

# 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

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**Abstract** The fossil remains of two species of Suoidea (Artiodactyla, Mammalia) from the Early/Middle Miocene locality of Sandelzhausen (MN5; Bavaria, Germany) are described. A skull and some isolated teeth and bones reveal hitherto unknown features of *Schizoporcus muenzenbergensis*, Schizoporcini, Taucanaminae, Palaeochoeridae (Old World peccaries), Suoidea. The phylogeny of the Taucanaminae is discussed and an updated classification of the Palaeochoeridae is presented. The new names *Schizoporcus* and Schizoporcini replace the junior homonyms *Schizochœrus* Crusafont and Lavocat (1954) and Schizochœrini Golpe-Posse (1974). Remains of several skulls and mandibles, over 50 associated tooth rows, over 300 isolated teeth, and over 200 bones, constitute one of the largest collections of a Miocene suid known, and are assigned to *Hyotherium soemmeringi wylensis*, Hyotheriini, Hyotheriinae, Suidae (pigs), Suoidea. *Hyotherium* is the oldest certain suid genus known and many assumed it to be one of the most primitive. While the postcranial bones of the Suidae and Palaeochoeridae differ in many ways, the bones of *Hyotherium* are already very similar in morphology to those of living pigs, although they are much more slender, suggesting that the genus was more fleet-footed. Features related to rooting behaviour indicate that *Hyotherium* was a more efficient rooter than Palaeochoeridae and living Dicotylidae, but not as efficient as living suids. The phylogeny of the Hyotheriinae is discussed. The subfamily is divided into Hyotheriini and Aureliachoerini, new tribe, and an updated classification is presented.

**Keywords** Suoidea · Suidae · Palaeochoeridae · *Hyotherium* · *Schizoporcus* · Miocene · Palaeoecology · Rooting behaviour

**Kurzfassung** Diese Studie enthält die Beschreibung der fossilen Reste zweier Suoidenarten (Artiodactyla, Mammalia) aus der unter-/mittelmiozänen Fundstelle Sandelzhausen (MN5; Bayern, Deutschland). Die eine Art ist durch einen Schädel und einige isolierte Zähne und Knochen repräsentiert, welche bisher unbekannte Merkmale von *Schizoporcus muenzenbergensis*, Schizoporcini, Taucanaminae, Palaeochoeridae (Pekaris der Alten Welt), Suoidea dokumentieren. Im Kontext wird die Phylogenie der Taucanaminae diskutiert und eine aktualisierte Klassifikation der Palaeochoeridae vorgestellt. Die neuen Taxa *Schizoporcus* und Schizoporcini ersetzen die Juniorhomonyme *Schizochœrus* Crusafont und Lavocat (1954) und Schizochœrini Golpe-Posse (1974). Die zweite Art ist mit Resten von einigen Schädeln und Unterkiefern, über 50 Zahnreihen, über 300 isolierte Zähne und über 200 Knochen vertreten, welche eine der größten Sammlungen eines miozänen Schweines darstellen und *Hyotherium soemmeringi wylensis*, Hyotheriini, Hyotheriinae, Suidae (Schweine), Suoidea zugeordnet werden. *Hyotherium* ist die bisher geologisch älteste Schweinegattung und viele Bearbeiter nahmen an, dass sie auch eine der primitivsten ist. Jedoch während die postkranialen Knochen der Suidae und Palaeochoeridae in vieler Hinsicht unterschiedlich sind, zeigen die Knochen von *Hyotherium* schon große Ähnlichkeit mit modernen Schweinen, obwohl sie sehr viel schlanker sind und größere Leichtfüßigkeit vermuten lassen. Merkmale, die im Zusammenhang mit dem Wühl-Verhalten stehen, zeigen an, dass *Hyotherium* ein wesentlich effizienterer Wühler war, als die Palaeochoeridae und die modernen Dicotylidae, aber nicht so effizient

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wie die modernen Schweine. Die Phylogenie der Hyotheriinae wird diskutiert. Die Unterfamilie wird unterteilt in Hyotheriini sowie den neuen Tribus Aureliachoeiini und eine aktualisierte Klassifikation wird vorgestellt.

**Schlüsselwörter** Suoidea · Suidae · Palaeochoeridae · *Hyotherium* · *Schizoporcus* · Miozän · Paläoökologie · Wühl-Verhalten

## Introduction

Sandelzhausen is a well known locality and certainly in the context of this volume, it is not necessary to introduce it further here. A recent overview of the locality and its literature was given by Fahlbusch 2003. A description of the Suidae was one of the first papers on Sandelzhausen to appear (Schmidt-Kittler 1971); the material was attributed to *Hyotherium soemmeringi*. This paper had a great influence on the classification of the Suidae; it contributed to the separation of the Hyotheriinae and Suinae, and the tribe Dicoryphochoerini within the Suinae was named. Sandelzhausen was excavated from 1969 to 1975 and from 1994 to 2001. It is not surprising that the present collection is much richer. Especially in the later excavations, remains of a second suoid species were found, it is an “Old World peccary” or palaeochoerid.

The first time I studied some of the Suidae from Sandelzhausen was in 1984. Later I came back many times to study other parts of the collection or material from the new excavations, and in various publications I used the Sandelzhausen collection as a reference (Van der Made 1990a, b, 1998a). A recurring problem in these comparisons was that *Hyotherium* from Sandelzhausen was small for MN 6, while otherwise the genus seemed to become large, the larger forms being known precisely from MN 6. Initially Sandelzhausen was placed in MN6 (Mein 1975, 1977, 1990; De Bruijn et al. 1992), but now the locality is placed low in MN5 Heissig 1997; Rössner 1997; Fahlbusch 2003; Moser et al. 2009). With this problem resolved, the large Sandelzhausen collection can serve as a standard to compare other *Hyotherium* for assessing their evolutionary level. This paper aims to describe all material of *Hyotherium* and the palaeochoerid in as much detail as possible, to place them in their evolutionary and taxonomic context and to interpret their ecology.

As in the previous paragraph, the well known MN units are used throughout the paper (Mein 1975, 1977, 1999; De Bruijn et al. 1992). The ages of the MN units are differently estimated, especially from the MN3–4 transition to the MN6–7 transition. There is a “long” and a “short chronology”. On the long side, and based on various lines of evidence, are Steininger (1999), Reichenbacher et al.

(1998), slightly shorter Kempf et al. (1997) based on palaeomagnetism in Switzerland, and Rögl (1999), and still shorter, based on palaeomagnetism in Spain: Krijgsman et al. (1994, 2003); Daams et al. (1999a, b), Agustí et al. (2001), Larrasoña et al. (2006), Van Dam et al. (2006), and Montes et al. (2006). The “short chronology” tends to fit my data and interpretations better (Van der Made 1992, 1996a, 2005).

## Materials and methods

The suoid material from Sandelzhausen is housed at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich under the inventory number prefix BSPG 1959 II, which is omitted in the following text.

Many specimens are listed in the tables. Some of these specimens do not have collection numbers yet, other means of identification are given in the tables, such as field numbers (usually given first and consisting of a four-digit number), the grit (Planquadrat PQ, indicated by a number–letter combination), the vertical position in cm above (ü = über) or under (u = unter) a particular layer (e.g. a coal layer K = Kohle) or the basis (B = Basis) and occasionally the date or year of collection (Moser et al. 2009).

The material from Sandelzhausen is compared with suoid fossils from other localities. When such a comparison is made, a bibliographic reference is given, or, more frequently, an acronym of an institute or collection where the material was studied. These acronyms and their collections are given below:

AMNH	American Museum of Natural History, New York
BNHM	Beijing Natural History Museum
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, München
CFE	Collection François Escuillé, Lyon
CH	Collection Mikko Haaramo, Helsinki
CJFV	Collection J. F. de Villalta, Barcelona
CTM	Collection Torres, Madrid
EBD	Estación Biológica de la Doñana, Sevilla
FISF	Forschungsinstitut Senckenberg, Frankfurt
GSMT	Georgian State Museum, Tbilisi
GSP	Geological Survey of Pakistan, Islamabad
HGSB	Hungarian Geological Survey, Budapest
HGSP	Howard–Geological Survey of Pakistan Project, material will be stored in GSP
HLD	Hessisches Landesmuseum, Darmstadt
HUJ	Hebrew University, Jerusalem
IGF	Istituto di Geologia, Firenze

IGL	Institut für Geowissenschaften/Geologie der Montan-Universität, Leoben	VMM	Vernadsky Museum, Moscow
IM	Indian Museum, Calcutta	ZMA	Zoölogisch Museum, Amsterdam
IPS	Instituto de Paleontología, Sabadell		
IPUW	Institut für Paläontologie der Universität, Wien		The material from Sandelzhausen is described and studied with the common methods in palaeontology. The terminology for the details of tooth morphology and method of measurement follow Van der Made (1996a). The measurements are indicated with the following acronyms:
ISEAK	Institute of Systematics and Evolution of Animals, Kraków		
IVAU	Instituut Voor Aardwetenschappen, Utrecht	d	Width of the facet for the cuboid in the astragalus
IVPP	Institute for Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing	DAP	Antero–posterior diameter of a tooth or bone
JGUM	Johannes Gutenberg Universität, Mainz	DAPd, DAPp	DAP of the distal or proximal end of a bone
LPVM	Laboratoire de Paléontologie des Vertébrés, Université Montpellier II	DAPdf, DAPpf	DAP of a facet at the distal or proximal side of a bone
KNM	Kenya National Museums, Nairobi	DAPh, DT	DAP and DT of the “head” of the calcaneum
KU	Kagoshima Univeristy	DAPmax	Maximum DAP
MGL	Museum Guimet, Lyon	DAPn, DTn	DAP and DT at the “neck” of a bone
MHMN	Museu Històric Municipal de Novelda	DAPps	Alternative DAPp in the phalanges (Van der Made 1996a, Fig. 19)
MHNT	Muséum d’Histoire Naturelle, Toulouse	DAPsf, DTsf	DAP and DT of the calcaneum at the level of the sustentacular facet
MNCN	Museo Nacional de Ciencias Naturales, Madrid	DLL	Linguo–labial diameter of incisors
MNHN	Muséum National d’Histoire Naturelle, Paris	DMD	Meso–distal diameter of incisors
MSNO	Muséum des Sciences Naturelles, Orléans	DMDo, DMDoc	DMD of I1, measured along the occlusal surface either as a total length of the crown or of the occlusal surface (Van der Made and Han 1994, Fig. 2)
MTA	Maden Tetkik ve Arama, Ankara		
NHM	Natural History Museum, London	DT	Transverse diameter (“width”) of a cheek tooth or bone
NMB	Naturhistorisches Museum, Basel	DTa, DTp	DT of the anterior or posterior lobe of a cheek tooth or DT of the anterior side or proximal end of a bone
NMBe	Naturhistorisches Museum, Bern		
NMM	Naturhistorisches Museum, Mainz	DTcem	DT including the cementum in the C <sup>m</sup> , when there is a thick cementum layer
NMNHK	National Museum of Natural History, Kiew	DTd	DT of the distal side of a bone
NMW	Naturhistorisches Museum, Wien	DTdf, DTpf	DT of a facet at the distal or proximal side of a bone
NNML	Nationaal Natuurhistorisch Museum, Leiden		
NSSW	Naturwissenschaftliche Sammlungen der Stadt Winterthur	DTm, DTpp	DT of the middle lobe in D <sub>4</sub> and of the third lobe in M <sub>3</sub>
PIMUZ	Paläontologisches Institut und Museum der Universität, Zürich	DTmax	Maximum DT of a bone
PIN	Palaeontological Institute, Moscow	H	Height of a bone or crown of a tooth
PDTFAU	Paleoantropoloji, Dil ve Tarih Cografiya Facultesi, Ankara Universitesi	Ha	H of a molar at the anterior lobe at the lingual side in M <sub>x</sub> and at the buccal side in M <sup>x</sup> . H of a bone at the anterior side
SLJG	Steiermärkisches Landesmuseum Joanneum, Graz		
SMNS	Staatliches Museum für Naturkunde, Stuttgart	Hla, Hli	Height of an incisor at the labial and distal sides
UCBL	Université Claude Bernard, Lyon		
UCM	Universidad Complutense, Madrid		
UNL	Centro de Estratigrafia e Paleobiologia da Universidade Nove de Lisboa	L	Length of a bone in proximo–distal direction
UPM	Laboratoire de sédimentologie et paléontologie, Université de Provence, Marseille		
UPVB	Departamento de Geología, Facultad de Ciencias, Universidad del País Vasco, Bilbao		
USR	Dipartimento di Scienze della Terra, Università “La Sapienza”, Roma		

La, Li, Po	Width of the labial, lingual and posterior sides of the $C_m$ . The limit of the enamel is not necessarily the limit of the labial side
Ll, Lu	Length of the lower, respectively upper, part of a bone
Lext, Lint, Lm	Length of the astragalus at the lateral and medial sides and in the middle
R	Diameter in an astragalus (F21)
R1–5	Five diameters of the distal trochlea of the humerus, taken at maxima and minima from the medial (R1) to the lateral (R5) side
Ri, Ro	Radius of curvature in male canines measured from the inner and outer sides
Ta	Thickness of enamel measured at the lingual side of the metaconid (or buccal side of the paracone)

The height of the mandibular condyle above the occlusal plane is measured as the distance from the condyle to a line that passes through the bottoms of the transverse valleys of  $M_1$  and  $M_2$ . Along this same line the distance is measured between the anterior edge of the  $M_1$  and the projection of the condyle on this line. A figure that shows how the measurement is taken on a cervid mandible is given elsewhere (Van der Made and Tong 2008). The measurements on suid mandibles were taken over many years and many of them have been used before (Van der Made 1989).

### Systematic palaeontology

Class Mammalia Linnaeus, 1758  
 Order Artiodactyla Owen, 1848  
 Superfamily Suoidea Gray, 1821  
 Family Palaeochoeridae Matthew, 1924  
 Subfamily Taucanaminae Van der Made, 1997

Tribe Schizoporcini new name

**Definition:** Taucanaminae with wide premolars (after Van der Made 1997a).

**Type genus:** *Schizoporcus*

**Remarks:** Crusafont and Lavocat (1954) introduced the generic and specific names *Schizochoerus vallesiensis* for a suiform from the lower Upper Miocene of Viladecavalls (Catalonia, Spain). However, *Schizochoerus* Poche, 1922, Schizochoerinae Poche, 1922, Schizochoeridae Poche, 1922, Amphilinidae is a widespread flat worm belonging to the Platyhelminthes (Rohde 1994, 2007; Bandoni and Brooks 1987). The name *Schizochoerus* Crusafont and Lavocat, 1954 is available, but it is a junior homonym of

*Schizochoerus* Poche, 1922. Likewise, Golpe-Posse (1972), not being aware of the name *Schizochoeridae* Poche, 1922, introduced the name *Schizochoerini* for a tribe within the Suinae, Suidae, but did not give a formal definition of the tribe at the place where the new name was mentioned in a schematic classification (p. 63). In her descriptive chapter, she included the genus along with other Suinae under the headings “Subfamilia SUINAE ZITTEL, 1893” and “Tribu SUINI nva. tribu” [!] (p. 149) and thus treated the genus as belonging to the Suini and not as an independent tribe. The genus is treated again on pp. 152–154, where the opinions of Crusafont and Lavocat (1954), Ozansoy (1957, 1965) and [Nikolov and] Thenius (1967) are explained and cited, but the author’s own opinion is not given, let alone a justification or definition of the tribe *Schizochoerini*. In the concluding chapter, the *Schizochoerini* are mentioned again, and it is explained why the genus *Schizochoerus* belongs to the Suinae and not to the Listriodontinae, but not why it should be placed in a tribe different from the Suini (pp. 185–186, and again on p. 187). The same is stated in the French (p. 189, p. 191) and German (pp. 193–194) concluding chapters. Because the name is not a replacement name and because no definition, description, or justification for the introduction of the new tribe *Schizochoerini* is given, nor a bibliographic reference to such a statement, the original publication does not meet the requirements of article 13.1 of the International Commission on Zoological Nomenclature (ICZN) to make the name available (ICZN 1999).

Nevertheless, the taxon *Schizochoerini* was treated as valid by later authors. Pickford (1978) transferred the taxon from the Suidae to the Tayassuidae and used the name at the subfamily level as “*Schizochoerinae* Golpe 1974”, but did not give a definition. The year of publication is a lapsus, the usage of the name at the subfamily level is probably no lapsus, because it was stated that “it [*Schizochoerus*] may require a subfamilial separation from *Doliochoerinae*”. McKenna and Bell (1997) included “*Schizochoerinae* Thenius, 1979” in the *Schizochoerini* Golpe-Posse, 1972, within the *Doliochoerinae* in the Tayassuidae. Van der Made (1997a) introduced the name *Taucanamini* next to the *Schizochoerini* within the *Schizochoerinae* and gave a diagnosis for the *Schizochoerini* Golpe Posse, 1972, which may have made the latter name available (although not valid).

Thus, at present the names *Schizochoerus* Crusafont and Lavocat, 1954, *Schizochoerini* Golpe-Posse, 1972, and *Schizochoerinae* Golpe-Posse, 1972 (or with author and year Golpe, 1974, or Thenius, 1979), are in use for Sui-forms, but all are either junior homonyms of *Schizochoerus* Poche, 1922, *Schizochoerini* Poche, 1922 and *Schizochoerinae* Poche, 1922, or not even available. New names for these taxa are thus needed. Bearing article 36 of the ICZN

in mind, which is on the principle of coordination, the name *Taucanaminae* Van der Made, 1997 takes the place of the *Schizochoerinae* Golpe-Posse, 1972.

*Schizoporcus* nom. nov.

**Type species:** “*Schizochoerus*” *vallesiensis* Crusafont and Lavocat, 1954.

**Diagnosis:** Schizoporcini with: 1) sublophodont or lophodont molars, or with molars that have cusps with a simple structure, which preserve those elements that play a role in lophodonty; 2) P<sup>3</sup> and P<sup>2</sup> with a small protocone, or with no protocone at all.

**Etymology:** as *Schizochoerus*, the name it replaces, but ending in *-porcus*, from the Latin for pig or wild boar.

*Schizoporcus muenzenbergensis* (Van der Made 1998)

### Synonymy:

- v.1909 *Choerotherium sansaniense* Zdarsky: 260–264 (the material from Münzenberg), pl. 7 Figs. 12–14.
- v.1934 *Choerotherium sansaniense* (Lart.).—Pia and Sickenberg: 183 (no. 1585), 187 (nos. 1616, 1618).
- v.1956 *Taucanamo sansaniense* (Lartet).—Thenius: 366–369 (only the material from Münzenberg, not no. 56633), Figs. 27–28.
- v.1967 *Taucanamo sansaniense* (Lartet).—Petronijevic: 77–78, 144, pl. 13 Figs. 2–5.
- v.1969 *Taucanamo sansaniense* (Lartet).—Pavlovic: 333–338 (Prebreza), 382, pls. 12–13.
- v.1970 *Taucanamo sansaniense* (LART.).—Mottl: 26.
- v.1983 *Taucanamo sansaniense* (Lart.).—Weber and Weiss: 122.
- v.1983 *Palaeochoerus (Aureliachoerus) aurelianensis* Stehlin, 1899.—Zapfe: 175–180, Figs. 6–10
- v.1993 *Taucanamo sansaniensis* lineage Van der Made: 128 (Münzenberg, Mala Miliva, Sandelzhausen).
- v.\*1998 *Taucanamo? muenzenbergensis* n.sp. Van der Made: 225–226, 234–239, 260–262.
- v.2003 *Schizochoerus muenzenbergensis* Van der Made: 153–155, 165.

**Holotype:** no. 56.697—a right mandible from Münzenberg with P<sub>3</sub>–M<sub>3</sub> (Zdarsky 1909: pl. 7, Figs. 16–17), stored in the Steiermärkisches Landesmuseum Joanneum in Graz.

**Type locality:** Münzenberg near Leoben.

**Age of the type locality:** Middle Miocene, MN5.

**Other localities:** Sandelzhausen, Neudorf Spalte, Baigneaux-en-Beauce (?), Prebreza.

**Diagnosis:** *Schizoporcus* with: (1) bunodont or “protolophodont” molars; (2) M<sub>3</sub> with a third lobe with the pentaconid in the middle and no hexaconid; (3) P<sub>4</sub> with the

hypoconid in the middle of the talonid; (4) M<sub>1–2</sub> moderately elongate; (5) upper molars not very elongate; (6) intermediate size.

**Material:** The material is indicated in Tables 2, 5, 6, 8, 10, 18, 19, and 21.

### Description and comparison

A fragment of a **skull** (Fig. 1) lacks most of what was situated anterior to the P<sup>1</sup> and most of what was behind the palate. It is crushed. Nevertheless, several interesting observations can be made.

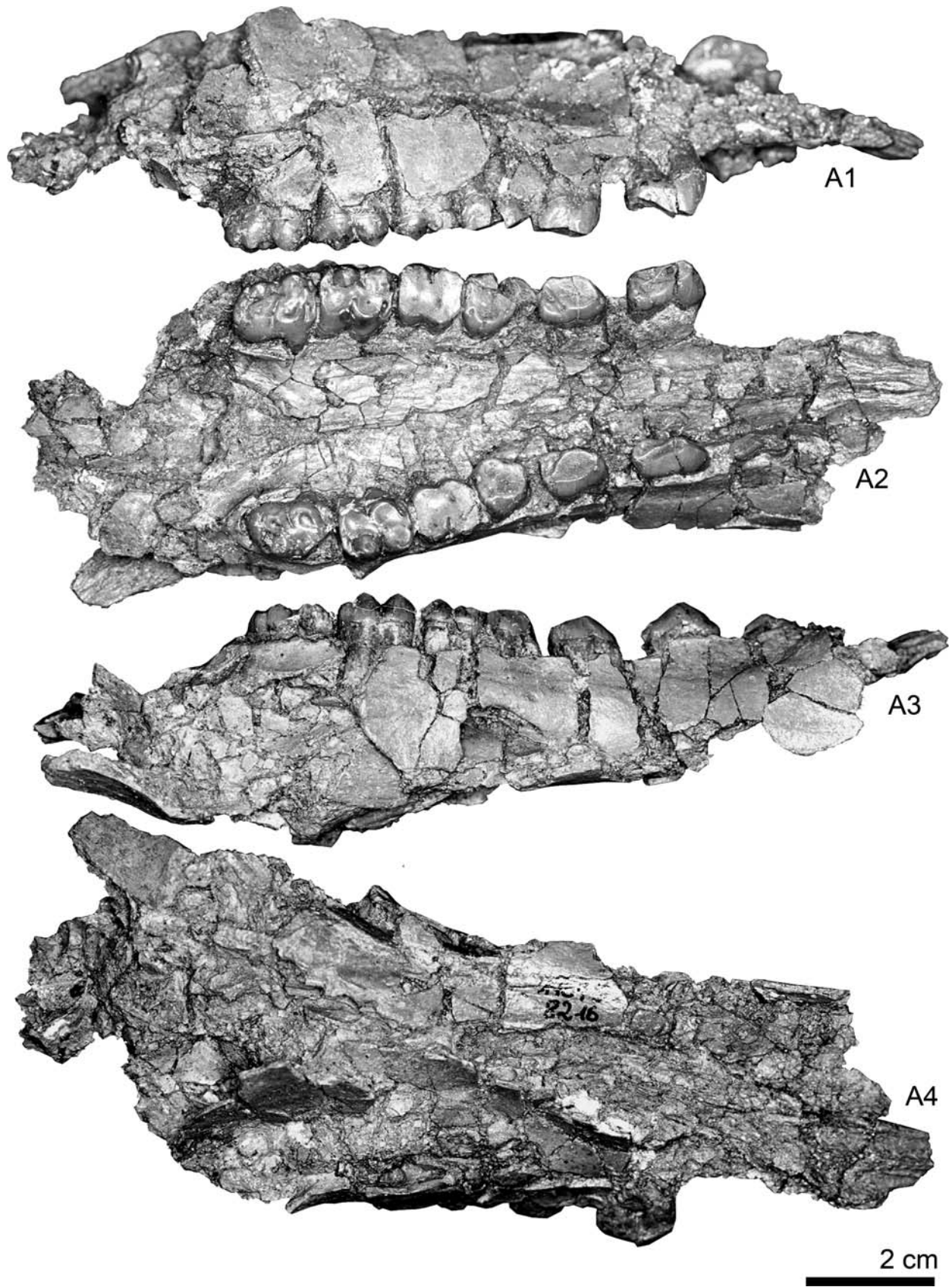
The posterior border of the palate has more or less a U-shape and is situated 5.2 (left) or 3.8 mm (right) behind the third molar. Dorsal to the palate the choanae are deformed but very wide, extending from the middle of one M<sup>3</sup> to the other. This morphology is as in the Suidae, while in the recent Dicotylidae the palate extends far behind the M<sup>3</sup>, where it becomes very narrow, with the pterygoid processes placed close together and reaching nearly to the tympanic bullae, with very narrow choanae between them. The choanae in *Doliochoerus quercyi* from the Quercy are intermediate (MNHN), while those of *Perchoerus* are already relatively narrow (Pearson 1923, Figs. 6, 7, 12, 13; 1927, Fig. 10). The skull of *Taucanamo* from Steinheim is juvenile and a little deformed in this area (Chen 1984, pl. 3, Fig. 1a).

The maxillary foramen is situated above the anterior lobe of the M<sup>1</sup>. There might be a palatine foramen at the height of the first lobe of the M<sup>1</sup>, but this cannot be seen well. What remains of the bone near the P<sup>1</sup> suggests that there was no large canine.

Some premolars are slightly displaced, suggesting the existence of small diastemas. However, the alveoles and the anterior and posterior wear facets on the premolars indicate that the premolars were in contact with each other, and that there were no diastemas between them.

The I<sup>1</sup> (Fig. 2H; Table 2) has simple morphology and a relatively low crown. There is a main cusp with well developed pre and postcristas, with styles at the lingual side. The endocrista is seen as a very low and wide structure. The lingual side of the crown is relatively flat, whereas the labial side is convex. There is a narrow and low lingual cingulum. The I<sup>1</sup> of *Taucanamo sansaniense*, *T. grandaevum* and *T. inonuensis* are similar to the specimen from Sandelzhausen, but have no lingual cingulum and no lingual styles and are much smaller (Fig. 3; Table 2).

In nearly all Suoidea, the I<sup>1</sup> occludes with the tips of I<sub>1</sub> and I<sub>2</sub>, which form an even crest, and the lateral side of the I<sub>2</sub> occludes with the I<sup>2</sup>. However, in *Taucanamo* the I<sub>1</sub> protrudes more than the I<sub>2</sub>, and the lateral side of the I<sub>1</sub> occludes with the I<sup>2</sup>. This is well seen in a specimen from



**Fig. 1** *Schizoporcus muezenbergensis* from Sandelzhausen 1959 II 8216—skull: A1 right lateral, A2 inferior, A3 left lateral, A4 superior views

Çandır (Van der Made 2003: pl. 2 Figs. h–l). This specimen might belong either to *Schizoporcus anatoliensis* or to *Taucanamo*. In a mandible of *S. vallesiensis* from Nsebar, there are two incisors (probably  $I_{1-2}$ , maybe  $DI_{1-2}$ ), which are large and have tips suggesting that both occluded with the  $I^1$ . In a skull of *S. sinapensis* from Sinap, the root of the  $I^1$  is preserved. It is massive. The large  $I^1$  from Sandelzhausen suggests the possibility that it occluded with  $I_1$  and  $I_2$ , as in later *Schizoporcus* and as suggested by the Nsebar specimen, but unlike in *Taucanamo*.

The  $C^x$  (Fig. 2B, C; Table 5) is represented by a much worn specimen and another one of which most of the crown is broken off. The latter has a massive root. It shows some torsion. At the anterior side of the tooth an enamel band can be seen, the presyncline, and the basal part of the anterior facet. The worn specimen has a large anterior facet, caused by occlusion with the lower canine. Such a large facet is not found in carnivores, so the specimen must belong to a suoid, despite its differences from the other canine. In this specimen the root is relatively small. Both specimens are large, especially the worn specimen (Table 5; Fig. 3).

Little is left of the  $P^1$  (Fig. 2A; Table 6). It was a small tooth and did not have a postero–lingual cusp (protocone).

The  $P^2$  (Fig. 2A; Table 6) has a narrow paracone with a long parapostcrista. There is a wide postero–lingual cingulum forming a small plateau, but not forming a distinct protocone. The tooth is larger than the  $P^2$  of *Taucanamo sansaniense*, *T. grandaevum* and *T. primum* and as wide as, but longer than the  $P^2$  of *Schizoporcus sinapensis* and *S. vallesiensis* (Fig. 4).

The  $P^3$  (Fig. 2A; Table 6) has the same structure as the  $P^2$ , but the paracone is much more massive with a shorter parapostcrista and there is a small protocone. The specimen is as long as in *T. sansaniense*, but it is wider. In this respect it resembles a specimen from Neudorf Spalte that was described as *Aureliachoerus* (Zapfe 1983), but that is here assigned to *S. muenzenbergensis*. Also the  $P^3$  of *Schizoporcus vallesiensis* is relatively wide (Fig. 4). The  $P^3$  of *Pecarichoerus* is known, but both specimens are damaged. The values indicated in Fig. 4 are approximate. The tooth is short and wide. There is a very massive protocone, much larger than in *Taucanamo*, later *Schizoporcus*, and in the material from Sandelzhausen.

The  $DP_3$  (Fig. 5A; Table 10) is represented by a specimen in a mandible. It has the simple morphology that is common in these teeth, with a main cusp and an anterior and posterior cristid and with divergent roots.

The  $P^4$  (Fig. 2A; Table 6) is too much worn to show the important details of its morphology. It is larger than its homologue in *Taucanamo*, except for *T. inonuensis*.

The  $DP^4$  (Fig. 2G; Table 6) is represented by a specimen in a maxilla with the  $M^2$  and part of the  $M^1$ . It has four

cusps, and an oblique anterior edge. What is peculiar, is that the anterior lobe is much narrower than the posterior lobe, thus resembling the  $D^3$  (with a single cusp in the anterior lobe) more than a normal  $D^4$ .

The  $DP_4$  (Fig. 5A; Table 10) is present in a mandible along with the  $D_3$ . It has three lobes each with two cusps.

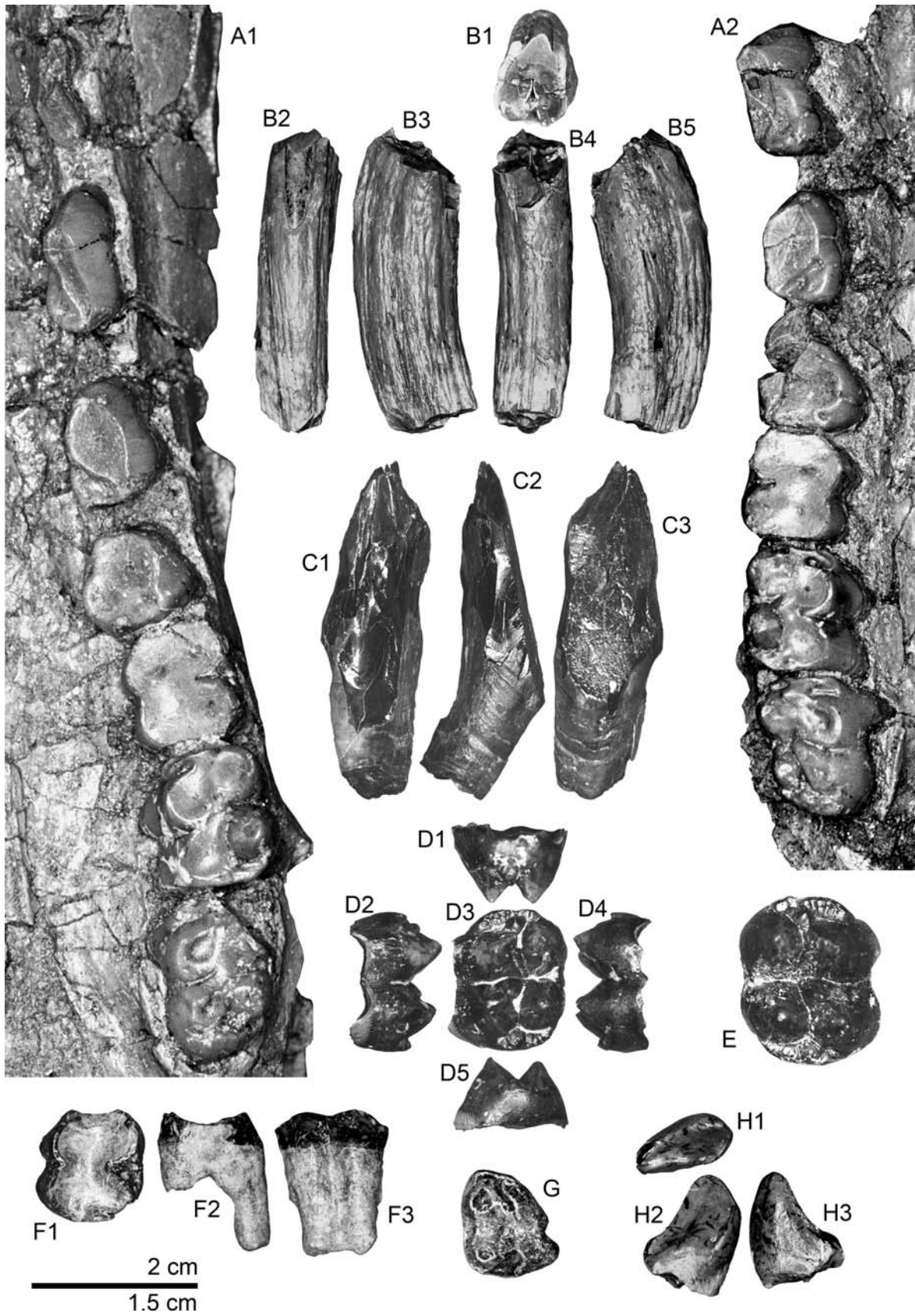
All  $M^1$  are much worn, but in *Suoidea* these molars tend to have the same shapes as the  $M^2$  (Fig. 2A, D–F; Tables 6, 8). The upper molars have a protoprecrista that ends in a separate protopreconule. The latter cusplet is clearly separate from the anterior cingulum, while in the Suidae, this cusplet is integrated in the cingulum and well separate from the protocone. There is a tetraprecrista, but no well separated tetrapreconule (central cusp). The tetrapostconule tends to be separated from the tetracone and to be incorporated in the posterior cingulum. The presence or absence of a postero–labial cingulum seems to be variable.

In one specimen it can be observed that the lingual roots are fused and convergent. The character state of fused convergent roots is common in the Artiodactyla and is probably primitive. The known Palaeochoeridae have fused roots, while Suidae have separate and divergent roots. Within the Palaeochoeridae, the fused lingual roots are convergent in *Taucanamo* and in some of the Palaeochoerinae, while in others they are divergent and connected with a thin bony platelike structure; this morphology has been compared with that of a webbed foot.

The  $M_1$  and the anterior lobe of the  $M_2$  are present in a mandible (Fig. 5A; Table 10). The structure is essentially bunodont; no lophes are formed and there is a small central cusp (hypopreconulid). The  $M_1$  is not shortened by wear. Geologically younger species of *Taucanamo* and *Schizoporcus* tend to have more elongate  $M_1$  (Fig. 4). The  $M_1$  is larger than in any species of *Taucanamo*, and its width is comparable with that of the type material of *T. muenzenbergensis* (Fig. 4).

The  $M^3$  (Fig. 2A; Table 6) has broadly the same shape as the  $M^2$ , but differs in having a narrower second lobe and a posterior cingulum that is expanded more at the lingual side, giving rise to what is the talon. The protoprecrista is well developed and there is no sign of a separation of a protopreconule. In the same way, the tetraprecrista is well developed and there is no separate tetrapreconule. There is a wide transverse valley. There is no protoendocrista, nor a metaprecrista. The morphology of this tooth is compatible with a possible evolution towards lophodonty. In later *Schizoporcus*, there is a metaprecrista that connects with the tetraprecrista.

The  $M^3$  of *Pecarichoerus* is known by two specimens with not much wear, which have nearly formed anterior lophes and have protoendocristas that meet the tetraprecristas in the transverse valleys. In this *Pecarichoerus* is more “advanced” than the suoid from Sandelzhausen, but





◀ **Fig. 2** *Schizoporcus muenzenbergensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...) **A** 8216—skull: 1 left P<sup>1</sup>–M<sup>3</sup>, a—occlusal view; 2 right P<sup>2</sup>–M<sup>3</sup>, occlusal view; **B** right C<sup>x</sup>: 1 apical, 2 anterior, 3 labial, 4 posterior, 5 lingual views; **C** 274 left C<sup>x</sup>: 1 post, 2 labial, 3 anterior views; **D** 280 left M<sup>2</sup>: 1 anterior, 2 lingual, 3 occlusal, 4 buccal, 5 posterior views; **E** 8918 right M<sup>2</sup>, occlusal view; **F** 272 left M<sup>2</sup>: 1 occlusal, 2 anterior, 3 lingual views; **G** 275 right D<sup>4</sup> (from maxilla D<sup>4</sup>–M<sup>1</sup>), occlusal view; **H** 283 right I<sup>1</sup>: 1 apical, 2 lingual, 3 labial views. The scale bar represents 2 cm for **A**, **D**–**H**; and 1.5 cm for **B**, **C**

it is similar to later *Schizoporcus* species. There is an additional crest between the tetracone and metacone, which is lacking in all *Schizoporcus*, and *Pecarichoerus* does not seem to be on an evolutionary pathway towards full lophodonty.

In **tooth proportions** (Fig. 6) the material from Sandelzhausen is close to the different species of *Taucanamo*, but it has a P<sup>3</sup> that is relatively large and a P<sup>2</sup> that is much larger than in that genus. It resembles *Schizoporcus sinapensis* in having wide premolars, but they are relatively large, while in *S. vallesiensis* the premolars became small compared with the molars. The earliest of these species, *T. primum*, has very small third molars, while the latest species (*T. inonuensis*, *S. sinapensis*, *S. vallesiensis*) tend to have the largest third molars.

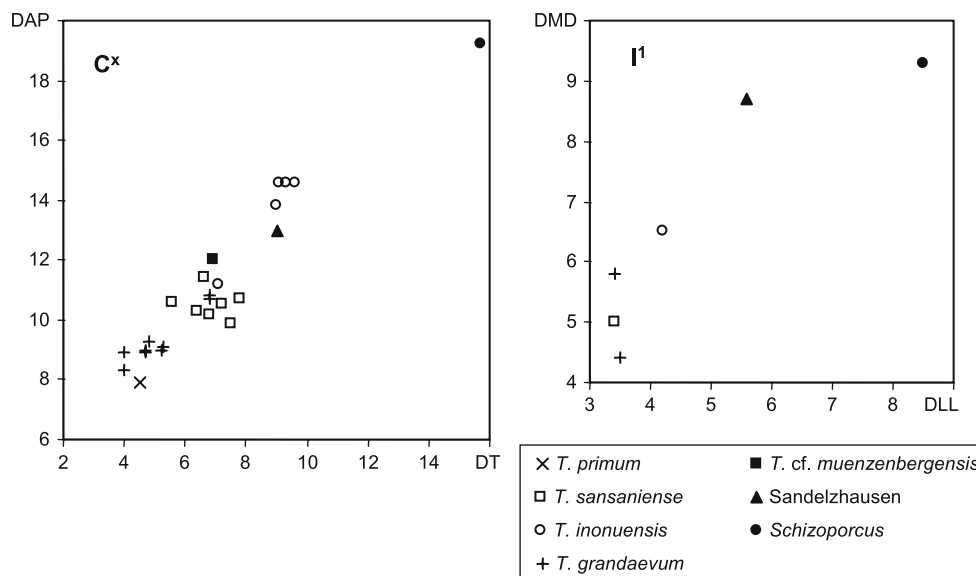
The **Mc III** (Fig. 5B; Table 16) is much smaller than that of *Hyotherium* (Table 16), but otherwise similar. There is a well developed tuberosity for the insertion of the tendon of the *extensor carpi radialis*.

The **calcaneum** (Fig. 5D, F; Table 19) is represented by two specimens of typical suoid morphology that are much

smaller than the calcanei attributed to *Hyotherium* (Table 19) and close in size to the calcanei of *T. sansaniense* from Sansan (MNHN). The sustentacular facet is typically concave in all directions. The most complete specimen is fully adult and seems to be more gracile than the *Hyotherium* specimens. A morphological difference with *Taucanamo* is that there is no deep longitudinal furrow in the middle of the lower part of the lateral side.

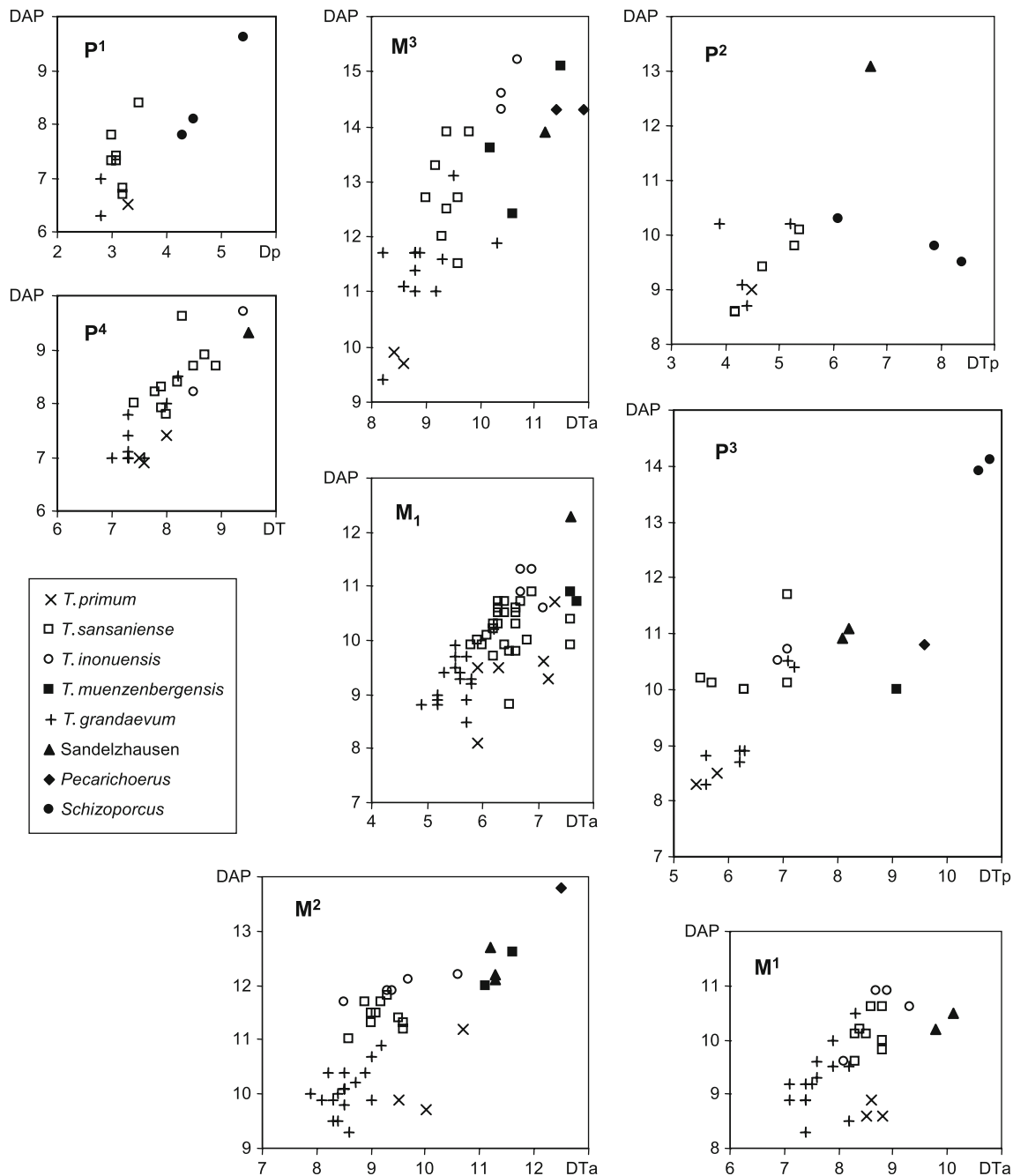
The **astragalus** (Fig. 5E; Table 18) has the common suoid morphology with cylindrical proximal and distal articular surfaces which have axes that are not exactly parallel, with well separated facets for the cuboid and navicular and with a sustentacular facet that is convex in transverse section. The specimen is about as large as the astragali of *Taucanamo sansaniense* (Fig. 7) and is close to two specimens from Neudorf Spalte. These two specimens either both belong to *Schizoporcus*, or the larger one belongs to *Hyotherium*, but the other remains of *Hyotherium* from that locality are large compared with their homologues from Sandelzhausen, while the astragalus is comparatively small. A maximum size for *S. muenzenbergensis* well above that of *T. sansaniense* is expected.

The **first phalanx III/IV** (Fig. 5C; Table 21) is long and slender. The two specimens are as long, as the specimens of *Hyotherium soemmeringi* from Sandelzhausen, but they are narrower (Fig. 31) and they are longer than the phalanges of *H. meisneri*. Palaeochoeridae tend to have elongate phalanges. The proximal articular surfaces of the phalanges have a depression in the middle at the plantar side, but not at the dorsal side. This is normal in the Palaeochoeridae, while



**Fig. 3** Bivariate plots of the I<sup>1</sup> and upper canines of *Taucanamo* and *Schizoporcus*: *T. primum* from Els Casots (IPS); *T. sansaniense* from Sansan (MNHN, MHNT); *T. inonuensis* from Pasalar (PDFAU) and Bonnefond (MNHN); *T. grandaevum* from Steinheim (SMNS), La

Grive (MGL, UCBL) and Anwil (cast IPS), *S. muenzenbergensis* from Sandelzhausen and (?) Baigneaux–en-Beauce (MGL) and *S. sinapensis* from Sinap (measurements taken on root; MTA)



**Fig. 4** Bivariate plots of the upper cheek teeth and  $M_1$  of *Taucanamo*, *Schizoporcus* and *Pecarichoerus*: *T. primum* from Artenay (MNHN), Petersbuch 2 (BSPG), Els Casots (IPS) and Bézian (cast MNHN); *T. sansaniense* from Mont Ceindre (MGL), Göriach (SLJG) and Sansan (MNHN, MHNT, NMB, NHM); *T. inonuensis* from Inönü I (MTA) and Pasalar (PDTFAU); *T. grandaevum* from Steinheim

(SMNS), Przeworno 2 (ISEAK), La Grive (UCBL), *S. muenzenbergensis* from Sandelzhausen, Münzenberg (SLJG) and Neudorf Spalte (NMW, IPUW), *P. orientalis* from the Chinji Formation (AMNH) and *S. sinapensis* from Lower (?) Sinap (MTA) and *S. vallesiensis* from Upper Sinap (MNHN). The very large molars of *Schizoporcus sinapensis* and *S. vallesiensis* are not included

the Suidae and recent Dicotyliidae have a dorso–plantar furrow across all the facet. In these families, the furrow articulates with the dorso–plantar crest in the middle of the distal articulations of the central metapodials (III and IV), while in the Palaeochoeridae the crest is only or mainly developed on the plantar side (Van der Made 1996b).

## Remarks

*Schizoporcus muenzenbergensis* has only relatively recently been described. From the start some specimens from Sandelzhausen were included (Van der Made 1998a). By now there much more material is available. The large

size, relatively large and massive P<sup>2</sup> and P<sup>3</sup>, and not much enlarged and simple M<sup>3</sup> differentiates the material from all species of *Taucanamo* on the one hand. On the other hand, the material indicates a smaller size than in *Schizoporcus anatoliensis*, *S. sinapensis* and *S. vallesiensis*, and the tendency towards lophodonty is less advanced. In the comparable characters, the material resembles other known material of *S. muenzenbergensis*.

Initially, the species was described as *Taucanamo? muenzenbergensis*, but it was stated that the species might be an evolutionary link between *Taucanamo* and *Schizochœrus* (now *Schizoporcus*) and later it was included in the latter genus (Van der Made 1998a, 2003). The material, described here, includes further elements that were not yet described for this species, including the skull, astragalus, calcaneum, Mc III, and first phalanx. The phalanx is an important element in the recognition of the Palaeochoeridae; it is elongate and has a typical morphology of the proximal articulation. The skull, having wide choanae, shows a similarity to the Suidae. The new material strengthens the links with *Schizoporcus*: the I<sup>1</sup> and canines are large as in *Schizoporcus sinapensis*, while in *Taucanamo* they are relatively small; the upper premolars, especially the P<sup>3</sup>, are wide and have massive paracones.

Family Suidae Gray 1821

Subfamily Hyotheriinae Cope 1888

*Hyotherium* Von Meyer 1834

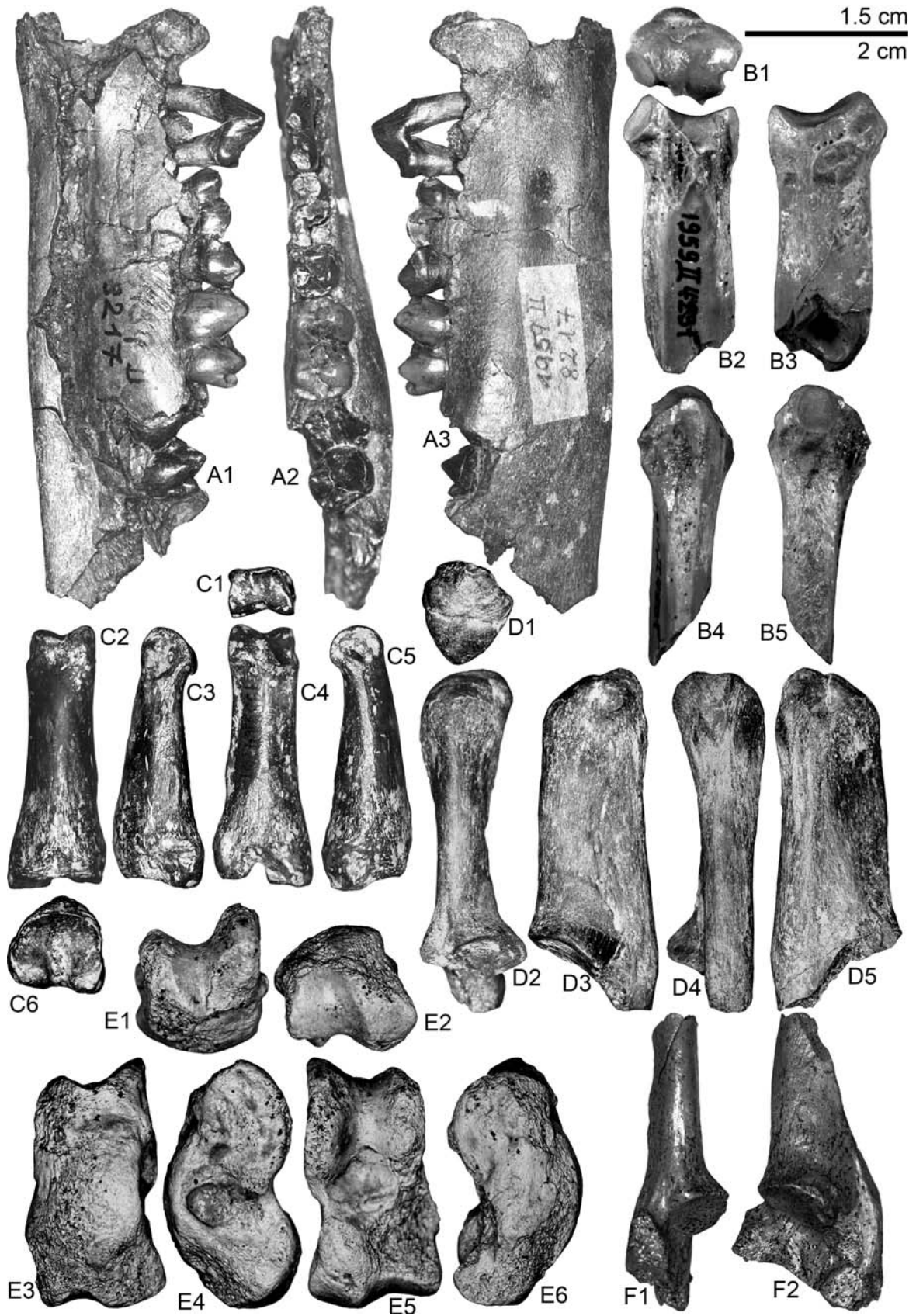
*Hyotherium soemmeringi* (Von Meyer 1829)

*Hyotherium soemmeringi wylensis* (Von Meyer 1859)

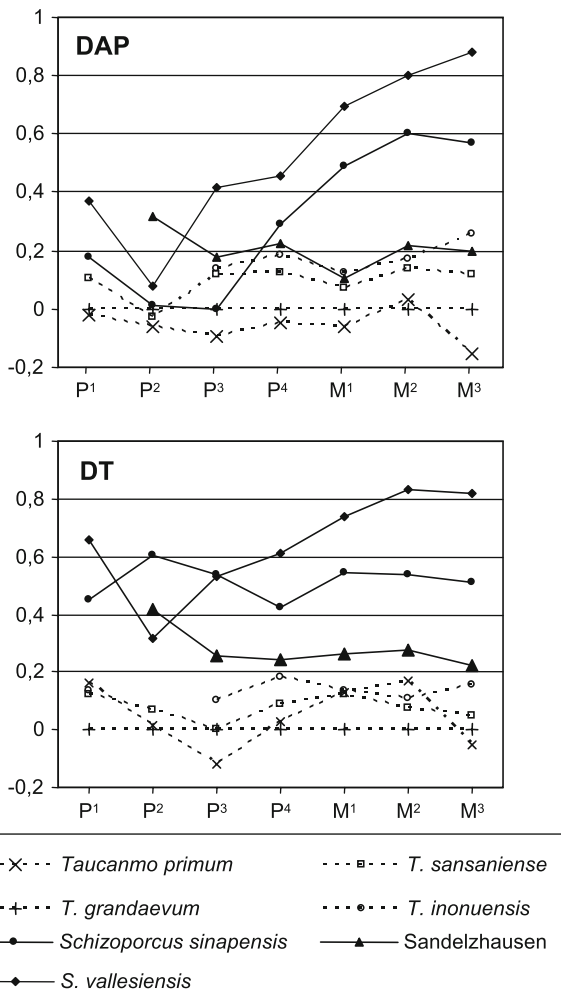
#### Synonymy (*H. s. wylensis*):

- v\* 1859 *Sus* (*Palaeohyus*) *Wylensis* Von Meyer: 429–430.
- v. 1859 *Hyotherium medium* Von Meyer: 429–430.
- v.1866 *Sus* (*Palaeohyus*) *Wylensis* Von Meyer: 577 (material from Nieder-Utzwyl; not Eggingen).
- v.1899–1900 *Hyotherium Sömmeringi* var. *medium* H. v. M.—Stehlin: 11, 44–45, 135–136, 236, pl. 1 Figs. 2–3.
- v.1907 *Hyotherium* cf. *Soemmeringi* H. v. M.—Stehlin: 528, 531.
- v.1907 *Hyotherium* cf. *Soemmeringi* var. *medium* H. v. M.—Stehlin: 528, 530.
- v.1908 *Hyotherium sömmeringi* Mayet: 54, 154?
- v.1908 *Palaeochoerus* aff. *Waterhousi* Mayet: 161–162 (Baigneaux), pl. 5 Fig. 16.
- v.1914 *Hyotherium Sömmeringi* Myr. var. *medium* Myr.—Stehlin: 192 (Buchental, other localities ?)
- v.1925 *Hyotherium* cfr. *Soemmeringi* var. *medium* Myr.—Stehlin: 70–72.

- v.1934 *Palaeochoerus Waterhousi* Pomel.—Roman and Viret: 43–44, pl. 4 Figs. 6–8 (not 9), pl. 5 Fig. 18?
- v.1946 *Palaeochoerus Waterhousi*.—Richard: 244, 246?
- v.1971 *Hyotherium soemmeringi* Meyer.—Ginsburg: 158, 159, 160?
- v.1971 *Hyotherium soemmeringi* H. v. Meyer, 1834.—Schmidt-Kittler: 129–168 (Sandelzhausen), Figs. 1–3, 5, 8–9, 12B, 13B, pls. 11–12.
- v.1972 *Conohyus cuspidatus* nva. sp.—Golpe: 149, Pl. 1 Fig. 1e, f.
- v.1975 *Listriodon lockharti* Leinders: Pl. 2 Fig. 3
- v.1976 *Listriodon lockharti* Leinders: 46–50, 53, pl. 2 Figs. 2–3.
- v. 1977 Suidae.—Daams et al.: Fig. 3 (Valdemoros 3a), Fig. 4.
- v.1980 *Hyotherium soemmeringi*.—Dehm: 49–56, Figs. 2–4 (Sandelzhausen).
- v.1990 *Hyotherium* cf. *soemmeringi* Meyer, 1841.—Ginsburg: 162.
- v.1990 *Hyotherium soemmeringi* Meyer, 1834.—Ginsburg: 164, 167?, 172.
- v.1990 ?*Hyotherium major* (POMEL, 1847).—Van der Made: 87, Fig. 3 (Valdemoros, Armantes).
- v.1990 *Hyotherium soemmeringi* VON MEYER, 1829.—Van der Made: 87 (excl. Montejo de la Vega), partially: 84, 93–94, Fig. 3.
- v.1990 *Hyotherium soemmeringi*.—Van der Made: 100, 104 (partially).
- v.1991 *Hyotherium soemmeringi* (H. v. Meyer).—Hellmund: 9–37 (material from Sandelzhausen), pl. 12 Figs. 1–3.
- v.1994 *Hyotherium soemmeringi*.—Van der Made: 11, 13, 14–15, 20r, Fig. 3, Tables 6, 10; partially: 2, 14, 16.
- v.1996 *Hyotherium soemmeringi* (MEYER, 1829).—Van der Made and Kowalski: 305–310 (the material from Belchatów).
- v.1996 *Hyotherium soemmeringi*.—Van der Made: 42, 81, 120, 128, Figs. 14a, 23, 24,
- v.1996 *Hyotherium soemmeringi* (Meyer, 1829).—Fortelius et al.: 355, 375 (partially).
- v.1997 *Hyotherium soemmeringi*.—Van der Made: 110 (partially), 111.
- v.1997 *Hyotherium soemmeringi*.—Van der Made: 148, 153 (Fig. 5).
- v.1998 *Hyotherium soemmeringi wylensis*. – Van der Made: 250–252, 260.
- v.1998 *Hyotherium soemmeringi*.—Van der Made et al.: 105,106 (Fig. 5 Baigneaux, Sandelzhausen).
- v. 2006 *Hyotherium soemmeringi*.—Orliac, Antoine and Duranthon: Fig. 6a.
- v. 2006 *Hyotherium lacaillei* n. sp.—Orliac, Antoine and Duranthon: 688–698, Figs. 2, 3, 4a, 4b, 5, 6b (material partially seen).

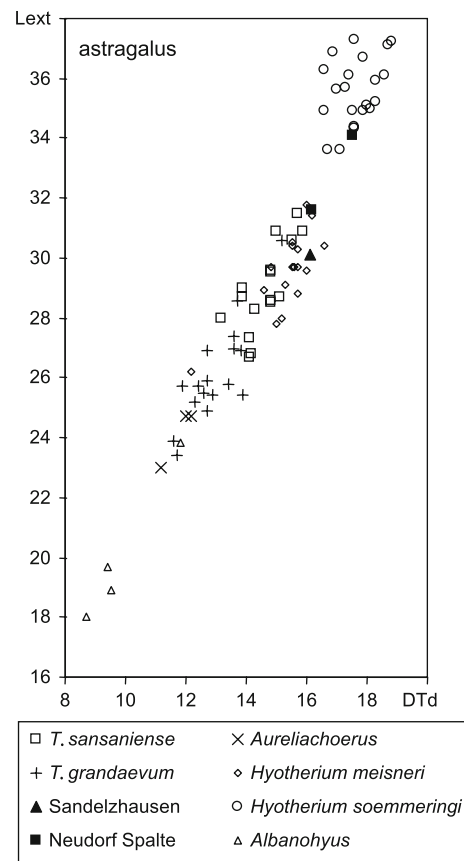


◀ **Fig. 5** *Schizoporcus muenzenbergensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...) **A** 2817 right mandible with D<sub>3</sub>–M<sub>2</sub>: 1 lingual, 2 occlusal, 3 buccal views; **B** 4231 left Mc III: 1 proximal, 2 posterior, 3 anterior, 4 lateral, 5 medial views; **C** 4761 first phalanx III/IV, left of axis of foot: 1 distal, 2 dorsal, 3 axial, 4 plantar, 5 abaxial, 6 proximal views; **D** 278 right calcaneum: 1 dorsal, 2 anterior, 3) medial, 4 posterior, 5 lateral views; **E** 277 right astragalus: 1 proximal, 2 distal, 3 posterior, 4 lateral, 5 anterior, 6 medial views; **F** 279 right calcaneum: 1 anterior, 2 medial views. The scale bar represents 1.5 cm for **B** and 2 cm for **A**, **C**–**F**



**Fig. 6** The proportions of the upper cheek teeth of different Palaeochoeridae compared. The value indicated for each cheek tooth is ln(sample/standard): average of *Taucanamo grandaevum* from Steinheim, La Grive and Anwil ( $n \leq 19$ ); average *T. primum* ( $n \leq 4$ ), *T. sansaniense* ( $n \leq 11$ ), *T. inonuensis* ( $n \leq 6$ ), *S. muenzenbergensis* from Sandelzhausen ( $n \leq 4$ ), *S. sinapensis* ( $n \leq 2$ ) and *S. vallesiensis* ( $n \leq 2$ ). Provenance of data as in Fig. 4

**Holotype:** A/V82 remains of left and right mandibles with left I<sub>1-3</sub>, C<sub>f</sub>, P<sub>2-3</sub> and right I<sub>1</sub> and M<sub>1-3</sub>, kept in the PIMUZ, illustrated by Stehlin 1899–1900, Pl. 1, Figs. 2–3.



**Fig. 7** Bivariate diagram of the astragalus of selected small Suoidea: *Taucanamo sansaniense* from Sansan (MNHN, MHNT, NMB), *T. grandaevum* from Steinheim (SMNS) and La Grive (MGL, UCBL, NHM, CFE), *Schizoporcus muenzenbergensis* from Sandelzhausen and from Neudorf Spalte (NMW; the larger specimen might belong to *Hyotherium*), *Aureliachoerus minus* from Wintershof West (BSPG), *Hyotherium meischeri* from Laugnac (UPM), Montaigu (NMB) and Hessler (FISF), *H. soemmeringi* from Sandelzhausen, *Albanohyus pygmaeus* from La Grive (MGL) and *Albanohyus castellensis* from Castell de Barberá (IPS)

**Type stratum and locality:** brown coal from Nieder-Utzswyl, near Wyl, Kanton St Gallen, Switzerland.

**Age of the type locality:** (based on evolutionary level of its *Hyotherium*) Early Aragonian, zone D of the Aragonian, early Middle Miocene, estimated as about 15.8 Ma (Daams et al. 1999).

**Other localities:** Estrepouy, Chilleurs, Belchatów C, Pellecahus, Pfetrachmühle, Buchental, Munébrega AB, Munébrega 1, Munébrega 2, Torralba 2, Torralba 4, Valdemoros 3a, Valdemoros 3c, Montréal du Gers, Baigneaux-en-Beauce, Sandelzhausen, Pontlevoy (oc).

**Diagnosis:** small *Hyotherium soemmeringi* with well developed, but not very large, distal cusp on the I<sup>1</sup>.

**Material:** The material is indicated in Tables 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, and 23.

**Table 1** The measurements (mm) of the associated upper incisors and canines of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/ right	I <sup>1</sup>			I <sup>2</sup>		I <sup>3</sup>		C <sup>f</sup>	
		DT	DMD	DMDoc	DMD	DLL	DMD	DLL	DAP	DT
307 <sup>a</sup>	l								11.2	6.5
307 <sup>a</sup>	r								11.0	6.3
16227	l	13.8	18.3	9.4	11.2	5.2	10.1	4.7		
16227	r	13.4	18.6	9.7			10.4	5.0		

<sup>a</sup> Specimens associated with cheek teeth

## Description and comparison

In addition to the anterior part of a **skull** and several other fragments described and illustrated by Schmidt-Kittler (1971, Figs. 1, 2, 12b, 13b, pls. 11 and 12; number 305) there is a nearly complete, although crushed, skull (number 8218) and a well preserved part of the anterior area of the zygomatic arch that has no deformation whatsoever (258; Fig. 8A) and some other fragments.

The shape of the skull in lateral view cannot be known because of the deformation of the specimens. However, it

**Table 2** The measurements (mm) of the isolated upper incisors and deciduous incisors of *Schizoporcus muenzenbergensis* (283) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/right	DT	DMD	DMDob	DMDoc	DLL	Hli	Hla
283	I <sup>1</sup>	r		8.7			5.6	8.1	
362	I <sup>1</sup>	l			12.8		8.6		
365	I <sup>1</sup>	r			12.2		8.1		
371	I <sup>1</sup>	l			10.8		5.8		
8856	I <sup>1</sup>	l			15.1		8.7		
8858	I <sup>1</sup>	l		>11.9			8.5		
8874	I <sup>1</sup>	r			14.2		8.3		
8218 <sup>a</sup>	I <sup>1</sup>	l	13.1	14.7	17.6	17.2	8.2		
8860	I <sup>1</sup>	r		>12.9	17.2		8.1		
8862	I <sup>1</sup>	r	_b	_b	_b	_b	_b		
8861	I <sup>1</sup>	r					8.2		
285	I <sup>1</sup>	l			13.6			7.8/8.8	
8855	I <sup>1</sup>	l		13.7	19.5	16.3	9.0		
1996 Baugelände	I <sup>1</sup>	l		12.1	19.2	15.2	8.6		
308 <sup>a</sup>	I <sup>1</sup>	r			13.4			~ 10.2	
11763	I <sup>1</sup>	l	_b	_b	_b	_b	_b		
16675	I <sup>1</sup>	r	_b	_b	_b	_b	_b		
PQ12-S. 30üB	I <sup>1</sup>	r	12.8	14.1	18.1	16.1	7.8		
11794	I <sup>2</sup>	l		11.0			5.6		
11732	I <sup>2</sup>	l		10.6			5.8		
11816	I <sup>2</sup>	l		10.5			5.7		
11764	I <sup>2</sup>	r		12.2			5.5		
368	I <sup>2</sup>	l		9.4			5.3		
16610 <sup>a</sup>	I <sup>2</sup>	l		10.4			5.8		
16641	I <sup>3</sup>	r		10.3			6.0	8.5	
370	I <sup>3</sup>	l		9.0			4.7		7.6
369	I <sup>3</sup>	r		8.6			4.9		
11751	I <sup>3</sup>	r		8.5			4.7		
16610 <sup>a</sup>	I <sup>3</sup>	r		9.2			5.3	8.5	
367	DI <sup>1</sup>	r		10.2			4.7		
11750	DI <sup>1</sup>	r		8.2			4.8		
11809	DI <sup>1</sup>	l		8.0			4.8		
11813	DI <sup>1</sup>	l		_b			_b		
7-N 135-140üO	DI <sup>1</sup>	l		7.2			5.1		
11820	DI <sup>1</sup>	l		7.7			4.5		
11792	DI <sup>2</sup>	l		7.2			3.5		
11815	DI <sup>2</sup>	l		7.1			3.6		
11819	DI <sup>2</sup>	l		7.3			3.9		

<sup>a</sup> Specimens associated with cheek teeth

<sup>b</sup> Measurement was not taken due to damage

**Table 3** The measurements (mm) of the associated lower incisors and canines of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/right	I <sub>1</sub>				I <sub>2</sub>		I <sub>3</sub>		C <sub>m</sub>			C <sub>f</sub>	
		DMD	DLL	Hli	Hla	DMD	DLL	DMD	DLL	Li	La	Po	DAP	DT
260 <sup>a</sup>	l	6.2	10			6.5	10.2						10.2	6.9
260 <sup>a</sup>	r					6.2	10.1							
315 <sup>a</sup>	l	5.3	8.7							– <sup>b</sup>	– <sup>b</sup>	– <sup>b</sup>		
315 <sup>a</sup>	r	5.6	8.8			6.1	9.8			– <sup>b</sup>	– <sup>b</sup>	– <sup>b</sup>		
317 <sup>a</sup>	l	6.5		>15.6	– <sup>c</sup>	6.0				– <sup>b</sup>	– <sup>b</sup>	– <sup>b</sup>		
317 <sup>a</sup>	r	6.4				6.3								
379	l	– <sup>b</sup>				5.4	9.5	4.4	8.8					
379	l	– <sup>b</sup>						4.3	8.8					
3721 <sup>a</sup>	r		9.8			6.1	9.9			13.5	9.3	11.1		
8218 <sup>a</sup>	l	– <sup>c</sup>	– <sup>c</sup>			– <sup>c</sup>	– <sup>c</sup>	8.2	5.0					
8218 <sup>a</sup>	r	– <sup>c</sup>	– <sup>c</sup>			– <sup>c</sup>	– <sup>c</sup>							
307 <sup>a</sup>	l	6.6	8.3			~6.2	8.9	– <sup>b</sup>	7.3				8.9	6.6
307 <sup>a</sup>	r	6.5	8.1			6.6	9.0	– <sup>b</sup>	7.1				8.0	– <sup>b</sup>

<sup>a</sup> Specimens associated with cheek teeth

<sup>b</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

<sup>c</sup> Measurement was not taken due to damage

is clear that the anterior part was not much elongated. The anterior rim of the orbita was situated a little behind the middle of the skull. The right orbita of specimen 8218 suggests the presence of a foramen lacrymale, but this is not clearly visible because of the state of the specimen.

The parietal lines meet and form a modest parietal crest. The occipital area is lacking but cannot have been very wide. The shape and extension of the supraorbital furrows cannot be seen well.

As indicated by Schmidt-Kittler (1971), there are minor diastemas anterior and posterior to the P<sup>1</sup> and a long diastema between the upper canine and the I<sup>3</sup>. The maxilla extends laterally over the C<sup>m</sup>. It is slightly elevated and forms a well developed crista alveolaris. In side view this structure curves up above the diastema for the C<sub>m</sub> and down lateral to the C<sup>m</sup>. It formed a niche for protection of the C<sub>m</sub> similar to that in living Dicotylidae. The maxilla does not have a pronounced dorsally directed process, as in, for instance, *Potamochoerus*.

Right premaxilla PQ20-N, 30-35üB has the alveoli of the I<sup>2</sup> and I<sup>3</sup>. The alveolus of the third incisor was in the process of closing at the moment of death, which implies the loss of this tooth a considerable time prior to death. The loss of I<sup>2-3</sup> during life does not seem to have been rare and is observed also in a skull of *Propotamochoerus provincialis* from Kardia (IVAU).

The foramen palatinum is at the level of the anterior lobe of the M<sup>2</sup> (305). In none of the specimens can the posterior border of the palate be well observed, but it extended some 2 cm behind the M<sup>3</sup> in no. 2805 and

>14.3 mm in 8218, which was a male. The variation of this character in some samples of recent *Sus* was described by Van der Made (1997b: 147, Fig. 6).

The zygomatic arch was described in great detail by Schmidt-Kittler (1971), who pointed out the similarities to the Chinese suid *Chleuastochoerus* and the sexually dimorphic nature of the structure: in the males the anterior part is much more developed. A more recently found specimen, 258, probably belonged to a male (Fig. 8B). It fits a maxillary fragment bearing the remains of the P<sup>3</sup> and P<sup>4</sup>. The zygomatic arch originates in an area that extends from lateral of the position of posterior lobe of the P<sup>3</sup> to the second lobe of the M<sup>3</sup>, and departs approximately at a right angle, curving even a little anteriorly. Its anterior part forms a horizontal plate, the prezygomatic shelf that is elevated about 23 mm above the occlusal surface. The lateral edge stands out approximately 24–28 mm from the vertical wall of the maxilla. This lateral edge has a beaded (or “cauliflower”) structure that is up to 14 mm thick, while the platelike structure medial to the edge is markedly thinner. Above the prezygomatic shelf and approximately above the posterior lobe of the M<sup>2</sup>, a part of the lower edge of the orbita is preserved. It is situated 48 mm above the occlusal surface and lateral to the buccal side of the M<sup>3</sup>. There does not seem to be an *incisura infra orbitalis*, but there is a marked infraorbital fossa, suggesting a well developed *levator rostri* muscle. The maxillary foramen is situated a short distance above the M<sup>3</sup> and is the entry to the maxillary canal, which opens at the lateral side of the maxillary as the *foramen infra orbitale*. This foramen is not

**Table 4** The measurements (mm) of the isolated lower incisors and deciduous incisors of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/right	DMD	DLL	Hli	Hla
315 <sup>a</sup>	I <sub>1</sub>	l	5.3	8.7		
372	I <sub>1</sub>	l	6.8	9.5	16.6	
376	I <sub>1</sub>	l	5.6	9.4	>14.6	>12.0
8864	I <sub>1</sub>	l	6.0	8.9	>16.8	
8865	I <sub>1</sub>	r	5.9	>8.5		
8871	I <sub>1</sub>	r		10.4	16	16.4
11675	I <sub>1</sub>	l	6.2			
11804	I <sub>1</sub>	r	5.5	8.8		
11805	I <sub>1</sub>	l	6.2	9.6		
374d	I <sub>2</sub>	r	6.4	9.5	>17.0	15
375	I <sub>2</sub>	l	5.2	9.1		
8863	I <sub>2</sub>	r	5.6	8.6		
8866	I <sub>2</sub>	r	5.7	8.5		
8867	I <sub>2</sub>	r	5.3	8.9		
8869	I <sub>2</sub>	r	6.9	9.6		
8870	I <sub>2</sub>	l	5.9	9.8	>16.6	>14.0
8872	I <sub>2</sub>	r	6.3	9.0		
8873	I <sub>2</sub>	l	6.8	8.9		
11676	I <sub>2</sub>	r	6.3			
11729	I <sub>2</sub>	l	6.9			
11822	I <sub>2</sub>	l	>5.4	>9.9		
11823	I <sub>2</sub>	l	5.4	8.2		
11785	I <sub>2</sub>	r	>6.0	>9.9		
11691	I <sub>2</sub>	r	5.9	10.0		
11776	I <sub>2</sub>	l		9.3		
11824	DI <sub>1</sub>	l	4.4	4.5		
8868	DI <sub>2</sub>	l	4.4	6.3		
11755	DI <sub>2</sub>	l	4.4	6.3		
11807	DI <sub>2</sub>	r	4.0	5.9		
			DMD	DLL	Dmax	Dperp
366	I <sub>3</sub>		5.2	9.5	8.0	— <sup>b</sup>
377	I <sub>3</sub>	r	5.7	— <sup>c</sup>	9.0	4.7
378	I <sub>3</sub>	r	5.4	— <sup>c</sup>		
11748	I <sub>3</sub>	r	4.5	6.9	7.6	5.8
11749	I <sub>3</sub>	l	4.4	7.1	8.7	4.5
11753	I <sub>3</sub>	l	5.1	7.4	9.1	5.9
11760	I <sub>3</sub>	r	5.8	7.4	7.9	4.9
11761	I <sub>3</sub>	l	4.8	5.9	7.8	4.2
11779	I <sub>3</sub>	r	5.1	7.8	8.2	6.0
16747	I <sub>3</sub>	l	6.7	8.1	9.0	4.4
16629	I <sub>3</sub>	l	6.5	9.0	10.4	5.3
11814	I <sub>3</sub>	r	5.6	6.1	7.9	4.9
11769	I <sub>3</sub>	r	4.5	8.3	9.8	5.6
11780	I <sub>3</sub>	r	4.7	6.3	8.0	5.1

<sup>a</sup> Some specimens are associated with cheek teeth<sup>b</sup> Measurement was not taken due to damage<sup>c</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)**Table 5** The measurements (mm) of the isolated canines of *Schizoporcus muenzenbergensis* (274, 282) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/ right	DAP	DT	DTcem	Ri	Ro
274	C <sup>f/m</sup>		>9.7	11.8			
282	C <sup>f/m</sup>		~13.0	8.0	9.0		
344	C <sup>m</sup>	l	15.2	12.3			
346	C <sup>m</sup>	r	16	15.5			
8847	C <sup>m</sup>	l	16	12.1	15.1	80	95
8848	C <sup>m</sup>	l	15.2	13.4	13.6	45	60
8852	C <sup>m</sup>	r	16.2	13.3	13.6	50	65
8851	C <sup>m</sup>	r	13.1	12.5	15.6	— <sup>a</sup>	— <sup>a</sup>
8853	C <sup>m</sup>	r	13.8	12.1	14.9	— <sup>a</sup>	— <sup>a</sup>
8849	C <sup>m</sup>	r	15.9	12.8	14.2	65	80
8917	C <sup>m</sup>	l?	— <sup>a</sup>	11.4	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
8854	C <sup>m</sup>	r	14	12.1	— <sup>a</sup>	65	65
16675	C <sup>m</sup>	r	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
342	C <sup>f</sup>	r	11.3	7.1			
252 <sup>b</sup>	C <sup>f</sup>	l	12.8	7.4			
308 <sup>b</sup>	C <sup>f</sup>	l	12.3	7.0			
308 <sup>b</sup>	C <sup>f</sup>	r	11.2	— <sup>a</sup>			
8071	C <sub>r</sub>	l	8.7	6.5			
312 <sup>b</sup>	C <sub>r</sub>	r	8.4	5.6			
313 <sup>b</sup>	C <sub>r</sub>	— <sup>c</sup>	— <sup>c</sup>	— <sup>c</sup>			
355	C <sub>r</sub>	l	8.2	6			
NB 20-Z 90üB	C <sub>r</sub>	r	>9.9	8.1			
11811	C <sub>r</sub>	r	tip				
16610 <sup>b</sup>	C <sub>r</sub>	r	9.6	6.4			
			Li	La	Po	Ri	Ro
93 <sup>b</sup>	C <sub>m</sub>	r	12.6	11.8	10.6		
350	C <sub>m</sub>	r	12.2	9.6	10.1	25	35
531	C <sub>m</sub>	l	— <sup>c</sup>	— <sup>c</sup>	— <sup>c</sup>		
357	C <sub>m</sub>	r	13.4	9.5	9.3	15–20	35
358	C <sub>m</sub>	r	13.2	9.0	10.0	35	— <sup>a</sup>
361	C <sub>m</sub>	r	9.8	~7.2	~9.3	30	40
356	C <sub>m</sub>	r	15.4	9.7	12.2	20	40
360	C <sub>m</sub>	l	12.9	8.9	9.9	25	35
8218 <sup>b</sup>	C <sub>m</sub>	l	13.8	8.7	11.4		
8841	C <sub>m</sub>	l	12.7	10.8	11	~25	40
8843	C <sub>m</sub>	l	12.1	9.6	10.4	25	35
11677	C <sub>m</sub>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
8842	C <sub>m</sub>	r	13.2	10.0	9.8	25	35
12-G 60-65	C <sub>m</sub>	l	11.7	7.2	9.0	— <sup>a</sup>	30
11691	C <sub>m</sub>	r	13.1	10.0	10.3	25	35
1929 30-M 5/9/ 73 <sup>b</sup>	C <sub>m</sub>	l	14.4	— <sup>a</sup>	— <sup>a</sup>		
1929 30-M 5/9/ 73 <sup>b</sup>	C <sub>m</sub>	r	15.8	10.0	12.4		

<sup>a</sup> Measurement was not taken due to damage<sup>b</sup> Some specimens are associated with cheek teeth<sup>c</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)



**Table 6** The measurements (mm) of the associated upper deciduous and permanent molars of *Schizoporcus muenzenbergensis* (8216, 275) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/right	P <sup>1</sup>		P <sup>2</sup>		P <sup>3</sup>		P <sup>4</sup>		M <sup>1</sup>		M <sup>2</sup>		M <sup>3</sup>							
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp					
8216	l	>10.0	- <sup>a</sup>	>3.8	13.1	5.9	6.7	11.1	6.4	8.2	9.3	9.5	10.1	10.1	12.2	11.3	11.5	13.9	- <sup>b</sup>	9.1	
8216	r				<14.0	5.8	6.8	10.9	6.7	8.1	- <sup>b</sup>	>10.3	10.1	10.2	12.1	11.3	11.3	13.9	11.2	9.1	
55	l								12.2	13.2	12.9	13.2	13.4								
252	r				14.4	7.4	- <sup>b</sup>	14.1	9.2	11.0	11.6	14.1	14.3	15.2							
252 + 261	l	10.9	5.1	5.4	14.4	9.1	10.8	14.4	9.1	10.8	11.9	14.2	14.9	15.1							
262	l				- <sup>b</sup>	- <sup>b</sup>	6.9	>14.3	9.4	- <sup>b</sup>	12.6	14.0			17.5	17.2	17.0				
265	l								12.7	14.5											
258	l								12.8	13.7					17.4	16.4	- <sup>b</sup>	20.2	15.6	12.5	
307	l	10.7	5.1	5.0				12.1	12.6	16.0	14.7	15.1	15.1	16.0	17.6	16.4	16.0	20.7	15.1	13.1	
307	r	11.5	5.2	4.7	14.1	5.8	6.2	15.3	8.2	9.6	12.4	12.7	<15.0	15.4	17.8	16.6	16.1	20.9	16.3	14.5	
268	r									15.5	14.2	15.4	16.4		18.2	≥16.5	16.4				
305	l	12.3	5.3	5.9	14.8	6.3	6.4	1.6	8.0	11.9	13.7	13.7	16.6	16.6	15.5	17.3	17.2	16.1	20.4	16.3	14.9
305	r	12.1	5.3	5.6	15.1	6.4	6.5	16.2	8.7	11.1	12.8	14.0	- <sup>b</sup>	17.0	17.7	17.3	18.0	20.3	16.5	14.9	
306	r				- <sup>a</sup>		- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	
309	l				14.5	9.0	11.2	12.6	13.6	16.0	15.0	15.0	15.0	17.3	19.0	17.3	17.0	21.9	16.7	15.2	
309	r				15.0	9.2	11.5	12.3	13.7	15.8	14.7	14.9	14.7	17.2	17.2	17.2	17.6	22.1	16.6	15.1	
310	l														18.0	- <sup>b</sup>	17.0	18.4	17.4	13.9	
310	r														17.2	17.4	16.5				
311	r				14.5		11.1	12.1	13.5	14.3	13.0				17.1	≥15.5	- <sup>b</sup>				
8218	l				14.9	- <sup>b</sup>	- <sup>b</sup>	14.4	- <sup>b</sup>	≥16.7	- <sup>b</sup>	- <sup>b</sup>	- <sup>b</sup>	- <sup>b</sup>	18.3	16.9	16.9	22.5	16.6	15.5	
8218	r	≥9.9	5.5	5.2	- <sup>b</sup>	6.9	7.8	- <sup>b</sup>	9.0	11.8	13.8	13.6			18.0	17.1	16.9	22.6	17.2	15.7	
8219	l				14.4	8.0	9.6	11.5	12.5	14.5	13.6	14.8	14.8	16.5	16.5	15.4	14.2	18.1	14.9	13.1	
8219	r														16.1	15.3	13.9	17.7	14.6	12.9	
8876	r				13.4	7.5	10.1	11.4	12.7	13.5	13.8	14.1									
8878	r									15.3	13.9	14.5	16.1		18.1	16.1	16.1				
8897	l							11.4	12.5	13.1	14.0	13.8	15.6		15.7	16.5	15.6	17.8	16.0	13.8	
308	l								<16.7	15.0	15.7	15.8						21.9	17.6	>14.4	
308	r				~16.2	- <sup>b</sup>	- <sup>b</sup>											21.1	16.9	>14.4	
16719	r				14.4	8.2	10.3	13.2	14.0	14.8	14.1	14.4									
D <sup>3</sup>																					
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	M <sup>1</sup>	DAP	DTa	DTp	M <sup>2</sup>	DAP	DTa	DTp			
275	r				9.8	8.1	8.9	- <sup>b</sup>	9.9	- <sup>b</sup>	12.7	11.2	11.0								
348	r				15.0	- <sup>a</sup>	10.9	14.7	- <sup>a</sup>	13.6											

<sup>a</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

<sup>b</sup> Measurement was not taken due to damage

**Table 7** The measurements (mm) of the isolated upper premolars of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/right	DAP	DTa	DTp
334	P <sup>1</sup>	l	12.1	5.9	5.4
352	P <sup>1</sup>	r	11.5	5.9	5.3
11741	P <sup>1</sup>	l	– <sup>a</sup>	– <sup>a</sup>	4.9
11746	P <sup>1</sup>	l	12.0	5.9	4.9
11767	P <sup>1</sup>	r	– <sup>a</sup>	5.8	– <sup>a</sup>
11759	P <sup>1</sup>	l	11.2	5.3	4.9
11786	P <sup>1</sup>	r	– <sup>a</sup>	5.6	– <sup>a</sup>
11803	P <sup>1</sup>	l	– <sup>a</sup>	6.1	– <sup>a</sup>
11791	P <sup>1</sup>	l	– <sup>a</sup>	– <sup>a</sup>	5.8
11806	P <sup>1</sup>	r	– <sup>a</sup>	5.3	– <sup>a</sup>
11787	P <sup>1</sup>	r	11.1	5.2	4.6
11795	P <sup>1</sup>	l	– <sup>a</sup>	– <sup>a</sup>	5.4
Baugelände 23-7-96	P <sup>1</sup>	r	11.0	5.3	3.6
WG 37-S 0-10üK	P <sup>1</sup>	l	– <sup>a</sup>	– <sup>a</sup>	5.3
330	P <sup>2</sup>	l	14.4	6.7	6.7
331	P <sup>2</sup>	l	13.7	6.1	5.9
332	P <sup>2</sup>	r	15.0	7.0	7.0
8973	P <sup>2</sup>	r	14.6	6.7	6.8
8974	P <sup>2</sup>	l	≥14.1	7.0	6.5
8975	P <sup>2</sup>	r	14.4	6.6	6.9
11744	P <sup>2</sup>	r	– <sup>a</sup>	7.0	– <sup>a</sup>
11772	P <sup>2</sup>	r	>13.6	7.4	7.7
11774	P <sup>2</sup>	l	14.9	6.3	6.1
382	P <sup>3</sup>	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
383	P <sup>3</sup>	l	19.1	9.8	– <sup>a</sup>
8070	P <sup>3</sup>	l	15.1	9.1	11
8976	P <sup>3</sup>	l	15.3	9.5	9.7
8974	P <sup>3</sup>	l	14.0	7.1	11.3
8977	P <sup>3</sup>	r	14.1	9.0	10.9
11770	P <sup>3</sup>	r	– <sup>a</sup>	8.8	– <sup>a</sup>
11797	P <sup>3</sup>	r	– <sup>a</sup>	>8.0	– <sup>a</sup>
11801	P <sup>3</sup>	l	– <sup>a</sup>	– <sup>a</sup>	9.0
8922	P <sup>3</sup>	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
11790	P <sup>3</sup>	l	– <sup>a</sup>	8.6	– <sup>a</sup>
11788	P <sup>3</sup>	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
30-U 20üK	P <sup>3</sup>	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
11768	P <sup>3</sup>	l	– <sup>a</sup>	8.5	– <sup>a</sup>
326	P <sup>4</sup>	l	13.7		14.0
327	P <sup>4</sup>	r	13.8		14.1
328	P <sup>4</sup>	r	12.7		12.8
329	P <sup>4</sup>	l	>11.3		12.7
8909	P <sup>4</sup>	l	12.3		13.1
8911	P <sup>4</sup>	r	12.5		12.8
8877	P <sup>4</sup>	l	12.1		12.8
8913	P <sup>4</sup>	l	12.3		13.0
8915	P <sup>4</sup>	r	– <sup>a</sup>		14.2
8912	P <sup>4</sup>	l	– <sup>a</sup>		14.2

**Table 7** continued

Specimen	Specification	Left/right	DAP	DTa	DTp
8910	P <sup>4</sup>	r	11.9		13.7
11694	P <sup>4</sup>	l	13.5		13.0
28-V 25üK	P <sup>4</sup>	r	– <sup>a</sup>		– <sup>a</sup>

<sup>a</sup> Measurement was not taken due to damage

preserved in the specimen and must thus have been situated anterior to the P<sup>3</sup>. In the male skull no. 8218, the prezygomatic shelf has an angular outline and extends anteriorly to above the anterior part of the P<sup>4</sup>. In a female illustrated by Schmidt-Kittler (1971, Fig. 13b) the shelf is more modestly developed, but nevertheless still large, and the character is interpreted to be sexually dimorphic. The zygomatic arch itself is a thin structure as shown by Schmidt-Kittler (1971, Fig. 2) and confirmed by 8218.

Similar prezygomatic shelves are seen in male or presumably male skulls of *Hyotherium meisneri* from Budenheim (FISF M4657) and a suid from Shanwang described as *H. shanwangense* (see the “Discussion” for its classification), but not in the female and juvenile male skulls of *H. major* from St Gérard-le-Puy (MNCN). The development of the prezygomatic shelf of the specimen described above in detail is even much stronger than in the specimen described and illustrated by Schmidt-Kittler and, as noted by this author, its general shape is very similar to that in *Chleuastochoerus*. Even the beaded edge is very similar to that in a specimen illustrated by Pearson (1928, Fig. 15). The structure differs greatly from the anterior part of the zygomatic arch in the Suinae, where this anterior horizontal platelike extension is totally absent, but where sometimes a more or less horizontal ridge is developed over the anterior side of the zygomatic arch.

The widths of the occipital condyles and foramen magnum are approximately 41 and >17.7 mm respectively in specimen 8218.

The **mandible** (Fig. 8C, D) is robust. The ascending ramus rises nearly vertically immediately behind the third molar. The *processus coronoideus* is well elevated above the condyle. In Suidae this process tends to be relatively elevated, pointed and directed backwards, while in living Dicotylidae it is less elevated, rounded and directed vertically. In the palaeochoerid *Taucanamo grandaevum* from Steinheim (SMNS) the processus is low, pointed and directed backwards. The lower border of the mandible is nearly straight and there is no clearly marked elevation of the lower border separating the angle of the horizontal ramus. In the few specimens that enable observation of this area, there are no important diastemas in the area between the canine and the P<sub>2</sub>.

The mandible of the Suidae tends to be more robust than that of the Palaeochoeridae. This is also the case in an early

**Table 8** The measurements (mm) of the isolated upper molars of *Schizoporcus muenzenbergensis* (272, 280, 8918) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/right	DAP	DTa	DTp
272	M <sup>1</sup>	l	10.2	9.8	9.9
280	M <sup>2</sup>	l	12.8	>10.6	>11.0
8918	M <sup>2</sup>	l	13.6	11.6	12.3
8881	M <sup>1</sup>	r	15.4	14.2	14.7
335	M <sup>1</sup>	- <sup>a</sup>	17.0	15.3	15.0
325	M <sup>1</sup>	l	15.4	14.0	13.8
8902	M <sup>1</sup>	l	14.5	13.7	14.3
8899	M <sup>1</sup>	r	15.5	14.7	15.4
8904	M <sup>1</sup>	l	15.4	14.5	14.5
8879	M <sup>1</sup>	l	15.7	13.8	14.5
8914	M <sup>1</sup>	r	- <sup>b</sup>	14.6	- <sup>b</sup>
8885	M <sup>1</sup>	- <sup>a</sup>	16.4	15.5	~15.0
8880	M <sup>1</sup>	l	15.7	14.7	15.8
5372	M <sup>1</sup>	l	14.7	~13.9	- <sup>b</sup>
323	M <sup>2</sup>	l	17.2	16.8	16.9
324	M <sup>2</sup>	r	19.5	18.4	17.9
336	M <sup>2</sup>	l	17.7	17.0	15.1
8882	M <sup>2</sup>	r	18.0	16.6	16.1
8898	M <sup>2</sup>	r	18.4	17.8	>16.8
8901	M <sup>2</sup>	r	17.0	17.5	15.9
8900	M <sup>2</sup>	l	18.3	17.7	≥17.4
8884	M <sup>2</sup>	r	17.7	16.8	17.2
8886	M <sup>2</sup>	l	- <sup>b</sup>	16.3	- <sup>b</sup>
8887	M <sup>2</sup>	r	18.8	16.1	15.3
8952	M <sup>2</sup>	l	- <sup>b</sup>	- <sup>b</sup>	17.9
8921	M <sup>2</sup>	r	≥17.1	- <sup>b</sup>	- <sup>b</sup>
16629	M <sup>2</sup>	r	18.8	16.4	15.6
318	M <sup>3</sup>	r	19.3	14.3	14.4
319	M <sup>3</sup>	r	20.0	15.2	12.8
320	M <sup>3</sup>	l	21.6	16.6	15.1
321	M <sup>3</sup>	r	20.8	16.7	15.1
333	M <sup>3</sup>	r	~19.9	~16.0	14.8
8907	M <sup>3</sup>	r	- <sup>b</sup>	- <sup>b</sup>	15.4
8906	M <sup>3</sup>	l	19.3	15.0	13.5
8889	M <sup>3</sup>	r	20.4	17.1	15.6
8896	M <sup>3</sup>	l	20.7	16.3	13.7
8892	M <sup>3</sup>	r	22.2	16.8	15.3
8875	M <sup>3</sup>	l	22.1	16.9	15.9
8888	M <sup>3</sup>	r	19.4	16.2	13.7
8890	M <sup>3</sup>	r	19.9	15.7	13.1
8895	M <sup>3</sup>	l	19.7	17.0	15.9
8893	M <sup>3</sup>	l	17.7	14.7	13.8
8894	M <sup>3</sup>	l	20.1	17.0	15.3
8908	M <sup>3</sup>	r	19.1	14.7	12.2
11-Q 90-100	M <sup>3</sup>	l	- <sup>b</sup>	- <sup>b</sup>	14.6

<sup>a</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

<sup>b</sup> Measurement was not taken due to damage

**Table 9** The measurements (mm) of the isolated deciduous molars of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/ right	DAP	DTa	DTp	
11731	D <sub>2</sub>	l	- <sup>a</sup>	- <sup>a</sup>	~5.1	
11756	D <sub>2</sub>	r	- <sup>a</sup>	4.6	- <sup>a</sup>	
11740	D <sub>2</sub>	r	14.2	4.1	4.8	
11802	D <sub>2</sub>	r	- <sup>a</sup>	- <sup>a</sup>	4.9	
11784	D <sub>2</sub>	r	- <sup>a</sup>	- <sup>a</sup>	5.5	
11745	D <sub>2</sub>	l	- <sup>a</sup>	≥4.5	5.8	
11728	D <sub>2</sub>	r	- <sup>a</sup>	3.5	4.6	
11813	D <sub>2</sub>	l	- <sup>a</sup>	3.9	- <sup>a</sup>	
11818	D <sub>2</sub>	r	- <sup>a</sup>	- <sup>a</sup>	5.1	
11795	D <sub>2</sub>	l	- <sup>a</sup>	- <sup>a</sup>	5.3	
12-N 75-85	D <sub>2</sub>	r	- <sup>a</sup>	- <sup>a</sup>	4.8	
11782	D <sub>2</sub>	l	- <sup>a</sup>	- <sup>a</sup>	4.8	
NB10-T 90üB	D <sub>2</sub>	l	12.3	4.0	4.9	
11719	D <sub>3</sub>	l	13.9	3.4	5.6	
11754	D <sub>3</sub>	l	- <sup>a</sup>	- <sup>a</sup>	5.9	
11771	D <sub>3</sub>	r	- <sup>a</sup>	- <sup>a</sup>	5.7	
11692	D <sub>3</sub>	r	13.8	3.9	6.0	
11754	D <sub>3</sub>	l	- <sup>a</sup>	- <sup>a</sup>	5.9	
11719	D <sub>3</sub>	r	>11.7	5.0	5.7	
11696	D <sub>3</sub>	r	12.7	~5.0	5.7	
15-N 80-90	D <sub>3</sub>	r	- <sup>a</sup>	- <sup>a</sup>	5.9	
11730	D <sub>3</sub>	l	13.6	4.5	5.9	
349	D <sup>2</sup>	r	13.9	4.9	5.6	
11747	D <sup>2</sup>	r	13.1	5.8	5.3	
11788 / 11789	D <sup>2</sup>	r	- <sup>a</sup>	- <sup>a</sup>	4.9	
Baugelände 1996	D <sup>2</sup>	r	13.5	5.9	4.7	
4341	D <sup>3</sup>	l	14.9	6.2	9.9	
11742	D <sup>3</sup>	l	- <sup>a</sup>	- <sup>a</sup>	9.9	
34-S 10-40uK	D <sup>3</sup>	r	- <sup>a</sup>	- <sup>a</sup>	9.2	
34-S 0-10üK 1995	D <sup>3</sup>	l	- <sup>a</sup>	- <sup>a</sup>	9.1	
8969	D <sup>3</sup>	r	14.3	6.1	9.4	
8903	D <sup>4</sup>	r	14.0	12.0	12.3	
11803	D <sup>4</sup>	r	14.1	11.6	12.0	
			DAP	DTa	DTm	DTd
8965	D <sub>4</sub>	r	17.9	6.2	8.3	9.0
8967	D <sub>4</sub>	l	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	8.9
8968	D <sub>4</sub>	r	- <sup>a</sup>	6.6	≥7.5	- <sup>a</sup>
11766	D <sub>4</sub>	l	- <sup>a</sup>	7.3	- <sup>a</sup>	- <sup>a</sup>
16576 <sup>b</sup>	D <sub>4</sub>	l	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	9.3
11808	D <sub>4</sub>	l	- <sup>a</sup>	6.4	- <sup>a</sup>	- <sup>a</sup>

<sup>a</sup> Measurement was not taken due to damage

<sup>b</sup> Specimens associated with cheek teeth

suidlike *Hyotherium* from Sandelzhausen. As is normal in the Suoidea, the right and left mandibles are well fused and the symphyseal area is robust. DAP is the distance from the

**Table 10** The measurements (mm) of the associated lower premolars or deciduous molars and permanent molars of *Schizoporcus muenzenbergensis* (8217) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/ right	P <sub>1</sub>		P <sub>2</sub>		P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>		M <sub>2</sub>		M <sub>3</sub>		Dfpp	Ta; Ha										
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	Ta; Ha	DAP			DTa	DTp	Ta; Ha							
93	r																										
299	l					- <sup>a</sup>		7.2	16.1	- <sup>a</sup>	10.0		>18.5	- <sup>a</sup>	1.1	23.5	12.7	- <sup>a</sup>	8.9								
263	l												19.1	15.1	14.9	1.3	28.3	14.9	13.3	9.8	11.3						
264	l												17.4	12.7	13.5	1.2	- <sup>a</sup>	13.2	12.2	- <sup>a</sup>	10.9						
312	l					15.7	6.6	7.0	13.7	8.4	9.7	16.1	11.9	11.7	0.8	18.2	13.8	12.9	1.1	- <sup>a</sup>	13.4	- <sup>a</sup>					
312	r			13.4	5.2	5.8	6.4	6.9	15.9	8.5	8.8	16.3	11.7	11.8	0.8	17.6	13.5	13.1	1.2	- <sup>a</sup>	13.4	- <sup>a</sup>					
314	r					15.6	6.8	7.5	14.5	8.6	10.1	- <sup>a</sup>	~10.6	~11.3	1.0	18.6	13.2	13.8	1.3	26.0	13.3	12.8	9.9				
315	l	11.2	5.6	5.4	13.9	4.9	5.3	6.5	6.6																		
315	r	11.0	5.6	5.1	13.5	4.7	5.3	6.4	6.9	15.4	8.1	8.5	15.7	- <sup>a</sup>	0.7	18.5	13.6	14.0	1.0	- <sup>a</sup>	13.6	- <sup>a</sup>	- <sup>a</sup>				
316	l	11.2	5.6	5.4	13.9	4.9	5.3	6.5	6.6	15.7	8.3	8.3															
316	r					13.7	5.2	5.7	7.4	14.9	8.5	10.3	15.1	10.5	10.8	0.8	≥17.9	12.9	13.2	0.9	25.1	- <sup>a</sup>	11.6	~8.5			
317	l					13.9	4.9	4.8				14.6	12.2	12.7		17.4	13.5	14.0									
337	r															18.1	14.1	14.2	1.2	25.9	14.4	13.3	9.3				
3721	r	10.7	4.2	4.7	13.3	5.6	5.9	7.2	15.6	8.8	9.5	15.8	11.4	11.7	0.9	18.0	14.0	14.0	1.3	25.9	14.3	11.0	9.2				
8218	l	>10.8	5.5	5.4		15.4	6.6	7.7	15.7	9.5	10.8	>16.9	12.7			18.0	13.9	14.3	1.4	~27.5	14	13.0	9.8	1.6			
8218	r	10.7	5.5	5.1	14.2	5.6	6.1	7.4	15.8	9.1	10.7	~18.1	~11.4	~12.4	0.8	17.8	14.0	14.3	1.4	26.3	14.2	13.0	9.8	1.6			
8929	r															18.0	12.7	13.6	11.3								
8942	l											15.2	10.7	11.5	0.7	17.4	12.8	13.5	1	24.8	13.5	11.8	8.9	9.8			
11758	r					>14.3	6.4	6.9	15.5	8.1	9.4																
11887	l	10.7	4.2	4.7	13.3	5.6	5.9	7.2	15.6	8.8	9.5	15.8	11.4	11.7		18.0	14.0	14.0	1.5	25.9	14.3	11.0	9.2	1.6			
11887	r					14.4	6.7	7.5																			
307	l					14.8	5.6	6.0	16.0	7.4	8.6	16.0	11.5	12.3	0.7	18.0	13.8	13.6	1.4	25.0	13.6	11.8	8.6	1.5			
307	r	9.3	4.8	- <sup>a</sup>		14.4	5.3	6.5	15.2	7.5	8.6	15.2	11.8	12.4	0.6	17.9	13.7	13.7	1.4	23.6	13.8	12.1	8.4	1.8			
16576	l								13.9	>8.0	>8.0	14.9	11.0	11.8													
16613	r					14.1	6.3	6.2	13.7	8.0	7.6	>13	- <sup>a</sup>	- <sup>a</sup>	0.6	15.8	13.1	12.5	1.3	25.1	12.7	11.4	8.1	1.5			
16612	r								16.5	12.8	13	10.1				19.3	>14.8	- <sup>a</sup>									
16610	l					13.9	-	5.9	15.6	6.7	7.6	15.5	8.6	10.4		19.2	14.1	14.5	1.3	24.1	14.1	12.4	10.1	1.9			
16610	r															18.6	14.5	14.1		23.8	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>	- <sup>a</sup>			
16584	l								- <sup>a</sup>	- <sup>a</sup>	7.3	15.9	8.2	8.5													
16583	r											15.7	11.6	12.0		18.3	13.1	14.1									
16227	r								- <sup>a</sup>	- <sup>a</sup>	7.4	16.4	8.8	10.0	≤16.1	10.9	- <sup>a</sup>	0.9	16.9	12.7	13.1	1.0	25.0	13.3	11.7	10.0	1.5
259	l								15.4	7.6	8.3	14.9	10.5	11.1	0.7					- <sup>a</sup>	- <sup>a</sup>	~12.1	- <sup>a</sup>	- <sup>a</sup>			
18/07/1996	r								- <sup>a</sup>	5.6	- <sup>a</sup>	7.1	7.1			17.9	13.7	14.1	1.2								
18/07/1996	r								- <sup>a</sup>	4.9	- <sup>a</sup>	14.5	6.2	6.7	>14.2	8.4	9.6										
																				- <sup>a</sup>	- <sup>a</sup>	11.9	- <sup>a</sup>	- <sup>a</sup>			

Table 10 continued

	D <sub>2</sub>			D <sub>3</sub>			D <sub>4</sub>			M <sub>1</sub>			M <sub>2</sub>			
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	Ta; Ha
8217	r			9.9	3.0	3.9		4.6	6.3	7.9	12.3	7.6	7.9	>12		
220	l			14.2	4.3	5.5		- <sup>a</sup>	8.7	11.6	15.4	10.8	11.6	17.7	13.2	10.5
317	l			13.8	4.9	5.8	19.1	7.3	~8.7	10.1						
249	l			13.6	3.9	5.3	21.1	7.4	- <sup>a</sup>	9.4	16.4	10.9	11.9	9.6		
16609	- <sup>c</sup>			13.9	- <sup>c</sup>	6.0	21.5	- <sup>c</sup>	10.6	13.2	16.3					
16583	r					5.1 <sup>b</sup>		7.5	8.6	12	15.7	11.6	12	18.3	13.1	14.1
267	- <sup>c</sup>					5.3		- <sup>a</sup>	8.6	11.8	16.3	11.8	12.5	18.3	13.9	14.3

For reasons of space, Ta and Ha are given in the same column; if the value is approximately 1.0 it is Ta, and when it is approximately 10.0, it is Ha

<sup>a</sup> Measurement was not taken due to damage

<sup>b</sup> Values correspond to an associated P<sub>2</sub>

<sup>c</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

Table 11 The measurements (mm) of the isolated lower premolars of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/right	DAP	DTa	DTp
380	P <sub>1</sub>	l	- <sup>a</sup>	5.1	- <sup>a</sup>
11682	P <sub>1</sub>	r	11.0	4.3	5.0
GrabOst B2 50-60üB	P <sub>1</sub>	r	10.3	4.8	4.9
11773	P <sub>1</sub>	l	11.0	5.4	4.3
381	P <sub>2</sub>	r	>12.8	5.2	- <sup>a</sup>
8976	P <sub>2</sub>	l	- <sup>a</sup>	- <sup>a</sup>	5.5
11724	P <sub>2</sub>	l	- <sup>a</sup>	- <sup>a</sup>	5.6
11726	P <sub>2</sub>	r	- <sup>a</sup>	5.5	- <sup>a</sup>
10685	P <sub>2</sub>	l	11.8	5.6	6.0
11810	P <sub>2</sub>	r	- <sup>a</sup>	5.1	- <sup>a</sup>
11725	P <sub>3</sub>	r	- <sup>a</sup>	6.3	- <sup>a</sup>
11757	P <sub>3</sub>	l	- <sup>a</sup>	6.7	- <sup>a</sup>
16575	P <sub>3</sub>	r	14.5	6.7	6.4
16577	P <sub>3</sub>	r	16.4	6.6	7.6
11695	P <sub>3</sub>	l	15.1	6.4	7.4
11812	P <sub>3</sub>	l	- <sup>a</sup>	6.9	- <sup>a</sup>
11768	P <sub>3</sub>	r	- <sup>a</sup>	7.5	- <sup>a</sup>
12399	P <sub>3</sub>	l	13.8	5.7	6.6
11727	P <sub>3</sub>	r	- <sup>a</sup>	- <sup>a</sup>	7.3
339	P <sub>4</sub>	r	15.9	9.5	10.7
340	P <sub>4</sub>	r	14.8	9.0	9.4
341	P <sub>4</sub>	r	14.6	8.2	- <sup>a</sup>
8931	P <sub>4</sub>	l	- <sup>a</sup>	- <sup>a</sup>	9.1
11777	P <sub>4</sub>	l	- <sup>a</sup>	- <sup>a</sup>	8.4
11743	P <sub>4</sub>	r	- <sup>a</sup>	- <sup>a</sup>	8.4
11817	P <sub>4</sub>	r	- <sup>a</sup>	8.6	- <sup>a</sup>

<sup>a</sup> Measurement was not taken due to damage

alveolus of the I<sub>1</sub> to the posterior side of the symphysis, measured at the lingual side, and H is the thickness measured perpendicular to DAP in the median plane (as indicated by Van der Made 1996a: Fig. 18). In the few specimens that could be measured little indication of sexual bimodality was found. There are three female specimens: specimen 314: DAP × H = ~59 × 19.9; specimen 260: 57.8 × 19.9; and specimen 93: 60.7 × 21.2. There is one male specimen, 33: 60.5 × 0.4.

The shape of the mandibular condyle is more or less cylindrical with a transverse axis. There is no plateau behind the articular surface. Such a plateau is normal in the more advanced Suidae and is present in all living species, but it is absent in the living Dicotylidae and in the Palaeochoeridae. In primitive suids, for example *Aureliachoerus* (MNHN), *Albanohyus* (SMNS), *Kenyasus* (KNM), and *Listriodon* (Kittl 1889: pl. 2 Fig. 1), the plateau is lacking, but a very small plateau is present in *Xenohyus* from Laugnac (UPM).

**Table 12** The measurements (mm) of the isolated lower molars of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/ right	DAP	DTa	DTp	DTpp	Ta	Ha
8935	M <sub>1</sub>	l	– <sup>a</sup>	– <sup>a</sup>	12.2			
8937	M <sub>1</sub>	r	16.3	11.2	11.3			
8940	M <sub>1</sub>	r	15.4	– <sup>a</sup>	11.8			
11775	M <sub>1</sub>	l	15.9	10.9	11.3			
338	M <sub>2</sub>	r	17.3	13.6	13.4			
8939	M <sub>2</sub>	l	17.5	12.8	13			11.4
8941	M <sub>2</sub>	r	16.6	12.5	12.7			
8944	M <sub>2</sub>	r	19.3	14	13.6			10.2
8945	M <sub>2</sub>	r	18.0	13.2	12.8			
8946	M <sub>2</sub>	l	18.7	13.2	13.6			12.6
8947	M <sub>2</sub>	l	18.3	13.2	14.0			1.4
8948	M <sub>2</sub>	l	19.2	13.4	14.1			
8949	M <sub>2</sub>	r	– <sup>a</sup>	14.2	13.5			1.2
8950	M <sub>2</sub>	l	17.5	12.8	13.1			
8953	M <sub>2</sub>	r	– <sup>a</sup>	13.2	– <sup>a</sup>			
16630	M <sub>2</sub>	– <sup>b</sup>	18.2	12.5	12.4			11.3
8950	M <sub>2</sub>	l	17.5	12.8	13.1			
11681	M <sub>2</sub>	r	17.5	12.7	13.3			11.7
1929 field number	M <sub>2</sub>	r	17.8	13.0	13.7			
12-S 64 ü B	M <sub>2</sub>	– <sup>b</sup>	18.3	13.9	14.3			
8938	M <sub>2</sub>	r	17.6	13	12.9			11.0
8955	M <sub>3</sub>	r	27.6	13.9	12.2	8.5		12.4
8956	M <sub>3</sub>	r	– <sup>a</sup>	13.8	12.0	– <sup>a</sup>		>9.9
8957	M <sub>3</sub>	l	– <sup>a</sup>	13.6	12.1	– <sup>a</sup>		1.2
8958	M <sub>3</sub>	l	– <sup>a</sup>	14.0	13.0	– <sup>a</sup>		
8961	M <sub>3</sub>	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	12.0		
8936	M <sub>3</sub>	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>		
8960	M <sub>3</sub>	l	≥25.0	– <sup>a</sup>	11.2	8.3		
8962	M <sub>3</sub>	r	– <sup>a</sup>	– <sup>a</sup>	12.6	– <sup>a</sup>		
8963	M <sub>3</sub>	l	– <sup>a</sup>	– <sup>a</sup>	11.6	– <sup>a</sup>		
8964	M <sub>3</sub>	r	– <sup>a</sup>	– <sup>a</sup>	12.0	– <sup>a</sup>		
16692	M <sub>3</sub>	r	– <sup>a</sup>	13.5	12.3			

<sup>a</sup> Measurement was not taken due to damage<sup>b</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

The mandibular condyle is not much elevated above the occlusal surface (Fig. 9). In specimen 313, the highest point of the condyle (H) is 34 mm above the occlusal surface and at 118 mm behind the anterior edge of the M<sub>1</sub> (128 mm for the posterior part of the condyle; measurements taken as indicated by Van der Made and Tong 2008). In number 312, which has the M<sub>3</sub> not completely erupted (Fig. 8C), and which is thus considered “sub-adult”, these values are 35 and 125 respectively.

**Table 13** The measurements (mm) of the distal humerus of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/ right	DAPd	DTd	DTdf	R1	R2	R3	R4	R5
4230	r		≥31.1	21.5	21.2	22.4	17.9	15.8	15.7
8924	r	30.2	>28.9	22.9	22.6	15.4	18.9	15.8	15.4
16621	l	30.6	31.7	23.5	22.6	15.8	18.5	15.9	15.6
16224	l	31.2	33.9	23.7	25.9	16.9	21.1	17.6	17.8
16570	r	– <sup>a</sup>	≥29.7	20.7	21.9	15.1	17.9	13.8	14.0
16568	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	14.8	14.3	17.8	15.7	– <sup>a</sup>
16581	r	– <sup>a</sup>	– <sup>a</sup>	21.3	17.4	17.3	18.4	16.0	22.7
4272	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	16.5	16.5	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16550	l	– <sup>a</sup>	– <sup>a</sup>	22.2	– <sup>a</sup>	16.0	≥17.1	15.3	15.3

<sup>a</sup> Measurement was not taken due to damage**Table 14** The measurements (mm) of the radius of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/ right	DAPp	DTp	L	DAPd	DTd	DAPdf	DTdf
11706	l	>13.9	>22.0	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
11737	r	14.8	22.1	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
11734	r	– <sup>a</sup>	– <sup>a</sup>	juv	15.1	19.9	9.7	18.8
4474	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	17.4	25.6	13.5	24.3
16552	r	14.8	22.5	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16551	l	14.7	22.4	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16785	r	15.2	24.6	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16555	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	13.2	– <sup>a</sup>	23.4
16625	– <sup>b</sup>	– <sup>a</sup>	– <sup>a</sup>	juv	– <sup>a</sup>	– <sup>a</sup>	12.8	23.9
11699	r	≥13.8	21.2	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
13-T 40- 60üB	l	14.7	22.6	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16562	l	≥14.5	22.1	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16582	l	15.5	23.0	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16655	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	≥17.6	≥28.0	13.8	24.6
16240	r	15.2	22.2	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16638	r	13.7	21.6	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>

<sup>a</sup> Measurement was not taken due to damage<sup>b</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

The I<sup>1</sup> (Fig. 10E, G, I, J; Tables 1, 2) are teeth with a massive, backward curving root and a crown with a large principal cusp on the mesial side, a large postcrista, and a lingual cingulum, as in nearly all Suoidea in which this tooth is known (excepting *Taucanamo*). The crown is not very high as in all primitive forms. The main cusp is displaced mesially and its tip is not even above the root; the crown is flattened somewhat in the linguo–labial direction.

There is a mesial facet caused by wear with the other I<sup>1</sup>, which indicates the orientation of the tooth with respect to

**Table 15** The measurements (mm) of the carpals of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Scaphoid	Left/right	DAP	DT	Ha	
16233	l	20.5	10.9	16.3	
16566	r	19.8	11.5	15.4	
16560	r	19.1	10.5	15.2	
Lunar	Left/right	DAP	DTp	DTd	Ha
16620	l	17.3	13.2	12.9	14.4
16234	l	16.9	13.4	12.8	15.6
16598	r	16.8	13.5	13.4	12.9
16616	r	16.6	– <sup>a</sup>	12.7	14.8
Ulnar	Left/right	DAP	DT	H	Ha
16232	l	12.5	7.3	15.1	12.4
Magnum	Left/right	DAP	DT	H	
16663	r	15.9	11.7	13.4	
16661	r	16.9	13.1	13.7	
16222	l	17.9	14.1	13.7	
16649	r	17.9	12.9	– <sup>a</sup>	
Unciform	Left/right	DAP	DT	H	Ha
38	r	18.1	16.1	16.5	15.6
11738	r	– <sup>a</sup>	15.0	– <sup>a</sup>	14.6
16671	r	13.8	12.5	15.2	13.8

<sup>a</sup> Measurement was not taken due to damage

the median plane. Right and left I<sup>1</sup> form a V-shape (Fig. 10J). This is an important feature (Van der Made 1997b), which is acquired within the Suidae; it is not present in the Cainochoerinae, nor in the Listriodontinae, and it is not well developed in the earliest Tetraconodontinae, but it is well developed in the later Tetraconodontinae and in the Hyotheriinae (except for *Chleuastochoerus*), Babyrousinae and Suinae.

Within the postcrista a distal cusp is formed, which is much smaller than the main cusp. This cusp is often absent in *Hyotherium meisneri* and *H. major*, but if present it is small. In *H. soemmeringi* it is always well developed. In *Hyotherium* from Munébrega AB (IVAU) and Montréal (MHNT), it is well developed, but less than in Sandelzhausen. It may be visible even in the labial wall by an elevation and a cleft mesial to it. Such a cusp is also seen in *Hyotherium* from Shanwang and in *Xenohyus*, but not in *Chleuastochoerus*.

The lingual cingulum, which may be inflated in the middle, is directed more or less transversely, but in its distal reaches it turns distally. There is a mesial ridge (precrista) that is marked by a style at the lingual side, and

**Table 16** The measurements (mm) of the metapodials of *Hyotherium soemmeringi wylensis* and *Schizoporus muenzenbergensis* (4231) from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Specification	Left/right	DAPp	DTp	L	l	DAPd	DTd
4231	Mc III	l	9.6	10.9	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16686	Mc III	r	14.1	15.5	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16572	Mc III	l	15.1	1.5	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16223	Mc III	r	14.2	15.6	68.8	– <sup>a</sup>	13.1	12.4
16558	Mc III	l	15.7	16.9	– <sup>a</sup>	– <sup>a</sup>	14.2	13.7
16235	Mc IV	r	12.3	1.3	72.0	– <sup>a</sup>	12.4	14.6
16611	Mc IV	l	11.4	13.2	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16627	Mc IV	– <sup>a</sup>	12.6	13.7	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16590	Mc IV	l	11.2	13.1	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16589	Mc IV	r	11.0	13.5	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16239	Mc V	l	9.7	5.9	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
8218	Mt II	l	7.7	4.9	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16238	Mt IV	r	19.2	12.2	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16557	Mt V	r	11.7	4.8	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16594	Mp III/IV	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	>11.7	12.8
16608	Mp III/IV	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	13.9	12.9
16595	Mp III/IV	l	– <sup>a</sup>	– <sup>a</sup>	juv	juv	15.1	>12.6
16561	Mp III/IV	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	13.3	10.9
16619	Mp III/IV	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	>11.2	>11.9
16648	Mp III/IV	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	14.1	13.0
16615	Mp III/IV	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	12.4
334 2uK	Mp III/IV	r	– <sup>a</sup>	– <sup>a</sup>	juv	juv	13.3	12.4
16591	Mp III/IV	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	10.4	5.9

<sup>a</sup> Measurement was not taken due to damage

**Table 17** The measurements (mm) of the tibia and fibula of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

	Left/right	DAPd	DTd	DTdf
Tibia				
11778	l	21.3	≥22.7	17.9
Fibula				
No number	l	13.3	7.7	6.9
16596	l	14.9	7.9	5.0
16241	r	13.3	7.6	5.1

there is an elevation of the lingual side of the main cusp (the endocrista). On the lingual cingulum, the lingual style of the precrista and on the endocrista and distal cusp, there is a transversely directed wear facet caused by occlusion with the I<sub>1</sub> and I<sub>2</sub>. In addition, there is a large wear facet on the tip of the main cusp, which is not caused by occlusion with the lower incisors; it is caused by rooting.

The I<sup>1</sup> from Sandelzhausen is a little larger than in *H. meisneri*, *H. major* and *Hyotherium* from Montréal, and comparable in size with the I<sup>1</sup> of other *H. soemmeringi* of the same age, and on average smaller than in *H. s.*

**Table 18** The measurements (mm) of the astragalus of *Schizoporcus muenzenbergensis* (273, 276, 277, 281) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/right	Lext	Lm	Lint	DTp	DTd	d	R
273	r	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	14.7	4.8	— <sup>a</sup>
276	— <sup>b</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	11.8	— <sup>a</sup>	— <sup>a</sup>	13.9
277	l	>30.1	26.1	>28.0	14.3	16.1	6.2	— <sup>a</sup>
281	l	29.2	≥23.6	— <sup>a</sup>	12.8	— <sup>a</sup>	4.3	≥13.1
4991	r	35.0	28.9	33.4	16.2	18.1	5.1	20.4
4992	r	34.9	27.8	31.4	15.7	16.6	5.8	19.4
4998	l	— <sup>a</sup>	28.9	>32.8	— <sup>a</sup>	17.3	5.1	20.4
4999	r	34.4	28.9	32.9	16.1	17.6	5.9	— <sup>a</sup>
5000	r	35.7	29.0	32.0	15.1	17.3	6.0	18.2
8813	l	36.7	— <sup>a</sup>	— <sup>a</sup>	16.2	17.9	6.1	20.6
8814	— <sup>b</sup>	37.3	— <sup>a</sup>	— <sup>a</sup>	16.1	17.6	6.0	21.1
8815	l	35.9	29.0	33.3	16.5	18.3	5.9	20.8
8816	l	35.2	— <sup>a</sup>	— <sup>a</sup>	16.0	18.3	6.3	19.9
8817	l	36.1	— <sup>a</sup>	— <sup>a</sup>	16.1	18.6	5.8	~21.9
8818	l	36.3	29.6	33.6	16.3	16.6	5.9	— <sup>a</sup>
8819	l	≥36.9	29.7	33.2	15.3	16.9	5.6	18.6
8820	l	34.9	27.9	32.0	16.0	17.5	5.7	19.6
8822	l	>33.3	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	≥16.4	5.0	18.2
8823	l	>33.5	— <sup>a</sup>	— <sup>a</sup>	14.9	≥16.7	— <sup>a</sup>	— <sup>a</sup>
8824	l	33.6	27.4	— <sup>a</sup>	15.2	17.1	6.5	18.8
8826	r	36.1	29.1	34.0	16.1	17.4	5.6	20.0
8827	r	33.6	— <sup>a</sup>	— <sup>a</sup>	15.2	16.7	5.8	17.7
8828	r	35.1	28.9	33.1	15.7	18.0	6.4	19.0
8829	r	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	15.6	— <sup>a</sup>	5.1	19.9
11670	l	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	16.6	6.3	— <sup>a</sup>
8825	l	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	17.6	5.8	— <sup>a</sup>
16592	l	37.2	30.5	34.3	16.8	18.8	6.0	— <sup>a</sup>
5000	— <sup>b</sup>	35.6	— <sup>a</sup>	— <sup>a</sup>	15.1	17.0	6.2	17.9
5060	— <sup>b</sup>	34.3	— <sup>a</sup>	— <sup>a</sup>	15.8	17.6	5.5	~19.0
8821	l	37.1	30.7	35.1	15.9	18.7	5.9	20.2
16573	l	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	16.1	— <sup>a</sup>	— <sup>a</sup>	19.7

<sup>a</sup> Measurement was not taken due to damage

<sup>b</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

**Table 19** The measurements (mm) of the calcaneum of *Schizoporcus muenzenbergensis* (278, 279) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Specimen	Left/right	DAPh	DTh	DAPn	DTn	DAPsf	DTsf	DAPmax	L	Lu	Ll
278	r	13.6	11.6	13.1	8.1	16.4	12.0	— <sup>a</sup>	— <sup>a</sup>	35.9	— <sup>a</sup>
279	r	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	≥15.8	≥11.2	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
4994	r	14.2	13.1	14.2	8.8	19.3	14.3	24.7	59.3	37.1	23.1
8831	l	— <sup>a</sup>	— <sup>a</sup>	15.4	9.2	19.3	14.5	26.3	juv	— <sup>a</sup>	24.9
8833	l	15.3	12.3	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	14.5	— <sup>a</sup>	— <sup>a</sup>	39.4	— <sup>a</sup>
8834	l	16.8	14.9	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	17.6	27.6	69.4	41.5	29.6
8835	— <sup>b</sup>	16.1	14.0	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	16.2	25.9	66.0	41.1	27.8
8836	r	14.5	13.2	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	14.1	25.2	66.7	41.0	27.0
8837	r	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	14.3	26.8	— <sup>a</sup>	— <sup>a</sup>	28.6
11733	l	15.2	14.5	15.2	8.3	20.3	15.3	— <sup>a</sup>	42.1	— <sup>a</sup>	— <sup>a</sup>
3358	l	— <sup>a</sup>	— <sup>a</sup>	<15.1	7.9	18.8	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
16688	l	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	18.6	14.9	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>

<sup>a</sup> Measurement was not taken due to damage

<sup>b</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)



**Table 20** The measurements (mm) of the cuboid, navicular and third cuneiform of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...)

Cuboid	Left/ right	DAP	DT	H	Ha
16636	r	19.0	13.6	24.9	17.5
11-N	– <sup>a</sup>	19.8	15.2	25.2	19.1
16618	r	19.9	15.8	27.9	17.6
16226	l	20.1	13.4	27.9	19.2
Navicular		DAP	DT	H	Ha
16634	r	23.4	13.9	10.7	
16693	l	>22.4	14.3	9.7	
16622	r	≥21.2	11.9	9.2	
11705	r	21.6	13.0	10.6	
11699	l	23.1	11.1	12.6	
16556	l	>22.1	>15.1	10.6	
16639	l	22.2	13.6	10.0	
32-L 0-15üK	r	>19.9	12.1	8.3	
39-N 0-10üK	r	23.7	12.3	8.7	
16658	r	19.7	12.1	8.7	
16660	r	20.4	12.7	9.1	
16659	l	20.6	12.5	9.7	
8218	l	23.4	14.6		
16242	l	22.9	14.1		
Cuneiform III		DAP	DT		
4730	l	11.6	10.4		
8218	l	12.6	11.4		
11736	l	10.8	9.9		
16605	l	12.3	9.7		
16601	r	11.9	10.2		
16640	r	11.6	10.0		
16645	l	10.3	9.2		
16243	l	11.2	10.0		
11735	r	11.0	9.8		

<sup>a</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

*soemmeringi* (Fig. 11). This reflects the general size differences in these species and subspecies. It is noteworthy that the  $I^1$  in *Chleuastochoerus* is much smaller, more than would be expected on the basis of the cheek teeth. This tooth also has a simpler crown without distal cusp and without meso–distal elongation, resulting in a less developed V-shape of right and left  $I^1$ . The  $I^1$  of *Xenohyus* is much larger than would be expected on the basis of the size of the cheek teeth. These incisors have also a distal cusp.

The  $DI^1$  (Fig. 10A; Table 2) has the same overall shape as the  $I^1$ , but differs in its smaller size (Fig. 12), in lacking a distal cusp, and in lacking a well developed lingual cingulum.

The  $I^2$  (Fig. 10C, F, H; Tables 1, 2) has a single root that is directed posteriorly and which at the end curves still further posteriorly. The main cusp is placed anterior to the middle of the crown. It has a short precrista and a long postcrista. In side view the crown is triangular, with the precrista being convex and the postcrista concave (Fig. 10H), or there may be an elevation, suggestive of a distal cusp (Fig. 10C, F). There is a facet that extends over the main cusp and precrista, and which is caused by occlusion with the lateral side of the  $I_2$ . The labial side of the cusp is convex and the lingual side is much flatter. There is a lingual cingulum that is best developed in the posterior half.

The general aspect of this tooth is similar to that of the  $I^3$ , but has a lower crown. It is also similar to the  $DI^2$ , although no  $DI^3$  was recognized in the sample. The  $I^2$  tends to be the largest and most elongate of these three teeth, although there is overlap with the  $I^3$  (Fig. 12). The  $I^2$  from Sandelzhausen are larger than those of *H. meisneri* and on average they are also larger than in *H. major* and *Hyotherium* from Montréal (Fig. 11). The  $I^2$  from Sandelzhausen is more elongate than in *Hyotherium* from Shanwang, *Chleuastochoerus* and *Xenohyus*. In those taxa, the main cusp is situated more in the middle of the tooth and the crown is thus more symmetrical in side view.

The  $I^2$  is an important tooth in suoid systematics, which is a reason for a comparison in this wider context. The general shape tends to be similar in all Suoidea, with the main differences concerning the extent and shape of the postcrista. Specimens with a more developed postcrista tend to be more asymmetrical and elongate. The generally early and primitive Palaeochoeridae tend to have small and short  $I^2$ , while fossil and recent Dicotylidae tend to have more elongate incisors and most Suidae have still more elongate  $I^2$  (Figs. 15, 16). Within the Suidae, Hyotheriinae and Babyrousinae (*Potamochoerus* and *Celebochoerus*) tend to have relatively short  $I^2$ , while Tetraconodontinae tend to have  $I^2$  with similar proportions, although in *Nyanzachoerus* (one specimen in Figs. 15, 16), the  $I^2$  may be much more elongate. Even the earliest known Suinae have  $I^2$  that are, on average, more elongate than in *Hyotherium*.

Not only the absolute, but also the relative size of the  $I^2$  varies among the Suoidea. Here the size relative to the width of the anterior lobe of the  $M^1$  is considered (Fig. 19). In this way, it is intended to “eliminate” size differences between the species. In this comparison, the width of the  $I^2$  does not vary much, although recent Dicotylidae tend to have relatively wider  $I^2$  than *Hyotherium*. Primitive Tetraconodontinae tend to cluster with *Hyotherium*, but *Nyanzachoerus* clusters with the Suinae. These observations indicate that the width of the tooth is stable and that more elongate shape is achieved by elongation (principally of the postcrista) and not by flattening of the tooth (or

**Table 21** The measurements (in mm) of the first central (III/IV) and lateral (II/V) phalanges of *Schizoporcus muenzenbergensis* (284 and 4761) and *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...). The left/right refers to the position relative to the axis of the foot

Specimen	Specification	Left/ right	DAPp	DAPpf	DTp	L	DAPd	DTd
284	III/IV	r	>10.4	>9.6	11.6	31.3	6.3	8.0
4761	III/IV	l	11.0	9.6	11.8	32.3	6.5	8.1
7867	III/IV	r	12.9	11.9	12.5	31.3	8.2	10.7
8218	III/IV	l	13.5	12.9	13.5	33.7	9.4	11.3
8218	III/IV	l	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	11.2
8926	III/IV	l	13.8	12.9	13.7	30.9	9.2	11.2
16553	III/IV	l	≥13.6	~12.4	≥13.3	30.8	8.8	11.2
16607	III/IV	r	≥13.0	— <sup>a</sup>	— <sup>a</sup>	32.1	9.5	10.8
16587	III/IV	l	≥12.4	11.7	13.1	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
16642	III/IV	l	>12.9	— <sup>a</sup>	≥13.7	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
16750	III/IV	r	— <sup>a</sup>	12.2	13.4	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
16231	III/IV	l	13.0	11.3	12.4	32.8	7.9	10.6
11704	III/IV	r	13.1	12.2	12.9	32.8	9.4	11.6
16687	III/IV	r	13.7	12.7	14.2	31.9	9.2	11.3
16682	III/IV	l	12.7	10.8	13.1	28.9	8.3	10.5
16644	III/IV	l	13.0	12.9	12.9	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
16626	III/IV	l	13.1	~11.1	~13.3	30.3	8.2	10.8
16230	III/IV	r	13.7	13.2	14.9	32.2	9.2	11.6
4770	III/IV	r	12.3	11.5	12.8	28.7	8.1	10.5
16559	III/IV	l	12.6	12.0	12.4	32.1	8.0	10.7
16564	III/IV	r	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>	9.5	11.9
16563	III/IV	r	13.2	12.5	13.3	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
16593	III/IV	r	12.3	11.7	13.4	— <sup>a</sup>	— <sup>a</sup>	— <sup>a</sup>
11796	II/V	r	8.1		6.6	12.4	6.6	5.8
16674	II/V	l	7.8		7.1	17.2	5.9	4.7
16602	II/V	r	8.7		8.6	19.7	6.6	6.0
16670	II/V	r	8.7		7.0	19.7	6.2	5.3
16221	II/V	r	9.9		9.7	20.8	7.1	6.8
16673	II/V	r	7.1		— <sup>a</sup>	9.7	4.9	5.6
16657	II/V	l	8.1		7.8	19.0	6.2	5.5
16666	II/V	r	>7.5		6.3	10.1	6.0	5.7
11784	II/V	r	8.2		7.2	18.6	5.7	4.6
16643	II/V	l	8.5		7.8	20.1	5.6	5.2
16740	II/V	r	— <sup>a</sup>		7.2	>19.1	5.2	4.7
16682	II/V	l	— <sup>a</sup>		— <sup>a</sup>	— <sup>a</sup>	6.9	6.8
13-G 95-110	II/V	r	9.1		7.3	13.0	7.5	6.5
16667	II/V	r	7.2		5.7	10.7	5.7	5.4
4772	II/V	l	9.8		8.7	21.3	6.6	5.9
4756	II/V	l	7.8		6.8	19.9	4.6	4.7
11720	II/V	r	8.7		8.4	19.6	6.2	5.9
11781	II/V	r	8.1		7.3	18.9	5.9	5.2
NB14-W 50üB vor 1964	II/V	l	9.5		9.6	20.9	6.9	6.4
16716	II/V	l	8.9		6.5	12.3	6.9	6.3
			8.7		8.0	18.9	5.7	5.5

<sup>a</sup> Measurement was not taken due to damage

reduction of its width). The observation that DLL is stable and DMD very variable contrasts with what is observed in the central incisors ( $I^1$  and  $I_{1-2}$ ), which mostly vary in absolute size and maintain the relationship between DMD

and DLL. It should be noted that in all these comparisons, *Hyotherium* from Shanwang and *Chleuastochoerus* have smaller and less elongate  $I^2$  than the European species of *Hyotherium*.

**Table 22** The measurements (in mm) of the second phalanges of *Hyotherium soemmeringi* wylensis from Sandelzhausen (Inventory No. BSPG 1959 II ...). The left/right refers to the position relative to the axis of the foot

Specimen	Specification	Left/ right	DAPp	DAPps	DTp	L	DAPd	DTd
16623	III/IV	l	13.2	12.6	10.6	21.0	9.5	9.2
16579	III/IV	l	13.0	12.1	10.9	20.9	9.0	9.1
16631	III/IV	r	14.1	12.9	10.8	~20.2	9.7	8.9
16632	III/IV	l	12.5	11.2	10.8	20.4	8.2	9.1
16571	III/IV	l	13.7	12.2	11.4	21.2	9.6	9.7
11784	III/IV	l	13.9	12.8	11.5	23.0	10.8	9.9
16662	III/IV	l	13.7	13.0	11.2	21.1	– <sup>a</sup>	9.1
4811	III/IV	r	16.3	15.2	13.3	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
4813	III/IV	l	12.4	11.7	11.1	19.9	– <sup>a</sup>	– <sup>a</sup>
4812	III/IV	r	13.1	12.2	10.6	>22.2	9.2	8.2
4814	III/IV	l	13.5	12.6	11.5	22.6	9.9	9.9
4815	III/IV	r	14.6	13.5	12.5	23.0	–	8.5
4661	III/IV	l	13.4	12.3	11.6	21.6	9.9	9.5
4808	III/IV	r	13.9	12.2	11.5	20.9	9.7	10.1
4809	III/IV	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	8.5
vor 1964	III/IV	r	12.4	11.4	10.5	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16604	III/IV	l	13.0	12.2	11.3	21.7	9.8	9.2
16565	III/IV	l	15.0	14.1	12.2	24.1	>10.2	9.2
16600	III/IV	l	13.5	12.8	11.3	22.7	9.1	8.6
16585	III/IV	l	13.6	12.2	>11.5	21.5	>9.1	9.6
16679	III/IV	r	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	>10.6
16569	III/IV	l	13.1	12.6	10.7	21.2	9.4	9.1
16606	III/IV	r	13.0	12.4	10.5	22.2	>8.5	8.8
16655	III/IV	r	>12.0	11.4	10.1	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
11783	III/IV	r	12.3	11.7	10.2	20.2	8.3	8.2
16666	II/V	r	>7.5	6.9	6.3	10.1	6.0	5.7
16673	II/V	r	7.1	≥6.9	– <sup>a</sup>	9.7	4.9	5.6
16668	II/V	r	8.1	7.2	6.6	12.4	6.6	5.8
16669	II/V	r	9.1	8.8	7.3	13.0	7.5	6.5
4851 <sup>b</sup>	II/V	r	7.2	7.0	5.7	10.7	5.7	5.4
vor 1964	II/V	l	8.9	7.7	6.5	12.3	6.9	6.3
16642	II/V	l	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	6.9	6.8
4810	II/V	l	8.2	7.3	6.7	12.3	6.9	6.2

<sup>a</sup> Measurement was not taken due to damage

<sup>b</sup> Associated with phalanx 16677

The **DI**<sup>2</sup> (Table 2) resembles the **I**<sup>2</sup>, but it has a lower crown, there is no hint of a distal cusp or inflation of the postcrista, and it is clearly smaller than both **I**<sup>2</sup> and **I**<sup>3</sup> (Fig. 12).

As indicated above, the **I**<sup>3</sup> (Fig. 10B; Tables 1, 2) is similar to the **I**<sup>2</sup>, but differs in having a higher crown, shorter postcrista, and less elongate shape and being on average smaller (Fig. 12). Occlusion with the **I**<sub>3</sub> causes a large facet on the anterior side of the main cusp and precrista.

The specimens from Sandelzhausen are larger than those of *H. meisneri* and are close in size to those attributed to *H. major*. The **I**<sup>2</sup> of *Hyotherium* from Shanwang is close in size, but relatively short, and those of *Chleuastochoerus* are small and short (Fig. 11).

Like the **I**<sup>2</sup>, the **I**<sup>3</sup> is an interesting tooth in the wider context of the evolution of the Suoidea. It can be seen that the *Hyotherium* **I**<sup>3</sup> has a wide range of degree of elongation, but that it is in general much wider than the *Sus* **I**<sup>3</sup> (Figs. 17, 18, 19).

The **I**<sub>1</sub> (Fig. 10K; Tables 3, 4) is a tooth with a single main cusp and a single root. The precristid and postcristid have well marked stylids at the lingual side; between them there is the endocristid. The labial side is rounded. The tooth is nearly symmetrical. The preanticiclid and post anticiclid are well marked and fairly high. The crown is high, but not very high compared with later Suidae. The endosynclonid is deeper than the ectosynclonid; in incisors with higher crowns, this tends to be the reverse. There is a mesial wear facet near the tip, which marks the median

**Table 23** The measurements (in mm) of the third phalanges of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...). The left/right refers to the position relative to the axis of the foot

Specimen	Specification	Left/ right	DAPp	DAPps	DTp	L
0207 field number	III/IV	r	≥10.7	≥14.1	9.4	– <sup>a</sup>
16672	III/IV	r	7.8	10.5	6.8	17.3
7-G 135 ü O	III/IV	l	7.7	9.8	8.9	19.5
16676	III/IV	l	10.1	11.1	8.2	21.4
10-N 100-105	III/IV	l	10.3	12.8	9.5	– <sup>a</sup>
16554	III/IV	r	11.1	14.4	10.5	>22.5
16-O 200-210	III/IV	l	9.1	11.6	8.8	– <sup>a</sup>
16599	III/IV	l	11.3	14.6	9.9	23.7
16588	III/IV	l	10.9	14.2	9.4	24.5
16574	III/IV	r	9.6	10.8	8.9	20.9
WG38-V 15üK	III/IV	l	8.4	9.7	8.0	19.1
16229	III/IV	l	9.0	10.6	8.9	– <sup>a</sup>
NBK 12-B 70üB	III/IV	l	9.8	11.8	8.2	– <sup>a</sup>
11721	III/IV	l	8.4	9.3	7.2	– <sup>a</sup>
16678	III/IV	l	9.8	11.6	8.0	21.1
8360	III/IV	– <sup>b</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>	– <sup>a</sup>
16741	II/V	r	6.2	6.7	4.7	9.0
11723	II/V	l	6.9	7.6	6.0	14.1
16665	II/V	l	6.2	6.8	4.8	11.3
16677 <sup>c</sup>	II/V	r	6.7	8.2	5.4	13.7
16664	II/V	l	7.6	9.1	6.5	15.3

<sup>a</sup> Measurement was not taken due to damage

<sup>b</sup> Measurement was not taken for another reason (covered by sediment, simply not taken, etc.)

<sup>c</sup> Associated with metapodial 4851

plane, and a similar one at the distal side, which is nearly parallel. These facets are caused by contact with the other incisors. There is a large apical facet, caused by occlusion with the  $I^1$  and another wear facet over the lingual side of the tooth, which may cause the dentine to surface on the endocrisid. This facet is not caused by occlusion, but by rooting.

The evolution of the Suidae is marked by an increase in hypsodonty in the central incisors. The values given in Table 4 allow for the calculation of some hypsodonty indices: 100 Hli/DMD = 244; 100 Hli/DLL = 175, 154; 100 Hla/DMD = 154; 100 Hla/DLL = 158. These values are broadly comparable with the few values that were published for *Hyotherium meisneri* (195, 184, 221–234, 207, respectively) and *Tayassu* (216–240, 166–203, 216–282, 169–231) (Van der Made 1996a: Table 18).

The  $I_1$  of *H. meisneri* are much smaller, those of *H. major* and *Hyotherium* from MN4 localities, including Montréal, are relatively small, whereas those of *H. soemmeringi soemmeringi* are relatively large compared with the Sandelzhausen sample (Fig. 13). *Xenohyus* is known for its enlarged incisors, and indeed, these are much larger, although most of the cheek teeth and the astragalus are not so much larger (Figs. 21, 30). If incisor size is compared with the  $M_1$  size (in order to “eliminate” general size), the difference does not seem so large, but still exists (Fig. 19).

The  $I_2$  (Fig. 10N; Tables 3, 4) is similar to the  $I_1$ , but is less symmetrical; its tip is curved a little mesially and the labio–lingual diameter is much less on the distal side than on the mesial side. Direct comparisons of the sizes of the  $I_2$  of the different *Hyotherium* samples give the same results as in the  $I_1$  (Fig. 13) and this is still valid if we compensate for general size (Fig. 19). The few hypsodonty indices that could be calculated: 100 Hla/DMD = 234; 100 Hla/DLL = 158. Again, values are similar, or even small, compared with those for *Hyotherium meisneri* (241–293 and 201–220) and *Tayassu* (248–271 and 182–213) (Van der Made 1996a: Table 18), although the large range of variation in these values and the small sample sizes have to be borne in mind.

The  $DI_1$  (Table 4) and  $DI_2$  (Fig. 10M, O, P; Table 4) are similar to the  $I_{1-2}$ , but differ from these teeth in being much smaller (Fig. 12) and less meso–distally flattened.

The  $I_3$  (Fig. 10D, L; Tables 3, 4) has the same morphological elements as the  $I_1$  and  $I_2$ , but is still more asymmetrical, and above all, it has a much lower crown. Partially caused by its greater asymmetry, its orientation in the mandible is more difficult to assess in isolated specimens, but specimens in situ also seem to have a more variable orientation. Moreover, there is a wide variation in morphology. Some specimens have flattened crowns (Fig. 10L), while in others this is much less (Fig. 10D); the latter teeth tend to have longer and more cylindrical roots.

As a result of all this variability, measurements are difficult to take in a standardized way.

The lower crown of the  $I_3$  seems to reflect the fact that, unlike the  $I_{1-2}$ , it does not (or only to a small degree) take part in the increase in hypsodonty so typical in the Suidae. In the upper tooth row, the  $I^2$  makes up for this difference in crown height between  $I_2$  and  $I_3$  by becoming more elongate.

Compared with the incisors and cheek teeth, the  $C^m$  (Fig. 14L; Table 5) is a high tooth, with a clear backward curvature, but compared with canines of other Suidae, the tooth is not very high.

The  $C^m$  is an important tooth that has several features in which the Suidae differ from the Palaeochoeridae and Dicotylidae. The crown is conical with an anterior and a posterior crest (the precristas and postcristas). Its lower edge curves much “down” (or away from the tip) at the places of these cristas, forming enamel bands, the pre and postsynclines, and curves a little down at the lingual side, forming a shorter, but wider enamel band, the endosyncline. These three enamel bands are typical of the suid  $C^m$ , whereas the upper canines of Palaeochoeridae have just the presyncline and postsyncline and recent peccaries have still a different model (Van der Made 1996a, b).

There is a large anterior facet, caused by occlusion with the lower canine. Striae on the surface indicate the direction of relative movement of the canines during occlusion. A skull fragment illustrated by Schmidt-Kittler (1971, pls. 11–12) shows the orientation of the canine: it points downwards and a little outwards. In Dicotylidae and Palaeochoeridae the canine is oriented nearly vertically, but in early Suidae, for example the Hyotheriinae, and earliest Listriodontinae and Tetraconodontinae, the canine is directed a little outward; in later species, including all Suinae, it is directed more outwards and may have an additional outward and even upward curvature, while in *Babyrousa* it even originates directed upwards and pierces the upper lip. In shape, size, orientation and outward curvature, the  $C^m$  in the Sandelzhausen material is typically primitive as in *Hyotherium*, as seen in the material from Georgensgmünd.

At first sight, the  $C^f$  (Fig. 14J; Tables 1, 5) might be believed to be an anterior premolar of a larger species. However, on closer examination there are morphological differences from premolars. The crown is relatively high compared with a premolar but low compared with most suid canines, and the lower edge of the crown is shaped in a different way. Besides there is a bulge in the middle of the lingual side, which corresponds to the endocrista, showing a downward curvature of the crown base, which is a faint indication of the endosyncline or lingual or ventral enamel band. The root shows a tendency to be divided into two, which may be noted by grooves on the lingual and labial

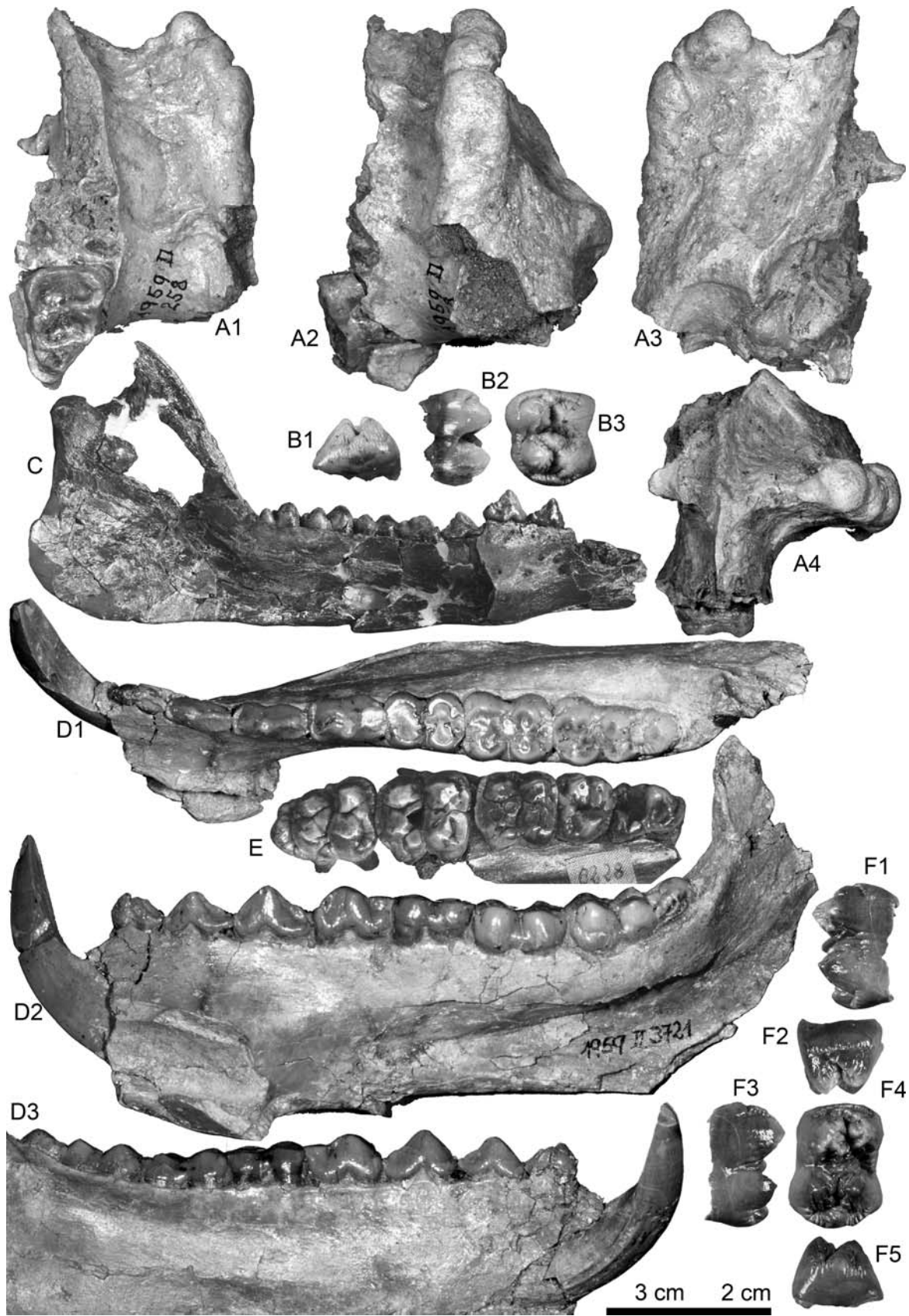
sides. Although the roots are not completely separated, each has a canal for the pulp cavity. Although two roots are peculiar for a canine, it is not unique: in *Conohyus si-morrensis* the  $C^f$  has two well separated roots.

The  $C_m$  (Fig. 14E, M, O; Tables 3, 5) is hypsodont with a triangular “scrofic” section (Fig. 20). The lingual and labial sides are covered with enamel, but the posterior side does not have enamel. The tooth is curved and may form as much as half of a circle in a fully adult individual (Fig. 14E). At the tip there is a large facet caused by occlusion with the upper canine. Wear is intense, and in old individuals much less than half of a circle is preserved (Fig. 14O). In the older individuals enamel no longer covers all the labial side (Fig. 14O1). This is also seen in the Listriodontinae on both the lingual and labial sides (Van der Made 1996: pl. 37, Fig. 1a, b). Here it is associated with irregular formation of the enamel, as seen by irregular “growth ridges” on the lingual side. The dark colour on the labial side of the specimen in Fig. 14E3 is cementum that covers the enamel. Such cementum is not found in all specimens.

The  $C_m$  have a small radius of curvature in comparison with the dimensions of their cross-section. One of the consequences of this is that a canine can never protrude much from the mandible, and this is seen in specimens which are in situ in the mandible (Fig. 8D), especially if compared with even very modest canines in *Bunolistriodon* (Van der Made 1996a: pl. 16, Fig. 8) or the large ones in *Listriodon* (Kittl 1889: pls. 14–15). This small size limits their value as weapons in inter or intraspecific combat. Whereas in *Listriodon splendens* the radius of curvature increased with evolution (Van der Made 1996a: Fig. 50), this does not seem to have been the case in *Hyotherium*, nor in *Chleuastochoerus* (Pearson 1928).

The section of the  $C_m$  is triangular, as stated above. The shape of this triangle is given much importance (eg. Stehlin 1899–1900; Pilgrim 1926). If the labial side is wider than the posterior side, as in *Sus verrucosus*, the section is said to be “verrucosic”. If the posterior side is wider, as in *Sus scrofa*, the section is said to be “scrofic”. Of course there is variability in any sample, and in juvenile animals, where the tip is not yet worn, the section is also different. A species may evolve from canines with a scrofic section towards canines with a verrucosic section (Van der Made 1996a: Fig. 48). *Hyotherium soemmeringi* from Sandelzhausen, and from other localities, and other species of Hyotheriinae clearly have a scrofic section.

The  $C_f$  (Fig. 14P; Tables 3, 5) has a high crown, but it is much lower than in the  $C_m$ . It also has a triangular section, but very different from that of the  $C_m$ ; the labial side is the widest side and the posterior side the narrowest. Another difference with the male canines is that the posterior side is covered by enamel. This is common in many Suidae,



◀ **Fig. 8** *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...). **A** 258–left maxilla and origin of zygomatic arch: 1 inferior, 2 left lateral, 3 dorsal, and 4 anterior views; **B** 8908 right  $M^{1/2}$ : 1 anterior, 2 buccal, and 3 occlusal views; **C** 312 left mandible (and fragment of the right mandible): medial view; **D** 3721 right mandible with  $C_m$  and  $P_1$ – $M_3$ : 1 occlusal, 2 lingual, and 3 buccal views; **E** 309 right maxilla with  $P^3$ – $M^3$ : occlusal view; **F** 8929 right  $M_{1/2}$ : 1 buccal, 2 anterior, 3 lingual, 4 occlusal, and 5 posterior views. The scale bar represents 2 cm for **F**, 3 cm for **A**, **D**, **E**, and 6 cm for **C**

although in the *Sus scrofa*  $C_f$  the posterior enamel ends a relatively small distance below the tip, leaving most of the posterior side uncovered.

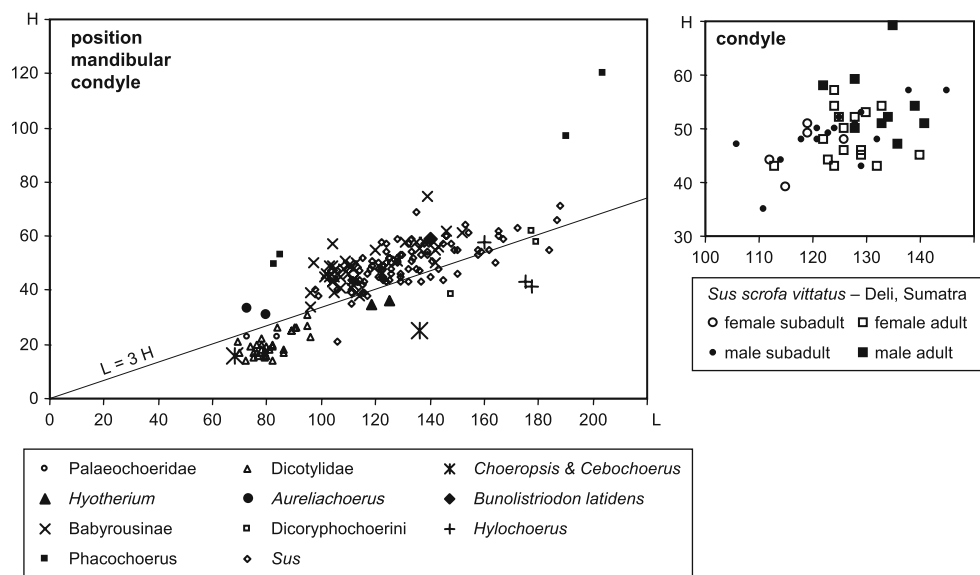
The  $P^1$  (Fig. 14C, D, G; Tables 6, 7) has a large paracone and well developed paraprecrista and parapostcrista. In side view the outline is triangular. The paraprecrista is directed anteriorly and a little lingually, ending at the antero–lingual “corner” of the tooth. The parapostcrista is directed towards postero–buccal, and at the lingual side of this structure a small plateau is formed. Occasionally on this plateau a small elevation is detected, which, if larger, would be called protocone. In contrast with the other

premolars, the anterior lobe of the  $P^1$  tends to be wider than the posterior lobe. There are two separated roots; the anterior one may be curved distally and thus converge on the posterior root, or be divergent from it.

The  $P^2$  (Fig. 14F, I; Tables 6, 7) is similar to the  $P^1$ , but is larger and its anterior cingulum tends to be better developed. Contrary to the normal state in Suidae, it does not have a much better developed protocone than the latter tooth (Fig. 12), and consequently it is narrow. Its roots are always divergent.

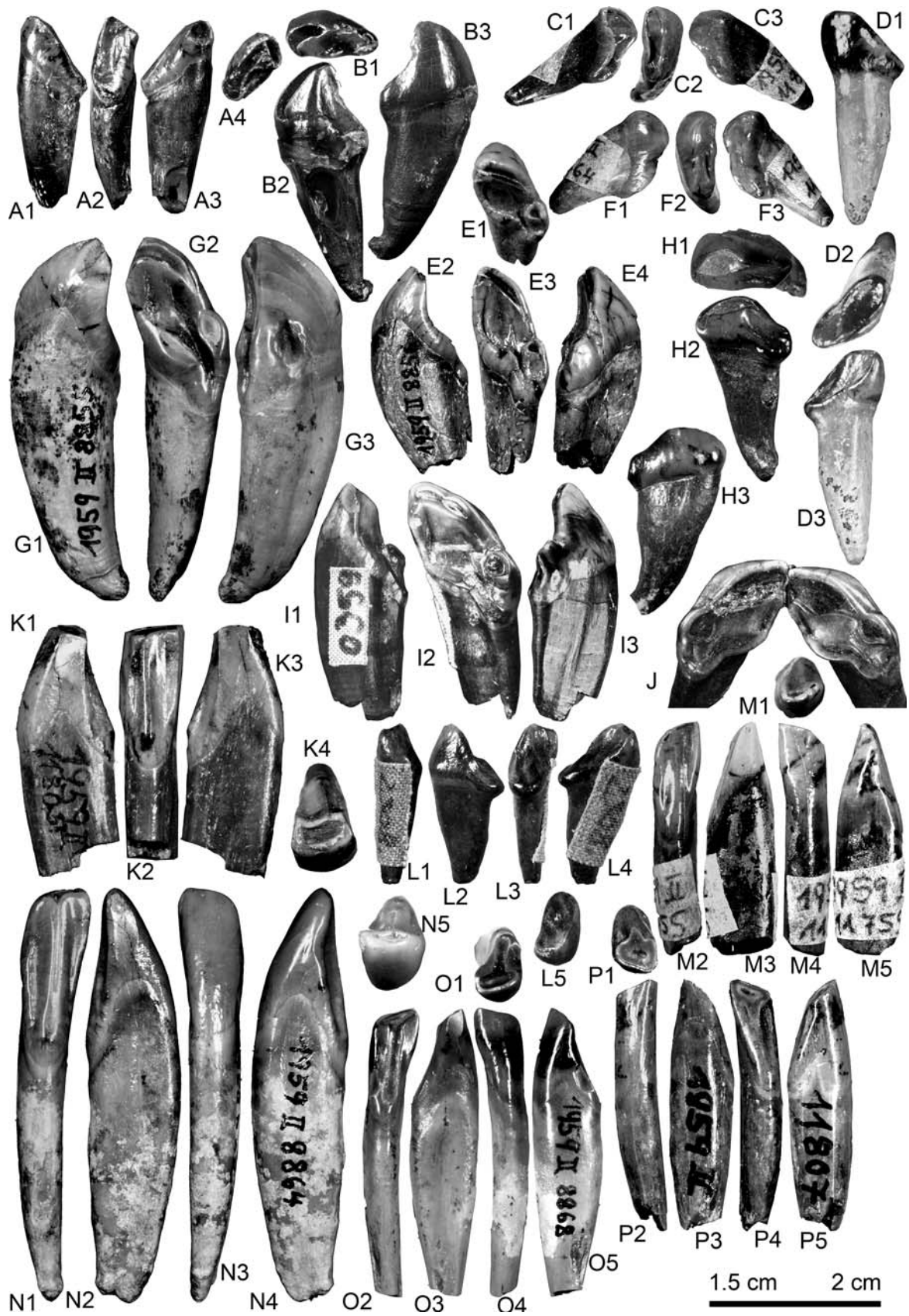
The  $D^2$  (Table 9) is similar to the  $P^1$  and  $P^2$ , but it is more elongate than the  $P^1$ , and always has divergent roots and thinner enamel.

The  $P^3$  (Fig. 8E; Tables 6, 7) has the same structure as the preceding three teeth, but its paracone is more conical and wide, although not as wide as in many other Suidae. Apparently the shape of the paracone is affected by the process of elongation of the premolars, which will be discussed below. The protocone is well developed as a cusp within a cingulum that encloses a talon basin. Both features result in a tooth that is wider at the anterior and posterior lobes than the anterior premolars and  $D^2$ , even though its



**Fig. 9** The position of the mandibular condyle of selected Suiformes: Palaeochoeridae including *Taucanamo sansaniense* from Sansan (MNHN), *Propalaeochoerus leptodon* from Puy-de-Dôme (cast MNHN) and *Propalaeochoerus* sp. from an unknown loc. (univ. Clermond Ferrand); Dicotylidae including *Dyseohyus stirtoni* from Observation Quarry (AMNH) and recent *Tayassu tajacu* (ZMA), *T. pecari* (ZMA) and *Catagonus wagneri* (NMW); *Hyotherium soemmeringi* from Sandelzhausen (BSPG); *Aureliachoerus aurelianensis* from Artenay (MNHN); *Bunolistriodon latidens* from Veltheim (NSSW); Babyrousinini including recent *Babyrousa* (ZMA) and *Potamochoerus* (ZMA, NNML, MNCN); Dicoryphochoerini including *Propotamochoerus provincialis* from Montpellier (UCBL) and Kardia (IVAUF); recent *Hylochoerus meinertzhageni* (ZMA, FISF);

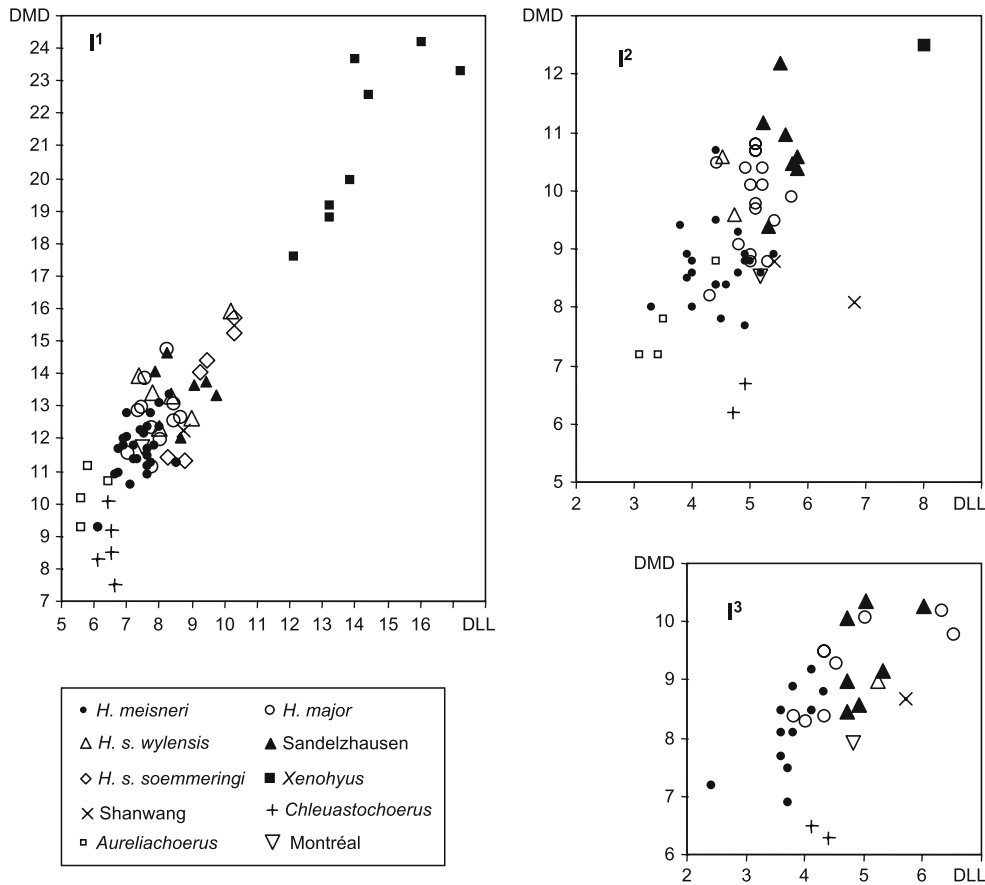
recent juvenile (small) and adult (large) *Phacochoerus* (ZMA); *Sus* including *S. strozzi* from Valdarno (IGF), *S. brachygnathus* from Trinil (NNML), and recent *S. celebensis* (ZMA, FISF), *S. barbatus* (ZMA), *S. verrucosus* (NNML), *S. scrofa vittatus* from Deli, Sumatra (ZMA), *Sus* from Tokunoshima (KU), *S. scrofa* from Japan, *S. scrofa* from Germany (NNML), Spain (MNCN), and Estland (CMH); non-suoid Suiformes including recent *Choeropsis liberiensis* (the large specimen) and *Cebochoerus* sp. from Los Barros (the small specimen; MNCN). The sample of *S. scrofa vittatus* from Deli is also used to show sexual dimorphism and ontogenetic change between subadult (M3 in the process of erupting) and adult (M3 fully erupted and worn). This is the same sample used by Van der Made (1991, 1997) and Guan and Van der Made (1993) to illustrate sexual bimodality





◀ **Fig. 10** The incisors of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...). **A** 367 right DI<sup>1</sup>: 1 labial, 2 occlusal, 3 mesial, and 4 apical views; **B** 370 left I<sup>3</sup>: 1 occlusal, 2 lingual, and 3 labial views; **C** 11861 left I<sup>2</sup>: 1 lingual, 2 apical, and 3 labial views; **D** 11764 left I<sub>3</sub>: 1 distal, 2 apical, and 3) mesial views; **E** 8856 right I<sup>1</sup>: 1 apical, 2 mesial, 3 occlusal, and 4 distal views; **F** 11764 right I<sup>2</sup>: 1 abial, 2 apical, 3 lingual views; **G** 8855 left I<sup>1</sup>: 1 mesial, 2 occlusal, and 3 distal views; **H** 368 left I<sup>2</sup>: 1 apical, 2 lingual, and 3) labial views; **I** 362 left I<sup>1</sup>: 1 mesial, 2 occlusal, and 3 distal views; **J** 16227 left and right I<sup>1</sup>: occlusal view; **K** 11805 left I<sub>1</sub>: 1 distal, 2 lingual, 3 mesial, and 4 apical views; **L** 16228 left I<sub>3</sub>: 1 labial, 2 distal, 3 lingual, 4 mesial, and 5 occlusal views; **M** 11755 germ of left DI<sub>2</sub>: 1 apical, 2 lingial, 3 mesial, 4 labial, and 5 distal views; **N** 8864–left I<sub>2</sub>: 1 lingual, 2 mesial, 3 labial, 4 distal, and 5 apical views; **O** 8868 left DI<sub>2</sub>: 1 apical, 2 lingual, 3 mesial, 4 labial, and 5 distal views; **P** 11807 right DI<sub>2</sub>: 1 apical, 2 labial, 3 mesial, 4 lingual, and 5 distal views. The *scale bar* represents 1.5 cm for **B, D, H, K, M–P**, and 2 cm for **A, C, E–G, I–J, L**

length is comparable with that of the P<sup>2</sup> and larger D<sup>2</sup> (Fig. 12). The anterior and postero–labial cingula are well developed.

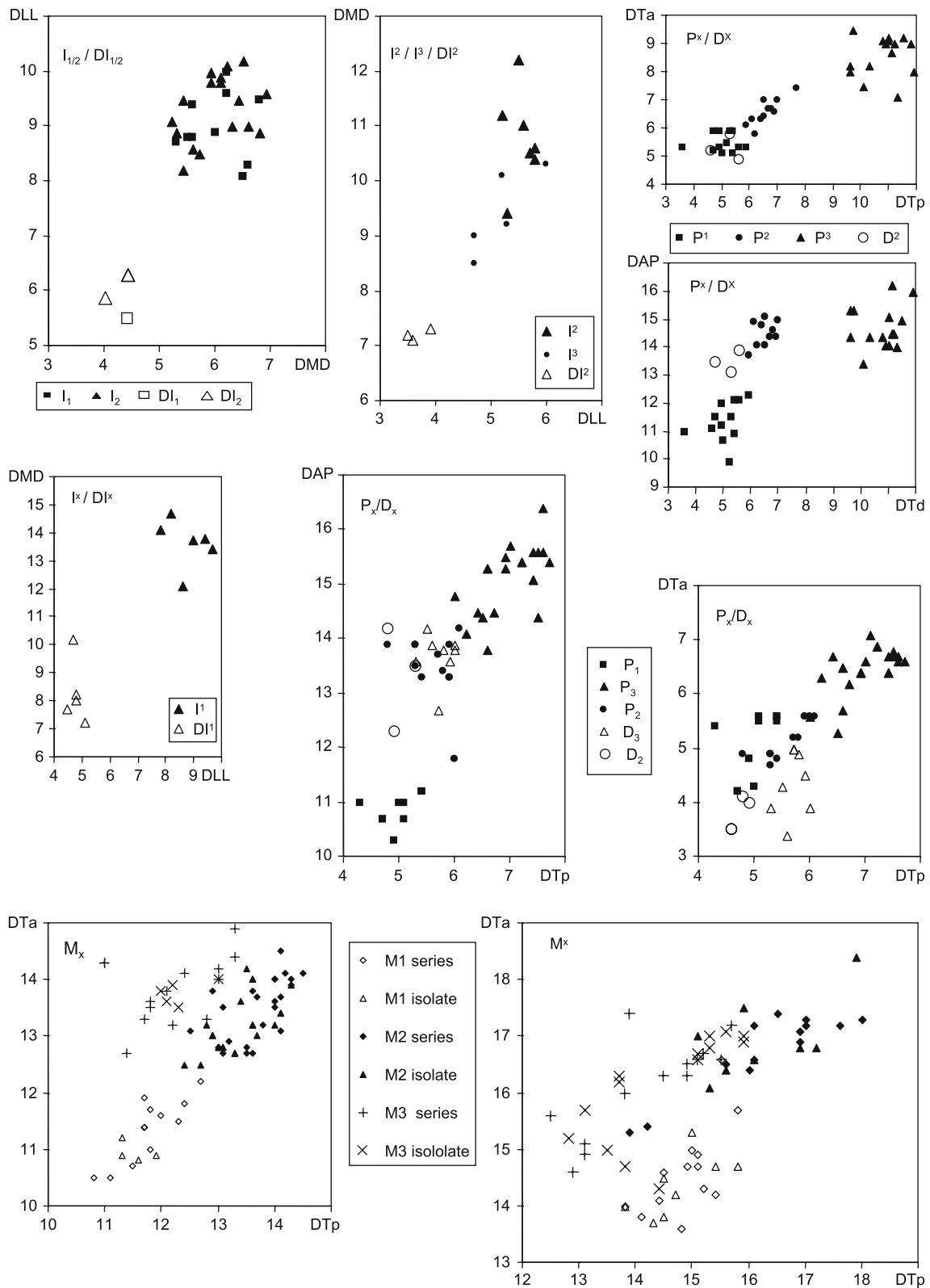


**Fig. 11** Bivariate diagrams comparing the upper incisors of selected Hyotheriinae: *Hyotherium meisneri* from Paulhiac (NMB), Cetina de Aragón (MNCN, IPS, IVAU), Grépiac (MHNT), Laugnac (UPM, UCBL, NMB), Montaigu (NMB) and Hessler (FISF); *H. major* from St Gérard-le-Puy (MNHN), Weisenau (FSIF) and Ulm Westtangente (SMNS); *H. soemmeringi wylensis* from Sandelzhausen (BSPG), from Montréal-du-Gers (MHNT for the I<sup>1</sup> and for the I<sup>2–3</sup> Orliac et al. 2006), and from Chilleurs-aux-Bois (NMB), Munébrege AB (IVAU),

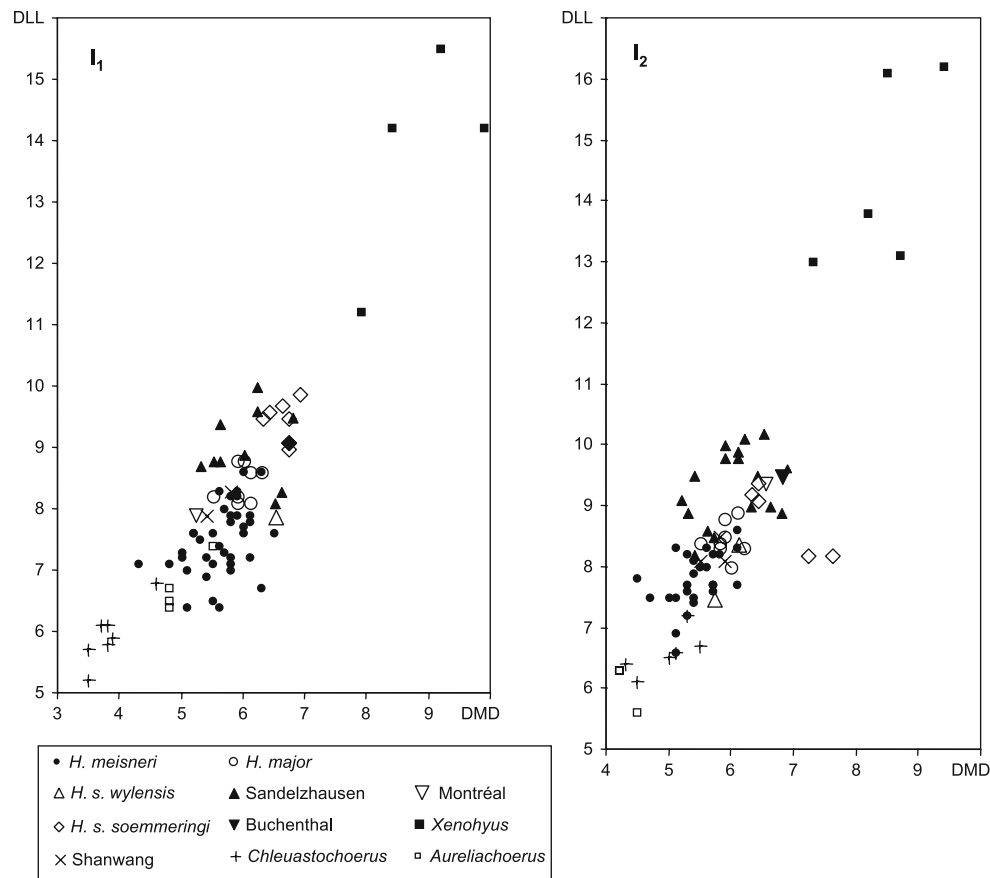
The P<sup>4</sup> (Figs. 8E, 14H; Tables 6, 7) is constructed on the same basis as the previous premolars, but has a large metacone, which developed from a cusplet in the parapostrista, and has a much enlarged protocone, which is also placed much anteriorly. The separation between the paracone and metacone is very well seen in an unworn tooth, but also in a worn tooth through separate dentine islets and a deep groove on the buccal wall. This separation is much better developed than in earlier species of *Hyotherium*.

There may be minor crests or enamel folds on the lingual sides of the para and meta-cones of the P<sup>4</sup> of *Hyotherium*, *Chleuastochoerus*, *Xenohyus*, and *Aureliachoerus*, but there are never separate cusplets at these places. Such cusplets, called sagittal cusps (Pickford 1988) or endoconules (Van der Made 1996a), are believed to define the Suinae (Pickford 1988), but occur occasionally in the Tetraconodontinae (Van der Made 2004) and in the

Baigneaux-en-Beauce (NMB) and Pontlevoy (MNHN); *H. s. soemmeringi* from Schöneck (SLJG) and Thannhausen (BSPG), *Hyotherium* from Shanwang (cast IVPP); *Chleuastochoerus* from Hsi K'ou (3 miles NW Yushe, AMNH); *Xenohyus* from Laugnac (UPM), various localities of the Faluns de Touraine et de l'Anjou (MNHN) and Loranca (MNCN); *Aureliachoerus minus* from Wintershof West (BSPG) and Gazapouy (UCBL) and *A. aurelianensis* from Artenay (NMB)



**Fig. 12** Bivariate diagrams comparing dental elements of *Hyotherium soemmeringi* with similar morphologies from Sandelzhausen



**Fig. 13** Bivariate diagrams comparing the lower first and second incisors of selected Hyotheriinae: *Hyotherium meisneri* from Paulhiac (NMB), Cetina de Aragón (MNCN, IPS), Laugnac (UPM, UCBL, MNHN, NMB), Montaigu (NMB), Budenheim (FISF, HLD) and Hessler (FISF); *H. major* from St Gérard-le-Puy (MNHN), Langy (MGL), Weisenau (FSIF) and Ulm Westtangente (SMNS); *H. soemmeringi wylensis* from Buchenthal (PIMUZ), from Sandelzhausen (BSPG) and from Munébraga 2 (IVAUA) and Baigneaux-en-Beauce

(NMB); *H. s. soemmeringi* from Labitschberg (SLJG), Seegraben (SLJG), Münzenberg (SLJG) and “Leoben” (IGL); *Hyotherium* from Shanwang (cast IVPP); *Chleuastochoerus* from Locality 73 (IVPP), Baodea (IVPP), Holinger (BNHM), and Lufeng (IVPP); *Xenohyus* from Laugnac (UPM), various localities of the Faluns de Touraine et de l’Anjou (MNHN) and Loranca (MNCN); *Aureliachoerus minus* from Wintershof West (BSPG) and *A. aurelianensis* from Artenay (NMB)

Babyrousiniae also. There are well developed anterior and posterior cingula. Metrically the  $P^4$  from Munébraga AB is situated in the middle of the Sandelzhausen sample (Van der Made 1998a, Fig. 7).

The  $D^3$  (Tables 6, 9) has a morphology that is intermediate between the previous teeth and the  $D^4$  and molars (although the cusps do not seem to be homologous). There are two lobes, one with just the paracone, and one with the metacone and protocone.

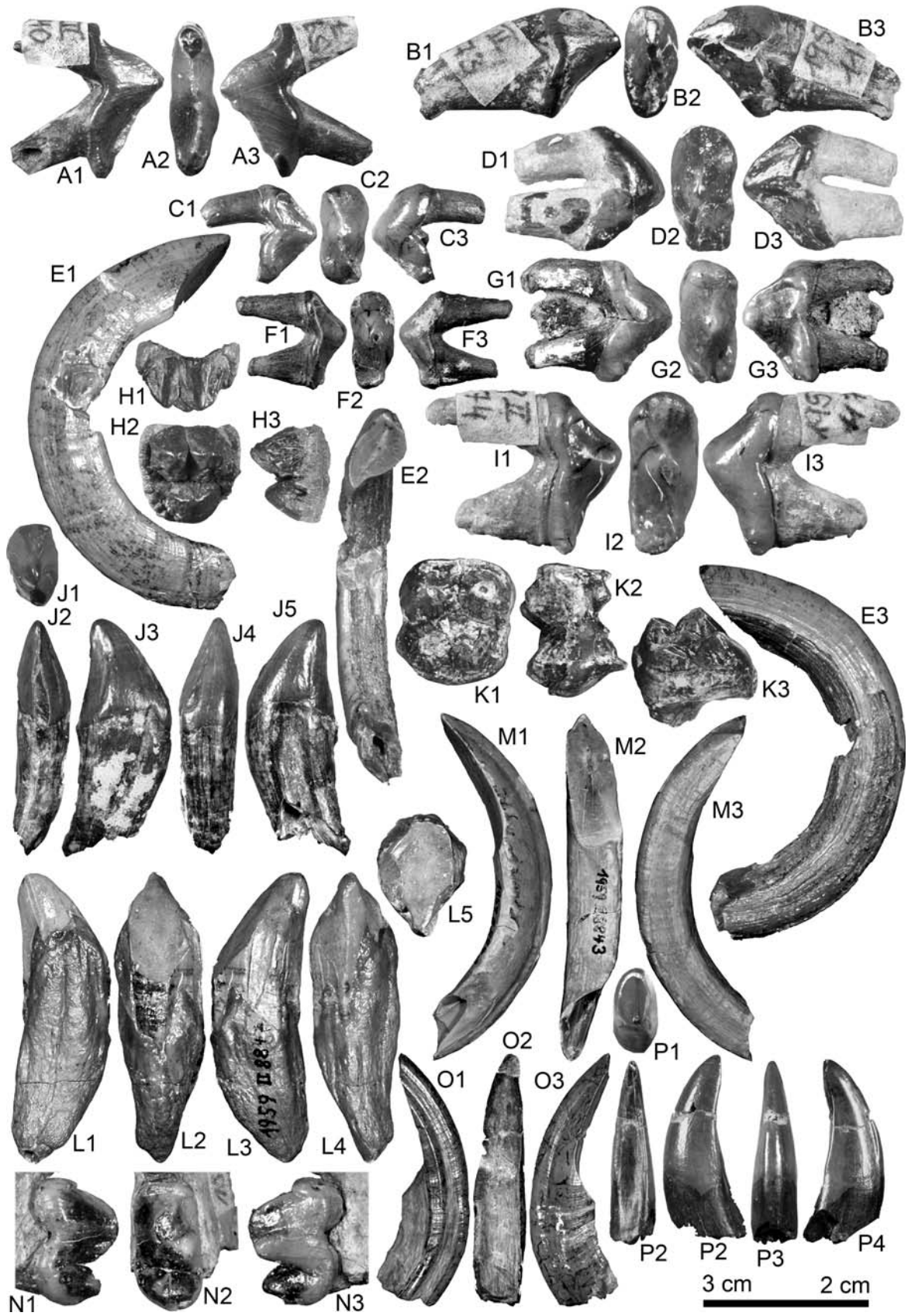
The  $P_1$  (Fig. 14B; Tables 10, 11) has an elongate protoconid with protoprecrestid and protopostcrestid; the former being directed slightly lingually and the latter slightly buccally. The crown has a triangular outline in side view. The tip of the protoconid is placed well anterior of the middle of the tooth. There are two roots, but they are fused and curved backwards. The  $P_1$  from Sandelzhausen is larger than that of *Hyotherium major* from its type locality St Gérard-le-Puy and other

localities, but it is close in size to that of other *Hyotherium soemmeringi* (Fig. 21).

The  $P_2$  (Fig. 8D; Tables 10, 11) is similar to the  $P_1$ , but its crown tends to be more elongate and relatively lower. It is larger, much more elongate and the posterior lobe is relatively wider (Fig. 12). The tip of the protoconid is placed closer to the middle of the crown. There is a small cusplet where the protoprecrestid reaches the anterior cingulum. The roots are separate and divergent. The  $P_2$  of *Hyotherium major* is smaller than in Sandelzhausen, the MN4 *Hyotherium*, including Armantes I and Montréal, is relatively small, whereas those of MN5 *Hyotherium* tend to be of similar size (Fig. 21).

The  $D_2$  (Tables 9, 10) is similar to the previous teeth, but with more divergent roots and thinner enamel. It is smaller and tends to be much more elongate (Fig. 12).

The  $P_3$  (Fig. 8D; Tables 10, 11) is similar to the previous teeth, but the anterior cusplet is better developed and



◀ **Fig. 14** Canines, premolars and an upper molar of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...). **A** 11740 right D<sub>2</sub>: 1 lingual, 2 occlusal, and 3 buccal views; **B** 11773 right P<sub>1</sub>: 1 lingual, 2 occlusal, and 3 buccal views; **C** 334 left P<sup>1</sup>: 1 lingual, 2 occlusal, and 3 buccal views; **D** 352 right P<sup>1</sup>: 1 buccal, 2 occlusal, and 3 lingual views; **E** 357 right C<sub>m</sub>: 1 lingual, 2 posterior, and 3 labial views; **F** 331 left P<sup>2</sup>: 1 lingual, 2 occlusal, and 3 buccal views; **G** 332 right P<sup>1</sup>: 1 buccal, 2 occlusal, and 3 lingual views; **H** 328 right P<sup>4</sup>: 1 buccal, 2 occlusal, and 3 anterior views; **I** 11774 left P<sup>2</sup>: 1 lingual, 2 occlusal, and 3 buccal views; **J** 342 right C<sup>f</sup>: 1 apical, 2 posterior, 3 lingual, 4 anterior, and 5 labial views; **K** 325 left M<sup>1</sup>: 1 occlusal, 2 buccal, and 3 antero-occlusal views; **L** 8847 left C<sup>m</sup>: 1 labial, 2 anterior, 3 lingual, 4 posterior, and 5 apical views; **M** 8843 left C<sub>m</sub>: 1 lingual, 2 posterior, and 3 labial views; **N** 16220 left P<sub>4</sub>: 1 buccal, 2 occlusal, and 3 lingual views; **O** 356 right C<sub>m</sub>: 1 labial, 2 posterior, and 3 lingual views; **P** 355 left C<sub>f</sub>: 1 apical, 2 posterior, 3 labial, 4 anterior, and 5 lingual views. The scale bar represents 1.5 m for **A**, **B** and **D**, it represents 2 cm for **C**, **G**, **H**, **J**, **K**, **N** and **P**, and 3 cm for **E**, **L**, **M** and **O**

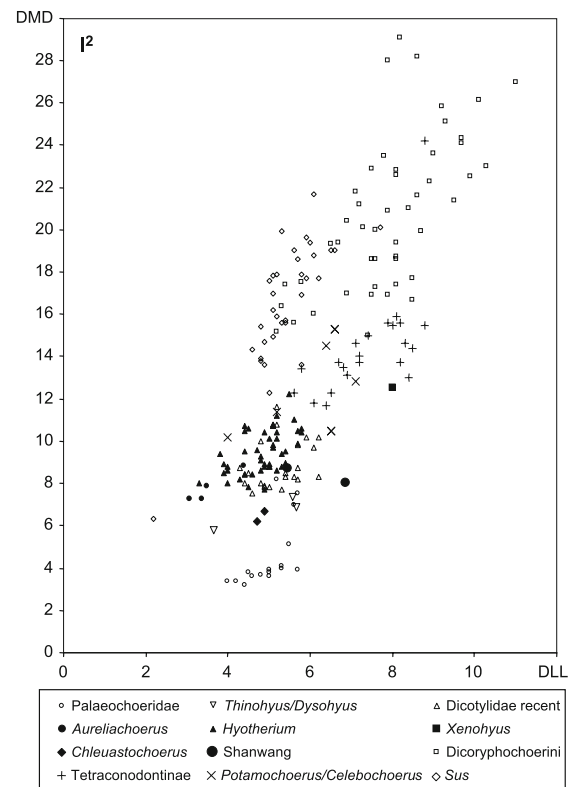
there is a thickening or cusplet in the protoposteristid. It is also larger, but it is not relatively wider than the P<sub>2</sub>. Although there is much variation in the index 100DAP/D<sub>Tp</sub>, the samples of Sandelzhausen, Baigneaux, and in part Buchenthal, have higher values than older samples. The still younger samples again may include wide specimens.

The D<sub>3</sub> (Tables 9, 10) is broadly similar to the previous premolars and milk molars, but tends to have a more inflated protoconid and may have multiple posterior crests, or bifurcated posterior crests. It has a relatively narrow anterior lobe, which is possibly because of its position between the wide and molariform D<sub>4</sub> and the very narrow D<sub>2</sub> (Fig. 12).

The P<sub>4</sub> (Figs. 8D, 14N; Tables 10, 11) differs from the previous premolars in having a well developed metaconid and a well separated talonid with a large cusp. Comparison with the sizes of the other samples of *Hyotherium* leads to similar results as for the previous premolars (Fig. 21). The width in the sample from Sandelzhausen seems to be more variable than in most other samples of *Hyotherium*, and in comparison with other suids (e.g. *Xenohyus*, Fig. 21) it is much more variable. Curiously, the length is not so variable, whereas it might be expected to be more variable because of shortening through wear. There are thus two types, one that is wide, and another one that became narrower. The P<sub>4</sub> from Armantes I is close to the smallest specimens of Sandelzhausen (Fig. 21). This is also the case for a specimen from Buchenthal, whereas another incomplete specimen from that locality is larger. A specimen from Montréal is large and elongate.

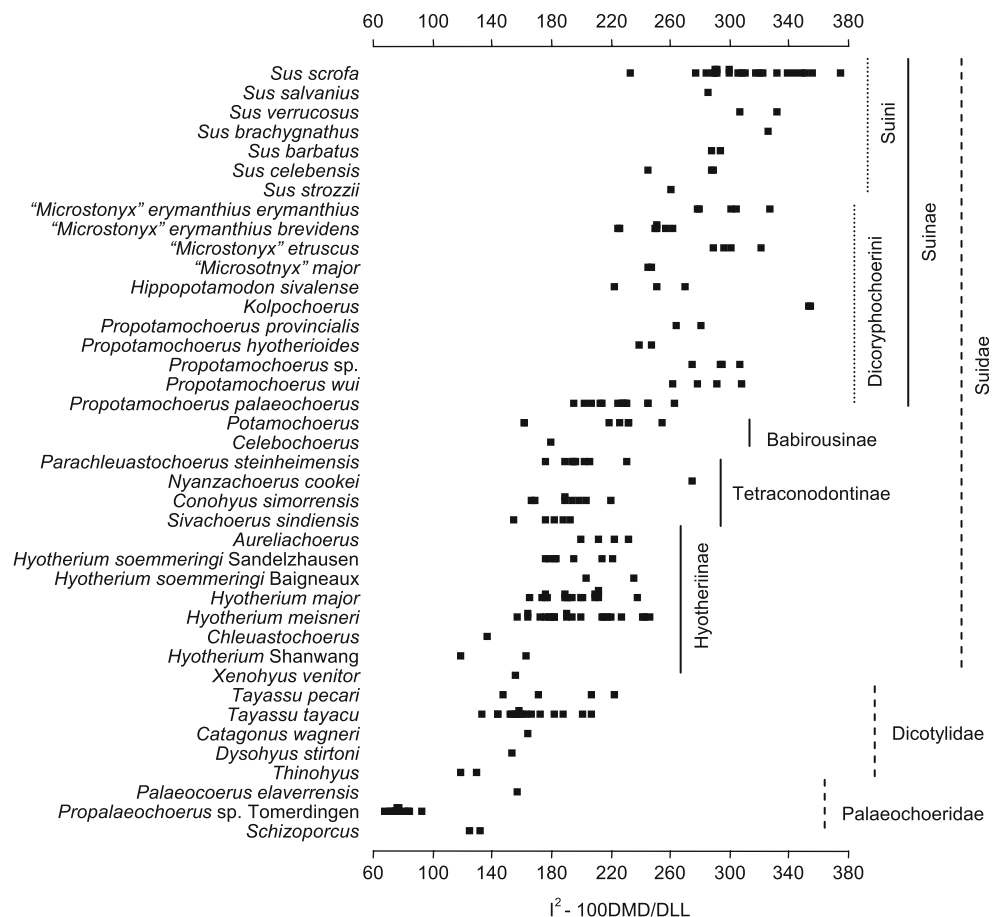
The D<sup>4</sup> (Tables 6, 9) has a structure similar to that of the M<sup>1</sup> and M<sup>2</sup> (see below), but is smaller and differs in having an oblique anterior edge that sticks out most anteriorly at the buccal side. As is common in milk teeth, it also has thinner enamel.

The D<sub>4</sub> (Tables 9, 10) is a molariform tooth, but differs from the M<sub>1</sub> and M<sub>2</sub> in having three lobes, each one with



**Fig. 15** Bivariate diagram of the  $I^2$  of selected Suoidea: Palaeochoeridae including *Schizoporcus sinapensis* from Sinap (MTA), *Propalaeochoerus* sp. from Tomerdingen (SMNS), and *Palaeochoerus aquensis* from the Quercy (MNHN); *Thinochus lentus* from Roundhouse Rock (AMHN) and *Dysochus stirtoni* from Observation Quarry (AMNH); recent Dicotylidae including *Tayassu tajacu* (ZMA), *Tayassu pecari* (ZMA) and *Catagonus wagneri* (NMW); *Aureliachoerus minus* from Wintershof West (BSPG) and Gazapouy (UCBL); *Hyotherium meisneri* from Cetina (MNCN), Laugnac (UPM), Grépiac (cast MHNT), Hessler (FISF), *Hyotherium major* from Weisenau (FISF), Ulm Westtangente (SMNS) and St Gérard-le-Puy, *Hyotherium soemmeringi* from Baigneaux-en-Beauce (NMB), Sandelzhausen (BSPG); *Xenohyus ventitor* from Laugnac (UPM); *Hyotherium* from Shanwang (cast IVPP); *Chleuastochoerus* from Hsi K'ou 3 miles NW Yushe (AMNH); Tetraconodontinae including *Conohyus simorreensis* from Göriach (SLJG) and Pasalar (PDTFAU), *Nyanzachoerus cookei* from Sahabi (USR; the large specimen), *Sivachoerus sindiensis* from the Siwaliks (IM, BSPG) and *Parachleuastochoerus steinheimensis* from La Grive (MGL, IGF), Przeworno (ISEAK) and Wissberg (HLD, NMM); recent *Potamochoerus* (ZMA, NNML, MNCN) and *Celebochoerus heekereni* from Sompoh (NNML); Dicoryphochoerini including *Propotamochoerus palaeochoerus* from Wissberg (NMM), Hostalets (IPS), Mariatal (IPUV) and Doué-la-Fontaine (MNHN), *P. wui* from Lufeng (IVPP), *Propotamochoerus* sp. from Samos (NMW), Baccinello V3 (NMB) and Maramena (JGUM), *P. provincialis* from Venta del Moro (MNCN), *Kolpochoerus* from East Rudolf (KNM), *Hippopotamodon sivalensis* from the Siwaliks (GSP), "*Microstonyx*" *major* from Crevillente II (MHMN) and Terrassa (IPS), "*Eumaiiochoerus*" *etruscus* from Monte Bamboli (Pisa) and Baccinello V2 (NMB), and "*M.*" *erymanthus* from Dorn Dürkheim (FISF), Csakvar (GSB), Samos (NMB) and Pikermi (NHM); *Sus strozzi* from Olivola (IGF), *Sus brachygnathus* from Trinil (NNML), and recent *S. celebensis* (FISF, NNML), *S. barbatus* (ZMA), *Sus salvanius* (MNHN) and *Sus scrofa* (HUJ, CMHH, MNCN, UPVB, ZMA, NNML)

**Fig. 16** The degree of elongation of the  $I^2$  in the Suoidea; provenance of data as in Fig. 15



two cusps. The width of the lobes increases from anterior to posterior. Any of these lobes is narrower than the lobes of a molar. The enamel is much thinner.

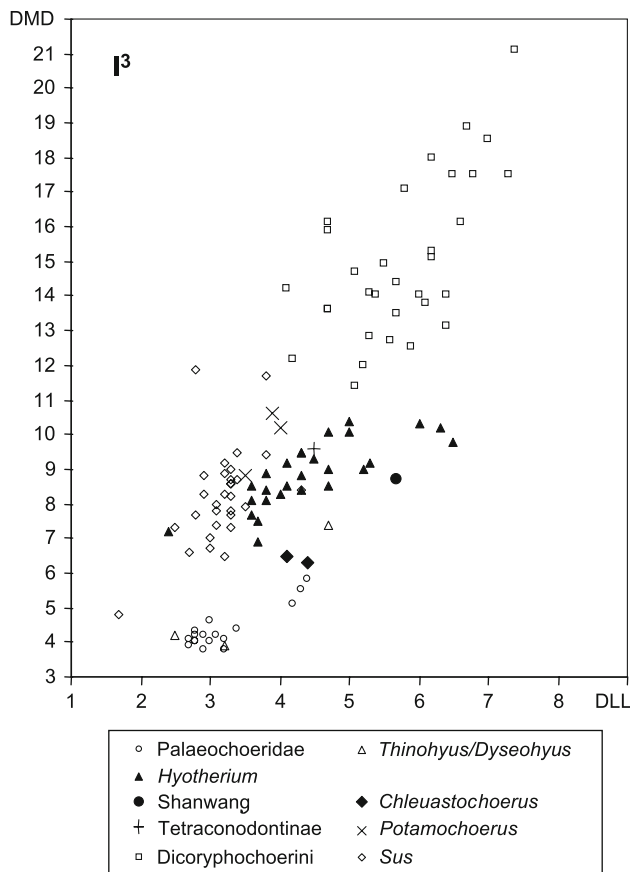
The  $M^1$  and  $M^2$  (Figs. 8B, E, 14K; Tables 6, 8) are teeth that have similar morphologies, but that differ in that the  $M^1$  tends to be smaller and has a relatively narrower anterior lobe (Fig. 12) and thinner enamel. These teeth have typically four main cusps. These cusps have wrinkled enamel, as seen in unworn specimens, but some of the grooves are better developed and delimit elevations. These elevations are clear lobes or crests in later species (Van der Made 1996a), but here it is difficult to recognize these crests unequivocally or the furrow pattern (or “Furchen”) of Hühnermann (1968).

A well developed cusp is present at the position of the protopreconule, but it is connected to the anterior cingulum and not to the protocone. A protopreconule that is fused to the cingulum is common suid morphology whereas in Palaeochoeridae this cusplet is connected to the protocone. In one isolated specimen from Sandelzhausen, the cusplet is connected to the protocone (Fig. 14K). Otherwise this specimen is like other *Hyotherium* teeth and different from and larger than the molars of *Schizoporcus*.

A large central cusp or tetrapreconule is situated on the posterior side of the transverse valley. The posterior cingulum continues below the tetrapreconule and does not form one continuous structure with the tetrapreconule, as may occur in primitive suoids. There is a buccal cingulum. There may be a cingulum or cusp, even a large one (Fig. 8E), at the lingual entrance of the transverse valley, or none at all (Fig. 8B).

The  $M^3$  (Fig. 8D, E; Tables 6, 8) has a structure that is similar to that of the previous teeth. It tends to have a relatively narrow second lobe (Fig. 12). However, the clearest difference is that it has a wider posterior cingulum, in particular at the posterolingual side, where a true cusp, the pentacone, may even have developed. A specimen from Munébrega AB, which is situated metrically in the middle of the Sandelzhausen sample (Van der Made 1998a: Fig. 8), is one of the types of “*Conohyus cuspidatus*”.

The  $M_1$  and  $M_2$  (Fig. 8D, F; Tables 10, 12) are teeth with similar morphologies. They differ in that the  $M_1$  is smaller (Fig. 12), and that it has absolutely thinner (Tables 10, 12) and on average relatively thinner enamel (enamel index  $1000Ta/DTa$ ; Fig. 22). These teeth have the simple bunodont structures that are common in primitive



**Fig. 17** Bivariate diagram of the  $I^3$  of selected Suoidea. Palaeochoeridae including: *Schizoporcus sinapensis* from Sinap (MTA), *Propalaeochoerus* sp. from Tomerdingen (SMNS) and *Palaeochoerus aquensis* from the Quercy (MNHN); *Thinohyus lentus* from Roundhouse Rock (AMNH) and *Dyseohyus stirtoni* AMNH); *Hyotherium* including *H. meisneri* from Cetina (MNCN), Grépiac (MHNT), Laugnac (UPM), “Ulm” (NMB) and Hessler (FISF), *H. major* from St Gérard-le-Puy (MNHN) and Ulm Westtangente (SMNS), *H. soemmeringi* from Munébrega AB (IVAU) and Sandelzhausen (BSPG); *Hyotherium* from Shanwang (cast IVPP); *Chleuastochoerus* from Hsi K’ou 3 miles NW Yushe (AMNH); Tetraconodontinae including *Nyanzachoerus cookei* from Sahabi (USR); recent *Potamochoerus* (ZMA, EBD, MNCN); Dicoryphochoerini including *Propotamochoerus palaeochoerus* from Castell de Barberá (IPS) and Johnsdorf (SLJG), *P. wui* from Lufeng (IVPP), *Propotamochoerus* sp. from Samos (NMW), Maramena (JGUM) and Baccinello V3 (NMB), *P. provincialis* from Venta del Moro (MNCN), “*Eumaiocherus*” *etruscus* from Monte Bamboli (Pisa), and “*Microstonyx*” *erymanthius* from Dorn Dürkheim (FISF), Samos (NMB) and Pikermi (NHM); *Sus* including *S. brachygnathus* from Trinil (NNML) and recent *S. celebensis* (FISF, NNML), *Sus verrucosus* (NNML), *Sus salvanius* (MNHN) and *Sus scrofa* (ZMA, NNML, HUJ)

pigs, and are relatively short and wide compared with their homologues in later suids. The crowns are also low, and whenever hypsodonty indices can be calculated ( $100Ha/DTa$ ) the value is  $\ll 100$  (raw data in Tables 10, 12), which is another primitive feature. Compared metrically with the

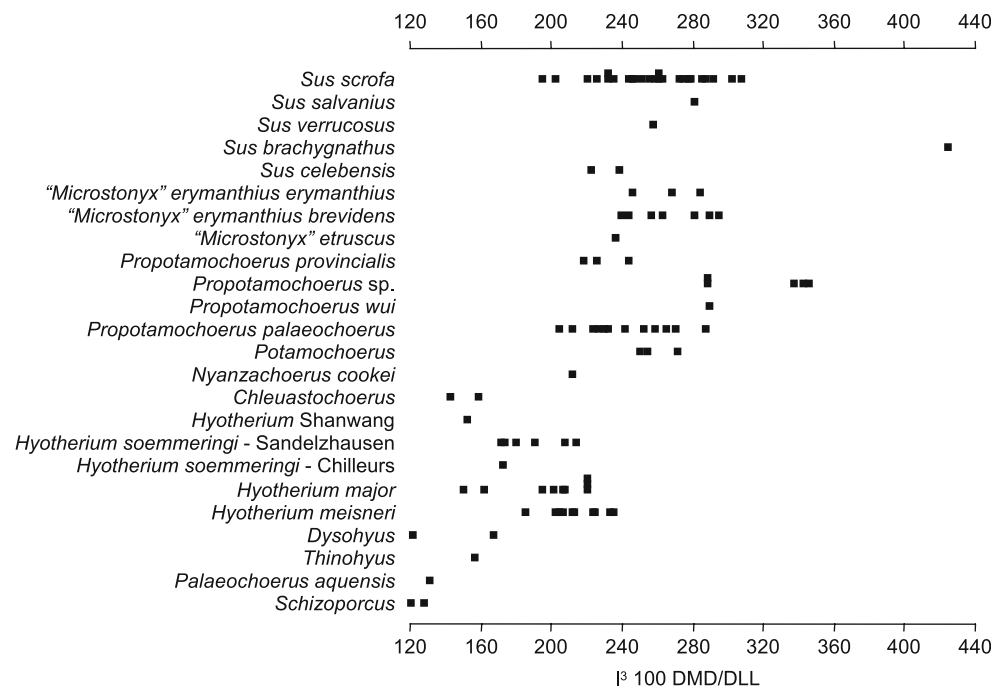
Sandelzhausen sample, the specimens of *H. major* are smaller, those from MN4 localities, such as Armantes I and Montréal are in the ranges, whereas those from Georgensgmünd are in the upper ranges (Figs. 21, 23). Comparison of the sizes of the Sandelzhausen  $M_2$  with a large number of samples reveals that, broadly, there is a size increase with time and that the sample from Sandelzhausen fits in this cline together with other localities of the same approximate age (Fig. 23).

The  $M_3$  (Fig. 8D; Tables 10, 12) is similar to the first two molars, but has a third lobe with a large cusp in the middle (the pentaconid), which is preceded by a smaller cusp (the pentapreconulid), which is flanked by smaller cusps or a beaded cingulum. It also differs in having a relatively narrower second lobe (Fig. 12) and thicker enamel (Fig. 22). Its morphology is common among the early Suidae. The St Gérard specimens are again smaller, and those from Georgensgmünd are again in the upper ranges of the Sandelzhausen sample (Fig. 21). As with the  $M_2$ , the  $M_3$  fits in the general trend in increasing size in *Hyotherium*, and in both cases the sample seems to fit just above Baigneaux, another large sample, and would even fit above the old collection from Pontlevoy.

The average **cheek tooth proportions** of some *Hyotherium* samples are compared in Fig. 24. Most samples are of respectable size, but from Georgensgmünd there are no more than two specimens for each measurement and also the sample from St Gérard is not very large. In addition, anterior premolars tend to be less represented. The standard is *Hyotherium meisneri* from Hessler. In the upper graph, which refers to tooth length, it can be seen that in general, the older samples have smaller values. It also seems that in the samples with larger values, the  $M_3$  and premolars tend to be relatively larger, at least in the  $P_4$  and  $P_2$ . In all samples, excepting the one from Hessler, the  $P_3$  seems to be relatively short compared with the neighbouring premolars. This probably is caused by an anomaly in the Hessler sample, but it is unlikely that this is because of the inclusion of isolated  $P_4$  in the  $P_3$  sample, because these are morphologically clearly different and inclusion of  $P_2$  would probably have led to a smaller average value and not a larger one. Variations in the size of the  $P_1$  may well be caused by the fact that this tooth is often poorly represented and thus the average value is not representative.

The figure for the width is a little more confusing, partly because usually two values ( $DTa$  and  $DTp$ ) are given per tooth. The anomaly of an apparently small  $P_3$  is magnified in most samples. Apart from this, the premolars seem, again, to be enlarged, particularly the  $P_1$  and  $P_2$ , but the  $M_3$  does not seem to be systematically enlarged. The  $M_3$  is usually a well represented tooth, and the two apparently contradictory observations can be reconciled assuming that the  $M_3$  is more elongate in the samples with larger values.

**Fig. 18** The degree of elongation of the  $I^3$  in the Suoidea; provenance of data as in Fig. 17



The degree of elongation of the premolars is shown in Fig. 25. Here it is seen that more elongate  $P_4$  appear in *H. soemmeringi* than in the earlier samples of the smaller species. In the  $P_3$  and  $P_2$  the elongate morphologies appeared already in older samples of the small *H. meisneri*. It is noteworthy that the younger samples of *Hyotherium* seem, again, to have short and wide  $P_3$  and  $P_4$ .

No diagram is given here for the proportions of the upper cheek teeth. Nevertheless, one peculiar feature should be mentioned. As is apparent from the previous descriptions, the maximum width of the upper premolars tends to increase from the  $P^1$  to the  $P^4$ , through a progressive increase in the size of the protocone. In many Suoidea, including the Listriodontinae and Suinae, this occurs gradually, but here there is a clear break between the  $P^2$  and  $P^3$ . This break is not as spectacular as in the Tetraconodontinae, but still it is there. In the Tetraconodontinae, there is a process of enlargement in the posterior premolars, and initially of elongation in the anterior premolars, causing a similar, but greater break in the gradual posterior increase of the width of the premolars (Van der Made 1999). This break is at the same place. At present, it is unclear whether this similarity is coincidence or caused by an underlying fundamental principle.

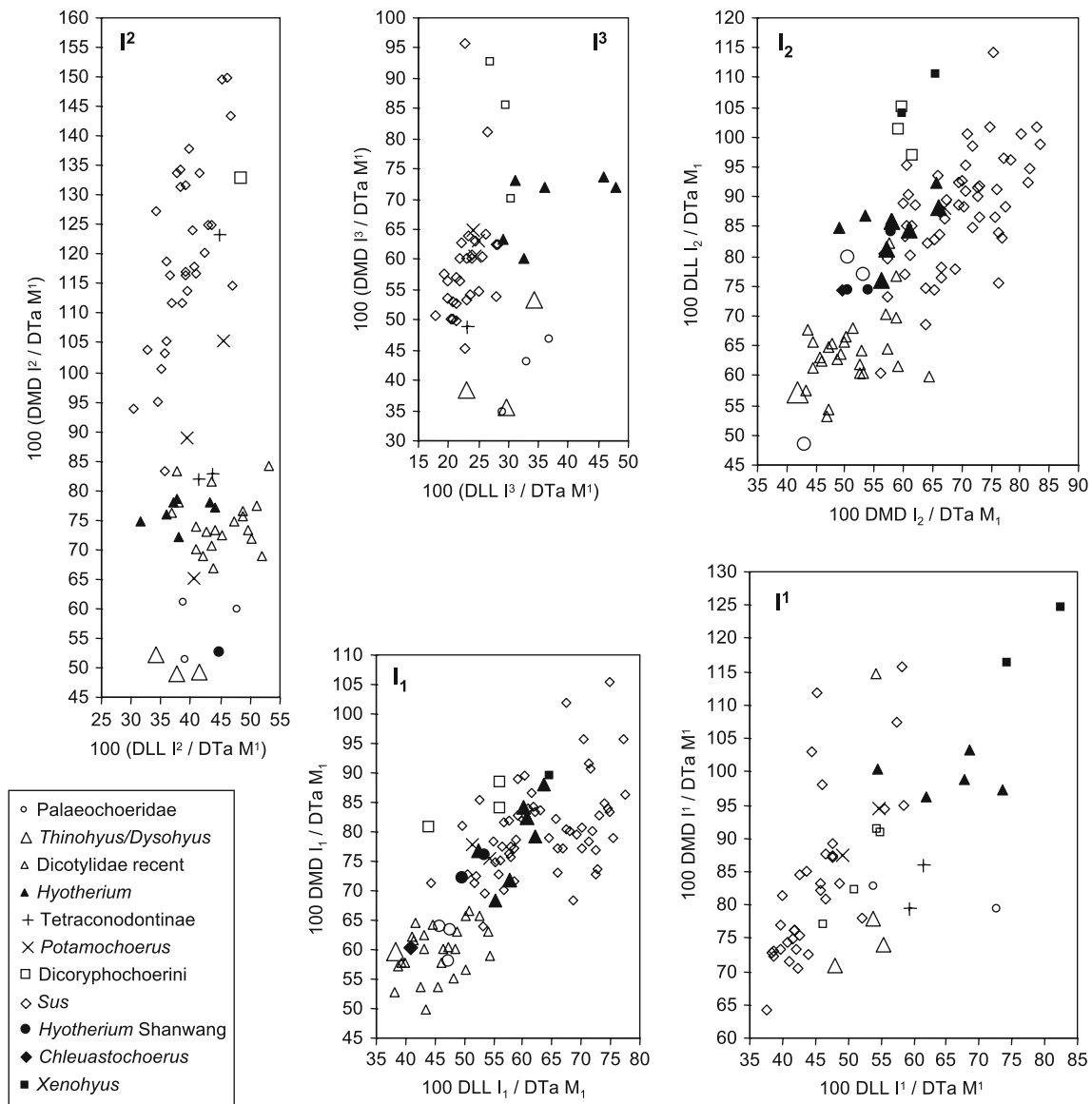
The **humerus** (Fig. 26A; Table 13) has a cylindrical distal articulation with a large radius of curvature and diameter at the lateral side (at the capitulum; diameters  $R_5$  and  $R_4$  of Van der Made 1996a: Fig. 19). It is large in comparison with the diameter at the crest near the middle of the articular surface ( $R_3$ ) and larger than at the constriction at the middle ( $R_2$ ):  $R_5 \sim R_4 \sim R_3$ ,  $R_5 \sim R_2$ ,

$R_4 > R_2$ , and  $R_5$  is only slightly smaller than  $R_1$  (at the medial side). In Ruminantia this is different:  $R_5 < R_4 > R_3$ ,  $R_5 < R_2$ ,  $R_4 < R_2$  and  $R_5 \ll R_1$ , whereas in recent *Sus scrofa*,  $R_5 > R_4 \sim R_3$  and  $R_5 \gg R_2$  and  $R_5$  is very close in size to  $R_1$ . The medial half of the articular surface is convex in transverse section as in recent *Sus scrofa*, whereas in the Palaeochoeridae it is concave and in Ruminantia the surface is much more convex than in the Suidae. In the Palaeochoeridae and Ruminantia, the ridge in the middle is more developed ( $R_3 > R_4$ ,  $R_3 > R_2$ ). In Listriodontinae (Van der Made 1996a: pl. 25 Fig. 1), the articular surface is more similar to that of the Palaeochoeridae than to *Sus scrofa*. The long axis of the shaft seem to be inclined medially in comparison with the axis of the cylinder of the distal trochlea. The medial epicondyle is well developed, resulting in a long DAPd. Within the Artiodactyla, marked differences are found in the proportions of the distal end of the humerus. This must have important biomechanical implications and is likely to reflect very different locomotory adaptations. However, these aspects have received little attention in the literature so far.

The proximal articular surface of the **radius** (Fig. 26B–C; Table 14) reflects the distal morphology of the humerus, but the differences are more difficult to describe metrically. The distal articular surface of the radius has well marked facets for the scaphoid and semilunar. The anterior borders of these facets do not curve much distally, and thus, unlike in *Sus scrofa*, do not create clear “stop facets”.

The **scaphoid** (Fig. 27I; Table 15) has an overall shape that is similar to that of *Sus scrofa*, with undulating or





**Fig. 19** The sizes of the upper and lower incisors of selected Suoidea as percentages of the width of the first lobe of the M<sup>1</sup> and M<sub>1</sub>, respectively, of the same individual and side. This is intended to “eliminate” body size. Palaeochoeridae including *Schizoporcorus sinapensis* from Sinap (MTA), *Taucanamo primum* from Els Casots (IPS), *Palaeochoerus typus* from St Gérard-le-Puy (MGL) and *P. aquensis* from the Quercy (MNCN); *Thinohyus lentus* from Roundhouse Rock (AMNH) and *Dyseoehyus stirtoni* from Observation Quarry (AMNH); Dicotyliidae including recent *Catagonus wagneri* (NMW), *Tayassu pecari* (ZMA) and *T. tajacu* (ZMA); *Hyotherium meisneri* from Cetina de Aragón (MNCN), Laugnac (UPM, MNHN), and Grépiac (cast MHNT), *H. major* from Ulm Westtangente (SMNS) and St Gérard-le-Puy (MNHN), *H. soemmeringi* from Sandelzhausen (BSPG), Buchental (PIMUZ); *Hyotherium* from Shanwang (cast

IVPP); *Chleuastochoerus stehlini* from Loc. 73 (IVPP); Tetraconodontinae including *Conohyus simorreensis* from Göriach (SLJG) and *Nyanzachoerus cookei* from Sahabi (USR); recent *Potamochoerus* (ZMA, MNCN); Dicoryphochoerini including *Propotamochoerus palaeochoerus* from Johnsdorf (SLJG), *Propotamochoerus* sp. from Samos (NMW) and Baccinello V3 (NMB), Hippopotamodon antiquus from Eppelsheim (HLD) and Middle Sinap (MNHN), *H. sivalensis* from the Siwaliks (IM); *Sus arvernensis* from Villafranca (NMB), *Sus brachygnathus* from Trinil (NNML) and recent *Sus celebensis* (ZMA, SMNS), *S. barbatus* (ZMA), *S. riukiuanus* (KU), *Sus florensianus* (ZMA) and *S. scrofa* (MNCN, NNML, ZMA, HUI, KU, CMH). *Xenohyus* I<sup>1</sup> from Pont Boutard (MNHN) and Chavaignes (MNHN) are used in combination with DT of the M<sup>1</sup> from Les Beilleaux (Ginsburg et al. 1988)

curving proximal and distal facets. However, the bone is more “elongate”, that is: it has a relatively long DAP. This is partly, but not only, caused by a posterior protuberance, which is hardly noticeable in the living species. The facets for the semilunar are less developed, while the lateral

projection of the proximal articular surface, that locks into a niche in the proximal articular surface of the semilunar, is more developed than in the recent species.

The **semilunar** (Fig. 27J; Table 15) is broadly similar to that of *Sus scrofa*, but has the above mentioned niche, for

the process of the scaphoid, in the proximal surface more developed. Also, in anterior view, the angle made by the facets for the unciform and magnum make a much sharper angle. In addition, these facets do not curve proximally at their anterior borders, whereas in *Sus scrofa* they do, forming a kind of “stop facet”.

The **ulnar** (Fig. 27H; Table 15) is again broadly similar to its homologue in *Sus scrofa*, but it is flatter, and the facets with the semilunar are less developed.

The **magnum** (Fig. 27F; Table 15) is in its general shape similar to that of *Sus scrofa*, but it is more elongate, that is: it has a longer DAP. In part this is caused by a posterior process, which at the distal side bears a continuation of the surface that articulates with the Mc III. In proximal view, the bone is narrower than in *Sus scrofa*, especially posteriorly, resulting in a triangular outline. In anterior view it looks narrower and higher. In these aspects it is more similar to the *Bunolistriodon* magnum (Van der Made 1996a: pl. 17 Fig. 7), while the *Listriodon* magnum tends to be a little more similar to that of *Sus scrofa* (Van der Made 1996a: pl. 43 Fig. 5; Van der Made 1998 b: pl. 2, Fig. 3). In anterior view, the facet for the semilunar is well separated from the facet for the Mc III by a facet for the unciform, whereas in *Chleuastochoerus* these facets meet nearly (and consequently, the magnum nearly does not articulate with the unciform; Pearson 1928). Observations in other suids, suggest that the latter character is probably variable.

The **unciform** (Fig. 27G; Table 15) is similar to that in *Sus scrofa*, but it is higher (compared with width) and its posterior process is much more developed. The facet for the ulnar slopes less laterally and is more curved at the

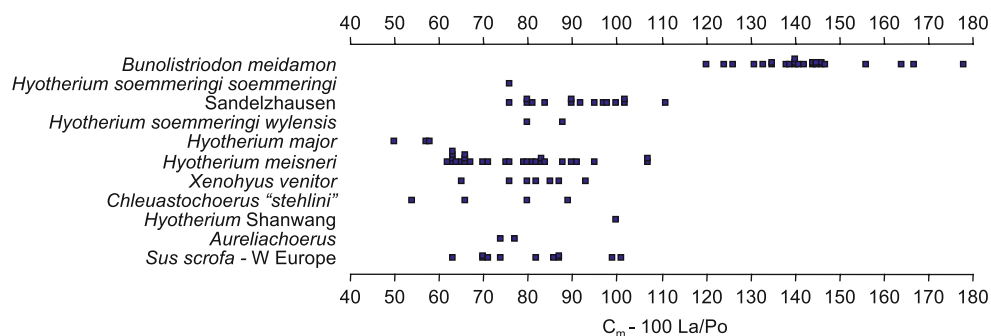
posterior side. The distal articular surface is a little flatter, or in other words, its radius of curvature is relatively longer. That holds also for the facet for the semilunar. The latter facet mirrors the “stop facet” morphology on the semilunar. All these differences from *Sus scrofa* are resemblances to the listriodont unciform (Van der Made 1996a: pl. 25, Fig. 4).

The **Mc III** (Fig. 28D; Table 16) is similar to that of *Sus scrofa*, but markedly more gracile (Fig. 29). Pearson (1928, Fig. 28) illustrated a fore leg of *Chleuastochoerus* from Locality 28 (numbers of “Lagrelus” localities; Kurtén 1952) and noted that the metacarpals were more robust than those of *Sus*, but unfortunately she did not give measurements. Figure 21 compares the robusticity index of the Mc III in a wider context; the higher the value of the index, the more gracile the metapodial. It can be seen that the Mc III of *H. soemmeringi* is gracile, even if compared with other species of the same genus, and in fact, it is gracile for any species of suid (Figs. 30, 31).

The posterior extension of the facet with the magnum gently curves and becomes inclined laterally, whereas in *S. scrofa*, the posterior extension of this facet has a greater inclination and is separated from the anterior part by a sharp angle.

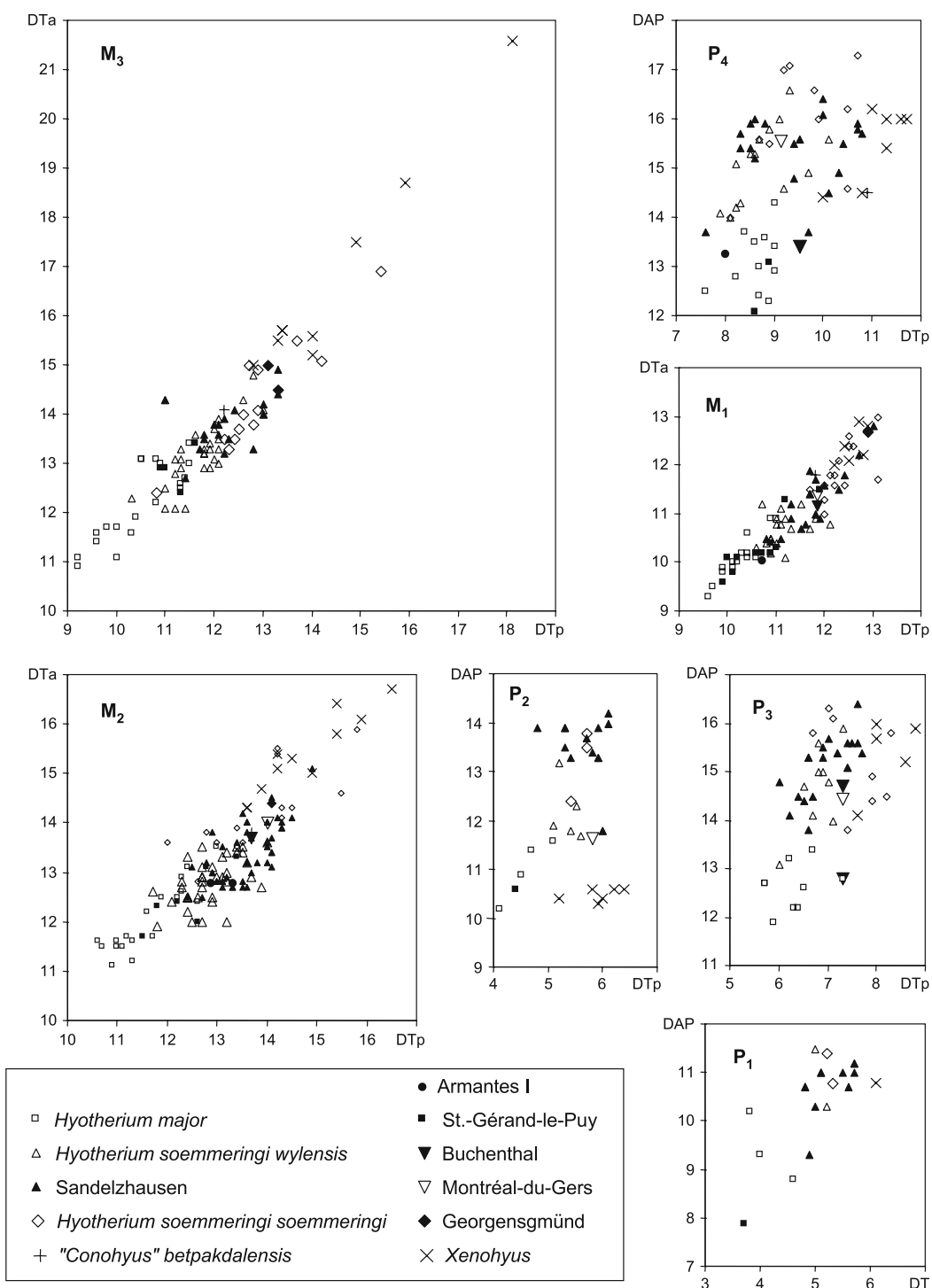
As the previous bone, the **Mc IV** (Fig. 28A; Table 16) is similar to that of *Sus scrofa* but more gracile, and in a wider context it is again a very gracile bone and definitely more gracile than in *Chleuastochoerus* from Locality 12 (Pearson 1928: Fig. 28).

The **Mc V** (Fig. 28F; Table 16) is recognized by its facets for the Mc IV and unciform. What remains of the



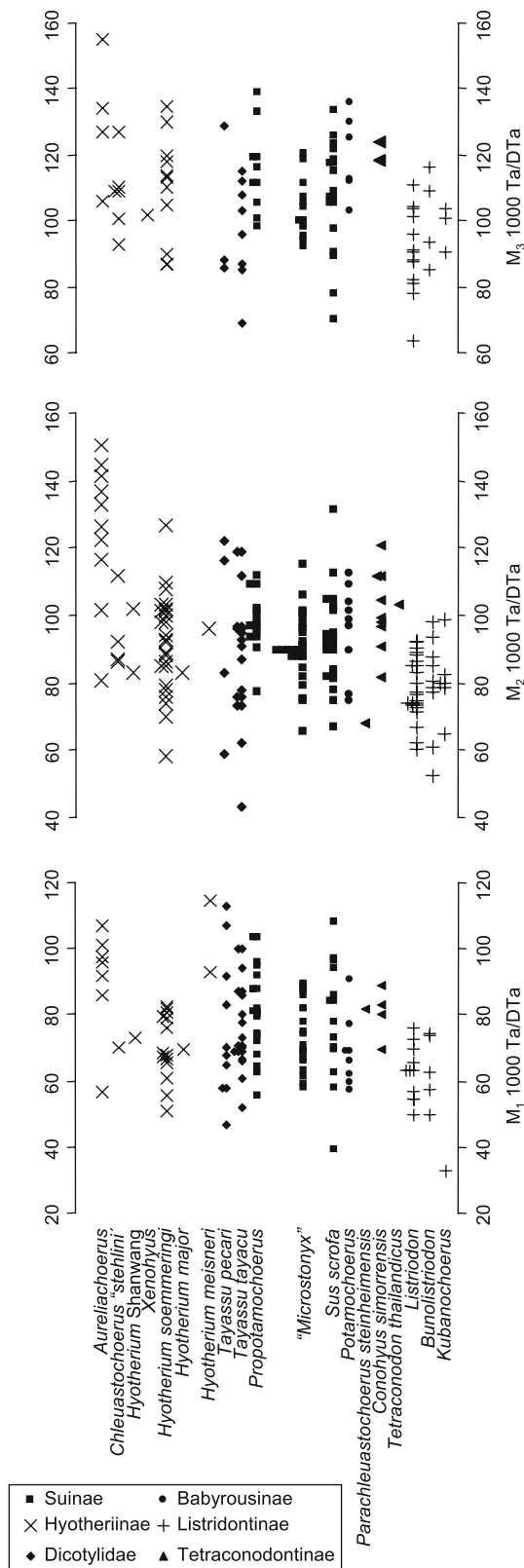
**Fig. 20** The section of the male lower canines of selected Suoidea as described by the index 100La/Po. Canines with values below 100 are of the “scrofic” type whereas those with values over 100 are called “verrucose”. An extreme “verrucose” form is *Bunolistriodon meidamon*. *Sus scrofa* from western Europe (ZMA, MNCN, NNML, UPVB, HUI); *Aureliachoerus minus* from Wintershof West (BSPG) and *A. aurelianensis* from Chilleurs-aux-Bois (MSNO); *Hyotherium* from Shanwang (cast IVPP); *Chleuastochoerus stehlini* from Locality 73 (IVPP), Baodea (IVPP), Lufeng (IVPP);

(UPM) and the Faluns du Touraine et de l’Anjou (MNHN); *Hyotherium meisneri* from Laugnac (UPM; MNHN; UCBL), Montaignu (NMB), Cetina (MNCN), Budenheim (HLD); Hessler (FISF) and Colomiers (CFE); *H. major* from Ulm Westtangente (SMNS) and St Gérard-le-Puy (SMNS); *H. soemmeringi wylensis* from Baigneaux-en-Beauce (NMB, MGL) and Sandelzhausen (BSPG); *H. s. soemmeringi* from Münzenberg (SLJG); *Bunolistriodon meidamon* from Pasalar (PDTFAU, PIMUZ)



**Fig. 21** Bivariate diagrams of the lower cheek teeth of selected Hyotheriinae: *Hyotherium major* from St Gérard-le-Puy (MNHN, NHM, MGL, MHNT), and from Ulm-Westtangente (SMNS), Weisenau (FISF), Langi (NMB) and Servilly (MGL); *H. soemmeringi wylensis* from Buchenthal (PIMUZ), from Montréal (Orliac et al. 2006), from Armantes I (IVAU), from Hohe Rone (PIMUZ), Valdemoros 3a (IVAU), Munébrega (IVAU), Pellecahus (NMB), Baigneaux-en-Beauce (NMB, MGL, MSNO) and Pontlevoy (MNHN) and from Sandelzhausen (BSPG); *H. soemmeringi soemmeringi* from Georgensgmünd (FISF, NMW) and from Hüllistein (PIMUZ),

Kalkgrube Schwanberg (SLJG), Seegraben (SLJG, IGL), Münzenberg (SLJG), Fohnsdorf (SLJG), Vordersdorf (NMW), Labitschberg (SLJG), Gamlitz (IPUW), Feisternitz (SLJG), Engelswies (NMB), Ar. da Lobeira (UNL), Quinta do Farinheira (UNL), Olival Susana (UNL), Stätzing (BSPG, NMB), Thannhausen (BSPG) and Neudorf Spalte (NMW); *Xenohyus betpakdalensis* from Betpakdala (PIN); *X. venitor* and *Xenohyus* sp. from Lagnac (UPM, MNHN), and from various localities of the Faluns de Touraine et de l'Anjou (MNHN), Brüttelen (NMB) and Loranca (MNCN)



bone suggests that it was gracile, as is definitively the case with the central metacarpals. The distal articulation is not preserved, but its morphology is expected to be similar for

◀ **Fig. 22** Enamel thickness in the lower molars as indicated by the index 1000Ta/DTa: *Kubanochoerus massai* from Gebel Zelten (MNHN; Van der Made 1996a); *Bunolistriodon adelli* from Armantes I and Munébrega I, *B. lockharti* from Chevilly, "Orléans", Araya, Pontlevoy and Avaray and *B. guptai* from locs. HGSP 8311 and 8412 in Pakistan (IVAUA, MSNO, MNHN; Van der Made 1996); *Listriodon pentapotamiae* from HGSP 8122 and 8304 and from the Chinji Fm. (IVAUA) and *L. splendens* from Paracuellos III and V, Arroyo del Val IV, Manchones I, Wien Heiligenstadt, Escanebrabe, Wartenberg, Merisor, Larroque de Magnoac, Sóoskut, Çandır, Klein Hadersdorf, Villefranche d'Astarac and "Gers" (MNHN, MNCN, IVAUA, NNML, NMW, HGSB, MTA, IPUW; Van der Made 1996); *Tetraconodon thailandicus* from Ban San Klang (LPVM); *Conohyus simorrensis* from Przeworno (ISEAK); recent *Potamochoerus* (ZMA, EDB), recent *Sus scrofa vittatus* from Deli at Sumatra (ZMA); "Microstonyx" from Grebeniki, Stratzing, Maragha, Csakvar, Samos, Pikermi, Chomateri, Baltavar and Polgardi (VMM, NMW, HGSB, NHM, MSNO, IPUW, HGSB); *Propotamochoerus* from Doué-la-Fontaine, Mariatal, Vösendorf, Magersdorf, Gross Mugl, Wien III Belvédère, Henersdorf, Rudabánya, Grytsev (MNHN, NMW, IPUW, NMNHK, HGSB, MNHN); recent *Tayassu tajacu* and *T. pecari* (ZMA); *Hyotherium meisneri* from Cetina de Aragón (MNCN), *H. major* from St Gérard-le-Puy (NHM); *H. soemmeringi* from Sandelzhausen, Fohnsdorf, Gamlitz, Labitschberg, Feisternitz, Münzenberg, Seegraben, Ameis and Pontlevoy (BSPG; SLJG, IGL, IPUW, MNHN), *Xenohyus* from Loranca sands (MNCN), *Hyotherium* from Shanwang (cast IVPP); *Chleuastochoerus stehlini* from Loc. 73 (IVPP); *Aureliachoerus minus* from Petersbuch 2, Can Canals and Costa Blanca (BSPG, IPS) and *A. aurelianensis* from Fay-aux-Loges, Chilleurs, Agreda, Tuchorice and Artenay (MSNO, NHM, MNCN, NMW)

all abaxial ("lateral") metacarpals and metatarsals, and is known on specimens without connection to the proximal parts (Fig. 28B; Table 16).

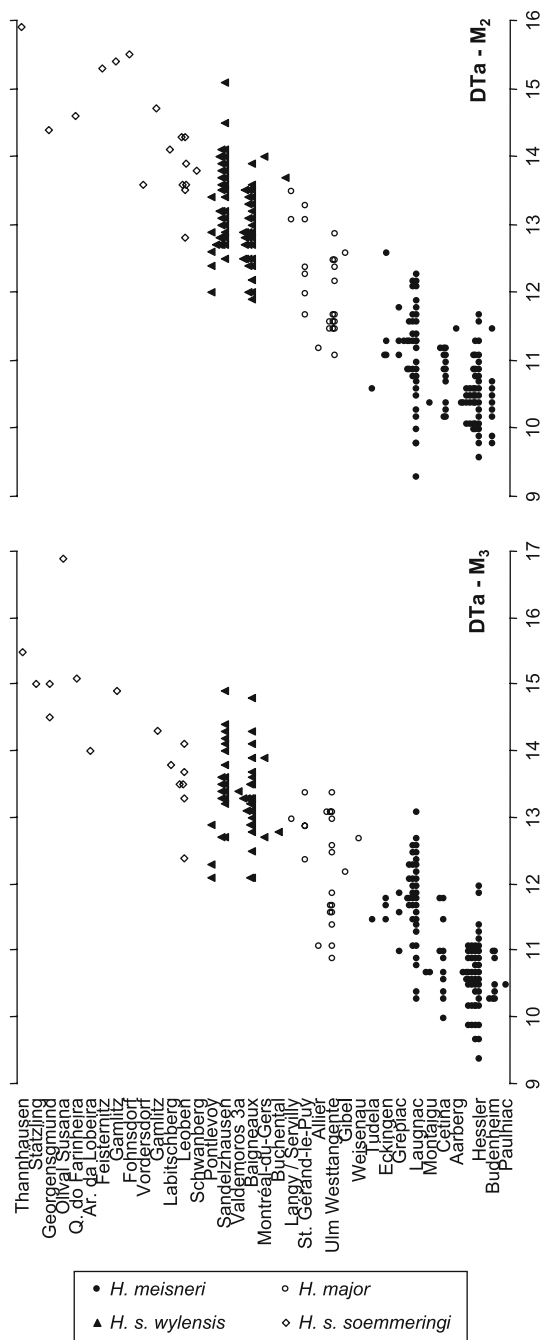
The **tibia** (Table 17) is similar to the tibia in *Sus scrofa*. Because no complete specimen is available, it is not possible to know whether the bone was more gracile than in the latter species.

The **fibula** (Fig. 26F; Table 17) illustrated is of a juvenile and the distal part is not fused to the shaft. The bone resembles its homologue in *Sus scrofa*.

The **calcaneum** (Fig. 26E; Table 19) is similar to that of *Sus scrofa*. The specimen described and illustrated by Leinders (1976) as belonging to "*Listriodon lockharti*", belongs to *Hyotherium soemmeringi*. The differences from the calcaneum of *Sus scrofa* noted by that author might be because of variability.

The **astragalus** (Figs. 26G, 30; Table 18) is, in general structure, similar to that of *Sus scrofa*. The sustentacular facet is convex in transverse section and is bordered by a ridge over which it extends. As a result, there is a proximo-distal depression in the sustentacular facet. In the Listriodontinae, the facet tends to be flat in transverse section and the ridge nearly not developed.

Dehm (1934) and Leinders (1976) compared the morphology of the astragalus of *Listriodon* with that of *Sus*



**Fig. 23** The size of the M<sub>2-3</sub> in the different samples of *Hyotherium*. The localities are arranged in approximate order from old (bottom) to young (top), but in any case with the localities of *H. meisneri* below: Paulhiac (NMB), Budenheim (HLD, FISF), Hessler (FISF), Cetina de Aragón (MNCN, IPS), Eckingen (NMB), Grépiac (MHNT), Montaigu (NMB), Laugnac (UPM, MNHN, NMB), Tudela (IPS), Weisenau (FSIF), Gibel (cast MNHN), Ulm Westtangente (SMNS), Allier (NHM), St Gérard-le-Puy (MNHN, NHM, MGL), Langy and Servilly (NMB, MGL), Buchental (PIMUZ), Montréal-du-Gers (Orliac et al. 2006), Baigneaux-en-Beauce (NMB, MGL, MSNO), Valdemoros 3a (IVA), Sandelzhausen (BSPG), Leoben (Seegraben, SLJG, IGL and Münzenberg, SLJG), Labitschberg (SLJG), Vordersdorf (NMW), Fohnsdorf (SLJG), Gamlitz (IPUW), Feisternitz (SLJG), Ar. da Lobeira (UNL), Quinta do Farinheira (UNL), Olival Susana (UNL), Georgenmünd (FISF), Stätzing (NMB), Thannhausen (BSPG)

*scrofa*. They paid attention to two or three features. One is the width of the facet for the cuboid. Leinders calculated the index  $P = 100(\text{width of the cuboid facet}/\text{width of the distal trochlea})$  and gave two values for *Sus* (40 and 44), one for *Tayassu tajacu* (37), two for *Listriodon splendens* (29 and 31), and one for “*Listriodon lockharti*” (34). These values for are *H. soemmeringi* from Sandelzhausen 27–38 ( $n = 24$ ) and from Baigneaux 35–37 ( $n = 2$ ; NMB, MGL), for *H. meisneri* from Laugnac 32–43 ( $n = 19$ ; UPM), for *Listriodon splendens* from Europe 29–44 ( $n = 32$ ; data from Van der Made 1996a), for *Bunolistriodon lockharti* from Europe 33–41 ( $n = 19$ ; data from Van der Made 1996a) and for *Taucanamo* from Sansan 31–40 ( $n = 17$ ; MNHN, MHNT, NMB). It is obvious that the values given by Leinders for *L. splendens* are in the lower ranges and those for *Sus scrofa* in the upper ranges of the values of a much larger sample of *L. splendens*. Although there may be some differences among the different species, they are very small (at least among the Miocene suoids considered here), and the overlap of the ranges is large, whenever the samples are large. Even if the differences between some of the species turn out to be real, their value for phylogenetic, biomechanical, and ecological interpretations is limited.

The second character is the shape of the sustentacular facet, which extends at its median side over a ridge in *Sus scrofa* but which is without a median ridge in *Listriodon*. The specimen assigned by Leinders to “*Listriodon lockharti*”, belongs to *Hyotherium soemmeringi*. It is more like *Sus scrofa* in this respect and this is also the case in the specimens from Sandelzhausen.

A third character was noted by Dehm (1934) but was given no further importance by Leinders (1976): the aforementioned ridge next to the sustentacular facet continues proximally and connects to the median elevation of the trochlea tibiae in *Sus*. This morphology is found in other Suinae, but not in the Hyotheriinae and Listriodontinae.

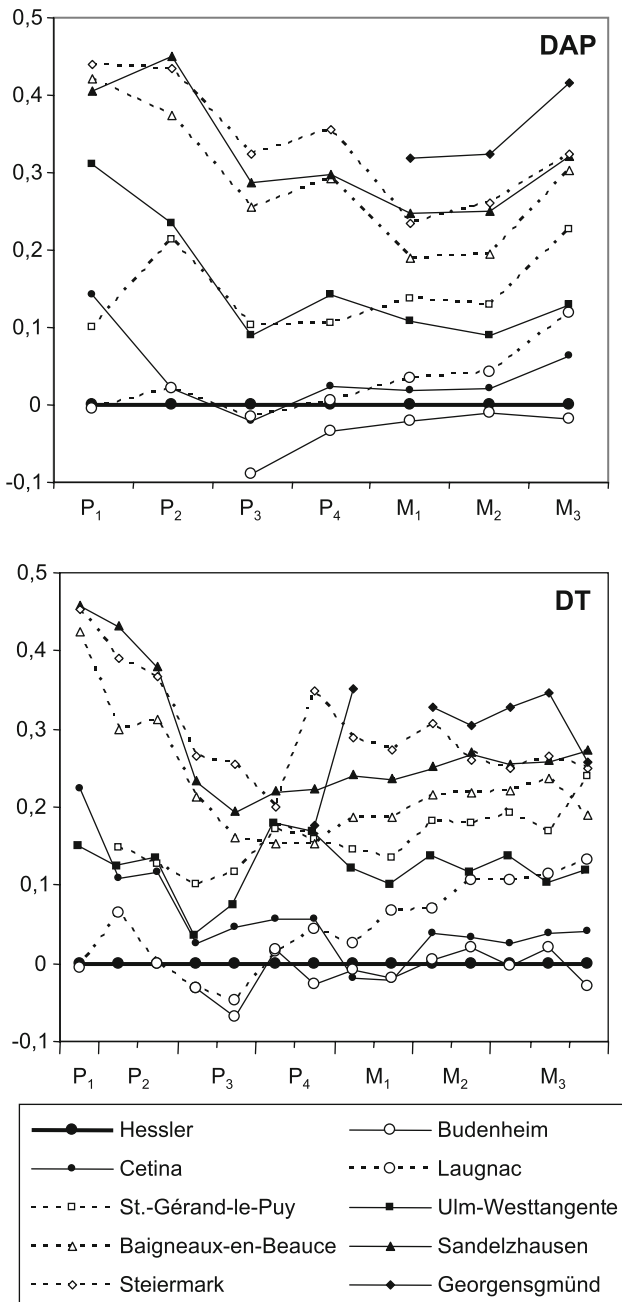
The **navicular** (Fig. 26H; Table 20) is similar to that of *Sus scrofa*. Maybe the posterior process is a little more developed.

The **cuboid** (Fig. 26D; Table 20) is similar to that of *Sus scrofa*, but is much higher (the proximo–distal dimensions are greater).

The **cuneiform III** (Fig. 26I; Table 20) is a very small and simple bone and does not show many characters.

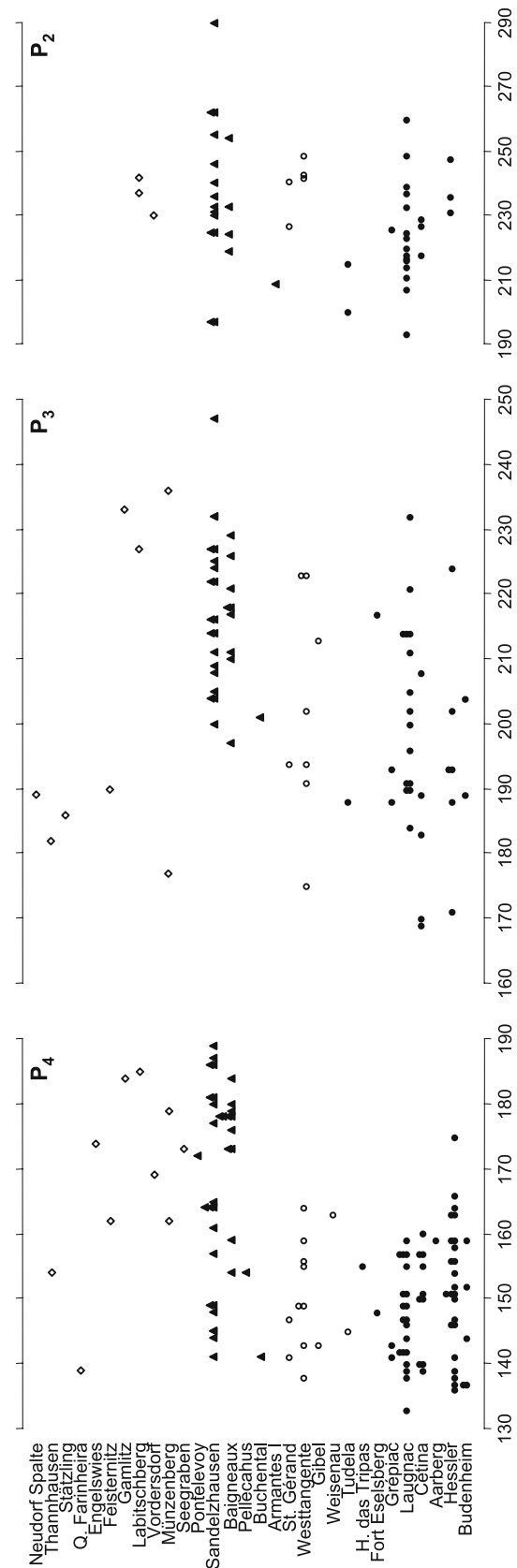
The **Mt II** (Table 16) resembles that of *Sus scrofa*.

The **Mt IV** (Fig. 28E; Table 16) is represented by proximal parts which suggest that it was a gracile bone, although it is not possible to quantify this with a value of the robusticity index. Pearson (1928, Fig. 27) noted that the central metatarsals of a hind leg of *Chleuastochoerus* from Locality 49 are robust, but the figure shows them to be relatively gracile, or at least much more gracile than the



**Fig. 24** Comparison of the proportions of the lower cheek teeth of different samples of *Hyotherium*. DT indicates maximum DT for P<sub>1</sub>, DTa and DTp for the remaining teeth, and DTpp for the M<sub>3</sub>. The value indicated for each cheek tooth is ln(average sample/average standard). The standard is the sample of *Hyotherium meisneri* from Hessler. “Steiermark” refers to all localities with *Hyotherium* studied by Van der Made (1998a): Seegraben, Münzenberg, Fohnsdorf, Vordersdorf, Zangal, Eibiswald, Ameis, Labitschberg, Schönegg, Hochtregist, St Peter and Kalkgrub bei Schwanberg; provenance of data as in Fig. 23

metacarpals from Loc. 12 (Pearson’s Fig. 28). The proximal part of the Mt IV from Sandelzhausen is similar to that in *Sus scrofa*.



**Fig. 25** Elongation of the lower premolars in *Hyotherium* as indicated by the index 100DAP/DTp; provenance of data as in Fig. 23

The **Mt V** (Fig. 28C; Table 16) has a relatively large posterior process at the proximal end. Its shaft is much more slender than in *Sus scrofa*.

The **first phalanx III/IV**, or first axial or central phalanx, has a morphology of the proximal articulation that is common in Suidae and different from that in Palaeochoeridae (see description of *S. muenzenbergensis* and compare with Fig. 5C). In all other aspects it is also a typical suid phalanx. Differences in the degree of robusticity suggest that some were of the *manus* (Fig. 27B; Table 21) and others of the *pes* (Fig. 27D; Table 21), and even in the bivariate diagram (Fig. 31) there are two clusters one of more gracile and another of more robust specimens. According to different locomotory adaptations of a species, the phalanges in the *manus* are larger or more robust than those of the *pes*, of equal size or robusticity, or smaller. However, more comparisons of the material from Sandelzhausen should establish whether the apparent separation in the diagram might correspond to a separation of manual and pedal phalanges. In any case, the phalanges are relatively gracile within the Suidae, although they are more robust than the phalanges of the Palaeochoeridae. This observation mirrors the observations made on the metapodials.

The **first phalanx III/IV**, or first abaxial phalanx, (Fig. 27C; Table 21) is similar in morphology to the first central phalanx, but differs in the shape of the proximal surface, which does not have a well marked dorso–plantar groove in the middle. It is also much smaller. Pearson (1928) noted that the lateral digits are more slender and in the hind foot also more shorter in *Chleuastochoerus* than in *Sus*. Also in living peccaries the side toes are reduced. A way to quantify such observations would be to compare the average measurements of the lateral and central phalanges of samples such as that from Sandelzhausen, but at present few or no comparative data are available.

The **second phalanx III/IV** (Fig. 27E; Table 22) is broadly similar to that of *Sus scrofa*, but it is, like the first phalanx, more gracile. This is caused not only by a greater length, but also the width is smaller in comparison with the antero–posterior diameter. In side view, the greater length of this phalanx makes the constriction on the middle less striking. The radius of curvature of the proximal and distal articular surfaces seems greater compared with the other dimensions of the bone, than in *Sus scrofa*. In distal view, the distal articular surface is separated in a large abaxial and a smaller axial half by a sharp furrow. In *Hyotherium*, this furrow makes a large angle with the plantar surface, whereas in *Sus scrofa* the angle is much sharper. The ridge that divides the proximal articulation into two halves is much more elevated in *Hyotherium* than in *Sus scrofa*.

In most of these features, the *Hyotherium* phalanges resemble those of *Dorcatherium*, which is also present at

Sandelzhausen. The larger *Dorcatherium* phalanges are close to those of *Hyotherium*. The following traits were used to separate the phalanges of these two genera. The proximal articular facet has convex axial and abaxial borders in *Hyotherium*, whereas in *Dorcatherium* the lower or plantar parts of these borders tend to be straighter and parallel. At the plantar side of this facet there is the “plateau post-articulaire” (in the sense of Heintz 1970). In *Hyotherium* this plateau has a hump or process at the abaxial side whereas in *Dorcatherium* there are subequal humps at the axial and abaxial sides, separated by a depression.

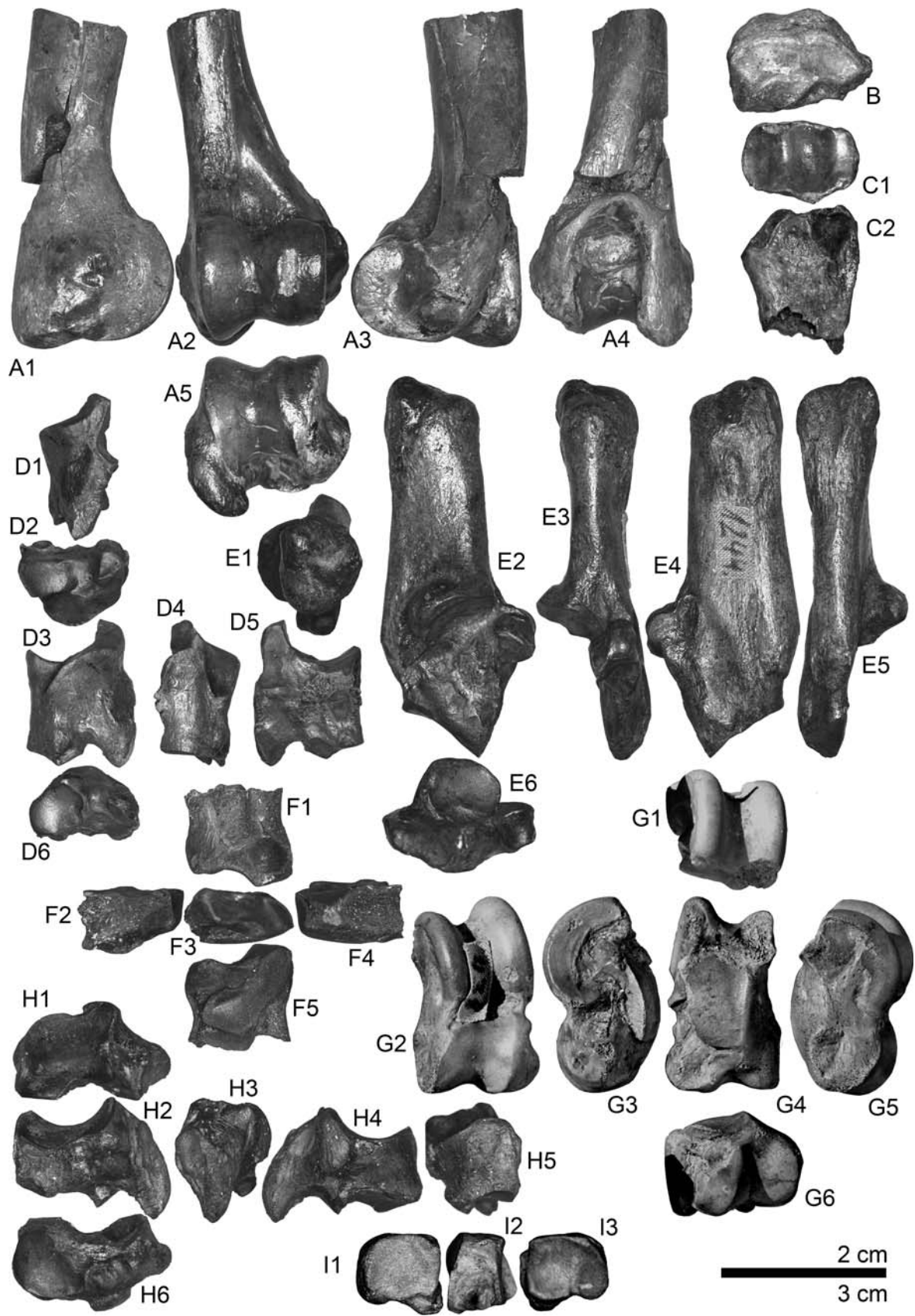
The **third phalanx III/IV** (Fig. 27A; Table 23) has a typical suid morphology, but compared with *Sus scrofa* it is elongate and the width is great in comparison with the antero–posterior diameter.

The **second phalanx II/V** (Table 22) and third phalanx II/V (Table 23) have overall shapes that are similar to the shapes of the central phalanges, but they are smaller and their articular surfaces tend to be flatter.

## Remarks

Part of the collection from Sandelzhausen was described before and assigned to *Hyotherium soemmeringi* Schmidt-Kittler (1971). This assignment was later confirmed by Dehm (1980), Van der Made (1990b), Hellmund (1991a), and Fortelius et al. (1996); still later the material was assigned to *H. soemmeringi wylensis* (Von Meyer 1866) (Van der Made 1998a). However, the name was already introduced by Von Meyer (1859), who described one specimen (which belonged to a male and which can be identified as specimen A/V85 in the PIMUZ) as *Hyotherium medium* and another which belonged to a female and can be identified as A/V82) as *Sus (Palaeohyus) Wylensis*. He also gave a short description and comparison which he considered to be a diagnosis. This implies that all requirements in the sense of the ICZN (1999) for the specific name to be available are met, and that the only specimen assigned to this species is to be regarded as the holotype. Although initially assigned to a different species, the other specimen (A/V85) and additional material from the same locality in the PIMUZ (A/V84, 86, 83) belong to the same taxon.

Von Meyer (1859, 1866) placed “wylensis” in the subgenus *Palaeohyus*. Roger (1887, p. 92) listed *Paläohyus Maraghanus* Pohl. whereas Pohlig (1885) listed *Palaeohyus maraghanus* Pohl. and gave some comments, but did not refer to an earlier description of this suid. I am not aware of other cases where the name *Palaeohyus* (or a variant) is used, and it seems thus that Von Meyer (1859) named not only a species but also the subgenus *Palaeohyus*. If this is the case, the type species is *Sus (Palaeohyus) wylensis*.





◀ **Fig. 26** *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...). **A** 16224 left humerus, distal end: 1 medial, 2 anterior, 3 lateral, 4 posterior, and 5 distal views; **B** 16225 left radius: distal view; **C** 16240 right radius: 1 proximal, and 2 posterior view; **D** 16226 left cuboid: 1 posterior, 2 proximal, 3 lateral, 4 anterior, 5 medial, and 6 distal views; **E** 8834 left calcaneum: 1 proximal, 2 medial, 3 anterior, 4 lateral, 5 posterior, and 6 distal views; **F** 16241 right distal fibula (juvenile): 1 lateral, 2 posterior, 3 distal, 4 anterior, and 5 medial views; **G** 8817 left astragalus: 1 proximal, 2 anterior, 3 lateral, 4 posterior, 5 medial, and 6 distal views; **H** 16242 left navicular: 1 proximal, 2 lateral, 3 posterior, 4 medial, 5 anterior, and 6 distal views; **I** 16243 left cuneiform III: 1 proximal, 2 posterior, and 3 distal views. The scale bar represents 2 cm for **F**, **H**, **I** and 3 cm for **A–E**, **G**

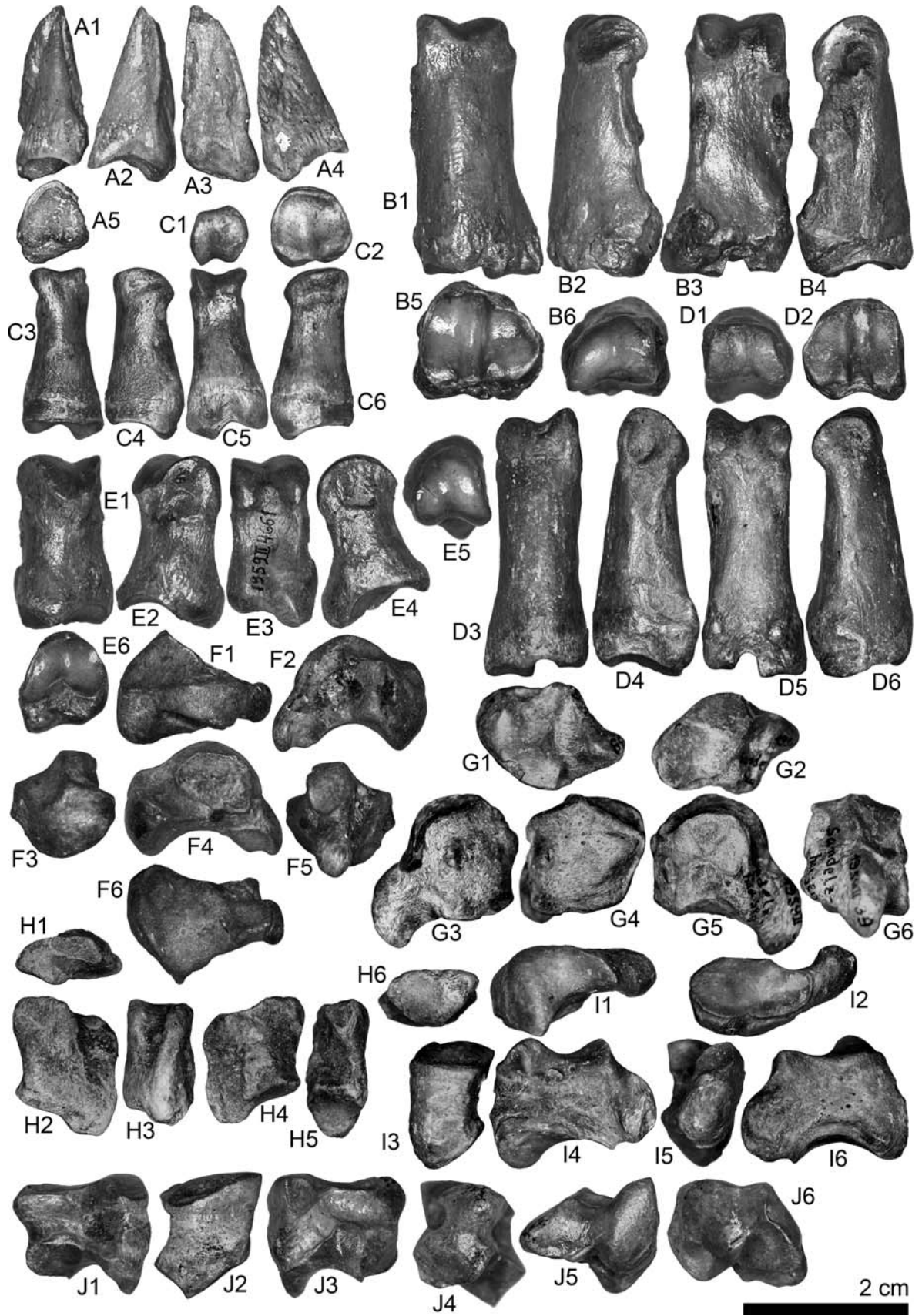
Because this taxon is included here as a subspecies within *Hyotherium soemmeringi*, the subgenus *Palaeohyus* becomes a junior synonym of *Hyotherium*.

Golpe-Posse (1972) introduced the name *Conohyus cuspidatus* for material from Armantes I. The holotype is a right  $M_2$  (IVAUA 41/541; cast IPS 1240) and the two syntypes are a left  $M^3$  (IVAUA Mun 5, IPS 1279 cast) and a  $P^4$  (IVAUA Mun 6, IPS 1283 cast) both from Munébrega AB. A formal diagnosis was given. The holotype and first lectotype were illustrated. The name is available. Later, different opinions were expressed on the type material. On the one hand, the lectotype  $P^4$  was illustrated as *Listriodon lockharti* (Leinders 1975: pl. 2 Fig. 3). On the other, the material was indicated belonging to *Hyotherium*, and it was indicated that neither *Bunolistriodon lockharti* nor *Conohyus* are present in these two localities, nor in other localities of the Calatayud area (Van der Made 1990a, 1996a). However, *Hyotherium soemmeringi* is common in these localities. It is present in Armantes I (additional specimens in IVAUA), Munébrega AB (additional specimens in IVAUA), Munébrega 1 (IVAUA), Munébrega 2 (IVAUA), Torralba 2 (MNCN), Torralba 4 (IVAUA), Valdemoros 3A (IVAUA), and Valdemoros 3C (IVAUA). The other suid that occurs in these localities is *Bunolistriodon adelli* (Van der Made 1996a). Typical morphological traits can be observed in the material, for example  $I^1$  with a distal cusplet (IVAUA Mun 13), morphology of the  $I^3$ ,  $P_4$  and  $P^4$ , molars, etc. The size of the specimens from Armantes I and Munébrega AB varies between the mean to above the upper end of the variation of material from St Gérard-le-Puy, between the mean and lower end of variation of the sample from Sandelzhausen, and is clearly smaller than the specimens from Georgensgmünd (Van der Made 1998a: Fig. 8). *Conohyus cuspidatus* is an available name for a form that is morphologically similar to typical *Hyotherium soemmeringi* although a little smaller, and is considered here a synonym of *H. s. wylensis* (Von Meyer 1859).

Orliac et al. (2006) used the name *Hyotherium lacaillei* for material from a locality that is indicated in the literature

with the names Montréal-du-Gers and Beón I. This is a late MN4 locality, which is only very slightly older than Armantes I, Munébrega AB, and the other localities of the Calatayud area. The diagnosis is given as: “*Hyotherium* with complete and continuous row of upper and lower cheek teeth;  $I^1$  with distal cusplet;  $P^1$  located lingually to canine alveolus; upper premolars globular in their anterior part;  $M^1$  without buccal cingulum”. These five characters will be discussed below, with another one.

1. *Hyotherium* with complete and continuous row of upper and lower cheek teeth. No *Hyotherium* species is known that lost premolars through reduction, but the description and discussion suggests that the lack of diastemas C-P1 and P1-2 is meant. The observation is based on a maxilla that is broken precisely in this area (compare photograph Fig. 2-1 with reconstruction Fig. 6B) and a mandible of the same individual, a female. A one-to-one comparison with one specimen of a male from Sandelzhausen is made (Fig. 6A). However, it is known that the size of the diastemas in recent pigs is subject to sexual bimodality and ontogenetic age and is variable even in a sample of individuals of the same sex and age (Van der Made 1991; Hellmund 1991b). For instance, recent *Sus scrofa vittatus* were reported to have C-P<sub>1</sub> diastemas in the ranges 0.6–6.3 (mean 3.5) in adult females and 0.0–7.8 (mean 5.3) in adult males. For the P<sub>1</sub>–P<sub>2</sub> diastema the values are: 0.0–2.1–7.3 in the adult females and 1.0–5.6–12.7 in the adult males (Van der Made 1991: Table 2). Orliac et al. (2006) did not give measurements for the diastema, but the largest diastemas I have observed in the Sandelzhausen sample are in the order of 5 mm, so that the greatest differences observed fit easily in the variation observed in a single *Sus scrofa* population. Therefore the diastemas are no grounds to recognize a new species.
2.  $I^1$  with distal cusplet. The large amount of material of *Hyotherium meisneri* and *H. major* included in this study shows that a small cusplet in the distal part of the postcrista of the  $I^1$  is occasionally present in those species. In *Hyotherium soemmeringi* it is always present and usually well developed. The development of the distal cusp in Montréal-du-Gers is as is expected in an early *Hyotherium soemmeringi*.
3.  $P^1$  located lingually to canine alveolus. The position of the  $P^1$  is lingual to the canine alveolus in the specimen from Montréal, while it is said to be behind the canine in the specimen from Sandelzhausen that was used for comparison. However, in Fig. 6 of Orliac et al. (2006) it can be seen that in both cases, the  $P^1$  is situated lingual to the canine, but that in Sandelzhausen, it is, in addition, behind the canine. This means that essentially



◀ **Fig. 27** Phalanges and carpals of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...). **A** 16229 third central phalanx, left of the axis of the foot: 1) dorsal, 2 axial, 3 plantar, 4 lateral, and 5 proximal views; **B** 16230 first central phalanx, right of the axis of the foot: 1 dorsal, 2 abaxial, 3 plantar, 4 axial, 5 proximal, and 6 distal views; **C** 16221 first abaxial phalanx, right of the axis of the foot: 1 distal, 2 proximal, 3 dorsal, 4 abaxial, 5 plantar, and 6 axial views; **D** 16231 first central or axial phalanx, left of the axis of the manus: 1 distal, 2 proximal, 3 dorsal, 4 axial, 5 plantar, and 6 abaxial views; **E** 4661 s central phalanx left of the axis of the foot: 1 dorsal, 2 axial, 3 plantar, 4 abaxial, 5 distal, and 6 proximal views; **F** 16222 left magnum: 1 proximal, 2 medial, 3 anterior, 4 lateral, 5 posterior, and 6 distal views; **G** 38 right unciform: 1 distal, 2 proximal, 3 lateral, 4 anterior, 5 medial, and 6 posterior views; **H** 16232 left ulnar: 1 proximal, 2 lateral, 3 posterior, 4 medial, 5 anterior, and 6 distal views; **I** 16233 right scaphoid: 1 proximal, 2 distal, 3 anterior, 4 lateral, 5 posterior, and 6 medial views; **J** 16234 left semilunar: 1 medial, 2 anterior, 3 lateral, 4 posterior, 5 proximal, and 6 distal views. The scale bar represents 2 cm for all figures

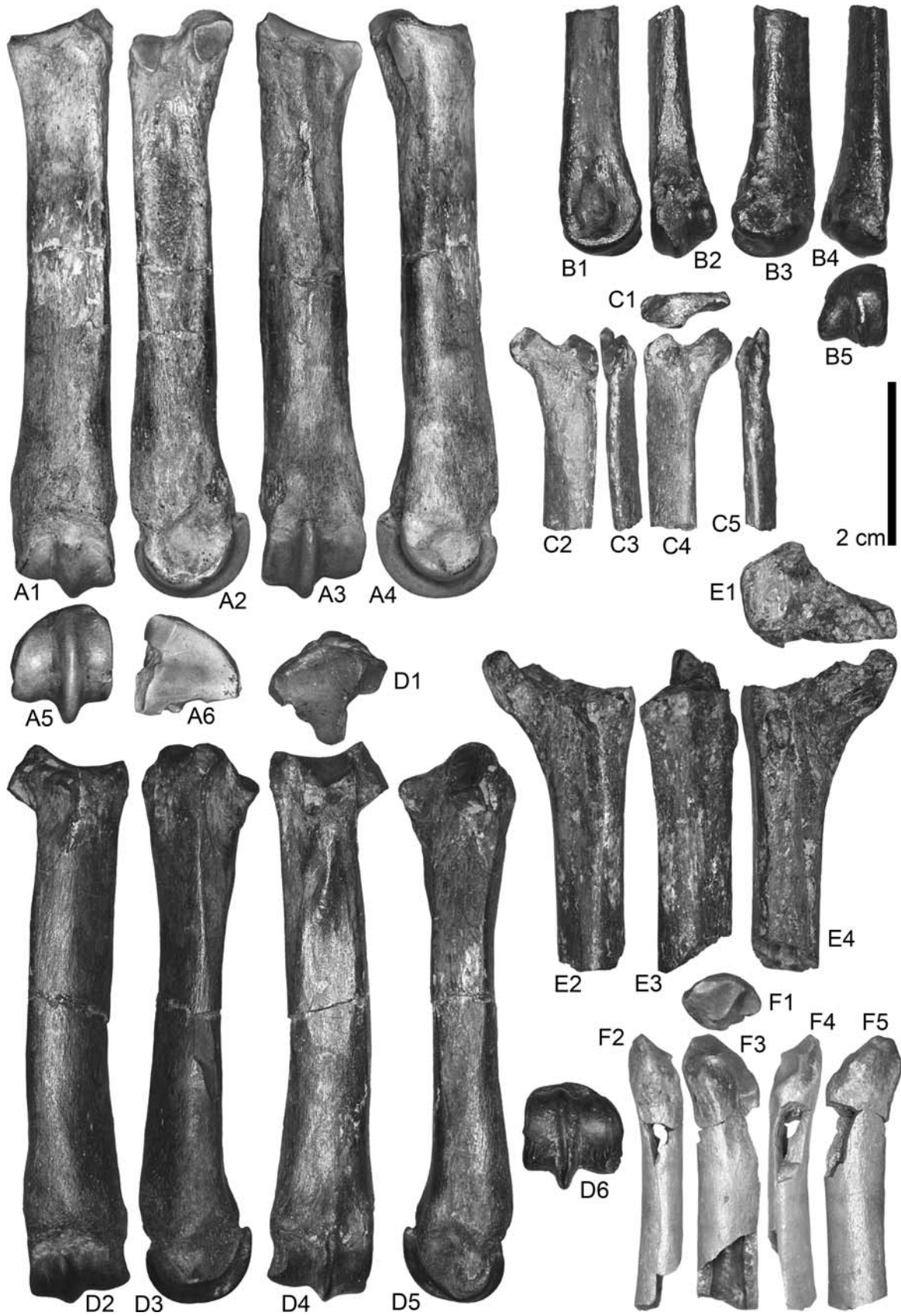
there is no difference in the position lingual to the canine, but that this position shows up because of a short diastema, which is a character that has been discussed already. In fact, if one studies the diastemas in recent pigs, one may observe that there are specimens in which the P<sup>1</sup> is situated lingually of the canine and as far forwards. One may observe resorption on the roots of the premolars and even loss of the P<sup>1</sup> because of this lack of space. In Fig. 6B of Orliac et al., solid and stippled lines are used, suggesting that the stippled lines indicate parts that are reconstructed and solid lines the actually observed morphology. However, a comparison with photograph Fig. 2-1 shows that some of the parts drawn as solid lines are absent in the specimen. This is precisely in the canine area. On the basis of the associated mandible, the individual is assumed to be female, but a large alveolus is drawn, as if for the canine of a male, and not the narrow or even “8-shaped” alveolus that is expected for a C<sup>f</sup> with two roots that are connected, though having a deep groove between them. All this suggests that the size and position of the canine is less well known than the authors claim.

4. Upper premolars globular in their anterior part. This is based on the left upper premolars of a single individual, which probably is again compared with the same specimen from Sandelzhausen. However, the large Sandelzhausen sample includes more globular (e.g. Fig. 14D) and more slender specimens (Fig. 14I).
5. M<sup>1</sup> without buccal cingulum. Note that on page 696, the authors state: “the lack of buccal cingulum in upper molars”. They use plural, whereas their observation is based on a single specimen. The published

photograph does not even allow good observation of this, but suggests a slight bulge of the base of the buccal side, which would be like a cingulum, but less well developed. Like any character, the development of cingula is variable.

6. In the discussion, the authors say that the material from Montréal has more slender lower and upper premolars, with a more developed posterior part of the teeth than in Sandelzhausen. The comparison is probably made with the only specimen illustrated in their Fig. 6. It can be seen that the P<sup>2</sup>, and to some extent the P<sup>1</sup>, in the specimen from Sandelzhausen (305) has a more developed postero-lingual shelf which projects further lingually than the base of the paracone. However, some of the specimens from Sandelzhausen illustrated here have this structure small and are narrow at this place (Fig. 14C, D, I), as in the specimens from Montréal. If the measurements given for Montréal are compared with Fig. 21, it can be seen that the premolars are not more slender; if anything is noted, it is that the P<sub>2</sub> from Montréal is wide for its length and is situated close to the smallest specimen from Sandelzhausen and that the P<sub>3</sub> has length and width within the ranges for Sandelzhausen, but that it is relatively wide for its length. Also the Buchental material has premolars that are slightly on the short side compared with Sandelzhausen.

The material from Montréal-du-Gers described by Orliac et al. (2007) is important in that it contributes to our knowledge of the MN4 *Hyotherium*, but it is similar to material from Armantes I, Munébrega AB, and Buchenthal, adding evidence that these forms may be primitive compared with later *Hyotherium* in characters, such as relatively small premolars and relatively small distal cusps on the I<sup>1</sup>. However, none of the samples have sufficient material to calculate indicative averages and to reveal the ranges of variation. While the character of small premolars may be real, its value at present is limited. Accepting provisionally the relatively small premolars in all these samples, the material from Armantes I, Munébrega and Montréal-du-Gers seems to represent the same taxon, for which the senior available name is *Hyotherium soemmeringi wylensis*, whereas “*Conohyus*” *cuspidatus* and *Hyotherium lacaillei* are junior synonyms. The transition of *H. s. wylensis* to *H. s. soemmeringi* is gradual at the scale of our observations, while the rich Sandelzhausen collection is intermediate between the types of these subspecies. Although new material may contribute to a better delimitation of the transition of one to the other subspecies, the name *H. s. wylensis* is used here as before (Van der Made



◀ **Fig. 28** Metapodials of *Hyotherium soemmeringi wylensis* from Sandelzhausen (Inventory No. BSPG 1959 II ...) **A** 16235 right Mc IV: 1 anterior, 2 medial, 3 posterior, 4 lateral, 5 distal, and 6 proximal views; **B** 16236 distal abaxial metapodial, right of the axis of the foot: 1 axial, 2 posterior, 3 abaxial, 4 anterior, and 5 distal views; **C** 16237 left Mt V: 1 proximal, 2 medial, 3 anterior, 4 lateral, and 5 posterior views; **D** 16223 right Mc III: 1 proximal, 2 anterior, 3 medial, 4 posterior, 5 lateral, and 6 distal views; **E** 16238 right Mt IV: 1 proximal, 2 lateral, 3 anterior, and 4 medial views; **F** 16239 left Mc V: 1 proximal, 2 posterior, 3 medial, 4 anterior, and 5 lateral views. The scale bar represents 2 cm for all figures

1998a), and the material from Sandelzhausen is assigned to that taxon.

## Discussion

The wider context of the Suoidea from Sandelzhausen will be discussed below in sections dedicated to the phylogeny of the Taucanaminae, the ecology of *Hyotherium*; the evolution and relationships among the species within *Hyotherium* and within the Hyotheriinae, and, finally, an updated classification of the Palaeochoeridae and Hyotheriinae will be given.

### Phylogeny of the Miocene Taucanaminae

The occasion of the description of *Schizoporcus muenzenbergensis* from Sandelzhausen is taken here as an opportunity to discuss the phylogeny of the Miocene Taucanaminae.

### Body weight

Body size is an important aspect of the ecology of a species (Damuth and MacFadden 1990) and changes in body size occur at several places in the phylogeny of the Taucanaminae. For this reason, the body weight of the species of Taucanaminae was estimated, although it is not the intention here to discuss all its aspects, nor the way of estimating these values.

Different methods are used to estimate body weight, including those of Legendre (1986), Fortelius (1990), and Damuth (1990). Legendre's (1986) method relates  $M_1$  size (length  $\times$  width) to body weight and has also been used for the Hyotheriinae (see below) and Listriodontinae (Van der Made 1996a). Fortelius' method estimates body weight on the basis of  $M^2$  length, and was applied to Miocene Suoidea of Europe (Fortelius et al. 1996) and extended to Chinese suoids (Liu 2003). Damuth (1990, Table 16.9) reported many possibilities of estimating body weight using dimensions of many different teeth.

Here estimates of body weights are given following Legendre, based on  $M_1$  "area", and Damuth, based on the

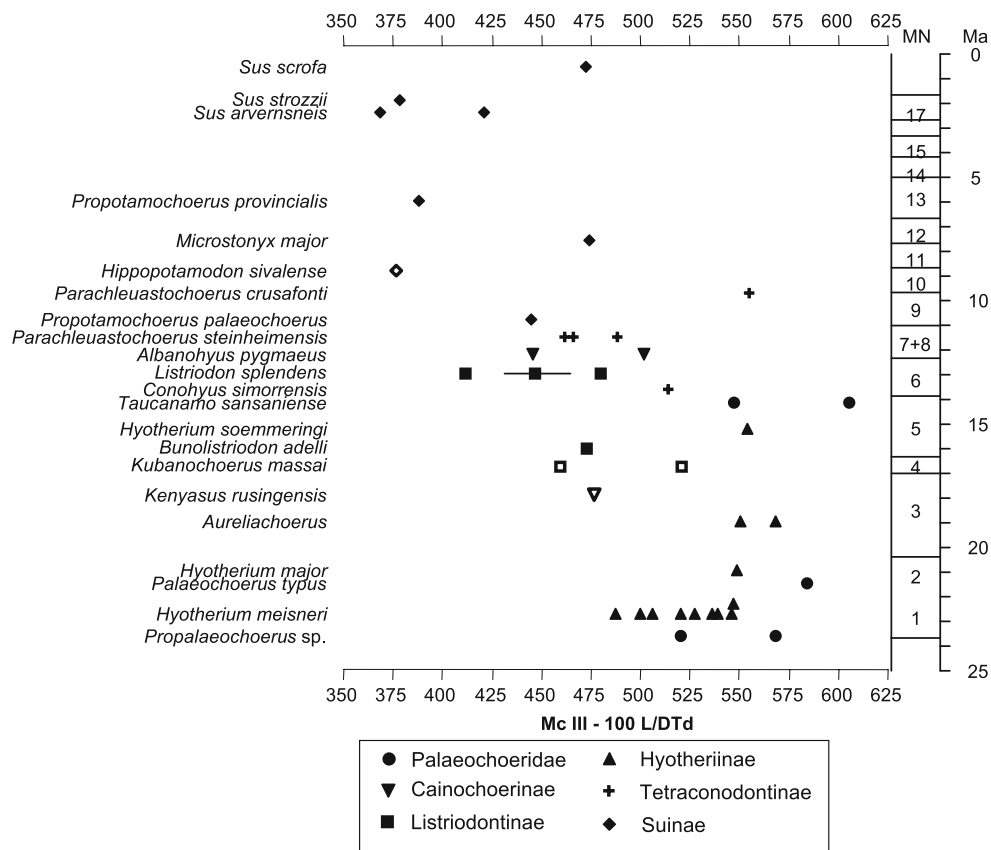
"area", DAP and DT of the  $M_1$ . The estimates are based on average  $M_1$  size: *Taucanamo primum* from Artenay, Els Casots and Bézian 19–15–14–15 kg, *T. sansaniense* from Sansan 19–16–18–13 kg, *T. inonuensis* from Pasalar 23–19–23–16 kg, *T. grandaevum* from Steinheim 13–11–14–9 kg, *Schizoporcus muenzenbergensis* from Münzenberg, based on 2 old specimens with  $M_1$  shortened through wear, 27–22–21–23 kg and on one unworn specimen from Sandelzhausen 33–27–31–24 kg, *S. vallesiensis* 109–86–101–70 kg, and *Yunnanochoerus gandakasense*, based on a single specimen, 54–44–71–28 kg. For comparison, with the same methods, *Tayassu tajacu* was estimated 47–38–29–45 kg and *Tayassu pecari* 80–64–48–77 kg. Most of these values for the living peccaries are rather high, which might be caused by the molars being very wide (because of the orthal mastication?), but for *Sus salvanius* 19–16–15–16 kg was estimated, values also slightly high compared with published body weight.

### Potentially interesting, but still problematic characters

Many characters are well known, and several have been discussed above, but some are still problematic. This is the case with some characters that are known for *Taucanamo*, but not for *Schizoporcus*, which are thus potentially interesting, but still problematic. These characters include:

- tips of  $I_1$  not forming a crest with those of  $I_2$ , but protruding more, resulting in the  $I^2$  occluding with the lateral side of  $I_1$  and tip of  $I_2$  and not with the lateral side of  $I_2$  and tip of  $I_3$ ,
- incisors with very low crowns,
- lower incisors relatively wide,
- lower incisors without lingual stylids that limit the mesial and distal edges of the crowns,
- small  $I^1$ , and
- $I^1$  without lingual cingulum and without styles that mark the mesial and distal edges at the lingual side of the crown.

Characters a–f are known from various *Taucanamo* species and characters a–d are known from a symphysis from Çandır that either belongs to *Schizoporcus anatoliensis* or to *Taucanamo* (Van der Made 2003). While characters b–d are probably plesiomorphic, character a (and the possibly related character e) are unknown from any other Suoidea, and might represent an apomorphy. A specimen from Nsebar (Nikolov and Thenius 1967) has  $I_1$  and  $I_2$  (or  $DI_1$  and  $DI_2$ ) that have higher crowns, faint mesial and distal stylids on the lingual sides, and the tips of both incisors forming a transverse crest, as is normal in Suoidea. Either there is here a reversal of character d, or the specimen from Çandır belongs to *Taucanamo* and not to *Schizoporcus* and the latter genus may be related to, but



**Fig. 29** Robusticity index 100L/DTd of the third metacarpal in the European (*solid symbols*) and some African or Asian (*open symbols*) Suidae. The *vertical axis* represents time (Ma and MN units) and the values of the species are arranged roughly in chronological order: *Propalaeochoerus* sp. from Saulcet (NMB) and Chavroches (NMB), *Hyotherium meisneri* from Lagnac (UPM) and Montaigu (NMB), *H. major* from St Gérard-le-Puy (MNHN), *H. soemmeringi* from Sandelzhausen (BSPG), *Palaeochoerus typus* from St Gérard-le-Puy (MGL), *Aureliachoerus minus* from Wintershof West (BSPG), *Kenyasus rusingensis* from Rusinga (KNM), *Kubanochoerus massai* from Gebel Zelten (MNHN), *Bunolistriodon adelli* from Bézian

(Ginsburg and Bulot 1987), *Taucanamo sansaniense* from Sansan (NHM, MNHN), *Conohyus simorreensis* from Klein Hadersdorf (IPUW), *Listriodon splendens* from Murrero (IVAU) and La Grive oc (MGL), *Albanohyus pygmaeus* from La Grive oc (IGF, MGL), *Parachleuastochoerus steinheimensis* from La Grive oc (MGL), *P. crusafonti* from La Tarumba (CJFV), *Propotamochoerus palaeochoerus* from Vösendorf (IPUW), *P. provincialis* from Librilla (MNCN), *Hippopotamodon sivalense* from the Siwaliks (IM), “*Microstonyx*” *major* from Inzersdorf (NMW), *Sus arvernensis* from Villafranche (NMB) and Kvabebi (GSM), *S. strozzi* from Poggiolino, Valdarno (IGF), *S. scrofa* from Cueva de Saldaraña (CTM)

not a descendant of, the former. In the following model (Fig. 32), most of these characters are ignored because of the uncertainties.

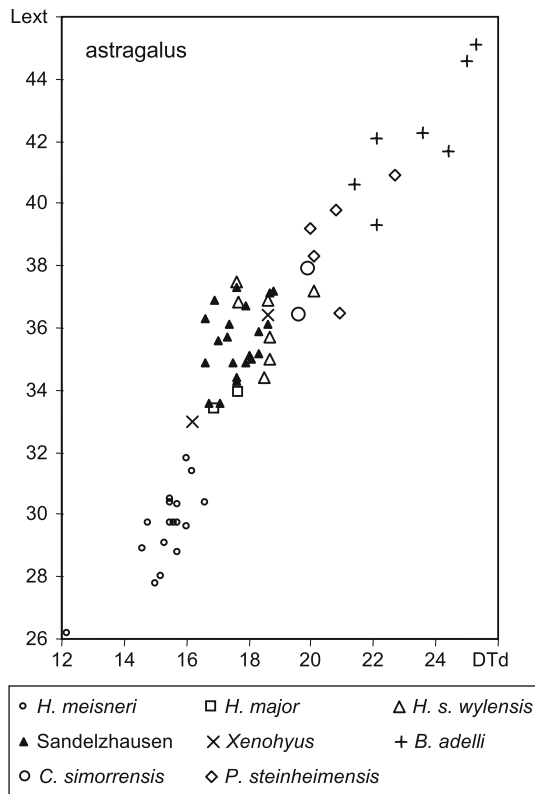
### Phylogenetic tree

Figure 32 gives a tree which is based on characters that are described above or elsewhere. As in the tree of the Hyotheriinae (Fig. 36), the basis of this tree is observation of morphological and metrical change in sequences of samples that belong to a species or lineage. There are gaps between relatively well documented segments of lineages and other lineages or samples. These different segments are united on the basis of shared derived characters. By default a species is derived from a similar but geologically older species, if no reversals of important characters have to be assumed for this. Numbers indicate any kind of change in

characters, including shared derived characters, which unite several lineages (or a “clade”), and simple observed changes, which mainly delimit stages in a lineage. Solid lines indicate known stratigraphic distribution, dashed lines indicate approximate stratigraphic distribution, and stippled lines indicate possible relationships.

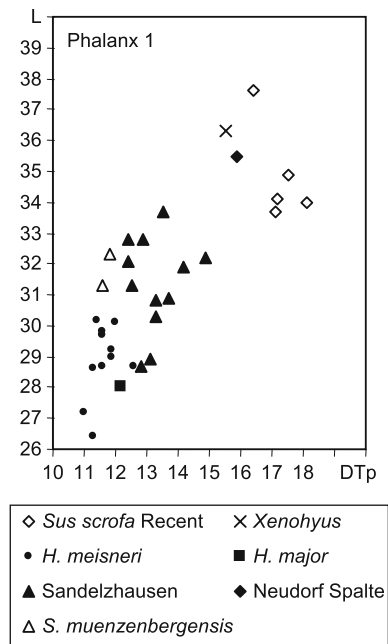
*Pecarichoerus* is known by very few specimens and its position is highly hypothetical.

The most important difference between *Yunnanocherus lufengensis* and *Y. gandakasensis* is size. In the context of this group, the larger size of the latter species seems to be derived. However, recent palaeomagnetism show Lufeng to be much younger than previously believed (Qi et al. 2006), and as a result, *Y. lufengensis* seem to be the younger species and a simple size increase in this genus is contradicted, leaving instead a size decrease as the more likely model.



**Fig. 30** Bivariate diagram of the astragalus of selected small Suoidea: *Hyotherium meisneri* from Laugnac (UPM), Montaigu (NMB) and Hessler (FISF), *H. major* from Ulm Westtangente (SMNS), *H. soemmeringi* from Torralba 4 (IVAU), Sant Mamet (IPS), Baigneaux-en-Beauce (NMB, MGL), Quinta Flamengas (CEPUNL) and Quinta Grande (CEPUNL), *H. soemmeringi* from Sandelzhausen, *Xenohyus venitor* from Laugnac (UPM), *Bunolistriodon adelli* from Olival Susana (CEPUNL), Quinta da Silveira (CEPUNL), Quinta Grande (CEPUNL), Quinta da Lobeira (CEPUNL), La Artesilla (MPZ) and Tarrazona (UPVB), *Conohyus simorrensis* from Puente de Vallecas (IPS) and Simorre (MNHN), and *Parachleuastochoerus steinheimensis* from La Grive (MGL, UCBL, IGF)

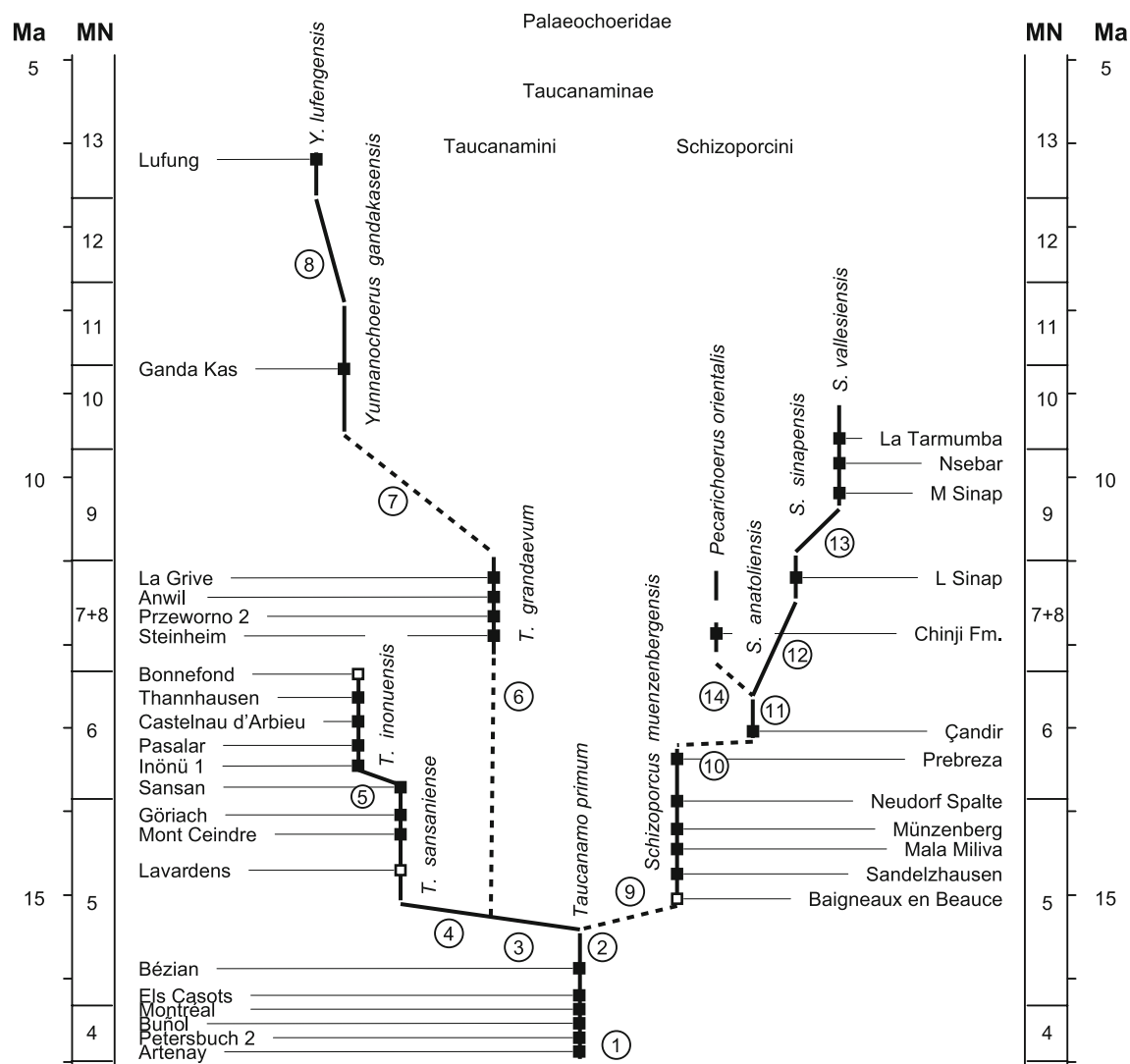
1. Characters present in the first representative: (a) lingual roots of upper molars fused and convergent, (b) two roots in lower molars, (c) small or no protocone on P<sup>3</sup> and P<sup>2</sup>, (d) lower canine with scrofic section.
2. The relative size of the M3 increases within *T. primum*, and a larger M3 is shared by all later Taucanaminae.
3. (a) More elongate premolars, (b) more elongate molars, (c) P<sup>4</sup> with DAP.DT (this is listed here as separate, because usually the P<sup>4</sup> is not affected by processes of elongation of the cheek teeth), d) M<sub>3</sub> occasionally with a second cusp in the third lobe.
4. (a) M<sub>3</sub> occasionally with a fourth lobe, (b) further elongation of premolars, (c) P<sup>4</sup> with marked anterior



**Fig. 31** Bivariate diagram of the first phalanx of selected Suoidea: *Schizoporcus muenzenbergensis* from Sandelzhausen, *Xenohyus venitor* from Laugnac (UPM), *Hyotherium meisneri* from Laugnac (UPM), *H. major* from Weisenau (FISF), *H. soemmeringi* from Sandelzhausen and from Neudorf Spalte (NMW) and recent *Sus scrofa* (BSPG)

cingulum, (d) P<sup>4</sup> very slender and with a high buccal cusp.

5. (a) Size increase, (b) probably relatively larger (not just more elongate) M3.
6. Size reduction?
7. (a) Formation of a complete anterior loph on both upper and lower molars, (b) size increase.
8. Size decrease.
9. (a) relatively larger I<sup>1</sup> (?), (b) I<sup>1</sup> with lingual cingulum and with styles that mark the mesial and distal edges at the lingual side of the crown (acquired here, or earlier see discussion 1?), (c) size increase.
10. (a) P<sub>4</sub> with prominent metaconid forming a transverse lophe, (b) P<sub>4</sub> talonid cusp reduced, (c) roots of lower molars probably starting to split into two pairs of roots (known only in Çandir), (d) size decrease and shortening of the premolars, (e) increase in general size.
11. (After Çandir, but before the split:) (a) Formation of anterior lophes on upper molars (or under 10), (b) formation of anterior lophes on lower molars (or under 12), (c) moderate size decrease.
12. (a) Formation of posterior lophes on upper molars, (b) formation of posterior lophes on lower molars, (c)



**Fig. 32** Proposed phylogeny of the Taucanaminae. Time in millions of years (Ma), MN indicate MN units (Mein 1975; De Bruijn et al. 1992). *Solid squares* indicate presence and *open squares* indicate possible or likely (cf., aff., ?) presence in a locality. *Solid lines*

indicate assumed time range and assumed relationships, *dashed lines* unknown time range, and *stippled lines* possible phylogenetic relationships. The *numbers in circles* indicate morphological and metrical changes that are discussed in the text

further size decrease and shortening of the premolars (e.g. in  $P^2$ ), (d) further increase of general size.

12 or 13 (b) second small cusp on posterior cingulum of  $M_{1-2}$

13. (a) Further reduction of premolars, (b) increase in general size.
14. (a) Formation of a complete loph on the anterior lobe of the  $M^3$  (morphology of other molars unknown), (b) large protocone on  $P^3$ , (c) general size decrease.

#### Ecology of *Hyotherium*

The morphological information relevant to the ecology of *Hyotherium* can be interpreted along several lines of

evidence, of which the following are treated here: (1) morphology related to the rooting behaviour, (2) mastication, (3) body size, (4) features that are related to social structure, (5) locomotion, and (6) temporal and geographical distribution.

#### Rooting

This is a typical behaviour in living species of pigs and peccaries. It consists of digging with the snout in the upper part of the soil, searching for roots, bulbs, other edible plant parts, and invertebrates in the soil. Many studies indicate the impact of this behaviour on the environment. The nasal disc, which is a unique structure in the Suidae,



serves for rooting. It is to be expected that the last common ancestor of the Suidae and the Dicotylidae had such a disc and all, or nearly all, its descendants, not just those on the lineages that survive today. The disc contains a bone, which in principle could fossilize, but as far as I know, this bone has never been described as a fossil. Therefore other characters related to this behaviour have to be studied. For the Listriodontinae, this was done and they were interpreted to be not very active rooters (Van der Made 1996a); they may have lost or reduced the behaviour. In the following text, several types of features related to rooting are discussed.

**Infraorbital fossa.** Powerful levator and depressor rostri muscles that move the nasal disc, originate in depressions such as the *fossa infra orbitalis* (see descriptions by Ewer 1958, 1970; Herring 1972b). In the Sandelzhausen material a deep *fossa infra orbitalis* indicates a powerful levator rostri muscle.

**Occiput.** Sicuro and Oliveira (2002) compared rooting in two species of peccary and feral *Sus scrofa*, coexisting in the Brazilian Pantanal wetland. Pigs were found to root extensive surfaces of 2 to over 50 m<sup>2</sup>, with a mean depth of 248 mm, whereas for peccaries these values are about 1 m<sup>2</sup> and 77 mm. The pigs were believed to be superior rooters because of the greater force rate of the complex muscle, and their bite force is similar or superior to that of the peccaries. These forces and force rates were estimated on the basis of cranial and mandibular measurements. A highly elevated and wide occiput contributes to a greater force rate of the complex muscle and thus a more forceful head elevation and superior rooting, whereas a long skull has the opposite effect. Only a few of the measurements taken by Sicuro and Oliveira (2002) can usually be taken on a particular fossil. Within the Suidae, the Hyotheriinae do not have very high, or very wide, occiputs, but their skulls are also relatively short. Compared with those of living peccaries, their skulls have wider occiputs and much shorter diastemas. The latter character results in shorter skulls. All this suggests they have a more powerful head elevation and thus that they may have been better at rooting.

**Incisors.** The Suoidea have highly adapted sets of incisors that are adapted to rooting. Apical wear on the I<sup>1</sup> and lingual wear on the I<sub>1-2</sub> is not caused by occlusion but by rooting (Herring 1972a). Such wear is found on the incisors in the Sandelzhausen collection. High crowned I<sub>1</sub> and I<sub>2</sub> form part of the complex of adaptations to rooting. Wear at their tips is intense and it is difficult to find unworn specimens that permit measuring the crown height (and if such specimens are present in a mandible the crown base tends to be hidden in the bone). There are two ways to obtain higher incisor crowns: (a) increasing the size of the incisors, but maintaining their proportions, (b) increasing the crown height relative to DLL, DMD, or to both.

a) The I<sub>1-2</sub> are much enlarged in the genus *Sus* (Fig. 19), a genus well adapted to rooting, while they are much smaller in *Tayassu*, which is a less able rooter. The incisors of most Suidae, including *Hyotherium*, tend to be relatively large compared with those of *Tayassu*, fossil Dicotylidae, and Palaeochoeridae (Fig. 19). Also the occluding I<sup>1</sup> is to some extent enlarged in the Suidae.

b) The proportions of the individual incisors may be changed, generally, in such a way that crown height increases most, and the labio–lingual diameter least. Low values for the DLL relative to DMD are seen in the *Sus* I<sub>1</sub> and I<sub>2</sub> in Fig. 19. Thus, this genus, in addition to increasing plain incisor size, acquired also more hypsodont incisors (that is with a greater value of H compared with DLL). If used in its proper context, changed proportions between DMD and DLL could be another, and more abundant, indicator of high crowned incisors and thus of rooting ability. Similarly, several later or “more progressive” species have I<sup>1</sup> with a large meso–distal diameter, but not such a large labio–lingual diameter; as a result the tooth is flattened.

As noted in the descriptions, hypsodonty indices of a few specimens of *Tayassu*, *Hyotherium meisneri*, and *H. soemmeringi* have more or less similar values. But then, the incisors of *Hyotherium* are more enlarged than those of *Tayassu*, leading to greater crown height (relative to the size of the remaining dentition). Even if the indices were calculated on worn *Sus scrofa* incisors, much higher values could be found than in *Hyotherium*, and thus the crown height is still higher.

The increase in size or hypsodonty of the I<sub>1</sub> and I<sub>2</sub> is usually seen in that the tips of these incisors protrude much more than the tip of the I<sub>3</sub>, leaving much of the lateral side of the I<sub>2</sub> exposed. The I<sup>2</sup> occludes with the lateral side of the I<sub>2</sub>, and this tooth is more elongate when the tip of the I<sup>2</sup> protrudes more. The I<sup>2</sup> is more elongate in these cases, not just larger; it is just its length or DMD that varies (Fig. 19). The degree of elongation of the I<sup>2</sup> can be used as a proxy for central incisor crown height, and thus for rooting ability. Also the I<sub>3</sub> may become a little more hypsodont, and the I<sup>3</sup> a little more elongate (Figs. 17, 18), but here the situation is more complex, because of the possibility of reduction of these teeth. Within the Suoidea, the I<sup>2</sup> became much more elongate (Figs. 15, 16, 19): the incisors are short in Palaeochoeridae and early Dicotylidae, a little longer in living Dicotylidae and Hyotheriinae, some Tetraconodontinae and Babyrousiniae, and much longer in the Suinae. Peculiar in this respect is the short I<sup>2</sup> in *Chleuastochoerus* and Chinese *Hyotherium*; either the length became reduced, or never became long in the evolutionary history of these forms.

**Rooting—conclusion.** A well developed preorbital fossa, occiput size and position, size of the central incisors,

and degree of  $I^2$  elongation suggest that *Hyotherium* was a much better rooter than living peccaries, and incisor size suggests that *Xenohyus* was a still better rooter. These early suids adapted to rooting by increasing incisor size, and *Sus scrofa* is a superior rooter that increased incisor hypsodonty.

### Mastication

There are various aspects of mastication, for example the position of the mandibular condyle relative to the tooth row, size of the posterior molars, enamel thickness, and hypsodonty.

**Mandibular condyle.** A relatively higher position of the mandibular condyle above the tooth row has various implications (Herring 1972a), but one is that the molar row closes more or less uniformly over all its length, which, in a straight tooth row (as in suoids), is advantageous during the lateral movement phase in chewing, and allows more food to be chewed at the same moment. If the condylar position is relatively lower, the  $M^3$  and  $M_3$  nearly occlude, while there is still some space between the  $M^1$  and  $M_1$ , which would be problematic in a grinding type of mastication, but not so in orthal mastication. The suid that is most adapted to a grinding type of mastication is *Phacochoerus* and it has the most elevated mandibular condyle.

It is well known that the mandibular condyle in recent peccaries is in a lower position above the occlusal plane than in recent pigs and that the glenoid is situated lower on the skull. Although the two observations may seem to refer to the same feature, but expressed in different bones, this is not the case. In peccaries, the glenoid is displaced on the skull and in recent species it is the lowest point of the zygomatic arch, as well seen in side view. As seen in posterior view, it descended from a level above the lower edge of the foramen magnum in primitive peccaries, to well below this level. It also moved forwards; as seen in side view, from a position nearly as far posterior as the occipital condyles towards a position next to the anterior half of the bullae. This is well documented (Pearson 1923; recent peccaries). However, the position of the mandibular condyle above the lower tooth row only became lower because it moved downwards and forwards relative to the tooth row. The condyles thus did not become relatively lower, but the mandibles became smaller relative to the skull.

In Fig. 9, the position of the mandibular condyle is compared in various suiforms. As explained above, the height of the condyle is measured as the distance from the condyle to a line that passes through the bottoms of the transverse valleys of the first and third molars. The other value is the distance along this line from the front of the first molar to the projection of the condyle on this line. A

sample of *Sus scrofa vittatus* collected in a short period from a small area near Deli (Sumatra) is used to illustrate sexual and ontogenetic variation. It is the same sample that was used elsewhere to study the variation of other dental, cranial, and mandibular characters (Van der Made 1991, 1997b; Guan and Van der Made 1993). It can be seen that Palaeochoeridae and Dicotylidae have low condyles that are situated below line  $L = 3H$ . This is also the case with the hippopotamus *Choeropsis* and the primitive suiform *Choerotherium*. Suidae tend to be above the line, and the most extreme form in this respect is *Phacochoerus* (Fig. 9; two measurements on a juvenile specimen and two on an adult).

In the position of the mandibular condyle *Hyotherium* groups with other Suidae, suggesting that its mandibular morphology was compatible with the grinding type of mastication that predominates in this family, although its morphology was still relatively primitive. It should be borne in mind that canine orientation is believed to be related to the type of mastication (Herring 1972a) and that *Hyotherium* still has relatively vertically directed upper canines.

**Size posterior molars.** In their evolution the Suidae tended to expand the occlusal surface distally through enlarging or elongating the third molar. Extreme examples are found in the Tetraconodontinae and Suinae (Cooke 1976; Harris and White 1979; Van der Made 1999a). As a result, their mandibles become relatively larger compared with the skulls and the glenoids may move backwards and upwards on the skull. Both trends are again seen in an extreme way in *Phacochoerus*. Distally expanded (and thus more elongate) or simply larger  $M_3$  (maintaining length-width proportions) enlarge masticatory surface. This is a common adaptation seen in grazers and enables mastication of larger quantities of food at the same time, and probably is an adaptation to the ingestion of larger quantities of less nutritive food. In Suidae and in some Palaeochoeridae, but not so much in Dicotylidae, the  $M_3$  tends to become clearly larger and distally expanded. In this respect, *Hyotherium* is still relatively primitive and has an  $M_3$  with a simple third lobe, and an  $M^3$  with little more than an enlarged posterior cingulum.

**Enamel thickness.** Much importance was given to bite force by Sicuro and Oliveira (2002), who used a great number of measurements to estimate bite force in feral hogs and two species of peccaries in the Pantanal wetland of Brazil, and who found that the two species of peccaries had different bite forces and used different resources. Many of their measurements cannot be taken on the fossil material. However, if great bite force is needed to crack seeds and nuts, the teeth need to withstand these forces. Such teeth are expected to have thicker enamel. Enamel thickness in Suidae was studied (Van der Made 1996a,

2004), and the Listriodontinae, which for other reasons had already been interpreted as folivorous, had relatively thin enamel, while Hyotheriinae were found to have particularly thick enamel. Here a large sample for *Hyotherium soemmeringi* is included, but fails to confirm the latter observation; its enamel thickness is comparable with that in most other Suidae, but it is thick compared with that of ruminants and the more grazing suid *Phacochoerus* (compare Van der Made 1996a, Van der Made and Tong 2008). However the increased data indicate that *Hyotherium meisneri* and *Aureliachoerus* do have thick enamel within the Suidae.

**Hypsodonty.** High crowned molars are common in species that eat abrasive food. Few data have been published on crown height or hypsodonty of the Suoidea, although some data on *Sus* are available (Van der Made 1988). Here some more data are given (Tables 10, 12), and if the index 100Ha/DTa is calculated, the values are well below 100, which is clearly lower than in living *Sus scrofa*.

**Mastication—conclusion.** The position of the mandibular condyle indicates that *Hyotherium* had a grinding type of mastication as in other Suidae, which is a more efficient mastication type for large quantities of food, but the genus is primitive in not having clearly distally expanded M3. Together with the evidence on enamel thickness and hypsodonty, this suggests that *Hyotherium soemmeringi* ingested moderate quantities of not very hard, and not very abrasive food. Compared with what is known of the diet of other species of pigs and peccaries (Sicuro and Oliveira 2002; and many others), it seems likely that *H. soemmeringi* may have had a similar diet to that of most living suoids (*Tayassu*, *Potamochoerus*, *Babyrousa*, *Sus*), but excluding the harder and more abrasive food items.

#### Body size

As noted above, body size has many implications for the ecology of a species (Damuth and MacFadden 1990). As with the Palaeochoeridae, Legendre's (1986) method based on M<sub>1</sub> "area" and Damuth's (1990) method based on M<sub>1</sub> "area", DAP and DT were used to estimate the body weight in different *Hyotherium* samples or "populations" on the basis of average M<sub>1</sub> size: *H. meisneri* from Budenheim 41–33–29–36 kg, Hessler 43–35–31–39 kg, Cetina 43–35–32–36 kg, Laugnac 51–41–34–47 kg and Montaigu 53–42–42–41 kg, *H. major* from Ulm Westtangent 60–48–43–51 kg and from St Gérard-le-Puy 66–53–48–56 kg, *H. soemmeringi* from Baigneaux 77–62–56–64 kg, Sandelzhausen 92–73–67–75 kg, Münzenberg and Seegraben 90–71–60–79 kg, and the average of the MN6 localities Georgensgmünd, Thannhausen and Stätzling gave 111–87–80–88 kg. For *Xenohyus* from Laugnac a body weight of 104–82–70–89 kg was estimated. For the

Middle Miocene *Hyotherium* from China this is 65–52–38–66 kg. For *Chleuastochoerus* from Loc. 73 this is 45–36–39–34 kg and from Loc. 49 it is 53–43–43–42 kg (based on data from Pearson 1928). The estimates should be considered with some reservation, because different methods may give very different results (e.g. using other teeth according to Damuth 1990; Fortelius 1990). For instance, Fortelius et al. (1996) estimated body size on the basis of M<sup>2</sup> length and found 63 kg for *Hyotherium* from Sandelzhausen (based on data published by Schmidt-Kittler 1971).

For comparison, the four methods used here gave 57–46–43–47 kg for *Sus celebensis*, 121–95–98–87 kg for *Sus barbatus*, 82–65–65–62 kg for *Sus verrucosus*, and 116–91–87–90 kg for *Potamochoerus*. Most species of hyotheres are thus larger than the Taucanaminae and comparable with species of *Sus* that are not very large.

#### Social structure

Obviously, we have no direct indications of the social structure in the fossil species of Suidae. However, morphological features in living species of Bovidae are well known to be related to social structure, and this may also be the case with some morphology in the living species of Suidae, providing thus a way to interpret the fossils in this respect.

Studies of African bovids lead to their grouping in four to five classes showing a gradual change from small bovids browsing in closed habitats, territorial, predominantly solitary or living in pairs, to large bovids grazing in open habitats, migratory and living in large mixed herds (Jarman 1974; Estes 1974). In the same way antipredator behaviour changes from run and hide, to outrun, and defence. Horn cores vary from small in males and absent in females in the smaller territorial species, to large in males and absent in females in the larger territorial species, to moderate in males and small in females in the smaller non-territorial species, and large subequal in large non-territorial species. Much of this seems also to hold for the Cervidae.

Large sexually dimorphic structures serve generally to enable estimation of strength and avoidance of unnecessary inter-male combats. Showy upper canines in male pigs have been interpreted in a similar way as bovid horns (Van der Made 2003). The small upper canines of *Hyotherium soemmeringi*, were probably hardly visible in a living animal, and suggest small social units and territoriality in a closed environment, whereas the large male and small female canines in the contemporaneous *Bunolistriodon* and *Listriodon* would suggest social units consisting of groups of females and a single territorial male in somewhat more open environments. To some extent such an interpretation is supported by the fact that fossils of *Hyotherium* are more

common in coal deposits whereas fossils of Listriodontinae tend to be more common in deposits that suggest more open environments.

### Locomotion

Locomotion is important in the ecology of any species because efficient locomotion facilitates acquisition of food, water, and mates, but also, as mentioned above, is important in anti predator behaviour. Giraffidae, with very long limbs, cover very large distances away from drinking water in search of food, while ungulates with shorter limbs tend to move over shorter distances or even be territorial. Obviously the actual antipredator behaviour in any situation is subject to many variables, for example predator size relative to prey size, number of predators cooperating in an attack, number of prey being attacked, etc. Species that tend to outrun predators tend to have fore and hind limbs of subequal length, with elongated radius and tibia and much elongated metapodials. Species that tend to run and hide tend to have hind limbs that are much longer than the fore limbs, and short metapodials in both fore and hind limbs. Short distal limb bones allow greater acceleration, while longer distal limb bones permit higher top speed. In the evolution of ruminants, the acquisition of longer metapodials led to fusion of the central metapodials and reduction of the abaxial metapodials. Compared with most living ruminants, Suoidea tend to have short metapodials that are not fused and tend to maintain functional side toes. *Phacochoerus*, which ventures short distances into open landscapes, has more gracile metapodials than *Sus* and *Potamochoerus*.

The Hyotheriinae are not particularly large, so their typical primary antipredator behaviour may have been to run and hide; their canines may have been used as a second line of defence. Within the Suoidea, there is an overall tendency to shorten the metapodials (e.g. Fig. 29). This tendency seems to be independent of body size and thus is not primarily allometric, but suggests a progressive locomotory adaptation. A progressively more robust postcranial skeleton in the Suidae, recalls a similar observation by Guérin and Eisenmann (1994) on tapirs (see also Van der Made and Stefanovic 2006). The reason for this tendency, which occurs across Perissodactyla and Artiodactyla, is not yet clear, but seems to be a common response to environmental change. *Hyotherium* is one of the most gracile suids, if not the most gracile, but it is more robust than a typical palaeochoerid. Possible explanations for the still very gracile postcranial bones in *Hyotherium* are that the species covered larger distances for access to food or water, that it had different anti-predator behaviour, or that the environment in which it lived is different from that in which Suidae live today. Such differences in the

environment may have been in the density of the vegetation or the average height of the dominant plants. For example, for an animal that is less than a metre tall, vegetation of that height allows a run-and-hide anti-predator strategy, and the spread of grassland or another landscape dominated by low plants would lead to the retreat of such animals to more densely vegetated landscapes.

### Distribution

During the nearly 10 Ma that the genus *Hyotherium* lived in Europe, it experienced marked fluctuations in its abundance: it was widespread in MN1–2, but became rare in MN3, recovering in MN4–5 and declining again in MN6. The comparison between tapirs and Suidae that was made in the previous paragraph can be extended: there was a “Tapir-vacuum”, a period without tapirs in Europe, but also in North America, covering the later part of MN3 till the later part of MN5, after which, the genus *Tapirus*, with a more robust postcranial skeleton, appeared in Europe and became abundant in MN9 (Van der Made and Stefanovic 2006). So the decrease in *Hyotherium* abundance after MN2 coincides with a total disappearance of tapirs.

To some extent the decline of *Hyotherium* after MN2 seems to coincide with a short lived increase in abundance of *Xenohyus* (Fig. 36). But this may be an artifact, because most of the localities of that genus are from the geographically restricted area of the Faluns de Touraine et de l’Anjou and have been interpreted as being reworked from MN3 (Ginsburg 1980). The only other specimen from MN3 is from Brüttelen, and the genus is known with certainty from MN2. There are thus insufficient grounds to assume that the decline in *Hyotherium* is because of competition with *Xenohyus*.

The recovery of *Hyotherium* after MN3 coincides with the dispersal of *Dorcatherium*, which was present with up to four species (Fahlbusch 1985). *Dorcatherium* species diversity was reduced in MN6 and *Hyotherium* went extinct. Later, tapirs and *Dorcatherium* became abundant again in MN9. Tragulidae, Tapiridae, and *Hyotherium* may have shared part of their diet and habitat preferences, and the record shows that abundance peaks of two of the three tend to coincide, but not of all three at the same time. This phenomenon might reveal more information about habitat preferences and competition among these ungulates and merits further study.

Listriodontinae have been interpreted as folivores that “grazed” on not very abrasive leaves, that did not root, and that may have lived in relatively large social units in relatively open habitats (Van der Made 1996a, 2003). In nearly all of the characters discussed here, *Hyotherium* differs markedly from the contemporaneous *Bunolistriodon* and *Listriodon*, which suggests that within the Suidae there

were very divergent habitat preferences or that habitats were used in very different ways. Its gracile postcranial skeleton suggests that *Hyotherium* was adapted to a kind of habitat different from that in which *Sus scrofa* tends to live, and its decline in abundance after MN2, parallel and simultaneously to that of gracile tapirs suggests that this kind of environment changed after MN2, although it may have recovered later.

#### *Ecology: conclusion*

The characters of the masticatory apparatus of *Hyotherium* suggest that it had evolved some distance “towards” the living Suidae, as confirmed by the morphology relative to the rooting behaviour. *Hyotherium* had already become a much more efficient rooter than the peccaries, but less so than *Sus scrofa*, and it must have lived on humid soils with a rich subsoil flora and fauna. Although its metapodials and phalanges are relatively long for a pig, the feet of *Hyotherium* were suited to life in closed habitats and on soft soils. The different species of *Hyotherium* may have been comparable in size with the not very large species of *Sus*, and may have been territorial, living in small social groups including only a single male, like *Sus scrofa*. Like any organism, *Hyotherium* may have been flexible in its lifestyle, but its remains are more common in coal deposits and in fossil associations that reflect closed or humid habitats, than in deposits and associations that reflect more open or arid landscapes. Other contemporary suids, for example the Listriodontinae, may have been more abundant in more open habitats.

#### Evolution of *Hyotherium*

In broad lines, the evolution of *Hyotherium* is marked by size increase and a few morphological changes, such as the distal cusplet on the I<sup>1</sup>, which initially was small and frequently not present at all, but which later was always present and large, and the progressive elongation of the premolars.

#### *A possible transition from Hyotherium meisneri to H. major*

There has been much confusion between *Palaeochoerus* and the earlier species of *Hyotherium*, but from Ginsburg (1974) onwards the genera have generally been properly separated. Ginsburg (1974) saw *H. meisneri* as a geographical subspecies of *H. major*. Subsequently, there has been some discussion on the priority of *H. meisneri* or *H. major* (Hellmund 1991a). Alternatively, they were recognized as two different species belonging to two parallel lineages, the small *H. meisneri* ranging MN1–3

and the slightly larger *H. major* ranging MN1–2 and evolving into the still larger *H. soemmeringi*, ranging MN3–6 (Van der Made 1990a, b, 1994).

*Hyotherium meisneri* seems to have been a very abundant species and is present in great numbers in several localities, although only some of this material has been described in detail (Van der Made 1994; Bouvrain and De Bonis 1999). The samples from these localities are not identical, but differ slightly in metrical and morphological characteristics. It is possible to arrange them in a sequence that would be a perfect morphological and metrical first segment of the *H. major*–*soemmeringi* lineage. The possibility of evolution from *H. meisneri* to *H. major* has not been studied previously: they were either considered to represent geographical subspecies (Ginsburg 1974) or different contemporaneous species (Van der Made 1990a, b, 1994; Bouvrain and De Bonis 1999). However, are they really contemporaneous?

*Hyotherium major* was supposed to be present in MN1 and MN2a in Weisenau, St Gérard, and Ulm Westtangente, whereas *H. meisneri* was supposed to be present in MN2b in Laugnac and in MN3 in Horta das Tripas, which implies a clear temporal overlap. This overlap would preclude a single lineage model. However, the relative positions of the localities do not seem to be well established in all cases.

**Laugnac.** Paulhiac (reference locality of MN1) is situated just above the Oligocene and low in the Agenian sequence whereas Laugnac (reference locality of MN2b; Mein 1977) is situated high in this sequence and below the Burdigalian (Richard 1946; Huguency and Ringead 1990). Both localities have *H. meisneri*.

**St Gérard-le-Puy.** The type material of *Hyotherium major* is from St Gérard-le-Puy, or Langy according to Bouvrain and De Bonis (1999). There are various localities around St Gérard-le-Puy which yielded fossils, such as Langy, Montaigu-le-Blin, and others, and for the older collections it is often not clear from where the material comes exactly, although it seems that the early collections came predominantly from Langy. “St Gérard” (with quotation marks) appeared in the earlier tables of the MN units in MN2a (Mein 1975), but later was substituted by Montaigu, which became the reference locality for MN2a (Mein 1977). However, even this is a very extensive locality, yielding fossils from different places. I do not know whether the lithostratigraphic positions of Montaigu and Langy relative to each other are clear. Montaigu has *H. meisneri* and as such, it is different from “St Gérard”, which has *H. major*. Material indicated in the collection (MGL) to come from Langy also belongs to *H. major*.

Ginsburg et al. (1991) discussed the age of Barbotan-les-Thermes relative to St Gérard and Laugnac. This discussion is illustrative of the stratigraphy of the MN2 localities and St Gérard in particular. Some arguments used by

Ginsburg et al. (1991) in correlation concern taxa that are assumed to appear or disappear at the MN2a–2b transition. However, alternatively, the distribution of such taxa could be related to ecology. In other cases, the level of evolution is compared, but this, as the authors admit, seems to be higher in St Gérard, as is the case with *Pseudotheridomys parvulus* and *Pomelomeryx gracilis*–*P. boulangeri*. One of the lines of evidence used concerned the Suidae and is chosen here to discuss in more detail. The appearance of *Aureliachoerus* was taken to mark the transition of MN2a to MN2b. This goes back to Ginsburg (1974, 1980), where this genus is supposed to replace *Palaeochoerus typus* and where its first appearance is indicated to be in Selles-sur-Cher, based on three teeth, which have not been illustrated, nor have their measurements been published (Ginsburg and Huguéney 1980). It should be remembered that Ginsburg (1974), considered the small *H. meisneri* a geographical subspecies of *H. major*. Ginsburg et al. (1991) indicated the presence of the small *Aureliachoerus* in Laugnac and Barbotan, along with *H. major*. I have studied the extensive collections of Laugnac in Marseille (UPM), and in other institutes, and have found *H. meisneri*, but not *Aureliachoerus*; this was confirmed by the study of Bouvain and De Bonis (1999). Likewise, the material from Barbotan seems to me to represent only *H. meisneri*. A revision of the Spanish *Aureliachoerus* did not reveal any MN2 record (Van der Made and Morales 1999), nor do I know the genus from any other MN2 locality. All this suggests that the arrival of *Aureliachoerus* may have been in MN3 and that size differences in *Hyotherium* in the French localities may have been incorrectly interpreted. If the reason for the extinction of *Palaeochoerus typus* were the arrival of *Aureliachoerus*, there is no compelling reason to place St Gérard low in MN2.

Rodents are generally important in assigning a locality to an MN unit, and in MN2, *Eucrietodon* is an important element. For instance, *E. gerandianus* from Montaigu and La Chau is more primitive than *E. aquitanicum* from Laugnac (Daams 1976). This seems to confirm an older age for St Gérard. However, the original type material of *E. gerandianus* from Langy was lost, and material from La Chau was taken as hypotypoid (Daams 1976), which implies that *E. gerandianus* in this concept may indicate the age of La Chau, but not of Langy or “St Gérard” (see also Huguéney 1999).

Material said to be from “St Gérard” is often of unknown exact provenance and fossils from MN2a and MN2b localities in the area of St Gérard and elsewhere may have played a role in discussions on: (1) the age of the “locality”, (2) the ages, relative to “St Gérard”, of other localities, (3) the ages of particular specimens from the area, (4) the evolution of lineages (and subsequent use in stratigraphy), and (5) faunal events (and

subsequent use in stratigraphy). This may have led to errors that are difficult to detect, because such assumptions are not always explicit, or because arguments build on earlier papers that used assumptions that may be not sound. Here it is considered possible that Langy and the material of *H. major* may derive from the uppermost part of MN2.

**Ulm-Westtangente.** This locality is placed in MN2a (Heizmann et al. 1989), but the reasons for such an age were not given. Werner (1994) studied the small mammals and discussed the position of the locality. The locality is in the Ulmer Schichten and was considered to be one of the youngest localities of the Untere Süßwasser Molasse (USM, Lower Fresh Water Molasse) of the area, and was placed in MN2a, while the apparent absence of MN2b in the area was explained as either not deposited or eroded by the Burdigalian transgression. Arguments for correlating Ulm Westtangente to Cetina and thus MN2a include: the presence of both *Pseudomys parvulus* and *Ritteneria molinae* and the presence of *Myoglis truyolsi*. Another argument for an MN2a age was the presence of *Eucrietodon* aff. *gerandianus*.

*Pseudotheridomys parvulus* occurs in MN1–4 and is thus irrelevant (Engesser 1999).

The species *Glis truyolsi* (not *Myoglis*) is extremely rare, and this is also true for the Miocene record of this genus, being represented in MN1–2, 4, and 9, whereas *Myoglis* appears in MN2b (Daams 1999), suggesting that the presence of “*Myoglis truyolsi*” in Ulm Westtangente does not contradict an age younger than MN2a.

Problems with *Eucrietodon gerandianus* are discussed above; the species was assumed to indicate an older age than La Chau.

*Ritteneria manca* is more advanced than its ancestor *R. molinae* in the degree of separation of the lophs, which in the lower molars shows La Chau to be well advanced over Ulm Westtangente and Schaffhausen, whereas in the uppers the difference between the first two localities is much less and the Schaffhausen sample is clearly the most advanced (Werner 1994, Figs. 41–42). La Chau is believed to be older than Laugnac.

A new subspecies “*Paraglis*” *infralactorensis ingens*, a descendant of *Bransatoglis fugax*, was named from Ulm Westtangente. Daams (1999) recognised a *Bransatoglis fugax*–*infralactorensis*–*astaraciensis* lineage, with the species being present in MN1–2b, MN3, and MN4–9, respectively. This lineage would thus suggest a younger age for Ulm Westtangente.

Whereas some of the evidence suggests that Ulm Westtangente is relatively old within MN2, and older than La Chau, other evidence suggest it might be younger. In the latter case, the problem of an apparent absence of an MN2b record in the area would be solved.

**Weisenau.** This is a classic locality and a rich collection was discussed by Von Meyer (1843), but not described in detail. Von Meyer (1841) based his species *Hyotherium medium* on material from Weisenau and Mösskirch. The latter locality probably has *H. soemmeringi*. The name *Hyotherium soemmeringi medium* became in use for small *Hyotherium soemmeringi* (Thenius 1956; Mottl 1970). I assume that the material of *Hyotherium* I studied (FISF) is a small part of the collection discussed by Von Meyer (1843), but it certainly does not represent the 12 individuals mentioned by him. The material that is available is dominated by elements that are more difficult to evaluate for taxonomy, such as incisors, milk teeth, and bones. Some premolars tend to be relatively large; this suggests an early MN1 *Hyotherium major* that was larger than *H. meisneri* from Cetina (Van der Made 1990b, 1994). Cetina was placed in MN2b (Mein 1975, 1977) and later in MN2a (De Bruijn et al. 1992).

Weisenau was placed in MN1 (Mein 1975, 1977; De Bruijn et al. 1992). However, there are various fossiliferous levels in the area of Weisenau, and Tobien (1972) described small vertebrate remains from the Cerithien, *Corbicula*, and Hydrobien Schichten. More material from these units was collected and the middle Cerithien Schichten were correlated to MP30, the upper Cerithien Schichten to MP30, MN1, and MN2a, and the *Corbicula* and lower Hydrobien Schichten to MN2a (Engesser et al. 1993). These authors also cited research that indicates that Von Meyer's collection comes from the "bone bearing earth" that was excavated for the construction of a beer cellar, and that this sediment is from the *Corbicula* Schichten.

Accepting a MN2 age for Weisenau and the apparent size increase in *H. meisneri*, this material might also enter the ranges of the later samples that have a larger average size, but also a large sample size and a wider range of variation.

**Horta das Tripas.** Four suid teeth from Horta das Tripas were described as *Palaeochoerus aurelianensis*, in present nomenclature *Aureliachoerus aurelianensis*, and anthracothere material was assigned to *Brachyodus onoideus* (Roman 1907). However, the suid teeth were assigned with some doubts to *Hyotherium meisneri* (Van der Made 1990a). The size increase of *Brachyodus intermedius* to *B. onoideus* suggests that the locality is from the younger part of MN3. This would be the youngest *H. meisneri* and would contradict a simple size increase from *H. meisneri* to *H. major*. However, the material is poor.

**Cetina de Aragón.** Most of the collection is known to come from a lower coal level and was assigned to *H. meisneri*, but some larger specimens, including a maxilla from a somewhat higher level, were assigned to *H. major*, although it was admitted that the "evidence ... is not overwhelming" (Van der Made 1994). This nearly

implies that the species were contemporaneous. However, other samples have a wider range of variation than the Cetina sample and it might be possible to include these few specimens in that sample.

Although some material or some ages, do not perfectly fit an anagenetic evolution from *H. meisneri* to *H. major*, most the data fit such a model. The model is presented here as a hypothesis.

#### *The transition Hyotherium major—H. soemmeringi*

The evolutionary link between *H. major* and *H. soemmeringi* has been suggested but has also been considered with some reservation (Ginsburg 1974; Hellmund 1991a). The doubts arise principally because of the poor record in MN3, resulting in a morphologically and metrically under-represented transition between the two species; also the earliest (MN4) material of *H. soemmeringi* is not very abundant. Hellmund (1991a) suggested that *H. meisneri* (including, in his view, also *H. major*) was abundant in Europe during MN1–2, that outside (western?) Europe *H. soemmeringi* may have descended from *H. meisneri*, and that *H. soemmeringi* dispersed into Europe during MN4. This scenario would explain well the poor *Hyotherium* record in MN3.

Bearing that scenario in mind, the question of a closer relationship between the Chinese *Hyotherium* and *H. soemmeringi* arises. However, enlarged anterior premolars had been acquired already in the more advanced *H. meisneri* populations and in *H. major*, and all European *Hyotherium* have elongate  $I^{2-3}$ , whereas in these respects the Chinese *Hyotherium* is more primitive. In addition, *H. major* from its type locality St Gérard-le-Puy is already larger than the Chinese *Hyotherium* and close in size to *H. soemmeringi*. New material described by Orliac et al. (2006) is interesting in that it helps to document the earlier *H. soemmeringi*. In all respects, there seems a more gradual transition between *H. soemmeringi* and the early European samples than between that species and the Chinese *Hyotherium*.

It seems thus likely that the transition between *H. major* and *H. soemmeringi* either occurred in Europe during a period when the genus was rare, or when it was living in an area, probably in western Eurasia, of which the fossil record remains to be explored, but not in China.

#### *Evolutionary change in Hyotherium soemmeringi*

In the earliest MN charts, Baigneaux was placed in the middle or upper part of MN4 and Sandelzhausen in MN6, while Pontlevoy is the reference locality of MN5 (Mein 1975, 1977; De Bruijn et al. 1992); since that time, however, Sandelzhausen has been placed in MN5 (Fahlbusch

2003). This change affects the perception of the evolution in *Hyotherium*, which appears more as a gradual size increase (as is seen here in Fig. 23). The Styrian localities with *Hyotherium* and *Aureliachoerus* were placed in the Karpatian (Mottl 1970), and of those, Leoben (= Seegraben and Münzenberg) and Eibiswald were placed in MN5 (Mein 1975, 1977; De Bruijn et al. 1992). Later Oberdorf was placed in the Ottnangian and in MN4, and Wies, Eibiswald, and Schönegg were tentatively placed at the MN4–5 transition (Daxner-Höck 2003; Strauss et al. 2003), well below Sandelzhausen. This raises the question whether all the Styrian localities are close in age or whether they represent different ages.

Little independent information about the ages of the Styrian localities relative to each other and to Sandelzhausen is known (or at least to me), but an indication could be the size of their material of *Hyotherium*. However, it is curious that the localities that yielded upper teeth tend to have short molars and those that yielded lower teeth tend to have longer molars (Van der Made 1998a: Fig. 8). This is even true for Seegraben, which has both upper and lower molars. In addition, Sandelzhausen has more upper than lower M3 and, as a result, the ranges of variation are much smaller in the lower M3. So these samples may not all be representative of the populations from which they derive and their comparisons may give a false impression. Here the position of all these localities above Sandelzhausen, is maintained, although this may not be correct. Obviously this placement has consequences for the classification of the suids, because the transition to *H. s. soemmeringi* is placed here above Sandelzhausen. The material studied from Pontlevoy is from the old collections, and may not originate exactly from the reference locality Pontlevoy-Thenay. The average size is smaller than at Sandelzhausen, and also the minimum values are well outside the ranges for Sandelzhausen and the size is small even compared with Baigneaux. The ordering of the localities shown here in Fig. 23 is thus conservative and not optimal with regard to the evolutionary tendencies in *Hyotherium*.

Dehm (1980) described material from Thannhausen (MN6), compared it with the Sandelzhausen collection (which he believed to be MN6) and to some data from Georgensgmünd from the literature, and named the new subspecies *Hyotherium soemmeringi bavaricum*. The new subspecies was believed to be a side branch that was contemporary with *H. s. soemmeringi*, but differing from the latter in having a wider P<sub>4</sub> and M<sub>2</sub>. My own measurements indicate that the M<sub>2</sub> is wide (Fig. 23), but not as wide as measured by Dehm (1980, Fig. 3). The material from Thannhausen is here considered to be similar to other material of this age and close to the type material of *H. s. soemmeringi* from Georgensgmünd.

## Relationships and evolution in the Hyotheriinae

*Hyotherium* became the type genus of the Hyotheriinae, and subsequently *Chleuastochoerus*, *Aureliachoerus*, and *Xenohyus* were placed in that subfamily (Simpson 1945, Ginsburg 1974, 1980). At some moment, these four genera constituted the Hyotheriinae (Van der Made 1997b), because other genera, for example *Palaeochoerus* and *Propalaeochoerus*, were transferred to the Doliochoerinae, Palaeochoerinae, or Palaeochoeridae (Van der Made 1990a, b, 1994, 1996b). This is still the accepted classification here, although other authors have suggested further modifications of the content of the Hyotheriinae, concerning *Xenohyus*, *Chicochoerus*, *Miochoerus/Sinapriculus*, *Chleuastochoerus*, and the species *Hyotherium pilgrimi*.

### Systematic position of *Xenohyus*

Ginsburg (1980) described the new genus and species *Xenohyus venitor* and stated that it was a suid, close to *Hyotherium soemmeringi*.

Pickford and Morales (1989) stated that *Xenohyus* belongs to the Doliochoerinae, Tayassuidae (current nomenclature Palaeochoerinae, Palaeochoeridae) and that it was ancestral to the Hippopotamidae. These authors compared that genus with the “*Doliochoerus*” material described by Dechaseaux (1959), which in reality belongs to *Palaeochoerus aquensis*. The discussion of the morphology is a lengthy enumeration of characters that are said to be present in both *Doliochoerus* and *Xenohyus*. Many of the characters mentioned are irrelevant, because they are common to both Suidae and Palaeochoeridae. Other characters are said to be similar, whereas they are in fact different. For instance, it is said that the P<sup>4</sup> are similar, but in *Xenohyus* the labial cusps are well separated and in *Palaeochoerus* they are not, and both are claimed to have a I<sup>1</sup> with a distal cusplet, but this is not the case in *Palaeochoerus*. It is said that the upper molars of both resemble each other in the position of the anterior accessory cusplets. The protocone in *Palaeochoerus* is fused to the protocone, as in all Palaeochoeridae, and in *Xenohyus* to the anterior cingulum, as in most Suidae (Van der Made 1996b). None of all characters mentioned separates *Xenohyus* from the Suidae and unites it with the Palaeochoeridae. The postcranial skeleton of *Xenohyus* includes common derived characters with the Suidae, e.g. central metapodials with a ridge in the middle of the distal articulation continuing dorsally and the corresponding morphology of the first phalanx (compare Van der Made 1996b).

The “tayassuid hypothesis” of the origin of hippos was considered unlikely (Van der Made 1999), its arguments



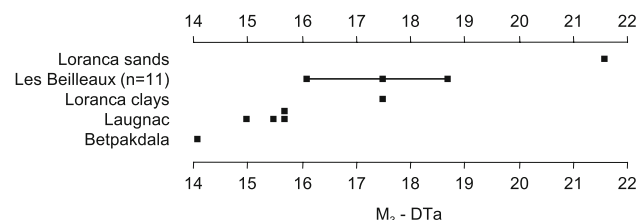
were criticized (Wright 1998) and it was plainly dismissed as being “mostly based on some incorrect observations”, and an origin from the Anthracotheriidae has been assumed (Boisserie et al. 2005).

*Evolution of Xenohyus*

The lack of a well developed metaconid on the P<sub>4</sub> of the type specimen of “*Conohyus*” *betpakdalensis* Trofimov (1949) suggested to the author affinities with *Conohyus*. However, the tooth is not enlarged as in *Conohyus* and the tip of the main cusp is inflated, not slender or sharp-pointed. The tooth has a morphology like other hyotheriine P<sub>4</sub> with a not well developed metaconid. It has been suggested that the species belongs to *Xenohyus* (Van der Made 1994), a genus which was described from MN2–3 in Europe (Ginsburg 1980). The attribution of the species to *Xenohyus* was one of the arguments used by Kordikova (2001, pp 73–74) to rejuvenate the upper member of the Askazansor Formation from Late Oligocene to MN2–3. However, the specimen from Betpakdala is small compared with *Xenohyus venitor* as known from Europe (Fig. 33).

It seems that the material described by Ginsburg (1980) as *Xenohyus venitor* is not homogenous in size; the material from Laugnac (MN2) is small compared with the material from the Faluns (Ginsburg 1980; Ginsburg et al. 1988), which is believed to be MN3. A specimen from the clays at Loranca is also larger, and a specimen from the sands at that locality is still larger (MNCN; Pickford and Morales 1989). This locality was previously believed to be MN3, but now it is placed in MN2. A P<sub>4</sub> from Brüttelen (NMBE; MN3) is also large.

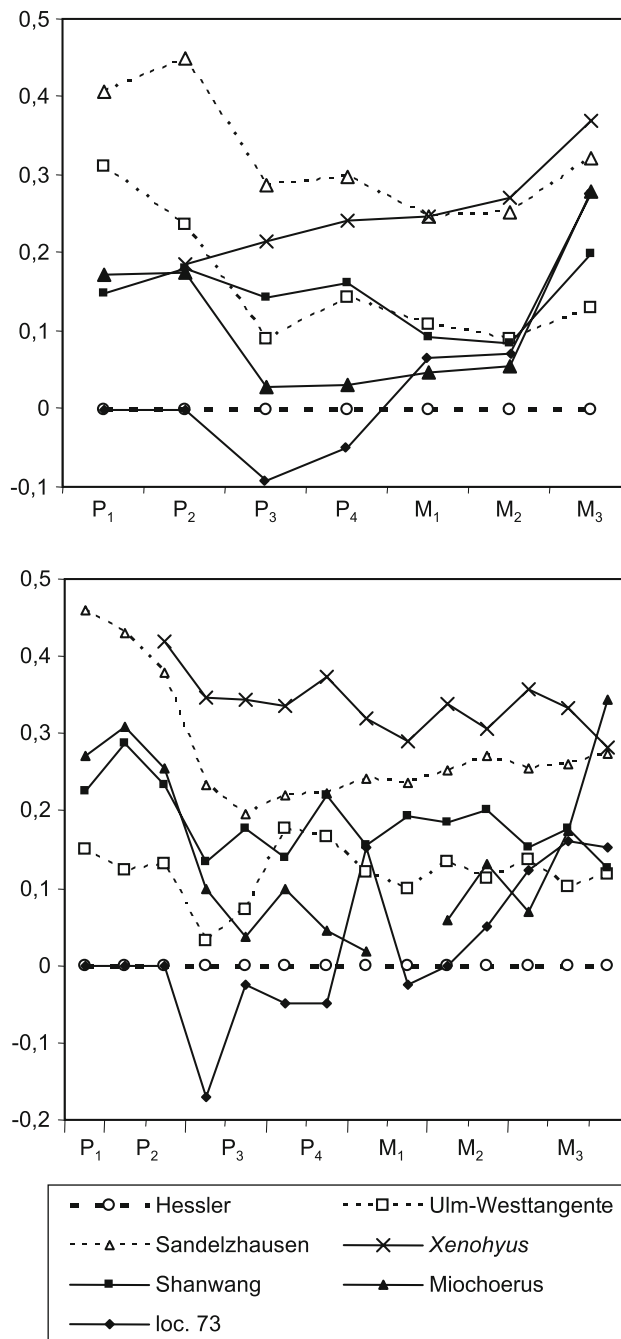
Although there is not very much *Xenohyus* material, there is more than just the M<sub>3</sub> given in Fig. 33. The observed range of variation in *Xenohyus venitor* is larger than expected in a single species, and suggests size increase with time. There may also be some morphological change, for example better separation of the metaconid on the P<sub>4</sub>. However, more material of known age is necessary to substantiate this.



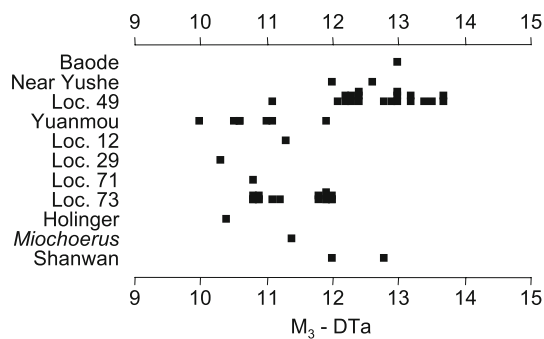
**Fig. 33** Variation in size of the third molar in *Xenohyus*: Betpakdala, holotype of “*Conohyus*” *betpakdalensis* (PIN), Laugnac, including the holotype of *Xenohyus venitor* (MNHN, UPM), Loranca clays (MNCN), Les Beilleaux à Savigné-sur-Lathan (minimum–average–maximum; Ginsburg et al. 1988), Loranca sands (MNCN)

Miochoerus/Sinapriculus

Chen (1997) introduced the new generic and specific names *Miochoerus youngi* for a suid mandible from



**Fig. 34** Proportions of the lower cheek teeth of the Chinese Hyotheriinae compared with some samples of European *Hyotherium* and *Xenohyus* from Laugnac (MNHN, UPM). As in Fig. 24, DT indicates maximum DT for P<sub>1</sub>, DTa and DTp for the remaining teeth, and DTpp for the M<sub>3</sub>. The value indicated for each cheek tooth is ln(average sample/average standard). The standard is the sample of *Hyotherium meisneri* from Hessler. Provenance of data as in Figs. 24 and 25



**Fig. 35** Variation in size in the Chinese Hyotheriinae: *Hyotherium* from Shanwan (casts IVPP), type of *Miochoerus youngi* (cast IVPP), and *Chleuastochoerus stehlini* from Holinger (BNHM), Loc. 73 (IVPP; Pearson 1928), Locs. 12, 29, 49, 71, 29 (Pearson 1928), Yuanmou (IVPP), Yushe (PIN) and Baode (IVPP)

Jianshan near Xinan city. The suid was described as belonging to the Suinae. Liu et al. (2002) gave the new generic and specific names *Sinapriculus linguensis* and the new specific name *Hyotherium shanwangense* to material from Shanwan and placed both taxa in the Hyotheriinae. The first new species name is based on a mandible of a female, with a long symphysis, diastemas between the canine and P<sub>3</sub>, shallow mandible, and P<sub>3</sub> and P<sub>4</sub> longer than M<sub>1</sub> (the latter character is contradicted by their Table 1). *Sinapriculus linguensis* is based on a mandible and maxilla of a slightly larger individual, a male, lacking a cingulum on upper molars, with less development of diastemas, and a P<sub>4</sub> without a metaconid. Some of the characters mentioned in the diagnoses of the two species do not serve to separate one from the other, because the characters are not represented in the material assigned to the other species (lower edge mandible, symphysis, upper molars). Other characters are notably variable (again the metaconid on the P<sub>4</sub> of the Hyotheriinae—Van der Made 1994). These two names are considered here to be based on a female and a male of the same species. The skull shows a well developed prezygomatic shelf as in *Hyotherium*. Liu et al. (2002) did not cite Chen (1997) and did not compare their material with *Miochoerus youngi*. This is unfortunate, because the resemblance is very great. If there is any difference that can be observed that might be significant, this might be a better development of the metaconid on the P<sub>4</sub>. This would not be strange, because the specimen is a little younger and later *Hyotherium* tends to have better separated metaconids on that tooth. Here all this Chinese material is classified as *Hyotherium youngi*.

In comparison with all European *Hyotherium*, the Chinese species is primitive in its short I<sup>2</sup> and I<sup>3</sup>, whereas in its degree of elongation of the premolars it is broadly intermediate between *H. meisneri* and *H. major*, although the premolar proportions are a little different (Fig. 34). The

only I<sup>1</sup> I know has a distal cusplet that is less developed than in *H. soemmeringi*. There is no evidence for a particularly close relationship with *H. soemmeringi*, nor with *H. major*, through common derived characters that appeared after *H. meisneri*. On the contrary, all European *Hyotherium* share more elongate second and third upper incisors. It thus seems likely that European and Chinese *Hyotherium* separated following the dispersal of the genus into Europe.

#### *Hyotherium pilgrimi*

Pilgrim (1926) named a great number of new species, several of which were recognised to be synonyms (Colbert 1935, Pickford 1988). “In order to impart stability”, Pickford (1988) named a new species of *Hyotherium*, *H. pilgrimi*, and included in it material of five species named by Pilgrim (1926) and placed in the genera *Dicoryphochoerus* and *Propotamochoerus*; the material does not include the holotypes of four of the five species, but one is included with doubts. Although this is not a 100% objective synonymy, it is as close as it can get. The attribution of the remaining holotypes remains unclear in this revision by Pickford (1988), but no other species of Hyotheriinae and Suinae were recognized from the Chinji Formation, raising even more questions about what these holotypes might represent. Liu et al. (2002) suggested that *H. pilgrimi* should not be included in *Hyotherium*, but left its affinities open.

Pickford (1988) proposed that the P<sup>4</sup> of the Suinae have sagittal cusplets in the sagittal valley whereas the P<sup>4</sup> of other Suoidea do not, and assumed that *Hyotherium pilgrimi* is ancestral to the Suinae. Both are interesting proposals. However in relation to the first proposal it should be noted that some Tetraconodontinae also may develop such a cusp in parallel (Van der Made 2004). The second proposal combines elements of divergent views of earlier authors. The selected holotype of *Hyotherium pilgrimi* is a skull fragment that was assigned by Pilgrim (1926) with some reservation to *Dicoryphochoerus haydeni*. In Pilgrim’s (1926) model, this genus was closely related to the strictly European genus *Hyotherium* whereas other authors included *Dicoryphochoerus* and *Propotamochoerus* in the Suinae (Simpson 1945, Schmidt-Kittler 1971).

The holotype of *H. pilgrimi* and other material included in the species show derived characters that unite them with the Suinae, but which are absent in the Hyotheriinae: the holotype has a P<sup>4</sup> with one sagittal cusp, and the M<sup>3</sup> is long. *Hyotherium pilgrimi* does not share any derived character with *Hyotherium*, but lacks derived characters seen in other species of *Hyotherium*, for example the morphology of the anterior part of the zygomatic arch and prezygomatic shelf and the particular way in which *Hyotherium* premolars are elongated.

In conclusion, there are no clear derived characters that unite *H. pilgrimi* or early *Propotamochoerus* / *Korynocochoerus* with *Hyotherium*. For the time being “*Hyotherium pilgrimi*” is considered here as an early representative of the Suinae (coinciding largely but not completely with Pickford’s (1988) opinion), and is not further discussed here.

#### Systematic position of *Chleuastochoerus*

Schlosser (1903) named *Sus stehlini* and *Sus microdon* on the basis of some isolated teeth from China. Pearson (1928) described splendid material including many skulls from China, and assigned the material to a new genus with one of Schlosser’s species as type species: *Chleuastochoerus stehlini*. The other species she considered to be a small variant or the same species. She used statistics to test the size differences between the different samples of *C. stehlini* and found significant differences, but nevertheless she was strongly against assigning part of the material to a different species. She believed *Chleuastochoerus* to belong to a lineage quite separate from *Hyotherium* and closely related to *Palaeochoerus*. Simpson (1945) placed all three genera in the Hyotheriinae (which in his view included *Palaeochoerinae*). Schmidt-Kittler (1971) showed that *Chleuastochoerus* and *Hyotherium* are closely related. This view was shared by Van der Made and Han (1994) and Pickford (1988, p. 10), but not by Pickford (1995), who placed *Chleuastochoerus* in the Dicoryphochoerini (page 248) and in the Propotamochoerini (p. 265), but in any case in the Suinae. No arguments were given for this drastic change. Nevertheless, this classification was adopted by Chen (1997).

Liu (2003) presented a cladogram in which *Chleuastochoerus* grouped with the Suinae and not with *Hyotherium*. Features that contributed to this grouping include: 7) protocone as far forwards as paracone (in *Hyotherium* behind paracone), 10) distinct central cusp (incipient in *Hyotherium*), 12) metacone same size as other main cusps (smaller in *Hyotherium*), 51) anterior lobe of lower molar higher than posterior lobe. I simply fail to see the differences between the character states in the fossils. Other characters are: 18) metacone on P<sup>4</sup> as large as paracone (incipient in *Hyotherium*), 75) diastemas inside tooth row short (absent in *Hyotherium*). Here certain character states are given for *Hyotherium*, while also the other states can be observed in the genus; this kind of character is very likely to evolve in parallel. Still another character is: 20) crest on sagittal groove of P<sup>4</sup> well developed in *Chleuastochoerus*. This must be Pickford’s (1988) sagittal cusp, but it is absent in *Chleuastochoerus*. Characters 73) and 81) can be observed in a specimen illustrated here (Fig. 8A). Character state 81) preorbital fossa shallow (absent in

*Hyotherium*), does not correspond to the deep fossa that can be seen here in Fig. 8A2 (lateral view—note the shadow marking the limits of the fossa), 1c (dorsal view) and 1d (anterior view—where the depth can be appreciated). Character 73, the prezygomatic shelf is scored as “0) absent” in *Hyotherium*, “1) weak” in *Hippopotamodon* and *Sus*, “2) medium and behind the infraorbital foramen” in *Chleuastochoerus* and *Propotamochoerus*, and “3) extends over infraorbital foramen” in *Microstonyx*, thus contributing to the grouping of *Chleuastochoerus* with the Suinae. However, I agree with Schmidt-Kittler (1971) that the prezygomatic shelf in *Hyotherium* and *Chleuastochoerus* is similar and different from the prezygomatic shelf in the Suinae.

Several very clear, but mostly primitive, characters place *Chleuastochoerus* apart from the Suinae: I<sup>1</sup> low crowned, I<sup>1</sup> not flattened, short I<sup>2</sup> and I<sup>3</sup>, low crowned lower incisors, generally one foramen lacrymale per orbita (two in Suinae), no *incisura infra orbitalis*, short jugular process, short or low (tip–root) C<sup>m</sup>, and C<sup>m</sup> not directed or curved outwards. These characters do not preclude a closer relationship with the Hyotheriinae, while the shape of the prezygomatic shelf plainly supports such a relationship. Here the genus is treated with the Hyotheriinae.

#### Evolution of *Chleuastochoerus*

As stated above, Pearson (1928) showed size differences in *Chleuastochoerus*. This was picked up by Van der Made and Han (1994), who suggested that these differences reflect evolution and time, not geography or ecological differences between contemporaneous populations, and presented a stratigraphic scheme in which the larger *Chleuastochoerus* evolved from the smaller one. This still remains the most likely explanation and is confirmed to some extent by palaeomagnetic dating of Yuanmou and Lufeng (Qi et al. 2006). In addition to a minor increase in size or length of the molars (Fig. 35), the P<sub>4</sub> seems to acquire a better developed metaconid, and there may be lengthening of the premolars (unfortunately, premolar sizes were not published by Pearson 1928). Schlosser’s (1903) type material is very poor, and its present whereabouts are not known to me, but the possibility exists that his name “*microdon*” applies to the smaller form.

Accepting *Chleuastochoerus* as a Hyotheriine, it is very tempting to search for a link with the Middle Miocene *Hyotherium* from China, the more since the relatively dense record in Europe indicates that *Hyotherium* went extinct there during or after MN6. The I<sup>2–3</sup> with short DMD relative to the width could support a link between the Chinese *Hyotherium* and *Chleuastochoerus* (Figs. 15, 16,

17, 18). However, *Hyotherium* from Shanwang has a somewhat flattened  $I^1$  with a distal cusplet, whereas *Chleuastochoerus* is more primitive in this respect. Also its premolars are much elongated whereas elongation of the premolars seems to occur in *Chleuastochoerus* much later. These observations, based on little material, suggest that there is no direct ancestor–descendant relationship between the Chinese forms. Description (and measurements) of more *Chleuastochoerus* premolars and incisors might resolve the problem.

#### Aureliachoerus

Ginsburg (1974) recognized that the small “*Palaeochoerus*” *aurelianensis* Stehlin, 1899 does not belong to *Palaeochoerus*, but that it is a suid and placed it in the new genus *Aureliachoerus*. *Palaeochoerus minus* was named and described by Golpe-Posse (1972, 1981). The species was transferred to the genus *Aureliachoerus* and the type material was described in more detail (Van der Made 1990a, b; Van der Made and Morales 1999).

Orliac et al. (2006) presented a cladogram in which “*minus*” is in a basal position to a group formed by *Aureliachoerus aurelianensis*, type species of that genus, various species of *Hyotherium* and *Xenohyus*. Apparently because *Aureliachoerus* appears here as paraphyletic, Orliac et al. (2006) introduced the new generic name *Chicochoerus* for *Aureliachoerus minus*. However, in that study some *Taucanamo* material, including an upper canine and a  $P^4$ , was included in “*minus*” (e.g. Fig. 8-2, 8-3), which resulted in an erroneous character state for that taxon: the  $P^4$  of *A. minus* is well known from the type material (Van der Made and Morales 1999) and the  $C^m$  is known from Petersbuch 2 (BSPG: it is not flattened, but has a suid type morphology. In addition, the  $P_4$  of *Aureliachoerus minus* was said to have no metaconid, but *A. minus* from Wintershof West (BSPG has this cusp well developed. This character is notably variable in the Hyotheriinae (Van der Made 1994). The concave postcrisid of the premolars appears twice in the data matrix (characters 3 and 11). The width of the lower premolars is an interesting character, but is treated in a simplistic way compared with the complex pattern that arises from the large amount of data that is available (compare here Fig. 25). In general, character states in the data matrix are based on few specimens, and do not take into account the variability that can be observed in the more extensive collections that are available. All the characters mentioned above contribute to the separation of *Aureliachoerus minus* and *A. aurelianensis* in the cladogram by Orliac et al. (2006).

Characters shared by the two species of *Aureliachoerus*, which present differences from the other Hyotheriinae include: they acquired early a much flattened  $I^1$ , but

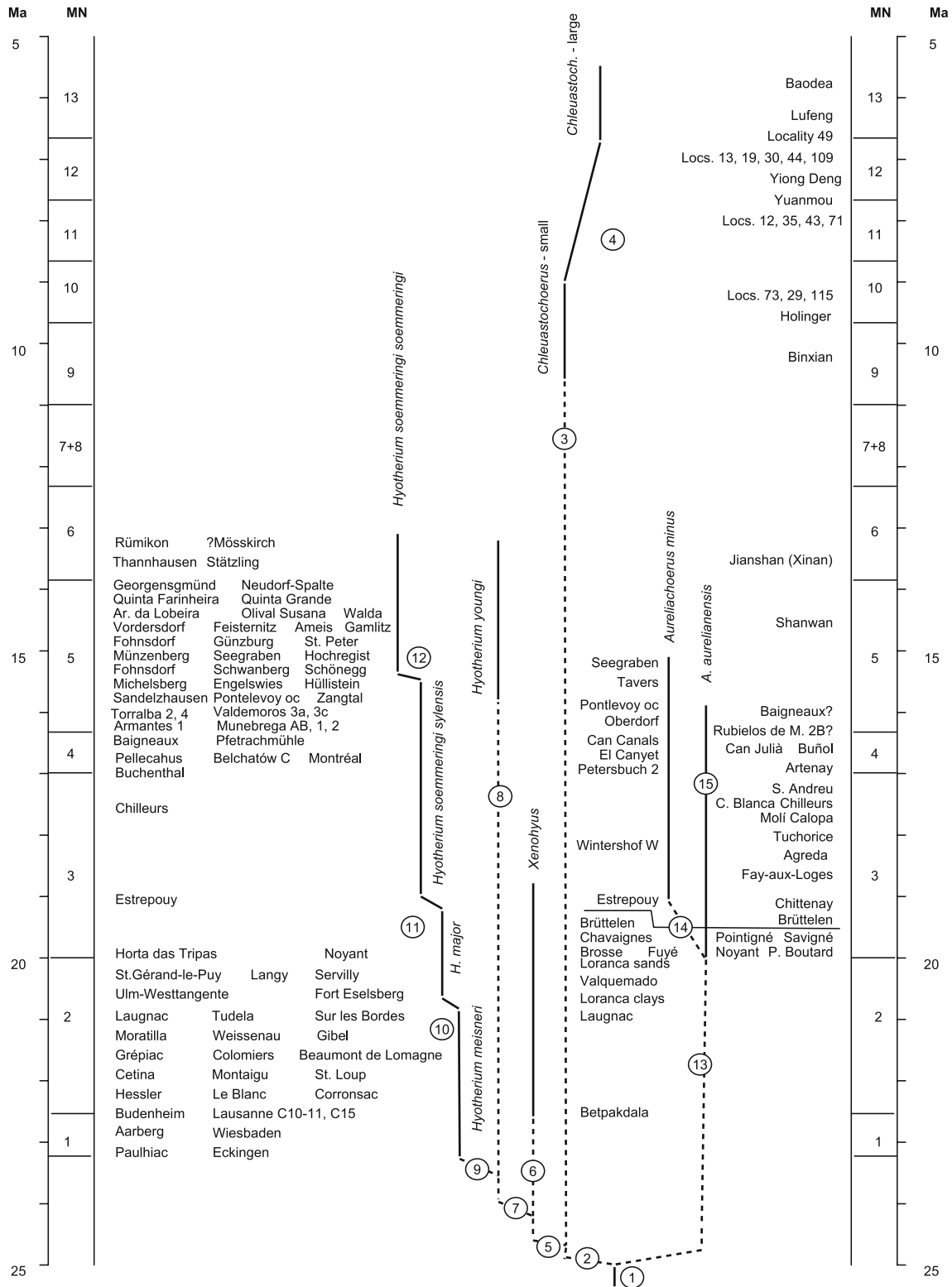
without distal cusplet; the lower central incisors have higher crowns; the proportions of the premolars are different; usually the  $P_4$  has a well developed metaconid, and if this is the case, it is placed more forwards than in the other Hyotheriinae. Most of these characters are derived within the context of the Hyotheriinae, while *Aureliachoerus* does not have a much anteriorly extended prezygomatic shelf (Collier and Guex 1977), which is a derived character in *Hyotherium* and *Chleuastochoerus*. *Aureliachoerus aurelianensis* has several characters that separate it in an even more fundamental way from the other Hyotheriinae. It has a well developed postglenoid process that may well function to limit the movement of the jaw to orthal mastication, as in living peccaries. It has an extremely developed sagittal crest, with a height of up to 15 mm (in such a small animal!; material from Artenay in NMB). This indicates much stronger temporal muscles than in *Hyotherium* and *Chleuastochoerus*. This is a feature that is commonly related to orthal mastication. In living Suidae, the masseter tends to be the dominant muscle in mastication, while the temporalis is much less important (Turnbull 1970), but *Aureliachoerus aurelianensis* seems to have a fundamentally different way of mastication than most or all other Suidae. It is not clear whether the apparent predominance of the temporalis is related to the presumed more orthal way of mastication. Nevertheless, the mandibular condyle is in a high position, which is different from what is commonly found in species with orthal mastication.

Instead of being paraphyletic, it seems that *Aureliachoerus* is monophyletic and separate from *Hyotherium*, *Chleuastochoerus*, and *Xenohyus*, which seem to form a closely related group, treated here as the Hyotheriini. *Aureliachoerus* is treated here as a different tribe, Aureliachoerini, including one genus, with two species: *A. minus* and *A. aurelianensis*. A formal definition of the tribe is given in the next section.

#### Phylogenetic tree

A hypothesis of a phylogeny is presented in Fig. 36. The same conventions are used as in the tree of the Taucanaminae (Fig. 32). The numbers in circles refer to the following characters.

- (A) Primitive characters within the Suidae: (a) short (tip–root)  $C^m$ ; (b)  $C^m$  directed downward and only slightly outward; (c)  $C^m$  nearly straight and without important outward curvature; (d)  $C^m$  with very faint development of lingual enamel band (endosyncline); (e)  $C^f$  with two roots (each one with its pulp cavity, although they may be externally fused); (f)  $C_m$  with scrofic section (probably primitive for Suidae); (g)



**Fig. 36** Proposed phylogeny of the Hyotheriinae. Conventions as in Fig. 32. European *Hyotherium* localities on the left, Chinese *Hyotherium* localities (Jianshan and Shanwan) on the right, *Chleuastochoerus* localities on the upper right, localities with *Aureliachoerus minus* in

the middle of the figure above the horizontal line, localities with *A. aurelianensis* on the right above the line, *Xenohyus* localities in the middle below the line

- $C_m$  hypsodont, but permanently growing: although it stops formation of continuous dentine on lingual and labial sides of the crown in old individuals; (h)  $C_f$  with posterior enamel, (i) bulla with short vertical axis; (j) short and posteriorly directed paroccipital process of squamosal (jugular process); (k) although variable: one foramen lacrymale (in each orbita) in most of the individuals, (l) no *incisura preorbitalis*, (m) low position of occipital, (n) relatively narrow occipital. (B) Common derived characters of the Hyotheriinae as compared with other Suidae: (a)  $P_4$  usually with metaconid, although in all genera there are specimens where this cusp is not well developed; (b) well developed preorbital fossa. (C) Primitive character states for the Hyotheriinae: (a)  $I^1$  without meso–distal elongation; (b)  $I^1$  without distal cusplet; (c) very short  $I^2$  and  $I^3$ ; (d) moderately elongate premolars; (e) small M3; (f) small body size; (g) saddle-shaped glenoid without important pre and postglenoid processes.
2. Large prezygomatic shelf present in males, but not always well developed in females.
  3. (a) Increase in ornamentation of the snout region (especially above the canines), at least so in the males; (b) increased development of the prezygomatic shelf; (c) reduction of premolar size relative to the molars (?); (d) occasional diastemas in the area C–P2; (e) increase in size of the posterior molars; (f) reduction in height of the  $C^m$  (?–compare 5d and 13i).
  4. (a) moderate size increase, at least in the molars; (b) elongation of molars; (c) better developed metaconid on  $P_4$ , (d) elongation of the  $P_3$  and  $P_4$ .
  5. (a) Enlargement of the central incisors ( $I^1$ ,  $I_{1-2}$ ); (b) occasional distal cusplet on the  $I^1$ ; (c) moderate enlargement of the M3; (d) more high crowned  $C^m$  (?–compare 3f).
  6. (a) Great enlargement of central incisors; (b) distal cusplet on  $I^1$  larger and more frequent; (c) possible reduction size  $P_1$  and  $P_2$ ; (d) progressive size increase within the genus; (e) possibly flattening of  $I^1$  (or meso–distal elongation) within the lineage.
  7. Flattening (or meso–distal elongation) of the  $I^1$ .
  8. (a) Size increase M3, (b) enlargement premolars.
  9. (a) Increased elongation of the  $I^2$  and  $I^3$ , (b) elongate  $P_2$  and  $P_3$ .
  10. Size increase, a tendency that is present already in *H. meisneri*, but which seems to accelerate here.
  11. (a) Prezygomatic shelf always well developed in females, but even better in males; (b) distal cusplet on  $I^1$  always present and large, and progressively becoming still larger in the lineage; (c) occasional development of a swelling in the postcrista of the  $I^2$ ; (d) metaconid on  $P_4$  always well developed; (e) appearance of high proportion of elongate  $P_4$  in the samples (morphologically this is reflected in a metaconid that is placed more posteriorly with respect to the protoconid); (f) decrease of the proportion of short  $P_3$  in the samples; (g) para and metacone on  $P^4$  progressively better separated; (h) continued size increase.
  12. (a) Still larger size; (b) occasional return to short  $P_3$  and  $P_4$ .
  13. (a) Well developed postglenoid process; (b) extreme development of the sagittal crest, reflecting very important temporalis muscles; (c) possibly acquired at this point: a high mandibular condyle; (d) a much flattened  $I^1$ ; (e) increase in crown height of lower central incisors; (f) elongation of  $I^2$ ; (g) usually a well developed metaconid on the  $P_4$ , placed lingually (and not linguo-distally) to the protoconid; (h) probably incisors more hypsodont (than in *Hyotherium*); (i) increase height of  $C^m$  (?–compare 3f).
  14. (a) Better separation of the buccal cusps of the  $P^4$ ; (b) probably initial size decrease and minor continued size decrease during the lineage.
  15. Within *A. aurelianensis* there is a tendency for the M3 to become distally expanded by the addition of cusps.

#### Updated classification of the Palaeochoeridae and Hyotheriinae

Although zoological classification and nomenclature describe nature, it should be recognized that they are man-made. Classification originated long before the acceptance of evolution and was originally based on morphology. Classification should not contradict evolution, but the best way to present the evolution of a group, is usually a phylogenetic tree, not a complex classification with numerous levels of classification that try to catch each node in a cladogram. Introducing new names for many morphologically similar branches of a paraphyletic taxon, is more likely to confuse than to help.

For a taxon to be formally named (or for use of an available name to continue), it should be possible to recognize the taxon on the basis of morphology or, in the case of a species or subspecies, size. There are authors who recognize within a genus one species per continent or subcontinent, without even considering the possibility of a wider distribution (see discussions on particular cases concerning the Suoidea: Van der Made 1996a, Van der Made 1999a, b), although the species *Sus scrofa* has a natural distribution in three continents. Lumping poor

material from distant localities into a single species, may give the false impression of a widespread species, while in fact there are several imperfectly known species. However, giving such specimens different names (even if such names are already available) equally gives a false impression and, moreover, accepts the lack of morphological data as a basis for classification.

If an available name is not considered to be “valid” here for the reasons mentioned above, it still may be available in the sense of the ICZN, and when new data or interpretations justify the use of such a name, it is available for use. Not to use all formally available names, is not a destructive act, but using too many names may be very destructive with respect to the wider view.

It occurs, often, that several species are named, and that later, after the record increased, it could be seen that these species could be arranged in lineages (as was the case with the European *Hyotherium*). The result is that the name-bearing types are usually not situated at regular distances along such a lineage. Moreover, the rule of priority does not allow free choice from the available names those based on types that are situated at convenient morphological or metrical distances from each other. This is a handicap in the classification of the stages of a lineage.

The fossil record is not complete. There are gaps in basins, there are times that are continent wide under-represented in the fossil record and there are fluctuations in the representation of a taxon because of environmental change. There are lineages that show marked changes in their geographical distribution. In combination with previous phenomena, this may lead to sections of a lineage being very well represented at different times and places, and poorly or not at all in other places. In such cases it is convenient to situate (arbitrarily) the limit between taxa in a gap of the record, if this is possible, rather than in the middle of a dense sequence of numerous samples showing a gradual morphological cline. Here the transition of *H. major* to *H. soemmeringi* is conveniently placed at such a position.

Here, the classification by Van der Made (1997) for the Palaeochoeridae and of Van der Made (1994) for the (European) Hyotheriinae is updated with additions and modifications as discussed above and in the following paragraphs. The method of classification is compatible with that of the Listriodontinae (Van der Made 1996a) and Tetraconodontinae (Van der Made 1999). In addition, some themes are discussed that were not covered by these earlier classifications.

***Egatochoerus*.** Ducrocq (1994) described *Egatochoerus jaegeri* as an early representative of the Tayassuidae from the Eocene of Thailand. Whereas upper molars and an astragalus are compatible with an assignment to the Suoidea, the holotype of the species is more problematic. Its mandible that is very deep, much deeper than in any early

suoid, and a deep and massive mandible is typical of the later Suidae and Dicotylidae. The molars in this mandible are much worn and difficult to evaluate. The P<sub>4</sub> has an extremely large metaconid and a not well differentiated hypoconid; in the Suoidea a large metaconid tends to be a derived character that appears well after the hypoconid is clearly differentiated. In addition, the metaconid is more separate from the protoconid than is the case in any suoid. The P<sub>1</sub> is lost (reduced), whereas this tooth tends to be present in the primitive Suoidea, and only much later gets lost. There are thus reasons to doubt the assignment of the type material of this species and genus to the Suoidea.

***Siamochoerus*.** Other Eocene Thai material that Ducrocq et al. (1998) described as *Siamochoerus banmarkensis* and placed in the Suidae, has clearly a suoid morphology and is said to have “unfused molar roots”, which indeed suggests similarities with the Suidae.

**Eocene of China.** Liu (2001) described material from the Eocene of China and named: *Eocenchoerus savagei* (two upper teeth; placed in the “Suidae?”), *Siamochoerus viriosus* (three lower molars and half a molar; Palaeochoeridae), *Huaxiachoerus guanxiensis* (tree upper molars; Palaeochoeridae), and a single upper molar was assigned to Tayassuidae gen. et sp. indet. The material is poor and many important characters cannot be observed; nevertheless, the material shows the presence of a variety of species with molars having a suoid morphology. The M<sub>2</sub> assigned to *S. viriosus* shows separate roots below the anterior lobe, which is a character suggesting affinities with the Suidae. The upper molar assigned to the Tayassuidae has a proto-preconule that is relatively well separated from the protocone and, although this separation is not complete as in the Suidae, it suggests affinities with this family. This molar is not very different in size from those assigned to *S. viriosus*, and might belong to the same species. *Huaxiachoerus* has upper molars with two lingual roots connected with a thin bony plate, giving a structure that has been compared with that of a webbed foot of a duck. The proto-preconule is fused to the protocone and the cusps have an angular outline similar to that of the lower molars of *Odoichoerus*. The size is also very similar. The enamel is thick, which is reported to be a difference from *Odoichoerus* (Liu 2001), but no measurements were given in support. The two genera are probably closely related, if not the same. In *Eocenchoerus*, the proto-preconule is fused to the protocone and the genus might belong to the Palaeochoeridae.

***Pecarichoerus sminthos*.** Pickford (1983) transferred *Anthracotherium sminthos* Forster-Cooper, 1913 to *Pecarichoerus*. The type from Bugti consists of a M<sub>2</sub> and M<sub>3</sub>, with a morphology and size that are compatible with an assignment to the Taucanamini, but which really are insufficient for a reliable classification. Although the type species *Pecarichoerus orientalis* is a taucanamine from the

Indian Subcontinent, the species “*sminthos*” could as well belong to a different genus, such as *Taucanamo*.

*Sanitherium* is now excluded from the Palaeochoeridae. Pickford (2004, Fig. 6–8) assigned an upper canine to a sanithere that seems to have a lingual enamel band, which up to now is only known from the Suidae (Van der Made 1996b). The possibility exists that the sanitheres are more related to the Suidae than to the Palaeochoeridae.

**Gryphon taxon.** Material that has been assigned to *Nguruwe kijivium*, *Lopholistriodon moruoroti*, and *Albanohyus* (Van der Made 1996a, b) was united with still other material and described as the new genus and species *Morotochoerus ugandensis*, belonging to the Schizochoerinae (Pickford 1998). However, there is no reason to doubt the earlier taxonomical assignments of that material, and because the diagnosis contains characters from several different taxa, *Morotochoerus* can be considered to be a gryphon taxon. The holotype of the type species *Morotochoerus ugandensis* probably represents an early form of *Lopholistriodon pickfordi*.

**Lorancahyus.** Pickford and Morales (1998) named a genus and two species: *Lorancahyus hypsorhizus* and *Lorancahyus daamsi*, which were placed in the Doliochoerinae, Tayassuidae. The type material of the latter species may well represent *Palaeochoerus typus*, while the former species shows characters that relates it to *Propalaeochoerus* sp. A of Van der Made (1994), such as simple molar structure, talon and talonid of third molars small, and massive fused roots of the molars.

**Aureliachoerini new tribe.** As indicated above, *Aureliachoerus* is considered to have a fundamentally different ways of mastication from other Hyotheriinae, and is placed here in a separate tribe. The definition of the Aureliachoerini n. tribe is: Hyotheriinae, with an extremely developed sagittal crest and a well developed postglenoid process.

**Dicotylidae.** Comparisons are made here between the Suoidea from Sandelzhausen and the New World peccaries. These are often placed in the Tayassuidae Palmer, 1897 (Simpson 1945; McKenna and Bell 1997), even though their synonymies indicate that other names have priority (Dicotylidae Turner 1849; Cynorcidae Cope 1867). Groves and Grubb (1993) applied the name Dicotylidae, and if these authors did not overlook a nomenclatorial problem, the use of this name must be justified and is followed here.

**Classification.** The classification of the Palaeochoeridae and Hyotheriinae is here given to subspecies level. As a

context, also the major divisions of the other Suidae are given. Detailed classifications of the Listriodontinae and Tetraconodontinae have been given elsewhere (Van der Made 1996a, Van der Made 1999a, b).

Order Artiodactyla Owen, 1848

Superfamily Suoidea Gray, 1821

Family Palaeochoeridae Matthew, 1924

Subfamily unknown.

*Odoichoerus* Tong and Zhao, 1986 (?=*Huaxiachoerus* Liu, 2001)

*O. uniconus* Tong and Zhao, 1986, type species (?=*H. guanxiensis* Liu, 2001)

*Huaxiachoerus* Liu, 2001

*H. guanxiensis* Liu, 2001, type species

? *Eocenchoerus* Liu, 2001

*E. savagei* Liu, 2001, type species

Subfamily Taucanaminae Van der Made, 1997 (=Schizochoerinae Golpe-Posse, 1972)

Genus unknown (attribution to Taucanaminae hypothetical)

“*Anthracoherium*” *sminthos* Forster-Cooper, 1913

Tribe Schizoporcini new name (=Schizochoerini Golpe-Posse, 1972)

*Schizoporcus* new name (=Schizochoerus Crusafont and Lavocat, 1954)

*S. muenzenbergensis* (Van der Made, 1998)

*S. anatoliensis* (Van der Made, 1997)

*S. sinapensis* (Van der Made, 1997)

*S. vallesiensis* (Crusafont and Lavocat, 1954) (= *Schizochoerus*

*arambourgi* Ozansoy, 1965), type species

Tribe Schizoporcini?

*Pecarichoerus* Colbert, 1933

*P. orientalis* Colbert, 1933, type species

Tribe Taucanamini Van der Made, 1997

*Taucanamo* Simpson, 1945

*T. primum* Van der Made, 1997

*T. sansaniense* (Lartet, 1851), type species

*T. inonuensis* Pickford and Ertürk, 1979

*T. grandaevum* (Fraas, 1870)

*Yunnanocherus* Van der Made and Han, 1994

*Y. gandakasensis* (Pickford, 1977)

*Y. lufengensis* (Han, 1983), type species

Subfamily Palaeochoerinae Matthew, 1924 (=Doliochoerinae Simpson, 1945)

Tribe Doliochoerini Simpson, 1945

*Doliochoerus* Filhol, 1882 (?=*Propalaeochoerus* Stehlin, 1899)

*D. quercyi* (Filhol, 1882), type species

*Propalaeochoerus* Stehlin, 1899

*P. leptodon* (Pomel, 1848)

*P. elaverensis* (Viret, 1929), type species

*Propalaeochoerus* sp. A Van der Made, 1994

*Propalaeochoerus* sp. B Van der Made, 1994

*Lorancahyus* Pickford and Morales, 1998

*L. hypsorhizus* Pickford and Morales, 1998, type species



- Tribe Palaeochoerini Matthew, 1924
- Palaeochoerus* Pomel, 1847 (= *Dubiotherium* Hellmund, 1992)
- P. paronae* (Dal Piaz, 1930)
- Palaeochoerus?* *pusillus* Ginsburg, 1974
- P. gergovianus* (De Blainville, 1846), type species
- P. typos* Pomel, 1847, type species (= *P. gergovianus*; = ?
- Lorancahyus daamsi* Pickford and Morales, 1998)
- P. aquensis* (Repelin, 1930) (= *Palaeochoerus massiliensis* Viret, 1929; = *Palaeochoerus waterhousi* Pomel, 1853 (type species of *Dubiotherium*))
- Family Suidae Gray, 1821
- Subfamily unknown.
- Siamochoerus* Ducrocq, Chaimanee, Suteethorn and Jaeger, 1998
- S. banmarkensis* Ducrocq, Chaimanee, Suteethorn and Jaeger, 1998
- S. viriosus* Liu, 2001
- ?Subfamily Sanitheriinae Simpson, 1945 (= Xenocherinae Thenius, 1979)
- Sanitherium* Von Meyer, 1866 (= *Xenocherius* Zdarsky, 1909; =
- Diamantohyus* Stromer, 1926)
- S. jeffreysi* (Forster-Cooper, 1913)
- S. africanus* (Stromer, 1926) (type species of *Diamantohyus*) (= ?
- Sanitherium nadirum* Wilkinson, 1976)
- S. schlagintweitii* Von Meyer, 1866, type species (= *Sus pusillus* Falconer, 1868; = *Xenohyus leobense* Zdarsky, 1909; = *Sanitherium cingulatum* Pilgrim, 1926; = *Sanitherium masticum* Paraskevaidis, 1940)
- Subfamily Hyotheriinae Cope, 1888
- Tribe Aureliachoerini new tribe
- Aureliachoerus* Ginsburg, 1974 (= *Chicochoerus* Orliac, Antoine and Duranthon, 2006)
- A. aurelianensis* (Stehlin, 1899-1900), type species
- A. minus* (Golpe-Posse, 1972) (type species of *Chicochoerus*)
- Tribe Hyotheriini Cope, 1888
- Chleuastochoerus* Pearson, 1928
- C. stehlini* Schlosser, 1903, type species
- C. stehlini* Pearson, 1928 - small (= *Sus microdon* Schlosser, 1903)
- C. stehlini* Schlosser, 1903 - large
- Hyotherium* Von Meyer, 1834 (?incl. subgenus *Palaeohyus* Von Meyer, 1859; incl. *Miochoerus* Chen, 1997; *Sinapriculus* Liu, Fortelius and Pickford, 2002)
- H. meisneri* (Von Meyer, 1829)
- H. major* (Pomel, 1847)
- H. soemmeringi* (Von Meyer, 1829)
- H. s. wylensis* (Von Meyer, 1859) (= *Conohyus cuspidatus* Golpe-Posse, 1972 = *H. lacaillei* Orliac, Antoine and Duranthon, 2006)
- H. s. soemmeringi* (Von Meyer, 1829) (= *Hyotherium soemmeringi bavaricum* Dehm, 1980) (= ?
- Choerotherium Dupuii* Lartet)
- H. youngi* (Chen, 1997), type species of *Miochoerus* (= *S. linquensis* Liu, Fortelius and Pickford, 2002, type species of *Sinapriculus*) (= *H. shanwangense* Liu, Fortelius and Pickford, 2002)
- Xenohyus* Ginsburg, 1980
- X. betpakdalensis* (Trofimov, 1949)
- X. venitor* Ginsburg, 1980, type species
- Xenohyus* sp. (Pickford and Morales, 1989)
- Subfamily Cainochoerinae Pickford, 1988
- ? *Kenyasus* Pickford, 1986
- Cainochoerus* Pickford, 1988
- Albanohyus* (= *Barberahyus*, Golpe Posse, 1977)
- Subfamily Listriodontinae Gervais, 1859
- Subfamily Tetraconodontinae Lydekker, 1876
- Subfamily Babyrousinae Gray, 1868 (incl. Potamochoerini Gray, 1873)
- Celebochoerus* Hooijer, 1948
- Potamochoerus* Gray, 1854
- Babyrousa* Perry, 1811
- Subfamily Suinae Gray, 1821
- Tribe Dicoryphochoerini Schmidt-Kittler, 1971 (= Propotamochoerini Pickford, 1993)
- Tribe Phacochoerini Gray 1868 (incl. Hippohyini Thenius, 1970; Hyosuinae Thenius, 1979)
- Tribe Suini Gray, 1821
- Family Dicotylidae Turner, 1849 (= Tayassuidae Palmer, 1897; Cynorcidiae Cope, 1867)

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