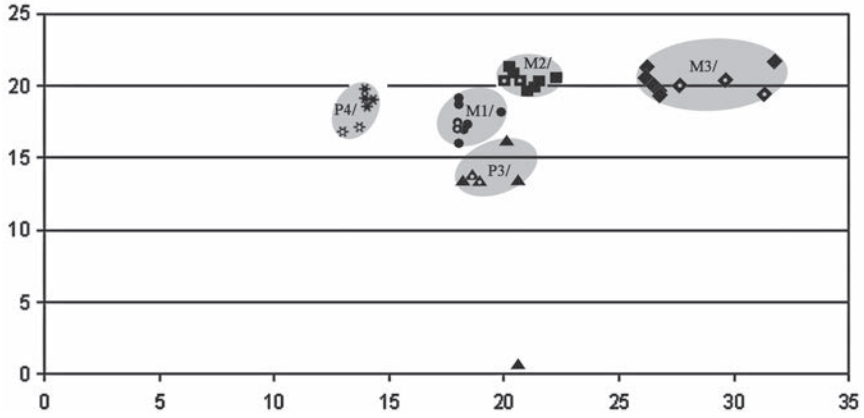

Fig. 8. Bivariate plot of upper cheek teeth of *Parachleuastochoerus valentini* from France (St Gaudens: type locality) and Spain (Mira, St Quirze) solid symbols, and Austria (Hollabrunn) open symbols.

P3/ and P4/ is flat and vertical, showing no sign of a root of a zygomatic arch or a facial crest. From this it is deduced that the root of the zygomatic arch in these maxillae was in a posterior position, as in *Parachleuastochoerus valentini*.

Hollabrunn has also yielded *Listriodon splendens*. The presence of this species in the same site as *Parachleuastochoerus valentini* indicates correlation to MN 8 or the base of MN 9.

Table 4. Measurements (in mm) of the teeth of *Parachleuastochoerus valentini* from Hollabrunn, Austria (lt = left, rt = right) (Own measurements).

Catalogue	Tooth	L	B
IPUW 61	M1/ lt	18.0	17.3
IPUW 4043	M1/ rt	18.0	17.0
IPUW 61	M2/ lt	20.7	20.2
IPUW 4043	M2/ rt	20.0	20.3
IPUW 168	M3/ lt	31.3	19.4
IPUW 61	M3/ lt	27.6	20.0
IPUW 4043	M3/ rt	29.6	20.4
IPUW 61	P3/ lt	18.9	13.4
IPUW 4043	P3/ rt	18.6	13.8
IPUW 61	P4/ lt	13.0	16.7
IPUW 4043	P4/ rt	13.7	17.0

Ilz

Thenius (1956: fig. 24) attributed an isolated p/3 (UMJGP 14140) to *Conohyus simorrensis*. The specimen falls at the low end of the range of metric variation of *Retroporcus matritensis* material from Göriach. The tooth plots within the range of variation of *Conohyus simorrensis*, but its relatively great breadth suggests that it probably belongs to *Retroporcus* rather than to *Conohyus simorrensis*, although, being an isolated tooth, there remains some doubt about its affinities (Van der Made *et al*. 2014).

Klein-Hadersdorf

An isolated suid p/3 was found at Klein-Hadersdorf. The specimen is most likely to represent *Parachleuastochoerus valentini* on account of its dimensions (Table 5) and relatively narrow morphology (Figs 9, 10), but being an isolated tooth other identifications cannot be ruled out. *Listriodon splendens* also occurs at the site, suggesting correlation to basal MN 09.

If the identification of the tetraconodont tooth is valid, then it would suggest a correlation of the site to early MN 9 in agreement with the conclusion of Mein (1986). The age of Klein-Hadersdorf is usually given as Badenian (Steininger 1986) but the correlation is controversial as Piller *et al*. (2000) give the age as MN 6? This locality yielded post-cranial remains attributed to the hominoid primate *Austriacopithecus weinfurteri* Ehrenberg, 1938 (later attributed to *Griphopithecus darwini* Abel, 1902, mainly on the basis of its age as the post-crania of this species are unknown). However, if the Klein Hadersdorf deposits are younger than previously thought, as indicated by the suid fauna, then the hominoid post-cranial remains could be attributed to *Dryopithecus fontani*, as they are compatible in dimensions and morphology with specimens from the type locality, St Gaudens, France, which also happens to be the type locality of *Parachleuastochoerus valentini*.

Mariathal

Suids from the site of Mariathal comprise two taxa, *Propotamochoerus palaeochoerus*, which is relatively common (Bauer 2009) and *Parachleuastochoerus kretzoii* which is represented by an isolated upper molar measuring 13.3 mm mesio-distal by 11.6 mm bucco-lingual (Fig. 9, Table 5).

Table 5. Measurements (in mm) of suid teeth from Klein Hadersdorf, Pitten and Mariathal, Austria (B = Bucco-lingual breadth, L = Mesio-distal length, lt = left, rt = right, *P*. = *Parachleuastochoerus*) (author's own measurements).

Catalogue	Tooth	L	B	Taxon	Locality
IPUW 4047	p/3 rt	23.0	12.3	*P. valentini*	Klein Hadersdorf
IPUW 4042	m/1 lt	19.4	15.0	*P. valentini*	Pitten
IPUW 4042	p/3 lt	23.0	12.4	*P. valentini*	Pitten
IPUW Mariathal	M1/ lt	13.3	11.6	*P. kretzoii*	Mariathal

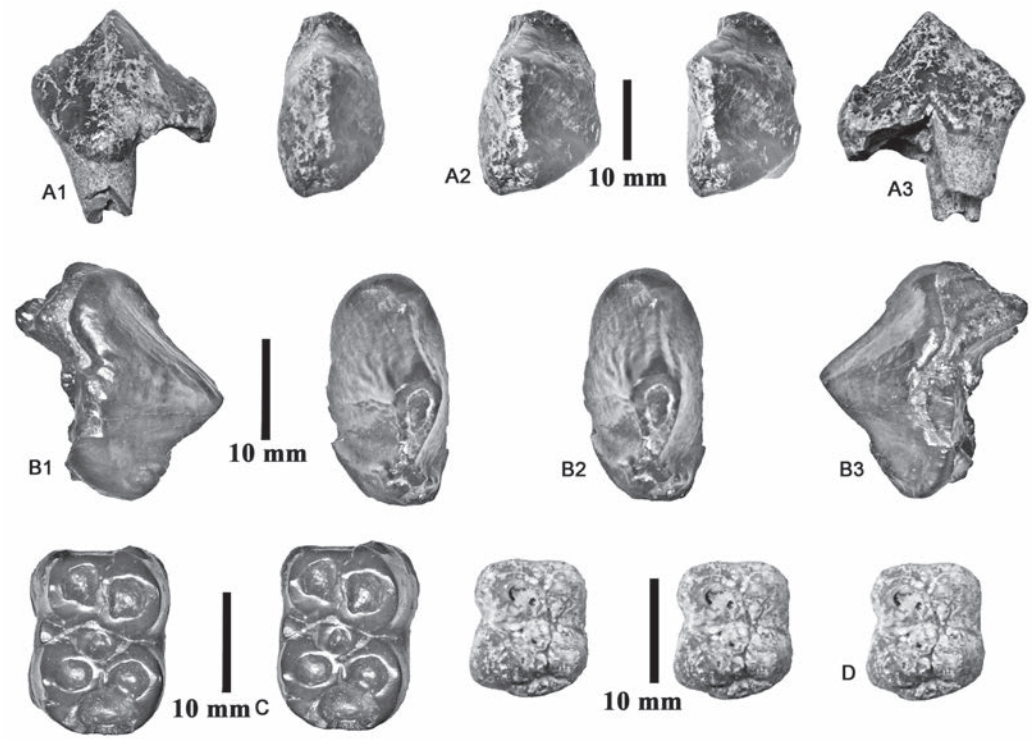

Fig. 9. Tetraconodont teeth from Klein Hadersdorf, Pitten and Mariathal, Austria. **A**: IPUW 4047, right p/3 from Klein Hadersdorf, Austria, tentatively attributed to *Parachleuastochoerus valentini* A1: stereo triplet, A2: buccal, A3: lingual views. **B–C**: *Parachleuastochoerus valentini* from Pitten, Austria. B: IPUW 4042, left p/3, B1: buccal, B2: stereo occlusal view, B3: lingual view; C: IPUW 4042, left m/1, stereo occlusal view; **D**: IPUW Mariathal, left M1/ of *Parachleuastochoerus kretzoii*, stereo triplet of the occlusal view.

Two features indicate that the small Mariathal tooth (uncatalogued M1/ in the IPUW: Table 5) is likely to be an upper molar of a tetraconodont. The premetacrista is well developed, forming a prominent ridge extending from the apex of the cusp towards the lingual end of the median transverse valley, and the broad and well developed distal cingulum. In M1/s of *Parachleuastochoerus* these structures tend to be less well developed, but in any case the character is variable. It is not a D4/ of *Propotamochoerus* (as indicated on its label).

The small Mariathal suid tooth (Table 5) is probably an M1/ of *Parachleuastochoerus kretzoii* a species known from the nearby site of Atzelsdorf (DAXNER-HÖCK & BERNOR 2009) and Rudabánya, Hungary (FORTELIUS *et al*. 2005).

The combined presence at Mariathal of *Propotamocheorus palaeochoerus* and *Parachleuastochoerus kretzoii* indicates a correlation of the site to MN 9. MEIN (1986) already reached this conclusion as did WOODBURNE (2009).

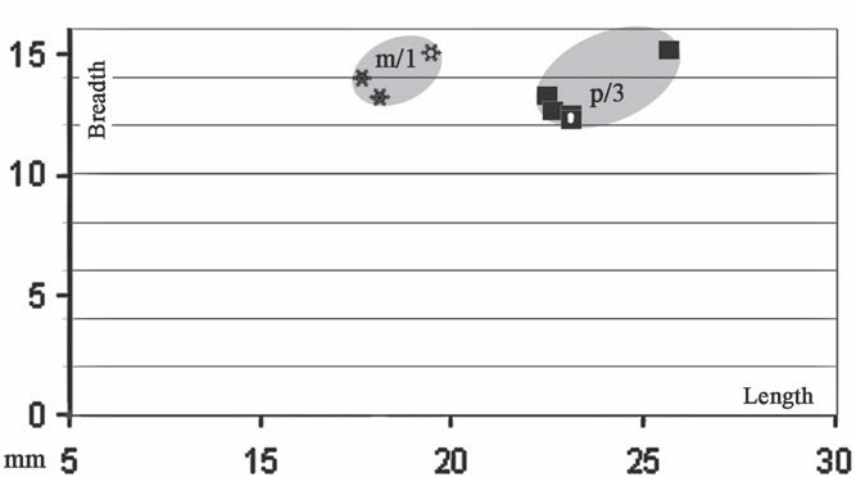

Fig. 10. *Parachleuastochoerus valentini* from Pitten and Klein Hadersdorf, Austria, open symbols, compared with material from France (St Gaudens: type locality), Spain (Mira, St Quirze) and Germany (Kleineisenbach, Tutzing) closed symbols.

Pitten

In their catalogue of Austrian mammals, Pia & Sickenberg (1934) listed a p/3 and m/2 from Pitten, which they attributed to *Conohyus* or *Hyotherium*. The specimens stored at the IPUW have the dimensions and premolar to molar proportions of *Parachleuastochoerus valentini* (Figs 9, 10, Table 5). The age of the site which yielded these fossils is likely to be MN 8 to MN 9. A Karpatian correlation was tentatively suggested by Huttunen (2002) on the basis of a deinothere tooth but this is unlikely as the specimen is compatible in dimensions with material from MN 08 (personal observation). Van der Made (1997) also doubted such an early age for the site.

Rosenthal bei Köpflach

Van der Made (1998) mentioned m/2 and m/3 from Rosenthal bei Köpflach, attributing the specimens to *Conohyus simorrensis goeriachensis*. As concluded by Van der Made (1998) the teeth (UMJGP 1511, 1512) are likely to represent *Retroporcus matritensis* which is the senior name for the species.

GERMANY

Breitenbrunn

Breitenbrunn is the type locality of *Conohyus huenermanni* Heissig. Van der Made (1990, 1998) discussed the material, and transferred it to the genus *Parachleuastochoerus*.

The holotype mandible agrees with the genus *Parachleuastochoerus*. The Breitenbrunn deposits were correlated to MN 6 by HEISSIG (1989) to MN 7/8 by VAN DER MADE (1989) and to MN 9 by BERNOR *et al*. (2004) although ERONEN & RÖSSNER (2007) correlated the deposits to MN 8. The deinotheres from Breitenbrunn indicate a correlation to MN 6 or less likely to MN 7 (personal interpretation of the fossils).

Derndorf

Tetraconodont fossils from Derndorf (MN 6 – Germany) (SEEHUBER 2009) are morphometrically compatible with *Retroporcus matritensis* rather than with *Conohyus simorrensis*. The overhang of the crown beyond the distal root of p/2 is greater than in *Conohyus simorrensis* and the apex of the tooth is in the anterior third of the crown, rather than being almost in its centre as in *Conohyus simorrensis* (PICKFORD 2013a; PICKFORD & LAURENT 2014). The P2/ from Derndorf has the characteristic disto-buccal swellings forming a low complex of ridges as in *Retroporcus*. An upper incisor (NMA 2005/204/1633) from Derndorf identified as *Parachleuastochoerus* by SEEHUBER (2009) could be a deciduous tooth of *Retroporcus* rather than a permanent tooth of *Parachleuastochoerus*.

Dinotheriensande

Fossil tetraconodonts from Eppelsheim, Esselborn and Gau-Weinheim (Wissberg) were recently revised by PICKFORD (2013b). Eppelsheim is the type locality of genus indet. *antediluvianus*, an isolated and moderately worn upper third molar which is basically unidentifiable, meaning that the species name *antediluvianus* is a nomen dubium. PICKFORD (2013b) thought it could be related to *Sivachoerus*.

Six tetraconodont taxa occur in the Dinotheriensande, indicating that the deposits span a considerable period of time (PICKFORD 2013b). The species present range in age from

Table 6. Distribution of Tetraconodontinae in the Dinotheriensande, Rhine Graben, Germany (fossils are listed in PICKFORD 2013b housed at NHMM, HLMD, SMF, SMNS-BSPG).

Locality	Taxon and number of teeth present	Biostratigraphic meaning
Eppelsheim	Cf. *Sivachoerus antediluvianus* – 1	MN 9
	Retroporcus matritensis – 3	MN 6
Esselborn	*Retroporcus matritensis* – 1	MN 6
Gau-Weinheim (Wissberg)	Genus inc. sed. *antediluvianus* – 6	MN 9
	Conohyus doati – 3	MN 7/8-9
	Retroporcus matritensis – 55	MN 6
	Parachleuastochoerus crusafonti – 1	MN 9
	Parachleuastochoerus kretzoii – 11	MN 9
	Parachleuastochoerus huenermanni - 4	MN 7/8-9

MN 6 to MN 9, with a maximum of Middle Miocene specimens at Gau-Weinheim, mixed in with some basal Late Miocene taxa. The distribution of the suid species in the Dinotheriensande is provided in Table 6. A revision of the Deinotheriensande biostratigraphy carried out by Pickford & Pourabrishami (2013; on the basis of Deinotheriidae) and Böhme *et al*. (2012) (on the basis of Cervidae) revealed that previous narrow correlations of the Deinotheriensande to MN 9 can no longer be considered valid because the deposits span the enitre Miocene epoch

Günzberg

Hünermann (1968) described an isolated tooth (NHMB TD 846) from Günzberg as *Hyotherium soemmeringi*. I have not seen the specimen, but a right upper first premolar (length and breadth: 16.1 × 5.5 mm) from the same site (SMNS 16706) belongs to *Conohyus*.

Hammerschmiede

Two upper cheek teeth from Hammerschmiede (Table 7) curated in the SNSB-BSPG can be attributed with some degree of confidence to *Conohyus doati* as the specimens, a P3/ and M3/ are morphometrically typical of this species, the teeth being typically tetraconodont in morphology (inflated P3/, bunodont M3/ with characteristic wrinkled enamel) and larger than *Conohyus simorrensis* and *Retroporcus matritensis*.

Hinterauerbach bei Wartenberg

Two suid teeth from Hinterauerbach bei Wartenberg (SNSB-BSPG 1953–I-484, right m/2–m/3) are compatible in dimensions and morphology with specimens of

Table 7. Measurements (in mm) of teeth from Hinterauerbach bei Wartenberg (1), Kleineisenbach (2) attributed to *Parachleuastochoerus valentini* and from Hammerschmiede (3) attributed to *Conohyus doati* (B = bucco-lingual breadth, L = mesio-distal length, lt = left, rt –right) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Locality	Data source and comments
SNSB-BSPG 1953 I 484a	m/2 rt	19.0	14.0	1	Own 2013; Hünermann 1968 as 19 × 14.2
SNSB- BSPG 1953 1484b	m/3 rt	25.8	15.0	1	Own 2013; Hünermann 1968 as 25.8 × 15.2
SNSB-BSPG 1972 XVI 2201	C1/m lt	26.5	16.8	2	Own 2013
SNSB-BSPG 1972 XVI 2202	C1/m rt	26.0	14.2	2	Own 2013
SNSB-BSPG 1972 XVI 2205	M3/ lt	22.8	16.8	2	Own 2013; Fortelius et al 1996, 22.8 × 17
SNSB-BSPG 1972 XVI 2203	p/3 rt	22.4	13.2	2	Own 2013; Fortelius et al 1996, 22 × 13.1
SNSB-BSPG 1972 XVI 2206	P3/ rt	18.7	14.6	2	Own 2013
SNSB-BSPG 1518	P3/ lt	20.0	15.2	3	Own 2013
SNSB-BSPG 1980 I 5	M3/ rt	27.0	22.4	3	Own 2013

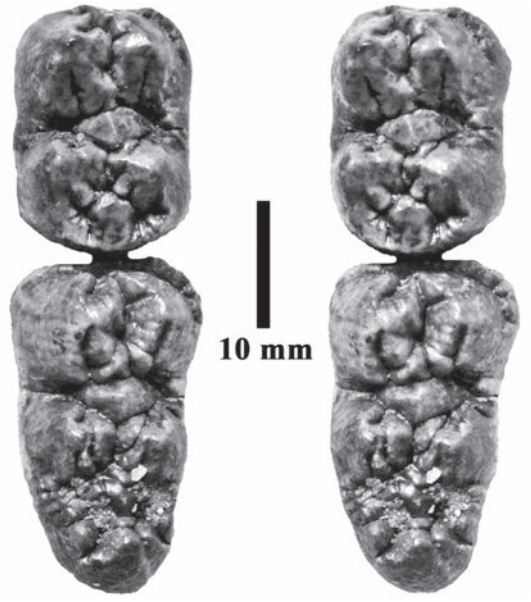

Fig. 11. BSPG 1953 I 484a, b, right m/2-m/3 from Hinterauerbach bei Wartenberg attributed to *Parachleuastochoerus valentini*, stereo occlusal view.

Parachleuastochoerus valentini (Fig. 11). HÜNERMANN (1968) identified these teeth as *Conohyus simorrensis*, but they are too large to belong to this species. The specimens are close in dimensions to *Versoporcus steinheimensis* and *Retroporcus matritensis* (Table 7) but the morphology of the unworn crowns is closer to material of *Parachleuastochoerus valentini*. VAN DER MADE *et al*. (2014) identified the fossils as *Parachleuastochoerus steinheimensis*, which is not impossible, but the symmetry of the m/3 suggests affinities with *Parachleuastochoerus valentini*, rather than with the Steinheim species, which has a twisted talonid cusp and distal root in the m/3.

Hinterauerbach was correlated to MN 9 by HEISSIG (1999) an indication that is supported by the presence of *Parachleuastochoerus valentini* at the locality.

Kleineisenbach

The site of Kleineisenbach yielded several suid teeth which are closest in morphology and dimensions to material of *Parachleuastochoerus valentini* from St Gaudens, France, with the exception of an upper M3/ which is closer in dimensions to *Versoporcus grivensis* (Figs 12, 13) (Table 7). However, the talon of the M3/ is distally elongated as in *P. valentini*, from which it is concluded that it represents the latter species.

FORTELIUS *et al*. (1996) attributed two of these specimens (M3/ and p/3) to *Conohyus simorrensis* and correlated the site to MN 8, which is rather too young to yield this taxon which is normally found in MN 6. However, the proportions of the p/3 and P3/ to the M3/ indicate a close relationship to *Parachleuastochoerus valentini*, an indication supported by the morphology of the upper canines which show the strongly developed

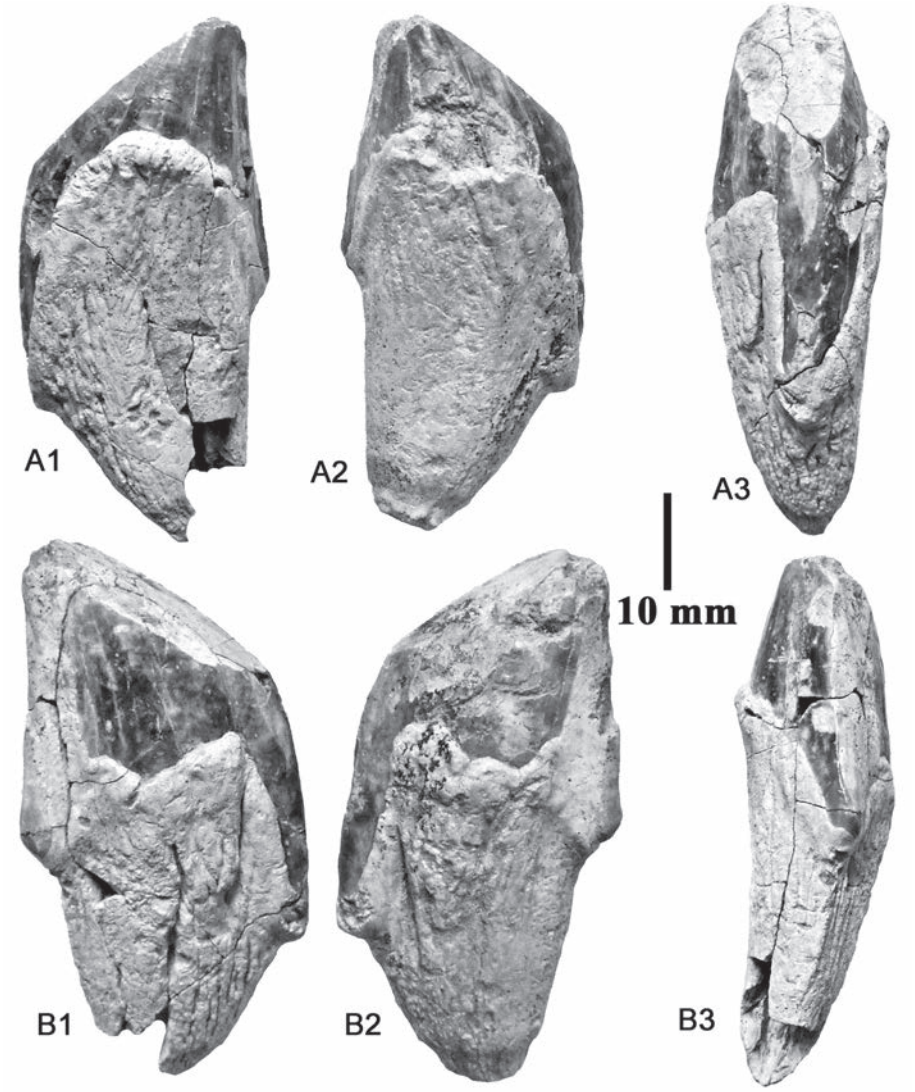

Fig. 12. *Parachleuastochoerus valentini* from Kleineisenbach, Germany. **A**: SNSB-BSPG 1972 XVI 2201, left upper canine A1: mesial, A2: labial, A3: lingual views; **B**: SNSB-BSPG 1972 XVI 2202, right upper canine, B1: lingual, B2: labial, B3: mesial views.

mesial and distal crests overhanging the root, as in material from St Quirze, Spain (Pickford 2014). Correlation of the deposits to MN 8 is supported by the attribution of these teeth to *Parachleuastochoerus valentini* which is known from St Gaudens, France and St Quirze, Spain, among other sites dating from the end of the Middle Miocene and the very base of the Late Miocene.

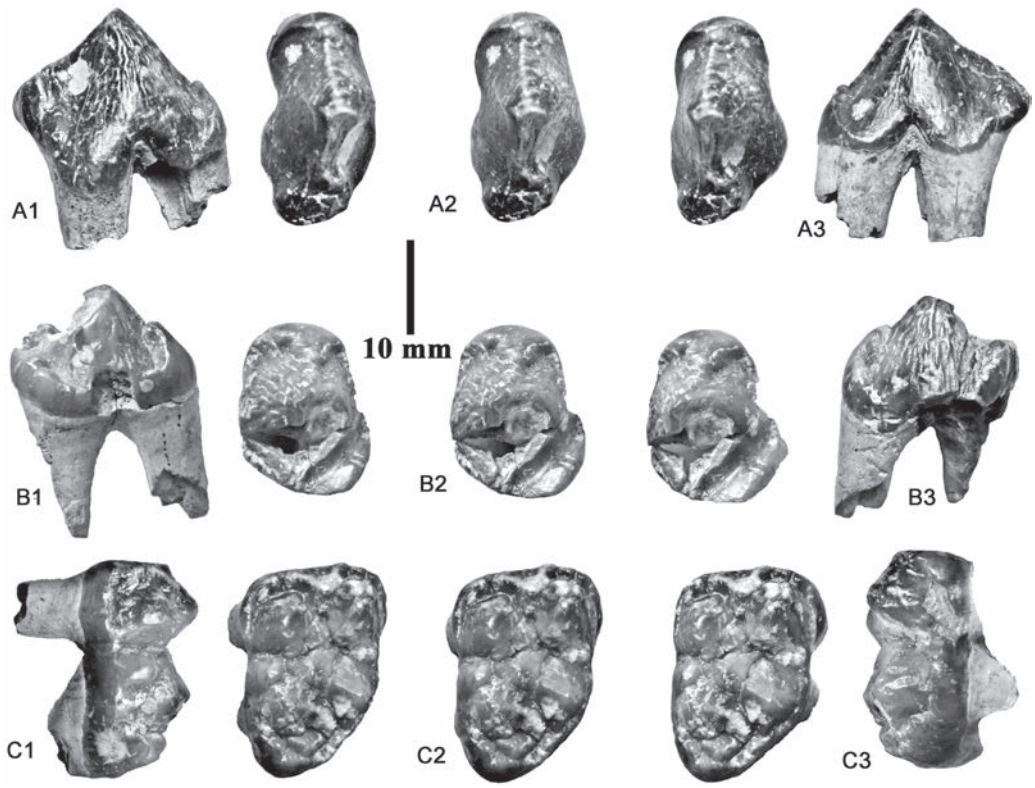

Fig. 13. *Parachleuastochoerus valentini* from Kleineisenbach, Germany. **A**: SNSB-BSPG 1972 XVI 2203, right p/3, A1: buccal, B2: stereo triplet occlusal view, A3: lingual view; **B**: SNSB-BSPG XVI 2204, fragment of left p/3, B1: buccal, B2: lingual views; **C**: SNSB-BSPG XVI 2206, right P3/, C1: lingual, C2: stereo occlusal, C3: buccal views; **D**: SNSB-BSPG 1972 XVI 2205, left M3/, D1: lingual, D2: stereo triplet occlusal view, D3: buccal view.

Laichingen

HÜNERMANN (1968) attributed several teeth from Laichingen to *Conohyus simorrensis*. The proportions of the premolars are closer to those of the species *Retroporcus matritensis* than to *Conohyus simorrensis* (Table 8). Other specimens from the site belong to *Listriodon splendens*, suggesting correlation to MN 6 or MN 7.

Melchingen

The karst deposits at Melchingen have yielded a mixed suid fauna comprising Vallesian and Turolian taxa. The Vallesian specimens are usually brown, whereas the Turolian teeth have white enamel (Fig. 14). The Vallesian suid fauna (Table 9) comprises *Parachleuastochoerus huenermanni* with the possibility of the presence of *Parachleuastochoerus*

crusafonti indicating correlation to MN 9 and possibly MN 10. The Turolian suids comprise *Hippopotamodon major* (Gervais, 1850).

Pischelsberg

Conohyus simorrensis is present at Pischelsberg according to Heissig (1989) who provided measurments of p/4 and m/2 (Table 10). Fortelius *et al*. (1996) listed the species at the site but provided no further details. Hünermann (1968) attributed an M3/ from

Table 8. Measurements (in mm) of suid teeth from Laichingen, Germany (L = Mesio-distal length, B = Bucco-lingual breadth, lt = left, rt = right, - measurement not possible, *L*. = *Listriodon*, *R*. = *Retroporcus*) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Taxon	Data source
GPIT MA 1178-29	M1/ rt	18.0	16.5	*L. splendens*	Own 2014
GPIT MA 2912	m/3 rt	-	18.9	*L. splendens*	Own 2014
GPIT MA 2917	m/1 lt	18.0	13.0	*L. splendens*	Own 2014
GPIT MA 2918	m/2 lt	21.8	16.9	*L. splendens*	Own 2014
SMNS M 20240	I1/	26.3	12.5	*L. splendens*	Hünermann 1968
SMNS M 20241	I1/	28.3	12.4	*L. splendens*	Hünermann 1968
SMNS M 20243	i/2	14.8	11.7	*L. splendens*	Hünermann 1968
SMNS M 20245	c/1	14.0	15.0	*L. splendens*	Hünermann 1968
SMNS M 20239	i/1	7.6	11.5	*R. matritensis*	Hünermann 1968
SMNS M 4867	m/1	17.0	13.7	*R. matritensis*	Hünermann 1968
SMNS M 4867a	p/4	19.4	14.0	*R. matritensis*	Hünermann 1968
SMNS M 4867b	p/4	19.6	14.1	*R. matritensis*	Hünermann 1968

Table 9. Measurements (in mm) of suid teeth from Melchingen (B = bucco-lingual breadth, L = mesio-distal length, lt = left, rt = right, *H*. = *Hippopotamodon*, *P*. = *Parachleuastochoerus*, - measurement not possible) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Taxon	Data source and comments
GPIT MA 2350	I1/ rt	24.0	10.5	*H. major*	Own 2014
GPIT MA 6-6-18	M3/ lt	-	26.8	*H. major*	Own 2014; Hünermann 1968 site erroneously listed as Salmendingen
GPIT MA 1178-1	m/3	-	18.0	*H. major*	Own 2014
GPIT MA 1319	p/4 lt	20.2	15.0	*H. major*	Own 2014
GPIT MA 4983	M3/ lt	-	14.4	*P. huenermanni*	Own 2014
GPIT MA 4985	Mx/ lt	-	15.1	*P. huenermanni*	Own 2014
GPIT MA 4981	p/4 rt	14.0	8.6	*P. crusafonti*	Own 2014

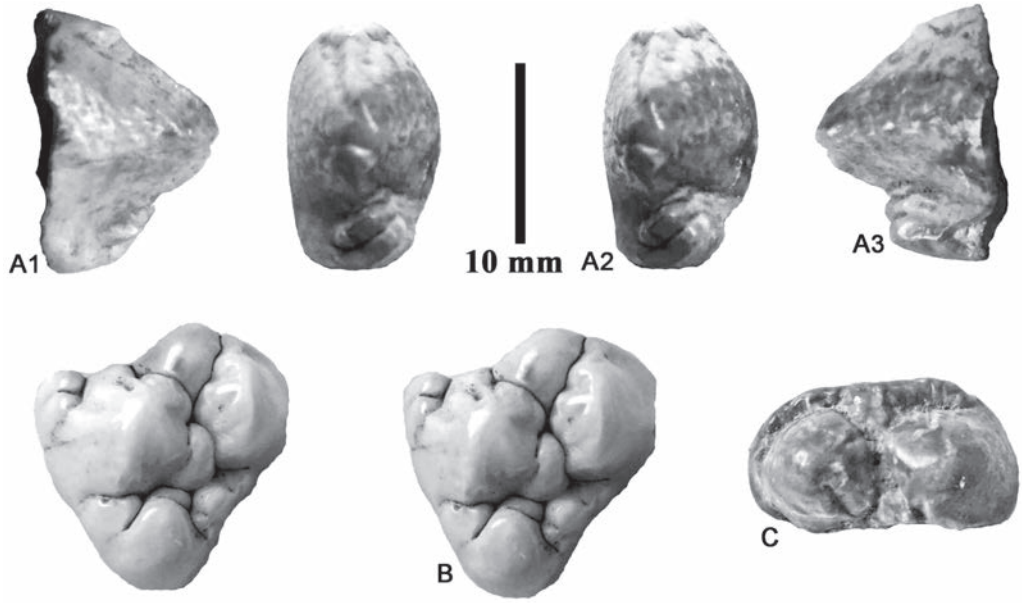

Fig. 14. *Parachleuastochoerus huenermanni* teeth from Melchingen, Swabian Alb, Germany. **A**: GPIT MA 4981, right p/4, A1: lingual, A2: stereo occlusal, A3: buccal views; **B**: GPIT MA 4983, distal part of left M3/, stereo occlusal view; **C**: GPIT MA 4985, anterior loph of left upper molar fragment occlusal view.

the locality to *Hyotherium soemmeringi*, but it is more likely to belong to *Conohyus simorrensis* along with the other two teeth mentioned by HEISSIG (1989). Correlation of Pischelberg to MN 7/8 is likely.

Steinheim

Steinheim is an important suid locality due to the relatively complete nature of some of the specimens and the large quantity of teeth that it yielded (FRAAS 1870; STEHLIN 1899–1900; HÜNERMANN 1968; CHEN 1984; VAN DER MADE 1998). It is the type locality of *Chaeropotamus steinheimensis* FRAAS, 1870, which is the type species of *Versoporcus* PICKFORD, 2014. Because of this, Steinheim is a reference locality for understanding the range of variation of the teeth of the species (PICKFORD 2014) (Figs 15–20). For this reason a complete updated list of measurements of teeth of *Versoporcus steinheimensis* is provided in the table of measurements (Table 11). The locality also yielded samples of *Listriodon splendens* and *Choeromorus sansaniensis* LARTET, 1851. The combination of suid taxa at the site indicates correlation to MN 7.

VAN DER MADE (1998) classified the Steinheim fossils in *Parachleuastochoerus steinheimensis* because of their relatively narrow and small premolars. However, the morphology of the molars differs from that of *Parachleuastochoerus valentini* and *Parachleuastochoerus crusafonti*, from which it is concluded that it does not belong to the

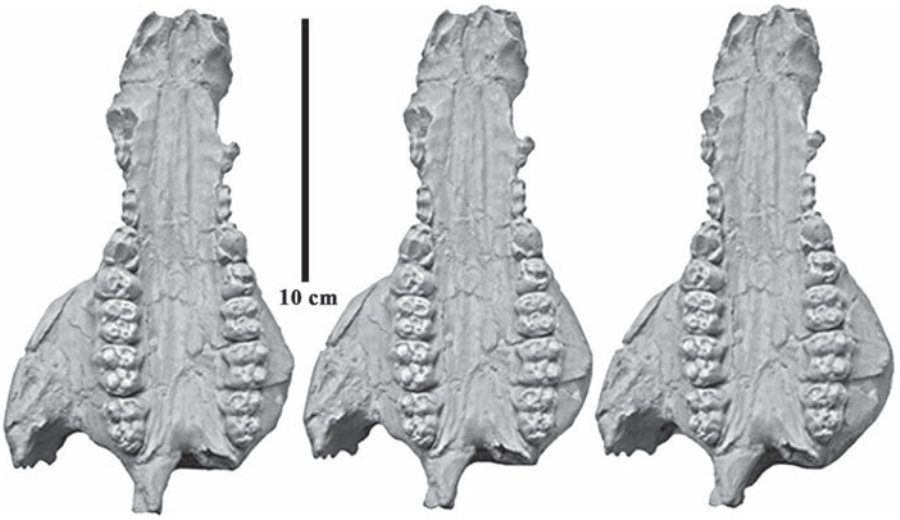

Fig. 15. SMNS M 20223, *Versoporcus steinheimensis* from Steinheim, Germany. Stereo triplet of the palatal view.

Table 10. Measurements (in mm) of the teeth of *Conohyus simorrensis* from Pischelsberg, Germany (B = Bucco-lingual breadth, L = mesio-distal length, lt = left, rt = right) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Data source and comments
SNSB-BSPG 1957 VII 86	M3/ lt	23.8	18.4	Own 2013; HÜNERMANN 1968 as 23 × 18.8 as *Hyotherium soemmeringi*
SNSB-BSPG 1959 I 140	m/2 rt	20.8	15.6	Own 2013; HEISSIG 1989 as 21 × 15.7
SNSB-BSPG 1959 I 140	p/4 rt	19.2	13.4	Own 2013; HEISSIG 1989 as 18.4 × 14.2

Table 11. Measurements (in mm) of suid teeth from Steinheim, Germany (B = Bucco-lingual breadth, L = mesio-distal length, f = female, m = male, lt = left, rt = right, - measurement not possible) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Data source and comments
SMNS M 20224	c/1 lt f	-	-	Own 2010, buccal 8.7
SMNS M 20231	c/1 lt f	10.0	6.3	Own 2010
SMNS M 5280	c/1 lt f	11.0	6.8	Own 2010
GPIT MA 1178-41	c/1 lt m	15.2	12.4	Own 2014; HÜNERMANN 1968 as 14.8 × 11.3
GPIT MA 1178-37	c/1 rt m	16.0	11.8	Own 2014; HÜNERMANN 1968 as 18.7 × 15
SMNS M 4024	C1/ lt m	23.7	17.4	Own 2010
SMNS M 12770b	d/2 rt	12.7	4.6	Own 2010
NHMB Sth 178	d/3 lt	13.3	6.9	Own 2012; HÜNERMANN 1968 as 16.3 × 7

Table 11. Continued

Catalogue	Tooth	L	B	Data source and comments
SMNS M 12770b	d/3 lt	17.4	7.1	Own 2010; HÜNERMANN 1968 as 16.3 × 7
NHMB Sth 178	d/3 rt	13.6	6.8	Own 2012; HÜNERMANN 1968
SMNS M 12770b	d/3 rt	16.2	6.9	Own 2010; HÜNERMANN 1968 as 16.6 × 7.1
SMNS M sans n°	d/3 rt	16.6	6.0	Own 2010
NHMB Sth 178	d/4 lt	19.3	9.3	Own 2012; HÜNERMANN 1968 as 17.6 × 9.6
SMNS M 12770b	d/4 lt	21.7	9.9	Own 2010; HÜNERMANN 1968 as 21.6 × 10.3
NHMB Sth 178	d/4 rt	19.2	9.6	Own 2012; HÜNERMANN 1968 as 17.8 × 9.7
SMNS M 12770b	d/4 rt	21.8	10.2	Own 2010; HÜNERMANN 1968 as 21.7 × 10.3
SMNS M 4972	d/4 rt	-	10.3	Own 2010
SMNS M 12270	D2/ lt	-	6.0	Own 2010
SMNS M 12270	D3/ lt	16	10.8	Own 2010
SMNS M 12270	D3/ rt	15.7	10.9	Own 2010
SMNS M 20225	D3/ rt	15.0	10.3	Own 2010
NHMB Sth 676	D4/ lt	-	11.3	Own 2012
SMNS M 12270	D4/ lt	15.7	13.9	Own 2010; HÜNERMANN 1968 as 14.5 × 13.7
SMNS M 20226	D4/ lt	14.0	12.0	Own 2010; HÜNERMANN 1968 as 13.9 × 12
SMNS M 20227	D4/ lt	15.0	13.5	Own 2010; HÜNERMANN 1968 as 14.9 × 13.5
NHMB Sth 675	D4/ rt	15.0	12.0	Own 2012
SMNS M 12270	D4/ rt	15.5	13.3	Own 2010; HÜNERMANN 1968 as 14.7 × 13.4
SMNS M 4972	D4/ rt	15.0	13.2	Own 2010
SMNS M 4972	D4/ rt	15.0	13.3	Own 2010
SMNS M 20229	i/1 lt	7.0	10.6	Own 2010; HÜNERMANN 1968 as 7.1 × 10.8
SMNS M 8545	i/1 lt	5.6	9.4	Own 2010
NHMB Sth 682	i/2 lt	6.8	10.4	Own 2012; HÜNERMANN 1968 as 6.2 × 10.6
SMNS M 12963	i/2 lt	7.0	-	Own 2010
SMNS M 20230	i/2 lt	6.6	12.2	Own 2010; HÜNERMANN 1968 as 7.5 × 12.6
SMNS M 5280	i/2 lt	7.9	12	Own 2010
GPIT MA 1178-42	i/2 rt	5.0	7.4	Own 2014; HÜNERMANN 1968 as 5.1 × 7.6 di/2
SMNS M 12963	i/2 rt	7.1	10.7	Own 2010; HÜNERMANN 1968 as 7.5 × 0
SMNS M 4024	i/2 rt	8.2	-	Own 2010
GPIT MA 1178-39	m/1 lt	17.5	12.0	Own 2014; HÜNERMANN 1968 as 17.1 × 12.3
GPIT MA 1178-43	m/1 lt	17.6	11.2	Own 2014; HÜNERMANN 1968 as 17.5 × 11
NHMB Sth 178	m/1 lt	15.8	12.0	Own 2012
SMNS M 12770b	m/1 lt	18.0	11.4	Own 2010; HÜNERMANN 1968 as 18.5 × 12.4
SMNS M 13235	m/1 lt	16.6	11.7	Own 2010
SMNS M 4024b	m/1 lt	17.3	12.3	Own 2010

Table 11. Continued

Catalogue	Tooth	L	B	Data source and comments
SMNS M 5280	m/1 lt	17.0	12.0	Own 2010
SMNS M 5280a	m/1 lt	18.7	12.0	Own 2010; Hünermann 1968 as 17.4 × 12.3
GPIT MA 1178-37	m/1 rt	16.8	12.6	Own 2014; Hünermann 1968 as 17 × 12.9
NHMB Sth 679	m/1 rt	18.0	12.2	Own 2012; Hünermann 1968 as 17.3 × 12.3 m/1
NHML M 7829	m/1 rt	17.9	11.9	Own 2012
SMNS M 5280	m/1 rt	18.0	12.2	Own 2010
SMNS M 5280	m/1 rt	-	13.3	Own 2010
SMNS M 5280	m/1 rt	17.2	11.9	Own 2010
SMNS M 5280b	m/1 rt	18.6	12.2	Own 2010; Hünermann 1968 as 17.6 × 12.1
GPIT MA 1178-39	m/2 lt	19.0	14.0	Own 2014; Hünermann 1968 as 18.7 × 13.9
GPIT MA 1178-8	m/2 lt	-	13.0	Own 2014
SMNS M 13235	m/2 lt	19.0	14.0	Own 2010
SMNS M 5280	m/2 lt	20.3	14.0	Own 2010
SMNS M 5280a	m/2 lt	20.3	14.6	Own 2010; Hünermann 1968 as 20.9 × 14.9
GPIT MA 1178-37	m/2 rt	20.0	14.1	Own 2014; Hünermann 1968 as 19.7 × 15.2
GPIT MA 1178-38	m/2 rt	18.0	13.5	Own 2014; Hünermann 1968 as 18.2 × 13.9
GPIT MA 1178-44	m/2 rt	19.7	14.0	Own 2014; Hünermann 1968 as 19.4 × 14.1
SMNS M 5280	m/2 rt	20.0	13.9	Own 2010
SMNS M 5280b	m/2 rt	21.0	14.7	Own 2010; Hünermann 1968 as 20.9 × 14.8
GPIT MA 1178-39	m/3 lt	25.0	14.9	Own 2014; Hünermann 1968 as 25.4 × 15
NHMB Sth 681	m/3 lt	24.2	14.5	Own 2012; Hünermann 1968 as 24.2 × 14.7
SMNS M 5280	m/3 lt	26.3	14.0	Own 2010
SMNS M 5280a	m/3 lt	26.4	15.0	Own 2010; Hünermann 1968 as 26.4 × 15.4
GPIT MA 1178-37	m/3 rt	-	15.0	Own 2014; Hünermann 1968 as 0 × 15.5
NHMB Sth 680	m/3 rt	25.2	14.6	Own 2012; Hünermann 1968 as 25 × 14.9
SMNS M 5280	m/3 rt	26.5	-	Own 2010
SMNS M 5280b	m/3 rt	26.4	15.2	Own 2010; Hünermann 1968
SMNS M 20223	M1/	16.4	15.4	H. 1968
NHMB Sth 676	M1/ lt	16.0	14.0	Own 2012
SMNS M 4972	M1/ lt	15.9	14.7	Own 2010
NHMB Sth 133	M1/ rt	16.3	15.0	Own 2012; Hünermann 1968 as 14.4 × 15
SMNS M 20228	M1/ rt	17.1	14.4	Own 2010; Hünermann 1968 as 16.8 × 14.3
SMNS M 20223	M2/	17.8	17.9	Hünermann 1968
SMNS M 20223	M2/	17.9	17.9	Hünermann 1968
SMNS M 5280	M2/ rt	17.6	16.0	Own 2010
SMNS M 5280	M2/ rt	-	17.9	Own 2010

Table 11. Continued

Catalogue	Tooth	L	B	Data source and comments
SMNS M 20223	M3/	20.9	17.4	HÜNERMANN 1968
SMNS M 20223	M3/	20.4	17.7	HÜNERMANN 1968
NHMB Sth 132	M3/ lt	21.1	18.0	Own 2012; HÜNERMANN 1968 21.4 × 17.3
NHMB Sth 180	M3/ lt	20.8	17.2	Own 2012; HÜNERMANN 1968 as 20.7 × 0
SMNS M 5280	M3/ rt	22.3	17.1	Own 2010
GPIT MA 1178-39	p/1 lt	12.8	5.0	Own 2014; HÜNERMANN 1969 as 12.9 × 5
NHMB Sth 181	p/1 lt	14.1	5.1	Own 2012; HÜNERMANN 1968 as 14 × 5.2 P1/
SMNS M 12963	p/1 lt	-	5.0	Own 2010
SMNS M 13235	p/1 lt	12.4	4.7	Own 2010
SMNS M 5280	p/1 lt	13.0	5.0	Own 2010
GPIT MA 1178-37	p/1 rt	13.4	4.9	Own 2014; HÜNERMANN 1969 as 13.9 × 5
SMNS M 5280	p/1 rt	13.4	5.1	Own 2010
GPIT MA 1178-39	p/2 lt	14.6	5.7	Own 2014; HÜNERMANN 1968 as 15.2 × 5.9
SMNS M 12963	p/2 lt	15.3	5.3	Own 2010; HÜNERMANN 1968
GPIT MA 1178-37	p/2 rt	14.8	5.5	Own 2014; HÜNERMANN 1968 as 15 × 5.8
NHMB Sth 683	p/2 rt	15.2	5.7	Own 2012; HÜNERMANN 1968 as 15,2 × 5,9
SMNS M 12963	p/2 rt	-	-	Own 2010
SMNS M 5280	p/2 rt	15.1	5.1	Own 2010
GPIT MA 1178-39	p/3 lt	19.6	11.0	Own 2014; HÜNERMANN 1968 as 19.3 × 11
SMNS M 13235	p/3 lt	19.3	10.0	Own 2010
GPIT MA 1178-37	p/3 rt	19.0	10.0	Own 2014; HÜNERMANN 1968 as 19.2 × 10.4
GPIT MA 1178-38	p/3 rt	20.3	10.3	Own 2014; HÜNERMANN 1968 as 19 × 10
NHMB Sth 683	p/3 rt	20.4	10.8	Own 2012; HÜNERMANN 1968 as 20.2 × 11.2
SMNS M 5280	p/3 rt	19.6	10.4	Own 2010
SMNS M 5280a	p/4	18.1	13.5	HÜNERMANN 1968
GPIT MA 1178-39	p/4 lt	17.6	12.6	Own 2014; HÜNERMANN 1968 as 17,8 × 12,7
SMNS M 13235	p/4 lt	17.0	12.6	Own 2010
SMNS M 4024b	p/4 lt	17.8	13.3	Own 2010
GPIT MA 1178-37	p/4 rt	16.7	12.6	Own 2014; HÜNERMANN 1968 as 16.5 × 12.6
GPIT MA 1178-38	p/4 rt	17.6	12.0	Own 2014; HÜNERMANN 1968 as 17.6 × 12.4
SMNS M 5280b	p/4 rt	17.5	12.8	Own 2010
SMNS M 20223	P1/	13.5	5.8	HÜNERMANN 1968
SMNS M 20223	P1/	13.6	5.8	HÜNERMANN 1968
SMNS M 13235	P1/ lt	14.5	5.3	Own 2010
SMNS M sans n°	P1/ rt	14.8	6.1	Own 2010
SMNS M 20223	P2/	16.0	7.2	HÜNERMANN 1968

Table 11. Continued

Catalogue	Tooth	L	B	Data source and comments
SMNS M 20223	P2/	16.1	7.0	Hünermann 1968
NHMB Sth 135	P2/ lt	16.4	7.0	Own 2012; Hünermann 1968 as 16.3 × 7.1 P1/
SMNS M 4024	P2/ lt	17.0	6.4	Own 2010
NHMB Sth 179	P2/ rt	16.8	6.5	Own 2012; Hünermann 1968 as 16.6 × 6.7
SMNS M 20223	P3/	16.8	15.4	Hünermann 1968
SMNS M 20223	P3/	16.8	15.2	Hünermann 1968
NHMB Sth 677	P3/ lt	16.8	14.4	Own 2012; Hünermann 1968 as 16.8 × 14.7
NHMB Sth 134	P3/ rt	17.0	14.3	Own 2012; Hünermann 1968 as 17 × 14.6
SMNS M 20223	P4/	12.5	16.9	Hünermann 1968
SMNS M 20223	P4/	12.8	17.9	Hünermann 1968
NHMB Sth 678	P4/ lt	13.0	16.0	Own 2012; Hünermann 1968 as 13.1 × 16.1
SMNS M 5280	P4/ lt	13.7	17.0	Own 2010
SMNS M 4811 (12770)	m/1 rt	18.4	12.1	Own 2010; Hünermann 1968, 16.8 × – lectotype
SMNS M 4811	m/2	19.7	14.0	Hünermann 1968 lectotype
SMNS M 4811	m/3	25.2	14.5	Hünermann 1968 lectotype
SMNS M 4811	M1/ rt	17.5	15.2	Own 2010 lectotype
SMNS M 4811	p/3	19.1	10.5	Hünermann 1968 lectotype
SMNS M 4811	p/4	16.3	11.8	Hünermann 1968 lectotype

genus *Parachleuastochoerus* (for details see Pickford 2014). However, it is morphologically close to material from La Grive-St-Alban attributed to *Versoporcus grivensis*, a slightly larger species from MN 8, indicating that it represents this genus.

Tutzing

The sample of fossil suids from Tutzing is limited, the only specimen seen by the author comprising a poor cast of a mandible fragment (NHMB TD 811) containing p/3 and p/4 which was illustrated by Stehlin (1899–1900: pl. 3, figs 20–21, Table 12). The teeth are compatible with specimens of *Parachleuastochoerus valentini*.

Urlau

The Urlau tetraconodont fossils were attributed to *Conohyus simorrensis* by Hünermann (1968). Heissig (1989) agreed with this identification (Table 12).

Wartenberg bei Erding

Hünermann (1968) divided the fossils from Wartenberg bei Erding between *Propotamochoerus palaeochoerus* and *Conohyus simorrensis* which would give rise to a peculiar

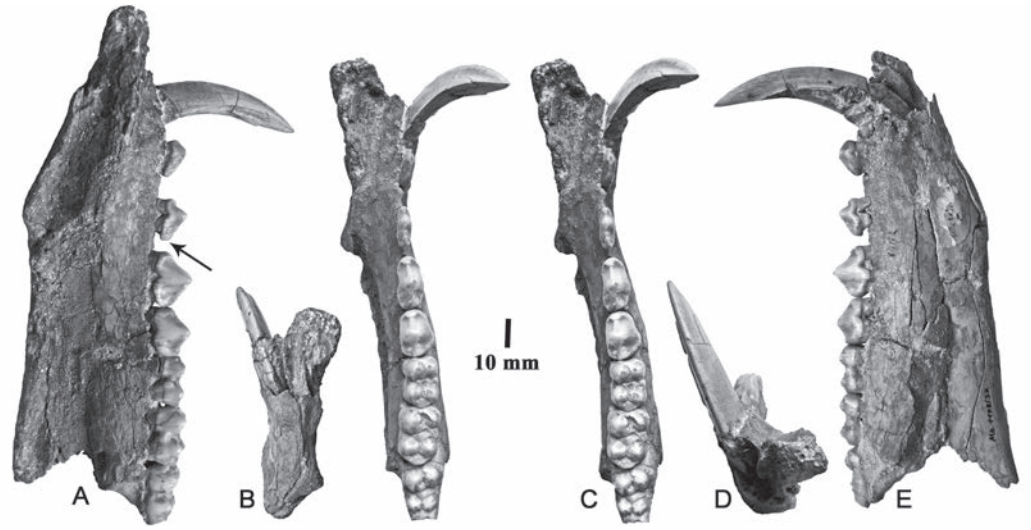

Fig. 16. *Versoporcus steinheimensis* from Steinheim, Germany. GPIT MA 1178-37, male right mandible containing canine, p/1-m/3. **A**: lingual view (arrow points to the distal overhang of the p/2), **B**: ventral view of symphysis, **C**: stereo occlusal view, **D**: anterior view, **E**: buccal view.

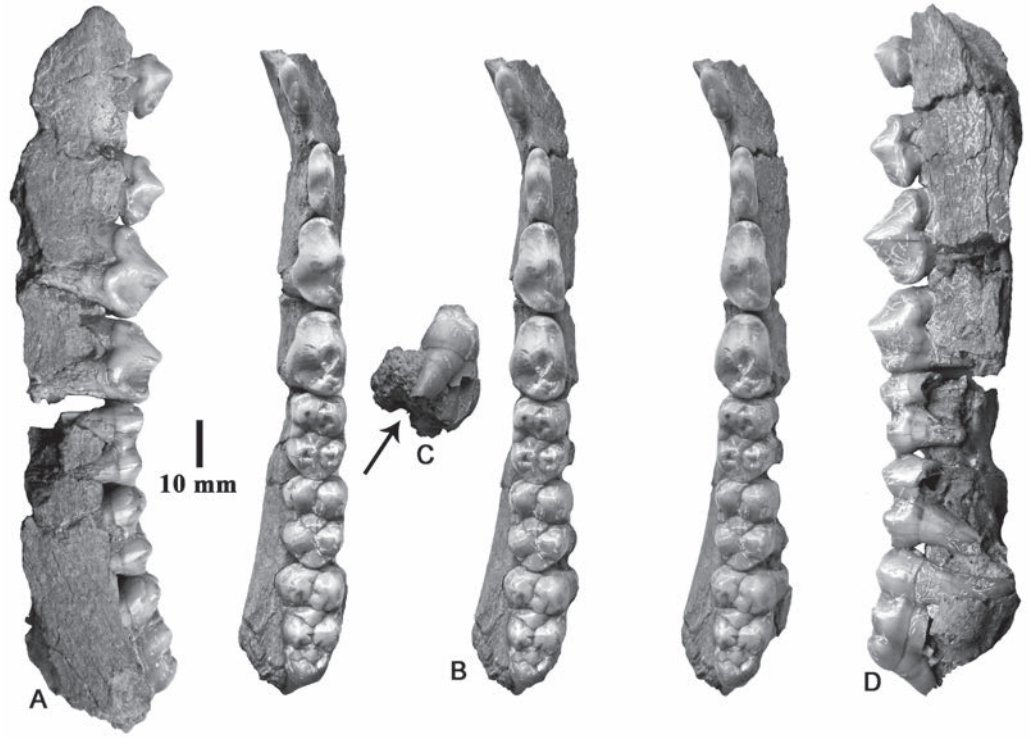

Fig. 17. *Versoporcus steinheimensis* from Steinheim, Germany. GPIT MA 1178-39, male left mandible containing canine alveolus, p/1-m/3. **A**: buccal view, **B**: stereo triplet occlusal view, **C**: distal view of m/3 (arrow points to the laterally tilted root of the m/3 talonid), **D**: lingual view.

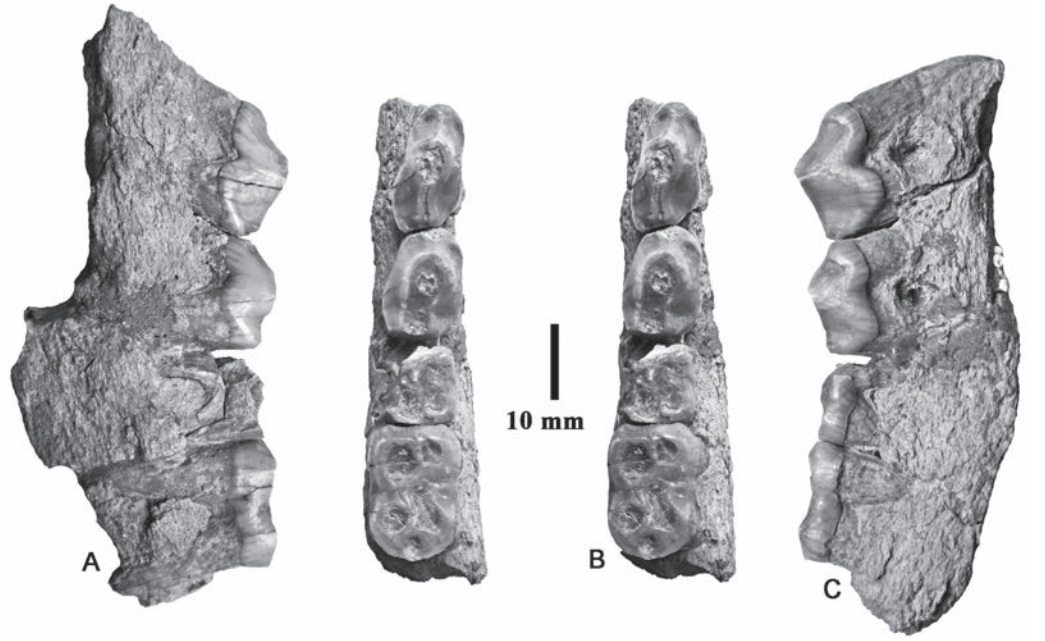

Fig. 18. *Versoporcus steinheimensis* from Steinheim, Germany. GPIT MA 1178-38, right mandible containing p/3-m/2. **A**: lingual view, **B**: stereo occlusal view, **C**: buccal view.

Fig. 19. *Versoporcus steinheimensis* from Steinheim, Germany. GPIT MA 1178-41, left male canine, **A**: buccal, **B**: radicular, **C**: lingual views.

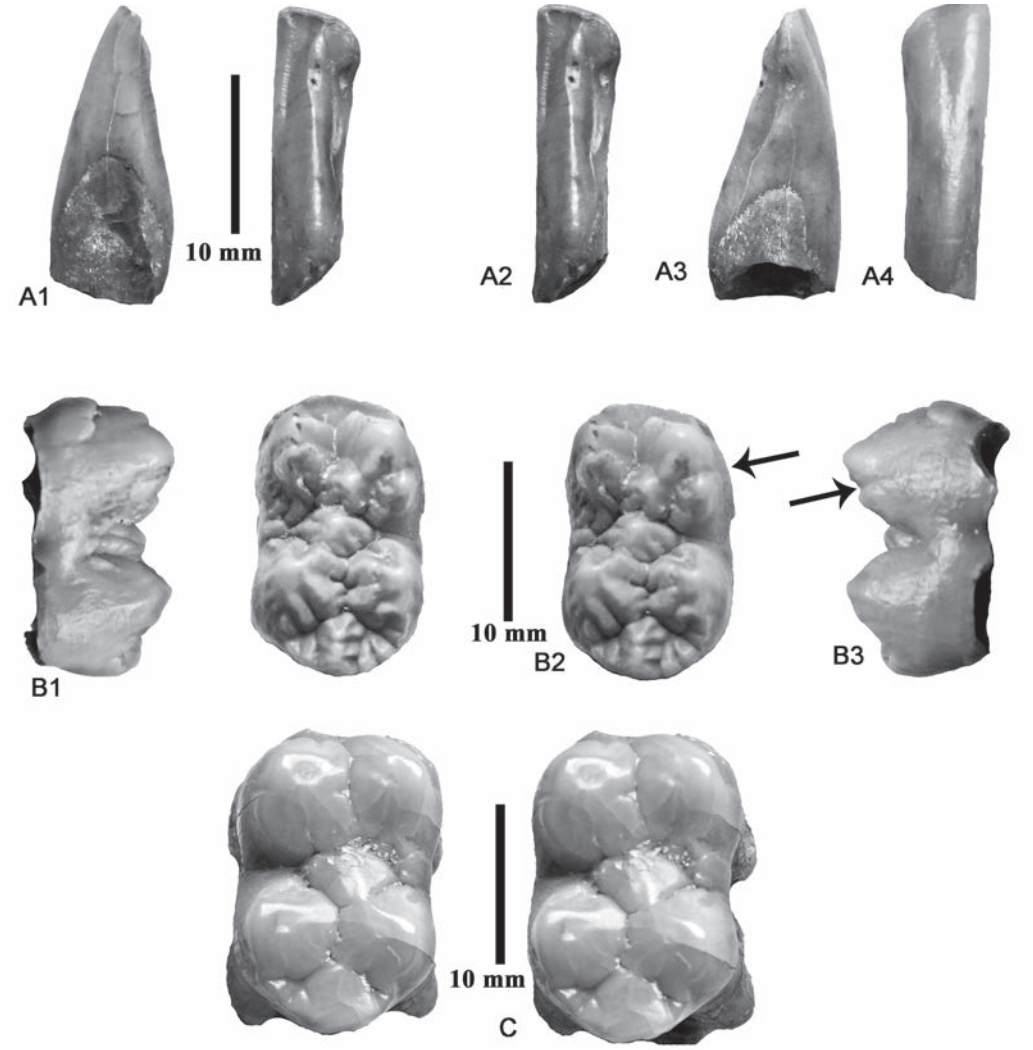

Fig. 20. *Versoporcus steinheimensis* from Steinheim, Germany. **A**: GPIT MA 1178-42, right i/2, A1: mesial, A2: stereo lingual, A3: distal, A4: labial views; **B**: GPIT MA 1178-43, left m/1, B1: buccal, B2: stereo occlusal, B3: lingual views (arrows show slit in metaconid; **C**: GPIT MA 1178-44, right m/2, stereo occlusal view.

situation from the point of view of biochronology. However, the material appears to be homogeneous and it is concluded that it represents a single taxon (Figs 21, 22), most likely *Parachleuastochoerus valentini*. Most of the dental measurements fall within, or slightly above, the range of variation of *Conohyus simorrensis*, some teeth, such as the M3/, plotting within the range of *Conohyus doati* and *Parachleuastochoerus valentini* (Table 13). The relatively elongated talon in the M3/ suggests appurtenance to *Parachleuastochoerus valentini* rather than to *Conohyus doati*, which would indicate a correlation to MN 8 or the base of MN 9

Table 12. Measurements (in mm) of tetraconodont teeth from Germany: (1) Urlau, attributed to *Conohyus simorrensis*; (2) Tutzing, attributed to *Parachleuastochoerus valentini* (B = bucco-lingual breath, L = mesio-distal length, lt = left, rt = right) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Locality	Data source and comments
SMNS M 20255	m/1 rt	16.0	12.6	1	Own 2010; Heissig 1989 as 16.1 × 13; Hünermann 1968 as 15.3 × 12.7
SMNS M 20255	m/2 lt	19.3	14.5	1	Own 2010; Heissig 1989 as 19.6 × 14.9; Hünermann 1968 as 19.2 × 14.6
SMNS M 20255	m/3 rt	25.8	15.3	1	Own 2010; Heissig 1989 as 26.6 × 16.2; Hünermann, 1968 as M 22255 25.8 × 15.8
SMNS M 20255	P3/ lt	17.8	16.6	1	Own 2010; Hünermann, 1968 as 17.9 × 16.9; Own 2012 cast 19 × 17 NHMB TD 809
SMNS M 20255	P3/ rt	18.0	16.7	1	Own 2010
NHMB TD 811 cast	p/3 lt	25.6	15.0	2	Own 2014
NHMB TD 811 cast	p/4 lt	19.0	15.0	2	Own 2014

Table 13. Measurements (in mm) of teeth from Wartenberg bei Erding, Germany, attributed to *Parachleuastochoerus valentini* (B = bucco-lingual breadth, L = mesio-distal length, lt = left, rt = right, - measurement not possible, *P.* = *Propotamochoerus*) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Data source and comments
SNSB-BSPG 1950 I 50	d/3 lt	15.5	6.4	Own 2013
SNSB-BSPG 1950 I 50	d/4 lt	21.0	9.5	Own 2013
SNSB-BSPG 1953 I 554	i/2 lt	8.5	9.6	Own 2013
SNSB-BSPG 1950 I 50	m/1 lt	19.0	13.4	Own 2013
SNSB-BSPG 1950 I 45	m/2 lt	21.8	15.9	Own 2013
SNSB-BSPG 1950 I 46	m/3 lt	26.7	15.6	Own 2013; Hünermann 1968 as 26.8 × 15.8
SNSB-BSPG 1953 I 486	M1/ rt	18.6	18.2	Own 2013; Hünermann 1968 as 18.7 × 18.1 *P. palaeochoerus*
SNSB-BSPG 1955 I 41	M2/ lt	20.0	19.0	Own 2013; Hünermann 1968 as 1955 I 47. 19.7 × 19.1
SNSB-BSPG 1953 I 487	M2/ rt	20.5	18.1	Own 2013; Hünermann 1968 as 20.8 × 18.7 *P. palaeochoerus*
SNSB-BSPG 1952 I 279	M3/ lt	26.0	20.5	Own 2013; Hünermann 1968 as 26.4 × 20.2
SNSB-BSPG 1968 I 100	M3/ lt	23.3	17.6	Own 2013
SNSB-BSPG 1950 I 12e	p/3 lt	-	12.8	Own 2013; Hünermann 1968 as 0 × 13.3
SNSB-BSPG 1950 I 49	p/4 lt	19.6	14.1	Own 2013; Hünermann 1968 as 20.3 × 14.9
SNSB-BSPG 1950 I 47	P4/ rt	14.2	19.1	Own 2013; Hünermann 1968 as 14.4 × 19.3
SNSB-BSPG 1950 I 48	P4/ lt	13.4	16.5	Own 2013; Hünermann 1968 as 13.4 × 16.7

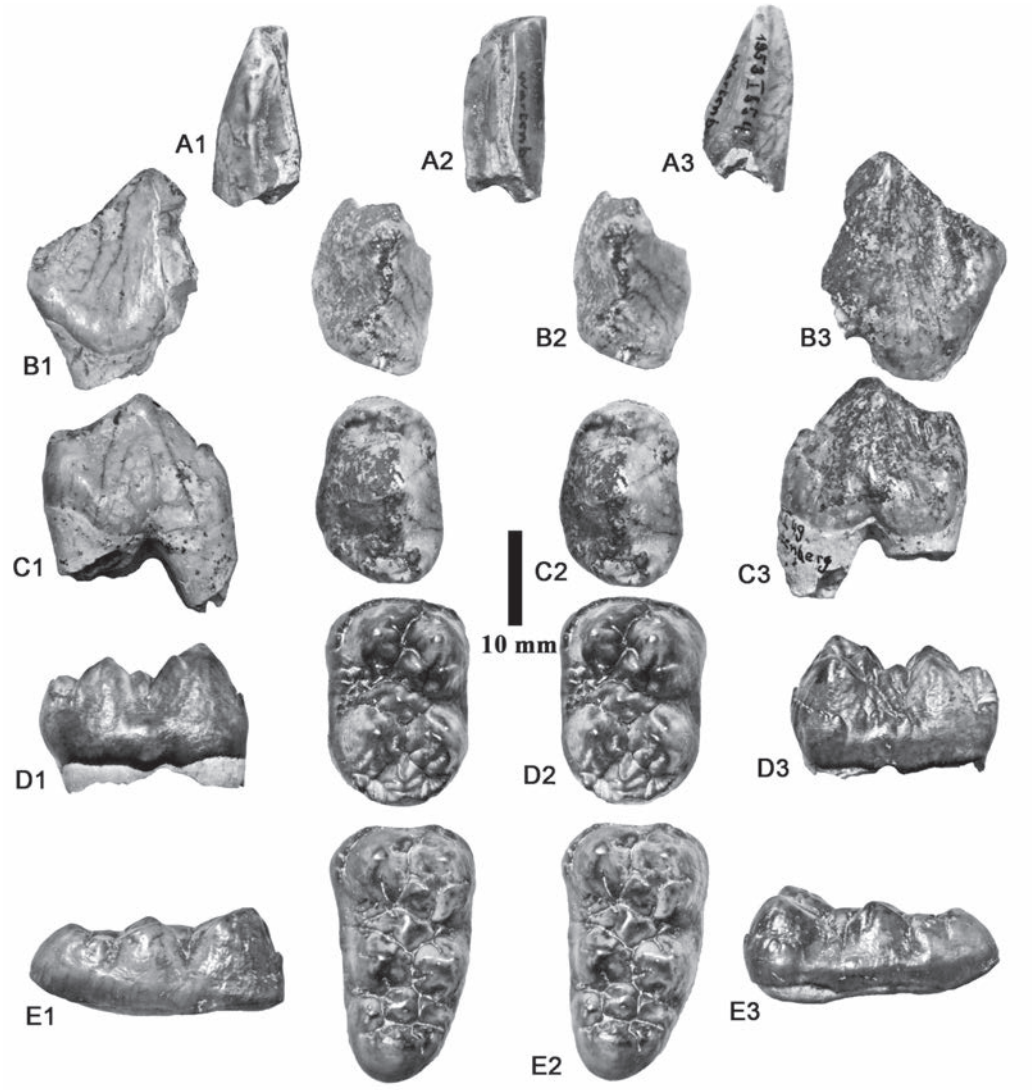

Fig. 21. Lower teeth of *Parachleuastochoerus valentini* from Wartenberg bei Erding, Germany. **A**: BSPG 1953 I 554, left i/2, A1: distal, A2: lingual, A3: mesial views; **B**: BSPG 1950 I 12e, left p/3, B1: lingual, B2: stereo occlusal, B3: buccal views; **C**: BSPG 1950 I 49, left p/4, C1: lingual, C2: stereo occlusal, C3: buccal views; **D**: BSPG 1950 I 45, left m/2, D1: lingual, D2: stereo occlusal, D3: buccal views; **E**: BSPG I 46, left m/3, E1: lingual, E2: stereo occlusal, E3: buccal views.

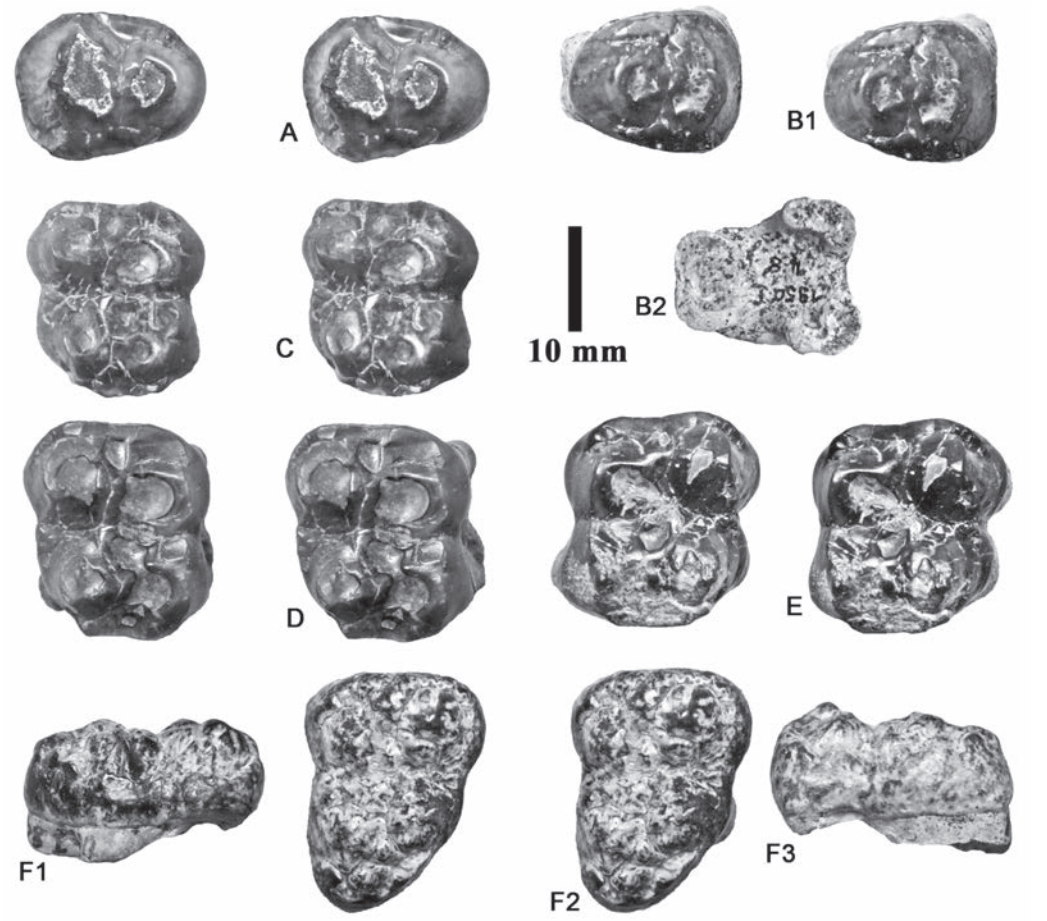

Fig. 22. Upper teeth of *Parachleuastochoerus valentini* from Wartenberg bei Erding, Germany. **A**: BSPG 1950 I 47, right P4/, stereo occlusal view; **B**: BSPG 1950 I 48 left P4/, B1: stereo occlusal view, B2: radicular view; **C**: BSPG 1950 I 486, right M1/, stereo occlusal view; **D**: BSPG 1953 I 487, right M2/, stereo occlusal view; **E**: BSPG 1955 I 41, left M2/, stereo occlusal view; **F**: BSPG 1968 I 100, left M3/ F1: buccal, F2: stereo occlusal, F3: lingual views.

SWITZERLAND

Aargau

The locality at Aargau yielded only a few fragmentary suid specimens among which there is a left third lower molar (PIMUZ A/V 2089, length times breadth: 29.0 × 16.4 mm) most similar to specimens of *Retroporcus matritensis* (Fig. 23) although attribution to another taxon cannot be ruled out.

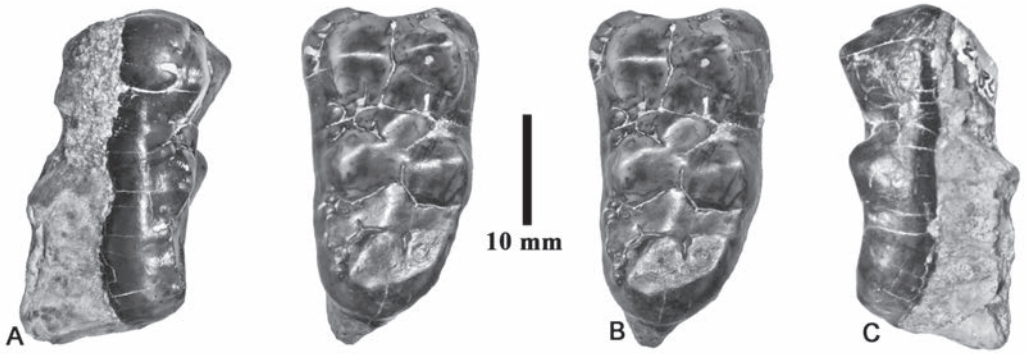

Fig. 23. PIMUZ A/V 2089, left m/3, probably of *Retroporcus matritensis* from Aargau, Switzerland. **A**: buccal, **B**: stereo occlusal, **C**: lingual views.

Anwil

Anwil yielded a restricted sample of suid teeth (ENGESSER 1972). The fossils are compatible in morphology and dimensions to *Versoporcus grivensis* (Figs 24, 25, Table 14) inviting correlation of the deposits to MN 8 (Annex).

PICKFORD & LAURENT (2014) considered that the Anwil suid specimens described by ENGESSER (1972) represented large individuals of *Retroporcus matritensis*, but since

Table 14. Measurements (in mm) of suid teeth from Aargau, Anwil and Charmoille, Switzerland (B = bucco-lingual breadth, L = mesio-distal length, *P. h.* = *Parachleuastochoerus huenermanni*, *P. v. Parachleuastochoerus valentini*, *R. m.* = *Retroporcus matritensis*, *V. g.* = *Versoporcus grivensis*, lt = left, rt = right, - measurement not possible) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Locality	Taxon	Data source and comments
PIMUZ A/V 2089	m/3 lt	29.0	16.4	Aargau	*?R. m.*	Own 2014
NHMB Anwil	d/4 lt	20.8	9.8	Anwil	*V. g.*	Own 2012
NHMB Anwil	m/1 lt	18.7	12.3	Anwil	*V. g.*	Own 2012
NHMB Anwil	M1/ lt	18.0	16.3	Anwil	*V. g.*	Own 2012; ENGESSER 1972 as 17.8 × 16.3
NHMB Anwil	M1/ rt	-	16.6	Anwil	*V. g.*	Own 2012
NHMB Anwil	M2/ lt	20.0	18.1	Anwil	*V. g.*	Own 2012; ENGESSER 1972 as 19.5 × 19.3
NHMB Anwil	M2/ rt	20.0	19.0	Anwil	*V. g.*	Own 2012; ENGESSER 1972 as 19.5 × 19.3
NHMB Anwil	M3/ rt	22.7	19.0	Anwil	*V. g.*	Own 2012; ENGESSER 1972 as 23.5 × 19
NHMB Al 175	P2/ rt	16.5	7.6	Anwil	*V. g.*	Own 2012
NHMB Anwil	P4/ rt	14.0	18.0	Anwil	*V. g.*	Own 2012; ENGESSER 1972 as 14 × 17.5
NHMB CM 440	m/3 lt	23.0	13.2	Charmoille	*P. h.*	Own 2012; HÜNERMANN 1968 as 22.9 × 13.4
NHMB CM 81	m/3 lt	30.6	16.0	Charmoille	*P. v.*	Own 2012; HÜNERMANN 1968 as 30.7 × 16
NHMB CM 439	M2/ rt	21.3	19.8	Charmoille	*P. v.*	Own 2012

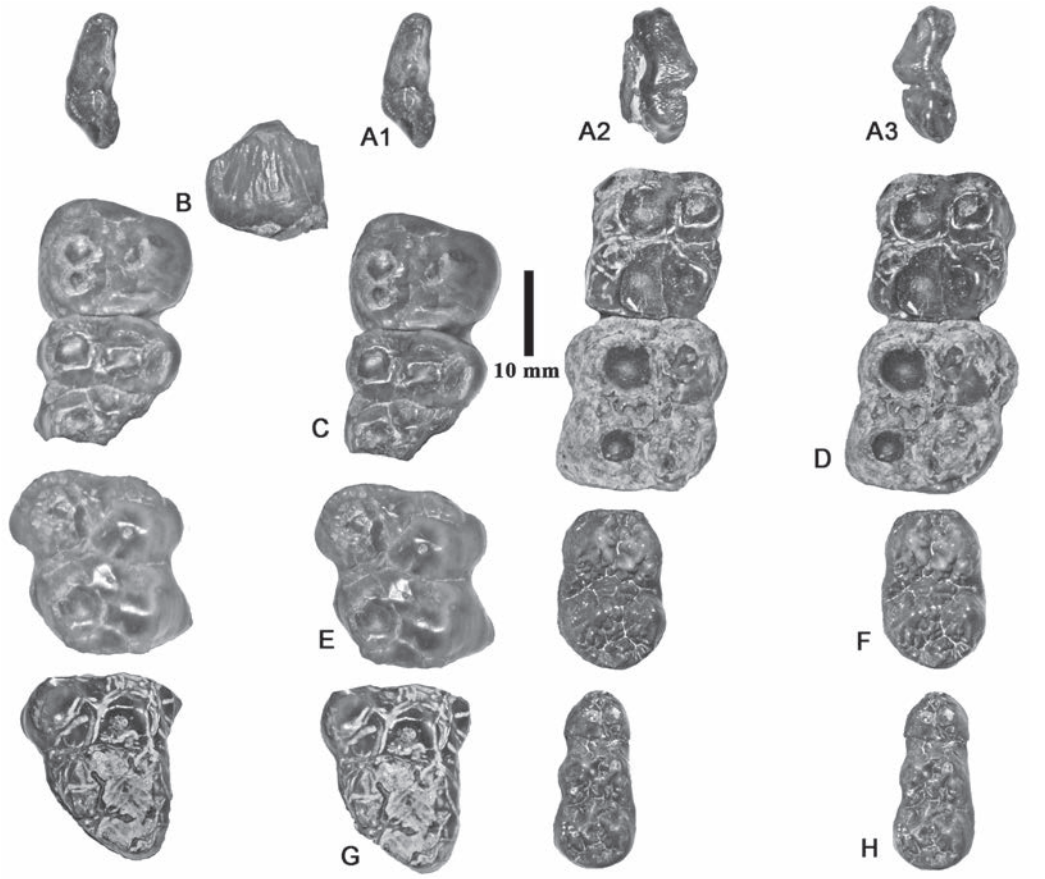

Fig. 24. Upper cheek teeth of *Versoporcus grivensis* from Anwil, Switzerland. **A**: NHMB AI 175, right P2/, A1: buccal, A2: stereo occlusal, A3: lingual views; **B**: right P4/, buccal view; **C**: right P4/-M1/, stereo occlusal view; **D**: left M1/-M2/, stereo occlusal view; **E**: right M2/, stereo occlusal view; **F**: left m/1, stereo occlusal view; **G**: right M3/, stereo occlusal view; **H**: left d/4, stereo occlusal view.

then a revision of the suids from La Grive-St-Alban (Pickford, 2014) has shown that the species *Sus grivensis* Gaillard, 1899, is valid and that it belongs to the genus *Versoporcus* Pickford (2014) of which the Steinheim suid is the type species (*Versoporcus steinheimensis* (Fraas, 1870)). The identification of the Anwil suids as *Versoporcus grivensis* is compatible with the reported age of Anwil as MN 8, whereas the identification of the fossils as *Retroporcus matritensis* would suggest an earlier correlation to MN 6.

Charmoille

The few suid fossils from Charmoille (Hünermann 1968; Van der Made 1998) fall into the range of variation of *Parachleuastochoerus valentini* and *Parachleuastochoerus*

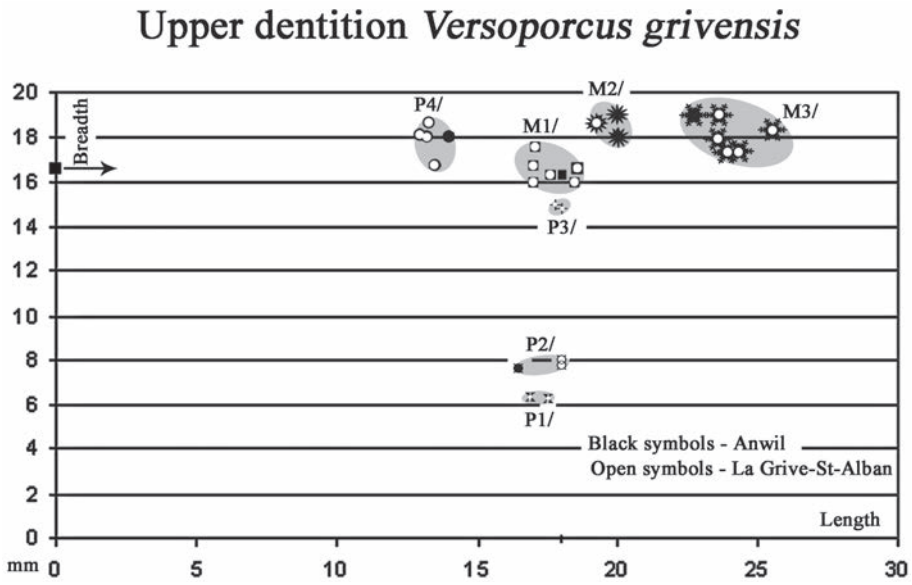

Fig. 25. Bivariate plot of upper cheek teeth of *Versoporcus grivensis* from Anwil (solid symbols) and the type locality, La Grive-St-Alban (hollow symbols). Arrow on the vertical axis is the breadth of an M1/ from Anwil.

huenermanni (Fig. 26). VAN DER MADE *et al*. (2014) listed *Conohyus steinheimensis* and *Parachleuastochoerus huenermanni* at the site. However, the upper molar from Charmoille, NHMB CM 439, is too large to belong to *Versoporcus steinheimensis* and is even too large for *Versoporcus grivensis*, but is close in dimensions and morphology to the M2/s in the holotype of *Parachleuastochoerus valentini* from St Gaudens, and has closely similar measurements to other material of the species from St Quirze. In particular, the presence of buccal cingular cusplets, the weak Furchen, relatively thin enamel (for a tetraconodont) and the rounded accessory cusplets agree with *Parachleuastochoerus valentini*. One of the m/3s from the site, NHMB CM 81, is large and falls outside the range of variation of *Versoporcus steinheimensis*, being closer in dimensions to the larger species *Versoporcus grivensis* and *Parachleuastochoerus valentini*. The other m/3 from the site, NHMB CM 440, is smaller and is compatible with *Parachleuastochoerus huenermanni*, as thought by VAN DER MADE *et al*. (2014).

Elgg

The lignites at Elgg have yielded a substantial quantity of suid remains (Figs 27–29, Table 15). There is an excellent, highly informative palate in the PIMUZ which provides good evidence that *Retroporcus matritensis* is represented at the site. Other material was illustrated by STEHLIN (1899–1900) and measured by VAN DER MADE *et al*. (2014) who identified the material as *Conohyus simorrensis*, but the latter specimens belong to *Retroporcus*

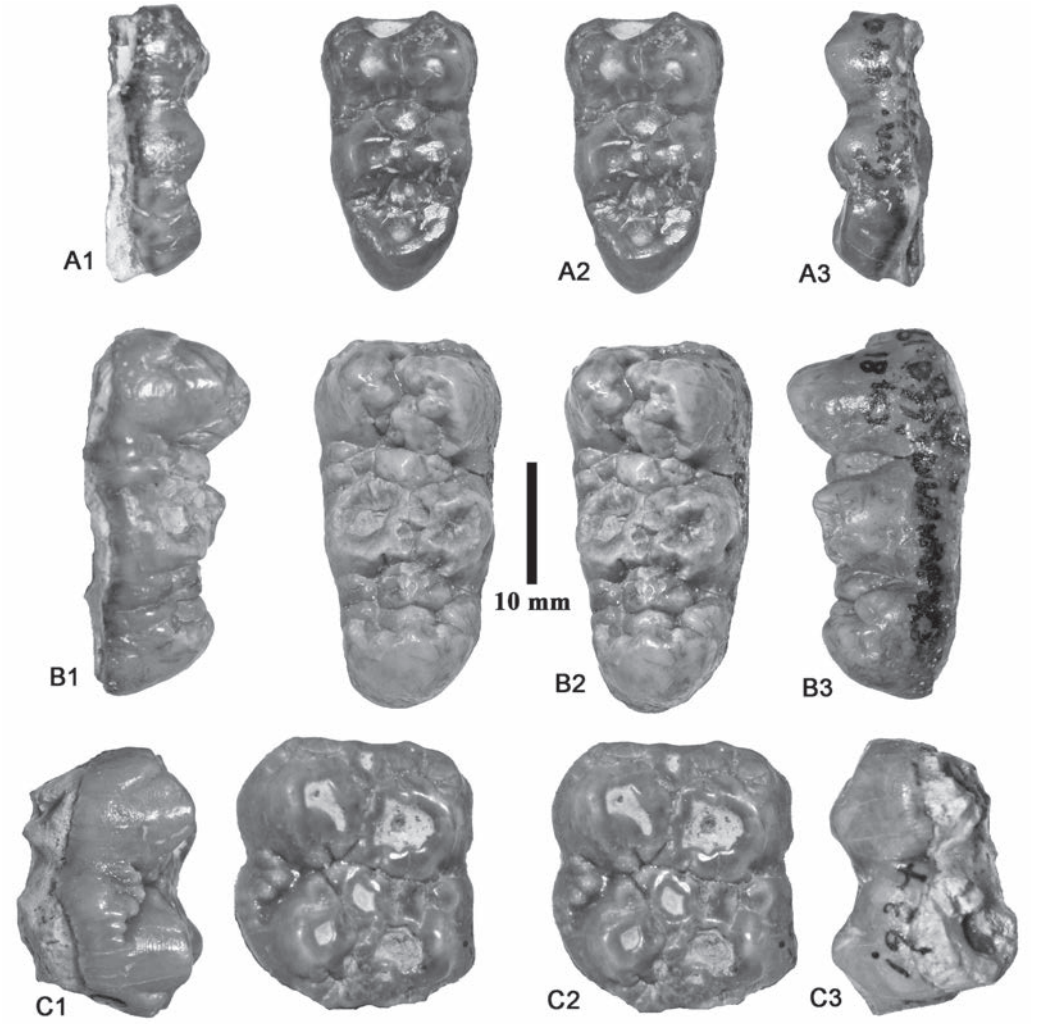

Fig. 26. Tetraconodonts from Charmoille, Switzerland. **A**: NHMB CM 440, *Parachleuastochoerus huenermanni*, left m/3, A1: buccal, A2: stereo occlusal, A3: lingual views; **B**: NHMB CM 81, *Parachleuastochoerus valentini*, left m/3, B1: buccal, B2: stereo occlusal, B3: lingual views; **C**: NHMB CM 439, *Parachleuastochoerus valentini*, right M2/, C1: buccal, C2: stereo occlusal, C3: lingual views.

There is a small suoid at the site (maxilla NHMUK M 2198) possibly representing a palaeochoerid considering the position of the anterior accessory cusplet in the upper molars, in between the protocone and paracone, rather than mesial to these cusps. Another small suoid labelled "Elgg? auch Köpfnach" (PIMUZ A/V 375) is attributed to *Hyotherium medium*. Given the confusing label, the latter species is not listed in the annex.

Stehlin (1899–1900 pl. 2, fig. 23) illustrated the occlusal view of a right P1/–P4/ from Elgg, but the current whereabouts of the fossil are unknown. This specimen is not the

Table 15. Measurements (in mm) of suid and palaeochoerid teeth from Elgg, Switzerland (B = bucco-lingual breadth, L = mesio-distal length, est.- estimated, lt = left, rt = right, *R. m.* = *Retroporcus matritensis*) (Own are the author's own measurements).

Catalogue	Tooth	L	B	Taxon	Data source and comments
CCECL B39 cast	M2/ lt	18.6	18.8	*R.m.* (labelled *Palaeogenus*) « *Mesochoerus* »	Own 2012
NHMB Elgg	p/4 lt	19.0	14.0	*R. m.*	Own 2012
NHMB Elgg	p/4 rt	18.7	14.5	*R. m.*	Own 2012
NHMB Elgg	m/2 rt	19.2	14.6	*R. m.*	Own 2012
NHMUK M 2198	M1/ lt	11.3	13.0	Palaeochoerid	Own 2012
NHMUK M 2198	M1/ rt	12.2	13.3	Palaeochoerid	Own 2012
NHMUK M 2198	M2/ lt	12.4	14.4	Palaeochoerid	Own 2012
NHMUK M 2198	M2/ rt	12.7	14.6	Palaeochoerid	Own 2012
NHMUK M 2198	M3/ lt	12.5	12.8	Palaeochoerid	Own 2012
NHMUK M 2198	M3/ rt	11.8	13.3	Palaeochoerid	Own 2012
NHMB OSM 932	M2/ rt	19.0	17.0	*R. m.* (labelled *Palaeogenus*)	Own 2012
NHMB OSM 932	M3/ rt	22.5	18.5	*R. m.* (labelled *Palaeogenus*)	Own 2012
PIMUZ A/V 1779	M1/ lt	16.6	16.0	*R. m.*	Own 2014
PIMUZ A/V 1779	M1/ rt	17.0	15.0	*R. m.*	Own 2014
PIMUZ A/V 1779	M2/ lt	19.0	18.6	*R. m.*	Own 2014
PIMUZ A/V 1779	M2/ rt	20.2	17.6	*R. m.*	Own 2014
PIMUZ A/V 1779	M3/ lt	22.2	19.0	*R. m.*	Own 2014
PIMUZ A/V 1779	M3/ rt	22.5	17.7	*R. m.*	Own 2014
PIMUZ A/V 1779	P2/ lt	21.0	8.7	*R. m.*	Own 2014
PIMUZ A/V 1779	P2/ rt	20.5	8.6	*R. m.*	Own 2014
PIMUZ A/V 1779	P3/ lt	21.4	15.9	*R. m.*	Own 2014
PIMUZ A/V 1779	P3/ rt	21.6	16.0	*R. m.*	Own 2014
PIMUZ A/V 1779	P4/ lt	14.4	17.9	*R. m.*	Own 2014
PIMUZ A/V 1779	P4/ rt	14.8	17.7	*R. m.*	Own 2014
PIMUZ A/V 51	M2/ rt	19.0	18.3	*R. m.*	Own 2014
PIMUZ A/V 51	M3/ rt	22.6	19.0	*R. m.*	Own 2014
PIMUZ A/V 1	C1/ rt	21.0	14.0	*R. m.*	Own 2014
Stehlin, pl. 2, fig. 23	P1/ rt	14.0	5.7	*R. m.*	STEHLIN 1899-1900 est. from figure
Stehlin, pl. 2, fig. 23	P3/ rt	20.0	7.0	*R. m.*	STEHLIN 1899-1900 est. from figure
Stehlin, pl. 2, fig. 23	P3/ rt	21.0	15.5	*R. m.*	STEHLIN 1899-1900 est. from figure
Stehlin, pl. 2, fig. 23	P4/ rt	14.0	18.0	*R. m.*	Stehlin 1899-1900 est. from figure

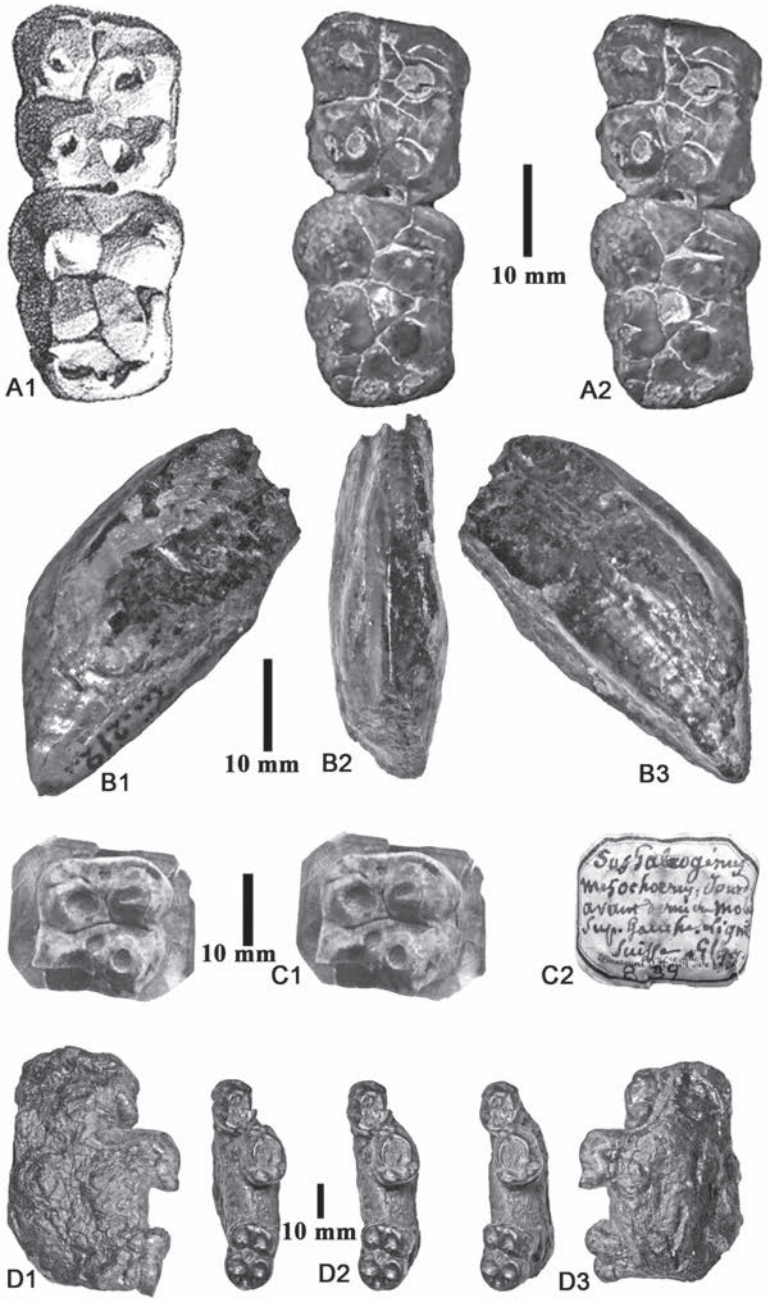

Fig. 27. *Retroporcus matritensis* from Elgg, Switzerland. **A**: PIMUZ A/V 51, right M2/-M3/, A1: illustration from Lortet & Chantre (1878: pl. VIII, fig. 7), A2: stereo occlusal view of original fossils; **B**: PIMUZ A/V 1, right upper canine (male), B1: lingual, B2: mesial, B3: buccal views; **C**: CCECL B 39 cast of left M2/, C1: stereo occlusal view, C2: label stuck to underside of cast, **D**: un-numbereed cast in NHMB of right mandible containing p/4 and m/2, with the left p/4 stuck to it D1: lingual, D2 stereo triplet of the occlusal view, D3: buccal view.

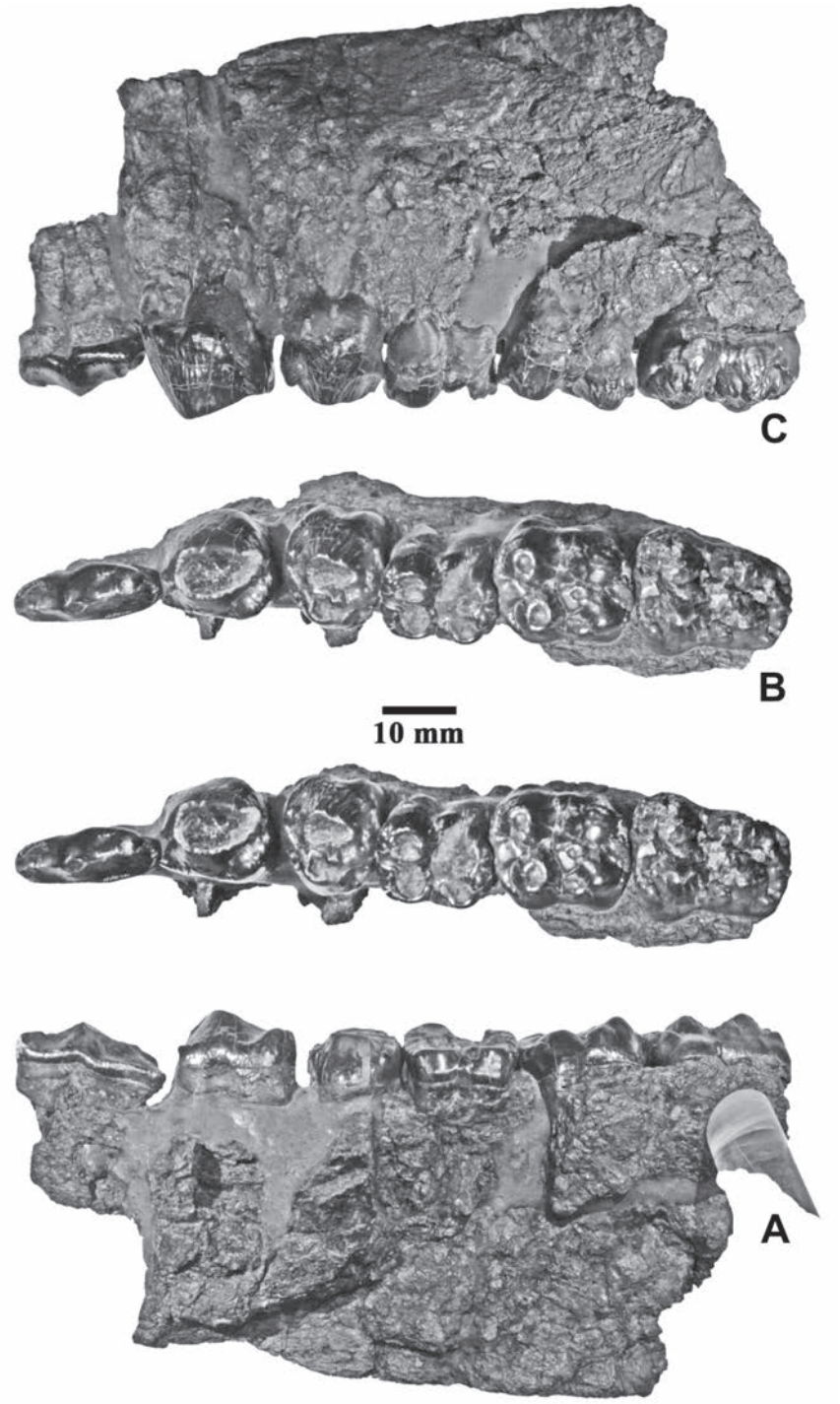

Fig. 28. *Retroporcus matritensis* from Elgg, Switzerland. PIMUZ A/V 1799, left maxilla containing P2/-M3/, **A**: lingual, **B**: stereo occlusal view, **C**: buccal view.

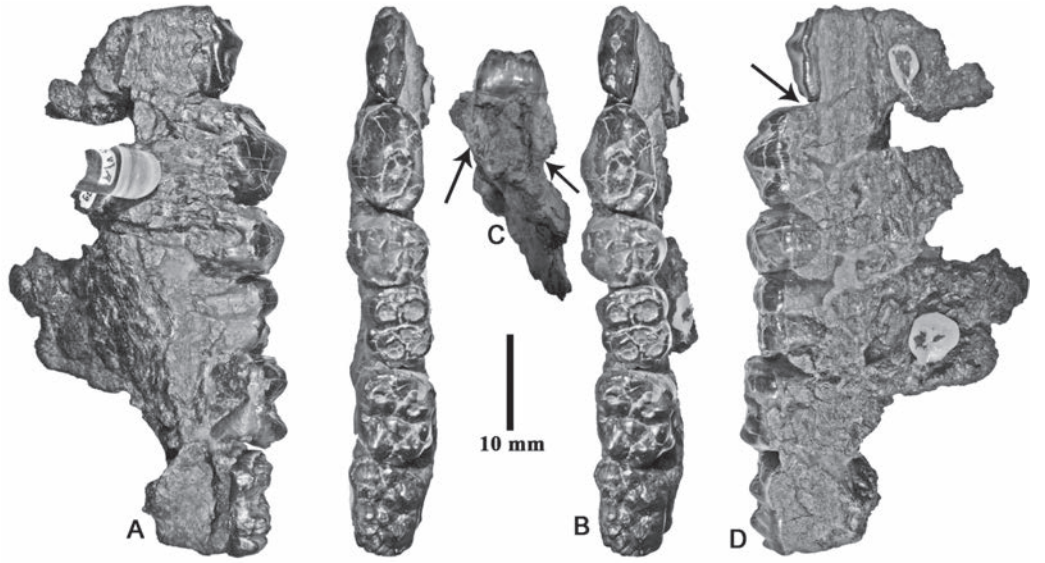

Fig. 29. *Retroporcus matritensis* from Elgg, Switzerland. PIMUZ A/V 1799, right maxilla containing P2/-M3/, **A**: buccal, **B**: stereo occlusal view, **C**: posterior view **D**: lingual view. Arrows in 'C' show broadened and bifurcate distal root of M3/, arrow in 'D' shows the offset in the cervical level of the P2/ with respect to P3/.

same as the maxilla PIMUZ A/V 1779 described above. The wear patterns of the teeth are not compatible. The interest of this specimen figured by Stehlin (1899–1900) is that it possessed the P1/ separated from the P2/ by a short diastema *c.* 12 mm long, one of the few specimens to retain both of these teeth in association with the posterior premolars.

Stehlin (1899–1900: pl. 4, fig. 4) illustrated the upper canine from Elgg (PIMUZ A/V 1) as a male individual of *Hyotherium simorrense*. My own study of the specimen, which shows a cross section like the fossils from Göriach, suggests that the specimen belongs to *Retroporcus matritensis*.

Lortet & Chantre (1878: pl. VIII, fig. 7) illustrated the right M2/–M3/ from Elgg under the genus name *Sus* whereas Stehlin (1899–1900: pl. 1, fig. 6) illustrated the same teeth under the name *Hyotherium simorrense*. A hand-written label kept with a cast of the specimen housed in the NHM Basel (NHMB OSM 932 cast of PIMUZ A/V 51) bears the words "*Sus palaeogenus* Meyer" but this name seems never to have been published formally although Stehlin (1899–1900) mentions it in the caption of Plate 1, Figure 6 of his monograph. A cast of an upper molar (B 39) from Elgg housed in the CCECL represents *Retroporcus matritensis*. The cast has a label stuck to it with the words "*Sus palaeogenus Mesochoerus* Jourd." But neither the genus name *Mesochoerus* nor the species name *palaeogenus* were published by Jourdan. The genus name *Mesochoerus* Shaw & Cooke, 1941, for an African suine, is a junior synonym of *Kolpochoerus* Van Hoepen & Van Hoepen, 1932.

There has been general agreement that the lignites at Elgg correlate to the Middle Miocene with slight differences of opinion about the precise age of the deposits: MN 5 according to HUGUENEY (1999) or MN 6 or 7 according to GÖHLICH (1999). The suids from Elgg (with the exception of the doubtful presence of *Hyotherium medium* VON MEYER, 1841) suggest correlation to MN 6.

Helsighausen

The deposits at Helsighausen have yielded suid specimens usually found in MN 6 and MN 7, comprising *Listriodon splendens* and *Retroporcus matritensis*. There is a valuable specimen from the site (PIMUZ A/V 3489) (Fig. 30) that retains several almost unworn upper teeth. The proportions of the P4/ to the upper molars are characteristic of *Retroporcus matritensis* (Table 16).

Käpfnach

KAUP (1859) described the species *Sus abnormis* on the basis of a palate from the lignite mine at Käpfnach, Switzerland (Fig. 31). The type specimen seems to be lost, but

Table 16. Measurements (in mm) of suid teeth from Helsighausen (Hohrain Waldi) (B = bucco-lingual breadth, L = mesio-distal length, lt = left, rt = right) (Own followed by a year are the author's own measurements).

Catalogue	Tooth	L	B	Taxon	Data source
Helsighausen Hohrain Waldi					
PIMUZ A/V 3747	M3/ lt	22.5	15.2	*Retroporcus matritensis*	Own 2014
NHMB OSM 1295	M3/ lt	22.0	15.7	*Retroporcus matritensis*	Own 2012
Helsighausen					
PIMUZ A/V 1236	m/2 rt	21.0	18.0	*Listriodon splendens*	Own 2014
PIMUZ A/V 1236	m/3 rt	33.0	21.1	*Listriodon splendens*	Own 2014
PIMUZ A/V 1236	p/3 rt	16.7	11.3	*Listriodon splendens*	Own 2014
PIMUZ A/V 1236	p/4 rt	17.0	14.0	*Listriodon splendens*	Own 2014
PIMUZ A/V 1237	I1/ lt	30.0	14.0	*Listriodon splendens*	Own 2014
PIMUZ A/V 3489	I3/ rt	11.5	5.0	*Retroporcus matritensis*	Own 2014
PIMUZ A/V 3489	M1/ lt	17.0	16.0	*Retroporcus matritensis*	Own 2014
PIMUZ A/V 3489	M1/ rt	16.6	16.2	*Retroporcus matritensis*	Own 2014
PIMUZ A/V 3489	M2/ lt	20.0	17.8	*Retroporcus matritensis*	Own 2014
PIMUZ A/V 3489	M2/ rt	19.9	17.7	*Retroporcus matritensis*	Own 2014
PIMUZ A/V 3489	M3/ rt	22.5	15.2	*Retroporcus matritensis*	Own 2014
PIMUZ A/V 3489	P4/ rt	13.5	18.6	*Retroporcus matritensis*	Own 2014

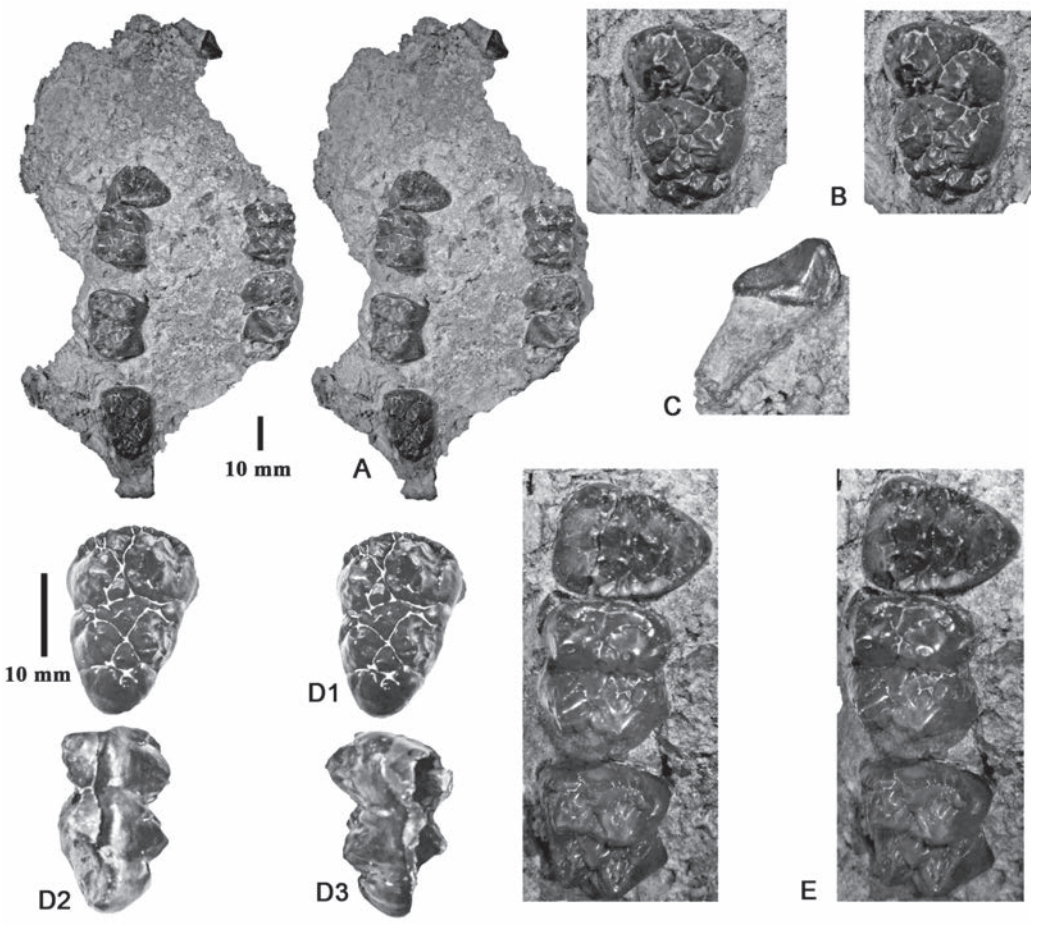

Fig. 30. *Retroporcus matritensis* from Helsighausen (Hohrain Waldi: Switzerland. **A-C+E**: PIMUZ A/V 3489, cheek teeth and incisor in consolidated sandstone, A: stereo occlusal view of cheek teeth, B: stereo occlusal view of right M3/, C: lingual view of right I3/; **D**: PIMUZ A/V 3747, left M3/, D1: stereo occlusal view, D2: lingual, D3: buccal view, E: stereo occlusal view of right P4/-M2/.

good illustrations of the specimen in occlusal and buccal views were published. The right tooth row comprises P1/–M3/ and the left one P3/–M3/. The M1/ is deeply worn but the M3/ is in light wear. The premolar to molar proportions are typical of *Conohyus simorrensis* (Table 17) and, although crushing in this area makes interpretation delicate, there appears to be no offset between the cervical level of the anterior and posterior premolars (ie the crown-root margins of all the premolars are at the same level, unlike in the genus *Retroporcus* in which the anterior premolars have cervical margins offset relative to those of the posterior premolars). The P1/ shows two roots close together and almost vertical whilst the P2/ has two widely separated roots.

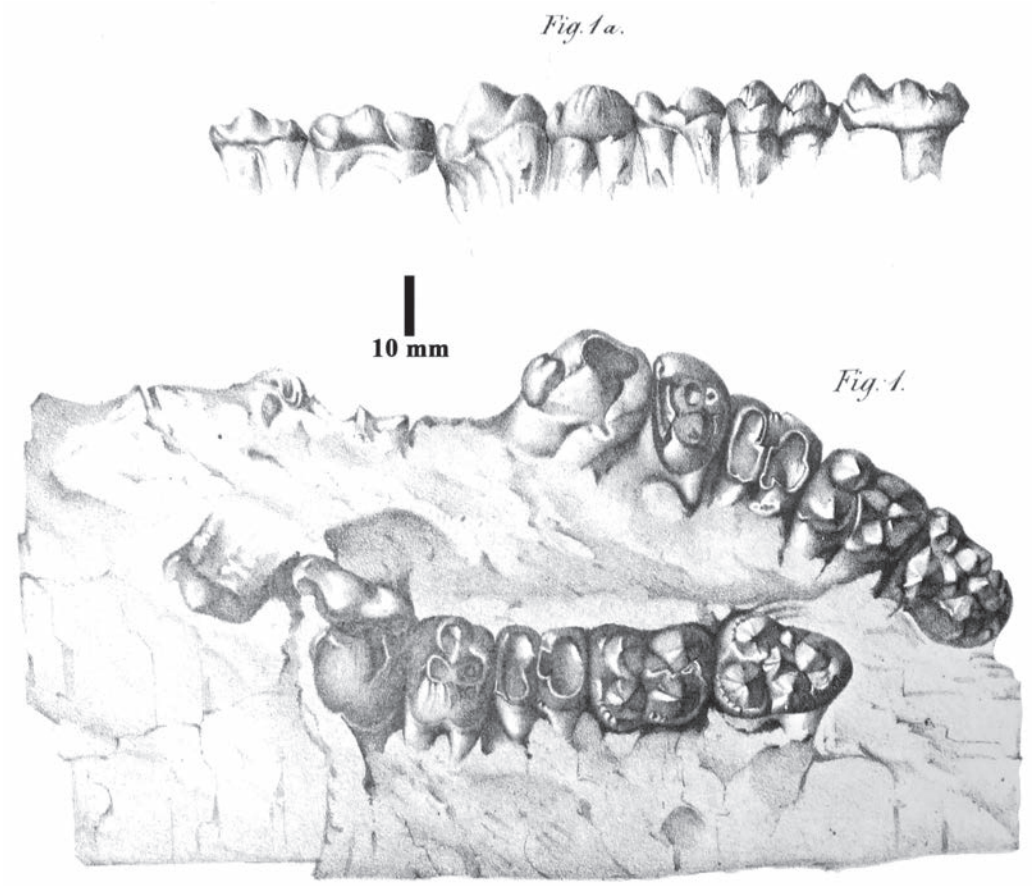

Fig. 31. Holotype of *Sus abnormis* Kaup, 1859, from Käpfnach, Switzerland, a crushed palate containing left P3/-M3 and right P1/-M3/ (image reproduced from KAUP, 1859).

The plate accompanying KAUP's (1859) description of the holotype of *Sus abnormis* from Käpfnach is re-illustrated (Fig. 31) and reveals that the specimen belongs to *Conohyus simorrensis* (LARTET, 1851). The name *abnormis* is therefore a junior synonym of *simorrensis*. The measurements of the teeth published by KAUP (1859) are compatible with the species determination save for the length of M1/ (19 mm in KAUP's 1859 text (obviously a misprint), 14 mm as measured in the figure).

There are other suids labelled Käpfnach housed in the PIMUZ and the NHMB which are identified as *Hyotherium soemmeringi* and *Hyotherium meisneri* (Table 17). The suids labelled Käpfnach thus yield a confusing biostratigraphic signal, because *H. soemmeringi* and *H. meisneri* are usually found in MN 4 or older deposits, whereas *C. simorrensis* is considered to occur in MN 6 and younger deposits. The possibility of two sedimentary units at Käpfnach is suggested by the suids.

Schlatt am Kohlfirst

A maxilla from Schlatt am Kohlfirst containing three molars (cast in NHMB OSM 1060) is, according to its label, preserved in Frauenfeld (without precision of where it is kept). The distal alveoli of the P4/ seem to be broader than the M1/ which indicates that the specimen is likely to be a tetraconodont. It is tentatively identified as *Conohyus* sp. (Table 18).

Table 17. Measurements (in mm) of the teeth of suids from Käpfnach, Switzerland. 1: *Conohyus simorrensis*, 2: *Hyotherium soemmeringi*, 3: *Hyotherium meisneri*. Kaup (1859) provided measurements of the teeth, but made an error in the length of the M1/ which he wrote was 19 mm long, the same length as the M2/. Reference to the figure shows that the M1/ is *c.* 15 mm long (lt = left, rt = right, - measurement not possible) (H = Hünermann, K = Kaup, S = Scherler, Own are the author's own measurements.

Catalogue	Tooth	L	B	Taxon	Data source and comments
Käpfnach (lost ?)	P1/ rt	16.0	6.0	1	Kaup 1859, holotype *Sus abnormis*
Käpfnach (lost ?)	P2/ r	20.0	7.0	1	Kaup 1859, holotype *Sus abnormis*
Käpfnach (lost ?)	P3/ rt	17.0	15.0	1	Kaup 1859, holotype *Sus abnormis*
Käpfnach (lost ?)	P4/ rt	13.0	16.0	1	Kaup 1859, holotype *Sus abnormis*
Käpfnach (lost ?)	M1/ rt	15.0	14.0	1	Kaup 1859, holotype *Sus abnormis* as 19 × 14
Käpfnach (lost ?)	M2/ rt	18.5	17.3	1	Kaup 1859, holotype *Sus abnormis*
Käpfnach (lost ?)	M3/ rt	21.5	16.0	1	Kaup 1859, holotype *Sus abnormis*
NHMB OSM 928	m/1 rt	15.0	11.7	2	Own 2012; Scherler 2011 as 16.5 × 11.5
NHMB OSM 928	m/2 rt	-	13.3	2	Own 2012; Hünermann 1968 as 0 × 13.4
NHMB OSM 928	p/4 rt	14.4	9.0	2	Own 2012; Scherler 2011 as 15.5 × 8.5
PIMUZ A/V 373	p/4 rt	15.5	8.7	2	Own 2014
PIMUZ A/V 374	D3/ lt	-	10.4	3	Own 2014
PIMUZ A/V 374	D4/ lt	12.3	12.3	3	Own 2014
PIMUZ A/V 374	M1/ lt	14.8	14.3	3	Own 2014; Scherler 2011 as 12 × 13
PIMUZ A/V 374	M2/ lt	16.5	16.0	3	Own 2014; Scherler 2011 as 14.5 × 14
PIMUZ A/V 374	M2/ rt	17.4	-	3	Own 2014
PIMUZ A/V 374	M3/ lt	19.5	-	3	Own 2014; Scherler 2011 as 16.5 × 15.5
PIMUZ A/V 374	M3/ rt	-	15.7	3	Own 2014
PIMUZ A/V 376	m/1 lt	14.6	11.5	3	Own 2014; Scherler 2011 as right 15 × 11
PIMUZ A/V 376	m/2 lt	16.5	12.6	3	Own 2014; Scherler 2011 as right 16 × 12.5
PIMUZ A/V 376	m/2 rt	16.8	-	3	Own 2014
PIMUZ A/V 376	m/3 lt	23.0	13.2	3	Own 2014; Scherler 2011 as right 24 × 12.5
PIMUZ A/V 376	m/3 rt	24.5	-	3	Own 2014
PIMUZ A/V 376	p/4 lt	-	8.7	3	Own 2014

TURKEY

Alçitepe

VAN DER MADE & TUNA (1998) attributed a right P4/ from Nuri Yamut, near Alçitepe, Turkey, to *Conohyus giganteus* (FALCONER & CAUTLEY, 1847) but VAN DER MADE *et al*. (2014) identified the specimen as *Conohyus simorrensis*.

The specimen from Alçitepe, of which a cast is preserved in the PIMUZ (A/V 2370), could represent the same species as the North African *Sivachoerus devauxi* (ARAMBOURG, 1968). Although *Sivachoerus giganteus* and *Sivachoerus devauxi* have similar sized P4/s (PICKFORD 1990) their upper third molars are markedly different in dimensions, those of *S. giganteus* being substantially bigger than those of *S. devauxi* (PICKFORD 2014). However, the Alçitepe tooth is not very far outside the range of variation of *Conohyus doati* (admittedly known from only a few specimens) so it is perhaps more likely that the specimen represents this species rather than *Sivachoerus devauxi* or *Sivachoerus giganteus*. The tooth is too large to belong to *Conohyus simorrensis* or *Retroporcus matritensis*.

Bayraktepe

Two teeth from Bayraktepe (m/3 and I2/) of which casts are available at PIMUZ (A/V 2375), are compatible with *Conohyus doati* in dimensions and crown morphology (the type of cusp wrinkling, the layout of the cusps, the shallow Furchen)

Paşalar

Suids from Paşalar were described by HÜNERMANN (1975) and FORTELIUS *et al*. (1996) (Figs 32, 33). The specimens housed in the PIMUZ are attributed to *Retroporcus matritensis* and *Listriodon splendens* typical of MN 6 in other parts of Europe (Table 19).

Table 18. Measurements (in mm) of suid upper molars from Schlatt am Kohlfirst, Switzerland, tentaively attributed to *Conohyus* sp. (B = bucco-lingual breadth, L – mesio-distal length, rt = right) (Author's own measurements).

Catalogue	Tooth	L	B	Data source
NHMB OSM 1060	M1/ rt	16.6	16.7	Own 2012
NHMB OSM 1060	M2/ rt	18.9	19.0	Own 2012
NHMB OSM 1060	M3/ rt	23.2	20.5	Own 2012

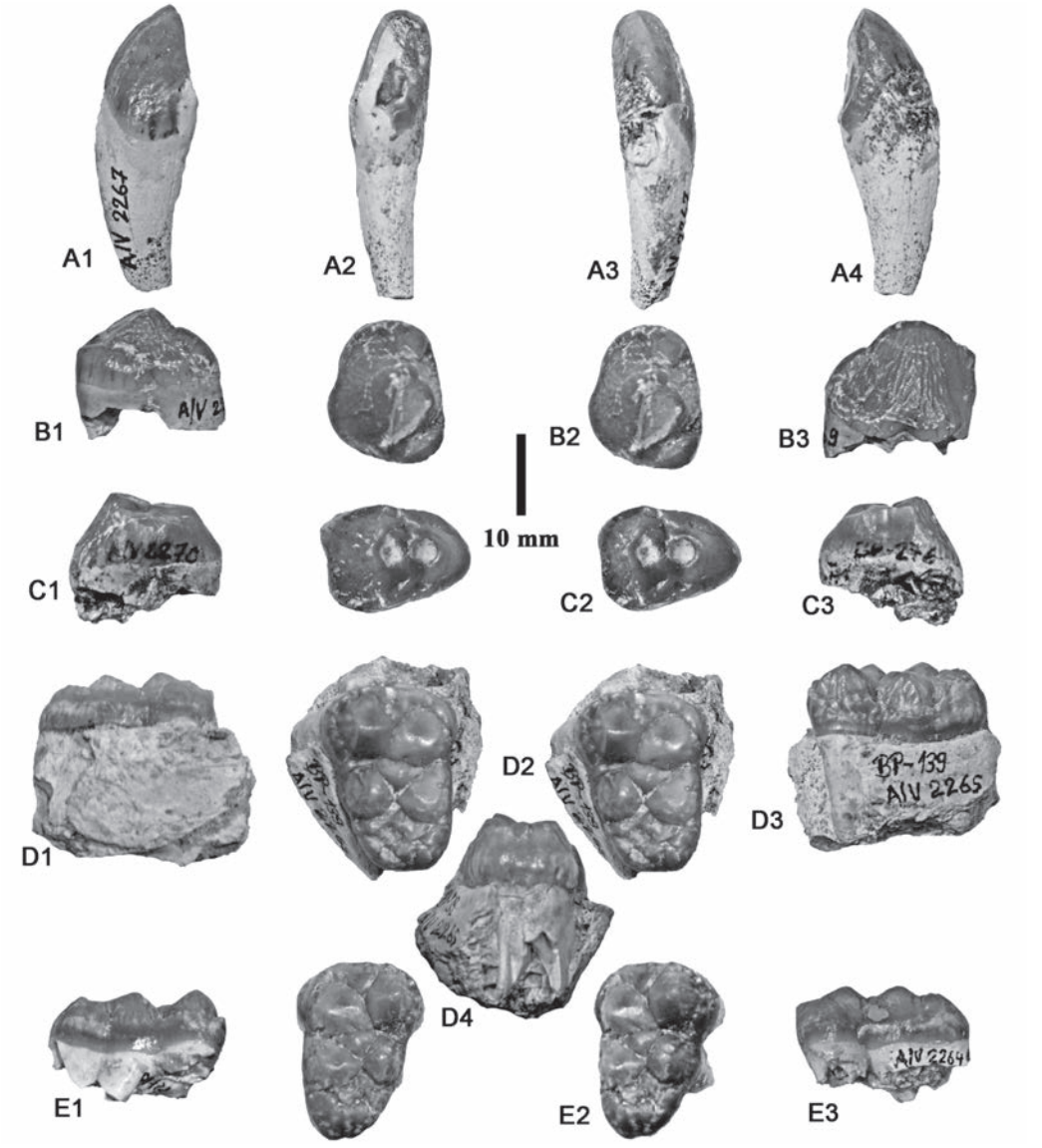

Fig. 32. Upper teeth of *Retroporcus matritensis* from Paşalar, Turkey, housed in the PIMUZ. **A**: A/V 2267, right I1/, A1: labial, A2: distal, A3: mesial, A4: lingual views; **B**: A/V 2269, right P3/, B1: lingual, B2: stereo occlusal, B3: buccal views; **C**: A/V 2270 left P4/, C1: distal, C2: stereo occlusal, C3: mesial views; **D**: A/V 2265, right M3/, D1: lingual, D2: stereo occlusal, D3: buccal, D4: distal view to show broadened, bifurcate, distal root; **E**: A/V 2264, left M3/, E1: lingual, E2: stereo occlusal, E3: buccal views.

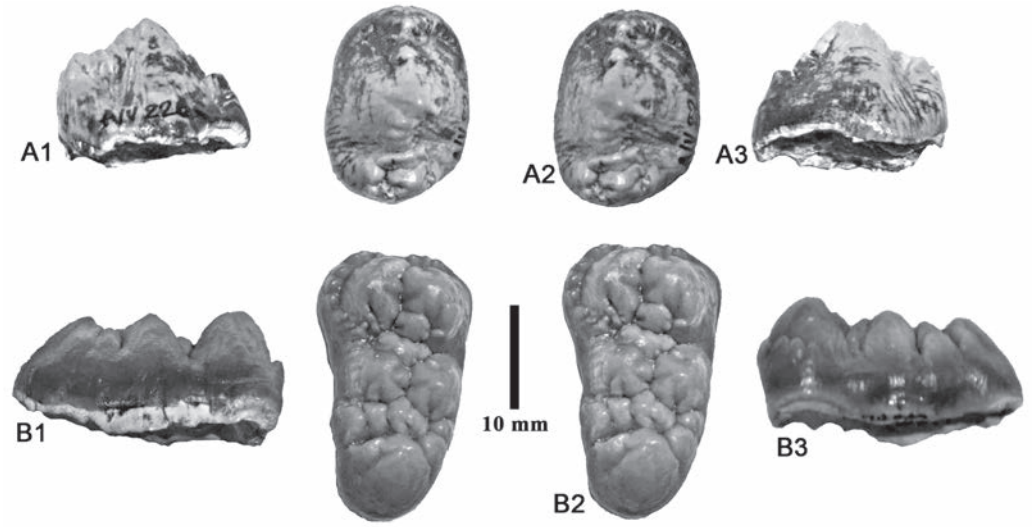

Fig. 33. Lower teeth of *Retroporcus matritensis* from Paşalar, Turkey, housed in the PIMUZ. **A**: A/V 2268, right p/4, A1: buccal, A2: stereo occlusal, A3: lingual views; **B**: A/V 2271, left m/3, B1: lingual, B2: stereo occlusal, B3: buccal views.

SLOVAKIA

Neudorf (Sandberg) (= Devinská Nová Ves, Sandberg)

THENIUS (1952) described and illustrated a p/4 and a fragment of left m/1 from Neudorf, Slovakia, as *Hyotherium soemmeringi* but the two specimens belong to *Conohyus simorrensis* (Fig. 34). The premolar shows the charactersitic enlargement relative to the first molar that occurs in tetraconodonts, and the style of wrinkling of the molar cusps accords with the usual condition in *Conohyus*, which does not occur in *Hyotherium*.The dimensions of the teeth are compatible with *Conohyus simorrensis*. The p/4 is too narrow to belong to *Retroporcus matritensis* (PICKFORD & LAURENT 2014).

ZAPFE (1983: figs 6, 7) attributed several heavily worn upper teeth and a lower canine from Neudorf to *Aureliachoerus aurelianensis* (STEHLIN, 1899–1900) but the specimens belong instead to *Choeromorus inonuensis* (PICKFORD & ERTÜRK, 1979), a palaeochoerid, as shown by the section of the canine, and the cusp layout of the molars allied to the high crown base. The isolated premolar that he described and illustrated (ZAPFE 1983: fig. 1) under the name *Hyotherium soemmeringi* belongs instead to *Conohyus simorrensis* as shown by its overall morphology, simple main cusp and its dimensions. Other suoids from Neudorf comprise the hyothere *Hyotherium soemmeringi*, the listriodont *Listriodon splendens*, and the palaeochoerids *Choeromorus sansaniensis* and *Choeromorus inonuensis*.

Table 19. Measurements (in mm) of listriodont and tetraconodont teeth from Paşalar, Turkey (B = bucco-lingual breadth, L = mesio-distal length, f = female, m = male, lt = left, rt = right, L = *Listriodon*, *R. = Retroporcus*) (Own are the author's own measurements).

Catalogue N°	Tooth	L	B	Taxon	Data source and comments
PIMUZ A/V 2300 cast	c/1 f	11.0	9.3	*L. splendens*	Own 2014
PIMUZ A/V 2324	c/1 f	12.7	8.7	*L. splendens*	Own 2014
PIMUZ A/V 2333	c/1 lt m	17.0	12.0	*L. splendens*	Own 2014
PIMUZ A/V 2333	c/1 lt m	17.0	11.9	*L. splendens*	Own 2014
PIMUZ A/V 2334	c/1 lt m	15.5	11.0	*L. splendens*	Own 2014
PIMUZ A/V 2333	c/1 rt m	16.8	11.6	*L. splendens*	Own 2014
PIMUZ A/V 2334	c/1 rt m	18.5	12.0	*L. splendens*	Own 2014
PIMUZ A/V 2326	C1/ f	13.0	8.4	*L. splendens*	Own 2014
PIMUZ A/V 2341 cast	D3/ rt	15.6	12.4	*L. splendens*	Own 2014
PIMUZ A/V 2305	i/1 lt	14.5	-	*L. splendens*	Own 2014
PIMUZ A/V 2308	i/1 rt	12.0	9.8	*L. splendens*	Own 2014
PIMUZ A/V 2317	i/1 rt	11.5	10.0	*L. splendens*	Own 2014
PIMUZ A/V 2322	i/1 rt	11.0	9.0	*L. splendens*	Own 2014
PIMUZ A/V 2299 cast	i/2 lt	15.0	10.6	*L. splendens*	Own 2014
PIMUZ A/V 2323	i/2 lt	13.0	10.0	*L. splendens*	Own 2014
PIMUZ A/V 2323	i/2 lt	13.0	10.6	*L. splendens*	Own 2014
PIMUZ A/V 2298 cast	i/2 rt	14.0	9.2	*L. splendens*	Own 2014
PIMUZ A/V 2321	i/2 rt	13.0	9.3	*L. splendens*	Own 2014
PIMUZ A/V 2320	i/3 lt	16.0	8.2	*L. splendens*	Own 2014
PIMUZ A/V 2320	i/3 lt	16.0	8.6	*L. splendens*	Own 2014
PIMUZ A/V 2297 cast	i/3 rt	15.0	8.0	*L. splendens*	Own 2014
PIMUZ A/V 2316	i/3 rt	16.0	9.0	*L. splendens*	Own 2014
PIMUZ A/V 2290 cast	I1/ lt	35.0	9.0	*L. splendens*	Own 2014
PIMUZ A/V 2293 cast	I1/ lt	38.0	11.0	*L. splendens*	Own 2014
PIMUZ A/V 2301 cast	I1/ lt	27.0	14.0	*L. splendens*	Own 2014
PIMUZ A/V 2302 cast	I1/ rt	24.0	11.4	*L. splendens*	Own 2014
PIMUZ A/V 2325	I3/ lt	13.0	6.0	*L. splendens*	Own 2014
PIMUZ A/V 2287	m/1 lt	18.0	13.0	*L. splendens*	Own 2014
PIMUZ A/V 2260 cast	m/2 lt	22.0	16.0	*L. splendens*	Own 2014
PIMUZ A/V 2263	m/2 rt	22.0	16.3	*L. splendens*	Own 2014
PIMUZ A/V 2286	m/2 rt	21.0	16.5	*L. splendens*	Own 2014
PIMUZ A/V 2337	m/3 rt	33.3	18.5	*L. splendens*	Own 2014
PIMUZ A/V 2337	m/3 rt	31.0	17.3	*L. splendens*	Own 2014
PIMUZ A/V 2337	m/3 rt	35.5	19.2	*L. splendens*	Own 2014

Table 19. Continued

Catalogue N°	Tooth	L	B	Taxon	Data source and comments
PIMUZ A/V 2339	m/3 rt	33.5	18.5	*L. splendens*	Own 2014
PIMUZ A/V 2367	m/3 rt	35.0	18.6	*L. splendens*	Own 2014
PIMUZ A/V 2307	M1/ lt	17.4	16.6	*L. splendens*	Own 2014
PIMUZ A/V 2292 cast	M1/ rt	17.2	15.1	*L. splendens*	Own 2014
PIMUZ A/V 2311	M2/ rt	23.0	23.0	*L. splendens*	Own 2014
PIMUZ A/V 2288	M3/ rt	23.0	18.9	*L. splendens*	Own 2014
PIMUZ A/V 2291 cast	M3/ rt	25.0	22.0	*L. splendens*	Own 2014
PIMUZ A/V 2312	M3/ rt	24.6	22.0	*L. splendens*	Own 2014
PIMUZ A/V 2314	p/2 lt	14.4	9.0	*L. splendens*	Own 2014
PIMUZ A/V 2315	p/2 lt	13.0	8.9	*L. splendens*	Own 2014
PIMUZ A/V 2313	p/3 rt	14.9	9.7	*L. splendens*	Own 2014
PIMUZ A/V 2318	p/3 rt	16.3	10.0	*L. splendens*	Own 2014
PIMUZ A/V 2309	p/4 rt	17.0	13.5	*L. splendens*	Own 2014
PIMUZ A/V 2310	p/4 rt	17.3	12.7	*L. splendens*	Own 2014
PIMUZ A/V 2303 cast	P2/ lt	14.0	9.3	*L. splendens*	Own 2014
PIMUZ A/V 2294 cast	P3/ rt	16.0	14.0	*L. splendens*	Own 2014
PIMUZ A/V 2295 cast	P3/ rt	16.5	13.5	*L. splendens*	Own 2014
PIMUZ A/V 2306	P3/ rt	18.0	14.9	*L. splendens*	Own 2014
PIMUZ A/V 2289	P4/ lt	14.2	16.0	*L. splendens*	Own 2014
PIMUZ A/V 2319	P4/ lt	14.5	18.2	*L. splendens*	Own 2014
PIMUZ A/V 2261 cast	p/4 rt	17.0	14.2	*R. matritensis*	Own 2014
PIMUZ A/V 2264	M3/ lt	22.2	16.5	*R. matritensis*	Own 2014
PIMUZ A/V 2265	M3/ rt	22.1	16.8	*R. matritensis*	Own 2014
PIMUZ A/V 2266 cast	m/1 rt	17.3	12.7	*R. matritensis*	Own 2014
PIMUZ A/V 2267	I1/ rt	14.0	9.3	*R. matritensis*	Own 2014
PIMUZ A/V 2268	p/4 rt	19.0	14.2	*R. matritensis*	Own 2014; HÜNERMANN 1975 as p/3
PIMUZ A/V 2269	P3/ rt	17.7	15.2	*R. matritensis*	Own 2014
PIMUZ A/V 2270	P4/ lt	13.3	18.5	*R. matritensis*	Own 2014
PIMUZ A/V 2271	m/3 lt	26.0	16.0	*R. matritensis*	Own 2014
PIMUZ A/V 2304 cast	i/1 rt	5.7	9.0	*R. matritensis*	Own 2014

This combination of suoids indicates a correlation to MN 6, younger than the MN 5 estimate made by ZAPFE (1983) and they could indicate the possibility of a mixed fauna.

Fig. 34. Neudorf, Slovakia, **A**: NHMW 2003z0089/0041, left p/4, A1: buccal, A2: stereo triplet occlusal view, A3: lingual view; **B**: NHMW 1997z0178/1987, left m/1 *Conohyus simorrensis*, stereo triplet occlusal view.

SPAIN

Montejo de la Vega

Retroporcus complutensis likely occurs at Montejo de la Vega. The poorly preserved fossils were previously identified as *Hyotherium soemmeringi* (Van der Made 1990) and then as *Conohyus simorrensis* (Mazo *et al*. 1998; Van der Made *et al*. 2014). The rounded cusps in the molars, the subdued Furchen and the occlusal outline of the teeth indicate that they do not belong to *Hyotherium* and the specimens are too small to belong to *Conohyus* (Pickford & Laurent 2014).

Molina de Aragon

The karst deposits at Molina de Aragon yielded a rich fauna correlated to the base of MN 9. Among the fossils from the site are several fragments of suid teeth which can be attributed with some degree of confidence to *Parachleuastochoerus valentini*. The unworn upper molars show a beaded lingual cingulum and low bunodont cusps with highly wrinkled enamel (Fig. 35, Table 20).

Discussion and conclusions

Fossil suids have long been known to be useful for biostratigraphy, especially in Africa where several lineages underwent rapid morphological and metric evolution (Cooke & Wilkinson 1978). For successful determination of the biostratigraphic meaning of fossils, correct identification is essential, as was pointed out by Van der Made (2010). Some European suids such as *Propotamochoerus palaeochoerus* were perceived by some

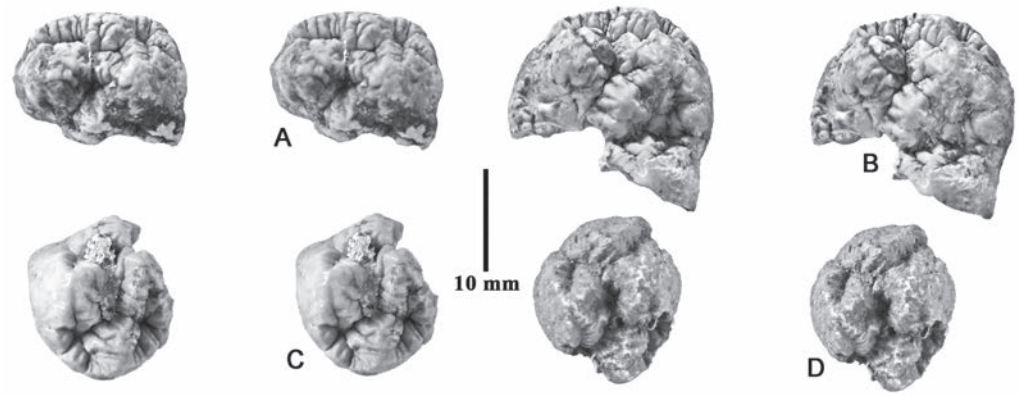

Fig. 35. Stereo occlusal images of tooth fragments from Molina de Aragon attributed to *Parachleuastochoerus valentini*. **A**: MNCN MLA 2, mesial loph of right M1/, **B**: MNCN MLA 1, mesial loph of right M2/, **C**: MNCN MLA 3, distal part of right m/2, **D**: MNCN MLA 4, distal part of right m/2.

authors to have survived through long time spans; in this case MN 9 to MN 13 (VAN DER MADE 1990) yet the only reliably identified specimens from Europe are restricted to MN 9. No fossils of this species have been reported from MN 10 to MN 12, and the material from MN 13 (HELLMUND 1995) attributed to it probably belongs to a distinct taxon. Records of *P. palaeochoerus* from MN 8 (ALBA *et al*. 2006) are based on misidentified molars of *Parachleuastochoerus valentini*, the premolars of the same suids being erroneously identified as *Conohyus simorrensis*. The difficulty of identifying isolated molars of large species of *Parachleuastochoerus* and *Propotamochoerus palaeochoerus* was recognised by VAN DER MADE *et al*. (2014) but the holotype snout of *Parachleuastochoerus valentini* from St Gaudens provides the crucial association between premolars and molars which resolves the issue (PICKFORD 2014). HÜNERMANN (1968) was aware of the problems but was overly influenced by his acceptance of the notion prevailing at the time of his studies that the Dinotheriensande of the Rhine Graben comprised deposits which accumulated only during MN 9. He thus identified 8 taxa of suids in the Dinotheriensande (six in the text plus two additional taxa in the tables of measurements) whereas there are at least 12 species in the deposits ranging in age from MN 4 to MN 12 (PICKFORD 2013b).

Table 20. Measurements (in mm) of teeth from Molina de Aragon, Spain, attributed to *Parachleuastochoerus valentini* (lt = left, rt = right, - measurement not possible).

Catalogue	Tooth	Length	Breadth
MNCN MLA 1	M2/ rt	-	20.4
MNCN MLA 2	M1/ rt	-	17.5
MNCN MLA 3	m/2 rt	-	14.5
MNCN MLA 4	m/2 rt	-	14.7

The rediscovery of Lartet's (1851) hypodigm of "*Sus*" *simorrensis* and Filhol's (1882) type specimen of "*Sus*" *valentini* throws new light on European tetraconodont evolution, and reveals that many European suid fossils ranging in age from MN 6 to MN 10 have been misidentified. The absence of these fossils from the palaeontological conscience for more than a century (Pickford & Laurent 2014; Pickford 2014) meant that authors were obliged to compare their fossils with samples from other localities. The retrieval of the type series reveals that the fossils used to define the species "*Sus*" *simorrensis* comprised two taxa (*Conohyus simorrensis* and *Retroporcus matritensis*) and the holotype of "*Sus*" *valentini* was for a long time mislabelled as *Conohyus simorrensis*.

Revision of European tetraconodonts (Pickford & Laurent 2014; Pickford 2014) based on revised diagnoses of genera and species (see Systematic Palaeontology section above) is now possible, and this paper presents a preliminary reassessment of many of the fossils. It is clear that there have been frequent misidentifications in the literature due principally to the "loss" of the type material of *Conohyus simorrensis* and *Parachleuastochoerus valentini*. It is also clear that there remains the possibility of other instances of misattributed fossils, in particular for samples that consist of a few isolated premolars or molars, especially if the specimens are moderately or heavily worn. Specimens or samples that contain associated premolars and molars are more reliably identified, because the premolar to molar proportions yield a reliable indication of the subfamily and the genus, whilst dimensional data provide reliable species determination once the genus has been properly identified.

This paper presents preliminary results of an examination of Middle and Late Miocene suids from many localities in Austria, Slovakia, Germany, Turkey, Switzerland and Spain and provides a biostratigraphy of the deposits based in their suid content (Annex). A pattern is emerging that tetraconodonts (and other suids) are indeed more reliable indicators of geological time than previously thought when many specimens were misidentified. There remain some contentious issues, but this is inevitable when dealing with localities that have yielded only a few isolated teeth. However, several cases where there were inconsistencies between the biostratigraphic conclusions of authors working on suids and non-suid mammals have now been resolved following more accurate identification of the suid specimens. Further detailed work will undoubtedly improve the reputation of European fossil suids for carrying out biostratigraphy.

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Annex

List of European suid localities and correlations to the MN Zonation, focussing on listriodonts, tetraconodonts and suines in the time span MN 05-MN 11.

1. *Listriodon latidens,* 2. *Listriodon lockharti,* 3. *Listriodon splendens,*

4. *Retroporcus complutensis,* 5. *Retroporcus matritensis,*

6. *Conohyus simorrensis,* 7. *Conohyus sp.* 8. *Conohyus doati,*

9. *Versoporcus steinheimensis,* 10. *Versoporcus grivensis,*

11. *Parachleuastochoerus valentini, 12. Parachleuastochoerus huenermanni,*

13. *Parachleuastochoerus crusafonti,* 14. *Parachleuastochoerus kretzoii,*

15. *Propotamochoerus palaeochoerus,* 16. *Hippopotamodon major.*

Country	Locality	Biostratigraphy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Croatia	Lucane	MN 05												X				
France	Hommes	MN 05							X									
France	Pontlevoy	MN 05		X				X										
France	Channay	MN 05						X										
France	Lublé	MN 05						X										
Spain	Puente de Vallecas	MN 05		X			X											
Serbia	Mala Miliva	MN 05	X			X												
Spain	Montego de la Vega	MN 05				X												
Spain	Somosaguas	MN 05				X												
Germany	Sigmaringen	MN 05/6			X													
Germany	Breitenbrunn	MN 06												X				
Germany	Günzberg	MN 06							X									
Turkey	Bâlâ	MN 06							X									
Switzerland	Elgg	MN 06					X	X										
Austria	Ilz	MN 06					X?	X										
Slovakia	Neudorf	MN 06			X			X										
Austria	Neufeld bei Ebenfurt	MN 06						X										
Germany	Pischelsberg	MN 06						X										
Spain	Carpetana	MN 06						X										
Switzerland	Käpfnach	MN 06						X										
Austria	St Oswald	MN 06						X										
France	Auverse	MN 06					X											
France	Faluns	MN 06					X											
France	Lasse	MN 06					X											
Germany	Laichingen	MN 06			X		X											

Country	Locality	Biostratigraphy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Turkey	Pasalar	MN 06			X		X											
Austria	Au bei Auflenz	MN 06					X											
Austria	Göriach	MN 06					X											
Austria	Rosenthal bei Köpflach	MN 06					X											
Germany	Derndorf	MN 06					X											
Germany	Helsighausen	MN 06					X											
Switzerland	Aargau	MN 06																
Austria	Mannersdorf	MN 06			X													
Austria	St Margarethen	MN 06			X													
France	Sansan	MN 06			X													
France	Gers	MN 06			X													
Germany	Stätzling	MN 06			X													
Spain	Arroyo de Val	MN 06			X													
Spain	Manchones	MN 06			X													
Spain	Las Gruas	MN 06			X													
Spain	Murrero	MN 06			X													
Spain	Paracuellos	MN 06			X													
Switzerland	Helsighausen	MN 06			X													
Turkey	Candir	MN 06			X													
Turkey	Inönu	MN 06			X													
Austria	Leithegebirge	MN 06			X													
Spain	M-407	MN 06			X													
Germany	Gau-Weinheim	MN 06 + MN 09					X			X				X	X	X	X	
Germany	Esselborn	MN 06 + MN 09			X		X										X	
Germany	Eppelsheim	MN 06 + MN 09					X										X	
Germany	Urlau	MN 06/7						X										
France	Laroque Magnoac	MN 06/7			X													
France	Castelnau de Barbarens	MN 06/7			X													
Austria	Kaisersteinbruch	MN 06/8			X						X							
Austria	Stützenhofen	MN 06/8			X													
France	Tri sur Brize	MN 06/8			X													
Germany	Mauer	MN 06/8			X													
Germany	Mehring (Mering)	MN 06/8			X													
Germany	Morslingen (Morsingen)	MN 06/8			X													
Germany	Prittlbach	MN 06/8			X													
Hungary	Sooskut	MN 06/8			X													
Romania	Krivadia	MN 06/8			X													

Country	Locality	Biostratigraphy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Spain	Cisterniga	MN 06/8			X													
Germany	Steinheim	MN 07			X						X							
Turkey	Yaylacilar	MN 07			X													
France	La Grive	MN 07/8			X			X			X	X		X				
Turkey	Bayraktepe	MN 07/8			X					X								
Switzerland	Schlatt am Köhlfirst	MN 07/8							X									
France	Castelnau d'Arbieu	MN 07/8						X										
Spain	Alhambra	MN 07/8						X										
France	Malartic	MN 07/8					X											
France	Simorre	MN 07/8			X		X											
France	Villefranche d'Astarac	MN 07/8			X		X											
France	Escanecrabe	MN 07/8			X													
Spain	Cerro del Ortero	MN 07/8			X													
Spain	Solera	MN 07/8			X													
Spain	Toril	MN 07/8			X													
Switzerland	La Chaux-de-Fonds	MN 07/8			X													
Switzerland	Le Locle	MN 07/8			X													
Turkey	Sariçay	MN 07/8			X													
Austria	Atzelsdorf	MN 08			X											X		
Spain	Saint Quirze	MN 08			X								X	X				
France	St Gaudens	MN 08			X								X					
Spain	Can Mata	MN 08											X					
Switzerland	Anwil	MN 08					X					X						
Spain	Can Feliu	MN 08			X						X							
Spain	Hostalets de Pierola	MN 08			X						X							
Spain	Can Almiral	MN 08									X							
France	Le Fousseret	MN 08						X										
Poland	Przeworno	MN 08						X										
Germany	Massenhausen	MN 08			X													
Spain	Mas de Olmo	MN 08			X													
Turkey	Lower Sinap	MN 08			X													
Germany	Wissberg	MN 08 + 09			X												X	
Turkey	Alcitepe (Nuri Yamut)	MN 08 + 09			X					X								
Switzerland	Charmoille	MN 08/9										X		X				
Germany	Kleineisenbach	MN 08/9						X					X					
Austria	Klein Hadersdorf	MN 08/9			X								X					
Austria	Hollabrunn	MN 08/9											X					

Country	Locality	Biostratigraphy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Austria	Pitten	MN 08/9											X					
Spain	Molina de Aragon	MN 08/9											X					
Austria	Eichkogel	MN 08/9			X								X					
Austria	Gratkorn	MN 08/9			X							X						
Spain	Castell de Barbera	MN 08/9			X						X							
Germany	Hammerschmiede	MN 08/9						X		X								
France	Bonnefond	MN 08/9			X					X								
Germany	Wartenberg bei Erding	MN 08/9			X								X					
Spain	El Buste	MN 08/9								X								
Portugal	Azambujeira	MN 08/9							X									
Germany	Hinterauerbach bei Wartenberg	MN 09											X					
Austria	Mariathal	MN 09														X	X	
Hungary	Rudabanya	MN 09														X	X	
France	Doué	MN 09					X	X									X	
Spain	Can Llobateres	MN 09			X												X	
Germany	Steineberg/Edelstahl	MN 09															X	
Austria	Belvedere Wien III	MN 09															X	
Austria	Brunn bei Vösendorf	MN 09															X	
Austria	Gross Mugl	MN 09															X	
Austria	Hainberg	MN 09															X	
Austria	Hennersdorf	MN 09															X	
Austria	Inzersdorf	MN 09															X	
Austria	Lassnitzhöhe bei Graz	MN 09															X	
Austria	Magersdorf	MN 09															X	
Austria	Meidling	MN 09															X	
Austria	Nexing	MN 09															X	
Austria	Pyhra	MN 09															X	
Austria	Saaz bei Feldbach	MN 09															X	
Austria	St Kind bei Riegersberg	MN 09															X	
Austria	St Peter bei Wies	MN 09															X	
Austria	Wien X (Wienerburg)	MN 09															X	
Austria	Wiessen	MN 09															X	
Austria	Götzendorf	MN 09															X	
Austria	Johnsdorf	MN 09															X	
France	Drôme	MN 09															X	
France	La Tour du Pin	MN 09															X	

Country	Locality	Biostratigraphy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
France	Labécède	MN 09															X	
France	Montréjeau	MN 09															X	
Germany	Dintesheim	MN 09															X	
Germany	Mörgen	MN 09															X	
Germany	München (Isarbett)	MN 09															X	
Germany	Neuhausen	MN 09															X	
Germany	Salmendingen	MN 09															X	
Germany	St Georgen	MN 09															X	
Germany	St Georgen bei Diesen	MN 09															X	
Germany	Wallertsheim	MN 09															X	
Germany	Westhofen	MN 09															X	
Germany	Wolfsheim	MN 09															X	
Hungary	Oedenberg	MN 09															X	
Moldova	Braila	MN 09															X	
Moldova	Ghidighici	MN 09															X	
Ukraine	Grytsiv	MN 09															X	
Spain	Ballestar	MN 09															X	
Spain	Can Ponsic	MN 09												X	X			
Spain	Seu de Urgell	MN 09												X				
Germany	Tutzing	MN 09											X					
Spain	Mira	MN 09											X					
Austria	Gaiselberg	MN 09								X								
Portugal	Fonte de Pinheiro	MN 09								X								
Spain	La Ciesma	MN 09								X								
Germany	Markt Rettenbach	MN 09			X													
Spain	Santiga	MN 09			X													
Spain	Can Cunile	MN 09			X													
Portugal	Aveiras de Baixo	MN 09			X													
Germany	Melchingen	MN 09 + Turolian												X	X		X	
Austria	Wien III	MN 09/10															X	
Spain	La Tarumba	MN 10															X	
France	Vareille	MN 11																X