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Aureliachoerus from Oberdorf and other Aragonian pigs from Styria

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(With 10 text-figures and 1 plate)

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Abstract

An important collection of fossil Suoidea (pigs) from nearly twenty localties in the Aragonian (Early and Middle Miocene) of Styria (Austria) has figured prominently in discussions on the evolution of the Suoidea. Recent work on the Suoidea revealed many problems in suoid systematics and evolution and the description of new finds from Oberdorf induced a redescription and discussion of the Styrian suoids.

European Suoidea belong to two families: Suidae (pigs) and Palaeochoeridae (their primitive relatives). The members of the two families have been mixed up frequently, and this was also the case with the Styrian fossils.

Aureliachoerus minus from the Early Aragonian (Neogene Mammal Unit MN 4) of Oberdorf and Middle Aragonian (MN 5) of Seegraben is a small suid, but has been confused with various spieces of the palaeochoerid *Taucanamo*. The types of this species have been considered to represent small individuals of the larger species *A. aureliachoerus*. The material from Styria shows that a smaller and a larger species of the same genus were coeval.

The evolution of *Taucanamo sansaniense* and the suid *Conohyus simorrensis* is becoming better known and suggests that the locality of Göriach, where both are found, is late MN5 or early MN 6. A new species is named for a palaeochoerid from Münzenberg, *Taucanamo? muenzenbergensis*.

Sanitherium schlagintweiti belongs to the Palaeochoeridae and may well be a descendant of *Palaeochoerus* or a closely related form. Its level of evolution suggests an age of less than about 14 Ma for the locality of Seegraben, which is placed in MN 5.

Hyotherium major and *H. soemmeringi* form one lineage, which is found all over western and central Europe. The lineage is characterised by an increase in the size of molars and increase in size and elongation of the premolars, along with other morphological changes. Within *H. soemmeringi*, two chrono subspecies can be recognized: *H. s. wylensis* (MN 3–5) and *H. s. soemmeringi* (MN 5–6). Fossils from over ten localities in Styria belong to the latter subspecies.

Listriodon splendens indicates a Late Aragonian age for two of the Styrian localities.

Zusammenfassung

Für die Diskussion der Evolution der Suoidea spielt die bedeutende Sammlung von fossilen Suoidea (Schweineartige) aus nahezu zwanzig Fundstellen des Aragoniums (Unter- und Mittel-Miozän) der Steiermark (Österreich) eine entscheidende Rolle. Neue Bearbeitungen der Systematik und Evolution der Suoidea machten viele Schwierigkeiten. Die Bearbeitung neuer Funde von Oberdorf zieht eine Neubeschreibung und Diskussion der Steirischen Schweineartigen mit sich. Die Europäischen Suoidea verteilen

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sich auf zwei Familien: Suidae (Schweineverwandte) und *Palaeochoerus* (ihre ursprünglichen Verwandten). Nicht immer wurden Schweinefossilien der richtigen Familie zugeschrieben, so auch in der Steiermark.

Aureliachoerus minus aus dem frühen Aragonium (Neogene Säugetiereinheit MN4) von Oberdorf und aus dem mittleren Aragonium (MN5) von Seegraben ist ein kleines Schwein, das mit verschiedenen Arten von *Taucanamo* (Palaeochoeridae) verwechselt wurde. Die Typen dieser Art wurden als kleine Individuen der größeren Art *A. aureliachoerus* angesehen.. Das Material aus der Steiermark beweist das gleichzeitige Vorkommen einer kleineren und einer größeren Art dieser Gattung.

Die zunehmende Kennnis der Evolution von *Taucanamo sansaniensis* und des Schweines *Conohyus simorrensis* zeigt, daß die Lokalität Göriach, wo beide Formen vertreten sind, in die späte MN5 oder frühe MN6 einzustufen ist. Aus Münzenberg wurde *Taucanamo muenzenbergensis*, eine Palaeochoeride, neu beschrieben.

Sanitherium schlagintweiti gehört zu den Palaeochoeridae und kann ein Nachfahre von *Palaeochoerus* oder einer nah verwandten Form sein. Sein Evolutionsniveau läßt für die Lokalität Seegraben, die in MN5 gestellt wird, ein geringeres Alter als etwa 14 Ma vermuten.

Hyotherium major und *H. soemmeringi* bilden eine Linie, die über ganz West- und Mitteleuropa verfolgt werden kann. Diese Entwicklungslinie ist neben anderen morphologischen Veränderungen duch die Größenzunahme der Molaren und die Verlängerung und Vergrößerung der Prämolaren charakterisiert. *H. soemmeringi* umfaßt zwei Chrono-Subspecies: *H. s. wylensis* (MN 3–5) und *H. s. soemmeringi* (MN5–6). Aus der Steiermark gehören Fossilien aus mehr als zehn Lokalitäten letzterer Subspecies an.

Zwei Fundstellen aus der Steiermark werden durch das Vorkommen von *Listriodon splendens* in das späte Aragonium eingestuft.

Introduction

Fossil pigs from Styria were mentioned or described as long ago as the 1860s (SUESS 1867; PETERS 1869). Large collections were made from the mines of Styria, but when the method of mining changed and mines closed, collecting stopped. Recently, the Oberdorf project added some new finds to the existing suoid collections. The finds come from the open-cast mine Oberdorf, north of Voitsberg, in the Köflach-Voitsberg coalfield, in Styria (Steiermark). The exact provenance is from the coal and clay layer O4 in the north section of the eastern part of the coal field.

A comprehensive description of the Styrian pigs was given by THENIUS (1956). However, since that time, much has changed in our understanding of suoid evolution and systematics. There are three palaeochoerids in the Styrian Aragonian localities. Two of these and the small suid from Oberdorf and Seegraben have been mixed up. It is only natural to discuss this material and the systematics of these species in one paper. There is abundant material of *Hyotherium soemmeringi* in Styria, which differs from material from other localities assigned to this species. The evolution of this species is discussed here. Göriach has the largest collection of *Conohyus simorrensis*. I described the evolution of this species (Van der MADE 1989), but since that time more material has become available from other localities that corroborates the evolutive tendencies found and that enables increasingly precise correlations.

It is the aim of this paper to describe the material from Oberdorf, as well as discuss other suoids from the Aragonian of Styria.

Synonymies are restricted to material from Styria.

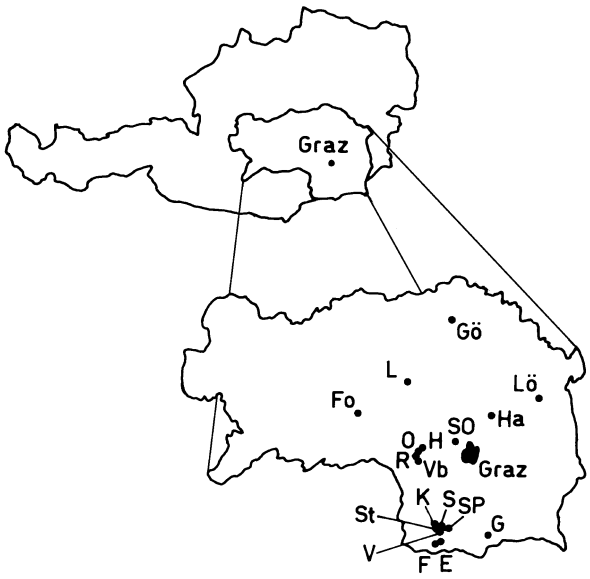

Fig. 1: Geographical distribution of the localities (mainly after MOTTL 1970).

E = Eibiswald;
F = Feisternitz;
Fo = Fohnsdorf;
Gö = Göriach & Au;
G = Gamlitz;
H = Hochtregist;
Ha = Haselbach;
K = Kalkgrub bei Schwanberg;
L = Leoben-Seegraben & Leoben-Münzenberg;
Lö = Löffelbach;
O = Oberdorf;
R = Rosental;
S = Schönegg;
SO = St. Oswald bei Gratwein;
SP = Sankt Peter;
St = Steieregg;
V = Vordersdorf;
Vb = Voitsberg-Zangtal.

The Palaeochoeridae – recent changes in their classification

There are several palaeochoerids in the Styrian localities and the suid from Oberdorf has been assigned to a palaeochoerid species. The recognition of new taxonomically useful characters and new interpretations of known characters, the study of holotypes, the recognition of synonymies and a more rigid application of priority rules has lead to many recent and drastic changes in the classification of the Palaeochoeridae, including their recognition as a distinct family of the Suoidea.

On the basis of basicranial features, PEARSON (1927) included the European genera *Doliochoerus* and *Choerotherium* in the Dicotylinae, which until then were believed to be a mainly or exclusively American subfamily of the Suidae. She included *Palaeochoerus* in the Suinae. The name *Choerotherium* was preoccupied and the suoid is now known as *Taucanamo* SIMPSON, 1945. The skulls which PEARSON believed to belong to *Palaeochoerus* belong to *Hyotherium* and consequently her observations are valid for the latter genus and not for *Palaeochoerus* (Van der MADE 1994), a fact that seems to interfere even with recent classifications. The evolution of *Doliochoerus*, *Palaeochoerus* and *Propalaeochoerus* is not yet sufficiently clear and there is probably one genus name too many.

The classification of SIMPSON (1945) has been followed by many palaeontologists. SIMPSON placed *Doliochoerus* and *Taucanamo* in the Doliochoerinae SIMPSON, 1945 and in the Tayassuidae PALMER, 1897 and *Palaeochoerus* in the Hyotheriinae, which he considered to be a senior synonym of Palaeochoerinae MATTHEW, 1924. SIMPSON considered Dicotylinae LEIDY, 1853 and Dicotylina TURNER, 1849 junior synonyms of Tayassuinae HAY, 1902 (!). Present nomenclatorial rules imply that Dicotylidae TURNER, 1849 have priority over Tayassuidae PALMER, 1897 (GRUBB & GROVES 1993) and Dicotylinae TURNER, 1849 over Tayassuinae PALMER, 1897.

Palaeochoerus is included in the Doliochoerinae in the majority of recent publications (GINSBURG 1974, 1980; Van der MADE 1990 a+b; HELLMUND 1992), though PICKFORD (1988) includes the genus in the Palaeochoerinae in the Suidae. The latter author may have based himself on PEARSON (1927). However, if *Palaeochoerus* is included in the Doliochoerinae, the name Palaeochoerinae is the valid name the whole group (Van der MADE 1994). Finally the group was given family status (Van der MADE 1996b).

Albanohyus GINSBURG, 1974 and *Barberahyus* GOLPE POSSE, 1977 have often been included in the "Doliochoerinae", but are synonymous and belong to the Cainochoerinae, Suidae (Van der MADE 1996b).

Along with basicranial morphology, the vertical orientation of the upper canines have been used to recognize the "Doliochoerinae". However, the earlier Suidae do not always have upper canines that flare out as much as is believed to be typical for the whole group. Consequently the character should be applied with caution. Differences between Suidae and Palaeochoeridae include the following characters (Van der MADE 1996b).

1) The anterior and posterior lobes in the M_1 and M_2 and the anterior lobe in the M_3 have each two separate roots in the Suidae; in the Palaeochoeridae, these roots are fused. In Cainochoerinae (Suidae) the two roots below one lobe may be fused over a certain distance. It is not to be excluded that in later Palaeochoeridae, parallel to the Suidae, the molars acquired two separate roots below each lobe.
2) Upper molars in Palaeochoeridae have the lingual roots fused and Suidae have two separate roots. Later palaeochoerids may have acquired two separate lingual roots in the upper molars.
3) The protoconule tends to be fused to the protocone in Palaeochoeridae and to the anterior cingulum in the Suidae (Listriodontinae are aberrant suids in this respect).
4) The C^m have two enamel bands in Palaeochoeridae and three in Suidae. However, in primitive Listriodontinae and primitive Hyotheriinae, the "bands" are still slight undulations in the lower limit of the crown and thus more difficult to recognize and interprete.
5) Metapodials have a median crest at the distal articulation which clearly continues on the dorsal side in Suidae, but not or not so clear in the Palaeochoeridae.
6) The proximal articulation of the first phalange reflects character 5.

The characters mentioned above include three or four independent character complexes, some of which might be well developed before basicranial morphology of the Suoidea diversified. Tooth morphology and the mandibulo-cranial joint are integrated in the masticatory apparatus; it is to be expected that certain aspects of basicranial morphology in suoids are not such reliable taxonomical indicators, if studied in isolation.

It is convenient to give a classification of taxa mentioned in the discussions on the suoids in this paper.

Superfamily Suoidea
- Family Palaeochoeridae
  - Subfamily Palaeochoerinae
    - *Palaeochoerus*
    - *Propalaeochoerus*
    - *Doliochoerus* (which might be synonymous to one of the two other genera)
    - *Sanitherium* (see discussion on *S. schlagintweiti*).
  - Subfamily Schizochoerinae
    - *Schizochoerus*
    - *Taucanamo*
- Family Suidae
  - Subfamily Cainochoerinae
    - *Albanohyus*
  - Subfamily Listriodontinae
    - *Listriodon*
  - Subfamily Hyotheriinae
    - *Hyotherium*
    - *Aureliachoerus*
    - *Xenohyus*
  - Subfamily Tetraconodontinae
    - *Conohyus*
    - *Parachleuastochoerus*
- Family Dicotylidae
  - Subfamily Dicotylinae
    - *Tayassu*

Stratigraphy

The Neogene Mammal Units (MN-units) are used (De BRUIJN et al. 1992). Magnetostratigraphic dating of the zones of the Aragonian and MN units was done by KRIJGSMAN et al. (1994). These dates were slightly corrected by KRIJGSMAN et al. (1996) and ALVAREZ SIERRA et al. (1997), who also included zone D of the Aragonian in MN 5. The latter is an attempt to minimize differences between MN 5 as it was used in Spain and as it was used in Central Europe. On the basis of the study of intercontinental dispersal events, I arrived independently at strikingly similar results (Van der MADE 1996). Differences remain with the estimates of the absolute ages or the MN units by, for instance, RÖGL & STEININGER (1984), RÖGL (1996) and STEININGER et al. (1996).

These different opinions affect the dating of Oberdorf. The locality of Oberdorf is placed in MN 4 and in Chron C5Dn as indicated by DAXNER-HÖCK et al. (this volume, p. 212–219); this implies an age of over 17 Ma. ALVAREZ SIERRA et al. (1997) estimate the MN3–4 transition at 16.7 Ma.

Nomenclature, measurements and abbreviations

In the descriptions of the teeth the nomenclature of Van der MADE (1996a) is used, see also Fig. 2.

Measurements taken as indicated by Van der MADE (1996a). All measurements in mm, unless indicated otherwise.

DAP Antero-posterior diameter in teeth and bones. "Length" of a tooth.
DLL Labio-lingual diameter of an incisor.
DMD Meso-distal diameter of an incisor.
DT Transverse diameter or width in teeth and bones.
DTa Transverse diameter of the anterior lobe of a tooth.
DTp Transverse diameter of the posterior lobe of a tooth.
Dtpp Transverse diameter of the third lobe of a M3.
Hla Height of the crown measured at the labial side.
Hli Height of the crown measured at the lingual side.
I Index of a tooth: 100 DAP/DT.
Li Width of the lingual side of the C_m, taken as low as possible, usually just above the alveolus.
La Width of the labial side of the C_m, taken as low as possible, usually just above the alveolus.
Po Width of the posterior side of the C_m, taken as low as possible, usually just above the alveolus.
Ta Thickness of the enamel measured at the metaconid.
Tp Thickness of the enamel measured at the entoconid.

Collections

BSPHGM Bayerische Staatssammlung für Paläontologie und Historische Geologie, München.
CEPUNL Centro de Estratigrafia e Paleobiologia da Universidade Nove de Lisboa.
FISF Forschungs-Institut Senckenberg, Frankfurt.
GML Geological Museum, Lisbon.
IGF Istituto di Geología, Firenze.
IGGML Institut für Geowissenschaften / Geologie der MontanUniversität, Leoben.
IGPKFUG Institut für Geologie und Paläontologie, Karl-Franzens-Universität, Graz.
IPS Institut Paleontológic M. Crusafont, Sabadell.
IPUW Institut für Paläontologie der Universität, Wien.
ISEAK Institute of Systematics and Evolution of Animals, Kraków.
IVAU Instituut Voor Aardwetenschappen, Utrecht.
MGPUSB Museo di Geologia e Paelontologia, Università degli Studi di Bologna.
MHNT Muséum d'Histoire Naturelle, Toulouse.
MNCN Museo Nacional de Ciencias Naturales, Madrid.
MNHNP Muséum National d'Histoire Naturelle, Paris.
MSNO Muséum des Sciences Naturelles, Orléans.
MTA Maden Tetkik ve Arama, Ankara.
MGL Muséum Guimet, Lyon.
MPZ Museo Paleontológico de la Universidad de Zaragoza.
NMB Naturhistorisches Museum, Basel.
NHMW Naturhistorisches Museum, Wien.
PDTFAU Paleoantropoloii, Dil ve Tarih Cografya Facultesi, Ankara Universitesi.
PIMUZ Paläontologisches Institut un Museum der Universität, Zürich.
SLJG Steiermärkisches Landesmueum Joanneum, Graz.
SMNS Staatliches Museum für Naturkunde, Stuttgart.
UCBL Université Claude Bernard, Lyon.

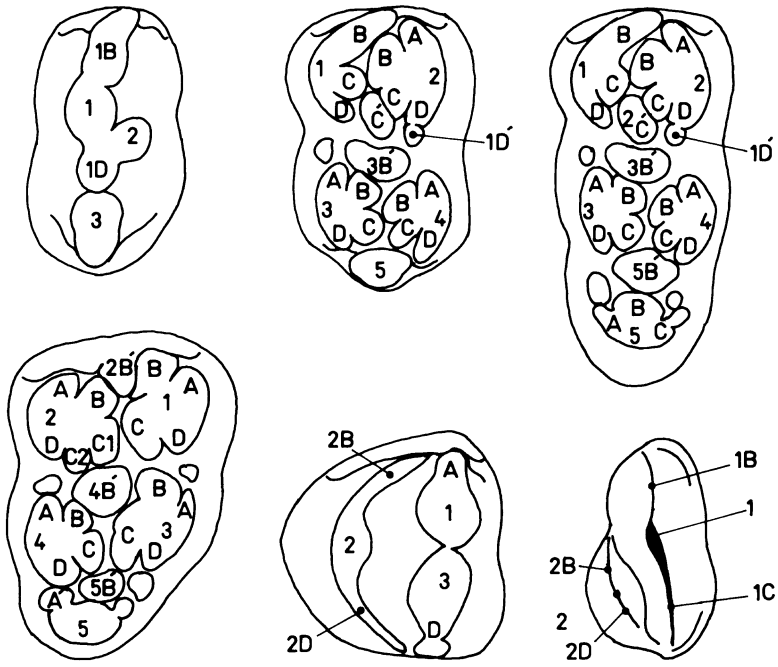

Fig. 2: Nomenclature for Artiodactyle teeth after Van der MADE (1996a). The crests or lobes (--crista, --cristid) and cuspules (--conule, --conulid) are named after the cusp from which they originate (proto-- , meta--, hypo--, tetra--, ento--, penta-- etc.) and according to their position or origin on those cusps (-ecto-, -pre-, -endo- and -post-).

Upper row, from left to right: P_4, $M_{1/2}$, M_3. Legend: 1 = protoconid, 1B = protoprecristid, 1C = protoendocristid, 1D = protopostcristid, 2 = metaconid, 2A = metaectocristid, 2B = metaprecristid, 2C = metaendocristid, 2C' = metaendoconulid, 2D = metapostcristid, 2D' = metapostconulid, 3 = hypoconid, 4 = entoconid, 5 = pentaconid etc.

Lower row, M^3, P^4 and P^2. Legend: 1 = paracone, 1A = paraectocrista, 1B = paraprecrista, 1C = paraendocrista, 1D = parapostcrista, 2 = protocone, 2A = protoectocrista, 2B = protoprecrista, 2B' = protopreconule, 2C = protoendocrista (2C1 = internal and 2C2 = external protoencrocrista, if the lobe is bifurcated as in Suinae), 2D = protopostcrista, 3 = metacone, 4 = tetracone, 5 = pentacone, etc.

The application is not always easy in Suoidea, where the lobes or crests are not very pronounced. For the application to selendont artiodactyls and for a full discussion of the nomenclature, see Van der MADE 1996a).

Systematics

Suoidea GRAY, 1821

Palaeochoeridae MATTHEW, 1924

Schizochoerinae GOLPE POSSE, 1972

Taucanamo SIMPSON, 1945

Taucanamo sansaniense (LARTET, 1851)

1893 *Cebochoerus suilus* FRAAS – HOFMANN: 82, Pl. 17, figs. 14–15.
1934 *Choerotherium* sp. – PIA & SICKENBERG: 187 (no. 1617).
1956 *Taucanamo pygmaeum* (DEPERET) 1892 - THENIUS: 369-371 (material from Göriach), Fig. 31.
1970 *Taucanamo pygmaeum* (DEP.) – MOTTL: 33, 35.
1983 *Taucanamo pygmaeum* (DEP.) – WEBER & WEISS: 139.
1993 *Taucanamo sansaniensis* lineage – Van der MADE: 128.
1994 *Taucanamo sansaniense* (LARTET, 1851) – Van der MADE & HAN: 35–43, Pl. 3, figs. 4–5.

M a t e r i a l:

Göriach:

SLJG 1880 – a left M_1 in a mandible fragment (HOFMANN 1893: Pl. 17, figs. 14–15; THENIUS 1956, Fig. 31).

SLJG 58.817 – a right M_2 (Van der MADE & HAN: Pl. 3, fig. 4).

SLJG 58.818 – a right P_4 (Van der MADE & HAN: Pl. 3, fig. 5).

?IGPKFUG – a canine, mentioned by PIA & SICKENBERG under no. 1679 which I was unable to locate.

?NHMW – M_2–M_3 listed by PIA & SICKENBERG under no. 1676 as *Palaeochoerus* sp. might represent *Taucanamo*. However, I could not find the specimen any more.

D e s c r i p t i o n a n d c o m p a r i s o n: A M_1 and what, based on its size, seems to be an M_2 have two roots, one below each lobe. The Göriach molars tend have the lobes not well developed; instead the cusps have an angle at the corresponding places. The endocristids are well developed and there is a hypoprecristid rather than a hypoprecónule ("central cusp"). The postcristids tend to be reduced. The teeth are not lophodont (with real anterior and posterior lophs) and not even sublophodont (with only a real anterior loph). However, the evolution of lophodonty involves several changes of the basic bunodont pattern (Van der MADE 1996a), some of which are found in the teeth from Göriach. These teeth could be called "protolophodont".

The pentaconid in the M_2 from Göriach is an isolated cusp that extends between the hypoconid and entoconid. In the M_1 it has a crest that is directed towards the hypoconid. In *Propalaeochoerus* the cusp is fused to the hypoconid and should be called a hypoendoconulid.

The P_4 has a worn tip. There is no indication of a large independent metaconid. There is no paraconid at the end of the protoprecristid. *Palaeochoerus* and *Propalaeochoerus* have P_4 with well developed para- and metaconids. *Schizochoerus* has a P_4 with a lophid formed by the protoconid and metaconid.

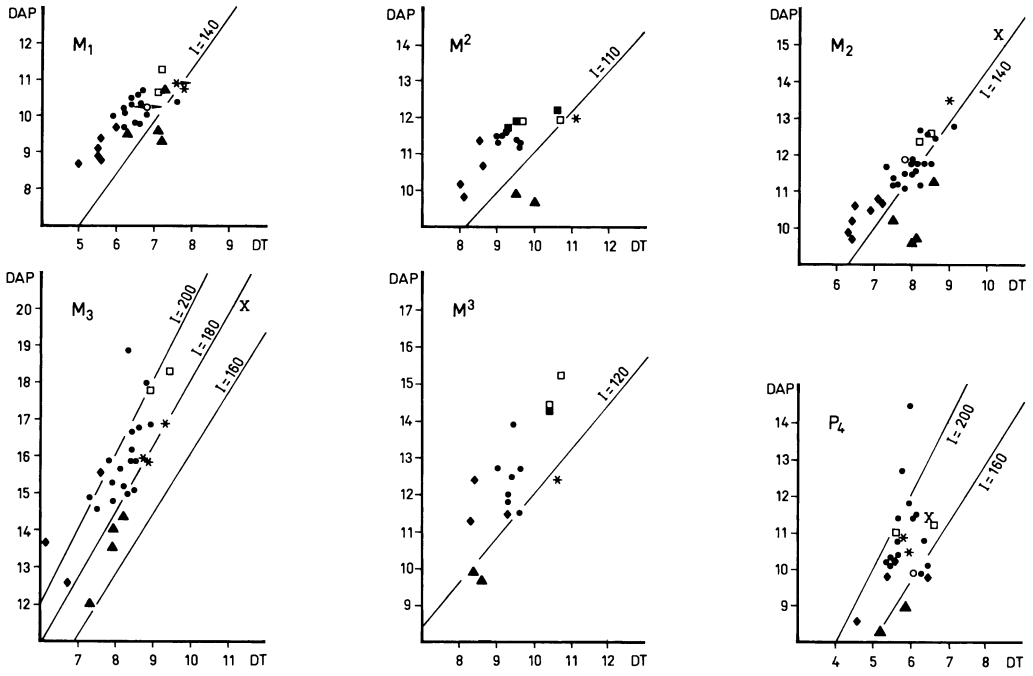

Fig. 3: Bivariate plots of the P_4, and M1–M3 in European Schizochoerinae.

● = *Taucanamo sansaniense* from type locality Sansan (MNHNP, MHNT, IPS).
○ = *T. sansaniense* from Göriach (SLJG).
◆ = *T. grandaevum* from typelocality Steinheim (SMNS).
▲ = *Taucanamo* sp. from MN 4 (Artenay – MNHNP; Els Casots – IPS; Bézian – cast in IPS).
✻ = Schizochoerinae from Münzenberg (SLJG).
■ = *T. inonuensis* from typelocality Inönü I (MTA).
□ = *T. inonuensis* from Paşalar (PDTFAU).
X = *Schizochoerus* sp. from Çandır (MTA).

The P_4 is not very elongate. Many of the P_4 of *Taucanamo* from Sansan are elongate. It is about as long as the smallest P_4 from Sansan and larger than the largest from Steinheim (SMNS) and a group of MN 4 localities, including Artenay, Els Casots and Bézian (Figure 3). The molars are within the ranges for Sansan, but larger than material from Steinheim and the MN 4 localities (Figure 3).

D i s c u s s i o n: Save for the earliest citations, the palaeochoerid from Göriach was assigned to "*Taucanamo pygmaeum* DEPERET". This species became the type species of *Albanohyus* GINSBURG, 1974. However, *Albanohyus pygmaeus* (DEPERET) turned out to be a suid (Van der MADE 1996b) and is different from *Taucanamo grandaevum*, which is the correct name for the late Aragonian palaeochoerid that was known for a long time as "*T. pygmaeum*" (FORTELIUS & BERNOR 1990). Since the two species were found in La Grive (type locality of *A. pygmaeus*) they have been mixed up during over a century. Is the suoid from Göriach: a) *Albanohyus pygmaeus*, b) *Taucanamo grandaevus*, or c) none of the two?

In addition to the six characters separating Palaeochoeridae and Suidae that were mentioned in the introduction, *Albanohyus* differs from *T. grandaevum* in having: 1) wider molars (index I), 2) shorter premolars relative to the molars, 3) a smaller overall size, 4) molars with rounded cusps, whereas those of *T. grandevum* have crests (Van der MADE 1996b). The latter species shows the beginning of a tendency towards lophodonty.

The lower molars of the small suoid from Göriach (circles in Fig. 3) have one root per lobe and a "protolophodont" pattern and are larger than those of *T. grandaevum* (diamonds), but have a similar degree of elongation (M_{1-2} with index I over 140). The small suoid from Göriach differs from *Albanohyus pygmaeus* in size and morphology. It is a palaeochoerid but it is too large for *T. grandaevum*. Its simple P_4 rules out any other European palaeochoerid than *Taucanamo*.

Taucanamo entered Europe in MN 4. These MN 4 forms (triangles in Fig. 3), *T. sansaniense* (MN 5?–6; dots) and *T. inonuensis* (later MN 6; solid and open squares) formed a lineage (Van der MADE in press), which increased in general size, their cheek teeth became more elongate and the distal part of the M3 became more complex and more elongate (the lines in Figure 3 indicate indices I). *T. grandaevum* replaced the earlier lineage of *Taucanamo* in Europe in MN 7+8. It is more advanced in cheek tooth elongation than the MN 4 forms, and resembles in this character *T. sansaniense*. The distal part of the M3 is more complex than in the MN 4 form, but not as much as in *T. sansaniense*. And it has advanced more in the direction of lophodonty than any other *Taucanamo*, though it is still far from lophodont. All this suggests that the MN 4 *Taucanamo* is a common ancestor, and that the *T. sansaniense – inonuensis* and *T. grandaevum* lineages diverged somewhere during late MN 4 or MN 5.

Taucanamo from Göriach has elongated cheek teeth as in the *T. grandaevum* and *T. sansaniense – inonuensis* lineages. It is too large for the former and is comparable to the "most primitive" specimens from Sansan. If the specimens from Göriach do not represent "primitive" extremes of the population but average types, Göriach is likely to fit in the lineage in an earlier position than Sansan. Larger samples of the bovid *Eotragus* from both localities also place Göriach anterior to Sansan (Van der MADE, submitted).

Taucanamo? muenzenbergensis n. sp.

1907 *Choerotherium sansaniense* – ZDARSKY: 260–264 (the material from Münzenberg), Pl. 7, figs. 12–14.
1934 *Choerotherium sansaniense* (LART.) – PIA & SICKENBERG: 183 (no. 1585), 187 (nos. 1616, 1618).
1956 *Taucanamo sansaniense* (LARTET) – THENIUS: 366-369 (only the material from Münzenberg, not no. 56633), Figs. 27-28.
1970 *Taucanamo sansaniense* (LART.) – MOTTL: 26.
1983 *Taucanamo sansaniense* (LART.) – WEBER & WEISS: 122.
1993 *Taucanamo sansaniensis* lineage – Van der MADE: 128 (Münzenberg).

D i a g n o s i s: Schizochoerinae with: 1) bunodont or "protolophodont" molars; 2) M_3 with a third lobe with the pentaconid in the middle and no hexaconid; 3) P_4 with the hypoconid in the middle of the talonid; 4) M_{1-2} moderately elongate; 5) upper molars not very elongate; 6) intermediate size.

D i f f e r e n t i a l d i a g n o s i s: *T.? muenzenbergensis* differs from: 1) *T. sansaniense* in its larger size and wider upper molars; 2) *T. inonuensis* in the lesser degree of elongation of the M3 and the simpler structure of the third lobes of the M3; 3) *T. grandaevum* in its much larger size, in the lesser degree of elongation of the upper molars, in having M_3 with third lobes with a simple structure; 4) early *Taucanamo* (MN 4) in its larger size; 5) *Schizochoerus* from Çandır in its smaller size and in having the hypoconid of the P_4 in the middle of the talonid; 6) other *Schizochoerus* in its smaller size and bunodont molar pattern.

D e r i v a t i o n o m i n i s: the species is named after the type locality.

H o l o t y p e: SLJG 56.697 – a right mandible from Münzenberg with P_3-M_3, figured by ZDARSKY (1909: Pl. 7, figs. 16-17) and stored in the Steiermärkisches Landesmuseum Joanneum in Graz.

P a r a t y p e s:

SLJG 56.634 – a left mandible from Münzenberg with P_4–M_3, roots of the P_3 and canine, figured by THENIUS (1956: Fig. 27).

SLJG 56.698 – a left mandible from Münzenberg with M_{2-3}, figured by THENIUS (1956: Fig. 28).

SLJG 56.699 – a left maxilla with M^2–M^3, figured by ZDARSKY (1909: Pl. 7, fig. 15) and THENIUS (1956: Fig. 26). This specimen was cited as from Seegraben by PIA & SICKENBERG (1934: no. 1585). However, it is kept in the SLJG with the other specimens from Münzenberg, it has the same fossilisation and may well be from that locality.

T y p e l o c a l i t y: Münzenberg near Leoben, Styria, Austria.

A g e o f t h e t y p e l o c a l i t y: MN 5, Middle Aragonian, Miocene.

D e s c r i p t i o n a n d c o m p a r i s o n: The lower part of the root of the **canine** is preserved; it is larger than in *T. sansaniense* from Sansan (MNHNP).

The **P_4** had a large protoprecristid, which created an incipient protofossid. There is no indication of such a protofossid in the Göriach P_4 (attributed to *T. sansaniense*), but *Schizochoerus* has a very shallow protofossid. The tooth is worn off flat and it cannot be seen whether there was a large metaconid or not. The wear pattern shows that there was a large hypoconid in the middle of the talonid. This morphology is common in *Taucanamo*. In *Schizochoerus* (including the material from Çandır described as *Taucanamo* sp. by PICKFORD & ERTÜRK, 1979), the hypoconid tends to be reduced and there is a large metaconid, forming a loph with the protoconid.

All **lower molars** are much worn and therefore is it not possible to see whether they were fully bunodont or whether they were "protolophodont" (see discussion on *T. sansaniense*). Since all molars are in mandibles, their roots cannot be studied. The pentaconid is displaced buccally and there is a small structure lingually of it. The latter may either be the cingulum (which lacks a postero-buccal end), or a tiny hexaconid. *S. vallesiensis* is peculiar in having a hexaconid on the M_1 and M_2. *Schizochoerus* sp. from Çandır and *Taucanamo* do not have a hexaconid.

The third lobe of the **M_3** has a pentaconid in the middle, but no hexaconid. In *Taucanamo sansaniense*, there is a tendency to add distal cusps and in the Sansan sample not only a hexaconid is common, but even specimens with a fourth lobe occur. In *Schizochoerus vallesiensis*, the third lobe of the M_3 is not known, but *Schizochoerus* sp. from Çandır has a simple third lobe with a pentaconid in the middle.

The **mandible** is shallow compared to molar size. This is common in Palaeochoeridae; Suidae have deeper mandibles.

The **palate** does not show a foramen palatinum next to the M^2 or M^3. This foramen may have been placed further forward.

The **upper molars** have a very small protopreconule or protoprecrista that is connected to the protocone. No protoloph is formed. The talon in the M^3 is simple and not much distally expanded. It cannot be seen whether the lingual roots of the upper molars are fused or not.

The M_1 from Münzenberg (asterisks in Fig. 3) are heavily worn, but they are still longer than any of the specimens of *T. sansaniense* from Sansan (dots). The width is not influenced by wear and is great in comparison to the Sansan sample. The M_2 shows the same pattern. The M_3 is also large, but some specimens from Sansan with an additional lobe are longer. The upper molars are larger, or in the case of the M^3 wider than any of the Sansan specimens. The M1–2 tend to be larger than their homologues in *T. inonuensis* from Inönü I (solid squares) and Paşalar (open squares), but the M3 are shorter, which is reflected in the simplar morphology of their talon and talonids. All M_x are much smaller than their homologues in *Schizochoerus* from Çandır.

D i s c u s s i o n: The fossils from Münzenberg and some upper teeth from Seegraben (SLJG 56633) have been described as *T. sansaniense*. However, there is a great size difference between these specimens. The specimens from Münzenberg indicate a larger species than *T. sansaniense* from Sansan, whereas the teeth from Seegraben (crosses in Fig. 4) indicate a much smaller animal than *T. sansaniense* (triangles pointing up in Fig. 4). It is therefore very unlikely that both samples belong to *T. sansaniense* and, since none of the samples is comparable to the one from Sansan, it seems even unlikely that any of these samples belongs to that species.

Taucanamo sp. entered Europe in MN 4 (Artenay – MNHNP, Petersbuch – BSPHGM), and increased in size and aquired more elongated cheek teeth (index I) and relatively longer M3 through the addition of distal cusps. In MN 6 it had evolved into *Taucanamo sansaniense* (Sansan – MNHNP, MHNT, NMB, IPS) and still later in MN 6 in the even larger *T. inonuensis* (Inönü I – MTA, Paşalar – PDTFAU, MTA). In MN 7+8 the lineage is replaced by the smaller species *T. grandaevus* (Steinheim - SMNS, NMB, SMNK, La Grive – UCBL, MGL, NMB, IGF, Anwill – cast in IPS). It has been suggested that the Münzenberg and Sandelzhausen palaeochoerids might be large members of the *T. sansaniense* lineage (Van der MADE 1993); they should represent *T. inonuensis* and be younger than Sansan.

However, Sandelzhausen is now placed in MN 5 (HEISSIG 1997; RÖSSNER 1997) instead of MN 6 (De BRUIJN et al. 1992). The fossils from Münzenberg come from the same sedimentological unit as those from Seegraben (PETRASCHECK 1922–29), the geographical distance is only a few hundred meters and the geological structure is well known (LACKENSCHWEIGER 1937: fig. 2). It seems very likely that both collections are of the same age. The evolutive stages of *Eotragus*, *Palaeomeryx* and *Procervulus* suggest a greater age for Seegraben (SLJG, NHMW) than for Sansan (MNHNP, MHNT, NMB). Either *T. inonuensis* is coeval with *T. sansaniense* and no descendant from that species, or the fossils from Münzenberg (and those of Sandelzhausen) do not belong to *T. inonuensis*.

The combination of, on the one hand, "primitive characters" (for the *T. sansaniense* lineage) such as wide upper molars and a simple third lobe in the M_3 and, on the other hand, the "progressive" large size suggests that the material from Münzenberg does not belong to the *T. sansaniense* lineage.

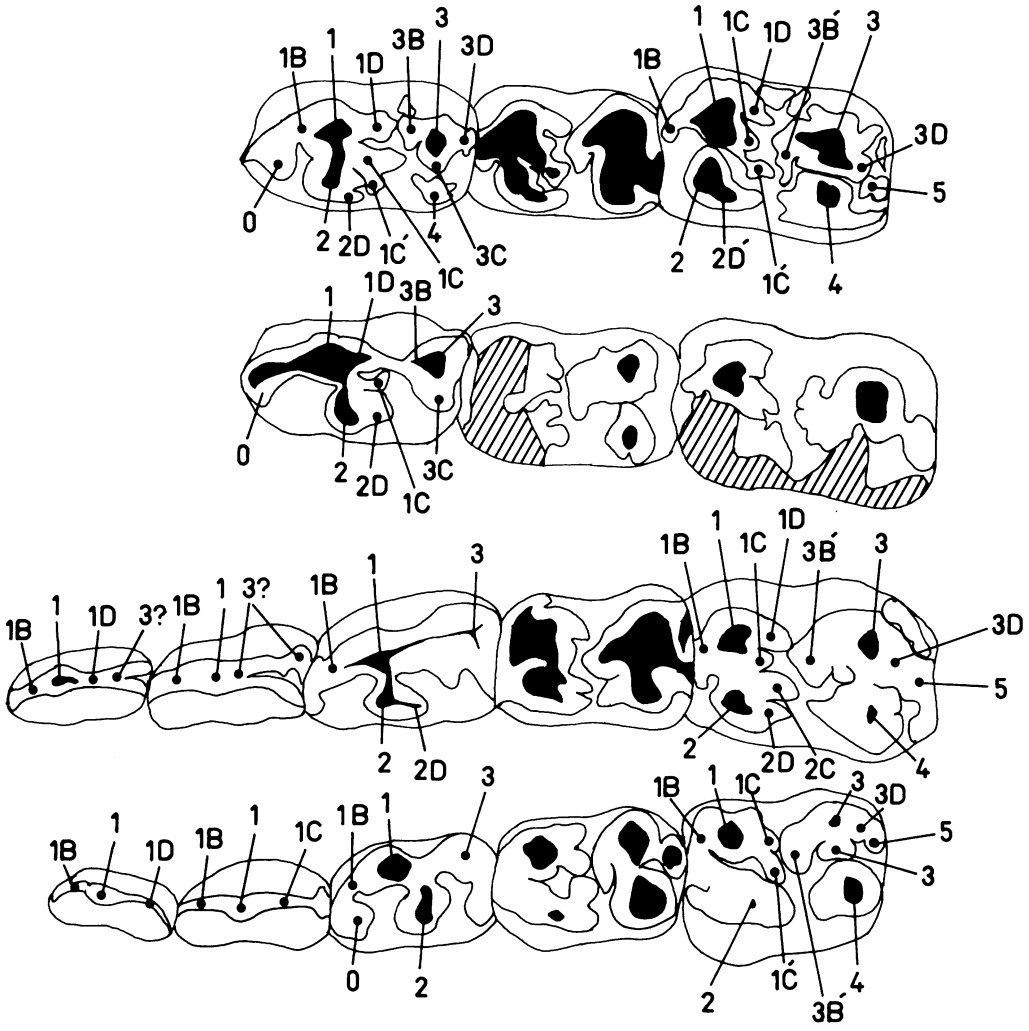

Fig. 4: The morphology of the lower cheek teeth of *Palaeochoerus* and two stages of evolution of *Sanitherium*.

From bottom to top: *Palaeochoerus* (P_2–M_2; general pattern), two specimens of *Sanitherium* stage II from Karungu (P_2–M_2 and P_4–M_2; KNM), *Sanitherium schlagintweiti* (= stage III) from Seegraben (P_4–M_2; SLJG). Legend as in Figure 2, moreover: 0 = paraconid.

The palaeochoerid from Çandır, described as *Taucanamo* sp. (PICKFORD & ERTÜRK, 1979), shares certain characters with *Schizochoerus* and is placed in that genus (Van der MADE, in press). The Çandır palaeochoerid (MTA) has a P_4 with a large metaconid (as in *Schizochoerus*), but its molars are not lophodont and do not have a hexaconid in the lower molars (as in *Taucanamo*). The *Schizochoerus* found in the youngest Aragoninan of Sinap is smaller than the Vallesian *Schizochoerus* (Van der MADE & HAN 1995: Fig. 6).

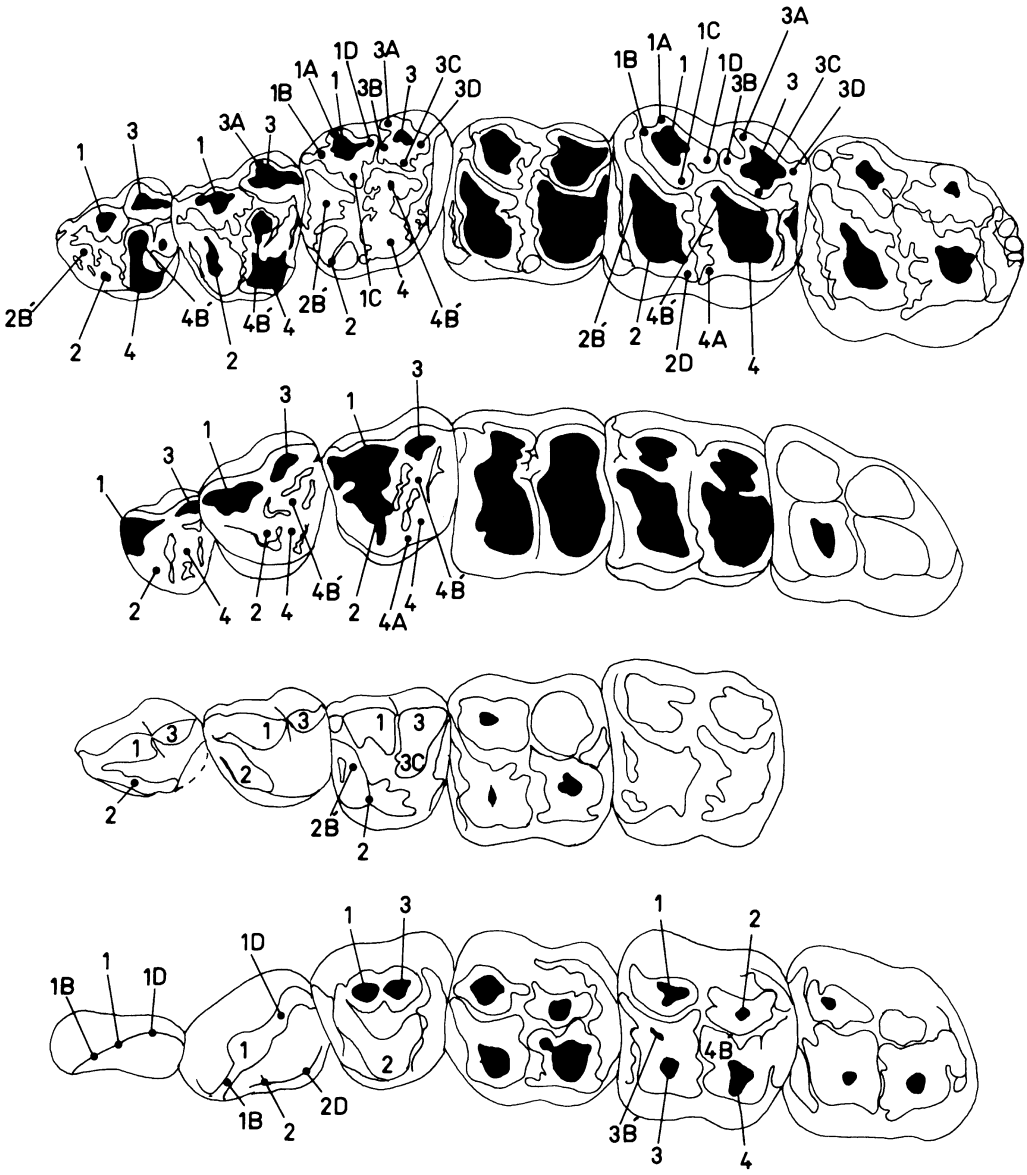

Fig. 5: The morphology of the upper cheek teeth of *Palaeochoerus* and the three stages of evolution of *Sanitherium*.

From bottom to top: *Palaeochoerus* (general pattern; P^2–M^3), *Sanitherium* stage I from Bugti (P^2 reversed; P^2–M^2), *Sanitherium* stage II from Karungu (KNM; P_2–M_2), *Sanitherium* Stage III (*S. schlagintweiti*) from Seegraben (P_2–M_2; SLJG). Legend as in Figure 2.

The current idea is that *Schizochoerus* is closely related to *Taucanamo* (PICKFORD & ERTÜRK 1979; Van der MADE 1990b). Two models come to mind: 1) *Schizochoerus* is a direct descendant from *T. inonuensis* and 2) it originated from an earlier form of

Taucanamo. The progressive elongation of the M3 and the premolars in the *T. sansaniense – T. inonuensis* lineage is not found in *Schizochoerus*, and makes this connection unlikely. The large canine, the suggestion of a protofossid and the position of the pentaconid in the molars suggest that the Münzenerg palaeochoerid does not belong to the *T. sansaniense* lineage and that it might belong to a lineage leading to *Schizochoerus*. More work on the matter is necessary, but at the moment the Münzenberg palaeochoerid fits best as an intermediate stage between *Schizochoerus* sp. from Çandır and early *Taucanamo*.

Whatever its affinities, the palaeochoerid from Münzenberg differs from any known species of *Taucanamo* and *Schizochoerus*, and a new species name is introduced here.

Palaeochoerinae MATTHEW, 1924

Sanitherium von MEYER, 1866

Sanitherium schlagintweiti von MEYER, 1866

1909 *Xenochoerus leobensis* nov. gen. nov. sp. – ZDARSKY: 264-269, Textfig. 1, Pl. 7, figs. 18–21.
1926 *Xenochoerus leobensis* – PILGRIM: 55–56, Plate 1.
1934 *Xenochoerus leobensis* ZDARSKY – PIA & SICKENBERG: 183, 188.
1940 *Sanitherium leobense* – PARASKEVAIDIS: 369–393.
1956 *Sanitherium leobense* (ZDARSKY) 1909 – THENIUS: 339–347, Figs. 1–2.
1970 *Sanitherium leobense* (ZDARSKY) – MOTTL: 22-23.
1983 *Sanitherium leobense* (ZDARSKY) – WEBER & WEISS: 121.
1984 *Sanitherium leobense* (ZDARSKY, 1909) – PICKFORD: 144-147, Figs. 15–16.
1989 *Sanitherium leobense* (ZDARSKY) – WEBER & WEISS: 121.
1990 *Sanitherium leobense* – Van der MADE: 100 & 104.
1992 *Sanitherium schlagintweiti* von MEYER, 1866 – Van der MADE & HUSSAIN: 90.
1992 *Sanitherium schlagintweiti* – Van der MADE: 87, 95.
1996 Stage III *Sanitherium* – Van der MADE: 137, Fig. 63.

M a t e r i a l:

Seegraben near Leoben:

SLJG 56.631 – a left maxilla with P^2–M^3 (ZDARSKY 1909: Pl. 7, fig. 18; PIA & SICKENBERG 1934: no. 1586; THENIUS 1956: Fig. 1; PICKFORD 1984: Fig. 16).

SLJG 56.632 – a right mandible with P_4–M_3 (ZDARSKY 1909: Pl. 7, figs. 19–21; PIA & SICKENBERG 1934: no. 1619; THENIUS 1956: Fig. 2; PICKFORD 1984: Fig. 15).

SLJG 56.635 – a right P^2.

D e s c r i p t i o n a n d c o m p a r i s o n: The **P_4** has a pronounced paraconid (code 0 in Fig. 5) and a large and independent metaconid (2). Its talonid has an independent entocondid (4) in addition to the hypoconid (3).

The **lower molars** have a buccal cingulum. Sanitheres are the only suoids with such a cingulum. Like in the upper molars the enamel is much wrinkled and certain crests or cusplets, such as the protopostcristid ("pli-*Palaeomeryx*"; 1D) and the protoendoconulid and metapostconulid ("metastylid"; 2D'), are well developed.

The upper **premolars** are complicated with many additional cusps (Fig. 6). As a consequence they have a great transverse diameter.

In the **upper molars**, the protopreconule ("protoconule"; 3B') is connected to the protocone (3). The molars have certain lobes or crests accentuated, such as the paraectocrista (1A) and metaectocrista (3A) and the enamel is wrinkled, giving a very irregular aspect. They have a buccal cingulum.

D i s c u s s i o n: ZDARSKY (1909) based a new genus and species on the specimens from Seegraben: *Xenochoerus leobense*. PILGRIM (1926) suggested the possibility that *Xenochoerus* and *Sanitherium* are synonymous and PARASKEVAIDIS (1940) decided to place *X. leobense* in *Sanitherium*. Van der MADE & HUSSAIN (1992) placed the material from Seegraben in *S. schlagintweiti* von MEYER, 1866, type species of the genus. The line of reasoning is the following.

The earliest sanitheres all had relatively simple and small premolars, later forms had larger and more complicated premolars. This is the case with specimens from Seegraben (types of *Xenochoerus leobense* ZDARSKY, 1909) and Chios (types of *S. masticum* PARASKEVAIDIS, 1940). These are from MN 5. Premolars cannot be studied in specimens from the Chinji Formation (including the types of *Sus pusillus* FALCONER, 1868 and *Sanitherium cingulatum* PILGRIM, 1926) and from Kushalgar (type of *S. schlagintweiti*). The specimens from the Chinji Formation are in the range MN 5–8, and more probably from the older than from the younger part. Von MEYER (1866) reported *Hipparion* from the same locality as *S. schlagintweiti*, suggesting MN 9 or later. Such a young age is somewhat suspect. The only Sanithere from central and western Europe is from Seegraben, though many localities are known. It must represent a shortlived and not far-reaching incursion in this area. Chios might represent the same event, since it is of the same age. In the absence of criteria for separating the Indian and European species, all are placed in the same species, *S. schlagintweiti*. This implies that *Xenochoerus* (type species *S. leobense*) is synonymous with *Sanitherium* (type species *S. schlagintweiti*).

Sanitheres have been placed in the Sanitheriinae, Suidae (SIMPSON 1945), in a family of their own (PICKFORD 1984), along with other suoids in the Palaeochoerinae, Tayassuidae (Van der MADE 1992) and finally in the Palaeochoeridae (Van der MADE 1996b).

Most authors recognized similarities between *Palaeochoerus* or *Propalaeochoerus* and *Sanitherium*. However, many followed PEARSON (1927) in placing *Palaeochoerus* in the Suidae. PICKFORD (1984: Fig. 19) believed the sanitheres closely related to the Suidae, but placed them in a separate family because of the relative position of the orbit and P^4 and the curvature of the upper tooth row. The former character is probably just primitive and in any case more similar to the state in some palaeochoerids than in most of the suids, and the latter character has been disputed (Van der MADE 1996b). According to PICKFORD (1984: Fig. 19), sanitheres and suids share the basicranial morphology. The basicranium is a complex area with many characters, but the only specimen of *Sanitherium* that includes the posterior part of the skull is a fragmentary skull from Karungu, lacking most of the basicranium. The glenoids are present and resemble those in the suids. Glenoid shape in *Palaeochoerus aquensis* (a species that was placed in *Doliochoerus*) from Wischberg (MN 1; NMB) is intermediate between the "dicotylid" and "suid" morphologies as described by PEARSON (1927). The glenoid in *Sanitherium* from Karungu (KNM-KA12577) is even more suid-like. This is possibly a parallel development related to the molarisation of the premolars and a greater lateral movement during mastication. PICKFORD (1984) did note, however, similarities to "Old World tayassuids" and was aware that sanitheres were considered by some to be related to *Palaeochoerus*. However, for PICKFORD (1988) the latter genus is a suid.

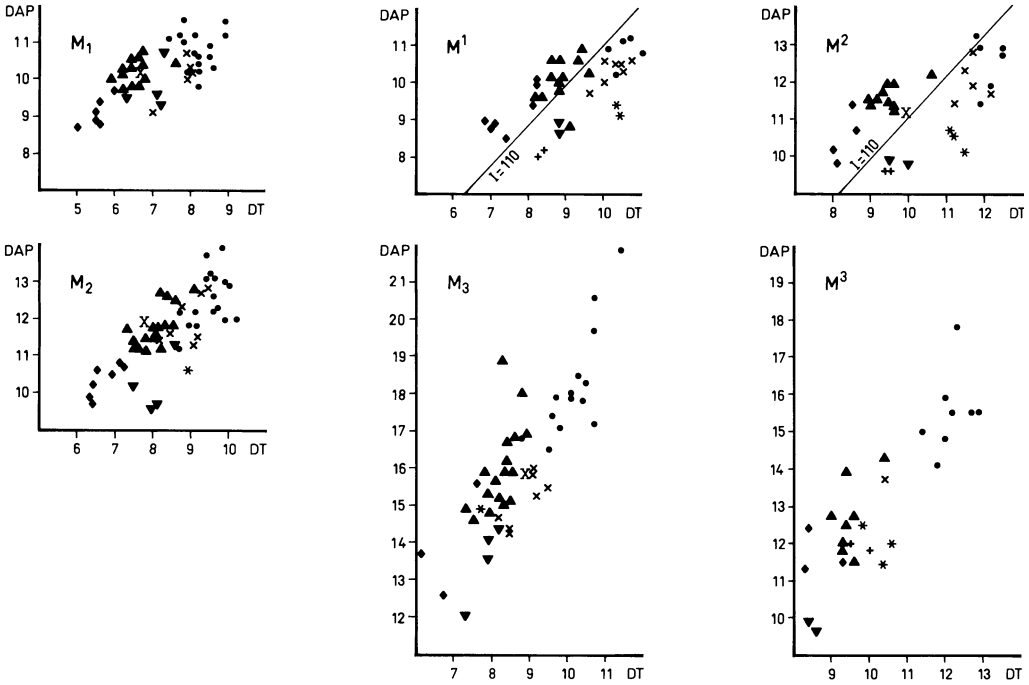

Fig. 6: Bivariate plots of selected Schizochoerinae and *Aureliachoerus* (Hyotheriinae; dots and crosses) from Europe.

● = *Aureliachoerus aurelianensis* from typelocality Artenay (MNHNP, NMB).
✻ = *A. minus* from Can Canals and El Canyet (Holo- and paratypes; IPS).
X = *A. minus* from Oberdorf oc (SLJG) and Oberdorf 4 (NHMW).
+ = *A. minus* from Seegraben (SLJG).
× = *Aureliachoerus minus* from Wintershof West (BSPHGM).
▲ = *Taucanamo sansaniense* from typelocality Sansan (MNHNP, MHNT, IPS).
▼ = *Taucanamo* sp. from MN 4 (Artenay – MNHNP; Els Casots – IPS; Bézian – cast in IPS).
◆ = *T. grandaevum* from typelocality Steinheim (SMNS).

I favor including the sanitheres in the Palaeochoeridae or "Old World tayassuids" (Van der MADE 1996b), but I have never discussed the matter in detail. I place *Sanitherium* in the Palaeochoeridae because they share a number of morphological features and because evolutive tendencies in the sanitheres seem to depart from a morphology identical to or close to that of *Palaeochoerus*. Let us review the six characters, mentioned in the introduction, that are typical for the Palaeochoeridae.

1) PICKFORD (1984) reported all sanithere lower molars to have "labio-lingually fused roots". This is typical of the Palaeochoeridae, while all Suidae have separate roots.

2) PARASKEVAIDIS (1940: 378) reported four roots in the upper molars. An upper molar (KNM-RU2751) from Rusinga has 3 lingual roots. This is highly unusual. In *Propalaeochoerus* the roots are convergent and well fused as is common in ruminants. In *Palaeochoerus* the roots are divergent and connected with a thin bony structure. The former state might be primitive, the latter is a step towards two

separate roots as in Suidae. *Sanitherium* is one step further than *Palaeochoerus*, possibly a parallel to suids. The specimen from Karungu might represent an aberrant morphology that could be formed at an evolutive stage, when the roots became separate, but when the exact morphology was not yet "established".

3) Sanitheres have the protopreconule connected to the protocone as Palaeochoeridae, whereas it is connected to the anterior cingulum in the Suidae (Listriodontinae are aberrant suids in this respect).

4–6) The C^{m}, metapodials and phalanges are not known in the sanitheres.

The balance is slightly in favor of palaeochoerid affinities. Let us compare the evolutive tendencies in *Sanitherium* to the supposed original morphology as in *Palaeochoerus*. It should be said from the start that the latest known *Palaeochoerus* is from MN 2 in Europe and the earliest known *Sanitherium* from the MN 3 equivalent in Africa and the Indian Subcontinent. There is a geographical, but no time gap. But then, Early Miocene large mammals are virtually unknown fom SE Europe and the Near and Middle East. Evolutive tendencies in *Sanitherium* involve an increase of the number of cusps and crests in the premolars, reflected in a larger size of these teeth, and an increase in folding of the enamel in all cheek teeth.

The sanithere P_4 has a pronounced protoprecristid or even paraconid and a large metaconid at the same level of the protoconid. The large paraconid is known in the Palaeochoerinae, but in no other European Suoidea. A large metaconid placed as far forward as the protoconid is known only in the Listriodontinae (Suidae), Palaeochoerinae (*Palaeochoerus*, *Propalaeochoerus*) and *Schizochoerus* (Schizochoerinae, Palaeochoeridae). The palaeochoerine P_4 is an ideal starting point for *Sanitherium*; the other taxa developed the large metaconid much later.

Figure 5 shows the lower cheek teeth of *Palaeochoerus* and two specimens of *Sanitherium* from Karungu (Set II, MN 3 equivalent) and one of *Sanitherium* from Seegraben (MN 5). The paraconid (code 0 in Fig. 4) and metaconid (2) are large in all specimens. *Palaeochoerus* and *Sanitherium* from Karungu have a buccally placed hypoconid (3); in *Sanitherium* from Seegraben there is an entoconid (4). The primitive position of the hypoconid in suoids is close to the axis of the tooth. The number of crests and wrinkles of the enamel increased; note the development of the metapostcristid (2D), protopostcristid (1C) and protopostconulid (1C'; "2/3 cusp" of PICKFORD 1984). At the end of the hypoendocristid (3C), a separate entoconid (4) developed. The protopostcristid (1D) and hypoprecristid (3B) became disconnected. Several of these developments are towards a morphology as in the molars.

The P_2 and P_3 of *Sanitherium* from Karungu have a morphology that is still close to that of *Palaeochoerus*, with short crowns, high and pointed protoconids and simple protopostcristids. In Suidae, these premolars tend to have more elongate crowns, lower and inflated protoconids, and protopostcristids with cuspules which may terminate in low hypoconids.

Figure 5 shows the upper cheek teeth of *Palaeochoerus* and *Sanitherium* from Bugti (early MN 3 equivalent), Karungu (late MN 3 equivalent) and Seegraben (late MN 5).

The P^2 of *Palaeochoerus* is a simple tooth, with a paracone (1). In *Sanitherium* first a metacone (3) and a lingual cingulum were added, then a protoconid (2) and still later the tooth becomes very complex, having a protopreconule (2B'), tetracone (4), tetraendoconule (4B') and other crests and wrinkles of the enamel.

The P^3 in P*alaeochoerus* has a paracone (1), may have a small protocone (2), placed far forward, and a large posterolingual cingulum. The protocone (2) became larger and separate from the lingual cingulum, and a metacone (3) was separated from the protopostcrista (1D). Next, complexity increased through the addition of cusps and folds of the enamel. In both P^2 and P^3 there was a marked increase in the width of the crown.

The geologically older P^4 is simple and has a paracone (1), a protocone (2) and may have an independent metacone (3). In the younger specimens, a large and separate protopreconule (2A´) is formed, as well as a tetracone (4) and a tetraendoconule (4C'). The number of crests and folds of the enamel increased as in the molars. Noteworthy is the prominent development of a buccally directed paraectostyle (1A) and metaectostyle (3A) as in the molars.

In *Sanitherium*, upper premolar width increased greatly, which certainly was related to the increasing complexity of the premolars. *P. typus* has relatively wide upper premolars, in particular the P^2, and seems to have been on the beginning of an evolutionary pathway similar to that in *Sanitherium*.

The sanithere molars have crests like many other Suoidea, including *Palaeochoerus* (Van der MADE 1996b). Some of these crests became more accentuated, which along with a more accentuated wrinkling of the enamel gives a pattern that appears at first sight to be rather irregular. The main crests of both upper and lower selenodont teeth are also present as crests or lobes in suoid molars. At certain stages of wear the sanithere molars call the selenodont pattern into mind. This is in particular the case in the later sanitheres, whereas the earlier sanitheres have molars that are still close to the common suoid morphology. The sanithere upper molars evolved particular paraectocristas (1A) and metaectocristas (3A). These crests are also present in other suoids, but are directed more anteriorly than buccally. The protopreconule (1B) and tetrapreconule (4B') became gradually larger in the sanitheres.

The evolution in *Sanitherium* started with a morphology close to that in *Palaeochoerus* and only later the sanithere cheek teeth acquired their extremely peculiar morphology. Both evolutive tendencies and morphologies present already in *Palaeochoerus* unite the sanitheres and the palaeochoerines.

Suidae GRAY, 1821

Hyotheriinae COPE, 1888

Aureliachoerus GINSBURG, 1974

Aureliachoerus minus (GOLPE POSSE, 1972)

1909 *Choerotherium sansaniense* LARTET – ZDARSKY: 260–264 (material from Seegraben), Pl. 7, fig. 12–14.
1934 *Choerotherium sansaniense* (LART.) – PIA & SICKENBERG: 183 (no. 1584) & 187 (no. 1615).
1956 *Taucanamo sansaniense* (LARTET) – THENIUS: 366-369 (SLJG 56633 from Seedorf, not Münzenberg).
1956 *Taucanamo pygmaeum* (DEPERET) – THENIUS: 369-371 (Oberdorf, not Göriach), Figs. 29–30.
1970 *Taucanamo pygmaeum* (DEP.) – MOTTL: 17.
1970 *Taucanamo sansaniense* (LART.) – MOTTL: 22.
1983 *Taucanamo sansaniense* (LART.) – WEBER & WEISS: 121.
1994 *Aureliachoerus* – Van der MADE: 11 ("Köflach").

M a t e r i a l:

Oberdorf 4:

NHMW1997z0190/0002/1 – Left M_3.

NHMW1997z0190/0002/2 – Posterior half of a left D_3.

Oberdorf bei Köflach, old collections:

SLJG 9781 - right series: P_1, D_2–M_2 (THENIUS 1956: Fig. 30; PIA & SICKENBERG 1934: no. 1615).

SLJG 9718 – a left $M^{1/2}$ (THENIUS 1956: Fig. 29).

PIA & SICKENBERG 1934 listed under no. 1681 three molars as from *Choerotherium sansaniense*. I do not know these specimens, but they might also represent *A. minus.*

Seegraben:

SLJG 56633 – right P^3, right (not left) P^4, right and left upper M^{1-3} (ZDARSKY 1909: Pl. 7, figs. 12–14; PIA & SICKENBERG 1934: no. 1584).

PIA & SICKENBERG 1934 listed under no. 1680 a M_2 of *Choerotherium sansaniense*. I do not know this specimen, but it might represent also *A. minus*.

D e s c r i p t i o n a n d c o m p a r i s o n: The **P_1** (suids do not change this tooth and it is not known whether it is a D_1 or a P_1; STEHLIN 1899–1900), the **D_2** and **D_3** have simple pointed cusps and no pronounced hypoconid (Plate 1, fig. 5). A fragment of a tooth from the recent collections (Plate 1, fig. 2) has the posterior root far backwards, leaving much space below the crown. Therefore it is interpreted as a milk tooth, despite its great DTp. The **D_4** has the common suoid morphology.

The roots of the **lower molars** are damaged, but the M_1 still has a part of the root below the metaconid, which shows that the roots below the metaconid and protoconid were not fused.

The **M_3** (Plate 1, fig. 1) has a simple third lobe with a pentaconid in the middle. Some *Aureliachoerus aurelianensis* from Artenay have the M_3 distally extended by the addition of cusps (in particular in the NMB collection).

The **upper premolars** have a buccal cingulum. The **P^3** has an elongate paracone and a small protocone. In the **upper molar** from Oberdorf (Plate 1, fig. 4) no roots are preserved, but the upper molars from Seegraben have the lingual roots well separated. The upper molars from Seegraben are much worn, but the specimen from Oberdorf has a very small protopreconule fused to the cingulum. Such a small protopreconule occurs also in other samples of *Aureliachoerus*.

The **M^3** have a small talon.

The molars from Oberdorf ("letter X" symbol in figure 4) are larger than those of *T. grandaevum* (diamonds), but close to those of *T. sansaniense* (triangles pointing up) and *A. minus* (oblique crosses and asterisks). The M1–2 from Oberdorf are not worn, which influences their apparent high degree of elongation; with wear they would become shorter and relatively wider (index I). The molars from Seegraben (crosses) are smaller than those of *T. sansaniense*, wider than those of *T. grandaevum* and equally wide as those of early *Taucanamo* (triangles pointing down) and *A. minus*, though they tend to be small compared to the latter species.

D i s c u s s i o n: The palaeochoerid *T. grandaevum* and the suid *A. pygmaeus* ("*T. pygmaeum*") have been mixed up. However, these suoids differ in a number of characters, as was mentioned in the discussion on *T. sansaniense*. The material from Oberdorf has been assigned to *T. pygmaeum* and the material from Seegraben to *T. sansaniense*. The material from Oberdorf is too large for such an assignation and that from Seegraben too small. To what species do the fossils from Oberdorf and Seegraben belong and are they suid or palaeochoerid?

The lower molars of Suidae have four roots and those of Palaeochoeridae two. The specimen from Oberdorf seems to have had suid type roots. All suids known have the lingual roots of the upper molars separated, but palaeochoerids, including *Taucanamo*, tend to have the roots fused. The Seegraben specimens are more suid like.

The smallest European suids belong to the genera *Aureliachoerus* and *Albanohyus*. The late Aragonian and Vallesian (MN 7–9) *Albanohyus* is even smaller than the Oberdorf and Seegraben suids and its molars lack wrinkling of the enamel and its premolars are relatively short and wide (Van der MADE 1996b), unlike the P^3 from Seegraben (Table 6).

Two species of *Aureliachoerus* are known: *A. aurelianensis* and *A. minus*. The former is the larger and has a tendency in the posterior molars to be distally extended, the latter is the smaller species and no such tendency is seen. The material from Oberdorf is close in size to *A. minus* from from Can Canals, El Canyet and Wintershof West (Fig. 4). Especially in the M_3 it is separated from *A. aurelianensis*, which is one of the earliest suoids in having a very clear tendency to elongate the M3. The material from Seegraben is relatively small, even small for *A. minus*. There might be a decrease of size through time.

The former assignation of the material from Oberdorf to "*Taucanamo pygmaeum*" would imply that the locality should best be placed in MN 7–9 if *Albanohyus pygmaeus* was meant, and in MN 7+8 if *T. grandaevum* was meant. An assignation of the material from

Oberdorf and Seegraben to *T. sansaniense* would imply an age of MN 6 or latest MN 5. This would obviously be in conflict with Oberdorf being MN 4 (HÖCK, pers. comm.).

Hyotherium von MEYER, 1834

***Hyotherium soemmeringi* (von MEYER, 1829)**

1867 *Hyotherium Sömmeringi* – SUESS: 7.
1869 *Hyotherium Sömmeringi* H. v. MEYER – PETERS: 196–214 (Eibiswald, not the bones), Pl. 1, figs. 1–10, Pl. 2, figs. 1–4 (not 5–8).
1888 *Hyotherium Soemeringi* H.v.M. – HOFMANN: 558-561, Pl. 9, figs. 1–2.
1890 *Hyotherium Meissneri* H.v.M. – HOFMANN: 524–525.
1890 *Hyotherium Soemeringi* H.v.M. – HOFMANN: 525.
1899–1900 *Hyotherium Sömmeringi* H. v. MEYER – STEHLIN: 41, 235, 238 (Eibiswald, Labitschberg bei Gamlitz).
1899–1900 *Hyotherium Sömmeringi-medium* – STEHLIN: 135–136 (Labitschberg, Eibiswald).
1899–1900 *Hyotherium Sömmeringi* var. *medium* (= *Sus wylensis*) – STEHLIN: 42, 313 (Feisternitz).
1899–1900 *Hyotherium medium* H. v. MEYER – STEHLIN: 42 (Feisternitz).
1904 *Hyotherium Sömmeringi* H. v. MEYER – HOFMANN & ZDARSKY: 585–586, Pl. 15, figs. 2–9.
1904 *Hyotherium Sömmeringi* H. v. MEYER – HOFMANN & ZDARSKY: 585–586, Pl. 15, figs. 2–9.
1906 *Hyotherium Sömmeringi* H. v. MAYER – REDLICH: 174.
1909 *Hyotherium Soemmeringi* H.v.M. – ZDARSKY: 225–260, Pl 7, figs. 1–11.
1909 *Hyotherium Soemmeringi* H.v.M. – BACH: 70–71. (Not Oberdorf. The footbones from "Wies" are probably those described by PETERS, 1869. These bones belong to a ruminant. I do not know the material from Hönigtal).
? 1909 (*Hyotherium medium* H.v.M.) – BACH: 72.
1909 (*Hyotherium Meissneri* H.v.M.) = *H. Soemmeringi* var. *medium* H.v.M. – BACH: 72.
1934 *Hyotherium soemmeringi* H. v. MEY. – PIA & SICKENBERG: 183–201 (most but not all).
1956 *Hyotherium soemmeringi* H. v. MEYER – THENIUS: 347–356, Figs. 3–7 & 12–13.
1956 *Hyotherium soemmeringi medium* H.v.M. – THENIUS: 350–353, Figs. 8–11.
1961 *Hyotherium soemmeringi* H. v. MEYER – MOTTL: 6–8, Pl. 1, fig. 2.
1970 *Hyotherium soemmeringi* H v.M. – MOTTL: 85–104.
1970 *Hyotherium soemmeringi soemmeringi* H.v.M. – MOTTL: 83–103.
1970 *Hyotherium soemmeringi medium* H.v.M. – MOTTL: 83–102.
1983 *Hyotherium soemmeringi soemmeringi* H.v.M. – WEBER & WEISS: 64, 65, 104, 121, 122.
1983 *Hyotherium soemmeringi medium* H.v.M. – WEBER & WEISS: 121, 122.
1990 *Hyotherium soemmeringi* large form – Van der MADE: 100, 104.

M a t e r i a l:

Seegraben near Leoben:

SLJG 3828 – left maxilla with P^{2-4} and M^{2-3} and right maxilla with P^2–M^3 (ZDARSKY 1909: Pl. 7, fig. 8.; THENIUS 1956: Fig. 4).

SLJG 3829 – right M_{1-3} (HOFMANN & ZDARSKY 1904: Pl 16, figs. 2–3).

SLJG 3831 – left M_1 (HOFMANN & ZDARSKY 1904: Pl. 16, figs. 6–7; THENIUS 1956: 347).

SLJG 3832 – left M_{1-2}.

SLJG 3833 – left D_2.

SLJG 3834 – left M^2.

SLJG 3835 – right P^1.

SLJG 3836 – symphysis with right and left I_{1-2} and right mandible with alveoles for C_f and P_{2-3} (ZDARSKY 1909: Pl. 7, fig. 9).

SLJG 3837 – right C^f (ZDARSKY 1909: Pl. 7, fig. 7; THENIUS 1956: Fig. 5).

SLJG 3839 – plaster cast of impression of D_4 and M_1 in coal (HOFMANN & ZDARSKY 1904: Pl. 16, fig. 5).

SLJG 3840 – left P^4–M^3 (THENIUS 1956: Fig. 10).

SLJG 3842 – left mandible with P_4–M_3, the first lobe of the M_3 is restored in plaster (THENIUS 1956: Fig. 11).

SLJG 3842 – right P^4.

SLJG 3843 – right M^3.

SLJG 3844 – right M_{2-3}.

SLJG 3845 – right C_f (ZDARSKY 1909: Pl. 7, fig. 6; THENIUS 1956: Fig. 9c–d).

SLJG 3846 – right C^f (ZDARSKY 1909: Pl. 7, fig. 3; THENIUS 1956: Fig. 9a–b).

SLJG 3848 – left I^1 (ZDARSKY 1909: Pl 2, figs. 1–2).

SLJG 56872 – right M_{1-3}.

Seegraben Tunnerschacht (This more exact indication of provenance is given in the IGGML. However, the material mentioned above is from the same place):

IGGML 32 – left M^3.

IGGML 6096 – left M_{2-3}.

IGGML 6109 – left astragalus.

Münzenberg near Leoben:

SLJG 3830 – right M_2 (HOFMANN & ZDARSKY 1904: Pl. 16, figs. 8–9).

SLJG 3838 – two fragments of left C_m (ZDARSKY 1909: Pl. 7, fig. 10).

SLJG 3847 – left and right I_1 (ZDARSKY 1909: Pl. 7, fig. 4).

SLJG 3849 – left I_3 (ZDARSKY 1909: Pl. 7, fig. 5).

SLJG 3850 – left D^4 (THENIUS 1956: 347).

SLJG 3851 – right mandible with M_{1-2} and in alveolus P_{2-4} and M_3 (ZDARSKY 1909: Pl. 7, fig. 11).

SLJG 3852 – right I_1.

SLJG 3853 – left mandible with P_3–M_3 (THENIUS 1956: Fig. 6).

SLJG 3858 – mandible with D_2–M_1 and P_3 and C_m in alveolus. (THENIUS 1956: Fig. 3).

SLJG 3859 – left mandible with D_4–M_1.

SLJG 3860 – right M_2.

SLJG 56873 – right I_2.

SLJG 56874 – left P_4.

SLJG 56875 – right M_1.

SLJG 56876 – left P_3.

SLJG 56877 – left fragmentary P_4.

SLJG 56878 – right M_3.

"Leoben":

IPUW — – left P^3.

Fohnsdorf:

SLJG 60250 – left M_{1-2} and fragmentary P_4 (MOTTL 1961: Pl. 1, fig. 2).

Vordersdorf bei Wies:

NHMW SK1646 – (C3877, 19882) – mandibles with left P_2, P_4–M_2, roots of P_3 and right P_4–M_3.

Zangtal:

SLJG 3821 – right and left P^4–M^3; much broken.

Eibiswald:

IPUW — – palate with left M^{2-3} and right P^1, P^4 and M^{1-3} (THENIUS 1956: Fig. 8, indicated provenance from Feisternitz. HOFMANN (1890) described a deformed skull from Feisternitz near Eibiswald with right P^{1-2} and M^{1-3} and left I^1, C^X and P^{1-2} and P^4–M^3 as *H. meisneri*. Possibly this fossil is the one described by HOFMANN).

IPUW — – left $M^{1/2}$ (PETERS 1868: Pl. 1, fig. 3).

IPUW — – left M^X.

IPUW — – fragment of molar.

IPUW — – fragment of left P^4.

IGGML 92 – right P^4 and left I_1.

A number of specimens were figured by PETERS (1869), which I was unable to find.

Feisternitz bei Eibiswald:

SLJG 2146 – right M^{1-3}.

SLJG 2147 – fragmentary P_{2-4} and M_2.

SLJG 3844 – left M^{2-3}.

SLJG 3855 – left M^2 (THENIUS 1956: 347).

NHMW 1896 – right P^3–M^2.

NHMW 17 – left I^1.

Ameis:

IPUW — – right M_2.

Labitschberg bei Gamlitz:

SLJG 1867 – right M_{2-3}.

SLJG 1878 – symphysis and mandibles with left and right I_{1-2}, left C_f, left P_{1-2} and right P_{1-4} (Half of the specimen figured by HOFMANN 1888: Pl. 10, figs. 1–2).

SLJG 1881 – left P^3.

SLJG 1968 – fragment of left M_1.

SLJG 1969 – fragment of left P^4.

IPUW — – left mandible with P_3–M_3 (Half of the specimen figured by HOFMANN 1888: Pl. 10, figs. 1–2; THENIUS 1956: Fig. 7).

Schönegg bei Wies:
SLJG 1822 – left I^1.
SLJG 1829 – right C^m.
SLJG 1847 – left P^4.
SLJG 1848 – right M^2.
SLJG 1849 – right M^1.
SLJG 1850 – left M^1.
SLJG 1864 – right M^3.
SLJG 1877 – left M^2.
SLJG 1882 – right P^3.
SLJG 1883 – left P^3.

Hochtregist NE von Voitsberg:
IGPKFUG 1877IV392 (P10) – left and right maxillas with much broken cheek teeth: (remains of) left P^3–M^3 and right P^2–M^3 (THENIUS 1956: Fig. 12).

St. Peter bei Wies:
SLJG 58774 – right M^2.

Kalkgrub bei Schwanberg:
SLJG 2149 – left M_x.
THENIUS (1956: Fig. 13) figured two premolars, that I was unable to find.

Göriach?:
SLJG 1819 – right I^1 (HOFMANN 1893: Pl. 16, figs. 7–8; THENIUS 1956: Fig. 20c).
IGGML 6068 – left I^1.
MOTTL mentioned *H. soemmeringi* from Kohlengrube Parschlug, Hochegger (Rosental)–Mulde and Steieregg bei Wies, but I could not find this material.

D e s c r i p t i o n a n d c o m p a r i s o n: Material from Styria has been described and figured in various papers. Therefore only the most relevant characteristics are discussed.

The $\mathbf{M_1}$ and $\mathbf{M_2}$ have four roots and the $\mathbf{M_3}$ has two roots below the first lobe, whereas the second and third lobes have the roots fused. The upper molars have the protopreconule fused to the cingulum and have two separate lingual roots. Palaeochoerids tend to have M_1 and M_2 with only one root per lobe and upper molars with one lingual root. Paleochoeridae and Listriodontinae tend to have the protopreconule fused to the protocone.

The $\mathbf{I^1}$ are distally expanded and have a distal cusp (the metacone), resulting in the two I^1 forming a "V-shape" (sensu Van der MADE 1996a: Fig. 25). The I^1 of *Conohyus* are not distally expanded, do not have a large metacone and do not form such a "V-shape". SLJG 1819, a right I^1 – assigned to *Conohyus* by THENIUS (1956: Fig. 20 c–d) and HOFMANN (1893: Pl. 16, figs. 7–8), and IGGML 6068, a left I^1 of the same morphology and fossilisation, belong to *Hyotherium soemmeringi* as indicated by its mesodistal elongation and distal cusp (metacone), resulting in a "V-shape", if the two would be put together. Both specimens are reported to be from Göriach. I do not know any locality

where the two species are found together. The fact that the specimens represent the only *Hyotherium* from Göriach suggests, that they do not come from that locality. The specimens have a dark fossilisation, like in Seegraben, Feisternitz etc. However, though not common, such colors also occur in Göriach.

The $\mathbf{I^2}$ is does not have such an elongate shape, as in the Suinae.

The **premolars** tend to be more elongate (index I) than in Listriodontinae, Suinae, Tetraconodontinae, Cainochoerinae and the hyotheriine *Xenohyus*. Size changes gradually from one premolar to the other, whereas in *Xenohyus* the P_2 is small and in *Conohyus* narrow compared to the P_3.

The $\mathbf{P_4}$ has a large and well separated metaconid that is placed clearly more distally than the protoconid. Tetraconodontinae do not have a large metaconid and in Listriodontinae it is placed at the same level as the protoconid.

The metacone of the $\mathbf{P^4}$ is larger and better separated from the paracone than in *H. meisneri* and *H. major*.

The material is much larger than the material assigned to *Aureliachoerus* and *H. meisneri* and a little larger than *H. major*, but smaller than *Xenohyus*. It is only slightly larger than that of Sandelzhausen and Baigneaux-en-Beauce (Figs. 7–8), which is currently assigned to *Hyotherium soemmeringi*. However, the material from Georgensgmünd, including the type material of that species, is larger (Figs. 7–8). This is not an isolated case, also a specimen from Quinta da Farinheira (ANTUNES & ESTRAVÍS 1986) is larger and DEHM (1980) introduced a new subspecific name for large material from Thannhausen: *H. s. bavaricum* (Fig. 7). Postcranial material from Neudorf Spalte (ZAPFE 1983) is also larger than that from Sandelzhausen (BSPHGM).

D i s c u s s i o n: At present three species of *Hyotherium* are recognized (Van der MADE 1994): the very small *H. meisneri* (MN 1–2, possibly MN 3), the small *H. major* (MN 1–2, possibly even MN5) and the large *H. soemmeringi* (MN 3?, MN 4–6).

The smaller *Hyotherium* from Styria have been assigned to *H. soemmeringi medium* (THENIUS 1956; MOTTL 1970). However, von MEYER (1841) introduced the name *Hyotherium medium* for material from Mösskirch and Weissenau. The fossils from Weissenau (MN 1) are currently placed in *H. major* and the material from Mösskirch (either a mixed fauna or MN 6) probably belongs to the later *Hyotherium*. I do not know

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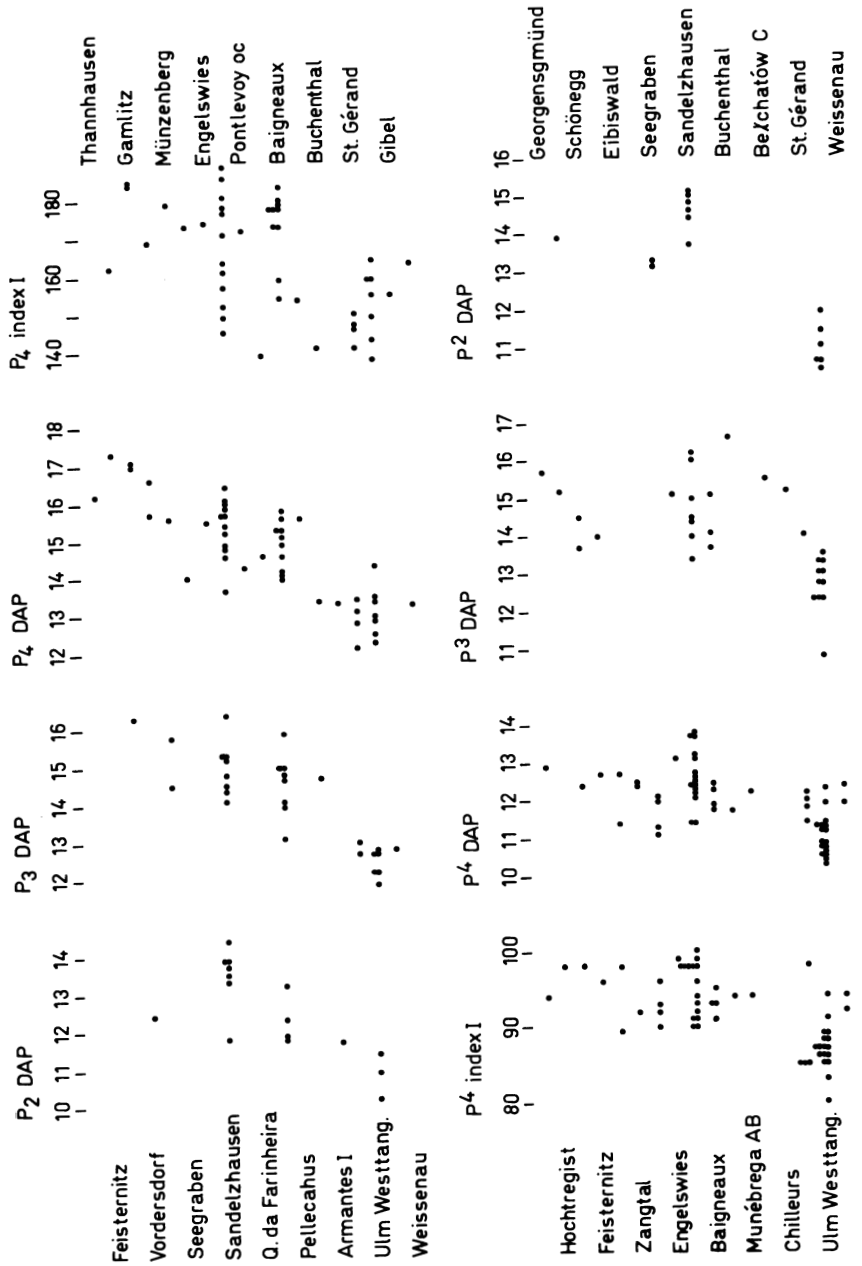
Fig. 7: Length and index I *Hyotherium* premolars. The localities are arranged in approximate stratigraphical order from old (bottom) to young (top) and alternate from right to left (but see also discussion in text).

Ages and collections for samples in figures 5 and 6: Weissenau (MN 1; FISF), Gibel (cast in MNHNP), Ulm Westtangente (MN 2; SMNS), St. Gérand-le-Puy (MN 2; MNHNP, MGL, MHNT, cast in SMNS), Servilly (MGL), Chilleurs (MN 3; NMB), Armantes I (MN4, formerly MN4a; IVAU), Munébrega AB (MN4, formerly MN 4a; IVAU), Belchatów C (MN 4; ISEAK) and Pellecahus (MN 4, formerly MN 4a; NMB), Buchenthal (PIMUZ), Baigneaux-en-Beauce (MN 5, formerly MN 4b; NMB, MGL, MSNO, BSPHGM), Quinta da Farinheira (MN 5; CEPUNL), Pontlevoy (MN 5; MNHNP), Engelswies (MN 5; NMB), the Styrian localities (all MN 5, formerly MN 5) and Georgensgmünd (MN 5, formerly MN 5; FISF, NMB) and Thannhausen (MN 6; BSPHGM).

St. Gérand-le-Puy is type locality of *Hyotherium major*, Buchenthal is type locality of *Hyotherium soemmeringi wylensis* and Georgensgmünd of *Hyotherium s. soemmeringi*.


P2 DAP
10 11 12 13 14
P3 DAP
12 13 14 15 16
P4 DAP
12 13 14 15 16 17 18
P4 index I
140 160 180
Feisternitz
Vordersdorf
Seegraben
Sandelzhausen
Q. da Farinheira
Pellecahus
Armantes I
Ulm Westtang.
Weissenau
Thannhausen
Gamlitz
Münzenberg
Engelswies
Pontlevoy oc
Baigneaux
Buchenthal
St. Gérand
Gibel
P4 index I
80 90 100
P4 DAP
10 11 12 13 14
P3 DAP
11 12 13 14 15 16 17
P2 DAP
11 12 13 14 15 16
Hochtregist
Feisternitz
Zangtal
Engelswies
Baigneaux
Munébrega AB
Chilleurs
Ulm Westtang.
Georgensgmünd
Schönegg
Eibiswald
Seegraben
Sandelzhausen
Buchenthal
Be/chatów C
St. Gérand
Weissenau

the Mösskirch material and therefore do not know whether it resembles the type material or the smaller material such as from Sandelzhausen. Because of the uncertainties about the taxon it is not used in recent literature (GINSBURG 1974; Van der MADE 1990a+b, 1994; HELLMUND 1991).

Small material from Sandelzhausen (formerly believed to be MN 6; De BRUIJN et al. 1992), large material from MN 5 (Styrian localities) and possibly even from MN 4 (Quinta da Farinheira) suggested a size decrease in *H. soemmeringi*, posing a problem to a lineage *H. major* – *H. soemmeringi* (Van der MADE 1990a, b). However, both rodents and ruminants suggest now that Sandelzhausen should be placed in MN 5 (HEISSIG 1997; RÖSSNER 1997). The deer from Sandelzhausen is more primitive than that from Seegraben (RÖSSNER, pers comm.). The change in stratigraphical position of Sandelzhausen has implications for our understanding of the evolution of *Hyotherium*.

Figures 5 & 6 show the DAP of cheek teeth of *H. major* and *H. soemmeringi*. The localities are arranged in approximate stratigraphical order. Key localities are: St. Gérand-le-Puy (typelocality of *H. major*), Buchenthal near Niederutzwyl (type locality of *Sus wylensis* von MEYER, 1866), Pontlevoy (reference locality of MN 5), Sandelzhausen, Georgensgmünd (type locality of *H. soemmeringi*) and Thannhausen (type locality of *H. s. bavaricum* DEHM, 1980). The material from Pontlevoy is from old collections; it has been suggested that those old collections may include material of different ages. Buchenthal is a poor locality (STEHLIN 1925) and therefore its stratigraphical position is based on the size of the *Hyotherium*.

In the way the localities are arranged in Figures 7 & 8, there seems to be a gradual size increase as well as an increase in the index of the premolars from *H. major* to *H. soemmeringi*. The specimens from Thannhausen, Quinta da Farinheira, Neudorf Spalte and the Styrian localities are very close in size to the type material of *H. soemmeringi* from Georgensgmünd. The material from Buchenthal, Sandelzausen, Baigneaux-en-Beauce, Munébrega etc. is morphologically similar, but smaller. It might be separated as a subspecies, which should be called *H. s. wylensis*. The cotypes of *H. s. wylensis* are stored in the PIMUZ and one of them has been figured by STEHLIN (1899–1900: Pl. 1, figs. 2–3) and can be considered as the lectotype.

Listriodontinae GERVAIS, 1859

Listriodon von MEYER, 1846

Listriodon splendens von MEYER, 1846

1908 *Listriodon splendens* H.v.M. – BACH: 117–118.
1909 *Listriodon splendens* H.v.M. – BACH: 73.
1934 *Listriodon splendens* H.v. MEY. – PIA & SICKENBERG: 206 (no. 1761).
1956 *Listriodon splendens* H.v.M. – THENIUS: 365-366, Fig. 25.
1970 *Listriodon splendens* H.v.M. – MOTTL: 46–47.

M a t e r i a l:

Haselbach:

SLJG 56636 – left M_1 (THENIUS 1956: Fig. 25; PIA & SICKENBERG 1934: no. 1761).

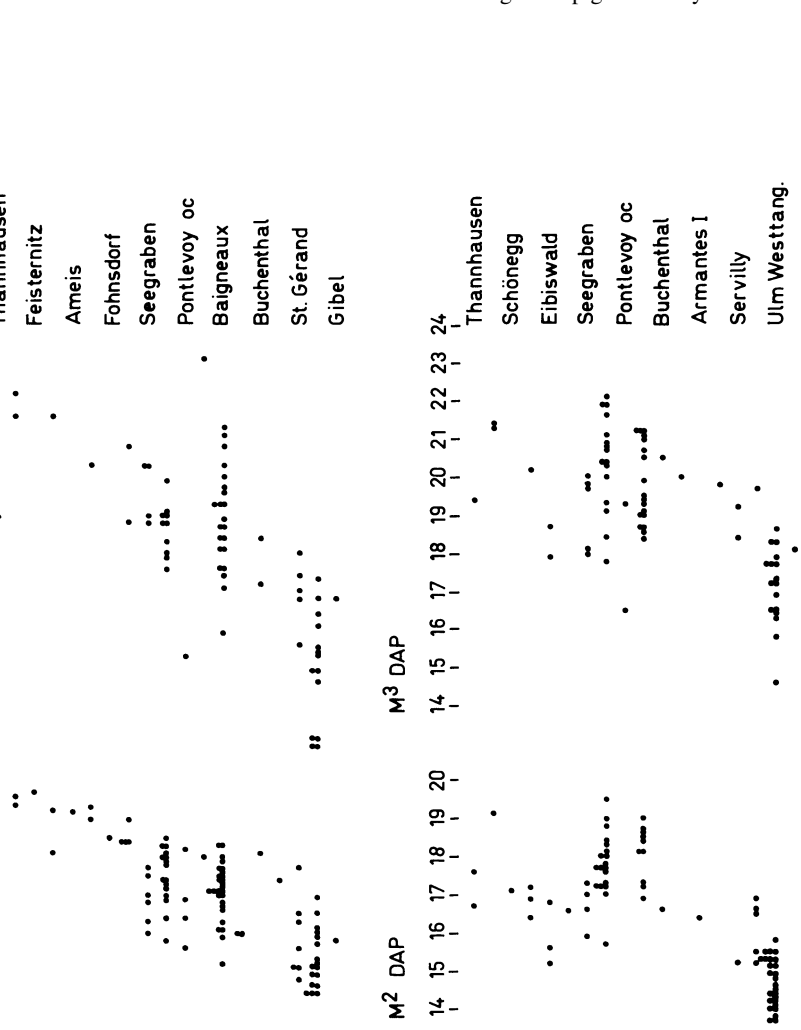


Fig. 8: Lengths of *Hyotherium* molars, arranged in approximate stratigraphical order from old (bottom) to young (top) (see also discussion in text). St. Gérand-le-Puy is type locality of *Hyotherium major*, Buchenthal is type locality of *Hyotherium soemmeringi wylensis* and Georgensgmünd of *Hyotherium s. soemmeringi*.

Löffelbach:

A C_m described by BACH (1908). The tooth should be in the IGPKFUG (BACH 1909), but I did not find it there.

D e s c r i p t i o n a n d c o m p a r i s o n: The lower molar is interpreted as a $\mathbf{M_1}$, because of its size. It has the common lophodont morphology of *Listriodon*.

BACH (1908) gave measurements of the $\mathbf{C_m}$: Li 29, La 24, Po 22. The canine from Löffelbach is particularly large and has a "verrucosic" section (with the labial side wider than the posterior side).

D i s c u s s i o n: The only fully lophodont suid in Europe is *Listriodon splendens*, which occurred from earliest MN 6 to latest MN 9 (Van der MADE 1990 a+b). The molar does not contain any further stratigraphical information.

Canine size in *Listriodon splendens* increased, particularly the width of the labial side, resulting in a shift from the "scrofic" to the "verrucosic" section. Size and morphology of the canine from Löffelbach suggest a latest Aragonian age. If the specimen is not an extreme of the Löffelbach population, the locality should be as old as St. Quirze or younger (Van der MADE 1996a).

Tetraconodontinae LYDEKKER, 1876

Conohyus PILGRIM, 1925

Conohyus simorrensis (LARTET, 1851)

1881 *Hyotherium Sömmeringi* v. MEYER – HOERNES: 330.
1893 *Hyotherium soemmeringi* H. v. MEYER – HOFMANN: 77–82, Pl. 15, figs. 13, 14 & 17 (figs. 15–16 ?), Pl. 16, figs. 1–10, Pl. 17, figs. 1–13.
1899–1900 *Hyotherium simorrense* LARTET – STEHLIN: 12, 50–51, 137–140, 246–247, 317–318, 333?
1934 *Conohyus simorrensis* (LART.) – PIA & SICKENBERG: 185–205.
1956 *Conohyus simorrensis simorrensis* (LARTET) – THENIUS: 357–365, Figs. 14–19, 20a+b, 20e+f, 21–24 (not Figs. 20c–d).
1969 *Conohyus simorrensis simorrensis* (LARTET) – MOTTL: 303.
1970 *Conohyus simorrensis simorrensis* (LART.) – MOTTL: 30, 33, 35, 38.
1983 *Conohyus simorrensis simorrensis* (LART.) – WEBER & WEISS: 139.
1989 *Conohyus simorrensis goeriachensis* nov. subsp. – Van der MADE: 19–28, Pl. 1.

M a t e r i a l:

Göriach:

SLJG 1426 – left I^2.

SLJG 1504 – right C^m.

SLJG 1513 – right I_1 (HOFMANN 1893: Pl. 16, figs. 16–18).

SLJG 1591 – anterior lobe of a left lower molar (probably M_3).

SLJG 1592 – fragments of two right upper molars ($M^{2–3}$?).

SLJG 1595 – right I^3 (?).

SLJG 1596 – $M_{1–3}$.

SLJG 1820 – right I^2 (HOFMANN 1893: pl. 16, figs. 9–10).
SLJG 1821 – left I^1.
SLJG 1826 – right C^m.
SLJG 1827 – left C^m (THENIUS 1956: Fig. 19).
SLJG 1828 – right C_x.
SLJG 1830 – right and left I^{1-2}, left C^m–M^3, right P^2–M^3 (HOFMANN 1893: Pl. 18, figs. 1–3).
SLJG 1831 – left P^{3-4}, right P^3, right P^1 and right C^f (HOFMANN 1893: Pl. 16, fig. 5).
SLJG 1833 – left C^m.
SLJG 1834 – right M^3 (THENIUS 1956: Fig. 18?).
SLJG 1836 – fragment of right P^3.
SLJG 1837 – right P^4–M^1.
SLJG 1839 – right P^4.
SLJG 1840 – right M^3.
SLJG 1841 – left M^3.
SLJG 1842 – left M_2.
SLJG 1843 – germ of right M_2.
SLJG 1844 – right M^3.
SLJG 1845 – left P^3 (HOFMANN 1893: Pl. 17, fig. 9).
SLJG 1846 – left P^3.
SLJG 1851 – right M^2.
SLJG 1852 – left M^2.
SLJG 1853 – left I^3.
SLJG 1856 – symphysis with the right and left I1–2 in alveolus, the roots of the DI1–2, I3 and Cf, and with P1 and a fragment of the P_2 or D_2.
SLJG 1857 – right P_3–M_3.
SLJG 1858 – left P_3–M_3 (same individual as SLJG 1857?).
SLJG 1859 – left C^f (HOFMANN 1893: Pl. 15, figs. 11–12).
SLJG 1860 – left P_4.
SLJG 1861 – right P_3–P_4.
SLJG 1862 – right P_4–M_3.
SLJG 1863 – right D_3–M_1 and P2–4 in alveolus and isolated M^1 and M^2 (HOFMANN 1893: Pl. 15, fig. 13).
SLJG 1865 – right M^{2-3}.
SLJG 1866 – right M^{2-3}.
SLJG 1868 – right P^1.
SLJG 1870 – right P^{2-4}.
SLJG 1879 – left C_f–P_3 and right C_f–M_2.
SLJG 1883 – right C_m.
SLJG 1896 – left M_3.
SLJG 2148 – left P_3–M_3.
SLJG 3820 – left and right P^3–M^3.

SLJG 3822 – left M_{1-3}.

SLJG 3823 – right M_{1-3}.

SLJG 3824 – right P^3–M^2.

SLJG 3825 – right P^2.

SLJG 3826 – tip of left C_m.

SLJG 3827 – left P_1.

SLJG 3856 – left I^2–P^4.

SLJG 3857 – right C^f–M^2.

SLJG 3861 – left and right M_3, right P^{1-2}, left M_2, fragment s of left and right P_3, right M_3, P^2 with fragments of P^{3-4}, not all of one individual.

SLJG 3861 – left M^1–M^3 and right M^3.

SLJG 9564 – left P_1–M_2 and right P_1–P_3.

SLJG 9569 – mandible fragment with: right I_1, root of left I_1, left and right P_{1-3}, left P_4–M_2.

SLJG 9582a – left P_4, 9582b – right P_3, 9582c – M_2, 9582d – left M_3, 9582e – right I_2, left C_f and left I_3, 9582f – right I_3.

SLJG 56692 – left P^4.

IGGML 3442 – much worn right I^1, right I^{1-2}.

IGGML 6019 – left M_3 (HOERNES 1882: Pl. 3, fig. 5).

IGGML 6069 – maxilla with buccal side of D^{3-4}.

?IGGML 6070 – mandible fragment with fragment of M_x.

IGGML 6263 – right M_{2-3}.

NHMW 1896 – right M_2 and M_3 of two different individuals (KITTL).

NHMW 1896 – left M^1 (KITTL).

NHMW 274/1958 – symphysis with right and left P_{1-2} (leg. HOFMANN).

NHMW 274/1958 – mandibles with left and right P_3–M_3 (leg. HOFMANN).

NHMW 274/1958 – posterior half of skull (compacted) with left M^{2-3} and right M^{1-3} (leg. HOFMANN).

NHMW 1980/2094 – left P_2, right D_4–M_1, left M_3, left and right I^1, right P^{2-3}, right P^4–M^1 (Simoniflöz; coll. ZAPFE).

NHMW 1980/2094 – right P_4–M_3, right M_{1-3}, left P_3, left P_4 (Simoniflöz; coll. ZAPFE).

IPUW 1835 – right P^3–M^3.

NMB TO 976 – right M_{2-3}.

Au:

SLJG 56693 – left P_3.

SLJG 56694 – left P^3.

SLJG 56695 – fragment left I^1.

SLJG 56696 – right M^2.

Rosenthal bei Köflach:

SLJG 1510 – impression in the coal of SLJG 1512 and of a M_2, which is no longer there.

SLJG 1511 – cast of the M_2 of SLJG 1510.

SLJG 1512 – right M_3.

St. Oswald bei Gratwein:

SLJG 9640 – a right P_4, figured by THENIUS (1956: Fig. 23) and described by MOTTL (1969).

D e s c r i p t i o n a n d c o m p a r i s o n: The major part of the material is from Göriach. It was described and figured by HOFMANN (1893), THENIUS (1956) and Van der MADE (1989). Therefore, only the features with a special interest are mentioned here.

There are several **skull** fragments, but most of their characteristics cannot be studied because they are badly crushed.

The $\mathbf{I^1}$ are of a primitive type. The facets caused by occlusion with the lower incisors indicate the transverse direction. The mesodistal axis of the crown is in transverse direction, not oblique to it as in most suids with "V-shaped" I^1 (sensu Van der MADE 1996a: Fig. 25), which is caused by distal expansion in oblique direction.

The $\mathbf{I^2}$ are not much elongated; they became larger in later *Conohyus* and the I^2 of later tetraconodonts that are known to me are also more elongate. The $\mathbf{I^3}$ are clearly smaller than the I^2, but the difference is not so accentuated as in later tetraconodonts. In hyotheriines and listriodonts there is less difference. SLJG 3820 has an incisor in the premaxilla. The specimen is deformed and it is not clear to me whether the line behind the tooth is a fracture or the suture between the premaxilla and the maxilla. The distance from this tooth to the C^f is only 16 mm. The morphology and size of the tooth suggest that it is an I^2, but its position immediately anterior to the possible suture and close to the canine suggests that it should be an I^3. A solution could be that the I^3 is lacking because of reduction; however, specimens like SLJG 1595 and SLJG 1883 seem to represent genuine I^3. Another possible solution is that the size and shape of the I^3 is very variable.

The **lower incisors** are not particularly hypsodont, compared to the more advanced Suinae, but more than in *Hyotherium*.

The $\mathbf{C_m}$ have an extreme scrofic section (with the posterior side much wider than the buccal side). Several later and larger tetraconodonts have this character less strongly developed or even have verrucosic sections (with the buccal side wider). This appears to be a common parallel trend and was documented in three listriodont lineages (Van der MADE 1996a: Figs. 39, 48, 49).

The **cheek teeth** have been described several times and this will not be repeated here, save for mentioning that the premolars are very large compared to the molars, the P_4 has but one main cusp and the P^4 has the metacone not well individualized.

There is one interesting aspect of the molars that should be mentioned here. **Enamel thickness** appears to be related to diet and receives much attention in the study of primates. The character has been studied in artiodactyles and in suoids in particular (Van der MADE 1996a) and it was found that folivorous animals tended to have thinnest enamel (measured at the lingual cusps and expressed as a promillage of the width of the same lobe); pigs that are known to root and/or eat hard food items such as nuts have thick enamel. The extinct hyotheriines had the thickest enamel in this study. However, data on tetraconodonts were virtually lacking, while it has been stated that Tetraconodontinae have thick enamel (PICKFORD 1988). With values for the M_2 ranging about 80–120, enamel thickness of *Conohyus* from Göriach (Table 11) is comparable to that of *Sus*, *Potamochoerus* and *Babyrousa*, less than that of the hyotheriines, which range

100–170, and more than in listriodonts, Dicotyline and the folivorous *Hylochoerus* (Van der MADE 1996: Table 19, Fig. 57).

Parachleuastochoerus steinheimensis was for a long time considered synonymous with *C. simorrensis* or only to be a subspecies (THENIUS 1956). Its premolars are much smaller and the molars tend to be more elongate than in *Conohyus simorrensis* (FORTELIUS et al. 1996: Figs. 28.6–28.7).

The size of the molars increases with decreasing geological age (Fig. 9 gives the width of the lower molars). On average, the specimens from Göriach are similar in size to those of MN 5 localities, and smaller than those of MN 6 localties.

There are but few specimens from Au and St. Oswald. These specimens belong to *Conohyus*, but the remains are insufficient to assess the evolutionary level. The few specimens from Rosenthal suggest an evolutive level close to that of Göriach; if the remains are representative for the population, they are even slightly more advanced.

D i s c u s s i o n: Most authors recognized that the material belongs to *C. simorrensis*. The P_4 with but one main cusp and the P^4 with a not well individualized metacone and the large size of the premolars are typical for the Tetraconodontinae, the large size of the premolars for *Conohyus* and the small size of its molars singles out *C. simorrensis*.

The type material of *C. simorrensis* seems to be lost. Dr. GINSBURG (pers. comm.) proposed to designate a mandible from Le Fousseret as a neotype (but did not do this in a formal way) and I named the material from Göriach *C. simorrensis goeriachensis* since it differs from the material from Le Fousseret in having smaller molars (Van der MADE 1989).

The European *Conohyus* lineage is characterized by an increase in molarsizes, especially in the M3. The size of the molars from Göriach and Puente de Vallecas suggests that the localities are close in age; the latter locality is placed in MN 5 and I proposed to place Göriach also in MN 5 (Van der MADE 1989). This proposal was also based on the evolutive stage of *Eotragus*, which is more primitive in Göriach than in Sansan (Van der MADE, submitted). A good collection of *Conohyus* from Paşalar became available for study (FORTELIUS & BERNOR 1990). The cheek teeth from Paşalar are larger than those from Göriach, suggesting a lesser age. Material from Elgg (mainly upper teeth) is intermediate between Göriach and Paşalar and specimens from Pitten (see THENIUS 1956: 365 for doubts about the provenance) and Klein Hadersdorf seems to be more progressive than that of Göriach.

S t r a t i g r a p h y

The older literature (THENIUS 1956; HÜNERMANN 1968; GINSBURG 1974) indicates long stratigraphical ranges for the suoid species. However, ranges seem to be much shorter for most suoids (GINSBURG 1980; Van der MADE 1990), and ongoing research reduces the ranges even more and proves suoids as being useful in stratigraphy. Figure 10 gives the stratigraphical position of Styrian (fat) and other (normal letters) localities, arranged per lineage (columns).

Taucanomo grandaevum (= *T. pygmaeum* of some previous authors) has a much shorter range than previously believed: not MN 4–9, but MN 7+8. The species was cited from Styria, and would suggest younger ages for Oberdorf and Göriach, if the species would be present there. However, these localities have *A. minus* and *T. sansaniense*, respectively.

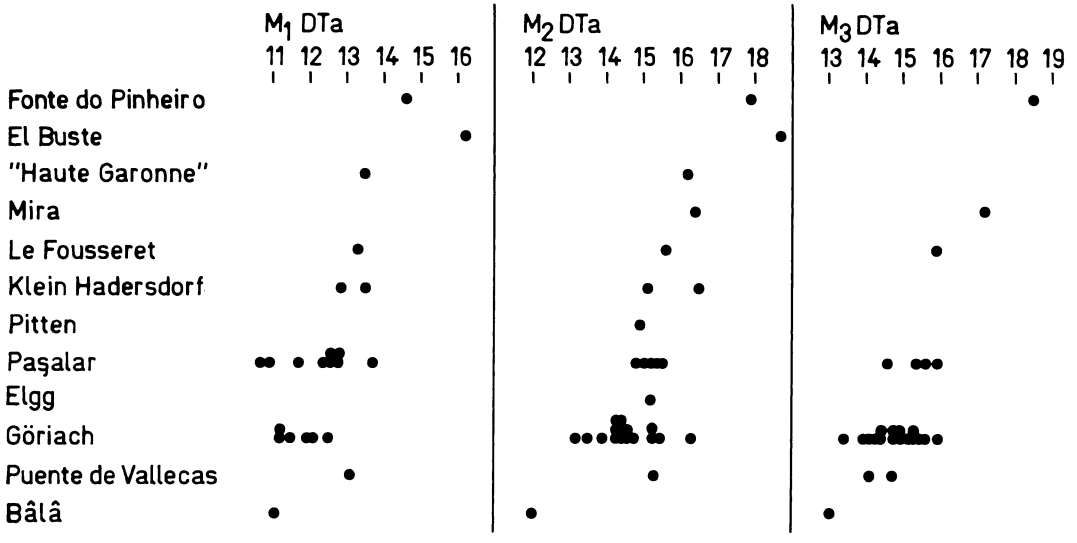


Fig. 9: Width of the first lobe of the lower molars of *Conohyus*, arranged in approximate stratigraphical order from old (bottom) to young (top).

Ages and collections: Bâlâ (isolated find MN 5; MTA), Puente de Vallecas (MN 5; casts in MNCN), Göriach (MN5; SLJG, NHMW,IGGML, NMB), Elgg (MN 6; NMB), Paşalar (MN 6; PDTFAU, MTA, PIMUZ), Pitten (MN 6; IPUW), Klein Hadersdorf (MN 6; IPUW), Le Fousseret (MN 7+8; MNHNP), Mira (isolated find MN 7+8; IPS), "Haute Garonne" (MN 7+8; MGPUSB), El Buste (MN 7+8; MPZ), Fonte do Pinheiro (MN 9; GML).

Aureliachoerus minus from Oberdorf and Seegraben suggests that the localities should be placed in MN 3–5.

T. sansaniense is a stage in a lineage *Taucanamo* sp. – *T. sansaniense* – *T. inonuensis*. This particular stage occurred in MN 5 and the earlier part of MN 6. It suggests for Göriach a slightly greater age than for Sansan.

There are three stages of evolution in the sanitheres: Stage I is found in Africa and the Indian Subcontinent, Stage II in Africa and Stage III (*S. schlagintweiti*) in Europe and the Indian Subcontinent (Van der MADE & HUSSAIN 1992; Van der MADE 1992, 1996a). Maboko in Africa has yielded a P_4 with a simple morphology, with only one cusp on the talonid. Maboko has a stage II sanithere.

Hyotherium soemmeringi ranges MN 3–6. The smaller subspecies *H. s. wylensis* occurred in MN 3 till the earlier part of MN 5 (zone D of the Aragonian), whereas the larger subspecies *H. s. soemmeringi* ranged from the later part of MN 5 (zone E) till the earlier part of MN 6 (zone F). The many localities from Styria have the latter subspecies. The combination of *Aureliachoerus minus* or an *Eotragus* that is smaller than *E. sansaniense* suggests that Seegraben and Labitschberg belong to MN 5. Münzenberg is lithostratigraphically correlated to Seegraben and should be of the same age.

The exact position of *T.? muenzenbergensis* is not certain, but, if it is ancestral to *Schizochoerus*, it is in line with Münzenberg being older than Çandır, and possibly being MN 5.

Taucanamo suggests that Göriach should be placed below Sansan, possibly even in MN 5. This coincides with data obtained on the bovid *Eotragus* from Göriach and Sansan (Van der MADE 1989).

The evolutive stage of *Conohyus* suggests that Göriach should be placed below Paşalar and possibly even in MN 5. These data are not isolated: *Eotragus* and *Taucanamo* from Göriach are more primitive than in Sansan and the deer *Euprox minimus* from Göriach has a lower evolutive level than *Euprox furcatus* from Arroyo del Val and Manchones.

Listriodon splendens ranged MN 6–9. The evolutive stage in Löffelbach suggests a latest Aragonian age (MN 8).

The bulk of the Styrian localities with suoids belong to late MN 5 (zone E) or earliest MN 6 (zone F). Micromammals suggest that Oberdorf 4 belongs to MN 4 (zone C), *A. minus* does not oppose this view. *Listriodon* places Haselbach in MN 6–9 and Löffelbach in the later part of MN 7+8.

Some of these biostratigraphical data can be translated into chronostratigraphy through correlation to radiometrically dated localities, to localities in palaeomagnetic sections and through "dated" migrations of suoids.

A stage II *Sanitherium* is found in Maboko and stage III in Seegraben: Seegraben should be younger than Maboko. The latter locality consists of a section of 50 m. A phonolite overlying the sequence is dated at 13.8 Ma and one overlying the richest fossil bearing bed at 14.7 Ma (FEIBEL & BROWN 1991). Since stage III (as in Seegraben) evolved from stage II (as in Maboko), Seegraben is likely to be younger than 14.7 Ma and possibly even younger than 13.8 Ma.

The entry of *Conohyus* in Europe was interpreted to be part of a dispersal event, occurring at the transition of zone D to zone E, and involving the primates *Pliopithecus* and *Crouzelia*

MN Unit	*Taucanamo inonuensis* *T. sansaniense* *Taucanamo* sp.	*Schizochoerus* *Taucanamo? muenzenbergensis*	*Sanitherium* Stage III Stage II Stage I	*Aureliachoerus minus*	*Hyotherium soemmeringi* *H. major*	*Listriodon splendens*	*Conohyus simorrensis*
7+8 6l		lower Sinap Çandır	?Chinji Fm.			St. Quirze **Löffelbach** **?Haselbach** La Grive oc Arroyo del Val IV Çandır	 Klein Hadersdorf
6e	Pasalar Inönü I Sansan		?Chnji Fm.		Thannhausen	Pasalar Sansan	Pasalar Elgg
5l/6	**Göriach**		?Chinji Fm.				**?St. Oswald** **?Au** **Göriach**
5l		**Münzenberg?**	Chinji Fm. Chios **Seegraben**	**Seegraben** Pontlevoy	Georgensgmünd **Hochtregist** **Schönegg** **Feisternitz** **Gamlitz** **Ameis** **Eibiswald** **Zangtal** **Vordersdorf** **Fohnsdorf** **Münzenberg** **Seegraben** Engelswies Sandelzhausen Pontlevoy oc Q. da Farinheira		Puente Vallecas
5e	Bézian		Maboko Ombo		Baigneaux Pellecahus		
4	 Artenay		Buluk Baragoi	**?Oberdorf oc** **Oberdorf 4** Can Canals El Canyet	 Buchenthal Munébrega Armantes I		
3			Karungu Rusinga Langenthal Loncherangan Bugti Napak		Chilleurs		
2					St Gérand Ulm-Westtangente		
1					Weissenau		

Fig. 10: Stratigraphical distribution of the Styrian suoid lineages. MN 5e is the former MN 4b (recently this part of MN 4 has been included in MN 5; ALVAREZ SIERRA et al. 1997). MN 5l is the former MN 5. Göriach is either earliest MN 6 or MN 5l. MN 6e is the earlier part of MN 6, MN 6l is the later part of MN 6.

as well as the rodent *Cricetodon*, all coming from or through the SE European – Anatolian land mass (Van der MADE 1996a). The event was believed to be related to the TD2.5 cycle of HAQ et al. (1987), dated at 13.8 Ma, and recently redated at 13.6 Ma (MILLER et al. 1996).

Magnetostratigraphic sections in the type area of the Aragonian yielded ages for the transitions of one zone to the other: the transition of zone D to E was estimated at 14.1 Ma, zone E–F = MN 5–6 at 13.8–13.9 and MN 6–7 at 12.7–13.0 Ma (KRIJGSMAN et al. 1994). More recent data suggest the respective ages: 14.05, 13.75 and 13.6 Ma (ALVAREZ SIERRA et al. 1997). ALVAREZ SIERRA et al. (1997) also redefined MN 5 as including zone D of the Aragonian (formerly in MN 4) in order to eliminate differences with central Europe.

These three lines of reasoning independently suggest for most of the Styrian localities (those of zone E) an age close to or slightly younger than 14 Ma. This contrasts with estimates of an age of about 15.5 to 17 Ma for the lower boundary of MN 5 (RÖGL & STEININGER 1984; RÖGL 1996), which implies an age at least 1.5 Ma older for these localities.

Biogeography

All localities mentioned were during the Miocene on the northern shore of the Paratethys and on the main Eurasian land mass (MOTTL 1970). Nearby was the northern edge of a subcontinent formed by SE Europe and Anatolia (RÖGL & STEININGER 1983).

During periods of low sealevel stands, this subcontinent formed a bridge between southern areas, such as Africa and the Indian Subcontinent and western and central Europe. It would be natural to expect a biogeographical separation at the place of the Paratethys. However, this is not indicated by the biogeography of the suoids.

Listriodon and *Conohyus* lived and evolved in an area that includes western and central Europe as well as the Balkan and Anatolia. Their distribution was not restricted.

Sanitherium is known from a number of African and Indian localities, from Chios and from Seegraben: it was on the Eurasian mainland, but it did not disperse further into this area.

Schizochoerus evolved in Anatolia, possibly from *Taucanamo muenzenbergensis*, which is known from Sandelzhausen and Münzenberg, but apparently did not disperse into western Europe until the Vallesian, millions of years later.

Other animals that seem to have been restricted permanently or temporarily like *Sanitherium* and *Schizochoerus* include the cervid *Euprox* and the bovid *Turcocerus*. The primitive species *E. minimus* was present in Göriach (MOTTL 1970), but only much later its probable descendant *E. furcatus* dispersed to western Europe (present in Arroyo del Val and Manchones; IVAU, MPZ). *Turcocerus* is known from Turkey (KÖHLER 1987), but is also found in the Vienna Basin (Mannersdorf, St. Margarethen; NMW), although it is not known from western Europe. Apparently Austria belonged to another palaeobioprovince than western Europe. The hypsodont *Turcoceros* may well have been restricted by a wooded central Europe, but whether this is also the case for the other species is questionable.

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	P_3			P_4			M_1				M_2					M_3			
	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	D	DAP	DTa	DTp	D	DAP	DTa	DTp	DTpp	D
Taucanamo																			
Münzenberg																			
SLJG 56697 r	12.4	4.9	5.6	10.5	5.8	6.0	10.7	7.7	7.8	--	12.0	>8.7	8.9	28.0	16.0	8.7	8.0	6.3	27.6
SLJG 56634 l				10.8	5.5	5.7	10.9	7.6	>7.5	>26.0	12.0	≥9.1	≥9.1	27.0	15.9	8.8	8.1	6.4	27.6
SLJG 56698 l											13.5	9.0	8.6	--	16.9	9.3	8.5	7.4	--
Göriach																			
SLJG 58818 r				9.9	5.6	6.1													
SLJG 58817 r											11.9	7.8	7.3						
SLJG 1880 l							10.3	±6.8	6.7	22.0									
Sanitherium																			
Seegraben																			
SLJG 56... d				11.3	6.2	6.3	9.7	6.5	6.6	22.3	11.6	7.9	7.9	23.9	--	7.5	--	--	--

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		P^2		P^3		P^4			M^1			M^2			M^3		
		DAP	DT	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp
Taucanamo																	
Münzenberg																	
SLJG 56699	l											12.0	11.1	10.5	12.4	10.6	8.3
Sanitherium																	
Seegraben																	
SLJG 56631	l	7.4	>6.4	8.2	>7.5	8.7	9.2	9.5	9.5	9.6	9.5	11.5	11.4	11.0	13.5	11.8	10.8
SLJG 56635	r	7.7	5.9														

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		I_1				I_2		I_3		C_m			C_f	
		DMD	DLL	Hli	Hla	DMD	DLL	DMD	DLL	Li	La	Po	DAP	DT
Hyotherium soemmeringi														
Labitschberg														
SLJG 1878	l	6.7	9.5			7.6	8.2	..	8.8				>12.9	--
	r	6.6	9.7			7.2	8.2							
"Leoben"														
IGGML 92	l	6.7	9.0											
Münzenberg														
SLJG 56873	r					6.4	9.4							
SLJG 3852	r	9.5	6.3	17.6	17.8									
SLJG 3838	r									13.9	8.0	10.5		
Seegraben														
SLJG 3845	r												8.7	6.7
SLJG 3847	l	6.7	9.1											
	r	6.7	9.1											
SLJG 3849	l							4.7	6.7					
SLJG 3836	l	6.4	9.6			6.4	9.1							
	r	6.9	9.9			6.3	9.2							
Conohyus simorrensis														
Göriach														
SLJG 1828	r									--	--	--		
SLJG 1856	l	±6.3	..			..	..							
	r	±6.2	..			±7.0	..							
SLJG 1883	r									16.1	8.0	12.8		
SLJG 3826	l									12.6	10.3	7.2	(tip)	
SLJG 9564	l					8.1	12.7							
SLJG 9582e	r					8.2	>13.0							
SLJG 9582e	l												>10.6	7.9
SLJG 9582e	l							--	--					
SLJG 9582f	r							..	±7.7					

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		I^1		I^2		I^3		C^m		C^f	
		DMD	DLL	DMD	DLL	DMD	DLL	DAP	DT	DAP	DT
Hyotherium soemmeringi											
Göriach?											
SLJG	r	13.5	8.4								
IGGML 6068	l	--	≥9.1								
Schönegg											
SLJG 1822	l	14.5	8.2								
SLJG 1829	r							--	--		
Feisternitz											
NHMW 17	l	12.4	8.0								
Seegraben											
SLJG 3846	r									11.7	6.3
SLJG 3848	l	11.4	8.7								
SLJG 3837	r									9.9	6.0
Conohyus simorrensis											
SLJG 1426	l			13.7	7.2						
SLJG 1504	r							20.7	14.8		
SLJG 1513	r	14.5	9.3								
SLJG 1595	r					>9.9	5.1				
SLJG 1820	r			12.3	5.6						
SLJG 1821	l	12.8	9.0								
SLJG 1826	r							--	--		
SLJG 1827	l							15.7	13.1		
SLJG 1830	l	13.6	9.7	13.1	6.9					..	..
	r	13.1	9.8	13.5	6.8						
SLJG 1833	l							20.5	14.1		
SLJG 1853	l					>8.4	5.0				
SLJG 1859	l									16.2	7.6
SLJG 3856	l					13.7	7.0			16.4	8.2
SLJG 3857	r									17.2	8.9
NHMW 1980/2094	l	13.2	9.4								
	r	12.7	8.7								
IGGML 3442	r	>11.6	>8.5	>12.3	>6.3						
IGGML 3442	r	--	8.6								
Au bei Aflenz											
SLJG 56695	l	13.7	10.5								

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Tab. 1: Measurements (in mm) of the lower cheek teeth of the Palaeochoeridae of the Aragonian of Styria. Where "--" is indicated, it means that the measurement could not be taken, because the specimen was broken or too worn. ".." indicates that this measurement was not taken because the

specimen was covered with sediment, a tooth was still in the alveolus, or that no standard measurement was possible because of the morphology of the tooth (for instance in the third lobe of the M^3).

		P_1			P_2			P_3			P_4			M_1			M_2			M_3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Hyotherium soemmeringi																							
Fohnsdorf																							
SLJG 60250	l										--	--	±10.5	15.9	12.4	12.5	18.5	15.5	14.2				
Kalkgrube Schwanberg																							
SLJG 2149	l																--	13.8	12.8				
Labitschberg																							
SLJG 1878	l	10.8	4.9	5.2	13.8	5.2	5.7																
	r	11.4	4.9	5.1	13.5	5.1	5.7	16.1	6.3	7.1	17.0	8.0	9.2										
SLJG 1867	r																18.1	14.1	14.3	--	13.8	12.8	--
SLJG 1968	l													--	--	--							
Feisternitz																							
SLJG 2146	r													16.6	±13.0	±13.1	±20.8	--	--	--	--	--	--
SLJG 2147	l							±15.8	±8.1	±8.3	17.3	10.2	10.7				19.7	15.3	--				
Gamlitz																							
IPUW --	l							16.3	6.3	7.0	17.1	8.2	9.3	16.9	12.6	12.5	19.2	15.4	14.2	27.6	14.9	12.9	9.5
Vordersdorf																							
NHMW sk1646	l				12.4	5.0	5.4				15.7	..	..	≥14.7	..	..	19.3	13.6	13.5				
	r										16.6	8.4	9.8	--	--	--	19.0	14.8?	..	26.2	..	..	..
Münzenberg																							
SLJG 56874	l										15.6	7.6	8.7										
SLJG 56878	r																			24.9	13.5	12.2	9.0
SLJG 56877	l										--	7.7	--										
SLJG 56876	l							15.8	5.9	6.7													
SLJG 56875	r													--	10.8	--							
SLJG 3860	r																18.4	13.6	13.0				
SLJG 3853	l							14.5	7.0	8.2	±16.0	±8.9	±9.9	15.9	11.0	12.0	18.4	13.9	13.4	26.8	13.5	12.4	10.2
SLJG 3851	r										±16.5	--	--	17.1	11.8	12.1	18.4	13.6	12.0				
SLJG 3830	l												19.0	13.7	13.5								
Seegraben																							
SLJG 3829	r													13.6	11.6	12.0	16.8	14.3	14.5	26.3	14.1	12.9	8.4
SLJG 3842	l										14.0	7.3	8.1	14.9	11.5	11.7	16.0	12.8	12.6	--	--	10.8	8.1
SLJG 3844	r																16.3	--	12.5	21.3	12.4	10.8	8.7
SLJG 56872	r													14.5	11.6	12.4	17.5	14.3	14.3	25.5	13.7	12.5	10.8
SLJG 3831	l													15.8	12.1	12.3							
SLJG 3832	l													15.2	11.3	12.0	17.0	13.5	13.4				
IGGML 6096	l																17.7	--	13.6	24.8	13.3	12.3	9.5
Aureliachoerus minus																							
Oberdorf 4																							
NHMW1997z0000/2/1	l																			15.9	8.9	7.4	6.1

		P^1			P^2			P^3			P^4		M^1			M^2			M^3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DT	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Hyotherium soemmeringi																						
Schönegg																						
SLJG 1849	r												16.5	14.3	14.2							
SLJG 1882	r							14.5	8.3	9.6												
SLJG 1848	r															17.1	16.2	15.7				
SLJG 1877	l															--	--	--				
SLJG 1850	l												15.1	14.7	13.9							
SLJG 1864	r																	--	--		13.4	--
SLJG 1883	l							13.7	8.9	10.1												
SLJG 1847	l										12.4	12.7										
St. Peter																						
SLJG 58774	r															18.0	--	>16.7				
Zangtal																						
SLJG 3821	l										12.4	--	--	--	--	--	--	--	20.0	17.0	15.5	··
	r										12.5	13.6	16.3	--	--	16.6	--	--	20.8	16.5	14.7	··
Hochregist																						
IGPKFUG 1877IV392	l							--	--	--	<14.3	14.6	<17.6	--	15.7	--	--	--	21.3	18.1	14.6	9.6
	r				13.9	6.5	7.5	15.2	9.0	11.4	14.0	14.3	16.8	15.7	--	19.1	17.3	15.9	21.4	--	14.6	10.3
"Leoben"																						
IPUW --	l							13.4	8.0	9.5												
Labitschberg																						
SLJG 1881	l							13.7	··	10.9												
SLJG 1969	l										12.4	--										
Eibiswald																						
IPUW --	l															15.6	16.1	15.4	17.9	15.8	13.7	5.5
	r	9.3	5.1	2.9							11.4	12.8	12.1	14.3	14.4	15.2	15.9	15.8	18.7	15.9	13.8	6.3
IPUW --	l															16.8	16.6	15.8				
IPUW --	l										--	--	14.6	--	--							
IGGML 92	r										12.7	12.9										
Feisternitz																						
SLJG 3855	l															17.2	16.3	15.4				
SLJG 3854	l															16.9	≥16.5	17.6	20.2	15.8	14.5	··
NHMW 1896	r							14.0	8.1	9.2	12.7	13.2	14.3	14.3	14.3	16.4	15.8	15.7				
Seegraben																						
SLJG 3828	l				13.3	6.0	--	--	8.4	--	12.0	12.9				17.3	16.4	≥15.1	19.8	16.5	14.7	8.4
	r				13.1	6.1	4.8	±14.0	8.4	--	12.1	12.6	14.6	13.8	13.8	17.0	16.2	15.9	19.7	16.3	15.1	7.7
SLJG 3840	l										11.3	12.3	14.5	13.8	14.5	15.9	15.1	15.0	18.1	14.7	13.4	··
SLJG 3843	r																		18.0	14.4	13.3	··
SLJG 3842	r										11.1	12.3										
SLJG 3834	l															16.6	15.8	16.5				
SLJG 3835	r	≥9.0	5.1	5.0																		
IGGML 32	l																		20.0	17.3	15.6	··
Aureliachoerus minus																						
Oberdorf oc																						
SLJG --																11.2	9.9	9.6				
Seegraben																						
SLJG 56633	l												8.0	8.2	8.2	9.6	9.5	9.3	12.0	9.5	8.3	
	r							>8.7	5.0	5.3	7.2	7.4	8.2	8.3	7.8	9.6	9.3	9.4	11.8	10.0	8.6	

		P_1			P_2			P_3			P_4			M_1			M_2			M_3			
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DTpp
Göriach																							
SLJG 1591	l																			--	15.9	(M_2/M_3?)	
SLJG 1842	l																18.9	14.3	14.5				
SLJG 1843	r																18.1	14.4	14.5				
SLJG 1856		13.1	5.1	5.6																			
SLJG 1857	r							--	12.6	--	18.9	13.4	14.9	16.1	--	--	17.9	14.6	14.2	24.8	14.1	12.8	10.6
SLJG 1858	l							26.1	13.7	16.5	18.5	13.0	15.2	--	>12.0	12.4	18.1	14.4	14.3	≤25.1	14.0	12.6	9.7
SLJG 1860	r										18.7	--	>12.6										
SLJG 1861	r							23.0	11.8	14.8	16.3	11.5	13.6										
SLJG 1862	r										16.9	≥11.8	≥12.2	15.9	11.2	11.7	17.8	13.2	13.7	24.4	14.4	12.5	10.9
SLJG 1868	r	15.7	4.9	5.9																			
SLJG 1879	l	14.3	5.4	5.7	19.5	6.9	7.9	25.6															
	r	14.5		5.9	19.5	6.0	8.0	29.1	--	15.8	20.5	13.9	15.0	17.7	12.0	≥12.2	±20.1	±14.8					
SLJG 1896	l																			24.8	14.9	12.6	10.6
SLJG 2148	l							23.1	11.9	14.6	17.7	12.0	14.0	15.6	12.5	12.8	17.2	15.3	15.7	24.8	15.3	13.3	12.5
SLJG 3822	l													15.6	--	--	17.9	14.3	14.0	25.2	14.3	12.6	11.6
SLJG 3823	r																--	14.4	≥13.7	25.5	14.4	12.3	10.4
SLJG 3827	l	13.3	4.9	4.7																			
SLJG 3861	l													--	--	13.0				25.4	15.3	--	11.3
	r																			25.5	16.6	13.2	12.3
SLJG 9564	l	16.2	6.0	6.4	19.8	7.3	8.9	24.3	12.0	15.9	17.9	13.0	14.9	16.1	≤13.0	12.6	--	15.4	14.3				
	r	15.8	6.0	6.1	19.8	..	±9.2	22.5	12.3	15.8													
SLJG 9582/a	l										20.0	14.4	16.3										
SLJG 9582/b	r							27.8	±12.7	16.4													
SLJG 9582/c																			13.6				
SLJG 9582/d	l																			28.4	14.9	13.3	13.1
IGGML 6019	l																			>21.9	--	11.8	9.7
IGGML 6263	r																17.2	13.5	12.6	23.8	13.4	11.8	10.4
NHMW 1896	r																			--	--	12.9	11.8
NHMW 1896	r																18.2	14.7	13.6				
NHMW 274/1958	l	14.3	5.6	6.0	--	--	--																
	r	14.2	5.8	6.0	--	--	8.3																
NHMW 274/1958	l							≥25.1	12.7	16.3	20.8	13.0	16.3	16.5	11.5	12.4	19.8	13.9	14.7	26.4	14.8	..	..
	r							--	--	15.6	>18.3	13.6	15.2	16.5	11.2	12.5	19.1	14.5	14.0	>22.4	14.8	..	..
NHMW1980/2094	l																			25.9	15.5	12.9	10.1
NHMW1980/2094	l				--	--	7.6																
NHMW1980/2094	r										17.8	12.4	14.3	16.4	12.1	13.0	18.8	14.3	14.4	26.0	15.2	13.1	10.1
NHMW1980/2094	r													--	--	--	19.8	15.4	14.7	25.7	15.4	13.1	10.5
NHMW1980/2094	l										18.5	12.5	15.1										
NHMW1980/2094	l							--	13.3	--													
NMB TO976	r																≤20.6	16.3	14.5	25.7	>15.2	>12.9	--
Au bei Aflenz																							
SLJG 56693	l							23.8	13.2	±18.8													
Rosenthal																							
SLJG 1512	r																			27.1	14.9	13.2	11.1
SLJG 1511	r																19.6	--	--				
St. Oswald																							
SLJG 9640	r										18.7	13.1	15.0										

		P¹ DAP	P¹ DTa	P¹ DTp	P² DAP	P² DTa	P² DTp	P³ DAP	P³ DTa	P³ DTp	P⁴ DAP	P⁴ DT	M¹ DAP	M¹ DTa	M¹ DTp	M² DAP	M² DTa	M² DTp	M³ DAP	M³ DTa	M³ DTp
Göriach																					
SLJG 1597	l							18.2													
SLJG 1830	l	17.9	··	··	19.4	7.0	8.4	20.0	15.0	17.7	13.4	17.6	15.8	15.8	15.2	18.7	18.6	18.0	21.1	18.1	14.0
	r				19.6	7.5	±8.6	20.1	··	±16.3	13.2	17.6	16.0	16.5	15.0	19.0	18.1	17.1	21.4	18.2	14.0
SLJG 1831	r	16.8	6.2	6.3																	
SLJG 1832	r				17.9	6.5	7.7	16.2	11.2	15.8	12.6	15.4									
SLJG 1834	r																		18.8	15.5	13.4
SLJG 1836	r							--	12.2	--											
SLJG 1837	r										12.7	17.3	--	15.1	--						
SLJG 1839	r										12.8	15.9									
SLJG 1840	r																		17.9	16.3	12.6
SLJG 1841	l																		18.3	16.2	13.0
SLJG 1844	r																		19.7	17.4	13.9
SLJG 1845	l							19.1	12.7	15.9											
SLJG 1846	l							16.9	±13.3	17.1											
SLJG 1851	r															18.6	17.0	16.1			
SLJG 1852	l																		20.8	16.4	13.2
SLJG 1866	r															17.8	--	--	20.3	16.2	15.2
SLJG 1870	l	--	--	--	16.7	6.3	7.9														
SLJG 3820	l										12.6	17.4	16.6	15.7	14.7	17.9	18.5	16.6	20.4	17.1	13.4
	r							17.9	14.4	17.8	12.7	18.3	16.4	15.5	14.9	18.3	18.1	16.9	22.5	17.2	13.8
SLJG 3824	r							19.2	13.6	17.4	12.9	17.9	16.1	≥14.5	14.6	18.1	17.7	16.6			
SLJG 3825	r				17.9	7.0	7.3														
SLJG 3856	l	18.7	6.4	7.2	20.6	7.2	8.4	20.8	14.1	18.8	13.3	19.0									
SLJG 3857	r	18.6	6.6	7.2	20.7	6.7	8.5	19.8	14.7	19.2	12.6	18.7	16.1	15.6	14.8	15.4					
SLJG 3861	r	14.6	6.1	6.3	20.4	7.7	9.1														
	l				±16.8	6.4	7.1	--	--	--	--	--	--								
SLJG 56.692	l										--	17.2									
NHMW 1896	l												15.7	--	13.9						
NHMW 274/1958	l															18.5	--	15.5	21.4	18.0	13.9
	r												16.2	14.9	14.2	18.9	17.6	16.0	··	17.3	··
NHMW1980/2094	r										12.9	≥18.7	15.6	14.7	14.2						
NHMW1980/2094	r				18.2	6.4	8.0	--	--	--											
IPUW 1835	r							19.6	13.3	18.7	13.4	18.4	15.3	16.1	15.4	17.8	17.5	15.7	20.6	17.3	13.5
Au bei Aflenz																					
SLJG 56696	r															19.0	18.4	16.7			
SLJG 56694	l							19.7	14.0	18.8											

Tab. 2: Measurements (in mm) of the upper cheek teeth of the Palaeochoeridae of the Aragonian of Styria.

		P_1			D_2			D_3			D_4				M_1			M_2		
		DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTp	DAP	DTa	DTm	DTp	DAP	DTa	DTp	DAP	DTa	DTp
Hyotherium soemmeringi																				
Münzenberg																				
SLJG 3858	l	12.4	4.2	3.4	13.8	5.0	5.6	19.8	--	8.6	9.8	15.1	12.1	12.0						
SLJG 3859	l							19.8	7.3	7.6	9.8	16.6	--	12.2						
Seegraben																				
SLJG 3833	l	12.0	3.6	4.7																
Aureliachoerus minus																				
Oberdorf oc																				
SLJG 9718	r	7.1	3.1	3.2	7.7	2.7	3.0	8.8	3.1	3.6	12.1	4.3	5.2	5.7	10.2	6.7	6.7	11.9	7.7	7.8
Oberdorf 4																				
NHMW1997z0000/2/2	l							--	--	4.1										
Conohyus simorrensis																				
Göriach																				
SLJG 1863	r							±16.7	--	--	±18.7	--	--	--	±16.0	--		--		
NHMW1980/2094	r										19.3	8.2	8.5	9.1	15.3	≥11.0	11.8			

		D^3			D^4		
		DAP	DTa	DTp	DAP	DTa	DTp
Hyotherium soemmeringi							
Münzenberg							
SLJG 3850	l				≥14.2	12.5	--
Conohyus simorrensis							
Göriach							
IGGML 6069		>14.2	--	--	≥14.0	--	--

Tab. 3: Measurements (in mm) of the lower incisors and canines of the Suidae from the Aragonian of Styria.

Tab. 4: Measurements (in mm) of the upper incisors and canines of the Suidae from the Aragonian of Styria.

		M_1				M_2				M_3			
		Ta	Tp	1000 Ta/DTa	1000 Tp/DTp	Ta	Tp	1000 Ta/DTa	1000 Tp/DTp	Ta	Tp	1000 Ta/DTa	1000 Tp/DTp
Hyotherium soemmeringi													
Fohnsdorf													
SLJG 60250	l	1.0	1.0	81	80	1.6	..	103	..				
Gamlitz													
IPUW --	l	1.0	1.0	79	80								
Feisternitz													
SLJG 2146	r	..	0.9	..	±69	--	1.5	--	--				
SLJG 2147	l					1.5	--	98	--				
Münzenberg													
SLJG 3853	l	0.9	--	82	--	1.3	1.3	94	97				
SLJG 3851	d	0.9	0.9	76	74								
Seegraben													
IGGML 6096										1.2	..	92	..
Labitschberg													
SLJG 1867	r					1.2	--	85	--	1.2	--	87	--
Taucanamo													
Münzenberg													
SLJG 56698	l					0.8	0.8	89	93	0.9	0.8	97	94
SLJG 56697	d	0.5	0.4	65	51	--	0.6	--	67	0.6	0.7	69	88
SLJG 56634	l									0.9	0.9	102	111
Göriach													
SLJG 1880	l	--	0.5										
SLJG 58817	r					0.6	0.6	77	82				
Sanitherium schlagintweiti													
Seegraben													
SLJG 566..	d	0.6	0.5	92	76	0.7	0.8	89	101				
Conohyus simorrensis													
Göriach													
SLJG 1842	l					1.6	1.9	112	131				
SLJG 2148	l	1.0	0.9	80	70	1.6	1.6	105	102	1.9	2.1	124	158
SLJG 3822	l	--	--	--	--	1.6	1.6	112	114				
SLJG 3823	r									1.7	1.4	121	≤102
SLJG 9564	l	0.7	0.5	54	40	1.4	1.6	91	112				
NHMW1980/2094	r	--	1.3	--	--								
NHMW1980/2094	r	1.0	1.1	83	85	1.4	1.7	98	118				
IGGML 6263	r					1.1	1.2	81	95				

Astraglus		Lext	Lm	Lint	DTp	DTd	R	d
IGGML 6109	l	36.4	29.3	33.2	16.5	18.6	..	..
Mandibular symphysis			L	H				
SLJG 3836			45.7	16.6				

Tab. 5: Measurements (in mm) of the lower permanent cheek teeth of the Hyotheriinae from the Aragonian of Styria.

Tab. 6: Measurements (in mm) of the permanent upper cheek teeth of the Hyotheriinae from the Aragonian of Styria.

Tab. 7: Measurements (in mm) of the lower permanent cheek teeth of *Conohyus* from the Aragonian of Styria.

Tab. 8: Measurements (in mm) of the permanent upper cheek teeth of *Conohyus* from the Aragonian of Styria.