

# Taxonomic study of the pigs (Suidae, Mammalia) from the late Middle Miocene of Gratkorn (Austria, Styria)

Jan van der Made · Jérôme Prieto · Manuela Aiglstorfer ·  
Madelaine Böhme · Martin Gross

Received: 21 November 2013 / Revised: 26 January 2014 / Accepted: 4 February 2014 / Published online: 23 April 2014  
© Senckenberg Gesellschaft für Naturforschung and Springer-Verlag Berlin Heidelberg 2014

**Abstract** The locality of Gratkorn of early late Sarmatian age (Styria, Austria, Middle Miocene) has yielded an abundant and diverse fauna, including invertebrates, micro-vertebrates and large mammals, as well as plants. As part of the taxonomical study of the mammals, two species of suids, are described here and assigned to *Listriodon splendens* Von Meyer, 1846 and *Parachleuastochoerus steinheimensis* (Fraas, 1870). As the generic affinities of the latter species were subject to debate, we present a detailed study of the evolution of the

European Tetraconodontinae. The morphometric changes that occurred in a series of fossil samples covering the known temporal ranges of the species *Pa. steinheimensis* are documented. It is concluded that *Parachleuastochoerus* includes three species, namely *Pa. steinheimensis*, *Pa. huenermanni* and *Pa. crusafonti*. Evolutionary changes are recognised among the *Pa. steinheimensis* fossil samples. In addition, it is proposed that the subspecies *Pa. steinheimensis olujici* was present in Croatia long before the genus dispersed further into Europe.

This article is an additional contribution to the special issue "The Sarmatian vertebrate locality Gratkorn, Styrian Basin".

J. van der Made (✉)

Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, c. José Gutiérrez Abascal 2, 28006 Madrid, Spain  
e-mail: mcnjv538@mncn.csic.es

J. Prieto

Department of Earth- and Environmental Science, Palaeontology, Ludwig-Maximilians-University Munich, Richard-Wagner-Str. 10, 80333 Munich, Germany  
e-mail: j.prieto@lrz.uni-muenchen.de

M. Aiglstorfer · M. Böhme

Fachbereich Geowissenschaften, Eberhard Karls Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany

M. Aiglstorfer

e-mail: manuela.aiglstorfer@senckenberg.de

M. Böhme

e-mail: m.boehme@ifg.uni-tuebingen.de

M. Aiglstorfer · M. Böhme

Senckenberg Center for Human Evolution and Palaeoenvironment (HEP), Sigwartstraße 10, 72076 Tübingen, Germany

M. Gross

Department for Geology and Palaeontology, Universalmuseum Joanneum, Weinzöttlstrasse 16, 8045 Graz, Austria  
e-mail: martin.gross@museum-joanneum.at

**Keywords** Listriodontinae · Tetraconodontinae · Middle Miocene · Sarmatian · Styrian Basin

## Introduction

Suoidea (pigs and their primitive relatives) are well represented in the Miocene deposits of Austria. Especially in the Styrian Basin, diversified faunas document this superfamily, and show its importance for biostratigraphic purposes (Mottl 1970; Van der Made 1998a). These finds are most often historical and the exact stratigraphic and faunal context is poorly documented, at least to modern standards. It is the contrary in the early late Sarmatian s. str. fossil locality of Gratkorn, where a large panel of plants, invertebrates and micro- and macrovertebrates have been brought to light (e.g. Gross et al. 2007, 2011; Harzhauser et al. 2008; Böhme et al. 2014, this issue). The geologic and sedimentary setting, as well as the stratigraphy of Gratkorn, is described by Gross et al. (2011; 2014, this issue). In the context of this special issue, which proposes a complete integrated overview of the terrestrial fauna from Gratkorn, we present here the well-preserved suids from Gratkorn, their taxonomy and autecology.

## Methods and material

The nomenclature of the dental elements and measurement methods follow Van der Made (1996). The measurements are indicated by the following acronyms:

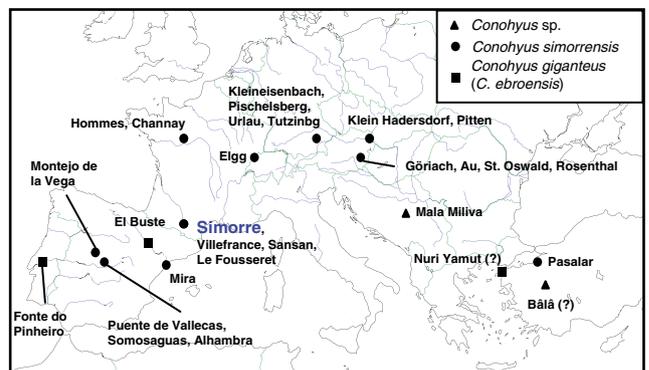
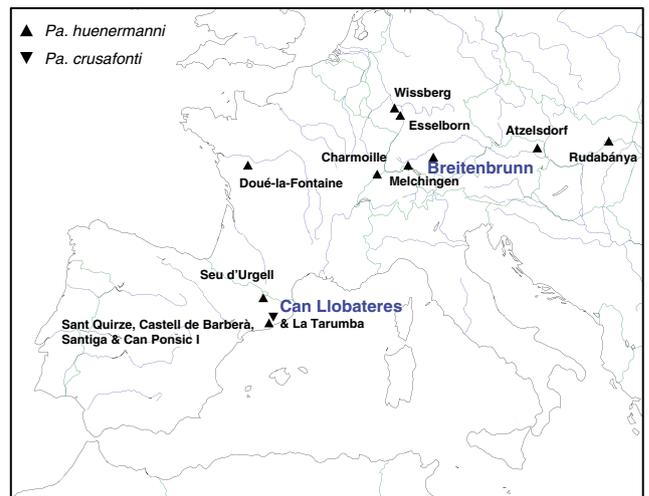
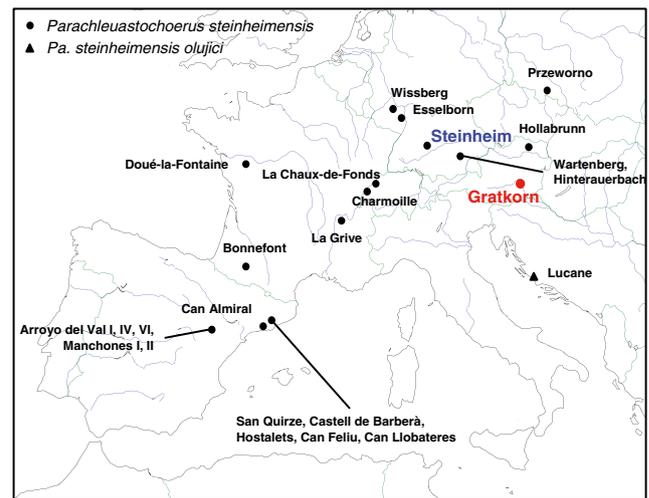
D	Depth of the mandible, measured on the lingual side, below the different cheek teeth.
DAP	Antero-posterior diameter.
DAPd	DAP at the distal end of a bone.
DLL	Linguo-labial diameter in incisors.
DMD	Mesio-distal diameter in incisors.
DT	Transverse diameter.
DTa	DT of the anterior lobe of a tooth.
DTd	DT at the distal end of a bone.
DTp	DT of the posterior diameter of a tooth.
DTpp	DT of the third lobe of a tooth.
H	Height of a tooth.
Ha	H measured at the anterior lobe of a tooth and, in lower molars, on the lingual side.
Hli	H of a premolar, measured on the lingual side.
Li	Width of the lingual side of a lower male canine.
La	Width of the labial side of a lower male canine.
Po	Width of the posterior side of a lower male canine.
Ri	Radius of outer curvature of a lower male canine.
Ro	Radius of inner curvature of a lower male canine.
W	Width of the mandible, measured below the different cheek teeth.
Ta	Enamel thickness, measured at the anterior lobe of a molar, in lower molars on the lingual side.

The fossils from Gratkorn are housed in the collections of the Universalmuseum Joanneum in Graz (Geology & Palaeontology), Austria (UMJGP) and in the Paläontologische Sammlung der Universität Tübingen, Germany (GPIT).

Comparative material of Listriodontinae is reported by Van der Made (1996). In the following, the comparative material for tetraconodontine suids and for *Propotamochoerus palaeochoerus* is listed in alphabetical order and the corresponding collections or publications are indicated. For the geographic position of the tetraconodontine localities see Fig. 1.

### *Parachleuastochoerus steinheimensis*

Arroyo del Val I	IVAU
Arroyo del Val IV	IVAU
Arroyo del Val VI	IVAU
Bonnefont	MNHN
Can Feliu	IPS
Can Almira	IPS
Can Llobateres	IPS
Castell de Barberà	IPS
Charmoille	NMM (cast)
Doué-la-Fontaine	MNHN



**Fig. 1** The geographic position of Gratkorn and of selected localities with Tetraconodontinae in Europe and Anatolia

Esselborn	HLD
Hinterauerbach	SNSB-BSPG
Hollabrunn (Oberhollabrunn)	IPUW
Hostalets	IPS
La Grive (old collections)	MGL, IGF
La Chaux de Fonds	MHNCHF
Manchones I	IVAU, IPS

Manchones II	IVAU
Przeworno 1	ISEAK
Przeworno 2	ISEAK
San Quirze	MLGSB, IPS, CVB
Steinheim	SMNS, NMB, MGL
Wartenberg	SNSB-BSPG
Wissberg	NMM, HLD

*Pa. steinheimensis olujici*

Lucane	Bernor et al. (2004)
--------	----------------------

*Parachleuastochoerus huenermanni* (“*Pa. kretzoï*”)

Breitenbrunn	Heissig (1989)
Can Ponsic I	IPS
Castell de Barberà	IPS
Charmoille	HLD (cast)
Doué-la-Fontaine	MNHN (cast)
Esselborn	FISF, HLD
?Melchingen	GPIT
Rudabánya*	HGSB
San Quirze	IPS
Seu d’Urgell	MLGSB
Vösendorf	NMW
Wissberg	NMM, HLD

*Parachleuastochoerus crusafonti*

Can Llobateres	IPS
La Tarumba	IPS

*Conohyus simorrensis*

Alhambra	MNCN
Au	UMJGP
Bâlâ	MTA
?Channay	Ginsburg (1977)
Elgg	NMB
Göriach	UMJGP, IGGML, NMW, NMB
Hommes	Ginsburg (1977)
Klein Hadersdorf I	PUW
Kleineisenbach	SNSB-BSPG
?Lublé	Ginsburg (1977)
Le Fousseret	MNHN
Mira	IPS
Montejo de la Vega	MNCN
Nuri Yamut	EUI
Paşalar	PDTCAU, PIMUZ
Pitten	IPUW
Pischelsberg	SNSB-BSPG
Puende de Vallecas	MNCN
Rosenthal	UMJGP
Sansan	Ginsburg (1977)
Simorre	MNHN
Somosaguas	UCM
St. Oswald	UMJGP

Tutzing	NMB (cast)
Urlau	SNSB-BSPG
Villefranche d’Astarac	MNHN

*Conohyus giganteus*

El Buste	MPZ
Fonte do Piheiro	GML

*Propotamochoerus palaeochoerus*

Ballestar	IPS
Can Ponsic I	IPS
Can Llobateres	IPS
Castell de Barberà	IPS
Doué-la-Fontaine	MNHN
Eppelsheim	HLD
Esselborn	HLD
Gaiselberg	HLD
Gau Weinheim	SNSB-BSPG, HLD
Götzendorf	NMW
Grossmugl	NMW
Grytsev	Van der Made et al. (1999)
Hennersdorf	NMW
Hostalets	IPS, CVB
Johnsdorf	UMJGP
Mariathal	IPUW
Magersdorf	NMW, IPUW
Montréjeau	NMB
München U-Bahntunnel	SNSB-BSPG
Steineberg/Edelstahl	NMW
Rudabánya	HGSB
Vareille	
Vösendorf	NMW, IPUW
Wien XII St. Oswald	NMW
Wissberg	NMM, HLD

The collections are indicated with the following acronyms:

SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
CVB	Collection Villalta, Barcelona.
EUI	Ege Universitesi, Izmir.
FISF	Forschungsinstitut Senckenberg, Frankfurt; presently Senckenberg Forschungsinstitut und Naturmuseum Frankfurt
GML	Geological Museum Lisbon.
GPIT	Paläontologische Sammlung der Universität Tübingen, Germany.
HGSB	Hungarian Geological Survey, Budapest.
HLD	Hessisches Landesmuseum, Darmstadt.
IGF	Istituto di Geologia, now Museo di Storia Naturale, Firenze.

IGGML	Institut für Geowissenschaften/Geologie der Montanuniversität, Leoben.
IPS	Instituto de Paleontología, Sabadell.
IPUW	Institut für Paläontologie der Universität, Wien (Vienna).
ISEAK	Institute of Systematics and Evolution of Animals, Kraków.
IVAU	Instituut Voor Aardwetenschappen, Utrecht.
IVPP	Institute for Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing.
MGL	Museum Guimet, Lyon.
MHNCHF	Musée d' Histoire Naturelle, La Chaux-de-Fonds.
MLGSB	Museu i Laboratori de Geologia del Seminari, Barcelona.
MNHN	Muséum National d'Histoire Naturelle, Paris.
MPZ	Museo Paleontológico de la Universidad de Zaragoza.
MTA	Maden Tetkik ve Arama, Ankara.
NMM	Naturhistorisches Museum, Mainz.
NMB	Naturhistorisches Museum, Basel.
NMW	Naturhistorisches Museum, Wien (Vienna).
PDTCAU	Paleoantropoloji, Dil ve Tarih Cografya Facultesi, Ankara Universitesi (Sección de paleoantropología, universidad de Ankara).
PIMUZ	Paläontologisches Institut und Museum der Universität, Zürich.
SMNS	Staatliches Museum für Naturkunde, Stuttgart.
UMJGP	Universalmuseum Joanneum in Graz (Geology & Palaeontology), Austria.

### Systematic palaeontology

Order Artiodactyla Owen, 1848  
 Superfamily Suoidea Gray, 1821  
 Family Suidae Gray, 1821  
 Subfamily Listriodontinae Gervais, 1859  
 Genus *Listriodon* Von Meyer, 1846

**Type species:** *Listriodon splendens* Von Meyer, 1846

**Other species included in *Listriodon*:** *Listriodon pentapotamiae* (Falconer, 1868)

Here, the classification of Van der Made (1996, 1997) is followed, which limits the genus to the lophodont Listriodontinae with  $C^m$  that curve outwards and upwards. Alternative classifications are by Orliac et al. (2006, 2009) and Pickford and Morales (2003), who include a variety of sublophodont and even bunodont species, but exclude others. The discussion of these differences is beyond the scope of this paper.

*Listriodon splendens* Meyer, 1846

2011 *Listriodon splendens* - Gross et al., figs. 4a,b.

A lengthy synonymy was given by Van der Made (1996, pp. 98–100). *Listriodon robustus* Yan 1979 was not included in this synonymy, but in that of *Bunolistriodon intermedius*, because the molars looked sublophodont on the published photographs. Later, Liu Liping showed JvdM at the IVPP the type material of this species. Despite some archaic features, it has reached full lophodonty. Therefore, it should be included in *Listriodon splendens*.

**Type material:** The lectotype is a right I1 figured by Stehlin (1899–1900, pl. 5, fig. 22) and Van der Made (1996, pl. 41, fig. 1). Paralectotypes were figured by Van der Made (1996, pl. 41, figs 2–6, 8–13) and Van der Made (1998, pl. 1, figs 1–6; pl. 2, figs 1–3).

**Type locality:** La-Chaux-de -Fonds (Switzerland), Middle Miocene, MN7–8.

**Material and measurements:** see Table 1

### Description and comparison

The  $M_3$  (Fig. 2f) has two well-formed lophes and a third lobe as is common in *Listriodon*. The paralectotypes of *L. splendens* include a fragmentary  $M_3$  with well-formed second loph. The related genus *Bunolistriodon* has a sublophodont structure: the lophes are not completely formed, and on the posterior side of the posterior loph there is a clear vertical furrow in the middle. The central cusp (hypopreconulid) is still relatively large for *Listriodon*, where it is usually more transformed into a low crest. However, in *Bunolistriodon*, it is less reduced and more clearly still a cusp. The lophes resemble those of tapirs, but those do not have a third lobe in the  $M_3$ .

The  $M_1$  (Fig. 2e) has a similar structure as the  $M_3$ , but lacks the third lobe.

The  $P_4$  (Figs. 2c, d) has a large metaconid that is situated lingually of the hypoconid and forms a perfect loph with that cusp. The talonid has a large cusp (hypoconid) with a large lingually directed crest (hypoendocristid). This is a progressive feature in *Listriodon* (Van der Made 1996).

The  $P_3$  (Fig. 2B) has a metaconid that is relatively well developed and separate from the protoconid. This is a progressive feature in *Listriodon*, more typical of the forms of MN8 and MN9. (Van der Made 1996 p. 107; see also pp. 100–101 for referred material and localities)

The  $C_m$  (Fig. 2a) has a triangular section. It is a hypselodont tooth. The shape of the section does not change much with ontogenetic age, and the size of the section increases only very little (save for the tip). The posterior side is a little wider than the labial side ( $100 \times La/Po=86$ ). In the evolution of *Listriodon splendens*, the labial side became relatively wider and this value increased gradually, the lowest extreme being

**Table 1** Measurements (in mm) of the teeth of *Listriodon splendens* from Gratkorn

Number	element	side	Li	La	Po	DTpp	Ha	Figured
UMJGP 203428	C <sub>m</sub>	Right	≥21.6	16.9	19.7			Fig. 2a
UMJGP 203429	C <sub>m</sub>	Left	24.2	17.3	–			Not figured
			<b>DAP</b>	<b>DTa</b>	<b>DTp</b>	<b>DTpp</b>	<b>Ha</b>	
UMJGP 203426	P <sub>3</sub>	Right	15.8	10.0	10.6			Fig. 2b
UMJGP 203424	P <sub>4</sub>	Left	16.9	12.8	12.0			Fig. 2c
UMJGP 203425	P <sub>4</sub>	Right	17.2	12.7	12.0			Fig. 2d
UMJGP 203423	M <sub>1</sub>	Left	16.3	13.4	12.9			Fig. 2e
UMJGP 203427	M <sub>3</sub>	Right	33.7	20.2	18.9	12.8	13.5	Fig. 2f
UMJGP 204671	D?	?	–	–	–			Not figured
UMJGP 204095+96	D <sub>4</sub>	Left	–	–	–	≥11.2		Not figured
UMJGP 211004	C <sup>f</sup>	Left	ca. 13.0	ca. 11.5				Fig. 2h
UMJGP 204679	M <sup>1</sup>	Right	17.9	16.3	>16.5			Fig. 2g
UMJGP 210906	P <sup>2</sup>	Left	14.3	9.8	≈13.2			Fig. 2i
UMJGP 210906	P <sup>3</sup>	Left	–	–	>15.3			Fig. 2j
UMJGP 210906	P <sup>4</sup>	Left	14.8	–	17.6			Fig. 2k
UMJGP 210906	M <sup>1</sup>	Left	–	–	–			Not figured
UMJGP 210906	M <sup>2</sup>	Left	–	–	–			Not figured
UMJGP 210911/1	M <sup>3</sup>	Right	≥27.9	25.8	24.0			Not figured
UMJGP 210911/2	M <sup>3</sup>	Left	27.7	25.5	23.18			Fig. 2l
UMJGP 210911/3	M <sup>2</sup>	Right	≥21.6	–				Not figured
			<b>DMD</b>	<b>DLL</b>				
UMJGP 210904	I <sup>1</sup>	Left	24.3	>11.4				Fig. 2m
GPIT/Ma/02744	I <sup>1</sup>	Left	ca. 30.2	–				Not figured
GPIT/Ma/02735	I <sup>1</sup>	Right	30.2	12.38				Not figured
UMJGP 210915	I <sup>2/3</sup>	Right	14.3	8.4				Not figured
UMJGP 204712	I <sup>2/3</sup>	Left	14.7	8.6				Fig. 2n
UMJGP 210909	I <sup>2/3</sup>	Left	15.5	8.7				Fig. 2o

close to 80 and the highest nearly 160. However, at any time, there was a wide range of variation (Van der Made 1996, fig. 48). In addition, to this trend, the male canines became much larger (Van der Made 1996, fig. 48). Both trends are thus characterised by the increase of the width of the labial side, from a minimum of 12 mm to a maximum of nearly 29 mm, but, again, the intraspecific variation is high. The specimens from Gratkorn show values of 16.9 and 17.3 mm respectively. These measurements are higher than in stratigraphically older samples (e.g. Paşalar), but correspond to samples ranging from Arroyo del Val (late MN6) to Hostalets (MN8–9).

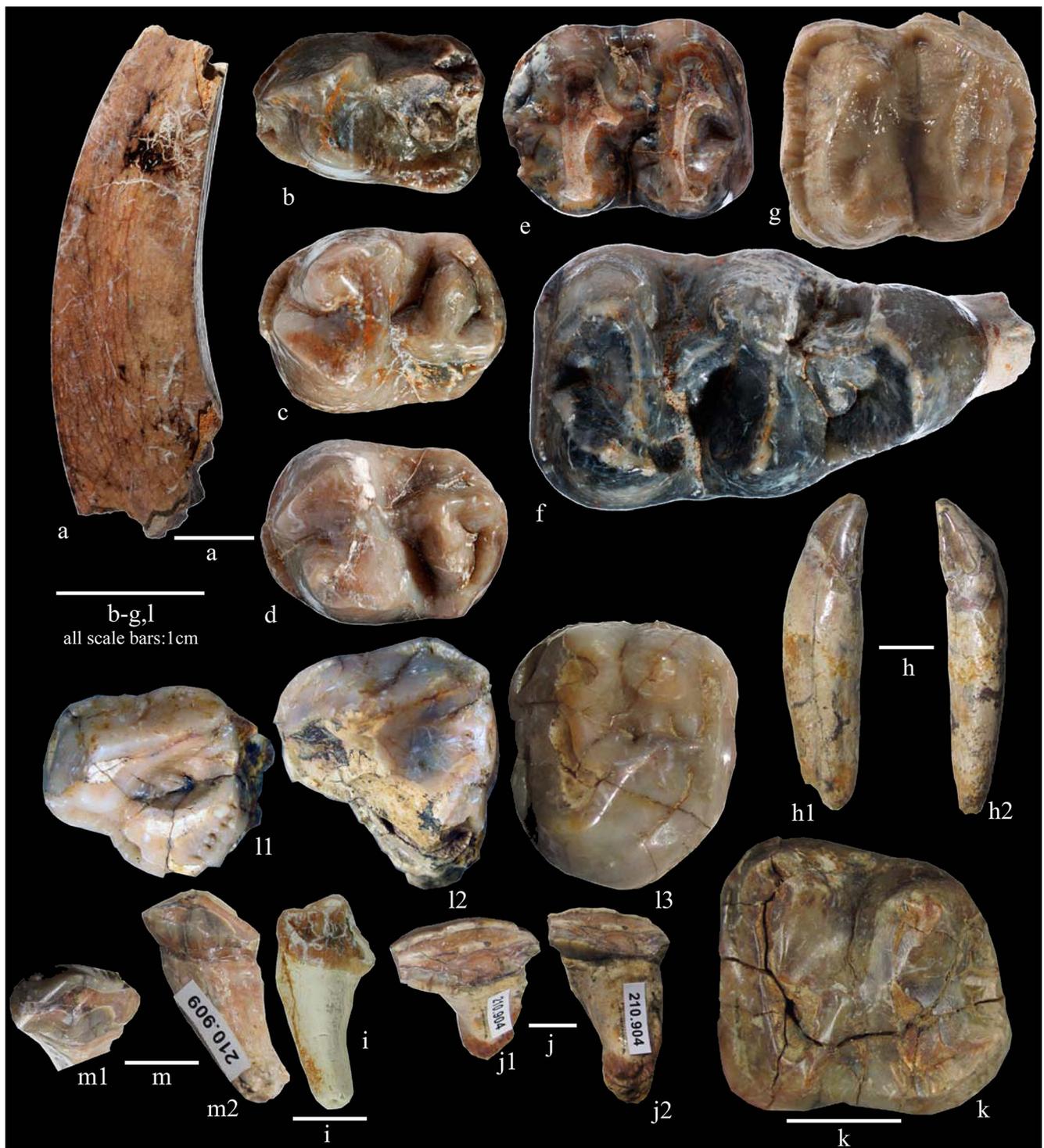
The M<sup>1–3</sup> (Figs. 2g, k) are fully lophodont. *Bunolistriodon* may acquire an anterior loph, but never a complete posterior loph as is the case here (in particular, Fig. 2g). Tapirs have upper molars with an ectoloph, which is completely absent here.

The P<sup>4</sup> (Fig. 2l) has a metacone that is large and well separated from the paracone, as in one of the paralectotypes of *L. splendens*. In *Bunolistriodon*, these cusps are usually less separated: an anterior loph is not completely formed. In *Listriodon pentapotamiae*, the P<sup>4</sup> shows a tendency to reduce the height of the metacone (Van der Made 1996, fig. 46, pl. 32, figs. 8–10, 12, pl. 33, figs. 1, 4).

The P<sup>3</sup> and P<sup>2</sup> (Fig. 2j, i) are wide, because of a well-developed protocone, which is surrounded by an also well-developed cingulum. In the course of evolution, these premolars became wider, which is illustrated by the index 100 DAP/DTp. The highest values (indicating narrow teeth) are around 160 and the lowest values below 100, but considerable variations within the samples are noticed (Van der Made 1996, fig. 56). For the P<sup>2</sup> from Gratkorn, this index is ≈108, indicating a very wide tooth comparable to what is known from Hostalets (a mixed fauna from MN8–9).

The female canine C<sup>f</sup> (Fig. 2h) of *Listriodon* is rarely documented, though male canines are common. The crown is low compared to that of *Bunolistriodon*. There is an extreme sexual dimorphism in *Listriodon splendens*, where, especially in the younger samples, male upper canines become huge (over 30 cm long with diameters of nearly 5 cm). In comparison, the C<sup>f</sup> from Gratkorn does not exceed a DAP of 13 mm.

The I<sup>2/3</sup> (Fig. 2m, i), if unworn, have a more or less symmetrical triangular outline. Among their suid analogues, they are easy to recognise, but the I<sup>2</sup> and I<sup>3</sup> are more difficult, if not impossible, to separate in the Listriodontinae.



**Fig. 2** *Listriodon splendens* Meyer, 1846 from Gratkorn. **a** Right  $C_m$  (UMJGP 203428), lingual view. **b** Right  $P_3$  (UMJGP 203426). **c** Left  $P_4$  (UMJGP 203424). **d** Right  $P_4$  (UMJGP 203425). **e** Left  $M_1$  (UMJGP 203423). **f** Right  $M_3$  (UMJGP 203427). **g** Right  $M^1$  (UMJGP 204679). **h** Left  $C^f$  (UMJGP 210911/3); **h1** lingual view, **h2** anterior view. **i** Left  $I^{2/3}$

(UMJGP 204712). **j** Left  $I^1$  (UMJGP 210904): **j1** apical view, **j2** lingual view. **k** Left  $M^3$  (UMJGP 210911/2). **l** Left  $P^2$  (**l1**),  $P^3$  (**l2**) and  $P^4$  (**l3**) (UMJGP 210906). **m** Left  $I^{2/3}$  (UMJGP 210909): **m1** apical view, **m2** lingual view. If not indicated, occlusal views

The  $I^1$  (Fig. 2j) are bilobed: a furrow on the labial side divides the tooth in two lobes as is the case in the paralectotype of *L. splendens*. In *Bunolistriodon*, a variety of

morphologies is found, with no, one or even two furrows, and, correspondingly, one to three lobes. The species with one furrow is believed to be ancestral to the genus *Listriodon*

**Table 2** Measurements (in mm) of the bones of *Listriodon splendens* from Gratkorn

Number	Element	Side	DTmax	DAPf	DAPmini						
UMJGP 204117	Ulna	d	30.4	25.4	28.5						
Number	Element	Side	DAPp	DAPpf	DTp	DTpf	L	DAPd	DAPd	DTd	DTdf
UMJGP 204077+240082	Radius	d	24.7	24.3	>33.2	>33.2	≈197.5	≥29.2	20.1	≥42.0	35.7
Number	Element	Side	DAPp	DTp	L	DAPd	DTd				
UMJGP 204077	Mc III	d	25,6	27,4	105,3	22,6	21,4				
UMJGP 204077	Mc IV	d	16.9	≥20,0	103,2	21,4	19,8				
Number	Element	Side	DAPn	DTsf	DAPsf						
UMJGP 205901	Calcaneum	s	23.5	>26	>26.7						
Number	Element	Side	Lm								
UMJGP 204092	Astragalus	s	35.8								

(Van der Made 1996). The first species of this genus to appear was *Listriodon pentapotamiae*, with relatively small incisors and canines, which gave rise to *L. splendens*, with larger incisors and canines. In the latter species, there was a further gradual evolutionary increase in the mesio-distal diameter (DMD) of the I<sup>1</sup> (while the size of the cheek teeth remained constant, but the index 100 DMD/DLL increased). The lowest DMD values are close to 20, and the highest close to 35 mm (Van der Made 1996, fig. 47). Wear at the mesial side affects the DMD and, as is usual, there is much variation within the samples. A worn I<sup>1</sup> from Gratkorn has a value of about 24.3 mm, while two almost unworn specimens have DMD values of 30.2 mm, which is much more than in *L. pentapotamiae*. Values as low as 24.3 mm are not found in samples that are younger than La Grive (old collection) and values of 32 mm are not found in samples that are older than La Grive.

**Postcranial bones:** A third and fourth metacarpal (Mc III and Mc IV) belong to the same individual. Their sizes (Table 2) are comparable to those of other specimens of *Listriodon splendens*, but they are slightly more gracile than the very few known complete specimens (Van der Made 1996, 2010). A radius of a juvenile is present in two parts, the distal epiphysis was not fused at the age of death. To our knowledge, no complete specimens of his species have been described. A radius fragment articulates well with this specimen. In addition, there are fragmentary calcanei and astragali.

#### Taxonomic assignment

The lophodont molars allow the recognition of *Listriodon*, their fully lophodont condition distinguishing them from the sublophodont *Bunolistriodon*. The incisors and canines of *Listriodon pentapotamiae* are smaller than those of *L. splendens* and its P<sup>4</sup> shows a tendency to reduce the height

of the metacone. All specimens from Gratkorn, including the canines, incisors and P<sup>4</sup>, which can be compared to their homologues among the lecto- and paralectotypes of *Listriodon splendens* (Van der Made 1996, pl. 41, 1998, pls. 1, 2), have a similar structure and size, and are therefore assigned to that species. Historically, *L. splendens* has been confused various times with a tapir, which can be easily ruled out here because of the third lobe of the M<sub>3</sub> and the less molarised premolars.

*Listriodon splendens* is recognised from over 100 localities from Europe and Anatolia, and even additional localities from China (Van der Made 1996, pp. 100–102). These localities range from middle Middle Miocene to the earliest Late Miocene (MN6–9). The documented higher degree of molarisation of the premolars in Gratkorn specimens as seen in the great width of the P<sup>2-3</sup> (Table 1; Fig. 21) and the presence of a well-developed separate metaconid on the P<sub>3</sub> (Fig. 2b) are progressive features within the evolution of this species (Van der Made 1996). The interpretation of the evolutionary state from the canines is not so clear, but the incisors are in favour of an age close to the classic collection of La Grive, that means in the later part of MN7–8.

Subfamily Tetraconodontinae Lydekker, 1876  
 Tribe Parachleuastochoerini Van der Made, 1999  
 Genus *Parachleuastochoerus* Golpe Posse, 1972

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

**Locality of type species:** Can Llobateres, Catalonia, Spain; early Late Miocene, MN9.

**Other species included in *Parachleuastochoerus*:** *Pa. steinheimensis* (Fraas, 1870) (= *Pa. parvulus* (Chang 1974); = *Pa. sinensis* Liu and Pickford, 2001), *Pa. huenermanni* (Heissig, 1989) (= *Pa. kretzoi* Fortelius et al. 2005). See below for details on the synonymies used here.

*Parachleuastochoerus steinheimensis* (Fraas, 1870)

2011 *Conohyus* sp. - Gross et al., Table 1, fig.4a

A synonymy list of this species was published by Chen (1984), and a selected synonymy highlighting new taxonomical decisions by Van der Made (1999a).

**Type material:** Fraas (1870, pl. 5, figs. 1–6, 14) figured a mandible with P<sub>2</sub>–M<sub>3</sub>, a series D<sup>3</sup>–M<sup>2</sup>, a series P<sub>4</sub>–M<sub>1</sub>, an incisor, and a series I<sub>1-3</sub>. Chen (1984, pl. 4, fig. 2) choose the mandible as a lectotype; the incisor is a *Listriodon* I<sub>3</sub>, and the remaining specimens are paralectotypes.

**Type locality:** Steinheim am Albuch, Germany, late Middle Miocene, MN7–8.

**Material and measurements:** see Table 3

#### Description and comparison

The M<sub>3</sub> (Figs. 3a, 4a) is bunodont, with the major cusps having four lobes separated by furrows, as is common in Suidae. The hypoconid has three lobes. Between the first two lobes, there is a central cusp and the third lobe is preceded by a similar cusp. This second “central cusp” is flanked by a smaller cusp on the lingual side and another one on the buccal side. There is a large terminal cusp on the axis of the tooth (pentaconid). One specimen is not much worn and the dentine is not yet exposed at the tip of the metaconid. The crownheight (Ha) is >9.4, resulting in an index 100 Ha/D<sub>Ta</sub> of somewhat more than 64. Though the complete crown height could not be measured, it can be inferred that the crown is very low. Suinae tend to have M<sub>3</sub> with clearly higher crowns.

Isolated molars of the tetraconodontine *Parachleuastochoerus* and the Late Miocene suine *Propotamochoerus palaeochoerus* are difficult to separate on morphological basis only, but *Pa. steinheimensis* from the older samples is on average much smaller. In most cases, this size difference serves to discriminate the two species, the M<sub>3</sub> from the Gratkorn cluster with those of *Pa. steinheimensis*, and are much smaller than those of *Pr. palaeochoerus* (Fig. 5).

The genus *Parachleuastochoerus* contains three species which are different in size: *Pa. steinheimensis*, *Pa. huenermanni*, and *Pa. crusafonti*. The M<sub>3</sub> from Gratkorn are larger than those from the latter two species and cluster with *Pa. steinheimensis*, particularly with the material from Steinheim. *Pa. parvulus* from type locality Xialongtan (China) is a little larger (Fig. 6; see below for synonymy). The size is also close to *Conohyus simorrensis*, a related species, of which, until recently, *Pa. steinheimensis* was believed to be a junior synonym.

The M<sub>2</sub> and M<sub>1</sub> (Figs. 3a, 4a) have similar morphologies, but the M<sub>2</sub> is a little larger. They are similar to the M<sub>3</sub>, but lack the third lobe; there is a small hypopostconulid or pentaconid on the posterior cingulum. These molars are a little less elongate

than most Suinae. Since these teeth are earlier in function than the M<sub>3</sub>, wear is more progressed and enamel thickness could be measured. The indices of 1000 Ta/D<sub>Ta</sub> are 69 and 79 for the M<sub>1</sub> and 72 for the M<sub>2</sub>. Though Tetraconodontinae are sometimes claimed to have very thick enamel, these values are quite normal within the Suidae (Van der Made 2004, Fig. 4).

Even more than in the M<sub>3</sub>, the anterior two molars are difficult to separate from their homologues of *Pr. palaeochoerus*. The M<sub>2</sub> of *Pa. steinheimensis* tends to be smaller than in *Pr. palaeochoerus*, but there are some large specimens from younger localities. Those from the type locality Steinheim tend to be small (as well as those from La Grive of about similar age). In the M<sub>1</sub> the separation between the two species is even worse than in the M<sub>2</sub>. This is because *Pr. palaeochoerus* has enlarged M<sub>3</sub> and, to some extent, M<sub>2</sub> which reflect masticatory adaptation. As with the M<sub>3</sub>, the M<sub>1-2</sub> are larger than in *Pa. huenermanni* and *Pa. crusafonti* (Fig. 6).

The P<sub>4</sub> (Figs. 3a, 4a) has one main cusp, the protoconid, like in the Tetraconodontinae and Babyrousinae. Listriodontinae, Hyotheriinae, and Suinae tend to have a clear metaconid. This main cusp is so dominant that the talonid is shortened and its cusp is very close and not well separated from the posterior crest of the protoconid (protopostcristid). In the Babyrousinae, the talonid cusp tends to be better developed. The P<sub>4</sub> does not have such an important bulge on the buccal side, making the tooth very wide as in *Conohyus*. The P<sub>4</sub> from Gratkorn clusters with that of *Pa. steinheimensis* from the type locality Steinheim as well as from other localities and with material from Xialongtan, but it is clearly larger than in *Pa. huenermanni* and *Pa. crusafonti* and smaller than in *Conohyus* (Fig. 7).

The P<sub>3</sub> (Fig. 3c) is similar to the P<sub>4</sub>, but longer and narrower. The different species are easier to separate metrically based on this premolar (Fig. 7), than using the P<sub>4</sub>. Even though the molars of *Pa. steinheimensis* are similar in size to those of *Conohyus* (Fig. 6), and the M<sub>1</sub> may be even bigger than in *C. simorrensis*, the premolars are always smaller.

The P<sub>2</sub> (Fig. 3b) and P<sub>1</sub> are similar to each other. They are very elongate. The main cusps are not very high, only extending a little above the talonid. Metrically, these teeth are close to those from Steinheim and other *Pa. steinheimensis* localities. They range between the smaller species of *Parachleuastochoerus* and *Conohyus simorrensis* (Fig. 7). However, the *Conohyus* P<sub>1</sub> are not reaching the size of *Pa. steinheimensis*, as is the case in the other premolars.

The male canine, C<sub>m</sub> (Fig. 8a), is hypselodont. Its section is triangular with the posterior side devoid of enamel, as commonly observed in the Suoidea (in many species, the female canine has posterior enamel). The posterior side is much wider than the labial sides. This is what is called a “scrofic” canine. The “verrucose” canine has a labial side that is wider than the posterior side. This is reflected in the index 100 La/Po (Van der Made 2010, fig. 20). Most primitive Suidae, as well as many Palaeochoeridae, have scrofic canines, including the species

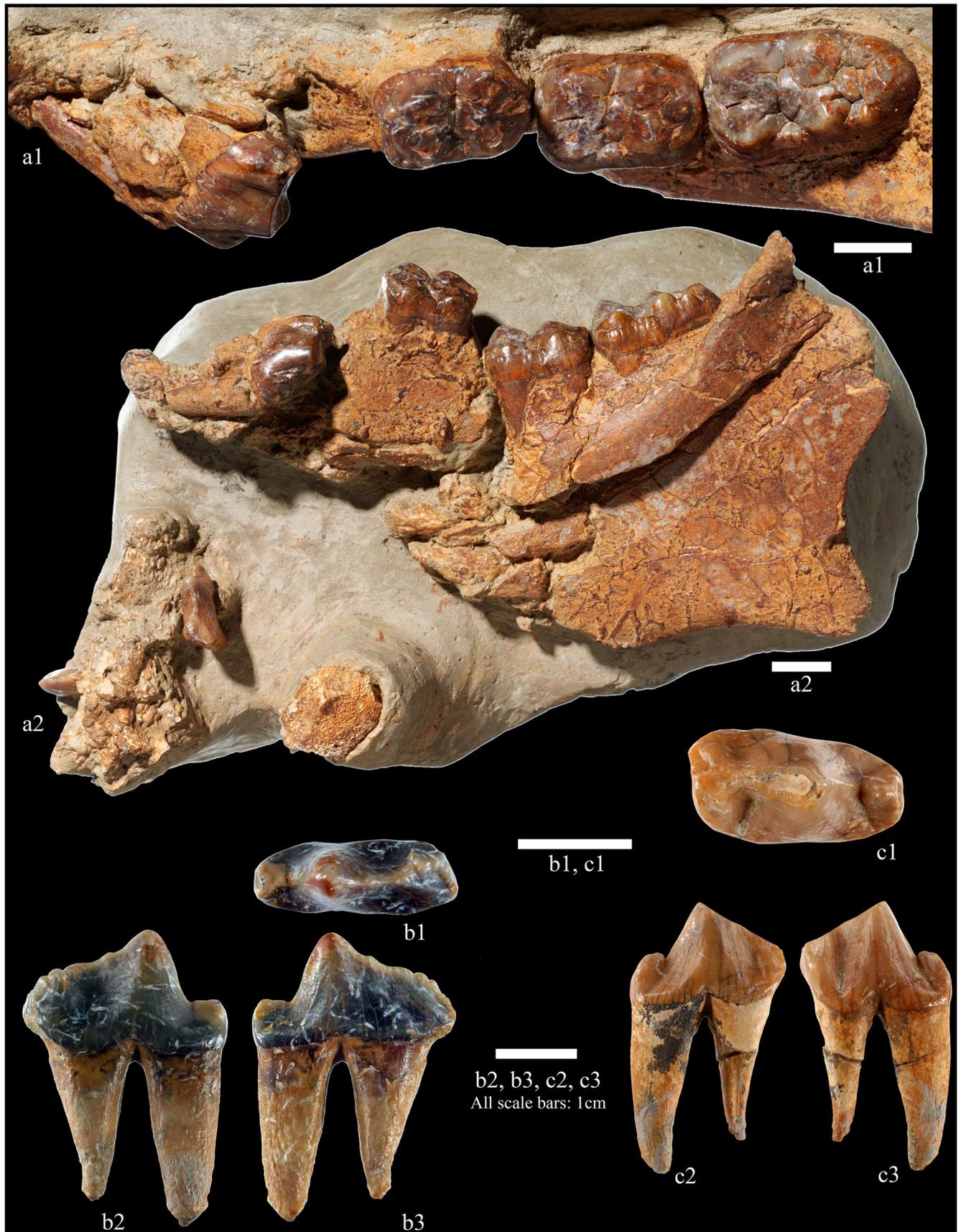
**Table 3** Measurements (in mm) of the teeth of *Parachleuastochoerus steinheimensis* from Gratkorn

Number	Element	Side	DAP	DTa	DTp	DTpp	Ha/Ta	D	W	Figured
UMJGP 204653+203713	P <sub>3</sub>	Left	≈20.2	9.0	10.5					Not figured
UMJGP 203698	P <sub>1</sub>	Left	>11.8	5.0	–					Not figured
UMJGP 203698	P <sub>2</sub>	Left	17.1	15.9	6.2					Fig. 3a
UMJGP 203698	P <sub>4</sub>	Left	17.0	10.8	11.6					Fig. 3b
UMJGP 203698	M <sub>1</sub>	Left	17.4	11.4	11.9		Ta=0.9			Fig. 3a
UMJGP 203698	M <sub>2</sub>	Left	19.9	14.0	13.3					Fig. 3a
UMJGP 203698	M <sub>3</sub>	Left	24.2	14.7	13.2	11.0				Fig. 3a
UMJGP 204655	P <sub>2</sub>	Right	17.2	6.0	6.4		Hli=9.8			Fig. 3b
UMJGP 204653	P <sub>3</sub>	Right	20.5	9.3	10.5					Fig. 3c
UMJGP 204652	P <sub>4</sub>	Right	16.2	10.2	11.5			≤51.7	18.0	Fig. 4a
UMJGP 204652	M <sub>1</sub>	Right	16.6	11.6	11.9		Ta=0.8	≤53.0	18.3	Fig. 4a
UMJGP 204652	M <sub>2</sub>	Right	19.3	13.9	13.3		Ta=1.0			Fig. 4a
UMJGP 204652	M <sub>3</sub>	Right	24.9	14.7	13.4	11.4	Ha>9.4		22.6	Fig. 4a
GPIT/Ma/02761	P <sub>4</sub>	Left	18.9	13.5	14.5		Hil=13.04			Not figured
GPIT/Ma/02761	M <sub>1</sub>	Left	18.2	–	–					Not figured
GPIT/Ma/02761	M <sub>2</sub>	Left	21.9	16.5	15.5					Not figured
GPIT/Ma/02761	M <sub>3</sub>	Left	27.3	15.9	14.2	11.8				Not figured
UMJGP 26/13	P <sub>2</sub>	Right	>13.5	–	–					Not figured
UMJGP 26/13	P <sub>3</sub>	Right	22.2	–	–					Not figured
UMJGP 26/13	P <sub>4</sub>	Right	18.7	–	–					Not figured
UMJGP 26/13	M <sub>1</sub>	Right	19.3	–	–					Not figured
UMJGP 26/13	M <sub>2</sub>	Right	21.2	16.3	14.8					Not figured
UMJGP 26/13	M <sub>3</sub>	Right	<29.0	<16.2	<15.9	11.6				Not figured
			<b>Li</b>	<b>La</b>	<b>Po</b>	<b>Ri</b>	<b>Ro</b>			
UMJGP 203699	C <sub>m</sub>	Right	19.1	10.1	15.1	30	55			Fig. 8a
UMJGP 204076	C <sub>m</sub>	Left	19.5	10.2	15.3					Not figured
			<b>DMD</b>	<b>DLL</b>	<b>DT</b>					
UMJGP 204651	I <sub>2</sub>	Left	7.5	11.2						Fig. 4b
UMJGP 204651	I <sub>1</sub>	Left	–	–						Fig. 4b
UMJGP 204651	I <sub>1</sub>	Right	6.8	10.0						Fig. 4b
UMJGP 204651	I <sub>2</sub>	Right	7.2	11.1						Fig. 4b
UMJGP 204653	I <sub>3</sub>	Left	9.8	6.2						Fig. 4c
UMJGP 204656	I <sub>3</sub>	Right	9.4	7.5						Not figured
UMJGP 203651	I <sup>1</sup>	Right	13.8	8.8	13.8					Fig. 8c
UMJGP 204658	I <sup>2</sup>	Right	13.2	6.4						Fig. 8b
UMJGP 204659	I <sup>3</sup>	Right	11.3	5.3						Fig. 8d

of *Parachleuastochoerus* and *Conohyus simorrensis*. Despite the fact that the canines of *Pr. palaeochoerus* are scrofic, their proportions allow their separation from those of *Pa. steinheimensis* (Fig. 8, bivariate diagram). The canines from Gratkorn are within the ranges of *Pa. steinheimensis*, and are a little larger than those of *C. simorrensis*.

The I<sub>1</sub> and I<sub>2</sub> (Fig. 4b) are relatively heavily worn compared to the other specimens of the same individual (Figs. 3a, 4a, 8a), of which the M<sub>3</sub> are nearly not worn. The crown bases are situated at a distance from the alveolus and a long part of the

roots is exposed. The lower boundaries of the crowns are easily seen as the enamel thins abruptly. In *Sus scrofa*, and other “advanced” suids, the enamel thins more gradually and often the crown base is covered by cement. Because of wear, the crown height of the incisors cannot be measured, but the morphology suggests that the height was not great. At the distal side of the I<sub>2</sub>, it can be seen that the postanticiclid is very low, and consequently the endo- and ectosynclonids are also shallow. This is typical of low-crowned incisors. The incisors have apical wear facets caused by occlusion with the



◀ **Fig. 3** *Parachleuastochoerus steinheimensis* (Fraas, 1870) from Gratkorn. **a** Left fragmentary mandible with P<sub>1</sub>–P<sub>2</sub>+P<sub>4</sub>–M<sub>3</sub> (UMJPG 203698): **a1** occlusal view of the M<sub>1</sub>–M<sub>3</sub> and lingual view of the P<sub>4</sub> of the specimen figured in (a2). **b** Right P<sub>2</sub> (UMJPG 204655): **b1** occlusal view, **b2** lingual view, **b3** labial view. **c** Right P<sub>3</sub> (UMJPG 204653/1): **c1** occlusal view, **c2** labial view, **c3** lingual view

I<sup>1</sup>, but also wear facets over the lingual side of the crowns. The latter are not caused by occlusion with other teeth, but are interpreted to have been caused by rooting (see “Discussion”). The I<sub>1</sub> and I<sub>2</sub> from Gratkorn have sizes comparable to those of *Propotamochoerus palaeochoerus*, *Conohyus simorrensis* and *Parachleuastochoerus steinheimensis* from type locality Steinheim and other localities. They are larger than those of *Pa. huenermanni* and *Pa. crusafonti*.

The I<sub>3</sub> (Fig. 4c) is a very asymmetrical tooth; asymmetry increases from the I<sub>1</sub> towards the I<sub>3</sub>. The crown is very low, but all the features, observed in the other lower incisors, are well developed.

The I<sup>1</sup> (Fig. 8c), if seen in apical view, has a triangular outline. There seems to be only one flat facet on the I<sup>1</sup>. However, in fact, it is composed of two facets in nearly the same plane, one is over the tip and the other is over the lower part of the crown and over the cingulum and is caused by the occlusion with the tips of the I<sub>1-2</sub>. In general, the apical facet of the I<sup>1</sup> is assumed to be caused by rooting (Herring 1972a). These facets, together with the facets on the I<sup>1</sup> of the other side, formed a flat and transversely-oriented surface and can be used to orient the tooth. There is a big main cusp, which is distally expanded (the postcrista), and both are outlined at the lingual side by a small cingulum. The lingual side of the crown is oriented transversely. This is a very primitive morphology for the Suoidea. In many suids, the distal crest is elongated and oriented partially posteriorly, so that the lingual sides of the two I<sup>1</sup> form a kind of “V-shape” (Van der Made 1996, fig. 25, 1997). This is the case in Hyotheriinae, Babyrousinae, Suinae and even in some Palaeochoeridae. Such incisors look flattened, but in fact, they are mesio-distally enlarged. These different proportions are observed in the bivariate diagram (Fig. 8), where the incisors of *Pr. palaeochoerus* tend to have longer DMD. These also have a well-developed cusp near the end of the postcrista, which is absent in Gratkorn, *Parachleuastochoerus* and *Conohyus*. The latter sample and genera are similar in size and are larger than *Pa. huenermanni* and *Pa. crusafonti*.

The I<sup>2</sup> (Fig. 8b) and I<sup>3</sup> (Fig. 8d) have a similar structure. There is a main cusp, situated much anteriorly from the middle of the tooth, which has an anterior and a posterior crest. The posterior crest is longer. In the I<sup>2</sup>, it tends to be higher than in the I<sup>3</sup>. There is a lingual cingulum. The I<sup>2</sup> has a large and anteriorly inclined wear facet over the main cusp, which is caused by occlusion with the lateral side of the I<sub>2</sub>. A second facet runs over the posterior crest, caused by occlusion with the tip of the I<sub>3</sub>. Both upper incisors are elongate and relatively low (compared to the Hyotheriinae and Palaeochoeridae).

The **symphysis** (Fig. 4b) has a length of 80.4 mm, a height of 30.5 mm and, at its narrowest point, the symphyseal area must have had a width of about 6 cm. The **mandible** (Figs. 3a, 4a) is relatively deep and not very wide for a suid.

#### Taxonomic assignment

The generic assignment of the species “*steinheimensis*” is subject to changes. It has been placed either in *Conohyus* or in *Parachleuastochoerus*. Since this species is present in Gratkorn, we have to discuss its generic affinities.

**Historical background:** Many problems arise when dealing with the taxonomy of the genus *Parachleuastochoerus* and its species. Since the naming of the species “*steinheimensis*” by Fraas (1870), most of the time it was included in the species *Conohyus simorrensis*; occasionally it was recognised as a separate subspecies (e.g. Thenius 1952). After a long period, Chen (1984) recognised it again as a separate species, namely *Conohyus steinheimensis*.

Meanwhile, *Parachleuastochoerus* and its type species *Pa. crusafonti* had been named by Golpe-Posse (1972) on the basis of material from Can Llobateres. Van der Made (1990a) (1) was of the opinion that “*Parachleuastochoerus* is a small copy of *Conohyus steinheimensis*”, (2) tentatively included *Conohyus huenermanni* Heissig, 1989 in *Parachleuastochoerus*, and (3) assigned the larger material from San Quirze and Can Ponsic, previously included in *Pa. crusafonti* (Golpe-Posse 1972; Pickford 1981), as well as some other material, to *Pa. huenermanni*. Fortelius et al. (1996) formally placed *C. steinheimensis* and *C. huenermanni* into *Parachleuastochoerus*. Later, Pickford and Liu (2001), on the basis of material from Xialongtan, named *Parachleuastochoerus sinensis* a species, which is considered to be synonymous to *Pa. parvulus* and possibly to *Pa. steinheimensis* (Sein et al. 2009). In this view, there are three species in *Parachleuastochoerus*: *Pa. steinheimensis* (= ? *Pa. sinensis* = *Pa. parvulus*), *Pa. huenermanni* and *Pa. crusafonti*.

However, in the meantime, Bernor et al. (2004) again placed *Pa. steinheimensis* and *Pa. huenermanni* in *Conohyus*, but retained the other material previously assigned to the latter species (San Quirze, Can Ponsic, etc.) as *Parachleuastochoerus* sp. These authors also named a new species: *Conohyus olujici*. Fortelius et al. (2005) gave the *Parachleuastochoerus* sp. of Bernor et al. (2004) the name *Pa. kretzoi*. In this view, *Parachleuastochoerus* contains two species: *Pa. crusafonti* and *Pa. kretzoi*, while *Conohyus steinheimensis* and *C. huenermanni* do not belong to this genus.

At present, there are two divergent views on the classification of *Parachleuastochoerus*, while “intermediate” views can also be found. The question whether “*steinheimensis*” belongs



◀ **Fig. 4** *Parachleuastochoerus steinheimensis* (Fraas, 1870) from Gratkorn. **a** Right fragmentary mandible with P<sub>4</sub>–M<sub>3</sub> (UMJGP 204652): **a1** lingual view, **a2** occlusal view. **b** Fragmentary mandible with left and right I<sub>1</sub>–I<sub>2</sub> (UMJGP 204651): **b1** lingual view, **b2** right lateral view, **b3** lower view. **c** Left I<sub>3</sub> (UMJGP 204653/2): **c1** mesial view, **c2** lingual view

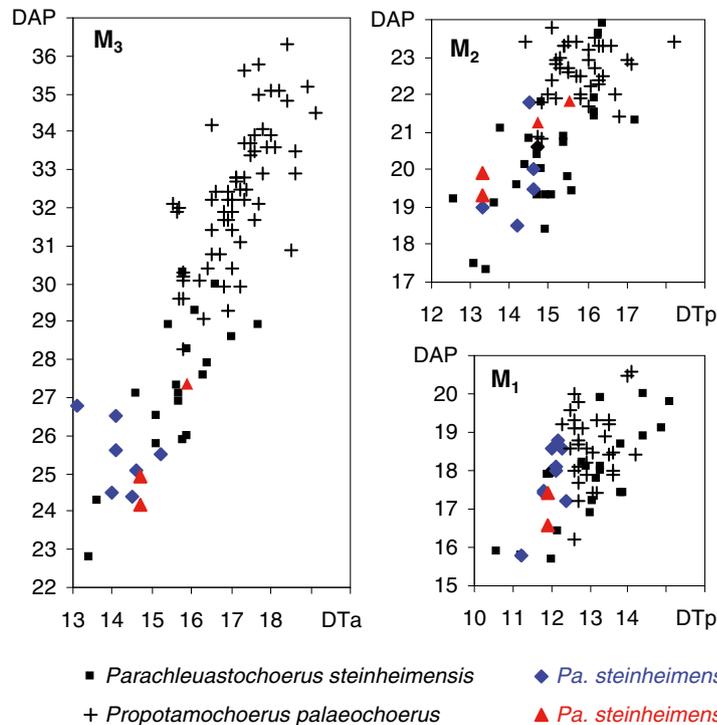
to *Conohyus* or to *Parachleuastochoerus* is entangled with the question of how the genus *Parachleuastochoerus* is delimited.

The progressive classification of “*steinheimensis*” in a subspecies, species, genus and even tribe different from *Conohyus simorrensis*, was justified by its smaller and narrower premolars (Thenius 1952; Chen 1984; Fortelius et al. 1996; Van der Made 1999).

Arguing that the approach of Van der Made (1999a) is too restrictive (no consideration of incisors, anterior premolars and skulls), Bernor et al. (2004) presented a biometric and a cladistic analysis based mainly on the lower cheek teeth, resulting in the transfer of *Pa. steinheimensis* and *Pa. huenermanni* to *Conohyus*. In our opinion, this proposal suffers from three types of weaknesses, namely: (1) the choice of *Hyotherium* for comparison in the metric analysis, (2) the choice of the outgroup and the polarity of the characters in the cladistic analysis, and (3) the definition/clarity of some of the characters.

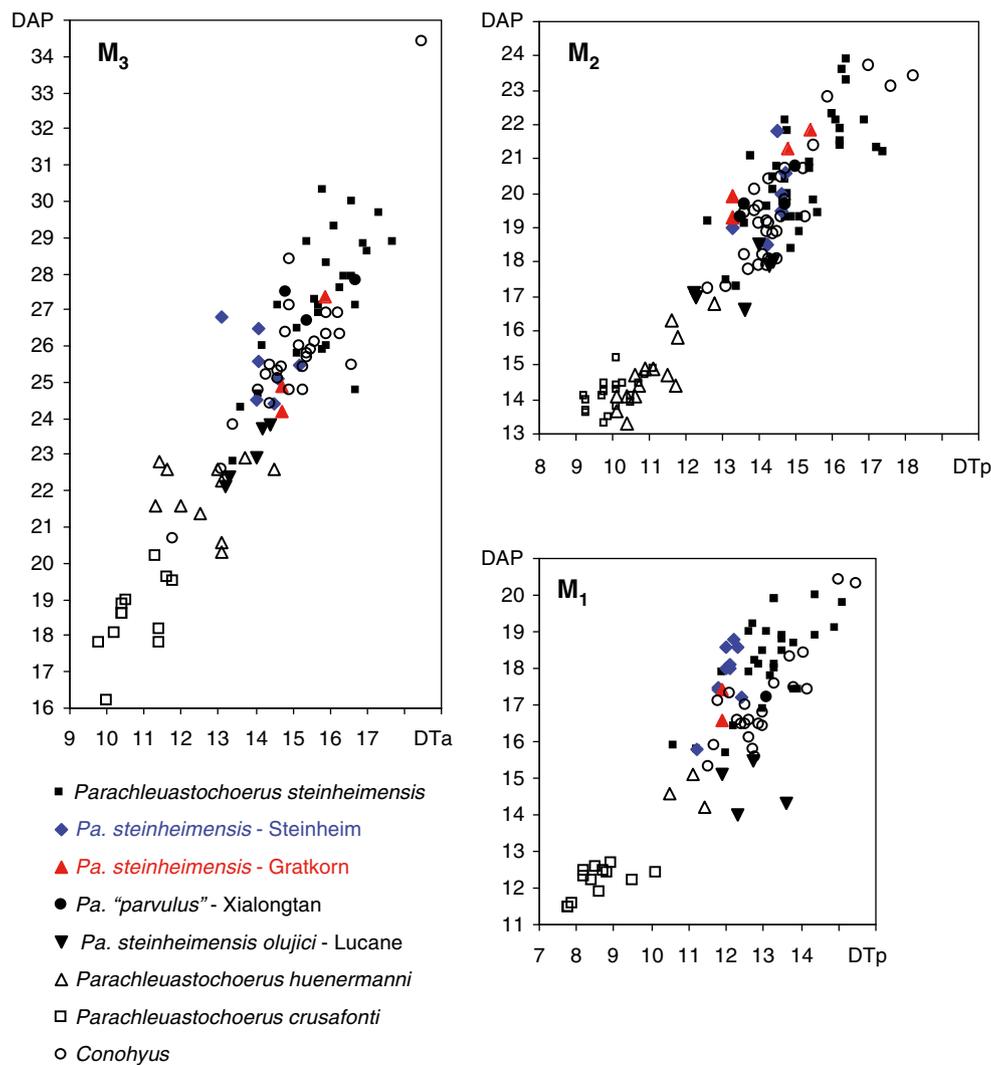
**Biometric analysis:** *Hyotherium* has little to do with the tetraconodonts and its inclusion in bivariate diagrams, which are used to discuss tetraconodont systematics, produces mainly noise. In the ratio diagram, a sample of *Hyotherium major* is used as a standard. The gradual increase in length and elongation of the premolars in the subsequent samples of *Hyotherium* is well documented (Van der Made 1998, fig. 7, 2010, figs. 24, 25). The use of a species with highly modified tooth proportions as a standard to study tooth proportions in other taxa mixes the different evolutionary signals and is not recommended in our opinion. Nevertheless, in their diagrams, Bernor et al. (2004) consistently found that *Conohyus simorrensis* is different from the tetraconodonts, which previously had been placed in *Parachleuastochoerus*.

This difference between *Conohyus* and the other species is indeed what the data show: Fortelius et al. (1996, fig. 27.7) used indices comparing premolar size to molar size and found that *C. simorrensis* has much larger premolars, while *Pa. crusafonti*, *Pa. huenermanni* and *Pa. steinheimensis* cluster and have smaller premolars. In the wider context of the Tetraconodontinae, this can also be observed (Van der Made 1999, fig. 3). This also appears very clearly in the ratio diagrams presented here (Fig. 9): *Conohyus simorrensis* is the standard, and the other European Tetraconodontinae show similar



**Fig. 5** Bivariate diagrams comparing the lower molars of *Parachleuastochoerus steinheimensis* and *Propotamochoerus palaeochoerus*. DAP length, DTa and DTp width of the anterior and posterior lobes. *Pa. steinheimensis* from Gratkorn and type locality Steinheim, as well as from: Manchones I, Arroyo del Val IV, La Grive, Can Almirall, Przeworno 2, La Chaux-de-Fonds, San Quirze, Hostalets, Castell de Barberà, Wissberg, Charmoille, Wartenberg, Hinterauerbach.

*Pr. palaeochoerus* from: Castell de Barberà, Ballestar, Montréjeau, Eppelsheim, Gaiselsberg, Götzendorf, Mariathal, Grytsiv, Magersdorf, Rudabánya, Vösendorf, Steinberg. In the case of localities where both species are present, molars in connection to other teeth that allow for a secure assignment were used, while isolated specimens of insecure assignment were omitted



**Fig. 6** Bivariate diagrams comparing the length (*DAP*) and width of the anterior or posterior lobes (*DTa*, *DTp*) of the lower molars of selected Tetraconodontinae. *Parachleuastochoerus steinheimensis* from Gratkorn and type locality Steinheim, as well as from: Manchones I, Arroyo del Val VI, La Grive, Can Almirall, Przeworno 2, La Chaux-de-Fonds, San Quirze, Castell de Barberà, Hostalets, Wissberg, Esselborn, Charmoille, Hinterauerbach and Wartenberg (selection criteria as in Fig. 5). *Pa. parvulus* from type locality Xialongtan. *Pa. huenermanni* from

Breitenbrunn, Charmoille, Castell de Barberà, Esselborn, Doué-la-Fontaine, Wissberg and Rudabánya. *Pa. crusafonti* from type locality Can Llobateres and from La Tarumba. *Conohyus simorrensis* from Puente de Vallecas, Göriach, Rosenthal, Villefranche d’Astarac, Paşalar, Alhambra, Klein Hadersdorf, Urlau, Le Fousset, Pischelsberg and Pitten. *Conohyus giganteus* from El Buste (type locality of “*C. ebroensis*”), “Haute Garonne” and Fonte do Pinheiro

proportions to each other, but diverge from *C. simorrensis*. The only irregularity is the  $P_1$  in *Pa. steinheimensis*, which is shorter than in the other species of *Parachleuastochoerus*. This is caused by specimens of one very small individual (SMNS 5280). The similarity of the curves of the different samples of *Parachleuastochoerus* is striking.

A drawback of ratio diagrams is that they do not adequately reflect variation. Figure 10 compares molar and premolar sizes of single individuals. It can also be seen that *Conohyus simorrensis* has much bigger premolars with regards to the species of *Parachleuastochoerus* as proposed here. There is one aberrant *Pa. steinheimensis* from La Grive, with a large premolar. The specimen

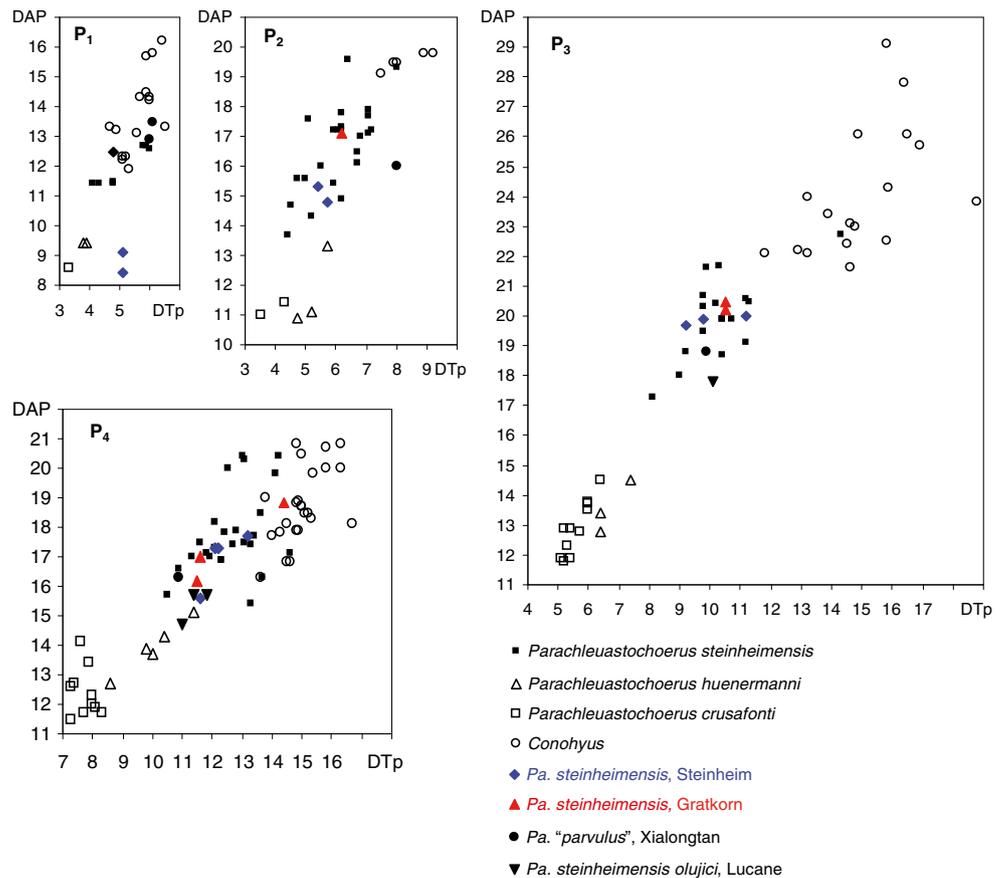
(MGL MGr1747) has been checked and measured more than once. It will be discussed again below.

**Outgroup and polarity of characters:** In some relevant features, the two species of *Hyotherium* chosen as outgroups in the study of Bernor et al. (2004) are derived; indeed, primitive and derived character states are confused.

The single main cusp in the  $P_4$  of the Tetraconodontinae (character 6) is assumed to result from the fusion of the principal cusp and the “innenheugel” (from the German Innenheugel, meaning “inner cusp”). In the Suoidea, in general and in particular lineages, a progressive separation of the “inner cusp” from the main cusp can be observed. Among the oldest suoids,

**Fig. 7** Bivariate diagrams comparing the length (*DAP*) and width of the posterior lobe (*DTp*) of the lower premolars of selected Tetraconodontinae.

*Parachleuastochoerus steinheimensis* from Gratkorn and type locality Steinheim and as well as from: Manchones I, La Grive, Can Almirall, Przeworno 1 and 2, Kaisersteinbruch, San Quirze, Hostalets, Castell de Barberà, Wartenberg, Wissberg and Can Llobateres. *Pa. parvulus* from type locality Xialongtan. *Pa. huenermanni* from: type locality Breitenbrunn, Esselborn, Rudabánya, and Can Ponsic I. *Pa. crusafonti* from type locality Can Llobateres. *Conohyus simorreensis* from Puente de Vallecas, Göriach, Au, St. Oswald, Villefranche d’Astarac, Klein Hadersdorf, Kleineisenbach, Paşalar, Tutzing, Elgg, Pischelsberg, Pitten, Le Fousseret and Mira. *Conohyus giganteus* from El Buste (type locality of *C. “ebroensis”*), “Haute Garonne” and Fonte do Pinheiro



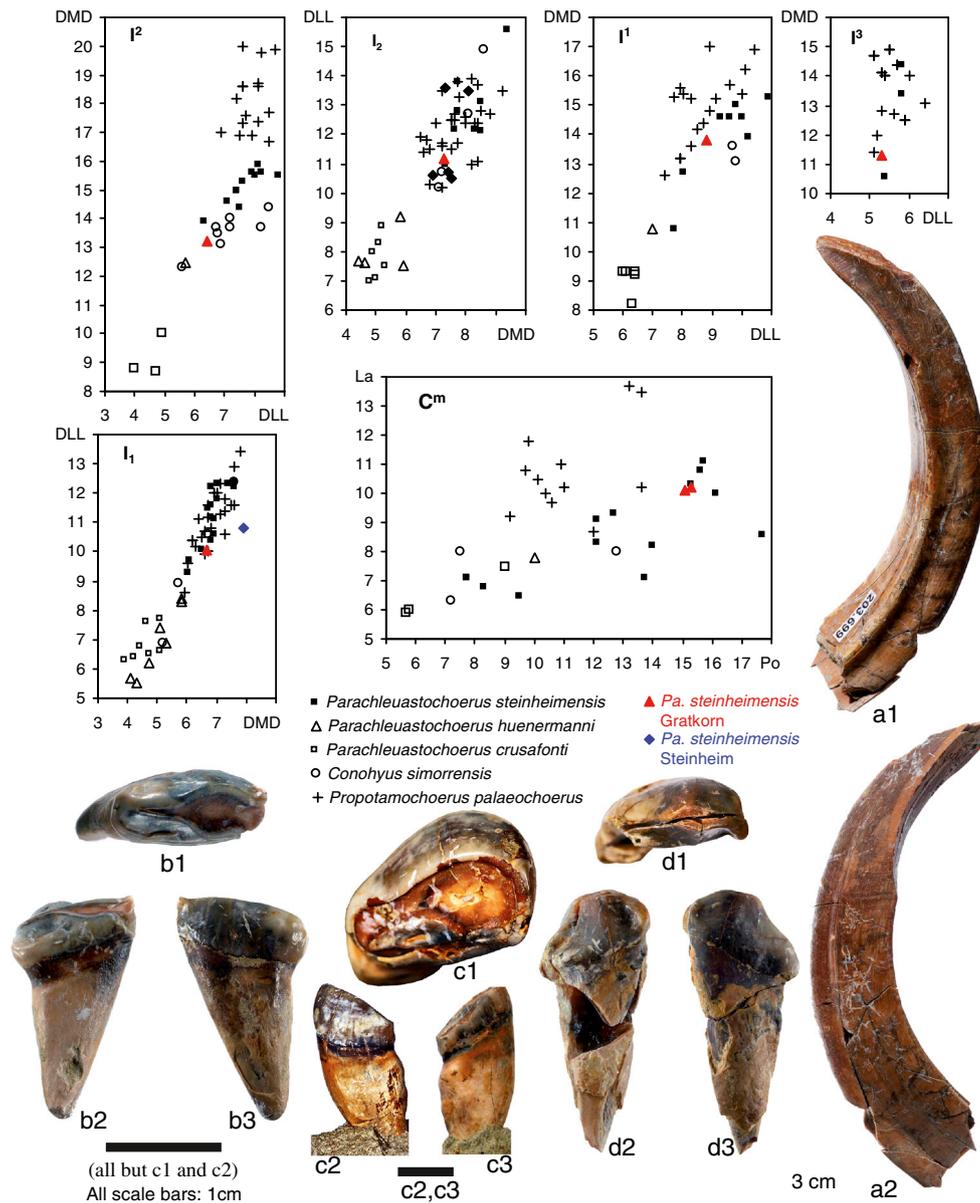
the  $P_4$  of *Odoichoerus uniconus* Tong and Zhao, 1986 has, as underlined by its name, only one cusp. A specimen from *Siamochoerus* has a large main cusp and a low and not far separated inner cusp (Ducrocq et al. 1998). A  $P_4$  which is part of the holotype of *Egatochoerus jaegeri* has a large inner cusp, but this specimen is believed not to be a Suoid (see discussion by Van der Made 2010). In the Hyotheriinae, the separation of the two cusps becomes clearer through time. Indeed, some of the older samples of *Hyotherium* and *Xenohyus* contain a  $P_4$  with a single main cusp (e.g. holotype of *Hyotherium shanwangense*) (Van der Made 1994, 2010). A similar trend in cusp separation is also observed in the Listriodontinae (Van der Made 1996). All these facts indicate that a  $P_4$  with a single main cusp is primitive in the Suoidea, not derived.

Similarly, the “paracone–metacone fusion” on the  $P^4$  (character 9) is not a progressive feature. A single buccal cusp on the  $P^4$ , or at least a not well-separated paracone and metacone, are common in the pre-Miocene species. In the Tayassuidae, Hyotheriinae and Listriodontinae, a progressive separation of the metacone from the paracone is observed. To some extent, this is also the case in the Tetraconodontinae. Most living species of Suidae belong to the Suinae and these have the two cusps well separated. There cannot be any doubt that the separation of a metacone on the  $P^4$  is a progressive feature in the Suoidea.

Short and wide (“square”) molars (character 7) are presented as an advanced character. However, since Stehlin (1899–1900), it has been known that primitive and early Suoidea have wide molars, and that evolution led to the elongation of these teeth. The Tetraconodontinae are presenting some well-known examples of this trend. Up to now, no detailed study documents a reversal of this trend.

**Definition/clearness of characters:** Character 1 of Bernor et al. (2004) documents the  $P_1$  and  $P_2$  crown shape. It is indicated as “tall and short” for *Parachleuastochoerus crusafonti* and *Parachleuastochoerus* sp. (Rudabánya) and “low and long” for the remaining Tetraconodontinae. Interestingly, Orliac et al. (2010) considered a low  $P_2$  a feature that is present in all Tetraconodontinae, including *Parachleuastochoerus crusafonti*. In general, narrow elongate premolars reach lower heights and both characters tend to be related. In Fig. 11, the elongation of these premolars is described with the index 100  $DAP/DTp$ . The  $P_2$  of *Conohyus* is relatively shorter than those of *Pa. crusafonti*.

Enamel thickness (character 11) was coded as thin for *Hyotherium*, *Parachleuastochoerus* from Rudabánya and *Pa. crusafonti* and thick for the remaining tetraconodonts. However, no measurements were provided. The only studies that gave measurements on suoid enamel thickness (as plain measurements or as indices) are provided by Van der Made



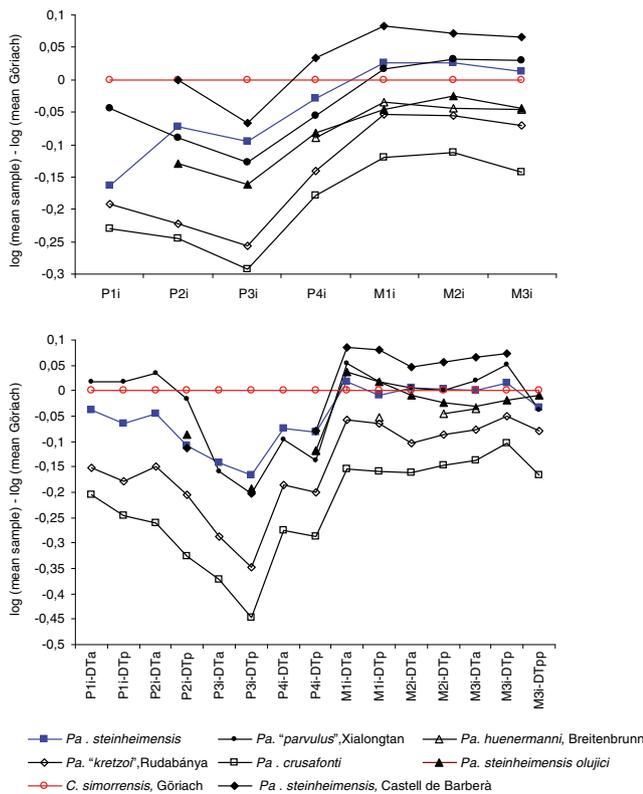
**Fig. 8** Bivariate diagrams comparing the mesio-distal diameter (DMD) and linguo-labial diameter (DLL) of the incisor and the width of the labial (La) and posterior (Po) sides of male lower canine (Cm) of *Parachleuastochoerus steinheimensis* from Gratkorn, selected Tetraconodontinae and *Propotamochoerus palaeochoerus*. *Pa. steinheimensis* from Gratkorn, type locality Steinheim, and: Arroyo del Val IV, Manchones I, Przeworno, La Grive, San Quirze, Hostalets, Castellde Barberà, Bonnefont and Wissberg. *Pa. huenermanni* from San Quirze, Rudabánya (type locality of “*Pa. kretzoi*”), Vösendorf/unknown locality (IPS). *Pa. crusafonti* from Can

Llobateres *Conohyus simorrensis* from Göriach, Paşalar, and Mira. *Pr. Palaeochoerus* from Castell de Barberà, Hostalets, Montréjeau, Gau-Weinheim, Wissberg, Eppelsheim (typelocality), Esselborn, München U-Bahntunnel, Doué-la-Fontaine, Johnsdorf, Vareille, Mariathal, WienXII, St. Oswald, Grytsev, Rudabánya, and Can PonsicI. *Pa. steinheimensis* from Gratkorn: **a** Right male canine (UMJPG 203699): **a1** labial view, **a2** lingual view. **b** Right  $I^2$  (UMJPG 204658): **b1** occlusal view, **b2** lingual view, **b3** labial view. **c** Right  $I^1$  (UMJPG 203651): **c1** apical view, **c2** labial view, **c3** lingual view. **d** Right  $I^3$  (UMJPG 204659): **d1** occlusal view, **d2** lingual view, **d3** labial view

(1996, 2004, 2010). In these studies, *Conohyus simorrensis* does not appear to have particularly thick enamel, while the few measurements of *Hyootherium meisneri* tend to be high. Some new data are available on the material from Gratkorn (Table 3), giving values for the index 1,000 Ta/D<sub>Ta</sub> of 79 and 69 for the M<sub>1</sub> and 71 for the M<sub>2</sub>. These are within the ranges of

most Suidae, slightly lower than the published data for *C. simorrensis*. These data do not support the coding for enamel thickness as used for the cladogram in Bernor et al. (2004).

Some of the features have never been described or figured. This is the case of the “cingular collar” of the P<sub>3</sub> and P<sub>4</sub>



**Fig. 9** Ratiodiagram of lower tooth row dimensions (DAP, DTA, DTP) of *Parachleuastochoerus* species relative to *Conohyus simorrensis* from Göriach. For each measurement, the value indicated is: log (average sample) – log (average Göriach). *Pa. steinheimensis* from type locality Steinheim and from La Grive together, Xialongtan (type locality of “*Pa. parvulus*”), and a single mandible from Castell de Barberà. “*Conohyus olujici*” from its type locality Lucane. *Pa. huenermanni* holotype from Breitenbrunn, and Rudabánya (type locality of “*Pa. kretzoi*”). *Pa. crusafonti* from type locality Can Llobateres. *Sivachoerus sindiensis* from Pakistan (IM, GSP, NHMI, HGSP, NMB, IVAU)

(characters 2 and 4, not mentioned in the description of the material from Lucane).

**The evolution of *Parachleuastochoerus*:** For these reasons, we consider that the cladogram of Bernor et al. (2004) is in need of re-adjustments, and their taxonomic conclusions are not followed here. Instead, it is preferred here to study the European Tetraconodontinae by ordering the samples according to relative age and observe the biometric tendencies. In this way, evolutionary trends, as well as the polarity of the characters and parallel evolution can be more easily recognised.

Figures 11, 12 and 13 document the gradual changes in size and proportions in the lower cheek teeth of the European Tetraconodontinae (similar changes are observed in the upper cheek teeth). A gradual increase of the elongation (100 DAP/DTP) occurs at the same time as a decrease in the length and width of in the P<sub>2-4</sub> of *Pa. steinheimensis*, while the molars increase in size. This suggests that the species evolved from a

species with larger and relatively wider premolars; proportions more similar to those of *Conohyus*. The presence of some very large P<sub>4</sub> and P<sub>3</sub> in the sample of La Grive (MGL LGr632) might reflect “conservative” individuals. The tendency to elongate the P<sub>3-4</sub> is even more advanced in *Pa. huenermanni* and *Pa. crusafonti*. A progressive decrease in width relative to the length might explain a P<sub>3</sub> which retains two roots in the holotype of *Pa. huenermanni* (Heissig 1989). The *Pa. huenermanni* samples indicate a continuous and gradual metrical change divergent from *Pa. steinheimensis*, towards *Pa. crusafonti*. This trend is partially documented at a high stratigraphical precision in the Spanish fossil record (bio- and lithostratigraphy after Agustí et al. 1984).

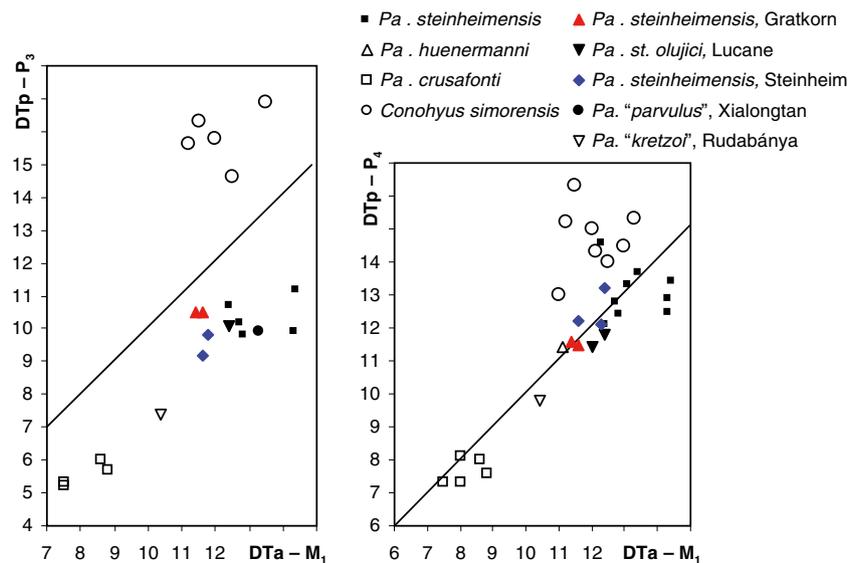
While *Parachleuastochoerus* and *Conohyus* share morphological features, such as the number of cusps in the upper and lower P<sub>4</sub>, the former genus differs from the latter in a much more progressive tendency to reduce premolar size and, above all, width (Fig. 9).

Accepting the tendencies of general size increase and relative premolar reduction in *Pa. steinheimensis*, the sample of Lucane fits very well in a basal position in this scheme. In fact in all metrics, it is very similar to the oldest samples assigned to *Pa. steinheimensis* (see Figs. 9, 10 and 11), but the measurements of some specimens fall outside the ranges. This is particularly the case with the M<sub>1</sub>, which are short in Lucane. Bernor et al. (2004) considered M<sub>1</sub> length in this sample not reliable. Because the suid from Lucane differs metrically from *Conohyus*, but is similar regarding the tooth proportions (Figs. 9, 12) to *Parachleuastochoerus*, the species from Lucane is here considered as belonging to the latter genus. And because it is a little smaller than *Pa. steinheimensis* from the type locality Steinheim, this stratigraphic earlier small subspecies is called *Pa. steinheimensis olujici* (the fossil horizon in Lucane is dated by Leeuw et al. 2010 to 15.0 Ma).

For Asian specimens, Sein et al. (2009) noted already the similarity between *Pa. parvulus* from Xialongtan and *Pa. steinheimensis*, but refrained from synonymising these species. This is mainly because of the short P<sub>2</sub> from Xialongtan compared to the samples of Steinheim and La Grive. Compared to the European samples, this difference remains, but is very small and based on a single tooth from Xialongtan. This minor difference is not sufficient to retain *Pa. parvulus* as a separate species.

Intermediate samples of *Pa. steinheimensis* and *Pa. crusafonti*, include the types of *Pa. huenermanni* and *Pa. kretzoi*. Based on the limited intraspecific variation, it is justified to consider these intermediate forms as belonging to a single species, for which the name *Pa. huenermanni* has priority.

**Taxonomic assignment of the species from Gratkorn:** The morphology of the P<sub>4</sub> indicates that the material from Gratkorn belongs to the Tetraconodontinae. In Europe,



**Fig. 10** Size ( $DTp$  posterior width) of the premolars ( $P_3$  and  $P_4$ ) compared to the size of the first lower molar ( $DTa$  width of the anterior lobe) of the same tooth row. *Conohyus simorensis* from Göriach, Le Fousseret, Paşalar and Kanam. "*Conohyus olujici*" from its type locality Lucane (Bernor, et al., 2004). *Parachleustochoerus steinheimensis* from La

Grive, Can Almirall, Przeworno 2, Gratkorn, San Quirze, Castell de Barberà and Xialongtan (type locality of "*Pa. parvulus*"). *Pa. huenermanni* from Rudabánya (type locality of "*Pa. kretzoi*"). *Pa. crusafonti* from its type locality Can Llobateres. The lines indicate the proportion  $DTp-P_{3/4}=DTa-M_1$

this subfamily was recorded by two species of *Conohyus* and three of *Parachleustochoerus* (Van der Made 1990b, 1999a). The  $P_4$  and  $P_3$  of *Conohyus simorensis* are much larger, while *C. giganteus* (= *C. ebroensis*) has much larger  $M_3$  and also  $M_2$ . Two of the species of *Parachleustochoerus* (*Pa. huenermanni* and *Pa. crusafonti*) are much smaller. The characteristics of the material from Gratkorn match perfectly those of *Pa. steinheimensis* from the type locality Steinheim and from other localities (e.g. La Grive).

## Discussion

### Biostratigraphic notes

The Suidae from Gratkorn belong to two species, namely *Listriodon splendens* and *Parachleustochoerus steinheimensis*. Both are common species in the late Middle and earliest Late Miocene of Europe (MN7+8, MN9).

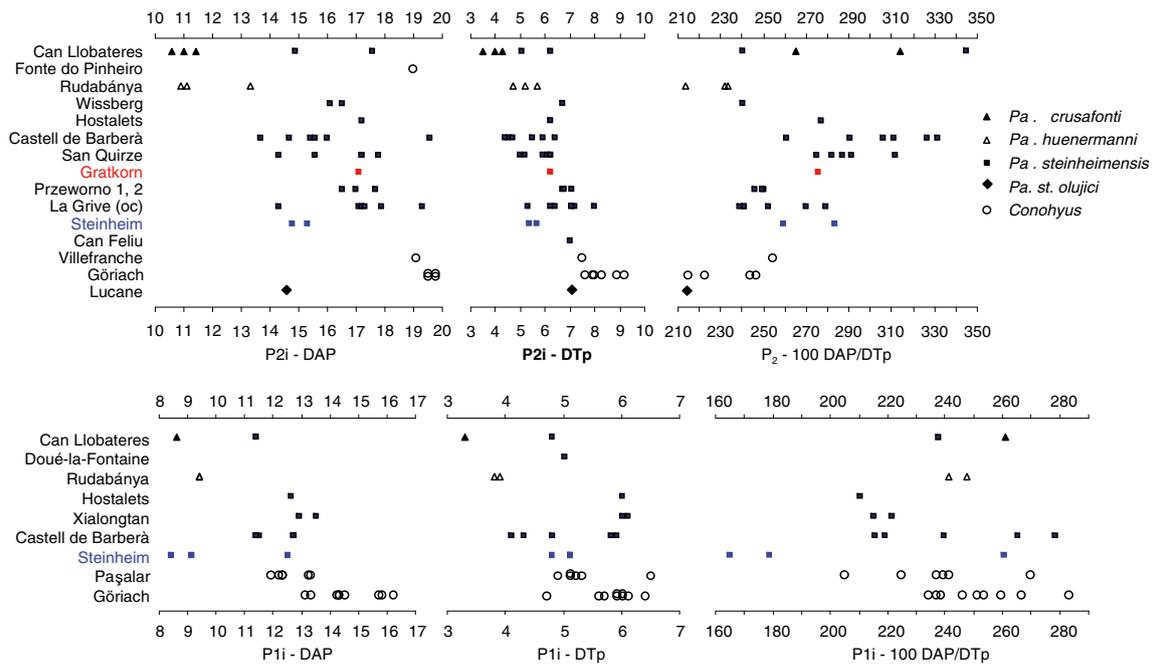
The entry of *Listriodon splendens* is at the beginning of MN6 in localities as far apart as İnönü I (Anatolia) and Sansan (France). Its last appearance is at the end of MN9 in Can Llobateres (Van der Made 1990a, 1996, 1999b). A major evolutionary trend consists of the increase of the transverse diameter of the first upper and first and second lower incisors. Additional trends are documented in the size increase of the male canines (section and the radius of curvature) as well as the appearance of a metaconid on the second and third lower

premolars, and of a metacone on the second and third upper premolars (Van der Made 1996). Based on these criterions, *Listriodon splendens* from Gratkorn is moderately advanced, comparable to the samples of stratigraphic positions within MN7–8 (e.g. La Grive). This is in accordance with the early late Sarmatian age proposed by integrative studies (e.g. Gross et al. 2011).

While in western Europe *Parachleustochoerus steinheimensis* appears a bit later than *Listriodon splendens* (later part of MN6, e.g. Manchones), their last appearance is in the same locality (Can Llobateres, latest MN9; Van der Made 1990a, 1999). Based on the evolutionary changes described above, the material from Gratkorn compares best to conspecific samples from MN7–8. In Hollabrunn *Pa. steinheimensis* is larger, as typical of latest MN8 and MN9 (e.g. San Quirze).

Diversity of the suids in Gratkorn with regards to the European fossil record during the late Middle Miocene (Sarmatian)

*Listriodon splendens* and *Pa. steinheimensis* are commonly found together in European localities of the second part of the Middle Miocene; e.g. Arroyo del Val and Manchones, Steinheim, La Grive (old collections, L7, L3), Bonnefont, La Chaux-de-Fonds, San Quirze, Hollabrunn. In some of these localities, the small suid *Albanohyus pygmaeus* and/or the small palaeochoerid *Taucanamo grandaevum* might also be documented.



**Fig. 11** Changes in size (*DAP* and *DTp*) and proportions (*100 DAP/DTp*) in the lower premolars (*P*<sub>1</sub> and *P*<sub>2</sub>) in *Conohyus* and *Parachleuastochoerus*. The localities are arranged according to their approximate biochronologic ages from old (*bottom*) to young (*top*)

In Austria, *Listriodon splendens* is well documented in the Sarmatian sediments of the Styrian and Vienna Basins (e.g. Mottl 1970; Gross et al. 2011, table 3). The presence of *Parachleuastochoerus steinheimensis* in the Miocene of Austria is well documented here for the first time. In Hollabrunn (Lower Austria), the remains of the species are restricted to a maxilla and an isolated M<sup>3</sup>, and the taxonomic assignment of the fossil from Ilz (Styria; Thenius 1956, fig. 24) is questionable. Most of the Austrian localities containing *Listriodon splendens* do not record other Suoidea, which may be a sampling effect.

**Ecologic notes**

On the basis of microwear analyses, *Listriodon splendens* has been interpreted as a browser (Hunter and Fortelius 1994). Because of its wide incisors, it was seen as a bulk feeder, and the incisor morphology and wear led Van der Made (1996) to hypothesise that *L. splendens* abandoned rooting as a major feeding strategy. Following these proposals, open or mosaic landscapes allowed *Listriodon* to feed on large quantities of herbs (or other low vegetation) in the environment of Gratkorn.

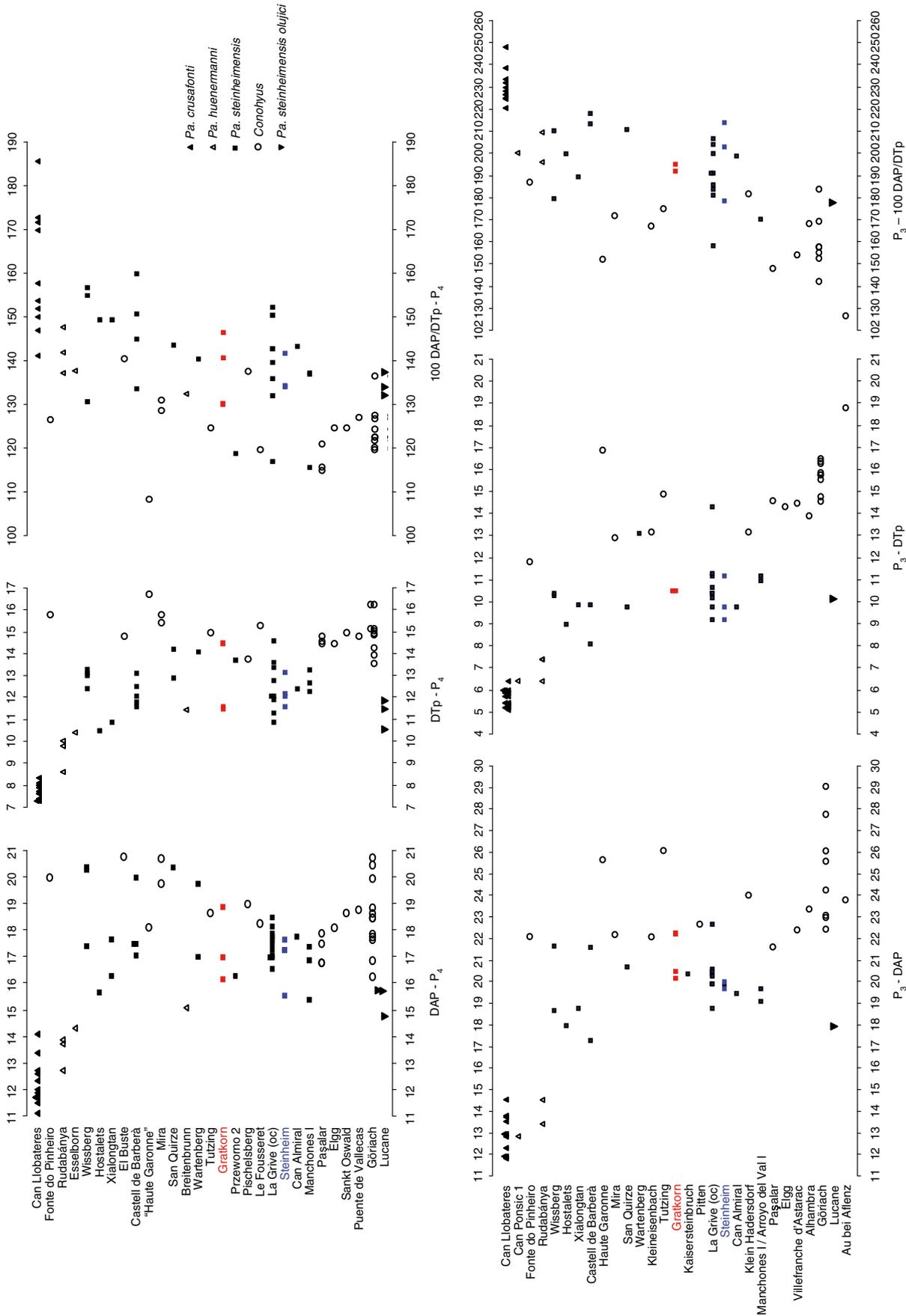
The *Listriodon splendens* sample from Gratkorn includes a female upper canine as well as lower male canines. These teeth prove a highly pronounced sexual dimorphism in this species. None of the contemporaneous Palaeochoeridae, Hyotheriinae, Tetraconodontinae and Suinae reached such a

degree of sexual dimorphism. The only other Middle Miocene example of comparable degree of dimorphism is, at the present state of knowledge, *Bunolistriodon meidamon* (Van der Made 2003).

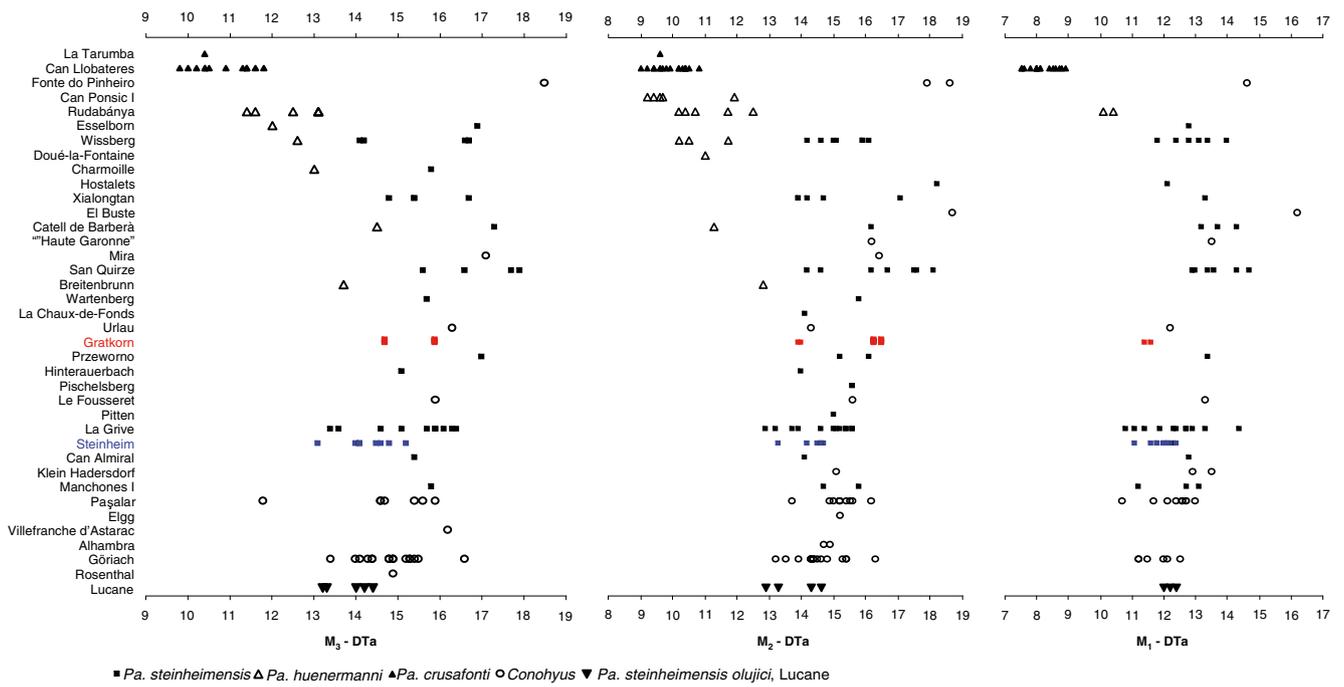
In bovids and cervids, extreme sexual dimorphism in horns and antlers occurs in species where males defend large territories, which overlap with the home ranges of several females. The antlers or horns are used for display and their sizes discourage males with smaller horns from contesting the territory. In case of equilibrate forces, the horns and antlers are used as weapons. The display functions occur only in relatively open landscapes, with good visibility, but not in very closed environments, as forests. In closed environments, species tend to live solitarily or in pairs. It has been suggested that the extreme sexual dimorphism in some Listriodontinae may have had a similar function, and that these species may have lived in more open landscapes than their pig contemporaries and may have had a different social structure (Van der Made 2003).

This ecology of *L. splendens* fits with the reconstructed relatively open, mesic woodland environment for Gratkorn (Gross et al. 2011; Aiglstorfer et al. 2014, this issue; Prieto et al. 2014, this issue) under semi-arid to sub-humid climate conditions (Böhme and Vasilyan 2014, this issue).

Rooting is the important ecological adaptation of the Suoidea. This defines the superfamily and gives the pigs access to food resources without competing with any other ungulate. The intensity of rooting varies through the year, and, in fact, helps the suids to get through the seasons



**Fig. 12** Changes in size (*DAP* and *DTP*) and proportions ( $100\ DAP/DTP$ ) in the lower premolars ( $P_3$  and  $P_4$ ) in *Conohyus* and *Parachleuastochoerus*. The localities are arranged according to their approximate biochronologic ages from old (*bottom*) to young (*top*)



**Fig. 13** Changes in size (*DAP* and *DTp*) and proportions ( $100 DAP/DTp$ ) in the lower premolars ( $P_1$  and  $P_2$ ) in *Conohyus* and *Parachleuastochoerus*. The localities are arranged according to their approximate biochronologic ages from old (*bottom*) to young (*top*)

when other food types are less abundant or less accessible. There are different rooting styles and abilities, which can be seen in skull architecture (Ewer 1958, 1970; Herring 1972b; Sicuro and Oliveira 2002) and in incisor size and morphology (Van der Made 2010). Incisors are present in the suid collection from Gratkorn and thus allow some degree of interpretation of the rooting abilities of *Pa. steinheimensis*, which gives insight into the ecology of the species in Gratkorn. The intense wear on these incisors (compared to the wear on the molars) suggests that this individual rooted intensively during its life. The  $I^2$  occludes with the lateral side of the  $I_2$ . In the evolution of the Suidae, and as an adaptation to rooting, the  $I_{1-2}$  become enlarged or higher crowned. The  $I_3$  remains much smaller or more low-crowned. As a result, there is a growing gap between the tips of the  $I^2$  and  $I^3$ . This is reflected in the  $I^2$  becoming more elongated. This is assumed to be related to retrieving food items from the soil (Van der Made 2010). The elongation of the  $I^2$  is mainly achieved by an elongation of the postcrista, and, as a result, the tip of the tooth is centrally placed in the primitive incisors, while it is situated more anteriorly in the most elongated incisors. This elongation can be observed (Fig. 8) from *C. simorrensis*, to *Pa. steinheimensis* and to *Pr. palaeochoerus*. As a consequence, the species from Gratkorn is better adapted to rooting than *Conohyus simorrensis*, but less than *Propotamochoerus palaeochoerus*. The rooting abilities of *Hyootherium*, judged from incisor morphology (Van der Made 2010, fig. 16) could have been close to those of *Pa. steinheimensis*.

Independently of morphology, different values for  $\delta^{18}O$  and  $\delta^{13}C$  of suid tooth enamel suggest that both suid species occupied different ecological niches in Gratkorn (Aiglstorfer et al. 2014, this issue). While *Listriodon splendens* was a browser with a certain amount of mixed feeding or ingestion of maybe upper canopy fruit, *Parachleuastochoerus steinheimensis* displays  $\delta^{18}O$  and  $\delta^{13}C$  values indicating a well-developed rooting behaviour (Aiglstorfer et al. 2014, this issue). Furthermore,  $^{87}Sr/^{86}Sr$  values give some evidence that the two species did not live sympatric in the surroundings of Gratkorn all their life, but occupied (at least temporarily) other regions (Aiglstorfer et al. 2014, this issue). Higher  $^{87}Sr/^{86}Sr$  values in tooth enamel of *Parachleuastochoerus steinheimensis* in comparison to the local ratio rather indicate that these individuals may have lived parts of their lives in mountainous habitats of the Eastern Alpine Mountain Chain, whereas *Listriodon splendens* was in comparison more resident with possible minor excursions to the coastal areas of the Sarmatian Sea in the south (Aiglstorfer et al. 2014, this issue).

**Conclusions**

The locality Gratkorn, among a large variety of terrestrial fossil vertebrates, has yielded fossils of the Suidae *Listriodon splendens* (Listriodontinae) and *Parachleuastochoerus steinheimensis* (Tetraconodontinae). This is the first time that the presence of the latter species is clearly demonstrated from

Austria, and the association of both species is in accordance with the chronostratigraphic age of the locality (early late Sarmatian).

For the generic assignment of *Parachleuastochoerus steinheimensis*, we provide a detailed study of the European Tetraconodontinae, leading to the conclusions that:

- Within the genus *Parachleuastochoerus*, the initially relatively wide and massive premolars became narrower and more elongate in the younger samples.
- The genus *Parachleuastochoerus* includes the species *Pa. steinheimensis* (= *Pa. parvulus*), *Pa. huenermanni* (= *Pa. kretzoi*) and *Pa. crusafonti*, while a subspecies rank is given to *Pa. steinheimensis olujici*.
- *Parachleuastochoerus steinheimensis* evolved a larger size, while the lineage *Pa. huenermanni* – *Pa. crusafonti* is an offshoot which became smaller.
- Incisor morphology suggests that *Parachleuastochoerus steinheimensis* was better adapted to rooting than *Conohyus*, but less than *Propotamochoerus palaeochoerus*.
- *Parachleuastochoerus steinheimensis* and *Listriodon splendens* occupied different ecological niches on the basis of dental and isotopic evidence, which allowed a co-habitation of both species in the late Sarmatian s. str. from Gratkorn.

**Acknowledgements** The community of Gratkorn financially supported excavation in 2008. We are indebted to the Wietersdorfer & Peggauer Zementwerke AG (especially Josef Plank). Norbert Winkler (Joanneum) meticulously prepared the specimens. We especially thank the reviewers K. Heissig (Bayerische Staatssammlung für Paläontologie und Geologie, München) and M. Orliac (Université Montpellier 2). The excavations of the Universalmuseum Joanneum were partly financed by the Land Steiermark/Wissenschaftsreferat. For the study of NHMW material Jérôme Prieto received support from the SYNTHESYS Project (ES-TAF-624), financed by the European Community Research Infrastructure Action under the FP6 “Structuring the European Research Area” Programme and from the Spanish Ministerio de Economía y Competitividad (CGL2011-28681). Jan van der Made received support from projects CGL2008-03881 and CGL2012-38434-C0 of the Spanish Ministerio de Economía y Competitividad and its predecessor. Over many years, the following persons gave Jan van der Made and/or Manuela Aiglstorfer access to material which is studied here or used for comparison, or helped in any other way: J. Agustí, B. Alpagut, B. Azanza, S. Calzada, E. Cioppi, G. Daxner-Höck, B. Engesser, V. Fahlbusch, J. Franzen, L. Ginsburg, C. de Giuli, W. Gräf, P. Havlik, K. Heißig, E.P.J. Heizmann, K.A. Hünermann, M.S. Jaquat, T. Kaya, L. Kordos, K. Kowalski, Liu Liping, H. Lutz, S. Mayda, H. Mayr, S. Moyà Solà, R. Niederl, M. Philippe, K. Rauscher, G. Rößner, G. Saraç, G. Scharfe, F. Schrenk, P.Y. Sondaar, M. Telles Antunes, L. Via and J.F. de Villalta Comella.

## References

Aiglstorfer M, Bocherens H, Böhme M (2014) Large mammal ecology in the late Middle Miocene Gratkorn locality (Austria). In: Böhme M, Gross M, Prieto J (eds) The Sarmatian vertebrate locality Gratkorn,

Styrian Basin. Palaeobio Palaeoenv 94(1). Doi: [10.1007/s12549-013-0145-5](https://doi.org/10.1007/s12549-013-0145-5)

- Agustí J, Moyà-Solà S, Gibert J (1984) Mammal distribution dynamics in the eastern margin of the Iberian peninsula during the Miocene. *Paléontol Cont Montpellier* 14(2):33–46
- Bernor RL, Bi S, Radovic J (2004) A contribution to the evolutionary biology of *Conohyus olujici* n. sp. (Mammalia, Suidae, Tetraconodontinae) from the early Miocene of Lucane, Croatia. *Geodiversitas* 26(3):509–534
- Böhme M, Vasilyan D (2014) Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). In: Böhme M, Gross M, Prieto J (eds) The Sarmatian vertebrate locality Gratkorn, Styrian Basin. *Palaeobio Palaeoenv* 94(1). Doi: [10.1007/s12549-013-0143-7](https://doi.org/10.1007/s12549-013-0143-7)
- Böhme M, Gross M, Prieto J (2014) The Sarmatian vertebrate locality Gratkorn, Styrian Basin. *Palaeobio Palaeoenv* 94(1). (Special issue)
- Chen G (1984) Suidae and Tayassuidae (Artiodactyla, Mammalia) from the Miocene of Steinheim a. A. (Germany). *Palaeontogr Abt A Palaeozool-Stratigr* 184(1–4):79–83
- Ducrocq S, Chamanee Y, Suthethorn V, Jaeger JJ (1998) The earliest known pig from the upper Eocene of Thailand. *Palaeontology* 41(1): 147–156
- Ewer RF (1958) Adaptive features in the skulls of African Suidae. *Proc Zool Soc Lond* 131:135–155
- Ewer RF (1970) The head of the forest hog, *Hylochoerus meinertzhageni*. *East Afr Wildl* 8:43–52
- Fortelius M, Made J van der, Bernor RL (1996) Middle and Late Miocene Suoidea of Central Europe and the Eastern Mediterranean: Evolution, biogeography and paleoecology. In: RL Bernor, V Fahlbusch, HW Mittmann (eds.) The evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press: 344–377
- Fortelius M, Armour-Chelu M, Bernor RL, Fessaha N (2005) Systematics and palaeobiology of the Rudabánya Suidae. *Palaeontogr Ital* 90:259–278
- Fraas O (1870) Die Fauna von Steinheim. Mit Rücksicht auf die miocenen Säugethier- und Vogelreste des Steinheimer Beckens. *Jahresh der Vereinigung vaterl Naturk Württembergs* 26:145–306
- Ginsburg L (1977) Sur la répartition stratigraphique de *Conohyus simorrensis* (Suidae, Artiodactyla, Mammalia) dans le Miocène européen. *CR Somm Soc Géol France* 4:203–205
- Golpe-Posse JM (1972) Suiiformes del Terciario Español y sus yacimientos. *Pal Evol* 2:1–197
- Gross M, Fritz I, Piller WE, Soliman A, Harzhauser M, Hubmann B, Moser B, Schlogger R, Suttner TJ (2007) The Neogene of the Styrian Basin – Guide to excursion. *J Geol Paläontol* 9:117–193
- Gross M, Böhme M, Prieto J (2011) Gratkorn: A benchmark locality for the continental Sarmatian s.str. of the Central Paratethys. *Int J Earth Sci* 100:1895–1913
- Gross M, Böhme M, Havlik P, Aiglstorfer M (2014) The late Miocene (Sarmatian s.str.) fossil site Gratkorn – the first decade of research, geology, stratigraphy and vertebrate fauna. *Palaeobio Palaeoenv* 94(1) doi: [10.1007/s12549-013-0149-1](https://doi.org/10.1007/s12549-013-0149-1)
- Harzhauser M, Gross M, Binder H (2008) Biostratigraphy of Middle Miocene (Sarmatian) wetland systems in an Eastern Alpine intramontane basin (Gratkorn Basin, Austria): the terrestrial gastropod approach. *Geol Carpathica* 59(1):45–58
- Herring SW (1972a) The role of canine morphology in the evolutionary divergence of pigs and peccaries. *J Mammal* 53(3):500–521
- Herring SW (1972b) The facial musculature of the Suoidea. *J Morphol* 137:49–62
- Heissig K (1989) *Conohyus huenermanni* n. sp., eine kleine Schweineart aus der Oberen Süßwassermolasse Bayerns. *Mitt Bayer Staatsslg Paläont hist Geol* 29:235–240
- Hunter JP, Fortelius M (1994) Comparative dental occlusal morphology, facet development, and microwear in two sympatric species

- Listriodon* (Mammalia, Suidae) from the Middle Miocene of western Anatolia (Turkey). *J Vertebr Paleontol* 14(1):105–126
- Leeuw A de, Mandic O, Vranjković A, Paveli D, Harzhauser M, Krijgsman W, Kuiper KF (2010) Chronology and integrated stratigraphy of the Miocene Sinj Basin (Dinaride Lake System, Croatia). *Palaeogeogr Palaeoclimatol Palaeoecol* 292:155–167
- Made J van der (1990a) Iberian Suoidea. *Pal Evol* 23:83–97
- Made J van der (1990b) A range chart for European Suidae and Tayassuidae. *Pal Evol* 23:99–104
- Made J van der (1994) Suoidea from the Lower Miocene of Cetina de Aragón, Spain. *Rev Esp Paleontol* 9(1):1–23
- Made J van der (1996) Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contrib Tert Quatern Geol* 33(1–4):3–254, Microfiche 54 pp
- Made J van der (1997) On *Bunolistriodon* (= *Eurolistriodon*) and kubanochoeres. *Proc K Ned Akad Wet* 100(1–2):141–160
- Made J van der (1998) *Aureliachoerus* from Oberdorf and other Aragonian pigs from Styria. *Ann Naturhist Mus Wien* 99: 225–277
- Made J van der (1999a) Biometrical trends in the Tetraconodontinae, a subfamily of pigs. *Trans R Soc Edinb Earth Sci* 89:199–225
- Made J van der (1999b) Intercontinental relationship Europe-Africa and the Indian Subcontinent. In Rössner G, Heissig K (eds) *The Miocene land mammals of Europe*. Verlag Dr. Friedrich Pfeil, München:457–472
- Made J van der (2003) Suoidea (pigs) from the hominoid locality of Çandır in Turkey. *Cour Forsch-Inst Senckenberg* 240:149–179
- Made J van der (2004) The status of *Conohyus giganteus* (Nyanzachoerini, Tetraconodontinae, Suidae) - Reply to Pickford (2001). *Trans R Soc Edinb Earth Sci* 94:157–167
- Made J van der (2010) The pigs and "Old World peccaries" (Suidae and Palaeochoeridae, Suoidea, Artiodactyla) from the Miocene of Sandelzhausen (southern Germany): phylogeny and an updated classification of the Hyotheriinae and Palaeochoeridae. *Palaeontol Z* 84:43–121
- Made J van der, Krakhmalnaya T, Kubiak H (1999) The pig *Propotamochoerus palaeochoerus* from the Upper Miocene of Grytsiv, Ukraine. *Estud Geol (Madr)* 55(5–6):283–292
- Mottl M (1970) Die jungtertiären Säugetierfaunen der Steiermark, Südösterreichs. *Mitt Mus Bergbau Geol Tech Landesmus Joanneum Graz* 31:1–92
- Orliac MJ (2009) The differentiation of bunodont Listriodontinae (Mammalia, Suidae) of Africa: new data from Kalodirr and Moruorot, Kenya. *Zool J Linn Soc* 157:653–678
- Orliac MJ (2006) *Eurolistriodon tenarezensis*, sp. nov., from Montreald-du-Gers (France): implications for the systematics of the European Listriodontinae (Suidae, Mammalia). *J Vert Paleontol* 26(4):967–980
- Orliac MJ, Antoine PO, Ducrocq S (2010) Phylogenetic relationships of the Suidae (Mammalia, Cetartiodactyla): new insights on the relationships within Suoidea. *Zool Scr* 39(4):315–330
- Pickford M (1981) *Parachleuastochoerus* (Mammalia, Suidae). *Estud Geol (Madr)* 37:313–320
- Pickford M, Liu LP (2001) Revision of the Miocene Suidae of Xiaolongtan (Kaiyuan), China. *Boll Soc Paleontol Ital* 40(2):275–283
- Pickford M, Morales J (2003) New Listriodontinae (Suidae, Mammalia) from Europe and a review of listriodont evolution, biostratigraphy and biogeography. *Geodiversitas* 25:1–58
- Prieto J, Angelone C, Casanovas-Vilar I, Gross M, Hír J, Hoek Ostende L van den, Maul LC, Vasilyan D (2014) The small mammals from Gratkorn: an overview. In: Böhme M, Gross M, Prieto J (eds) *The Sarmatian vertebrate locality Gratkorn, Styrian Basin*. *Palaeobio Palaeoenv* 94(1): Doi:10.1007/s12549-013-0147-3
- Sein C, Made J van der, Rössner G (2009) New material of *Propotamochoerus* (Suidae, Mammalia) from the Irrawaddy Formation, Myanmar. *N Jb Geol Paläont, Abh* 251(1):17–31
- Sicuro FL, Oliveira LFB (2002) Coexistence of peccaries and feral hogs in the Brazilian Pantanal wetland: an ecomorphological view. *J Mammal* 83(1):207–217
- Stehlin HG (1899–1900) Ueber die Geschichte des Suidengebisses. *Abhandlungen der schweizerischen paläontologischen Gesellschaft*. (First part, 1899, 26:1–336, second part, 1900, 27: 337–527)
- Thenius E (1952) Die Säugetierfauna aus dem Torton von Neudorf an der March (CSR). *N Jb Geol Paläont, Abh* 96(1):27–136
- Thenius E (1956) Die Suiden und Tayassuiden des steirischen Tertiärs: Beiträge zur Kenntnis d. Säugetierreste d. steir. Tertiärs VIII.-Sitzungsberichte d. Österr. Akademie d. Wissenschaften. Math.-naturwiss. Klasse Abt 1165:338–382
- Tong Y, Zhao Z (1986) *Odoichoerus*, a new Suoid (Artiodactyla, Mammalia) from the early Tertiary of Guangxi. *Vert Palasiatica* 24(2):129–138, pl.1