The Suoidea from the Middle Miocene of Gračanica (Bugojno Basin, Bosnia and Herzegovina) - Evolution, Taxonomy & Biostratigraphy

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ABSTRACT

The Suoidea from Gračanica in the Bugojno Basin (Bosnia and Herzegovina) are assigned to: *Choeromorus lemuroides* (previously *Taucanamo sansaniense*) (Taucanaminae, Palaeochoeridae), *Bunolistriodon latidens* (Listriodontinae, Suidae), and *Conohyus simorreensis* (Tetraconodontinae, Suidae). These belong to three anagenetic lineages, known from Western Europe to Anatolia. The fossils from Gračanica and these lineages are described in detail. Biostratigraphic correlations in an area extending from Western Europe to Anatolia are proposed on the basis of these lineages. These correlations are consistent with known independent age estimates of the large mammal localities in the different areas. Because the Suoidea from Gračanica belong to groups which have suffered from recent taxonomic inflation, their systematics has been discussed for a correct classification.

Key words: Suidae, Palaeochoeridae, Old World peccaries, Phylogeny, Biochronology

ACKNOWLEDGEMENTS

I thank U. Göhlich for inviting me to study the Suoidea from Gračanica, the following persons for discussions on themes related with this paper: M. Böhme, U. Göhlich, O. Mandic, P. Peláez Campomanes, J. Prieto, G. Rössner, D. Vasilyan, W. Wessels, and as reviewers M. Orliac and an anonymous person. The following persons gave me access to fossils used for comparison, or helped me in any other way: J. Agustí, L. Alcalá, F. Alférez, B. Alpagut, M. Arif, B. Azanza, O. Bardot, Basu, P. Brewer, S. Calzada, E. Cioppi, A. Curren, G. Daxner Höck, F. Duranthon, T. Engel, B. Engesser, V. Fahlbusch, M. Fortelius, S. Fraile, J.L. Franzen, J. Galkin, L. Ginsburg, C. de Giuli, U. Göhlich, A. González Alonso, W. Gräf, C. Guérin, E. Güleş, O. Hampe, K. Heissig, E. Heizmann, J. Hooker, M. Hugueney, K.A. Hünemann, S.T. Hussain, K. Kowalski, Y. Laurent, H. Lutz, E. Menéndez, S. van der Mije, J. Morales, R. Niederl, R. O'Leary, S. Pavic, M. Philippe, K. Rauscher, M. Raza, L. Rook, G. Rössner, M. Rummel, G. Saraç, U. Schmid, H.K. Schmutz, P.Y. Sondaar, I. Stefanović, M. Telles Antunes, E. Ünay, L. Via, R. Ziegler. This paper benefited from projects Synthesys GB-TAF-4119 and AT-TAF-3663, and from projects CGL2004-04169/BTE, CGL2008-03881 of the Spanish Ministry of Science, and CGL2015 65387-C3-3-P from the Spanish Ministry of Economy and Competitiveness.

Funding information This paper benefited from projects Synthesys GB-TAF-4119 and AT-TAF-3663 and from projects CGL2004-04169/BTE, CGL2008-03881 of the Spanish Ministry of Science, and CGL2015 65387-C3-3-P from the Spanish Ministry of Economy and Competitiveness.

INTRODUCTION

The interplay between tectonics and sea level greatly changed European Miocene geography and the reduction of the Paratethys to what are now the Black and Caspian Seas is part of this process (Rögl & Steininger 1983; Rögl 1998; Popov et al. 2004). Superposed climatic change, led to complex biogeographic changes, which are still far from understood. Europe was not biogeographically homogenous and even in western Europe there were many differences in the timing of faunal events (Van der Made et al. 2006; Kálin & Kempf 2009; Van der Meulen et al. 2011, 2012). Today, the limit between the Palearctic and Saharo-Arabian biogeographic realms passes just south of Anatolia (Holt et al. 2013), but there is evidence that from the Mio- till the Pleistocene a long standing biogeographic limit between Anatolia + Greece and West + central Europe existed (Van der Made & Mateos 2010). This could reflect a different position of the limit between the two biogeographic realms in the Neogene, though alternatively it may reflect that a wide transition zone with limits of individual taxa at different geographic positions.

The Middle Miocene fossil locality of Gračanica in Bosnia and Herzegovina is thus biogeographically in a very interesting position. Its fauna is a welcome addition to the relatively poor Middle Miocene fossil record of the area between west + central Europe and Greece + Anatolia. It should not be strange, that there are difficulties of biostratigraphic correlation between those areas. Fossil localities in the intermediate area are of interest in that they provide information on biogeography and correlation. Fahlbusch (1991, p. 168) recognized the difficulties arising from the complex biogeographic history of Europe and the need of unequivocal boundary definitions of the biozones. Since dispersal events may be diachronic, he considered the use of stages-of-evolution in continuously evolving lineages as the best method for the objective definition of time boundaries. The fossil Suoidea from Gračanica belong to three lineages, which are known from the Iberian Peninsula to Anatolia. Without pretending that these lineages should be used to define the boundaries of biozones, they have been used previously in correlation between these areas (Van der Made 2003, 2005). At present, there is much more material available to describe the evolution of these lineages which could support or contradict these correlations.

All three suoid lineages were subject to publications, which greatly complicated their taxonomy (eg. Pickford 2011, 2014, 2016a, 2016b, 2017; Pickford & Laurent 2014). In general there is much splitting, but also the rules of the International Code of Zoological Nomenclature are not followed. This obscures evolution and biostratigraphy and affects the classification of the Suoidea from Gračanica at the species, genus, subfamily and family level. Therefore it is necessary to discuss taxonomy of the taxa from Gračanica in detail.

The aims of this paper are: 1) to describe the fossil Suoidea from Gračanica, 2) to classify them, which implies discussions to clarify taxonomy, 3) to describe their evolutionary lineages quantitatively, and 4) to use these lineages in correlation in the area extending from western Europe to Anatolia. The major taxonomical problems will be discussed in the Suppl.-Information.

MATERIAL AND METHODS

Tooth nomenclature follows Van der Made (1996a) and Prieto et al. (2017). Upper teeth are indicated with superscript (e.g. M^3 , P^2), lower teeth with subscript (M_3 , P_2) and if no separation between upper and lower is made, neither sub- nor superscript is used ($M3$, $P2$). The measurements are taken as indicated by Van der Made (1996a) and are given in mm (unless indicated otherwise). The measurements are indicated in Tabs. 1-5 and in the figures with acronyms, which are explained in the Suppl.-Tab. 1.

The material presented here is housed in the Natural History Museum of Vienna, Austria (NHMW). The specimens from Gračanica are compared with specimens from other localities (Fig. 1; Suppl.-Fig. 1; Suppl.-Tab. 2). In Suppl.-Tab. 2, descriptions of those materials are also listed, with the classification used in those publications. In this table, acronyms are used to indicate in which institutes the material was studied, or where it is kept presently. These acronyms are explained in Suppl.-Tab. 3. If no acronym of a collection is given, the data used come from these publications. The stratigraphy of many of these localities is discussed in the Suppl.-Information and the ages are summarized in Suppl.-Tab. 4, where also the relevant literature on stratigraphy or age is given.

SYSTEMATICS

The material from Gračanica is described in this section, while information and discussions on taxonomy are

presented in the Suppl.-Information. The classification of the taxa mentioned in the text is given in Suppl.-Fig. 2, where it is compared to the classification of other authors.

Palaeochoeridae Matthew, 1924

Selected synonymy:

- 1899-1900 Palaeochoeren - Stehlin: pp. 29-522 (intentionally not used as a formal name).
- 1899-1900 Palaeochoeriden - Stehlin: pp. 182, 225, 269, 320, 328, 331, 410-411, 432, 433, 439-440, 453, 481-482 (intentionally not used as a formal name).
- 1909 Palaeochoeridés - Stehlin: p. 505 (not used as a formal name).
- 1924 Palaeochoerinae - Matthew: p. 176.
- 1996b Palaeochoeridae Matthew, 1924 - Van der Made: p. 302.
- 2011 Yunnanchoerini nov. - Pickford: p. 571.
- 2017 Siderochoeridae nov. - Pickford: p. 43.
- 2017 Schizoporcidae Van der Made, 2010 - Pickford: p. 34.
- 2017 Doliochoeridae Simpson, 1945 - Pickford: p. 24.

Taucanaminae Van der Made, 1997a

Selected synonymy:

- 1997a Taucanamini new tribe - Van der Made: p. 131.
- 2010 Taucanaminae Van der Made, 1997 - Van der Made: pp. 46, 47, 114.
- 2017 Choeromorinae nov. - Pickford: p. 55.

Choeromorus Gervais, 1850

Selected synonymy:

- 1850 *Choeromorus* Lartet - Gervais: p. 7. Type species: *Choeromorus mamillatus* Gervais, 1850.
- 1851 *Choerotherium* Lart. - Lartet: p. 33. Type species: *Choerotherium sansaniense* Lartet, 1851.
- 1945 *Taucanamo*, new name - Simpson: p. 146. Type species: *Choerotherium sansaniense* Lartet, 1851.
- 2017 *Siderochoerus* nov. - Pickford: p. 43. Type species: *Siderochoerus minimus* Pickford, 2017.

Choeromorus lemuroides (Blainville, 1847)

Selected synonymy:

- 1847 *S. lemuroides* - Blainville: p. 231, pl. 9.
- 1850 *Choeromorus mamillatus* - Gervais: p. 7, Pl. 33 fig. 4.
- 1850 *Choeromorus simplex* - Gervais: p. 7, Pl. 33 fig. 5.
- 1851 *Choerotherium Sansaniense* - Lartet: p. 33.
- 1949 *Taucanamo* (= *Choerotherium*) *sansaniensis* (Lart.) - Thenius: 163 (only the material from Sansan).
- 1956 *Taucanamo sansaniense* (Lartet) - Thenius: p. 366 (only the material from Sansan).
- 1956 *Taucanamo pygmaeum* (Depéret) - Thenius: fig. 31 (the material from Göriach, not figs. 29-30).
- 2012 *Choeromorus mamillatus* Gervais, 1850 - Pickford: pp. 251-265, figs. 1-23.
- 2017 *Choeromorus lemuroides* (Blainville, 1847) - Pickford: pp. 57-73, figs. 42-57.

Holotype: MNHN Sa 4593, symphysis with right I₂ and roots or alveoles of the remaining incisors, canines and right and left P₁₋₃, figured by De Blainville (1847, Genus *Sus* plate 9) and Pickford (2017, fig. 42).

Type locality: Sansan, France.

Age of the type locality: Middle Miocene, Middle Aragonian, early Astaracian, MN6.

Material:

- NHMW 2013/0008/0001a - left maxilla with P³ to M³, of the M³ only the anterior lobe is preserved.
- NHMW 2013/0008/0001b - right M².
- NHMW 2013/0008/0001c - left P₃.
- NHMW 2013/0008/0001d - left P₄.
- NHMW 2013/0008/0001e - left M₁.

Description and comparison

Of the M³ (Fig. 2) only the first lobe is preserved. It is similar to that of the M².

The M² (Figs. 2, 3) has the roots close together and still fused at a distance of the crown. Fused lingual

roots are typical of the Palaeochoeridae (“Old World peccaries”) and unlike in the Suidae. All roots are fused till some distance below the crown (taurodonty), what also occurs in the Palaeochoeridae. The crown is relatively low. The protopreconule (protoconule) is fused to the protocone as in the Palaeochoeridae and not to the cingulum as in most Suidae. The protoprecrista and paraprecrista meet anterior of the proto- and paracone, but posterior of the cingulum. This is a step towards lophodonty. This is like in the later species of *Choeromorus* and in *Pecarichoerus*, while *Schizoporcus* and *Yunnanocherus* have better developed lophs. No tetrapreconule (central cusp) is developed and there is only a tetraprecrista, which probably was low. Palaeochoeridae tend to have a small or no tetrapreconule, while most Suidae have a well-developed tetrapreconule. While the tetraprecrista is directed forwards, there is no metaprecrista and no loph is formed by the fusion of these two crests. A longitudinal valley keeps these cusps separate. Such sublophodont morphologies are common in the Taucanaminae. The tetraprecrista meets a protoendocrista. This is unlike in *Schizoporcus muenzenbergensis*, where the latter crest is not developed. In the sample from Sansan, it is variable. In *Choeromorus inonuensis* it is better developed, but also not universal. There is no cusp in the middle of the posterior cingulum (tetrapostconule) and the tetrapostcrista ends as a narrow crest. This is like in many Palaeochoeridae and unlike in the Suidae. The M^2 is narrow as *Ch. lemuroides*, *Ch. inonuensis* and *Choeromorus grandaevus*, while those of *Choeromorus primus* and *S. muenzenbergensis* are wider (Fig. 3). The size (Tab. 1) is comparable to those of the first two species.

The M^1 (Fig. 2) is much worn and little is preserved of the crown. As far as can be seen, the lingual roots are fused as in the Palaeochoeridae and unlike in the Suidae, where they are separate. They are convergent, as in the Taucanamini and Doliochoerini, and not divergent as in the Palaeochoerini. The proportions are as in the M^2 . While the M^2 is in the upper range of the *Ch. lemuroides* sample, the M^1 is in the lower range (Fig. 3). A large $M2$ and large $M3$, compared to the $M1$, are related features in Suoidea. In *Choeromorus* this is a progressive feature.

The P^4 (Fig. 2) has the para- and metacone placed very close together. They are not separated by a deep or clear furrow on the lingual, nor on the buccal side. Seen from the side, they form a pointed structure, rising far above the cingulum. There is no paraprecrista and no parapreconule (“sagittal cusp”). The protopre- and protopostcristas are short and there is no protoendocrista. All these features are primitive in the Suoidea and common in the Palaeochoeridae. The posterolingual cingulum forms a wide plateau. The tooth is longer than wide (Tab. 1; Fig. 3), which occurs in some of the species of *Choeromorus*, unlike what is common in the Suidae, Palaeochoerinae and *Schizoporcus*. The size is in the lower ranges of *Ch. lemuroides*.

The P^3 (Fig. 2) has a large paracone with pre- and postcristas. The protocone is a low cusp, arising from the posterolingual cingulum. The tooth is relatively elongate as in *Ch. lemuroides* and unlike in *Ch. primus* or *Ch. grandaevus* or *S. muenzenbergensis*. The size is in the range of *Ch. lemuroides* (Fig. 3).

The M_1 is much worn and nothing of the crown morphology is preserved. The tooth is elongate. The value indicated in Fig. 4 for the length (DAP) is a minimum value because of wear; the tooth was longer. The tooth is in the ranges of *Ch. lemuroides* and is smaller than the M_1 of *Ch. inonuensis* (Fig. 4).

The P_4 (Fig. 4/2) has only one main cusp. This is the primitive state for the Suoidea. In the Palaeochoeridae, it occurs in the Taucanamini and in the Suidae in the Tetraconodontinae and is occasionally known from some Hyotheriinae. *Schizoporcus* has a P_4 with a well-developed metaconid. There is a well-developed protoprecrista and where this reaches the wide anterior cingulum, a protopreconulid is formed. There is a protopost- and protoendocristid. The latter is directed posterolingually. There is a very low and well worn hypoconid. The low hypoconid correlates to the paracone and metacone on the P^4 being very close together and high, a primitive feature in the Suoidea. Primitive Suidae, like *Hyotherium* have already a larger hypoconid, and as a result, the para- and metacone on the P^4 form a lower and less pointed structure. Next to the hypoconid, there is another small cusplet on the talonid. The tooth is very elongate for a P_4 and in this respect, it is similar to *Ch. lemuroides* and *Ch. inonuensis* and it is also in their metrical ranges (Fig. 3).

The P_3 (Fig. 4/1) has a shape that is similar to that of the P_4 , but it is simpler. In particular, the hypoconid is very small and not well differentiated from the protopostcristid. In side view the tooth is triangular and this cusp does not even show up. This is a primitive morphology. Compared to the premolars of suids like Hyotheriinae, Listriodontinae and Suinae, the P_4 is relatively high and pointed. Metrically, it is within the ranges of *Ch. lemuroides*.

Specific and generic classification of the palaeochoerid from Gračanica

The fused lingual roots and shape of the protopreconule of the upper molars are similarities to the Palaeochoeridae. The molars with crests that suggest lophodonty are a similarity to several Taucanaminae, while the later species of *Schizoporcus* and *Yunnanocherus* have better developed anterior lophs in the upper molars.

The P₄ with a single main cusp is a difference with *Schizoporcus*. The elongate molars and premolars are a similarity to the later species of the genus *Choeromorus* (= *Taucanamo*). The size is relatively large for this genus and best fits *Ch. lemuroides* (= *T. sansaniense*). The material is assigned here to the latter species. The classification by Van der Made (2010) is used to arrive to this identification. However, subsequently a more complex classification of these Suoidea has been proposed (Pickford 2011, 2012, 2016b, 2017), which would change the species, genus, tribe, subfamily and family name of the suoid from Gračanica. Those proposals are discussed in the Suppl.-Information.

Suidae Gray, 1821
Listriodontinae Gervais, 1859
Bunolistriodon Arambourg, 1963

Selected synonymy:

- 1933 *Bunolistriodon* - Arambourg: p. 137 (name not available, because no type species was indicated).
1963 *Bunolistriodon* Arambourg, 1933 - Arambourg: pp. 903-904, with type species *Bunolistriodon lockharti*.
1995 *Eurolistriodon* nov. - Pickford & Moyà Solà: p. 344 (name not available, because no type species was indicated).
2006 *Eurolistriodon* gen. nov. - Orliac: pp. 968-969, with type species *Eurolistriodon adelli* Pickford & Moyà-Solà, 1995.

Bunolistriodon latidens (Biedermann, 1873)

Selected synonymy:

- 1873 *Sus latidens* m. - Biedermann: p. 11, pl. 7.
1899-1900 *Listriodon latidens* Biedermann - Stehlin: pp. 13, 85, 173, 285, 327, 426, 462, pl. 1, fig. 15, pl. 3, figs. 31-33.
1990a *Bunolistriodon latidens* (Biedermann, 1873) - Van der Made: pp. 86, 93.
1995 *Eurolistriodon latidens* - Pickford & Moyà Solà.

Holotype: NSSW no. 99 - mandible with left and right P₂-M₃, C_m, I₁ and left I₂, figured by Biedermann (1873, pl. 1, fig. 15), Stehlin (1899-1900, pl. 1 fig. 15, pl. 3, fig. 31-33) and Van der Made (1996a, pl. 18, figs. 2-3).

Type locality: Veltheim, Switzerland.

Age of the type locality: Middle Miocene, MN5.

Material

- NHMW 2013/0012/0001 - right maxilla with M²⁻³; same individual as 0002.
NHMW 2013/0012/0002 - left M³ and lingual half of left M²; same individual as 0001.
NHMW 2013/0012/0003 - left maxilla with P⁴ and roots of a completely worn M¹.
NHMW 2013/0012/0004 - right I₁₋₃ and left C_m.
NHMW 2013/0012/0005 - right premaxilla with root of the I¹ and an alveolus of the I^{2/3} and part of the maxilla with flattened C^m.
NHMW 2013/0012/0006 - right maxilla with P³⁻⁴ and M³ and with roots/alveoles of M¹⁻².
NHMW 2013/0012/0007 - left maxilla with P⁴-M³; probably same individual as 0008.
NHMW 2013/0012/0008 - left mandible with M₁₋₃ and right mandible with P₂-M₃, pressed together.
NHMW 2013/0012/0009 - left I¹.
NHMW 2013/0012/0010 - left P₄.
NHMW 2013/0012/0011 - fragment of left M₃; lingual wall of second and third lobes.
NHMW 2013/0012/0012 - second phalanx III or IV, right of the axis of the foot.
NHMW 2013/0012/0013 - right astragalus, proximo-medial fragment.

Description and comparison

The M₃ (Fig. 6/6) has the protoendocristid and metaendocristid directed to each other and connecting behind the centres of the proto- and metaconid. The protoconid and metaconid are massive cusps; between them and anterior to the endocristids, there is a clear anteroposterior furrow. The result is close to a loph, as occurs in *Bunolistriodon* and not a complete loph, as in *Listriodon*. There is a hypopreconulid in the middle of the transverse valley, as in many Suidae, including *Bunolistriodon*, while in *Listriodon* there is just a hypoprecristid.

The hypoconid and entoconid remain well separated by a clear antero-posterior directed valley. With a primitive loph in the anterior lobe and no loph in the posterior lobe, the tooth is sub-lophodont. Nearly all Suidae are bunodont, without any lophs, while within the Listriodontinae sub-lophodonty and lophodonty are found. All sublophodont Palaeochoeridae are much smaller. The third lobe consists of a large pentaconid and a pentapreconulid close to the axis of the tooth.

The M_2 and M_1 have a similar structure, but lack a third lobe. These molars are relatively small. Though there is a large overlap in size between the larger *B. lockharti* and the smaller *Bunolistriodon adelli* and *B. latidens*, the size of these molars is more similar to that of the latter species.

The M^3 (Figs. 6/1, 6/5) has a protoprecrista that is directed to the anterior side of the paracone. When it reaches that cusp it is very low, but the two connect, forming a primitive loph. No protopreconule is formed on the cingulum. The tetraprecrista is directed to the center of the tooth, where it ends, without connecting to the metacone, nor giving rise to a well individualized tetrapreconule in the middle of the transverse valley. This structure is called sub-lophodont, as occurs in *Bunolistriodon*. The third lobe consists of a pentacone, situated lingually of the axis of the tooth.

The M^2 and M^1 (Fig. 6/1) have morphologies similar to that of the M^3 , save for lacking a third lobe.

The P_4 (Fig. 6/3) has a well-developed metaconid placed lingually of the protoconid, forming a transverse loph. There is a flat transverse facet extending over the posterior side of this loph (Fig. 6/3e). There is a furrow on the anterior side between these two cusps (Fig. 6/3a), as in *Bunolistriodon*, while in *Listriodon*, there is a wide depression but no furrow. The hypoconid is placed on the buccal side of the talonid.

The P_3 and P_2 do not have any indication of a metaconid and the talonids do not have a clear hypoconid. Their morphologies are simple as in *Bunolistriodon*.

The P^4 (Figs. 6/1, 6/2, 6/4) has a large protoprecrista directed anterobuccally, ending near the axis of the tooth and without forming a loph with the paracone, even though in a worn tooth, the dentine pattern suggests such a structure (Fig. 6/4b). The metacone may be more (Figs. 6/1, 6/2) or less individualized (Fig. 6/4).

The P^3 (Fig. 6/2) consists of a large paracone and a small protocone, which is not connected to the cingulum. The latter morphology is common in the Listriodontinae. The protocone and cingulum do not extend much lingually and the tooth is not so wide as in the later *Listriodon*. There is no cusp or cusplet formed within the protopostcrista. Especially in the later *Listriodon splendens*, such a cusp is formed. Both morphologies are as in *Bunolistriodon*.

The C_m (Fig. 7) is high and probably it was hypselodont. It has a triangular section, with the lingual and labial sides covered with enamel, but the posterior side not. The earliest Suoidea have such triangular teeth with the lingual sides much wider than the labial sides. These teeth are said to be “scrofic”, because they are as in *Sus scrofa*. In several lineages, the width of the labial side increased, giving rise to “verrucosic” canines. When the labial side became wider, the posterior side became relatively narrower. The different canine types can be well recognized in bivariate diagrams, or using ratios of the widths of the different sides (Fig. 7). *Bunolistriodon lockharti* and *B. adelli* tend to have canines with relatively wide posterior (Po) and narrow labial sides (La), while in *B. latidens* the posterior side is relatively narrower and in *Bunolistriodon meidamon* it is much narrower (Fig. 7). In both the labial side is relatively wider. As seen in an index comparing the widths of the labial and lingual sides (Li), there is a tendency from *B. adelli* to *B. latidens* and *B. meidamon* to increase the width of the labial side (Fig. 7). The tooth from Gračanica fits best *B. latidens*.

The C^m has three enamel bands, as is normal in the Suidae: the pre-, post-, and endosyncline. The tooth has little wear and the tip, where the three synclines meet, is preserved. The tooth is flattened by diagenetic compression. It was directed outwards.

The I_1 is damaged and the labial side of the crown is gone, what is left of the relevant morphology is similar to that in the I_2 .

The I_2 (Fig. 8/1) has a transverse or mesio-distal diameter (DMD) that is much longer than the labio-lingual diameter (DLL). This occurs only in Listriodontinae, *Celebochoerus*, *Kolpochoerus* and *Hylochoerus*. The pre- and postanticiplinid are very low, as only occurs in the Listriodontinae. There is no endocristid. This crest is weak or absent in the Listriodontinae; *Listriodon* retains a weak crest, but in *Bunolistriodon* it tends to be weaker or absent. The DMD and DLL fit *B. latidens*, while the incisors of *B. lockharti* and *B. adelli* are narrower and those of *B. meidamon* wider (Fig. 8).

The I_3 (Fig. 8/2) is damaged, but what is left shows that the crown was very wide, as in *B. latidens* and *B. meidamon*.

The I^1 (Fig. 9/1) has a low and very elongate crown, with a marked lingual cingulum. The mesial facet is perpendicular to the long axis of the crown. This means that the two incisors formed a transverse crest, as in

the Listriodontinae, and not a V-shape as in most Suoidea (see Van der Made 1996a, fig. 25; 1997b, fig. 7). It has two clear, equally deep and long, grooves on the labial side, separating the main cusp in the middle, from the pre- and postconules. This is as in *Bunolistriodon*, while *Listriodon* has only one large groove, which in very elongate specimens it is flanked by two minor grooves. *Bunolistriodon lockharti* and *B. adelli* have incisors with a DMD that is about twice as long as the DLL, but *B. latidens* and *B. meidamon* have relatively much longer DMD (Fig. 9). The tooth from Gračanica fits *B. latidens* in size and proportions.

The **premaxilla and anterior maxilla** are crushed. The maxilla contains the C^m and the premaxilla the alveolus of the I¹. The I²⁻³ are not present and no alveolus of the I² can be seen, while it is not clear whether a depression is the alveolus of the I³. It is not clear whether these alveoles cannot be identified because the bone is crushed or whether the individual lost these teeth during life and the alveoles closed. In any case the snout is very wide as is normal in the Listriodontinae.

Some **foot bones** are preserved, but add little additional information.

Classification of the listriodont from Gračanica

The low crowned and wide incisors from Gračanica, are indicative of the Listriodontinae. The two equally long and deep labial furrows on the I¹ and the sublophodont molars indicate the genus *Bunolistriodon* (= *Euolistriodon*). This is supported by the sublophodont molars, while *Listriodon* has fully lophodont molars. Here the classification of *Bunolistriodon* of Van der Made (1996a, 1997b) is used. Other opinions on the classification of these Suidae are discussed in the Suppl.-Information.

The clearest differences between the different species of *Bunolistriodon* are seen in the proportions and sizes of the incisors and canines (Van der Made 1996a, figs. 35, 49), differentiating four species. Increased samples of the European and Anatolian I¹, I₂ and C_m of *Bunolistriodon* still show four clusters for each of these teeth (Figs. 7-9). The clusters of the oblique crosses include a specimen from Chevilly (red circle), type locality of *B. lockharti*, supporting that these clusters belong to that species. The clusters of the black triangles consist mainly of fossils of the type locality of *B. meidamon*. The clusters of blue rhombs include material from type locality Veltheim of *B. latidens*. *Bunolistriodon adelli* from type locality Els Casots (red dot) clusters with the small black squares (Fig. 9), which in part represents material previously assigned to that species (Van der Made 1996a), supporting this assignation. These graphs support four distinct west Eurasian species: *B. lockharti* (= *B. giganteus* = *B. tenarezensis*), *B. adelli* (= *B. retamaensis* =? *B. michali*), *B. latidens* and *B. meidamon*.

The incisors from Gračanica (red inverted triangles in Figs. 8-9) are far away from those of *B. lockharti* and *B. adelli*, as well as from *B. tenarezensis/giganteus* and *B. retamaensis* (whether these species are valid or not). They are also far away from *B. meidamon*, while they are closest to the clusters of *B. latidens* (Figs. 8-9). This is also the case with the canines (Fig. 7). All other morphology described above is compatible with assigning the listriodont fossils from Gračanica to *B. latidens*.

Tetraconodontinae Lydekker, 1876
Conohyus Pilgrim, 1925
Conohyus simorreensis (Lartet, 1851)

Selected synonymy:

- ?1850 *Listriodon Lartetii* - Gervais: p. 50, plate 20 fig. 1.
- 1851 *Sus Simorreensis* - Lartet: p. 33 (partially).
- ?1851 *Sus? doati* - Lartet: p. 33.
- 1859 *Sus abnormis*, Kaup - Kaup: pp. 7-9, pl. 2, fig. 1.
- ?1882 *Sus Valentini* - Filhol: pp. 123-124.
- 1972 *?Hyotherium sommeringi* MEY. *matritensis* n. sp. - Golpe-Posse: p. 122
- 1972 *Hyotherium sommeringi* MEY. *matritensis* nova. sp. - Golpe-Posse: pp. 155-156.
- 1972 *Hyotherium soemmerringi matritense* GOLPE, 1971 - Golpe-Posse: p. 197, pl. 6, fig. 6b.
- 1972 *Conohyus melendezi* n. sp. - Golpe-Posse: pp. 149, 157.
- 1972 *Conohyus melendezi* n. sp. GOLPE, 1971 - Golpe-Posse: pl. 2, fig. 2b.
- 1986 *Conohyus ebroensis* nov. ap. - Azanza Asensio: pp. 95-105, pl. 2, fig. 1, figs. 2-3?
- 1989 *Conohyus simorreensis goeriachensis* nov. subsp. - Van der Made: pp. 27-28, pl. 1.
- ?2014 *Parachleuastostochoerus valentini* (Filhol, 1882) - Pickford: pp. 181-185 (partially).
- 2014 *Conohyus simorreensis* (Lartet, 1851) - Pickford & Laurent: pp. 6-9, fig. 2.
- 2014 *Retroporcus matritensis* nov. comb. (Golpe-Posse, 1972) - Pickford & Laurent: pp. 15-24, figs. 14-26.
- 1999 *Conohyus giganteus* (Falconer & Cautley, 1847) - Van der Made: 211-212 (European material).

Lectotype: MHNT PAL2011.0.84.1 right mandible with P₂-M₂ and PAL 2011.0.84.2 left mandible with P₄-M₃ of the same individual, figured by Pickford & Laurent (2014, fig. 2).

Type locality: Villefranche d'Astarac, Gers, France.

Age of the type locality: Middle Miocene (Ginsburg, 1971).

Diagnosis: *Conohyus* with relatively large premolars and relatively small M₃. M₁ length about 14-21 mm, M₃ length about 24-35 mm, M₃ length as a percentage of M₁ length about 140-200. (Adapted from Van der Made 1999).

Material

NHMW 2014/0081/0001 right and left M₁₋₃ and left P₃ of the same individual.

Description and comparison

The P₃ (Fig. 11a-e) has a very simple structure. It has a single main cusp with a pointed tip. From this anterior and posterior crests (protopreclistid and protopostclistid) descend towards the base of the crown. There is no clearly developed posterior cusp (hypoconid or protopostconulid). There is a bulge on the posterior part of the buccal side. This simple structure is typical of the Tetraconodontinae. Other Suidae tend to have a main cusp that is not so pointed, but that has a wider and blunter tip, especially if seen from the side. They also tend to have a cusp on the talonid (hypoconid) or a cusplet in the protopostclistid (protopostconulid). The tooth is very large (Tab. 3) and it is much bigger than the P₃ of the different species of *Parachleuastochoerus* (save for a single aberrant specimen from La Grive) and of *Retroporcus sindiensis*, while it clusters with the P₃ of *Conohyus* (Fig. 11). Its length must have been a little over 183% of its width.

The M₃ (Fig. 12/1) has a structure that is similar to that of the anterior molars, save for that it has a third lobe. There is one main cusp in the third lobe, the pentaconid, and it is situated a little buccally of the axis of the tooth. It is preceded by a pentapreconulid. The tooth is not very elongate and its length is 158 % of its width and $\geq 153\%$ the length of the M₁. Both M₃ are unworn and their crowns are low with a hypsodonty index of 56 to 68. Compared to other *Conohyus* samples, these M₃ are among the shortest (Fig. 12).

The M₁ (Fig. 13/2) and M₂ (Fig. 13/1) have the same morphology, but differ in size (Tab. 3). They are bunodont and they had four roots. The M₂ are worn, but not enough to expose the dentine and when unworn the crowns must have been slightly higher than the values in Tab. 3. With a hypsodonty index (100 Ha/DTa) of 75, which must have been only a little higher, the crowns are markedly lower than wide. They are also wide (length about 122-127 % of the width in the M₂ and 131-132% in the M₁). The length of the M₂ is about 115% the length of the M₁. The latter value may be much more in a late tetraconodont and in most Suinae, this is near 140%. These three proportions are typical in the primitive or early Suidae. Compared to other samples of *Conohyus*, these teeth are among the smallest (Fig. 13).

Classification of the tetraconodont from Gračanica

The teeth from Gračanica described here belong probably to the same individual. The P₃ with a high main cusp and a low talonid and a size which is large in absolute terms (Fig. 11), but also relative to the molars, suggests that the species belongs to the Tetraconodontinae.

The suid from Gračanica does not belong to *Parachleuastochoerus* (= *Versoporcus*; Suppl.-Information) because its P₃ is much larger and relatively wider (Figure 11). In *Conohyus* the P₃ is large compared to the molars whereas in *Parachleustchoerus* it is much smaller (Fortelius et al. 1996: fig. 28.7; Van der Made 1999: fig. 3). The P₃ from Gračanica is large relative to the molars like in *Conohyus*. The size of the molars from Gračanica (in particular of the M₁) is comparable to the earlier stages of *C. simorreensis* (Figures 11-13, Supplementary Figure 9). The P₃ from Gračanica is longer and relatively narrower than those from Mala Miliva and Somosaguas and of *R. sindiensis* from Pakistan (Figure 11). These fossils from Gračanica are assigned here to *C. simorreensis*. This implies that Gračanica is younger than Somosaguas (zone E, 14.05-13.75 Ma), Sansan (just over 14.163 Ma), Mala Miliva, Petrovac and Bâla, which have *R. sindiensis* (see Suppl.-Information).

THE GRAČANICA SUOIDEA AND BIOSTRATIGRAPHY

Fig. 14 is a further developed version of previously published figures (Van der Made 2003 fig. 9, 2005, fig. 1). It includes the three suoid lineages described here in detail, as well as some others, which are of interest here. The

lineage of *Hyotherium* is included in Fig. 14. This lineage was described in detail by Van der Made (2010), recognizing two subspecies of *H. soemmerringi*. Recent literature on this lineage is discussed in the Suppl.-Information. The central part of Fig. 14 gives the evolutionary lineages and solid squares indicate the presence of the different chrono-species or chrono-subspecies in the localities. Open squares indicate possible presence. The localities are ordered in the same way as in Figs. 5, 7-10, 12-13. The localities with more than one lineage indicate the positions of the grades of evolution of different species relative to each other and the relative positions of localities. Though there is still some possibility to move localities up and down in this scheme, this is limited, and the more lineages are included, the more rigid the scheme becomes. The scheme is based on biometry.

On the left of Fig. 14, the Astronomically Tuned Neogene Time Scale (ATNTS2012) after Hilgen et al. (2012), the Spanish biozones and their ages and the proposed correlations the MN units as well as the Spanish and Portuguese localities (largely after: Daams et al. 1999a, 1999b; Hernández Bailarín & Peláez Campomanes 2017; Mein 2000). As indicated above, for most of the large mammal localities only the time range of the biozone is available. This results in a long time interval for sites from a long zone like Dc, but a short time interval for sites in a short zone like F. On the right, Fig. 14 gives localities from other parts of Europe, when available with their published ages or age ranges based on paleomagnetism, radiometric dates, etc., as well as the Central Paratethys stages, MN units and the ATNTS2012. It should be noted that MN units have different estimated ages in Spain and Germany + Switzerland (Van der Meulen et al. 2011). Most of the localities on the right side do not have reliable and precise age constraints. The ages or age ranges of many localities are discussed in the Suppl.-Information and the localities and their published or inferred ages are listed in Suppl.-Tab. 4.

The central part of Fig. 14 provides a scheme in which localities have ages relative to many of the other localities (older/younger than). The addition of chronological information of many localities, does not only provide absolute ages (or age ranges) to the scheme, but also more rigidity. This still does not provide a precise ages for many localities. It is not possible to indicate graphically the possible age ranges for each site in the figure, but regarding the figure well, the age constraints of the sites can be seen. There is much more material and much better age control than when these lineages were first proposed Van der Made (1989, 1996a, 1997a, 1997b, 2003, 2005, 2010).

What strikes in Fig. 14, is that the Iberian large mammal localities are not evenly distributed in time, or at least the localities with the large mammals studied here. There are biozones without a single locality with these taxa. On the right side of the figure this is not so apparent, but there are similar hiatuses for Germany, Austria and possibly France as well. Different basins might have hiatuses at different times. It was noted before that the European fossil record in general is not evenly distributed (Van der Made 2011: fig. 1).

The replacement of *Hyotherium* by *Conohyus*/*Retroporcus* in Central and western Europe

Conohyus simorrensis replaced *Hyotherium soemmerringi* in the Central Paratethys (Mottl 1970; Rabeder & Steininger 1975). The appearance of *Conohyus* was taken as indicative of MN6 (eg. Mein 1975, 1977). Later, on a European scale, there appeared to be an overlap (Van der Made 1990b; De Bruijn et al. 1992), but with improved dating the extinction of *Hyotherium* in Europe appeared to be earlier (Van der Made 2010). The question, whether such a replacement existed or not, and when it may have happened, has relevance for the age of Gračanica where *Conohyus* is present.

At present it appears, that the latest *Hyotherium* is in Rümikon (14.163-14.609 Ma) and Thannhausen (a little older than 14.55 Ma). Given the fact that Rümikon and Thannhausen have inferred ages close to or younger than 14.55 Ma, occurrences of *C. simorrensis* which are younger than 14.55 Ma, would fit the model of *Conohyus* replacing *Hyotherium*. However, the new species *Conohyus olujici* was named and some fossils have been reclassified as *Retroporcus sindiensis*.

Bernor et al. (2004) described the species *C. olujici* from Lučane (~15.0 Ma). It is tempting to believe that this represents the first *Conohyus* in Europe, but Van der Made et al. (2014) classified it as *Parachleuastochoerus steinheimensis olujici* and Pickford (2016b) as *Parachleuastochoerus huenermanni*.

Fossils previously included in *C. simorrensis* were placed in various species in the genus *Retroporcus* (Pickford & Laurent 2014) and are here classified as a single species *R. sindiensis*, which is present in Bălă, Petrovac, Mala Miliva, Sansan, Somosaguas and Montjeu de la Vega (Suppl.-Tab. 2). The latter two localities are in zone E (14.05-13.75 Ma). Sansan is in the top of C5ADn (close to 14.163 Ma; see discussion in the Suppl.-Information). The specimens from Bălă and Petrovac seem to be isolated finds. Mala Miliva is in sediments which interfinger with the marine Badenian, suggesting it is older than 13.8 Ma (Suppl.-Information). The faunal list is short, but includes two other species of Suoidea. The specific identity of the palaeochoerid from this site has been a problem. It is probably *Choeromorus lemuroides* (see Suppl.-Information). The other species is

Bunolistriodon latidens. The temporal ranges of these species are discussed below and are compatible with Mala Miliva being younger than Rümikon, but still within chron C5ADn (14.609-14.163 Ma).

With such an age for Mala Miliva, the model of *Conohyus*/*Retroporcus* replacing *Hyotherium* is possible. The dispersal of *R. sindiensis* into western Eurasia would then be anterior to 14.163 Ma (Sansan, top of chron C5ADn), but younger than Rümikon (chron C5ADn, 14.609-14.163 Ma) with the latest *Hyotherium*. Considering the historic model of a replacement of *Hyotherium* by *Conohyus*, which did not recognize *Retroporcus* as different from *Conohyus*, (Mottl 1970; Rabeder & Steininger 1975), Gračanica with *Conohyus* should be younger than 14.069 Ma, the oldest possible date of the last *Hyotherium*.

The replacement of *Bunolistriodon lockharti* by *Listriodon* as a criterion for the MN5-6 transition

Gračanica has been placed in MN4-6 on the basis of rodents (Wessels et al. 2019), MN5 on the basis of Rhinocerotidae (Becker & Tissier 2019), MN5-6 on the basis of ruminants (Aigelstorfer & Mayda 2019), beavers (Stefen 2019) and chalicotheres (Coombs & Göhlich 2019) and MN6 on the basis of carnivores (Bastl et al. 2018). These papers do not necessarily contradict each other, but more probably reflect that different definitions of the MN units were used. The MN units were defined using many different criteria (Mein 1975a, 1975b, 1977, 1979, 1990), but it should not be surprising that the use of different criteria may give different results.

The appearance of *Listriodon splendens* is consistently used to separate MN6 from MN5 (Mein 1975a, 1975b, 1977, 1979, 1990). The replacement of *Bunolistriodon* by *Listriodon* is the only faunal event indicated by De Bruijn et al. (1992, tabs 8-12), which separates MN5 from MN6 in both western and central Europe. The event is thus an important one. It should be noted that at the time of these publications, *B. lockharti* was the only species of that genus recognized in Europe. The presence of a second European species (Van der Made & Alférez 1988) and eventually of the lineage *Bunolistriodon adelli* - *B. latidens* - *B. meidamon* (Van der Made 1996a) was later. *Bunolistriodon lockharti* was a contemporary of *B. adelli* and even occurred in the same localities (Córcoles) and later *B. latidens* and *B. meidamon* were contemporaries of *L. splendens* and occurred in the same localities (Inönü 1, Paşalar, Çandır). By contrast, *B. lockharti* and *L. splendens* are not known from the same localities and there is no evidence that were contemporaries. It seems thus, that the replacement of *B. lockharti* by *L. splendens* is a relevant event for the MN5-6 transition in western Eurasia. *Listriodon* is known from over one hundred localities in Europe and Turkey (Van der Made 1996a) and its stratigraphic distribution can be more reliably known than of many other taxa which are used in biostratigraphy.

A similar replacement occurs broadly at the same time in China, where *Bunolistriodon intermedius* is replaced by *L. splendens*. *Bunolistriodon intermedius* has verrucose C_m , like *B. lockharti* and could be closely related or identical to that species. The Chinese *Listriodon* were named *L. mongoliensis*, *L. lishanensis*, *L. xinanensis*, and *L. robustus*, but there are no convincing features that show them to be different from *L. splendens*. I have previously listed *L. robustus* as a synonym of *B. intermedius* on the basis of published photographs (Van der Made 1996a). Liu Liping showed me the originals and indeed these belong to a primitive *Listriodon*, not to *Bunolistriodon*. The appearance of *L. splendens* and the replacement of a local species of *Bunolistriodon* could prove to be a good criterion for the correlation of the MN5-6 transition across Eurasia from Spain and Portugal to China.

Castelnau d'Arbieu has *B. lockharti* and is one level lower in the local stratigraphic sequence than Sansan (about 14.163 Ma) with *L. splendens*. Other late *B. lockharti* are from Lisbon Vb (later half of zone Dc, 15.2-14.75 Ma) and Ravensburg. The latter locality is in the Upper Fresh Water Molasse (OSM) and is probably latest MN5, but no precise age is known. A molar from Georgensgmünd (NMB) was assigned to *Bunolistriodon* sp. (Van der Made 1996a), but more material (MNB) belongs clearly to *B. lockharti*. Berger (2010, 2011) described and figured all presently known material and assigned it to that species. Georgensgmünd is in the OSM. Its age is controversial (before/after the Riss Event), but probably is slightly less than 15 Ma (see Suppl.-Information).

From Sansan (top C5ADn, a little older than 14.163 Ma) and Inönü 1 onwards, there is a dense record of *Listriodon* in Europe. A fragmentary incisor from Rümikon (14.163-14.609 Ma) (NMB OSM1080) belongs to a listriodont, but its identification is insecure. A cast from Stätzling (BSP) was assigned to *Listriodon* (Van der Made 1996a). This locality is similar in age to Thannhausen (close to, but older than, 14.55 Ma).

The replacement of *B. lockharti* by *L. splendens* seems to have occurred between about 15 and 14.55 Ma. This is in either in zone Dc or Dd and well before zone F, which in Spain has the first record of *L. splendens*. Puente de Vallecas is probably the only Iberian record of *Bunolistriodon* in zones Dd and E and was previously assigned to *B. lockharti* (Morales & Soria 1987). Even though these fossils were later assigned to *B. latidens*, the first appearance of *Listriodon* at 13.75 Ma in zone F was not questioned (Van der Made 1996a). Daams et al. (1998, fig. 1) indicated “Bunodont *Listriodon*” in zones C to E and “Lophodont *Listriodon*” in zones F to G1 and

correlated the E-F transition to that of MN5-6. It seems now, that the replacement of *B. lockharti* by *L. splendens* is a much older event between about 15 and 14.55 Ma. A correlation of Sansan to just below the top of C5ADn at 14.163 Ma dates Sansan within the time range of zone Dd (14.75-14.05 Ma). The position of Sansan is thus well above the MN5-6 transition, if this is taken at the replacement of *B. lockharti* by *L. splendens*. The following section will provide arguments that Gračanica is younger than the appearance of *Listriodon* and, based on this criterion, should be placed in MN6.

Faunal events and the age of Gračanica

A series of faunal events, both older and younger than Gračanica, are of biostratigraphic interest and help to date the locality (Figs. 14 and Suppl.-Fig. 10).

The first is the evolution of *Choeromorus primus* to *Ch. lemuroides* (Suppl.-Information). Since Gračanica has *Ch. lemuroides*, this event puts a maximum age on the locality. The evolution occurred after Els Casots (zone C, 16.45-15.98 Ma). The earliest *Ch. lemuroides* might be from Lavardens, in a level between those of La Romieu and Castelnau d'Arbieu. None of these sites have independent age estimates.

The second is the evolution of *B. adelli* to *B. latidens* (Suppl.-Information). *Bunolistriodon adelli* is well known from the Iberian peninsula, but might be present in Chios and *B. latidens* is mainly known from Serbia and Turkey, though there are some records in the Iberian Peninsula. *Bunolistriodon adelli* is present in various localities of zone C and Dc (15.47-14.75 Ma) and evolved into *B. latidens* present in Lisbon Vb (Olival da Susana, Quinta do Farinheira, etc.; zone Dc, 15.47-14.75 Ma; Fig. 14). The latter identification is mainly based on one I_1 from Olival Susana, but it is wider than any *B. adelli* I_1 (Suppl.-Fig. 8). Given the number of sites with *B. adelli* in zone Dc, this evolution may have happened closer to 14.75 than to the 15.47 Ma. This further limits the possible age of Gračanica.

The third event is the replacement of *Bunolistriodon lockharti* by *L. splendens*, which was discussed in the previous section. In Europe and Anatolia, it seems to have happened between about 5 and 14.55 Ma and a similar event occurred in China. It is of relevance, since it is one of the criteria used to define the transition of MN5 to MN6. Gračanica is younger than this event.

The fourth event is the replacement of *Hyotherium* by a *Retroporcus*, which is discussed in a previous section. This event happened within chron C5ADn (14.609-14.163 Ma).

The fifth event is the evolution of *Retroporcus* to *Conohyus* (Suppl.-Information). The youngest localities with *Retroporcus* and age control are Sansan (just over 14.163 Ma) and Montejo de la Vega and Somosaguas (zone E, 14.05-13.75 Ma). One of the oldest localities with *Conohyus* is Puente de Vallecas (zone E). This suggests that this transition occurred within zone E and between 14.05 and 13.75 Ma. A P_4 from Sankt Oswald is generally assigned to *C. simorrensis* and is longer and more elongate (measurements: Van der Made 1998, Tab. 7) than in *R. sindiensis*. The site is said to be in sediments that interfinger with marine sediments of the "Lagenidenzone" (Rabeder 1978), which would imply an age older than 13.9 Ma (Mandic et al. 2019, fig. 10). This suggests that, the replacement of *Retroporcus* by *Conohyus* happened between 14.05 and 13.9 Ma. Since Gračanica has *Conohyus*, this indicates a maximum age of 14.05 Ma for this site.

The sixth event is the evolution of *Ch. lemuroides* to *Choeromorus inonuensis* (Suppl.-Information). The fifth and sixth events bracket Gračanica, which has already *Conohyus*, but retains *Ch. lemuroides*. The event must be younger than Sansan (slightly older than 14.163 Ma), because that locality still has *Ch. lemuroides*. None of the localities with *Ch. inonuensis* has independent age control, so the only thing that can be said is that this event must be older than the next faunal event.

The seventh event is the evolution of *B. latidens* to *B. meidamon* (Suppl.-Information). The *B. latidens* I^1 from Gračanica is outside the range of the older samples of the species and comparable to Prebreza, a late, possibly the latest, locality with this species, suggesting that Gračanica was relatively close to this faunal event. The latest *B. latidens* with an independent indication of numerical age is from Carpetana (zone F, 13.75-13.60 Ma). This identification is based on only one incisor, but it is clearly outside the size range of the large sample from Paşalar (Suppl.-Fig. 8). The oldest locality with *B. meidamon* is Paşalar, but it lacks independent age control.

The eighth event is the replacement of *Ch. inonuensis* by *Choeromorus grandaevus*. This must have happened between Paşalar, without independent age control, and Steinheim with *Megacricetodon gregarius*, which in the Swiss molasse is restricted to the top of C5ACn (Kälin & Kempf, 2009). So the event must have happened before 13.739. Gračanica should be clearly older than this date.

The ninth event is evolution of *B. m. meidamon* to *B. m. ultimus*. This between Paşalar, without independent age control, and Çandır. The latter locality has a palaeomagnetic section with four possible correlations to the global scale (Suppl.-Information). The two most likely are to C5ACn (13.739-14.070 Ma) or to

C5ABn (13.363-13.608 Ma). A correlation of Çandır to C5ACn would concentrate the last three faunal events in the top of C5ACn and the base of zone F (13.75-13.739 Ma). It seems more likely that Çandır should be correlated to C5ABn.

Despite the fact that the localities are from an area extending from Lisbon to central Anatolia, and despite the known problems of correlation with MN units, all evolutionary events in these lineages are consistent with the known ages or age ranges of the localities. There are however, some remarkable implications. For instance, Sansan is not to be correlated to zone F, as previously believed, but more likely to the top of zone Dd. This follows from the age estimates from zone D and Sansan being placed in the top of chron C5Adn, but now this is also supported by biostratigraphy. The combination of various lineages provides more precise and robust age estimates. For instance, Petersbuch 39 and 108 date probably from between 14.163 (Sansan, where *Ch. inonuensis* is not yet present) and 13.363 Ma (the youngest possible age of Çandır, where *Ch. inonuensis* is replaced by *Ch. grandaevus*). The estimated age ranges for each of the localities, for which no previous age estimate was available, and for each of the faunal events, are testable hypotheses.

Gračanica is bracketed between events 1-5 and 6-9 (after 14.05 and well before 13.739 Ma). The use of multiple events to date Gračanica implies enhanced support for its estimated age.

Improved biochronology and the biogeography and evolution of *Bunolistriodon*

The anagenetic lineage *B. adelli-latidens-meidamon* was described and the origin of this lineage was discussed over 20 years ago (Van der Made 1996a), but it was not resolved whether *B. lockharti* and *B. adelli* appeared in Europe by dispersal at the same time, at different times, or whether one evolved from the other within Europe. The increased biochronologic resolution, as synthesized in Suppl.-Fig. 11, is relevant for the understanding and dating of the biogeography and evolution of *Bunolistriodon*.

In the Iberian Peninsula, the first localities with *Bunolistriodon* are in zone Ca (after 16.45 Ma), but in Germany this is in Grimmelfingen (17.6-17.2 Ma), Langenau (17.2-16.8 Ma), Gerlenhofen (16.8-16.6 Ma) and Engelswies (~16.6 Ma), which are all older. At the first sight, the same happens as with several micromammal events, that are used in biostratigraphy (Van der Meulen 2011, 2012): the taxa appear later in Spain than in the Molasse Basin. However, there are no large mammal localities in the Iberian Peninsula placed in zone B and those of zone A are much rarer than those of zones C and D. It is possible that this later appearance of *Bunolistriodon* in the Iberian Peninsula is apparent. This can only be solved when more large mammal localities of these ages are found. So it is not clear whether the later appearance of *Bunolistriodon* in the Iberian Peninsula is real or an artefact.

While the oldest European *Bunolistriodon* localities have all *B. lockharti*, nearly all *B. adelli* localities are from the Iberian Peninsula. It was cited from two localities in France and Spain: Echzell and Bézian (Van der Made 1996a). *Bunolistriodon michali* (Paraskevaidis 1940) is a small species, of which the incisors and canines are not known. It was considered to be a possible synonym of *B. latidens* (Fortelius et al., 1996). More recent age estimates for Chios (Koufos 2006) suggest that it is older than *B. latidens* and that it might rather be a synonym of *B. adelli*. The oldest *B. adelli* from zone C are more similar to *B. lockharti* than those of zone D. The available data suggest the following scenario (Suppl.-Fig. 11):

- 1) *B. lockharti* dispersed into Western Europe (17.6-17.2 Ma).
- 2) Not later than early zone Ca (16.45 Ma), it spread into the Iberian Peninsula.
- 3) *B. adelli* evolved there from *B. lockharti* (later in zone Ca, before 16.3 Ma). *Bunolistriodon adelli* inherited its three-lobed I^1 from *B. lockharti*, even though in the oldest samples the tripartite division is still variable and mainly visible near the tip of the tooth in little worn molars.
- 4) *B. lockharti* dispersed again into the Iberian Peninsula (zone Cb, 16.3-15.98) and *B. adelli* dispersed into Europe reaching Chios (not later than 15.974-15.16 Ma). The two species were sympatric.
- 5) *B. adelli* evolved into *B. latidens* (zone Dc, 15.47-14.75 Ma).
- 6) *B. lockharti* went extinct, when *L. splendens* dispersed into Europe (about 15-14.55 Ma).
- 7) In the Balkans and Anatolia, *B. latidens* gave rise to *B. meidamon* (after the onset of zone F, 13.75 Ma).
- 8) The lineage went extinct before 13.363 Ma.

ECOLOGY OF THE SUOIDEA OF GRAČANICA

With three species, the Suoidea are prominent in the fauna of Gračanica. There are at least two individuals of *Bunolistriodon latidens*, while the other species are represented each with at least one individual.

The most important feature of the Suoidea is their adaptation to rooting. This is a unique adaptation and

provides the Suoidea with access to food sources that are not used by other ungulates. They are omnivores and target animals that live in the soil or hide underground (invertebrates and small vertebrates) as well as nutrient rich underground plant parts (roots, tubercles, etc.). Depending on the climates in which they live, rooting provides the Suoidea access to food during dry or cold seasons, when other food sources are restricted (e.g. African wart hogs in the dry season; Cumming 1975). Suoidea have a variety of rooting styles, some root to an average depth of 8 cm and others to 25 cm, and adaptations to rooting, which can be seen in the fossils (Ewer 1958; Sicuro & Oliveira 2002). When Suoidea root, they push their snout into the soil and subsequently elevate the snout. Species that root deep have wide occiputs, for the insertion of powerful neck muscles, which are high above the occipital condyles, so that the muscles have a greater momentum. Long narrow snouts are another adaptation. Species with large canines probably do not root very deep, as is the case with the living African wart hog. When the snout is in the soil, the snout disc is moved for searching food items. This disc is moved with muscles, of which the size and power can be judged from the origin on the skull. The incisors are used in digging and in the extraction of food items. Narrow high crowned incisors are an adaptation to rooting. The lingual crests in the lower incisors are another feature, which probably is related to rooting, providing grip when wrenching roots. In many species the I_3 does not evolve a higher crown, while related to this, the I_2 becomes elongated, occluding with the lateral side of the I_2 (Van der Made 2010).

All Suidae of which the skulls are known have wider and higher occiputs than the Palaeochoeridae (“Old World peccaries”) and the Tayassuidae (American peccaries). The highest and widest skulls appear from the Late Miocene onwards. The skull of *Conohyus* is not known, but the skull of its ancestor *Retroporcus sindiensis* has already a clearly more elevated and wider occiput than in the peccaries, while its snout was narrow (Colbert 1938). Its incisors have high, but not extremely high, crowns and the I_2 is moderately elongated. Its I_{1-2} have clear lingual crests. *Conohyus simorrensis* was clearly adapted to rooting and presumably targeted deeper food items than the living peccaries. It may have had a broadly similar level of adaptation as *Hyotherium*, while later Suidae improved on that. *Conohyus* is far less abundant in the Middle Miocene of Europe, than its relative *Parachleuastocherus*. It tends to be represented by few specimens in the localities where it occurs. An exception is Göriach, where it is very common. The site is in coal, suggesting possibly dense vegetation or forest and certainly a humid soil with a thick organic layer. Such a soil would be rich in food items for *Conohyus*. Also the fossil locality of Gračnica is in coal and probably the environment had optimal conditions for *Conohyus*.

All known skulls of the Palaeochoeridae have narrow and low occiputs. There is no indication for powerful snout muscles on the face. Their incisors tend to be low crowned and in *Choeromorus* they lack lingual crests (Suppl.-Fig. 5). The I_2 is not elongated. This suggests that they are not powerful rooters. However, the Palaeochoeridae have elbows which allow some rotation, which is rare in the Artiodactyla, and third phalanges, which suggest the existence of powerful nails or claws, different from the typical hoofs of other Suoidea. These and other features, such as a long pisiform, suggest that they may have dug with their feet. Living species of Suoidea are known to dig occasionally with their forefeet (Cumming 1975). The localities where the Palaeochoeridae are most abundant tend to be fissure fillings: Coderet, Tomerdingen, various sites at Petersbuch and also La Grive. The fissures are in limestone. Landscapes with limestone, tend to have soils that are not very deep. *Choeromorus* evolved towards lophodonty, without fully reaching this state. Lophodonty in Suoidea is taken as an adaptation to folivory. All this suggests that *Choeromorus lemuroides* may have specialised more on folivory than other Suoidea and that it depended relatively less on rooting.

Bunolistriodon latidens evolved very wide incisors. The Listriodontinae in general show the trend to decrease the crown height and increase the width of the incisors. The lingual crests on the I_{1-2} tend to become less prominent. They also lack lingual wear facets on these incisors. This has been interpreted as an evolution away from the rooting habit (Leinders 1977; Van der Made 1996a). The Listriodontinae evolved towards lophodonty and the species of the lineage of *B. latidens* reached a stage which is called sublophodont. Morphology and microwear suggests that the listriodonts specialised in folivory and the wide incisors have been interpreted to be a specialisation to bulk feeding, perhaps on herbs (Leinders 1977; Hunter & Fortelius 1994; Van der Made 1996a). If this species abandoned rooting and was a specialized folivore, maybe also frugivore, there must have been abundant edible leaves all year round. This suggests a lesser degree of seasonality than today, or at least a lesser impact of the seasons on the vegetation. Another feature which suggests, that rooting was not important to *B. latidens* and *Bunolistriodon meidamon*, are the gigantic canines of the males, which had lengths of over 30 cm (Van der Made 1996a, Pl. 18 fig. 1, Pl. 37 fig. 6): these would not allow deep rooting. While the lower canines have sharp edges and could have been used as weapons, especially the upper canines are large and would be well visible from a distance. The upper canines had a display function and served to impress competing males. Bovidae use horns to fight and to display. The smaller horns occur in species which are territorial and live in pairs in closed habitats, while the largest and most ornamented horns occur in species which live in more open

environments and in which a male defends a territory and attempts to retain many females (“harem”) in this territory, while in non territorial species there are large mixed herds and also the females tend to have large horns (Jarman 1974; Estes 1974). In Suidae, this has a parallel in that most living species are territorial, live in pairs and the males have relatively small upper canines, while in the African warthog (*Phacochoerus*) both males and females have large canines, the females live in groups and one male defends his position near the group of females. On the basis of the canine as a display structure, the social structure of *B. meidamon* has been interpreted as males living with large groups of females in environments where these canines are visible from far (Van der Made 2003). *Bunolistriodon latidens* may have been folivorous, feeding on large quantities of herbs in a landscape with open spaces.

The rate of evolutionary change in the *Bunolistriodon adelli-latidens-meidamon* lineage was not constant, but increased greatly after 13.75 Ma. This is within a period of major climatic change, called the Mid-Miocene Crisis (Krijgsman et al. 1994). Probably these morphological changes are related to environmental change. At this time, the geographical distribution of the lineage became progressively restricted ending in Anatolia. This may reflect a response to the Mid-Miocene cooling, perhaps causing greater impact of seasonal fluctuations on the vegetation, first at higher latitudes, later at lower latitudes. The presence of *B. latidens* in Gračanica suggests that this locality shared aspects of its environment (i.e. those to which this listriodont adapted) with Anatolia, but not with West and central Europe. During MN6, the environment in which *B. latidens-meidamon* lived progressively disappeared from Europe.

Two of the three species of Suoidea from Gračanica seem to have been more specialised in folivory (perhaps also frugivory) rather than in rooting. This suggests the presence of abundant herbs or other low vegetation, either as an under storey in a forest or in open spaces during all or most of the year. The impact of the seasons on the vegetation may have been less than today, which is compatible with a higher inferred temperature, based on insects (Wedmann & Skartveit 2019). The canines of *Bunolistriodon* suggest open spaces, while *Conohyus* is more suggestive of closed environments, or at least soils with a thick horizon of organic material, which in turn suggests humid conditions. This is not strange, given the presence of coal and beavers at Gračanica (Stefen 2018). This interpretation is compatible with others of the environment of Gračanica having habitats ranging from swampy forest to drier and more open environments (Harzhauser et al. 2018; Becker & Tissier 2019; Coombs & Göhlich 2019).

CONCLUSIONS

The study of the Suoidea from Gračanica led to the following conclusions:

- The species *Choeromorus lemuroides* (Taucanaminae, Palaeochoeridae), *Bunolistriodon latidens* (Listriodontinae, Suidae), and *Conohyus simorreensis* (Tetraconodontinae, Suidae) have been identified.
- The Suoidea from Gračanica belong to anagenetic lineages, which are known from Europe and Anatolia. Many new fossils of these lineages have become available since these lineages were first described and dating of these materials has improved. The new data support these lineages.
- A biostratigraphic scheme is presented based on the evolutionary stages of these three lineages and some other Suoidea. The proposed correlations across Europe and Anatolia appear to be consistent, despite known provincialism in rodents, which are widely used in used for biostratigraphy.
- The Suoidea suggest an age for Gračanica between 14.05 and 13.739 Ma and probably more towards the middle of this period
- The ages of many other localities can be estimated more precisely. Among these, of particular interest are the hominoid localities Çandır (13.608-13.363 Ma) and Paşalar (13.75-13.739 Ma) and the locality Mala Miliva (14.609-14.163 Ma).
- The Suoidea suggest the presence of abundant vegetation, possibly forest, but also of open spaces at Gračanica. Seasonality may have had less impact on the vegetation than today. The soil may have been humid with a thick layer of organic material.
- A revised phylogeny of the Taucanaminae is presented.
- The early history of *Bunolistriodon* in Europe was not clear. The available information suggest, that *Bunolistriodon lockharti* dispersed first into central Europe and later into the Iberian Peninsula, where it may have given rise to *Bunolistriodon adelli* (= ? *Bunolistriodon michali*). The two species became sympatric in an area stretching from Portugal to Greece.
- The evolution in the *Bunolistriodon adelli-latidens-meidamon* lineage was not constant and the rate of evolution increased greatly around 13.75-13.739 Ma, which might be related to climatic change.

- *Retroporcus sindiensis* dispersed into Anatolia and Europe, which may have happened between 14.609 and 14.163 Ma. Between 14.05 and 13.75 Ma, it gave rise to *Conohyus simorrensis*.
- The Suoidea from Gračanica belong to groups which have suffered taxonomic inflation, taxa have been named on too little evidence and disregarding the rules of the ICZN (1999). The cases, which affect the classification of the Suoidea from Gračanica, have been discussed in the Suppl.-Information.
- *Choeromorus lemuroides* is not classified as Choeromorinae and Siderochoeridae, nor as Yunnanchoeridae, because of articles 36.1 and 40.1 of the ICZN (1999) the Choeromorinae is a junior synonym of Taucanaminae and Siderochoeridae and Yunnanchoeridae would be synonyms of Taucanamidae, if such a family would be recognized.
- *Choeromorus lemuroides* is classified as Palaeochoeridae, because *Palaeochoerus* does not belong to the Suidae (as has been claimed) and the Palaeochoeridae, Schizoporcidae, Siderochoeridae and Doliochoeridae share many apomorphies and are here retained in a single family, the Palaeochoeridae.
- The genus *Choeromorus* and its likely direct ancestor *Siderochoerus minimus* share a clear apomorphy and as a result *Siderochoerus* is included in *Choeromorus*. Several other synonymies concerning genera and species are discussed.
- The species *Retroporcus complutensis* is a synonym of *R. sindiensis*.
- The designation of a lectotype for *C. simorrensis* by Pickford and Laurent (2014) may not be valid, but changed the definition of the species.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest: The author declares that he has no conflict of interest.

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Tab. 1

Measurements in mm of the cheek teeth of NHMW 2013/0008/0001 of *Ch. lemuroides* from Gračanica.

		DAP	DTa	DTp
P ₄	s	10.9	5.5	5.8
P ₃	s	11.3	4.7	5
M ₁	d	>9.5	6	6.1
M ₃	s	--	9.2	--
M ₂	s	11.8	9.3	8.8
M ₁ ¹	s	9.7	7.8	7.8
P ₄ ¹	s	7.7		7.7
P ₃ ¹	s	10.7	5.3	6.8
M ₂ ¹	d	12.2	9.3	8.4

Tab. 2

Measurements in mm of the cheek teeth of *Bunolistriodon* from Gračanica.

		DAP	DTa	DTp	DTpp	Ha	Ta	
NHMW 2013/0012/0001	s	M ³	25.0	21.7	18.7			
		M ²	19.4	--	--			
NHMW 2013/0012/0002	s	M ³	25.2	21.3	>18.1			
		M ²	?19.8	--	--			
NHMW 2013/0012/0003	s	P ⁴	14.0		16.1			
NHMW 2013/0012/0006	d	M ³	>24.2	22.1	19.1			
		P ⁴	13.9		15.8			
		P ³	16.1	10.0	14.6			
NHMW 2013/0012/0007	s	M ³	25.8	19.7	16.1			
		M ²	18.3	18.0	17.0			
		M ¹	17.4	15.7	16.3			
		P ⁴	13.8		16.0			
		C ^m	20.7	--				
NHMW 2013/0012/0008	s	M ₃	32.2	18.3	16.1	12.2	13.4	0.8
		M ₂	?19.8	--	--			
		M ₁	?15.6	--	--			
NHMW 2013/0012/0008	d	M ₃	31.9	17.8	15.9	11.9	11.4	0.9
		M ₂	21.2	15.4	14.9			
		M ₁	16.9	11.4	12.1			
		P ₄	16.0	--	--			
		P ₃	14.5	--	--			
		P ₂	13.0	--	--			
NHMW 2013/0012/0010	s	P ₄	16.4	10.1	11			
NHMW 2013/0012/0011	d	M ₃	>>23.6	--	--	--		

Tab. 3

Measurements in mm of the incisors and lower canine of *Bunolistriodon* from Gračanica.

		DMD	DLL	Dmax		
NHMW 2013/0012/0009	s	I ¹	33.4	13.2		
NHMW 2013/0012/0004	d	I ₁	14.5	10.7		
		I ₂	14.5	10.7		
		I ₃	--	--	>15.9	
		Li	La	Po	Ri	Ro
NHMW 2013/0012/0004	s	C _m	17.7	14.7	13.8	65
						20?

Tab. 4

Measurements in mm of the bones of *Bunolistriodon* from Gračanica.

			DAPp	DTp	R	Rm
NHMW 2013/0012/0012	Phalanx 2	r	16.7	19.2		
NHMW 2013/0012/0013	astragalus	d			24.2	16.1

Tab. 5

Measurements in mm of NHMW 2014/0081/0001 lower cheek teeth of *C. simorreensis* from Gračanica.

		DAP	DTa	DTp	DTpp	Ha	Ta
M ₃	s	24.2	15.3	13.0	10.9	8.7	
M ₃	d	>24.2	14.9	12.8	10.9	10.1	
M ₂	s	18.4	14.5	14.5		10.9	
M ₂	d	18.1	14.8	14.3		11.1	
M ₁	s	15.8	12.0	12.0			0.8
M ₁	d	15.8	12.0	12.1			0.6
P ₃	s	>21.6	11.8	14.3

Figure 1

Geographic position of the localities with *Choeromorus* and *Schizoporcus* (top), the different species of the *B. adelli* – *latidens* - *meidamon* lineage (middle) and *Conohyus* and *Retroporcus* (bottom).

Figure 2

Choeromorus lemuroides from Gračanica: NHMW 2013/0008/0001a - left maxilla with P³-M³: a) buccal, b) occlusal, and c) lingual views.

Figure 3

Choeromorus lemuroides from Gračanica: 1) NHMW 2013/0008/0001b - right M²: a) anterior, b) posterior, c) buccal, d) occlusal, and e) lingual views. Bivariate diagrams comparing the widths of the anterior (DTa) or posterior lobes (DTp) and length (DAP) of the teeth from Gračanica with: *Ch. primus* from Petersbuch 2 and Els Casots (IPS); *Ch. lemuroides* from Sansan; *Ch. inonuensis* from İnönü I and Paşalar; *Ch. grandaevus* from Steinheim, La Grive and Anwil; *S. muenzenbergensis* from Münzenberg, Sandelzhausen and Neudorf Spalte. The lines indicate average proportions.

Figure 4

Choeromorus lemurooides from Gračanica: 1) NHMW 2013/0008/0001c - left P₃; a) buccal, b) occlusal, and c) lingual views; 2) NHMW 2013/0008/0001d - left P₄; a) buccal, b) occlusal, and c) lingual views. Bivariate diagrams comparing the width of the anterior (DTa) or posterior lobe (DTp) and length (DAP) of these premolars and the M₁ with: *Ch. minimus* from Petersbuch 62; *Ch. primus* from Petersbuch 2 & 7, Artenay, Montréal-du-Gers, Bézian and Els Casots; *Ch. lemurooides* from Petersbuch 31 & 68, Göriach, Thannhausen and Sansan and; *Ch. inonuensis* from İnönü I, Paşalar, Petersbuch 39 & 108 and Prebreza; *Ch. grandaevus* from Steinheim, Przeworno and La Grive; *S. muenzenbergensis* from Münzenberg, Neudorf Spalte, Sandelzhausen and Petersbuch 54. The lines indicate average proportions.

Figure 5

The size of the M³ and the size of the M³ relative to the M¹ in *Choeromorus* and *S. muenzenbergensis*. The localities are ordered from old at the bottom to young at the top. Provenance of data as in Table 6.

Figure 6

Bunolistriodon latidens from Gračanica: 1) NHMW 2013/0012/0007 - left maxilla with P⁴-M³: a) occlusal view, b) buccal view of the P⁴; 2) NHMW 2013/0012/0006 - right maxilla: a) occlusal view of the P³, b) buccal view of the P⁴, c) occlusal view of the P⁴; 3) NHMW 2013/0012/0010 - left P⁴: a) anterior, b) buccal, c) occlusal, d) lingual, and e) posterior views; 4) NHMW 2013/0012/0003 - left P⁴: a) buccal, and b) occlusal views; 5) NHMW 2013/0012/0002 - left M³: occlusal view; 6) NHMW 2013/0012/0008 - left M₃: a) buccal, b) occlusal, and c) lingual views.

Figure 7

Bunolistriodon latidens from Gračanica, NHMW 2013/0012/0004: 1) left C_m : buccal view. Bivariate diagrams comparing the width of the lingual (Li), buccal (Bu) and posterior sides (Po) of the C_m from Gračanica with those of the *B. adelli-latidens-meidamon* lineage and *B. lockharti* from: Pellécahus, La Artesilla, La Romieu, Chevilly, Buñol, Córcoles, Langenau 1, Tavers and Montréal du Gers (type locality of *B. tenarezensis*; MHNT). The lines indicate average proportions. Diagrams showing the changes in time in La and index 100 La/Li through time. The localities are in approximate order from old at the bottom to young at the top. Chevilly is the type locality of *B. lockharti*, Montréal du Gers is the type locality of *B. tenarezensis*, Veltheim is the type locality of *B. latidens*, Paşalar is the type locality of *B. meidamon* and Çandır is the type locality of *B. meidamon ultimus*.

Figure 8

Bunolistriodon latidens from Gračanica, NHMW 2013/0012/0004: 1) right I_2 : a) apical, b) labial, and c) lingual views; 2) right I_3 : labial view. Bivariate diagram comparing the meso-distal diameter (DMD) and labio-lingual diameter (DLL) of the I_2 from Gračanica with: *B. lockharti* from: La Romieu, Baigneaux-en-Beauce, Gerlenhofen, Langenau 1, Engelswies, Pontlevoy, Tavers and Montréal du Gers, *B. adelli*, *B. latidens* and *B. meidamon*. The lines indicate average proportions. Diagrams showing the changes in time in mesio-distal diameter (DMD) and index 100 DMD/DLL through time. The localities are in approximate order from old at the bottom to young at the top. Montréal du Gers is the type locality of *B. tenarezensis*, Veltheim is the type locality of *B. latidens*, Paşalar is the type locality of *B. meidamon* and Çandır is the type locality of *B. meidamon ultimus*. The provenance of the data is indicated in Table 6.

Figure 9

Bunolistriodon latidens from Gračanica. NHMW 2013/0012/0009 - left I¹: a) apical, b) lingual, c) mesial, d) lingual, and e) distal views. Bivariate diagram comparing the meso-distal diameter (DMD) and labio-lingual diameter (DLL) of the tooth from Gračanica with: *B. lockharti* from: La Romieu, Baigneaux-en-Beauce, Córcoles, Gerlenhofen, Langenau 1, Ravensburg, Pontlevoy, Tavers, Montréal du Gers and Can Canals, and with *B. adelli*, *B. latidens* and *B. meidamon*. The lines indicate average proportions. Montréal-du-Gers is the type locality of *B. tenarezensis*, Can Canals is the type locality of *B. giganteus*, Els Casots is type locality of *B. adelli*, La Retama is type locality of *B. retamaensis*, Veltheim is the type locality of *B. latidens*, Paşalar is the type locality of *B. meidamon* and Çandır is the type locality of *B. meidamon ultimus*. In the lower graphs the localities are ordered from old (bottom) to young (top). Provenance of data as in Tble 6.

Figure 10

Diagram comparing the 100 DMD/DLL indices of the I_1 , I_2 and I^1 as a percentage of the mean of the same tooth in the sample of Paşalar. The localities are in approximate order from old at the bottom to young at the top and the provenance of data is as indicated in Table 6.

Figure 11

Conohyus simorrensis from Gračanica: NHMW 2014/0081/0001 - left P₃; a) anterior, b) buccal, c) posterior, d) occlusal, and e) lingual views. Bivariate diagrams comparing the width of the posterior lobe (DTp) and length (DAP) of the P₃ of: *Conohyus simorrensis* from: Puente de Vallecas, Göriach, Au, Villefranche d'Astarac, Alhambra, Paşalar, Carpetana, Elgg, Klein Hadersdorf, Kleinenbach, Tutzing and Pitten; *R. sindiensis* from Mala Miliva, Somosaguas and from the Indian Subcontinent; *R. indicus* from the Indian Subcontinent; *P. steinheimensis* from: Manchones I, La Grive oc, Steinheim, Can Almira, Hostalets, Castell de Barberà, and Wissberg; *P. steinheimensis olujici* from Lučane; *P. huenermanni* from Rudabánya and Can Ponsic I; *P. crusafonti* from Can Llobateres. Provenance of data as indicated in Table 6.

Figure 12

Conohyus simorrensis from Gračanica, NHMW 2014/0081/0001: 1) left M₃: a) buccal, b) occlusal, c) lingual, and d) anterior views. Change in the anterior width (DTa) and length (DAP) of the M₃ of *Conohyus* and *R. sindiensis* through time - localities from old to young and *R. sindiensis* of different ages at the bottom. Provenance of data as indicated in Table 6.

Figure 13

Conohyus simorrensis from Gračanica, NHMW 2014/0081/0001: 1) left M2: a) buccal, b) occlusal, c) lingual, d) anterior, and e) posterior views; 2) left M1: occlusal view. Change in the posterior width (DTp) and length (DAP) of the M₁₋₂ of *Retroporcus* and *Conohyus* through time - localities from old to young and *R. sindiensis* of different ages at the bottom. Provenance of data as in Table 6.

Figure 14

The temporal distribution of the species of *Choeromorus*, *Bunolistriodon*, *Conohyus* and various other selected suoid lineages. To the left the localities from the Iberian Peninsula, the local biozonation (Z to G3) and its correlation to the MN units and ATNTS2012 mainly after Daams et al. (1999b), Hernández-Bailarín & Peláez-Campomanes (2017). To the right localities from the rest of Europe and of Anatolia, MN units and Central Paratethys stages modified after Hilgen et al. (2012). Lines indicate estimated ages of localities according to various authors (see text). In some case there are alternative ages (dashed lines) or age ranges. Solid squares indicate presence of a species in a locality and open squares indicate uncertainty (normally indicated with: cf., aff., sp. or ?).

Fig. 14
The temporal distribution of the species of *Choeromorax*, *Bunolistrion*, *Conchylus* and various other selected snail lineages. To the left the localities from the Iberian Peninsula, the local biozonation (Z to G3) and its correlation to the MN units and ATNTS2012 mainly after Daams et al. (1999b), Hernández-Bailarín & Peñáz-Campanones (2017). To the right localities from the rest of Europe and of Anatolia, MN units and Central Paratcheys stages modified after Hilgen et al. (2012). Lines indicate estimated ages of localities according to various authors (see text). In some case there are alternative ages (dashed lines) or age ranges. Solid squares indicate presence of a species in a locality and open squares indicate uncertainty (normally indicated with: cf., sp. ?).

Supplementary Information

LITHO- AND BIOTRATIGRAPHY OF RELEVANT LOCALITIES

Many of the fossils of the Suoidea, belonging to the three lineages present in Gračanica, have been found in stratigraphic contexts, which provide relevant information. These will be discussed below, but Suppl.-Tab. 4 recapitulates the main stratigraphical and chronological information. The MN units (Mein 1975a, 1977b, 1977, 1979, 1990; De Bruijn et al. 1992) are used throughout Europe and Anatolia. These units were defined using many different criteria, including a single reference locality and first appearances, grades of evolution and typical associations of taxa. This was meant as a help, but the use of different criteria may give different results. Hilgen et al. (2012, fig. 29.9) indicated the ages of boundaries of the MN units as “defined” by taxa and the inferred ages of the reference localities and gave the ages of the reference localities of MN7 and MN9 outside the temporal range of their MN units. This illustrates the problems arising from the use of different criteria. These problems have to be borne in mind.

Calatayud-Daroca and Madrid basins

In the West, in Spain many of these localities have known positions in a local biozonation, which is based on rodents (Daams & Freudenthal 1981, 1988; Freudenthal 1988; Daams et al. 1987, 1999a, 1999b; etc.). A long paleomagnetic section provides ages for the biozones (Krijgsman et al. 1994, 1996; Daams et al. 1999a). Many of the micromammal localities are in the paleomagnetic sections, or can lithostratigraphically be correlated to these sections. The use of sedimentation rates may provide additional precision. Precise age estimates have been published for many of those sites (Daams et al. 1999b; Van Dam et al. 2006). These are mostly micromammal localities, but include the large mammal sites Manchones (13.25 Ma) and La Artesilla (16.49/16.51 Ma), while Armantes is low in C5Br. For the remaining macromammal localities only the temporal range of the biozone is available. The published ages of some sites are subject to the small changes in the dating of the GPTS.

The same biozonation is used in the Madrid basin (Hernández-Ballarín & Peláez-Campomanes 2017). Paleomagnetic sections provide ages for the lithostratigraphy of the Madrid basin as well as for the fossiliferous localities sites: Paracuellos 5 (top of C5ABr, a little older than 13.608 Ma) and Paracuellos 3 (top of C5Ar.1n, a little older than 12.735 Ma) (Montes et al. 2006). This biozonation was applied also to other basins in Spain and occasionally outside Spain.

Lisbon area

Around Lisbon there are interfingering marine and continental sediments. There are various regression-transgression cycles. Of relevance here are the levels: Lisbon Val, which is marine with foraminifera of Blow zone N8, Lisbon Va2, which is continental with mammals attributed to MN4a, Lisbon Va3 with N8 foraminifera, Lisbon Vb, with MN4b/5 mammals, overlain by marine sediments with N9 foraminifera (Antunes 1984). This would situate level Lisbon Va1 between the upper and lower limits of zone N8 (about 16.3-15.1 Ma) and level Lisbon Vb below the top of N9 (15.1-14.8 Ma).

Localities from Lisbon Va have been placed in MN4 and others from Lisbon Vb in MN5, including Quinta da Farinheira (Mein 1975a, 1977b, 1977; De Bruijn et al. 1992). Mein (2000) correlated localities in the level Va2 to zone C of the Aragonian (16.45-15.98 Ma) and localities in the lower part of level Vb to zone Db (15.91-15.47 Ma) and the upper part of level Vb to zone Dc (15.47-14.75 Ma).

The localities Quinta da Pedreira, Quinta la Barbacena and Quinta da Conceição are situated in level Va and yielded *Bunolistriodon lockharti*, while 9 localities in level Vb yielded *B. adelli* (Van der Made 1996). Several localities of level Vb yielded *H. soemmerringi* (Antunes & Estravis 1986), which is the large *H. s. soemmerringi* (Van der Made 2010). The localities Olival da Susana and Quinta do Farinheira share both species.

Aquitaine Basin

Since the 19th century, many fossiliferous sites are known from the Aquitaine Basin (Richard 1946). Ginsburg (1971) and Ginsburg & Bulot (2000) gave the lithostratigraphic sequence of the Armagnac area and recognized from bottom to top levels 1 to 17 and gave the faunal lists of the main fossiliferous localities of these levels. Some of the levels are of relevance here. Level 3 is the Pellécahus Limestone (Calcaire de Pellécahus) with the locality Pellécahus. Level 4 Lower Limestone of Lectoure with La Romieu. Level 7 the Auch Limestone with the locality Lavardens. Level 8 the Lower Astarac Limestone with Castelnau d'Arbieu. Level 9 the Sansan Limestone with the locality Sansan. Level 10 the Monlezun limestone with Rajégats (=Rajogats, Arrajogats) near

Simorre. Level 12 the (upper) Astarac Limestone with Simorre and Villefranche d'Astarac. Level 13 the Fousseret Molasse with the locality Le Fousseret, level 14 has St. Gaudens (Valentine) and the next level is with *Hipparion*. Bézian is a site near La Romieu and lithostratigraphically intermediate between that site and Pellécahus and all three have *Democricetodon* and *Megacricetodon* (Bulot & Ginsburg 1993). The locality Montréal-du-Gers (Béon 1) is situated between Pellécahus and Bézian (Bulot et al. 2006).

The localities La Romieu and Sansan in this sequence are the reference localities of MN4 and MN6, respectively (De Bruijn et al. 1992). The fossil locality of Sansan is situated in the top of a normal polarity zone in a short paleomagnetic section with some hiatuses and Sen (1997) correlated the fossiliferous level to C5Bn.2n (15.160-15.032 Ma). However, Daams et al. (1999b) correlated it to C5ABn (13.369-13.605 Ma) and Kálin & Kempf (2009) to C5ACn. Hilgen et al. (2012, fig. 29.9) proposed an age of 14.1 Ma. Considering the position of the site in the top of a normal polarity zone, this should be the top of C5ADn (slightly older than 14.163 Ma), rather than the top of C5ACn (older than 13.739 Ma). Possibly, there is an error in the figure, given the fact that next to the arrow marking the 14.1 Ma of Sansan, there is a dashed line marking 14.0 Ma, but it is lower instead of higher in the figure. The correlation to the top of C5ADn is preferred here. In that interpretation the normal chrons C5Bn.1n and C5Bn.2n would correspond to a hiatus in the Sansan section by Sen (1997).

The sequence of localities in the Aquitaine Basin record the local appearance of *Bunolistriodon* and the replacement of *B. lockharti* in Castelnau d'Arbieu (Bulot et al. 1992) by *Listriodon splendens* in Sansan (Pickford 2012). The latter event was one of those that defined the MN5-6 transition (Mein 1975a, 1975b, 1977, 1979, 1990).

Loire Basin

In the Loire Basin, the older localities of Chitenay and Artenay and the younger localities of Baigneaux-en-Beauce, Chevilly (type locality of *B. lockharti*) are in the Sables de L'Orléanais (Orleans Sands) and Pontlevoy is in the "Faluns" (Ginsburg 1971). Pontlevoy is the reference locality of MN5, Thenay and Tavers are in the same marine sediments and based on molluscs and foraminifera, these are of Langhian age (15.97-13.82 Ma) (Hilgen et al. 2012).

West Paratethys

In Southern Germany and Switzerland the sequence OMM (Obere Meeres Molasse = Upper Marine Molasse), OBM or BM (Brackwasser Molasse = Brackish Molasse), and OSM (Obere Süßwasser Molasse = Upper Freshwater Molasse) covers most of the time of interest here. The BM contains from top to bottom the Grimmelfingen, Suevicus and Kirchberg Beds (Sach & Heizmann 2001). Moser et al. (2009) give further information. The OSM consists of a lower, middle and upper series. The Brockhorizont is situated within the OSM and is found in an extensive area. It is a result of the impact of a meteorite (Ries-Impact) and in turn these deposits are assumed to have blocked a valley, which caused a lake (Berger 2010). Localities in these lake sediments are assumed to date from after the Ries Event. There is also a biozonation OSM A to F. In Germany and Switzerland there are a number of dated bentonites.

The ages of the lithostratigraphic and biostratigraphic units have been estimated using paleomagnetism and other methods (Abdul Aziz et al. 2008; Reichenbacher et al. 2013). The Grimmelfingen Beds date from about 17.6 to 17.2 Ma, the lower Kirchberg Beds to about 17.2-16.8 Ma, the upper Kirchberg Beds to about 16.8-16.6 Ma. The Brockhorizont has been dated and redated. A recent estimate is 14.93 to 15.00 Ma (Rocholl et al. 2018). This horizon is situated between OSM zones E and F.

The locality of Grimmelfingen is in the Grimmelfingen Beds (17.6-17.2 Ma), Langenau 1 is in the lower Kirchberg Beds (17.2-16.8 Ma), Gerlenhofen is in the upper Kirchberg Beds (16.8-16.6 Ma), and Engelswies is at the top of the Kirchberg Beds (close to 16.6 Ma).

The fossil locality Sandelzhausen is in the lower series of the OSM and in zone C+D and it has a paleomagnetic reversal which was interpreted to correspond to C5Cn.1r-1n (Moser et al. 2009). Later this was revised to C5Cn.2r-2n (Reichenbacher et al. 2013) at 15.160 Ma.

Georgensgmünd is in the OSM and was believed to be in lake sediments formed after the Ries Event (14.93-15.00 Ma). It was placed in MN6 (Mein 1990; De Bruijn et al. 1992) or in MN5, because of *Palaeomyx* and because of the presence of *Bunolistriodon* sp., which was not known from MN6 in western Europe (Van der Made 1996). Material studied posteriorly (MNB) shows the species to be *B. lockharti*. Berger (2010) was of the opinion that the formation of the fossil site of Georgensgmünd is not related to the Ries Event, that it is not MN6 but MN5 because of *Palaeomyx* and *Bunolistriodon*, and he estimated on the basis of *Megacricetodon bourgeoisi* the age of the locality as 17.1 Ma. This *Megacricetodon* material from Georgensgmünd is close to *M. b. bezianensis* from Bézian and its size, if compared to the size increase in the *M. bavaricus* lineage, would

suggest an age close to Langenmoosen (Berger 2010, figs. 18-21). Oliver & Peláez-Campomanes (2016) considered that in *Megacricetodon* there are different parallel lineages, including *M. bezianensis* in France, which remained of the same size, and the *M. bavaricus* lineage in Germany, which increased rapidly in size. Occasional dispersals between the different areas occurred. It is thus also possible, that *M. bezianensis* arrived in Georgensgmünd long after 17.1 Ma by dispersal from France. This seems even more likely, because Georgensgmünd also yielded *Megacricetodon minor* (Berger 2010) and the entry of this species in Germany is in zone OSM E (Van der Meulen et al. 2011), which is after 15 Ma.

Ravensburg is in the OSM. Molluscs from there are claimed to be MN6 (Salvador et al. 2015), but it is not clear in how far this is applicable to the mammals. The largest (and most evolved) *B. lockharti* incisor is from there and the site was believed to be latest MN5 (Van der Made 1996).

The localities Stätzing and Thannhausen are in the middle series of the OSM. Thannhausen is above the Brockhorizont and just below a bentonite and a hiatus (Heissig 1989). The bentonite just below the hiatus is dated to 14.55 Ma (Moser et al. 2009). As a result, Thannhausen should be close to, but older than, 14.55 Ma.

In Switzerland there are various paleomagnetic sections, which are correlated to each other and which together cover this period (Kälin & Kempf 2009). These paleomagnetic sections date the Molasse sequence and many mostly micro-mammal localities. The localities Anwil and Rümikon date to 13.2-13.8 and 14.2-14.6 Ma respectively.

Steinheim is a locality in southern Germany, which is not in the molasse. It has the rodent *Megacricetodon gregarius*. In the Swiss Molasse in a sequence with fossil faunas and paleomagnetism, the total temporal distribution of this species is in the top of chron C5AC (Kälin & Kempf 2009). This suggests that, Steinheim is very slightly older than 13.739 Ma.

Central Paratethys

In the Central Paratethys the series of stages Ottnangian (18.2-17.2 Ma), Karpatian (17.2-16.0 Ma), Badenian (16.0-12.7 Ma) and Sarmatian (12.7-11.6 Ma) are defined in marine sediments (Piller et al. 2007). There are many mammal localities in the margin of this basin and it is tempting to apply the Central Paratethys stages (and corresponding dates) to these localities. However, apparently this was not always done with sufficient stratigraphic control. Mottl (1970) and Rabeder & Steininger (1975) cited work that correlated a series of localities to the Karpatian, including Seegraben and Münzenberg near Leoben, Eibiswald, Wies, Zangtal, Köflach as well as Oberdorf. Mein (1975b) included Leoben and Eibiswald in MN5. Of these, Oberdorf is now considered to be Ottnangian, having an age of 17.6-17.25 Ma and is placed in MN4 (Daxner-Höck et al. 1998). This might raise questions about the age of the other localities. Nevertheless, a Karpatian age for the remaining localities does not contradict the interpretations in the present paper.

Sankt Oswald bei Gratwein is in sediments, which interfinger with marine sediments of Early Badenian age or “Lagenidenzone” (Rabeder 1978) (about 16.4-14.2 Ma; Harzhauser et al. 2002; Mandic et al. 2019). Occasionally localities are placed in the Badenian, correlated to nanoplankton or foraminifera zones and are assigned numerical ages on this basis, without well-documented relationship to the marine strata. The fissures of Neudorf (Devínska Nová Ves) are overlain by sediments of late Badenian age, but the hill with the fissures is surrounded by sediments of Early Badenian age and for this reason, the fissures are assumed to predate the Badenian and have an age of 16.0 Ma (Steininger et al. 1996: 30). However, for such an inference, the fissure fillings should be overlain by lowermost Badenian sediments.

Dinarides

The fossiliferous locality of Lučane (Bernor et al. 2004) in Croatia is in a Paleomagnetic section, which is calibrated by three $^{40}\text{Ar}/^{39}\text{Ar}$ dates (De Leeuw et al. 2010). The fossils come from a level at the top of the section tentatively correlated to the reversed chron C5Bn.1r and based on sedimentation an age close to 15.0 Ma was suggested.

In Bosnia and Herzegovina there are two fossiliferous localities called Gračanica. One is a locality in the Gacko Basin, which yielded molluscs (Mandic et al. 2011) and the other is in the 120 km WNW located Bugojno Basin and yielded molluscs and mammals (Mandic et al. 2016). The present publication deals with the latter locality. The fossils come from a coal mine from the lower part of the coal beds. The section shows several trans-regressive cycles. The first occurrence of *Illyricongergeria frici* is recorded in the upwards continuation of the section. The first appearance of this mollusc is dated in the Gacko Basin to 15.5 Ma (Mandic et al. 2011). If the appearance of this bivalve is synchronous in these basins, this would suggest that the mammals studied here are older than 15.5 Ma.

Serbia

Mala Miliva and Prebreza in Serbia are placed in MN5 and MN6, respectively (Mein 1975a, 1977, 1990; De Bruijn et al. 1992). Mala Miliva is in sediments which interfinger with lacustrine deposits in the base of the marine Middle Badenian (Petronijević 1967, Rabeder 1978, Mandić et al. 2019) (>13.8 Ma). No independent information on the age of Prebreza is available.

Greece

The “locality” Chios is known since a long time (Paraskevaidis 1940). More recent work led to the excavation of various localities called Thymiana A-C, with paleomagnetism correlated to chrons C5Bn-1n to C5Cr, the fossiliferous level corresponding to ~15.5 Ma (Kondopoulou et al. 1993; Koufos 2006). The locality Antonios is placed on the basis of biostratigraphy either in the top of MN4 or the base of MN5 (Koufos 2006).

Anatolia

In Anatolia, a series of “faunal groups” (Faunengruppen) was established, named after a reference locality (Becker-Platen et al. 1975). The three lower ones are from old to young the Paşalar, Çandır and Sofça-Faunengruppe, which were correlated to Sansan, La Grive M, and to Steinheim / La Grive L3 / Anwil, which would correspond to MN6, 7 and 8 respectively (Mein 1977). Sariçay was placed in the later Çandır faunal group.

There are but few localities in paleomagnetic sections or associated to dated rocks. The locality of İnönü 1 is in the lower Sinap Formation and the base of this formation is mapped as overlying a basalt dated to 15.2 ± 0.3 Ma with reversed polarity correlated to C5Br (Kappelman et al. 1996, 2003). From this it appears that İnönü 1 is younger than 15.2, but it is not known how much younger. Mein (1975) indicated the appearance of *Listriodon* and *Kubanochoerus* to be indicative of MN6. Both are present in İnönü 1, while the latter is a rare suid in the area covered by the MN units, the former is very common and its presence is indicative. The locality of Çandır is in a paleomagnetic section and was initially correlated to C5ACn (13.734–14.095 Ma) or C5ABn (13.369–13.605 Ma), but when pressured for an older age, the alternative correlations to C5Cn.1r or C5Cn.2r (about 16.5 / 16.3 Ma) were also given (Krijgsman 2003).

SUPPLEMENTARY DISCUSSION ON THE SYSTEMATICS OF THE SUOIDEA FROM GRAČANICA

Specific and generic classification of *Choeromorus lemuroides* (= *Taucanamo sansaniense*).

It was known that the name *Taucanamo sansaniense* (Lartet, 1851) is not the name with priority, but other names were forgotten or not used for other reasons. Blainville (1839–1864) figured and named a specimen from Sansan as *Sus lemuroides*. The publication appeared in parts during many years. Lartet (1851: 32) cited this part as fascicule 22 published in 1847. Gervais (1848–1852) named the genus and species *Choeromorus*, *Ch. simplex* and *Ch. mamillatus*. He also published his work in parts. The part where the names *Choeromorus*, *Ch. simplex* and *Ch. mamillatus* were introduced was published in 1850 (Bibliographie de la France, 23–11–1850; Wagner 1851). Finally, Lartet (1851) published the name *Choerotherium sansaniense*. All these species represent a small suoid and all are based on material from Sansan. Since only one species of small suoid is recognized presently in this locality, Gervais’ names are junior synonyms of “*Sus*” *lemuroides*. “*Sus*” *lemuroides* was not used by later authors (e.g. synonymy lists by Pickford 2012, 2017) and would be a nomen oblitum, while for the sake of stability the name *Ch. sansaniense* could be retained as a nomen protectum (ICZN, 1999, article 23.9.2). Nevertheless, Pickford (2017) revived the name *C. lemuroides* and article 23.9.2 does not apply anymore.

Pickford (2017) states that Gervais (1850) erected the name *Choeromorus*, but incorrectly credited Lartet for the name. However, it was and still is possible that the person who is responsible for a new taxonomic name is not the person who publishes it (ICZN 1999, article 50.1.1) and it looks like Gervais gave credit to the person who recognized the taxon as new. However for Lartet being the author, the present criteria of availability are not met and thus Gervais (1850) is indeed to be considered to be the author of the name. This does not mean that Gervais (1850) made an error, nor that Lartet could not be considered author of the genus prior to the present nomenclatorial rules. With the present rules, the species from Sansan is named *Choeromorus lemuroides*.

Pickford (2017) proposed the name *Choeromorus petersbuchensis* for material from Petersbuch localities 31, 39, 68, 71 and 108. This species is very similar to *Ch. lemuroides* and *Choeromorus inonuensis* and therefore the material from Gračanica could also belong to this species, if it were a valid species. The first feature mentioned in the diagnosis of the new species is its size: it is on average larger than the *Ch. lemuroides* from Sansan and a little smaller than *Ch. inonuensis*. In all measurements, the type specimen of *Ch. petersbuchensis* is

within the ranges of the sample of *Ch. lemuroides* from Sansan, save for the size of the M^3 and M_3 (Pickford 2017, figs. 81, 85). However, Pickford (2012, Tab. 2) gave the length of specimen Sa4589 as 18.0 mm and Pickford (2017, Tab. 11) indicated some dashes at the place where its length should be indicated and did not include this specimen in his fig. 85, where a comparison between *Ch. lemuroides* from Sansan and the new species *Ch. petersbuchensis* is made. As a result, both M_3 of the holotype of *Ch. petersbuchensis* appear longer than all specimens from Sansan. If Sa4589 would have been included, these M_3 would be within the metrical ranges of the sample from Sansan. Most of the morphological features in the diagnosis do not serve to separate *Ch. petersbuchensis* from the other two species. It is indicated that the M_3 has a third lobe with a second large cusp (a hexaconid, in addition to the pentaconid). To some extent, this is a difference with *Ch. lemuroides*. Among around 25 M_3 from Sansan, a third lobe with only a pentaconid prevails. However, the two cusps are present in MNHN Sa4582 (holotype of *Ch. simplex*), Sa4589 and in a not numbered specimen from Sansan in the IPS. The holotype of *Ch. mamillatus* (Sa4580) has an even more complex morphology with a third lobe with two cusps and a fourth lobe with one (heptaconid). The latter specimen is also the longest M_3 . Figure 5 shows the sizes of the M_3 and it can be seen that there are two outliers from Sansan, which are longer than those from Petersbuch 108; these are specimens with a more complex morphology mentioned above. The M_3 of *Ch. petersbuchensis* are more similar to those of *Ch. inonuensis*, where a third lobe with two cusps is more common. In addition, it can also be seen that, the M^3 from Petersbuch 108 and those from Inönü 1 are all larger than all specimens from Sansan. Also the relative sizes of both M^3 and M_3 are large in Petersbuch 108 (Fig. 5, Suppl.-Fig. 4). Whereas the separation of *Ch. petersbuchensis* from *Ch. lemuroides* is not perfect, its size and morphology fit *Ch. inonuensis* better. It does not seem to be a new species and most probably it is a synonym of the latter species.

Classification of *Choeromorus lemuroides* at the levels of subfamily and tribe

Following Van der Made (2010), the *Ch. lemuroides* from Gračanica (= *T. sansaniense*) should be classified as Taucanamini, Taucanaminae, Palaeochoeridae, Suoidea. Pickford (2017) proposed a complex classification with five families of Old World Suoidea, instead of two as has been common usage for many years (Simpson 1945; Viret 1961; Van der Made 1996b; Hünemann 1999) or just one (Liu 2003: 18, fig. 2). A comparison between Pickford's (2017) classification and the more conservative one used here is made in Suppl.-Fig. 2. What cannot be seen in this figure is the classification of the individual specimens, in some cases the hypodigm of a species was changed nearly completely, which further complicates taxonomy.

In Pickford's classification, the *Choeromorus* from Gračanica would be classified as Choeromorinae, Siderochoeridae. The latter two new names, given by Pickford (2017), were introduced with disregard of the rules of the International Code for Zoological Nomenclature. Pickford (2011) named the Yunnanchoerini, but Pickford (2017) did not mention the Yunnanchoerini and placed *Yunnanchoerus* in "Siderochoeridae subfamily indet.". However, a name established at any rank within the family group is deemed to have been simultaneously established for all other ranks in the family group (ICZN 1999, article 36.1). As a consequence, Yunnanchoeridae Pickford, 2011 has priority over Siderochoeridae Pickford, 2017. The subfamily Choeromorinae is based on the genus *Choeromorus*, which is a senior synonym of *Taucanamo*. Pickford (2017) may have introduced this name, because he considered that Taucanaminae became invalid since *Taucanamo* is a junior synonym. However, family group names remain valid, even if their type genera are junior synonyms (ICZN 1999, article 40.1). The names Taucanamini and Taucanaminae remain thus valid. Because of these 2 articles of the ICZN, Taucanaminae Van der Made, 1997a is a senior synonym of Choeromorinae Pickford, 2017 and Taucanamidae Van der Made, 1997a would be a senior synonym of Siderochoeridae Pickford, 2017 and Yunnanchoeridae Pickford, 2011, if such a family would be recognized. Pickford's (2017) publication contains all the information necessary to reason these names to be junior synonyms.

Classification of *Choeromorus lemuroides* at the family level

The correction of names in the previous section still leaves the question, whether there should be several families for these suoids or one. In Pickford's (2017) classification, the families and subfamilies consist of few genera, one family (Schizoporcidae) consists of just a single genus and one subfamily (Siderochoerinae) of a single species. This inflates taxonomy and it is not clear, why the same groups cannot have lower level names (e.g. subfamilies, tribes and genera instead of families and subfamilies). The choice to classify a small group as a separate family (for instance, the single genus *Schizoporcus* in the Schizoporcidae) should be based on a sound phylogenetic analysis, but this is not the case. In the chapter "Phylogeny", Pickford (2017) mentioned problems in the study of the phylogeny and criticised other authors, but did not propose any phylogeny that could serve as a justification for naming new families and subfamilies. As an introduction, he included a history of the study of

the “Old World peccaries” (here included Palaeochoeridae), where under “Phase 3” he cited a cladistic analysis by Orliac et al. (2010), who gave a list of suoids of uncertain phylogenetic position. He argued that these taxa were represented by poor fossils and that the authors mixed the species up and that therefore the homogeneity of the Palaeochoeridae was in doubt. “Phase 4” refers to his own publication, where he claimed that a bipartite subdivision of the Old World Suoidea into Suidae and Palaeochoeridae is no longer tenable, because of different opinions on the classification of the genera *Sanitherium* and *Schizoporcus*. Therefore, he claimed, each of these should be placed in its own family. Such arguments do not resolve the phylogeny, and naming new taxa merely disguises that the phylogeny is not well known. Such arguments are no valid justification for the naming of new families (and subfamilies). Should all the “Old World peccaries” be included in a single family, or should they be classified in various families?

Pickford (2017) cited Orliac et al. (2010) in support of his inflated classification of the Old World peccaries. However, Orliac (2010) presented a cladogram of the Suoidea in which *Yunnanchoerus*, *Taucanamo*, *Palaeochoerus*, *Doliochoerus* and *Schizochoerus* (= *Schizoporcus*) are on different but not very distant positions and Orliac (2012) studied the petrosal and presented a cladogram based on a data matrix including 30 new petrosal characters. In this cladogram, *Taucanamo*, *Palaeochoerus* and *Doliochoerus* form one clade, called Palaeochoeridae, being a sister group to Suidae and Tayassuidae. Pickford (2016a, 2017) classified these three genera in the Suidae, Doliochoeridae and Siderochoeridae (Suppl.-Fig. 2).

The Palaeochoeridae share many features. Some of the species of the “Old World peccaries” are not well known, but all species, in which the features can be observed, share: 1 upper molars with the protoconule fused to the protocone; 2) upper molars with fused lingual roots (in species with divergent roots, these are connected by a thin bony plate, which occasionally may be lacking); 3) lower molars with a single root below the anterior and a single root below the posterior lobe; 4) a small or no protocone at all on the P² and P³, 5) male upper canines with well-developed pre- and postsynclines, but no endosyncline; 6) I² short (DAP short relative to DT and to molar size; see Van der Made 2010, figs. 15, 16, 19), 7) I³ short (Van der Made 2010, figs. 17, 18, 19) and very high (compared to its DAP and DT, but also compared to the I²), 8) anterior limbs much shorter than posterior limbs, which is well seen in the metapodials and phalanges; 9) elbow joint allows rotation of radius; 10) high cuboid; 11) central metapodials without well-developed median crest on dorsal side or at least less developed than in the Suidae, a feature reflected in the articular surface of the first phalanges; 12) first phalanges with shorter dorsoplantar diameter than in the Suidae; 13) third phalanges with proximal articular surface extending more proximally on the dorsal side (as opposed to other Artiodactyla, where it is the plantar side), reflecting a greater plantar flexion; 14) third phalanges more elongate with a wider plantar surface and morphology suggesting strong nails, possibly more adapted to digging than normal hoofs (this would be a morphological resemblance to armadillos). Some of these features are primitive, but others are probably shared derived features. It is not possible to figure, describe and discuss them all here. The upper canines evolved differently in the Suidae and Palaeochoeridae, providing an apomorphy for each of these families.

The upper canines of the Suidae may be strongly sexually dimorphic, while in the Tayassuidae and Palaeochoeridae dimorphism is very slight or absent and sexual bimodality (in the size) is moderate. Given the shape and crown height of female suid canines, the earliest canines may have had relatively low crowns, with a crown base that is more or less straight. In Palaeochoeridae the crown height increased and the crown base started to form prominent enamel bands at the anterior and posterior sides (pre- and postsynclines; Suppl.-Figs. 6/1, 6/9), particularly so in the males (Suppl.-Figs. 6/2, 6/4). In the females these pre- and postsynclines tend to be less deep (Suppl.-Fig. 6/3, 11/5). In the Suidae, the female canines remained much the same (Suppl.-Fig. 6/8) until the Pleistocene, when in some lineages these started to resemble male canines. The male canines developed deep pre- and postsynclines, but were also wider (with a greater transverse diameter), than those of the Palaeochoeridae. Possibly related to the greater width, an endosyncline developed. In Suppl.-Fig. 6/7, the endosyncline seems shallow, but its base is covered by cementum. Initially, the crown covered a substantial part of the tooth and the depth of the synclines was moderate. Later the canines became ever-growing, the tip with enamel covering all around the tooth became a minor part of the tooth and the synclines developed in three enamel bands, thin ones at the anterior and posterior side and a very wide one on the lingual or inferior side. At this stage, enamel covered a minor part of the tooth. Later lineages, lost the enamel bands. Suppl.-Fig. 6/7 shows the male canine of the early suid *Hyotherium* and Suppl.-Fig. 6/6 a male canine of the later suid *Kolpochoerus*. The endosyncline is visible as a ribbed enamel band all along the right side of the latter tooth. The thin pre- and post synclines and wide endosyncline are an apomorphy of the Suidae. The specimens shown in Suppl.-Figs. 6/1-5 belong to *Choeromorus*, *Propalaeochoerus* and *Palaeochoerus* and they share the apomorphy of the flat male canine with an anterior and a posterior enamel band or pre- and postsyncline, typical for the Palaeochoeridae. Pickford (2017) classified these three genera in the three separate families of Siderochoeridae, Doliochoeridae and Suidae.

Given the synapomorphy of the canine shape, and the lack of sound arguments for splitting it up, it seems best to retain the Old World peccaries as a single family. Is the name Palaeochoeridae the correct name for this family?

Pickford (2016a) still retained the “peccary-like Suoidea” as a group different from the Suidae (“Ächten Schweine” as opposed to “Echte Schweine” according to Pickford 2016a: 22 [sic]), but classified *Palaeochoerus typus* in the Suidae. As a result, the Old World peccaries would not include the type species of *Palaeochoerus*, nor the type genus of the Palaeochoeridae. Instead he used the younger name Doliochoeridae for the Old World peccaries.

Pomel (1847) named a new genus and two new species: *Palaeochoerus major* and *P. typus*. The latter is not a “lectotype species” (Pickford 2016a: 30), but, because of its species name, *P. typus* is the type species by original designation (ICZN 1999, article 68.2.2). Pomel (1847) figured a left maxilla and premaxilla and mentioned a metapodial. Both constituted the type series and the maxilla is now the lectotype. The other species was subsequently placed in the Hyotheriinae as *Hyotherium major* (e.g. Ginsburg 1974; Van der Made 2010). Pickford (2016a: 22) used five features to classify *P. typus* in the Suidae: 1) the zygomatic root, 2) the distance from the third incisor to the canine, 3) the lingual roots of the upper molars, 4) the position of the posterior edge of the palate, 5) the position of the P^{1-2} .

The first feature is that the posterior side of the root of the zygomatic arch of *P. typus* was said to be far forwards at the level of the M^2 as in the Suidae and unlike in the Doliochoeridae, where it is further back. In *Doliochoerus* it is behind the M^3 (Pickford 2017, fig. 140A), but in some of the specimens, which Pickford (2016a, figs. 147, 159, 161) included in the Doliochoeridae, it is behind the M^2 . This is at a similar place as in the type of *P. typus*, where it is not at the level of the M^2 , but behind this tooth (Pickford 2016a, arrow 4). In the suid *Hyotherium* it is not at the level of the M^2 (as stated by Pickford), but at the level of the posterior lobe of the M^3 (Pickford 2016a, figs. 79c, 83a, 88a), which is a position between the positions in *Doliochoerus* and the other Doliochoeridae. It is clear that, based on Pickford’s (2016a) figures, the feature does not support Pickford’s classification.

The second feature, the short distance between the I^3 and the canine of the type specimen of *P. typus* was used to place the species in the Suidae, while the type specimen of *Palaeochoerus suillus* was placed in the Doliochoeridae (Pickford 2017). Hellmund (1992) placed both in the same species. The distance between these teeth is one of the most variable measurements of a suoid skull, it varies with age and sex and between individuals (Van der Made 1991). It is more likely that the type specimen of *P. typus* Pomel, 1847 was a female and the type of *P. suillus* Pomel, 1853, which in all relevant features are very similar, are a male of the same species, rather than two individuals of two different species of two different families, as proposed by Pickford (2016a, 2017).

The third feature concerns the lingual roots of the upper molars. In the Old World peccaries, the roots are convergent and fused, as in *Choeromorus* and *Pecarichoerus* (Taucanaminae) and *Doliochoerus* and *Propalaeochoerus* (Doliochoerini, Palaeochoerinae), they are divergent and there is a thin plate of bone between them, as in *Palaeochoerus* (Palaeochoerini), whereas in the Suidae the lingual roots of the upper molars are separate and divergent. The type with connected divergent roots seems to be on the evolutionary path towards separate roots and it would not be surprising if occasionally such a morphology would be found in a sample with otherwise fused roots, though only Suidae have always separate roots (a shared derived feature within the Suoidea). The separation of the molar roots happened several times in parallel (e.g. in the Hippopotamidae). Pickford (2016a: 22) cited Van der Made (1994) and Hellmund (1992) for noting that the type specimen of *Palaeochoerus typus* does not have fused lingual roots in the upper molars and used this argument to transfer *P. typus* to the Suidae. Van der Made (1994: 12) did not make observations on the roots, but cited Hellmund (1992: 7, footnote), who mentioned that X-ray research on the type specimen of *P. typus* showed a division between the two lingual roots. He did not indicate who did the study and no image is given. It is possible that the roots were divergent, but that a thin bone plate connected them, which was not well visible in the X-ray image. The type specimen of *Palaeochoerus suillus* is a skull, which Hellmund (1992) included in *P. typus*. Pickford (2016a, fig. 162) described it as *Propalaeochoerus suillus*, indicated the lingual roots of a M^2 with an arrow and stated that they are fused. The morphology and size of this specimen clearly indicate that it belongs to *P. typus*. Another specimen from the type locality St. Gérard-le-Puy (France) shows very clearly lingual roots, which are divergent and connected by a bony plate (Suppl.-Fig. 5/1). There is no published evidence, that the lingual roots of the M^{1-2} in the type specimen of *P. typus* are separate and as a consequence, this feature cannot be used for the classification of this species.

The fourth feature. Pickford (2016a) stated that the posterior edge of the palate is situated between the M^3 in many early Suidae while in the Doliochoerinae it extends further back and that based on this feature,

Palaeochoerus belongs to the Suidae. The holotype of *P. typus* does not preserve the M^3 and the palate is broken off just behind the M^2 (Pickford 2016a, fig. 5). Nothing can be said about this feature in the type specimen. The holotype of *P. suillus* was classified by Pickford (2016a) as Doliochoeridae, but in reality it is a skull of a male of *P. typus*. It retains more of the palate, which is also broken, but what is left of it extends well behind the M^3 (Pickford 2016a, figs. 161-162). Pickford's argument is not applicable to the holotype of *P. typus* and incorrect with respect to the species *P. typus*, if the male skull of this species is taken into account.

The fifth feature is the position of the P^{1-2} , which in the Doliochoerinae were supposed to be placed more lingually with respect to the molars than in the Suidae, and was used to place *P. typus* in the latter family (Pickford 2016a). The type of *P. typus* does not preserve a P^1 and the exact orientation of the tooth row with respect to the median plane is not clear and therefore the exact position of the teeth cannot be known. Pickford (2016a, figs. 157, 193) figured two specimens in which the feature can be observed, which he assigned to the Doliochoeridae. The first one (fig. 157), also without P^1 , gives an idea what might have been meant, while the second one is equivocal. This is no basis for taxonomic decisions.

The five arguments used to place the type species *P. typus* in the Suidae are not convincing and the family Palaeochoeridae is retained as valid.

Not content with claiming that Palaeochoeridae is not the valid name for the Old World peccaries, Pickford (2016a) also claimed that its author and name of publication is not what everyone believes. Matthew (1924) is usually cited as the author of the Palaeochoerinae (Simpson 1945; McKenna & Bell 1997) and thus also of the Palaeochoeridae (Van der Made 1996, 2010). Pickford (2016a) argued that this should be Stehlin (1909), who used the term "Palaeochoeridés" in a diagram indicating the stratigraphic distribution of the different taxa, but did not use the word in the text, even though he discussed *P. typus*. Stehlin (1899-1900) used Anthracotherien, Hyopotamen, Dichobunen, Anoploteriden, Choeromoriden, Palaeochoeriden, etc. in an informal way and in one occasion indicated that the indication was "provisional". In a section on systematics in the same publication, he was critical with classification, or at least how it was being applied, and did not use any formal family name in the 527 pages of the paper, not even Suidae. It seems unlikely that Stehlin (1899-1900, 1909) had the intention to formally introduce the name Palaeochoeridae. Family-group names published before 1900 in non-latinized form, may, in certain cases, be valid after latinization (ICZN 1999, article 11.7.2). However, Stehlin's (1909) "Palaeochoeridés" does not meet the criteria and cannot be taken as the first publication of the name Palaeochoeridae.

The known Old World peccaries belong to a single family and *Ch. lemuroides*, present in Gračnica, is classified as Taucanamini, Taucanaminae, Palaeochoeridae Matthew, 1924.

"Pecarichoerus" inonuensis: part of the Choeromorus lineage or a species ranging from MN5 to MN7+8

The evolution of *Ch. lemuroides* to *Ch. inonuensis* is of stratigraphic interest for correlations from central Europe to Anatolia (Van der Made 1997a, 2003, 2005, 2010) and for the stratigraphic position of Gračnica. However, it was proposed that the latter species belongs to *Pecarichoerus* and that material from Inönü 1 and Pasalar, Mala Miliva, Thannhausen, Castelnau d'Arbieu, Neudorf Spalte (fissures Devínska Nová Ves), and Münzenberg belongs to this species (Pickford 2017). As a result, *Ch. inonuensis* was not only placed in a different genus, but could not have evolved from *Ch. lemuroides*, because it appeared much earlier than its ancestor and this evolution could be used in biostratigraphy. Pickford's proposal was the result of a series of changes, proposed in several publications (Pickford 2011, 2012, 2017). First Pickford's proposals are discussed and because these imply the relationship with other Taucanaminae, an update on the evolution of *Choeromorus* and these taxa is presented.

Pickford & Ertürk (1979) named the species *Taucanamo inonuensis*. Other authors, who later dealt with this species agreed with this classification (e.g. Fortelius & Bernor 1990; Fortelius et al. 1996a; Van der Made 1997a, 2010). When Pickford (2012) revived the senior synonym *Choeromorus* for *Taucanamo*, the species was classified as *Choeromorus inonuensis*. Pickford (2017: 1) redescribed the holotype of *Ch. inonuensis*, 2) noted similarities to the *Ch. lemuroides* from Sansan (type species of *Choeromorus*), 3) surprisingly continued "it is also similar in the parts that can be compared, to the genus *Pecarichoerus* from Pakistan and it is concluded that this is where it should be classified"; 4) but did not indicate any of those similarities. As a result, the species was transferred (Pickford 2017) to the genus *Pecarichoerus*, without justifying this with morphological or biometrical features. The reclassification of *S. muezenbergensis* from Sandelzhausen and Münzenberg as *Pecarichoerus* appears to be the reason for this change.

The classification of the material from Sandelzhausen and Münzenberg has been problematic: it has been assigned to four different species and five genera. Fossils from the Münzenberg were initially assigned to *Choerotherium sansaniense* (Zdarsky 1909), *Taucanamo sansaniense* (Thenius 1956; Weber & Weiss 1983) and

later, along with those from Sandelzhausen to *Taucanamo inonuensis* (Fortelius et al. 1996a). Subsequently, the fossils from these two sites were recognized as a different species *T. ? muenzenbergensis*, transferred to *Schizochœrus* and, after the recognition that the latter genus is a homonym, to *Schizoporcus* (Van der Made 1998, 2003, 2010).

Pickford's reclassification of the fossils from Sandelzhausen and Münzenberg as *P. inonuensis* happened in several steps.: 1) assignation of some fossils from China and Pakistan to *P. orientalis*, 2) use of supposed similarity between those fossils and a skull from Sandelzhausen to include the latter in *P. orientalis*, 3) use of a difference between a fossil from Kanatti and a skull from Sandelzhausen to re-classify the latter as the species "*inonuensis*", 4) use of a similarity between these same fossils to transfer *Ch. inonuensis* to *Pecarichoerus*. All of these steps are questionable.

First step. Pickford (2011) assigned two molars from China and two M³ from Chinji to *Pecarichoerus orientalis*. The figures of the Chinese specimens are so poor (Pickford 2011, fig. 6) that no relevant morphology can be seen. One of the specimens from Chinji is so much worn that nearly no morphology is left, while the other one, which retains indicative features (Pickford 2011, fig. 7a and 7b, respectively). It has a large protopreconule and a large tetrapreconule (central cusp). Wear on both cusps formed wide dentine islands, whereas the type of *P. orientalis* has a protopre- and tetraprecrista (Suppl.-Figs. 5/3-4), which are high and narrow and do not have such large dentine islands (Suppl.-Figs. 5/3-5). In *P. orientalis*, there are narrow protoendo- and tetraendocristas (Suppl.-Figs. 5/3-5), which cannot be detected in the tooth from Chinji. These very different morphologies preclude the classification of the new M³ as *P. orientalis*.

Second step. Pickford (2011) was of the opinion that the new M³ from Chinji, he assigned to *P. orientalis*, is similar to the M³ of the skull of *S. muenzenbergensis* from Sandelzhausen and therefore included that skull in *P. orientalis*. However, a direct comparison of the Sandelzhausen M³ and the *P. orientalis* type specimens shows clear differences: *P. orientalis* has long and thin protoendo-, tetrapre- and tetrapostcristas (Suppl.-Figs. 5/3-5), while the tooth from Sandelzhausen lacks the protoendo- and tetrapostcristas and has a massive tetraprecrista (Suppl.-Fig. 5/2). In the same features, the teeth from Münzenberg and Neudorf Spalte are similar to the molars from Sandelzhausen and differ from those of *P. orientalis*, precluding their classification as *P. orientalis*.

Third step. Pickford (2017) assigned a maxilla with a P² and a damaged P¹ from Kanatti (Chinji Formation, Pakistan) to *P. orientalis* and because the P² is different from that from Sandelzhausen, he re-classified the material from Sandelzhausen to the species "*inonuensis*". The P² is not represented in the type material of *Ch. inonuensis* and it is not known of *P. orientalis* at all. As a consequence, there is no solid basis for the classification of the specimen from Kanatti, nor for the use of its morphology as typical of *P. orientalis*.

Fourth step. Pickford (2017) stated that the maxilla from Kanatti and the skull from Sandelzhausen share "a zone of vermiform bone" and on this basis transferred *Ch. inonuensis* to *Pecarichoerus*. The vermiform bone has not been described or figured in a way that makes clear what is meant and therefore cannot be used as an argument to reclassify a fossil or a species. The skull from Sandelzhausen had previously been placed in *Schizoporcus* (Van der Made, 2010), but Pickford (2017) claimed that the zone of the posterior nares in the Sandelzhausen skull is different from that in *Schizoporcus*. However, this zone is damaged in the skull from Sandelzhausen and the argument cannot be used.

None of these four steps are based on sound evidence. It should be noted that the transfer of *Ch. inonuensis* to *Pecarichoerus* occurred without a direct comparison of the type materials of *Ch. inonuensis* and *P. orientalis* (type species of *Pecarichoerus*). It also should be noted that Pickford (2011, 2017) did not address the differences between *Ch. inonuensis* and the material from Münzenberg and Sandelzhausen, which were the reason to establish the species *S. muenzenbergensis* (Van der Made, 1998). Therefore any inference based on the morphology of the fossils of *S. muenzenbergensis*, does not have any relevance for the classification of *Ch. inonuensis*.

The new species *Ch. minimus* provides data on the relationship between the suoid from Sandelzhausen and Münzenberg, *Choeromorus* and *Schizoporcus*. Previously, *S. muenzenbergensis* was believed to be an offshoot of the *Choeromorus* lineage after *Ch. primus* (Van der Made 2010). The incisors of the latter species are not known, in *Ch. minimus* the I₁ protrudes more than the I₂, the lower incisors lack a well-developed endocristid and pre- and poststylids, and the I¹ has no lingual cingulum and no marked pre- and postcristas were present already in this *Choeromorus* lineage. The I¹ of *S. muenzenbergensis* shows these structures and that is probably correlated to the lower incisor morphology. In *Schizoporcus*, the I₁ and I₂ or DI₁ and DI₂ protrude equally far (Nikolov & Thenius 1967), as in most Suoidea, though they may be placed wide apart (Pickford 2017, figs. 25e, 26a, 26c), which is a modification of the common pattern. The morphology of *Ch. minimus* implies that neither the palaeochoerid from Sandelzhausen and Münzenberg, nor *Schizoporcus* are offshoots of the *Choeromorus*

lineage (contrary to what was previously believed, e.g. Van der Made 2010).

Pickford (2017) assigned the material from Mala Miliva to *P. inonuensis*. This material is problematic, because most teeth are incomplete. Previously it has been assigned to various species. Its M_3 retains a simple third lobe with one main cusp, which argues against a classification as *P. inonuensis* with two cusps. The teeth from Mala Miliva are large for *Ch. lemuroides* (e.g. Suppl.-Fig. 3). This material could represent *S. muenzenbergensis* or a large *Ch. lemuroides*.

It is concluded here that *Ch. inonuensis* is different from *S. muenzenbergensis*, that no valid arguments have been forwarded that show that *Ch. inonuensis* is not a descendant of *Ch. lemuroides* and that the use of this evolution for stratigraphy is possible.

The long lineage of *Choeromorus*

The long lineage of *Choeromorus* (= *Taucanamo*) is of biostratigraphic relevance for Gracianica. Since it was proposed and described in detail (Van der Made 1997a, 2003, 2005, 2010), there is much new material and some new species have been named: *Siderochoerus minimus* Pickford, 2017, *Siderochoerus ibericus* Pickford, 2017 and *Ch. petersbuchensis*, which all belong to this lineage. The species *Ch. petersbuchensis* (= *Ch. inonuensis*) was discussed above. The species *S. ibericus* is based on material, which previously was included in *Ch. primus* (*T. primum*) (Van der Made, 1997a) and this interpretation is retained here.

The newly named *Siderochoerus minimus*, placed in a subfamily of its own, the Siderochoerinae (Pickford 2017), is the earliest member known of this lineage. It shares with other species of *Choeromorus* the feature of the tips of the I_1 protruding much more than those of the I_2 (Suppl.-Figs. 5/6-8). Noteworthy is that the I_1 have facets near the tip on the lateral side, which are caused by occlusion with the I_2 . This is a common feature observed in various specimens of different species of the genus *Choeromorus*. The common condition in Suidae, Tayassuidae and Palaeochoerini is that the tips of the I_{1-2} form a transverse crest (Suppl.-Figs. 5/9-11) and that the I_2 (not the I_1) have a lateral facet caused by occlusion with the I_2 . The incisors of *Ch. minimus* and other species of *Choeromorus* also lack clear endocristids and pre- and poststylids on the lingual side. American Tayassuidae, like “*Prosthennops*” *niobrarenensis* (AMNH 113380) also have the first incisors protruding more than the second one, but this is probably a parallel evolution and these incisors differ from those of *Choeromorus* in being oriented more convergently and having higher crowns with a different morphology. The I_1 protruding more than the I_2 and the morphology of the incisors are apomorphies shared by *Choeromorus* and *S. minimus*. As a consequence, *Siderochoerus* Pickford 2017 is synonymised with *Choeromorus* Gervais, 1850 and Siderochoerinae Pickford, 2017 is a junior synonym of Taucanaminae Van der Made, 1997a.

Four species of the genus *Choeromorus* present progressive changes and the most parsimonious interpretation is that they form an anagenetic lineage: *Ch. minimus* - *Ch. primus* - *Ch. lemuroides* - *Ch. inonuensis*. The species *T. inonuensis* was mentioned from Europe and Anatolia (Fortelius et al. 1996a), but later the European fossil representatives were classified as *S. muenzenbergensis* (e.g. Van der Made 1998, 2010), restricting the former species to İnönü 1 and Paşalar in Anatolia. Pickford (2017) described fossils from Castelnau d’Arbieu and Thannhausen as *P. inonuensis* and fossils from Petersbuch 31, 39, 68, 71 and 108 as *Ch. petersbuchensis*. These fossils belong to *Ch. inonuensis* and show that the species lived in Europe. This provides opportunities for correlation between Europe and Anatolia. However, the fossils from Sandelzhausen and Münzenberg, which Pickford (2017) assigned to *P. inonuensis*, belong to *S. muenzenbergensis* (previous section). It is possible that *P. orientalis* is a fifth species in this lineage and should better be included in the same genus. Many of the changes in this lineage can be described very well with biometry. In the following, the numbers refer to Suppl.-Fig. 7 (modified from Van der Made 2010).

- 1) Characters present in the common ancestor: a) the features typical of the Palaeochoeridae (see previous section), b) lingual roots of upper molars fused and convergent, c) molars generally with cusps that tend to be more rounded without very marked crests or angles, upper molars without well-developed protoendo- and tetrapostcrista, d) upper molars with wide and generally short tetrapreocrista, e) molars wide, f) premolars not very elongate; g) P_4 with a single main cusp; h) choanae are wide and open close to the posterior end of the M^3 . Lower incisor morphology unknown.
- 2) Features present in *Choeromorus minimus*: a) I_1 protrudes more than I_2 , b) endocristid and pre- and poststylid on the lower incisors not developed or weak, c) simple I^1 without lingual cingulum and without pre- and poststyles, d) protoendo- and tetrapostcrista on the upper molars may be present.
- 3) *Choeromorus primus*: a) general size increase (absolute size of the M_3 increased, but not the relative size of the M_3 ; Fig. 5, Suppl.-Figs. 3-4), b) in general, the crests on the molars tend to become more pronounced.
- 4) *Choeromorus lemuroides*: a) more elongate M_1 -2 (Fig. 3), b) more elongate premolars (Fig. 4) (this is not

necessarily related to the elongation of the molars, see *Hyotherium* and *Conohyus*), c) even the P^4 is elongate (with often $DAP \geq DT$; usually the P^4 is not affected by processes of elongation of the cheek teeth), d) M_3 and M^3 larger relative to the $M1$ (Fig. 5, Suppl.-Fig. 4) and in absolute measurements clearly bigger than in the previous species (Fig. 5, Suppl.-Fig. 3), e) M_3 occasionally with a second cusp in the third lobe or with a fourth lobe, f) P^4 with wide anterior cingulum, g) P^4 with a high buccal cusp, h) progressively better development of the cristas and cristids on the molars.

- 5) a) Second cusp in the third lobe of the M_3 always present or at least predominant (because this is shared by *Ch. grandaevus* and *Ch. inonuensis*), b) progressive better development of the cristas and cristids on all molars.
- 6) *Choeromorus inonuensis*: a) size increase (Fig. 4), b) relatively (Suppl.-Fig. 3) and absolutely larger $M3$ (Fig. 5, Suppl.-Fig. 3).
- 7) *Choeromorus orientalis* is not well known and features 2a-c, 4b-g, 5a, 6b, and 8 are not known. If a direct descendant of *Ch. inonuensis*: a) protopre-, protopost-, tetrapre- and tetrapostcrista higher and more slender, b) valleys between the paracone and protopre- and protopostcrista and between the metacone and tetrapre- and tetrapostcrista deeper, c) size increase.
- 8) *Choeromorus grandaevus*: size reduction. The species must have branched of the main lineage somewhere outside Western Europe. The second cusp in the third lobe of the M_3 suggests that, this species did not branch off before *Ch. lemuroides*, where this cusp is present but not predominant.

Though Pickford's (2017) interpretation that *Ch. inonuensis* belongs to *Pecarichoerus* is not based on solid arguments, it raises the interesting question of the possible relationship between the *Choeromorus* and *P. orientalis*. In the *P. orientalis* upper molars, the protoprecrista is directed towards the anterior side of the metacone and gives the impression of a loph. This was interpreted as a shared feature with *Schizoporcus* (Van der Made 2010: 97, feature 11). However, the structure is slightly different in *Schizoporcus*, where the anterior loph is formed by the protoprecrista that connects with the metaprecrista between the two cusps. In *Schizoporcus*, the proto- and paracone and the meta- and tetracone are connected by crests, while in *Pecarichoerus* there is a long and slender protoendocrista directed towards the middle of the tooth, where it meets the tetraprecrista, which is also long and slender. Between the round metacone and the tetrapre- and tetrapostcrista, there is a deep semicircular valley in *Pecarichoerus*, but not in *Schizoporcus*, and there is a similar valley between the proto- and paracone. There is no connection between the tetra- and metacone. The molar morphology of *Pecarichoerus* is thus more similar to that of *Choeromorus* than to that of *Schizoporcus*. *Pecarichoerus orientalis* is a little larger than *Ch. inonuensis* and might be younger. If it is a descendant of *Choeromorus*, it might be considered to include it in that genus.

The small suoid from Sandelzhausen and Münzenberg is primitive in most of its features and no apomorphies are known linking the species to any of these genera in particular. It is evident the fossils from Sandelzhausen and Münzenberg do not interfere with the use of the *Choeromorus* lineage in stratigraphy, but it is also evident that the affinities of *S. muenzenbergensis* will continue to be problematic. The phylogenetic position of *Yunnanchoerus* is problematic, since its morphology remains badly known. Suppl.-Fig. 7 gives a new interpretation of the phylogeny of these suoids.

- 9) *Schizoporcus muenzenbergensis*: I^1 with lingual cingulum and with styles that mark the mesial and distal edges at the lingual side of the crown.
- 10) a) endocristids in the lobes of the lower molars directed towards each other, but not yet forming lophs, b) Completely formed anterior loph in the upper molars? (not known for *S. anatoliensis*), c) well-developes metaprecrista, directed towards the end of the tetraprecrista? (not known for *S. anatoliensis*). Features b and c are present in *Yunnanchoerus* and *S. sinapensis*. If both are closely related, these features may have been present in *S. anatoliensis*, but if *Yunnanchoerus* is more closely related to *Choeromorus*, features b and c may have appeared after *S. anatoliensis*.
- 11) *Schizoporcus anatoliensis*: a) P_4 with prominent metaconid forming a transverse loph, b) P_4 talonid cusp reduced, c) roots of the lower molars probably starting to split up in two pairs of roots (known only in Çandır), d) increase in general size.
- 12) *Schizoporcus sinapensis*: a) complete anterior and posterior lophs on lower and upper molars, b) larger size, c) here or earlier: shorter premolars and relatively wider upper premolars, d) large I^1 and upper canines (may have been acquired earlier); e) opening of the choanae further behind the M^3 (here or already at 9-10).
- 13) *Schizoporcus vallesensis*: a) further reduction of the premolars, b) increase in general size.

- 14) *Yunnanocherus* is not well known. It has two contradicting derived features: elongate premolars, a feature shared with *Choeromorus* and a high degree of lophodonty, shared with *Schizoporcus*. The third lobe of the M₃ and the second lobe of the M³ are small, while in *Choeromorus* there is a tendency to enlarge the M₃ distally. The affinities are not satisfactorily resolved. If originating from an early *Choeromorus*: a) complete anterior lophs in the upper and lower molars and a complete posterior loph in the upper molars, b) a nearly complete loph in the second lobe of the lower molars, c) reduction of the third lobe of the M₃ and second loph of the M³. If closely related to *Schizoporcus*: a) complete anterior lophs in the molars and complete posterior lophs in the upper molars, if not acquired already under 10, b) elongation of the M1-2, if not acquired already under 10, c) size increase.
- 15) *Yunnanocherus lufengensis*: a) size decrease, b) formation of a posterolingual crest originating from the protocone (protoendocristid).

Generic classification of the species “*latidens*”: *Listriodon*, *Bunolistriodon* or *Eurolistriodon*?

Biedermann (1873) named the species *Sus latidens*. Later, the species was placed in *Listriodon* (Stehlin 1899-1900; Pickford & Morales 2003; Orliac 2009), *Bunolistriodon* (Van der Made 1990a, 1990b, 1996) and *Eurolistriodon* (Pickford & Moyà Solà 1995). The species is present in Gračanica and its generic classification is relevant here.

Listriodon Von Meyer, 1846 is the first named listriodont genus and several species were placed in this genus, before other listriodont genera were named. Arambourg (1933) conditionally named *Bunolistriodon*, but this name is not available because no type species was indicated (ICZN 1999, article 13.3). Later, Arambourg (1963) indicated *Sus lockharti* Pomel, 1848 as the type of *Bunolistriodon*, gave a diagnosis, and the name is available from then onwards. Van der Made (1990a, 1990b, 1996, 1997b) placed *Bunolistriodon lockharti*, *B. latidens*, *B. adelli* and *B. meidamon* in *Bunolistriodon*. Pickford & Moyà Solà (1995) were of the opinion, that Arambourg's (1963) diagnosis is not good and therefore named the genus *Eurolistriodon*, but, like Arambourg (1933), they did not indicate a type species. The ICZN (1999) does not give criteria for good or bad diagnoses or definitions, but it does indicate that a type species should be selected for a genus name to be valid. Orliac (2006) used the same name for a genus with a somewhat different content. Whereas Pickford & Moyà Solà (1995) included the species *E. adelli*, *E. lockharti* and *E. latidens* in *Eurolistriodon* Pickford & Moyà Solà, 1995, Orliac (2006) included *E. adelli* and a new species *E. tenarezensis* in *Eurolistriodon* Orliac, 2006.

Orliac (2006) placed *B. lockharti* in *Listriodon*, based on a cladogram that groups on the one hand *E. adelli* and *E. tenarezensis* and on the other *B. lockharti*, *Bunolistriodon retamaensis*, *B. latidens*, *B. meidamon* and *L. splendens* (type species of *Listriodon*). *E. adelli* and *E. tenarezensis* are separate from the other two species because of the plesiomorphies they retain (features 3, 4, 7, 22) and the two are united, not because they share unique apomorphies, but they share a number of apomorphies which are coded as unknown in several of the other group of species (57-60, 63, 65, 70, 74, 76). Many of these features are more variable than admitted in this analysis: e.g. both character states of feature 4 can be observed in a single sample (Van der Made 1996, pl. 23 fig. 3 and pl. 22 fig. 4 would be coded 0 and 1, respectively). It is not possible to discuss all the features here in detail, but one, concerning the I¹, is of particular interest.

Leinders (1975) figured the labial profile of the I¹ of different species and noted that those of *L. splendens* are clearly bilobate and different from those of what is called here *B. adelli*, which in his figures show a small third lobe in the middle or a flat surface there. It is well known that in little worn listriodont incisors, there are cusplets along the crest of the I¹ (Stehlin 1899-1900). These cusplets are separated by shallow furrows developed near the crest. These shallow furrows are not normally taken into account. A grouping of incisors with no, one or two labial furrows is normally accepted (Leinders 1975; Van der Made 1996, 1997b; Pickford & Morales 2003). If the teeth are more “elongate” (with long DMD), both large and small furrows tend to be deeper and to reach further down on the labial side. The two furrows are a shared derived feature of the European *Bunolistriodon*. There is variability and the furrows are not always well-developed further from the apex (compare Leinders 1975, fig. 1/1 and 1/2, both from Munébrega). This is more likely the case in the earlier samples (those which contain the types of *B. tenarezensis* and *B. adelli*); apparently the feature evolved and became clearer. Orliac (2009) redefined the feature as one/two/several lobes and coded the species with three and *L. splendens* as having several. *Listriodon splendens* and *L. pentapotamiae* are generally accepted to have two lobes, separated by one furrow (Leinders 1975, Van der Made 1996; Pickford & Morales 2003), but may have some additional furrows that are not equally well-developed as the main furrow in the middle. The result of Orliac's redefinition is that: 1) a well known feature of the European species of *Bunolistriodon* is not recognized, and 2) that most, but not all, of the samples of these species are grouped with *L. splendens*. The three lobed I¹ seems to be an apomorphy of the monophyletic group of European *Bunolistriodon*, since the species in the Indian

Subcontinent and Africa assigned to *Bunolistriodon* of which the I^1 is known have one or no labial furrow on this tooth (Van der Made 1996: pl. 4 fig. 1, pl. 27 figs. 3 and 7). Here, the sublophodont Listriodontinae of Europe and Anatolia with I^1 with three lobes are considered to be a monophyletic group, to which the name *Bunolistriodon* is applied.

Which are the European species of *Bunolistriodon*?

For a long time, *B. lockharti* (Pomel, 1848) was recognized as the only fully bunodont listriodont in Europe, until it was recognized that there are two species in the locality of Córcoles (Van der Made & Alférez 1988; Van der Made 1991). The Listriodontinae were revised (Van der Made 1996a, 1997) and four species of *Bunolistriodon* were recognized, some of them recently named: *B. lockharti*, *B. adelli* Pickford & Moyà Solà, 1995, *B. latidens* (Biedermann, 1873) and *B. meidamon* Fortelius et al., 1996b. However, since that time *Listriodon retamaensis* Pickford & Morales, 2003 and *Eurolistriodon tenarezensis* Orliac, 2006 were named. The suid from Gračanica could belong to one of six species, if there are really six species. In the following section, it is argued that there are four species and in the main text, the material from Gračanica is classified on the basis of comparisons with these four species.

The diagnosis of *L. retamaensis* indicates the following features to justify a new name: 1) small size, 2) short diastemata (compared to *Eurolistriodon*), 3) all upper premolars present, 4) three lobed I^1 with length-width index of about 177, 5) bunolophodonty, 6) robust metapodials.

1) The species “*L. retamaensis*” is smaller than *B. lockharti* and similar in size to *B. adelli*.

2) Pickford & Morales (2003) compared diastema measurements of three *Bunolistriodon* skulls. Diastema length is one of the most variable features in a suid, and tends to be less in the females (Van der Made 1991). As it happens, the type of “*L. retamaensis*” is a female and the type of *B. adelli* a male, explaining perfectly well the observed different diastema sizes. Despite having studied material from over 50 localities, Van der Made (1996, table 13) could give only diastema measurements for one mandible of European *Bunolistriodon*. This illustrates well that there are not enough specimens to know the variability of diastema length in *Bunolistriodon* and to use it in taxonomy.

3) The reported lack of the second upper premolars in *B. adelli* (Pickford & Moyà Solà 1995) might be pathologic. However, the feature was not documented by adequate photographs and it cannot be ruled out that the absence is due to taphonomic reasons.

4) I^1 with three lobes, which are separated by two furrows on the labial side, are typical the European *Bunolistriodon*. These incisors evolved from incisors without grooves on the labial side and early European I^1 from Armantes and Munébrega tend to have these grooves not well-developed (Van der Made 1996, plate 1, figs. 3, 4, 16, plate 17, fig. 5). This is like in the type of *B. adelli*, even though Pickford & Morales (2003) include them in “*L. retamaensis*”. The proportions and size of the holotype of *B. adelli* and paratype of *B. retamaensis* are nearly the same (Fig. 9; data from Pickford & Moyà Solà 1995 and Pickford & Morales 2003).

5) Both “*L. retamaensis*” and “*E. adelli*” are sublophodont.

6) The robust metapodials are not only mentioned in the diagnosis, but appear in several places in the text, e.g.: “... the evidence afforded by the postcranial skeleton, in particular the long and slender metapodials of *E. adelli* which contrast with the shorter more robust metapodials of *L. retamaensis* n. sp. ...” (Pickford & Morales 2003). No measurements were given to substantiate this and the only metapodial figured (Fig. 2E) or of which measurements are given are not of *B. retamaensis* but of *L. splendens*. Subsequently new fossils from several localities, including Barajas 17, were described and assigned to this species (Pickford 2016b), but no mention was made of MNCN Bar17-5, a very gracile Mc IV from Barajas 17. The metapodials of *E. adelli* from Els Casots are crushed, so it is not possible to calculate a robusticity index, but they look indeed long and gracile. The specimen from Barajas has the index $100 L / DTD = 589$ and is the most gracile of all Suoid Mc IV that I have measured. Gracile metapodials seem to be a shared feature of *E. adelli* and *L. retamaensis*, or maybe all *Bunolistriodon*, while those of *L. splendens* are more robust.

In these and any other relevant features, *B. retamaensis* and *B. adelli* are similar and therefore are here considered to be synonymous. Another taxon, smaller than *B. lockharti*, is *B. michali*, based on material from Chios (Paraskevaidis 1940). The type material does not include incisors or canines. It was believed to be a possible synonym of *B. latidens* (Van der Made 1996). However, new work on Chios suggests that these fossils might be much older (C5Br, 15.974–15.160 Ma; Kondopoulou et al. 1993; Koufos 2006) and contemporary of *B. adelli* and *B. retamaensis* of which it may turn out to be a senior synonym. Until more material from Chios becomes available, the name *B. adelli* is applied here to the species that gave rise to *B. latidens*.

The diagnosis of *E. tenarezensis* includes the following features, which are claimed to differentiate it from *B. lockharti*: 1) the distal sulcus on the labial side of the I^1 is deeper, 2) the C^m is smaller, 3) the buccal

cingula on M^x are interrupted at the level of the paracone, 4) a different orientation of the metaendofossid on the M_{2-3} (Orliac 2006).

1) The development of the labial furrows of the I^1 has been described and figured in quite some detail (Van der Made 1996, Plates/figs. 4/1, 15/3-4, 17/5, 17/8, 18/6, 20/3, 20/9, 22/4-5, 22/12, 24/2, etc.). The labial side of the I^1 of early species of *Bunolistriodon* tends to have no furrows, while those of the earliest European *Bunolistriodon* tend to have two shallow furrows, mainly developed in the apical area and which may disappear with wear, and the later ones have two deeper furrows. Besides, there is individual variation. Using the depths of the furrows relative to each other is not warranted.

2) The upper male canine was claimed to be smaller in *E. tenarezensis* than in *B. lockharti*, however no measurements were given to support this (Orliac 2006, table 2). Canines of later *Bunolistriodon* species tend to be ever-growing and their size is very variable. There is much variation in upper and lower canine size in listriodont samples of a single species or even from a single locality (e.g. Van der Made 1996, figs. 39, 48, 49, 50, 53, 54).

3) The cingulum of the molars at the level of the paracone was claimed to be continuous in *B. lockharti* and discontinuous in *E. tenarezensis*. Within a sample of *B. lockharti* from Baigneaux-en-Beauce, the cingulum may be continuous (Van der Made 1996, Pl. 23, figs. 7, 8, 9, 10, 12), or interrupted (Pl. 23, figs. 11 and 13).

4) A difference in the orientation of the metaendofossid on the M_{2-3} would differentiate *E. tenarezensis* from *B. lockharti*. Some prefer to describe the fossids or furrows, but their orientation and position depend on the development of the lobes or crests and in this case are related to the tendency to lophodonty. In the listriodonts, the lobes of the cusps tend either to be converted into the crests that later form the lophs or to be reduced. These crests become oriented transversely (modifying the shape of the adjacent fossas), and when they fuse to the crest coming from the other cusp, a transverse loph is formed. Within a single tooth row, there are differences in the degree lophs are formed. In general it is clear when full lophodonty is acquired, but splitting up the sublophodont morphologies and assigning them to different species is one step further, very likely one step too far. There are no studies that quantify or describe the variability in this feature.

It seems that for all four features the variability was underestimated. If variability is systematically underestimated, this has dramatic consequences for the data matrix and resulting cladogram. There seem to be insufficient morphological grounds for maintaining *B. tenarezensis* as a species different from *B. lockharti*. Even if *B. tenarezensis* would be considered to be a separate species, there is a reason not to use this name. Orliac (2007, p. 33) included *Palaeochoerus giganteus* Golpe-Posse, 1972 from Can Canals in the synonymy of *E. tenarezensis*, which implies that *Bunolistriodon giganteus* would have priority.

The foregoing reduces the number of species in *Bunolistriodon* again to four. There are also other reasons to be suspicious of many species. Orliac et al. (2009, fig. 4) assumed that the species *E. adelli*, *E. tenarezensis*, *L. retamaensis* and *L. lockharti* appeared at the same time during MN4 in Europe. All these species are known from an area in south of France and the northern half of Spain with a diameter of less than 500 km. Would features like a minor difference in the depth of a furrow on an incisor, or a continuous/interrupted cingulum along the paracone allow four very similar species to be sympatric? This is very unlikely. *B. lockharti* and *B. adelli* differ as much in size as two recent sympatric peccary species (Van der Made 1991). This suggests that such a size difference is ecologically relevant. The species *E. adelli*, *E. tenarezensis*, *L. retamaensis* and *L. lockharti* can be separated into two size groups and this same separation is congruent with a separation using some morphological or morphometrical differences: *B. lockharti*/*B. tenarezensis* on the one hand and *B. adelli*/*B. retamaensis* on the other. The minor differences between *B. tenarezensis* and *B. lockharti* most probably concern features which evolved in this lineage and passed through a stage where both character states were found within a single population. The same is the case with the pair *B. adelli* and *B. retamaensis*. The latter gave rise to *B. latidens* and *B. meidamon*. Though there are four species, at any time there were not more than two contemporaneous species of *Bunolistriodon* in Europe.

Metrically these four species can be recognized. The black squares in Fig. 9 represent fossils, which previously have been assigned to *B. adelli* and *L. retamaensis* (Van der Made 1996; Pickford & Morales 2003; Pickford 2016) and specimens from the type locality of both (red dot and open triangle) indeed cluster with the black squares: *B. retamaensis* is a junior synonym of *B. adelli*. There is not much material from Can Canals (type locality of *P. giganteus*), but there is an I^1 , which is close to the cluster of *B. lockharti*, which supports the synonymy of the two species (Van der Made 1996). The I^1 , I_2 and particularly the C_m from Montréal du Gers (type locality of *B. tenarezensis*) are in the ranges of *B. lockharti* (Figs. 7-9) and there is little reason to maintain the two species separate. This leaves four reasonably well-defined species of European and Anatolian *Bunolistriodon*.

The lineage *B. adelli* - *B. latidens* - *B. meidamon*

The evolutionary lineage *B. adelli* - *B. latidens* - *B. meidamon* is considered to be of biostratigraphic interest for correlations in Europe-Anatolia (Figs. 7-9, Suppl.-Fig. 8; Van der Made 1996, 2003, 2005). In the phylogenetic tree of Pickford & Morales (2003, fig. 18), there is a similar lineage: *L. retamaensis* - *L. latidens* - *L. meidamon*. Orliac et al. (2009, fig. 4) presented a phylogenetic tree, based on a cladogram by Orliac (2009, fig. 9), in which *B. latidens* and *B. meidamon* form a clade with two parallel lineages, one of them being a ghost lineage for most of the time. This seems to be an artefact of the cladistic method or the computer program applied. Cladistics was developed as a method to study the relationships between living species, which are all presented as terminal species. It does not take time, anagenetic lineages and common ancestors into account, but it is inconceivable, that we never find fossils of a species that is the ancestor of another species. In Orliac's (2009) data matrix, *B. latidens* and *B. meidamon* differ only in features, which for one of the two are coded as unknown. In this case, a single anagenetic lineage is more parsimonious than two lineages, part of one being a ghost lineage. Apparently, cladistic methodology or the computer programs applied interfere with the interpretation of paleontological data.

The species *B. adelli* and *B. lockharti* differ in general size and in Figs. 7-9, these size differences are seen in their canines and incisors. These two species tend to have similar proportions of the cheek teeth and anterior dentition, while *B. latidens* and *B. meidamon* differ from them in the proportions of the anterior dentition. However, the C_m of *B. adelli* has a labial side (La) which is on average wider compared to the lingual side (Li) than in *B. lockharti*. The latter species has a canine with a primitive section of the "scrofic" type (as in *Sus scrofa*) with a relative narrow labial side. Within the Suidae, various species evolved canines with wider labial sides, the "verrucosic" type (as in *Sus verrucosus*). In this feature, *B. adelli* is already like *B. latidens* and *B. meidamon*, supporting the idea that they form a lineage. In this lineage, the width of the labial side (La) and the index $100La/Li$ increased gradually (Fig. 7). The increase in the transverse or mesio-distal diameter (DMD) of the incisors is pronounced (Figs. 8-9, Suppl.-Fig. 8) and is of biostratigraphic interest.

The increase in DMD can be observed as a plain measurement or as the index $100DMD/DLL$ (DLL = labio-lingual diameter) (Figs. 8-9, Suppl.-Fig. 8). In the lower incisors the increase in DMD is accompanied by a slight decrease in DLL from *B. latidens* to *B. meidamon* (Fig. 8). Since the I^1 occludes with the I_1 and I_2 , the increase in width of the all these teeth follows the same pattern (Figs. 8-9, Suppl.-Fig. 8), but the elongation of the three different teeth (I^1 , I_1 and I_2), expressed as the index $100DMD/DLL$ are not directly comparable. In order to have a comparable value for all three teeth, the value of that index is taken as a percentage of the average of the same tooth in the large sample of Paşalar. So the value of the index $100DMD/DLL$ of the I^1 of a specimen can be expressed as a percentage of the average of the same value of all specimens from Paşalar. The same is done for the I_1 and I_2 . These values are comparable and are used together in Fig. 10. In this figure, the evolution from *B. adelli* to *B. latidens* seems to be gradual and that of *B. latidens* to *B. meidamon* seems to be more rapid. The reason for this is that there is an additional change: the labio-lingual diameter of the incisors decreased from *B. latidens* to *B. meidamon*, accentuating the change in the index.

Classification of the European *Conohyus* and other Tetraconodontinae

There are five species of European Tetraconodontinae (Van der Made 1990b), which were classified as two species of *Conohyus* three of the related genus *Parachleuastochoerus* (Fortelius et al. 1996a, Van der Made 1999). Pickford (2014, 2016c) and Pickford & Laurent (2014) revived taxa in disuse and named new ones, increasing the number of tetraconodontine genera in Europe to four and species ten and transferred species from and to *Conohyus* (Suppl.-Fig. 2). In order to classify the tetraconodontine pig from Gračanica, these changes have to be discussed or mentioned at least.

Lartet (1851) named *Sus simorreensis*, stated that fossils of the species come from Simorre and Villefranche d'Astarac and described or indicated canines and molars, but he did not mention the premolars, which are now considered to be the most typical feature of the species. If he would have known the premolars, he might have referred to Gervais' species *L. lartetii*. Lartet (1851) did not give an indication which allows to identify the cheek teeth on which he based *Sus simorreensis*, but referred to a publication by Blainville, where an upper and a lower canine from Simorre are figured. The fact that Lartet united bunodont molars with the canines from Simorre, suggests that bunodont molars were present in Simorre. Bayle (1856) recognized that the canines from Simorre and figured by Blainville belong to *L. splendens*. Pilgrim (1925) named the genus *Conohyus* with type species *C. simorreensis*. This implies that *Sus simorreensis* was based on a type series consisting of remains of more than one species and that it remained an open question, which of them are the type species of *Conohyus*. Stehlin (1899-1900) searched for Lartet's specimens in the collections in Paris and Toulouse, but could not find them.

Several other species have been named, which are currently considered to belong to *Conohyus*: *Sus*?

doati Lartet, 1851 based on material from Bonnefond, *Sus abnormis* Kaup (1859) on the basis of material he indicated to be from Käpfnach, but which seems to be from Elgg (Stehlin 1899-1900, pp. 45-46), *Sus valentini* Filhol, 1881, based on material from St. Gaudens, *Hyotherium soemmerringi matritensis* Golpe-Posse, 1972 based on material from Puente de Vallecas, *Conohyus melendezi* Golpe-Posse, 1972) based on material from Mira, *Conohyus ebroensis* Azanza Asensio, 1986, based on a mandible from El Buste and finally *C. simorreensis goeriachensis* Van der Made, 1989, based on material from Göriach.

The lack of the type material of *C. simorreensis* was a problem. Leonard Ginsburg told me that the original specimens studied by Lartet were lost, that mandible HGP16 and palate HGP17 were from Le Fousseret, and that he was going to designate MNHN HGP16 as a neotype of *C. simorreensis* (pers. comm. 1986). I mentioned this issue (Van der Made 1989: 21) and named the subspecies *C. simorreensis goeriachensis* because it was much smaller than the fossils from Le Fousseret. In 1990, L. Ginsburg told me that he had excavated at Rajégats, one of the different fossiliferous points near Simorre, that also Lartet had collected there, and that he intended to select a neotype from this material, since this was more appropriate than the mandible and palate from Le Fousseret (Van der Made 1999a). This would change the definition of the species, since the material from Rajégats is much smaller than that from Le Fousseret. However, a neotype was never formally designated.

Pickford & Laurent (2014) re-discovered material from the Lartet collection in the MHNT and chose the mandibles PAL2011.0.84.1 and PAL2011.0.84.2 (assumed to belong to the same individual) to be the lectotype of *C. simorreensis*. No other specimens were indicated to have been known by Lartet, despite the fact that on p. 25 they suggest they found also suid fossils from Simorre studied by Lartet. There is, however, some doubt that these two mandibles were really part of the original type series, out of which a lectotype could/should be selected. As a proof that these specimens were syntypes, the authors indicated that the fossils have a paper label stuck to them with the indication “collections Edouard et Louis Lartet”. Louis Lartet (1840-1899) is the son of Édouard Lartet (1801-1871) and must have been 11 years old at the moment when his father gave the name *Sus simorreensis*. It does not seem likely that a fifty years old father stuck labels on the fossils which he had collected over many years, with the name of his 11 year old son. It is very likely that these labels date from much later, when the son had substantially contributed to the collections, and therefore do not provide a proof that Édouard Lartet had these fossils when he named the species. They could have been collected much later. The facts that the chosen lectotype-mandible contains the premolars which are so typical of the Tetraconodontinae and that Lartet (1851) did not mention the premolars, leads to the assumption, that he did not know these two mandibles when he named the species. In addition, Lartet (1851) indicated that *Sus? doati* from Bonnefond is a larger species than *C. simorreensis*, but the newly designated lectotype of the latter indicates a species of similar size, while material from Rajégats, one of the sites at Simorre and known to Lartet, is indeed smaller. As a consequence, there is reasonable doubt that these specimens were among the syntypes. If it is demonstrated that a designated lectotype was not part of the original type series, it loses its status as a lectotype (ICZN 1999, article 74.2). For sure, there is no proof, that the “neotype” was part of the original type series, but there is also no conclusive proof that it was not.

As mentioned above, Lartet (1851) based the species “*Sus*” *simorreensis* on fossils of two species: bunodont molars and canines which belong to the lophodont pig *L. splendens*. Pilgrim (1925) chose *C. simorreensis* to be the type species of *Conohyus*. Pickford & Laurent (2014) failed to see that their selection of a lectotype (if valid) formally establishes that the specific and generic names *Conohyus simorreensis* go with a bunodont species and that these names are no junior synonyms of *Listriodon splendens* (which would be the case, if one of the canines from Simorre were made lectotype).

The selection of a lectotype was accompanied by much incorrect information. For example, (Pickford & Laurent 2014: 3) stated that Van der Made (1989) proposed a specimen from Le Fousseret as a neotype and lamented how wrong or disadvantageous such a proposal was. However, Van der Made (1989) did not propose a neotype but mentioned Ginsburg’s intentions to do so. Nevertheless, these authors stated (p. 6) that they selected a lectotype a specimen from Villefranche similar to the specimens of Le Fousseret for the sake of nomenclatorial stability. Such a statement suggests that, the selection of the lectotype may affect the content of the species *C. simorreensis*.

Lartet (1851) indicated that *C. simorreensis* is present in Simorre and Villefranche d’Astarac. There are several fossiliferous sites at Simorre (Richard 1946), including Rajégats, in level 10, and Le Seignou in level 12 of the local stratigraphy and of a similar age as Villefranche d’Astarac (see section on stratigraphy). Pickford & Laurent (2014) designated a lectotype from Villefranche, but they did not provide measurements of the specimen. Therefore the measurements of the type and other specimens from Villefranche are given here in Suppl.-Tab. 5. Of these, an isolated molar is interpreted as a M₁ on the basis of its small width, and would be a very large M₁, but could be a small M₂. The material from Villefranche is clearly larger than that from Göriach, Puente de

Vallecas or Elgg (Figs. 12, 13). By contrast, the material from Rajégats (MNHN) is not very large. It includes M¹ (DAP = 16.2, 17.1) and M² (DAP = 19.0, 19.5). The lengths (DAP) of these teeth are broadly comparable with the lengths of the M₁ and M₂, respectively of Göriach, Puente de Vallecas and Elgg (Fig. 13). Indeed, the choice of the lectotype of one or another locality changes the content of the species *C. simorrensis*.

Lartet (1851) named *Sus? doati*, based on material from Bonnefond (Bonnefont) and indicated that it is larger than *C. simorrensis*. Pickford & Laurent (2014) revived Lartet's *Sus? doati* as *Conohyus doati*. Lartet (1851) wrote that *Sus? doati* from Bonnefond is a larger species than *C. simorrensis*. All that is known of the type series of this species is a canine (MNHN), a cast of the M³ (HLD) and a figure of the M₃ (Stehlin 1899–1900: pl. 1, fig. 9). Pickford & Laurent (2014) selected the M³-cast as the lectotype of the species. The canine has a section, which fits both *Conohyus* and *Parachleuastochoerus steinheimensis* and the same can be said for the morphology of the M³. Both teeth are large and it is not clear whether this material represents a large form of *Conohyus* or a large *Parachleuastochoerus*. The cast of the M³ (HLD) measures 25.2 x 21.6 (mm; DAP x DTa). It is much larger than material from Göriach and Puente de Vallecas and comparable to specimens from Mira and St. Gaudens ("Le Fousseret"; Van der Made 1989: fig. 4). The lower molars from Mira are comparable in size to the lectotype of *C. simorrensis* (Figs. 12–13). An M³ from Rajégats measures 21.1 x 16.6 (MNHN). Evidently, *Sus? doati* is larger than *Conohyus* from Rajégats and similar in size to *C. simorrensis* from Villefranche. This has two implications. 1) *Conohyus simorrensis* as defined by its lectotype is not smaller than *Sus? doati*, as Lartet (1851) indicated, but is of similar size and as a consequence is not what Lartet pretended. 2) If the species from Bonnefond belongs to *Conohyus*, it is similar to *C. simorrensis*, as presently defined, and is a junior synonym. Even though, Pickford & Laurent (2014) pretended to achieve nomenclatorial stability, their designation of a lectotype changed the species with respect to the concept of it by Lartet and many later workers.

The smaller material of *Conohyus* has generally been assigned to *C. simorrensis* and *C. abnormis* (from Elgg), *C. matritensis* (Puente de Vallecas) and *C. s. goeriachensis* (Göriach) were included in *C. simorrensis*. Names applied to the larger material are *C.? doati* (Bonnefond), *C. valentini* (St. Gaudens), *C. melendezi* (Mira), and *C. ebroensis* (El Buste). There are still more names for large *Conohyus*, based on type material from the Indian Subcontinent or Africa (Van der Made 1999), including *C. giganteus*.

A gradually evolving lineage is subdivided into chronospecies or –subspecies, with each occupying a section of the lineage. The boundaries between the chronospecies are situated somewhere in the middle between the type material of each species. Because the type material of *Conohyus simorrensis* is selected from a position higher in this lineage, the species became younger and larger. The newly designated type material is in the lower metrical ranges (Figs. 12, 13) of what previously was considered to be a larger species, for which the names *C. melendezi* (type locality Mira), *C. valentini* (type locality St. Gaudens) and *C. ebroensis* (El Buste) were proposed. These species should now be included in *C. simorrensis*.

Though we use the name *C. simorrensis*, this may not be the oldest name for this species. *Sus antediluvianus* Kaup, 1833 has been considered to be a synonym of *C. simorrensis* (Hünemann 1968). It is based on a molar from the Dinotheriensanden, where *P. steinheimensis* is common and it probably does not represent *Conohyus*, which is not known from these deposits. Gervais (1848–1852) named the species *Listriodon lartetii* in a part of his monograph, which was published in 1850 (Bibliographie de la France, 23–11–1850; Wagner 1851). He figured four specimens (plate 20, figs. 1–4) from "les graviers à Dinotherium du département du Gers", which constitute the type series. One of them is a P₄ with the morphology of what now is known as *Conohyus* and the other three are molars of *Listriodon*. I do not know where the originals are. Bayle (1856) and later also Gervais (1859, Atlas p. VI) himself considered *L. lartetii* a synonym of *L. splendens* and the name was not used later. Conform Gervais' own intention and in order to avoid the name "*lartetii*" being revived as a senior synonym of *C. simorrensis* or a species of *Parachleuastochoerus*, provoking new nomenclatorial instability, the M₃ (Gervais 1848–1852, plate 20, fig. 3; 1859 pl. 20, fig. 3) is selected here as a lectotype of *L. lartetii*.

Because the species *C. simorrensis* moved up in its evolutionary lineage, some space became free at the lower end of this lineage, which is filled by a species of *Retroporcus*. The name *Retroporcus* was first used by Pickford & Laurent (2014), though this genus is valid only from 2016, when Pickford (2016c) provided a diagnosis. Two European species, type species *R. complutensis* Pickford & Laurent, 2011 and *R. matritensis* (Golpe-Posse, 1972) and one Indian species, *R. sindiensis* (Lydekker 1878) were included in the genus. Pickford & Laurent (2014) assigned material from Mala Miliva to *R. complutensis*. This recalls the earlier proposal that *C. sindiensis*: 1) dispersed into Europe and gave rise to *C. simorrensis*, and 2) evolved in the Indian Subcontinent divergently from *Conohyus* and therefore was placed in a different genus (Van der Made 1999).

Retroporcus sindiensis is the best known species of this genus. It is on average smaller than the small European *Conohyus*, which is commonly called *C. simorrensis* (Figs. 11–13, Suppl.-Fig. 9) and its premolars are relatively wider (Fig. 11, Suppl.-Fig. 9), which was noted already before (Van der Made 1999a). The premolars

from Mala Miliva and Somosaguas are wide and all cheek teeth are well within the ranges of *R. sindiensis* (Figs. 11-13, Suppl.-Fig. 9). Other localities with similar material are Bâlâ and Petrovac (Figs. 12-13). Some fossils from Montejo de La Vega are particularly small and are more or less of the same age as Somosaguas (Mazo et al. 1998). On the basis of morphometrics, all this material could be assigned to *R. sindiensis*, while the detailed morphology of the different cheek teeth does not contradict this. Nevertheless, two other species were named or revived.

Pickford & Laurent (2014) named the species *R. complutensis* on the basis of material from Somosaguas. It is the type species of *Retroporcus*. Poor material from this site was previously noted to be very small and assigned to *C. simorreensis* (Van der Made & Salesa 2004). The new material allows to establish that the premolars are relatively short and wide as in *R. sindiensis* and unlike in *C. simorreensis* (Fig. 11, Suppl.-Fig. 9). Pickford & Laurent's (2014) diagnosis of *R. complutensis* gives only differences with *R. matritensis* but not with *R. sindiensis*. Since *R. complutensis* is in all features very similar to *R. sindiensis*, there is no compelling reason to keep them apart.

Golpe-Posse (1972) named a variety or subspecies *Hyotherium soemmerringi matritensis*. It is based on material from Puente de Vallecas in Madrid, a site placed in zone E of the Spanish biozonation. Van der Made (1990a, p. 89, fig. 1) noted that it is identical to *C. simorreensis goeriachensis* and there is no evidence that it is different from most other European early and small *Conohyus* (e.g. Figs. 12-14, Suppl. Fig. 9). Pickford & Laurent (2014) raised the subspecies to species rank and included it in *Retroporcus* as *R. matritensis*. Like Puente de Vallecas, the type locality of *R. matritensis*, Somosaguas is in Madrid and is placed in the same short biozone E (14.05-13.75 Ma). Given the proximity in age and geography of the type localities, the question arises, whether the two species are really different. While, the premolars of *R. complutensis* are smaller and relatively wider than in *C. simorreensis*, the premolars from Puente de Vallecas are larger and more elongate than in *R. sindiensis* and are within the ranges of *C. simorreensis* (Fig. 11, Suppl.-Fig. 9). Here *R. matritensis* is retained within *C. simorreensis*.

Ginsburg (1977) identified a single tooth from Sansan as a P¹ of *C. simorreensis* and gave the measurements 16.4 x 8.1 mm. Pickford (2012) identified it as a P₂ and gave the measurements 16.5 x 8.5 mm. If it were a P₂ it is wider and shorter than the same tooth in *C. simorreensis* and in the ranges of the P₂ of *R. sindiensis* (Suppl.-Fig. 9). If it were a P¹, the same would happen. Given its proportions it is more likely to belong to *R. sindiensis*. De Blainville (1839-1864) named *Sus choerotherium*, based on a maxilla with M²⁻³ from Sansan. Pickford (2012, 2017) indicated the year of publication of this part to be 1847 and noted that this material represents a tetraconodont. That is well possible and it seems likely to represent the same species as the premolar described by Ginsburg (1977). The consequence of this is that in case of synonymy, *S. choerotherium* would have precedence over *C. simorreensis* or any species placed in *Retroporcus*. *Sus choerotherium* is not a nomen oblitum anymore, since Pickford (2017: fig. 6) figured the type specimen under that name.

Here, the fossils from Sansan, Somosaguas, Mala Miliva, Petrovac and Bâlâ are classified as *R. sindiensis* and this species is considered to have dispersed into Europe and then to have given rise to *C. simorreensis*. The implication is that these five localities should be older than any locality with *C. simorreensis*.

For the correct classification of the fossils from Gračanica, some more recently named or revived taxa should be discussed. Pickford (2016c) named the genus *Versoporcus* with type species *V. steinheimensis* and included another species, which was in disuse, *V. grivensis*. This genus and two species correspond to *Parachleuastochoerus steinheimensis* as it is used here. Pickford (2014) claimed that HGP17 was not from Le Fousseret, but from St. Gaudens and that it is the holotype of *Sus valentini* Filhol, 1881. Filhol did not figure the specimen and indicated measurements, which in some cases differ significantly from my measurements of HGP17 (Van der Made 1989). In any case, HGP17 is considered here a large *C. simorreensis* (cf. Van der Made, 1989) and no *Parachleuastochoerus*, as claimed by Pickford (2014).

The lineage of *Hyotherium*

Hyotherium was a common suid in the Early and early Middle Miocene of Europe. This lineage is of relevance here for two reasons: 1) it strengthens the stratigraphic scheme presented here (Fig. 14) and the temporal distribution of suoid species of the lineages discussed here, and 2) it helps to delimit the age of Gračanica.

In addition to an insular species on Sardinia, there was the long lineage *H. meisneri* - *major* - *soemmerringi wylensis* - *s. soemmerringi* on the European main land, ranging MN1-5/6), which was described in detail by Van der Made (2010). There have been comments on the classification of these taxa, which need clarification here. Berger (2010, 2011) indicated that the correct spelling is *H. soemmerringi* with two "r" and not *H. soemmeringi*. He reported finding the lost type material of *H. soemmerringi*, and argued that for several reasons no two subspecies could be recognized, in part, because of the great age of the type locality

Georgensgmünd. However, the type material was not lost (Van der Made 1994). The age of Georgensgmünd is not 17.1 Ma, as argued by Berger, but more likely close to 15 Ma, and thus does not contradict a size increase. This size increase is documented (Van der Made 1998, figs. 7-8; 2010, figs. 21, 24). Another feature is the gradual increase in size of a distal cusp on the I¹ as observed in specimens from a series of localities, which are indicated by Van der Made (2010: 75). *Hyotherium medium* Von Meyer, 1841 is based on fossils from Weissenau and Mösskirch (= Mösskirch = Messkirch). Weissenau (MN 2) has *H. meisneri* and Mösskirch (MN5/6) has a larger species of *Hyotherium*. *Hyotherium medium* was thus, what Pickford (2016a) uses to call, a chimera, but he decided to select a lectotype from Mösskirch. This possibly makes the species a senior synonym of *Hyotherium wylensis* Von Meyer, 1859, a well defined taxon, used at the subspecies rank (Van der Made 2010). The proposal needs some checking, but does not affect stratigraphy. Here the model as presented by Van der Made (2010) is essentially followed.

The evolution of *H. s. wylensis*, still present in Sandelzhausen at about 15.2 Ma, to *H. s. soemmerringi*, present in Georgensgmünd (about 15 Ma, see section on stratigraphy above), occurred thus in a short time span. Various localities of Lisbon Vb (zone Dc, ranging 15.47-14.75 Ma) have *H. s. soemmerringi* and *Bunolistriodon latidens* (e.g. Olival da Susana and Quinta do Farinheira) and should thus be between <15.2 and 14.75 Ma. This situates the evolution of *B. adelli* (also present in zone Dc) to *B. latidens* in the later half of zone Dc.

The replacement of *Hyotherium* by *Conohyus* (or its ancestor) relevance for the age of Gračanica, in that Gračanica should be younger than the latest *Hyotherium* and in any case clearly younger than *H. s. wylensis*, meaning clearly younger than 15.2. The timing of this event is discussed in the main text.

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Suppl.-Fig. 1

Geographic position of the localities with *B. lockharti* and *Parachleuastochoerus*. Tooth nomenclature after Van der Made (1996) and Prieto et al. (2017), shown for a $M_{1/2}$ and a $M_{1/2}$.

Suppl.-Fig. 2

The classification of different groups of Suoidea treated in this paper after Van der Made (2010) and this paper, compared with the classification by Pickford (2016a, 2016b, 2017) for the Palaeochoeridae, Pickford & Morales (2003), with the addition of the species *E. tenarezensis* named by Orliac (2006), for the Listriontinae and Pickford (2016b) for the Tetraconodontinae.

Suppl.-Fig. 3

The size of the M3 in *Choeromorus*. The localities are ordered from old at the bottom to young at the top. Provenance of data as in Table 6.

Suppl.-Fig. 4

The size of the M³ relative to the M¹ in *Choeromorus* and *S. muenzenbergensis*. Large M³ relative to M¹ tend to be an adaptation to the consumption of large quantities of food generally low in nutrients. The localities are ordered from old at the bottom to young at the top. Provenance of data as in Tab. 6.

Suppl.-Fig. 5

The molars of selected Palaeochoeridae and the incisors of *Choeromorus* compared to those of other Suoidea. 1) MNHN SG3565 left upper molar of *P. typus* from St. Gérard-le-Puy: a) lingual, b) occlusal, and c) buccal sides. Note that the lingual roots are divergent, but connected by a thin bony plate. 2) BSP 1959 II 8216 right upper M³ of a skull of *S. muenzenbergensis* from Sandelzhausen: occlusal view. 2-3) AMNH 22955 right and left M³ type specimens of *P. orientalis* from the Chinji Fm: occlusal views. 5) Nomenclature of the relevant structures of the upper molars: note that the protoendocrista and tetrapostcrista are developed as long thin crests in *P. orientalis* and are absent in *S. muenzenbergensis*. 6) PDTFAU no number left and right I₁₋₂ of *Ch. grandaevus* from Çandır. 7) MNHN Sa4592 left I₁₋₃ and right I₁₋₂ of *Ch. lemuroides* from Sansan. 8) NMA 205/1760 left I₁₋₂ and right I₁₋₃ part of the holotype of *Ch. minimus* from Petersbuch 62. 9) MNHN Qu16-585a left and right I₁₋₃ of *P. aquensis* from the Quercy. 10) SLJG 1878 left I₁₋₃ and right I₁₋₂ of *H. soemmeringi* from Labitschberg. 11) NBC ZMA10512 left and right I₁₋₃ of *Tayassu tayacu*. (recent). All incisors lingual view and brought to the same size for comparison.

Suppl.-Fig. 6

The upper canines of the Palaeochoeridae (1-5) without and of the Suidae (6-8) with endosynclines in the C^m . 1) MGL LGr6003 left C^x of *Choeromorus* from La Grive (old collections: a) lingual, b) buccal views. 2)) SMNS 45032 left C^m of *Propalaeochoerus* sp. from Tomerdingen: a) lingual, b) buccal views. 3) SMNS 45034a left C^m of *Propalaeochoerus* sp. from Tomerdingen: a) lingual, b) buccal views. 4) MNHN Qu16-585b right C^m of *P. aquensis* from the Quercy: a) lingual and b) buccal view. 5) UCBL 8798 left C^f of *Palaeochoerus aquensis* from St. Henri: a) lingual and b) buccal view. 6) MNHN 1948-1-152 right C^m of *Kolpochoerus heseloni* from Ain Hanech: linguo-posterior view. 7) BSP 1959II16734 left C^m of *H. soemeringi* from Sandelzhausen: a) lingual, b) buccal views. 8) BSP1952II342 right C^f of *H. soemeringi* from Sandelzhausen: a) buccal, b) lingual views. 9) Names of the enamel bands of the canines. The 1 cm scale bar corresponds to figs. 1-4 & 6 and the 5 cm scale bar to fig. 5.

Suppl.-Fig. 7

The phylogeny of the Taucanaminae, modified after Van der Made (2010). The numbers in circles refer to features mentioned in the text.

Suppl.-Fig. 8

Diagrams showing the changes in time in DMD and index 100 DMD/DLL of the I_1 in the *B. adell-latidens-meidamon* lineage through time. The localities are in approximate order from old at the bottom to young at the top and the provenance of data is as indicated in Table 6.

Suppl.-Fig. 9

Bivariate diagrams comparing the width of the posterior lobe (DTp) and length (DAP) of the P₂ and P₄ of: *Conohyus simorrensis* from: Sankt Oswald, Göriach, Puente de Vallecas, Villefranche d'Astarac, Paşalar, Carpetana, Elgg, Pichelsberg, and Tutzing; *Retroporcus sindiensis* from Bâla, Mala Miliva, Petrovac, Somosaguas and from the Indian Subcontinent; *R. indicus* from the Indian Subcontinent; *Parachleuastochoerus steinheimensis* from: Manchones I, La Grive, Steinheim, Can Amiral, Przeworno 1 & 2, Gratkorn, Wartenberg, San Quirze, Hostalets, Castell de Barberà, and Wissberg; *P. steinheimensis olujici* from: Lučane; *P. huenermanni* from Breitenbrunn, Rudabánya, and Esselborn; *P. crusafonti* from Can Llobateres. Provenance of data as indicated in Table 6.

Suppl.-Fig. 10

The temporal distribution of the species of *Choeromorus*, *Bunolistriodon*, *Conohyus* and the ages of selected localities. Detail of Figure 14.

Suppl.-Fig. 11

The evolution of *Bunolistriodon*. The numbers in circles refer to features mentioned in the text.

Suppl.-Tab. 1

The acronyms, which are used to indicate the measurements in figures and tables.

Acronym	measurement
DAP	Antero-posterior diameter
DAPp	DAP of the proximal part of a bone
DLL	Linguo-labial diameter of an incisor
Dmax	Maximum diameter of the crown of a third lower incisor
DMD	Mesio-distal diameter of an incisor
DTa	Transverse diameter of the anterior lobe of a tooth
DTp	Transverse diameter of the posterior lobe of a tooth or the proximal part of a bone
DTpp	Transverse diameter of the third lobe of a tooth
Ha	Height of a lower molar at the metaconid (or upper molar at the paracone), with no or little wear (no dentine exposed), otherwise indicated as >.
La	Width of the labial side of the lower male canine
Li	Width of the lingual side of the lower male canine
Po	Width of the posterior side of the lower male canine
R	Diameter at the medial side of the articular surface of the astragalus with the tibia
Ri	Radius of curvature of the inner side of a canine
Rm	Diameter in the middle of the articular surface of the astragalus with the tibia
Ro	Radius of curvature of the outer side of a canine
Ta	Thickness of the enamel of a lower molar measured at the metaconid (or upper molar measured at the paracone)

Suppl.-Tab. 2

The material from Gračanica is compared here to fossils of the same and other species indicated in the table. When an acronym is given, this means that the material was studied in that institute (see Suppl.-Tab. 3) or that it is presently kept there. The column “literature” indicates papers that describe fossils of those species from those localities; the classification used in those papers is also given. If no collection is indicated, the data used are taken from the literature.

Species	Locality	Collection	Literature	Classification in literature
<i>C. minimus</i>	Petersbuch 62, 29	CRW, NMA, CS	Pickford 2017	<i>Siderochoerus minimus</i>
<i>C. primus</i>	Petersbuch 2	BSP	Pickford 2017	<i>S. minimus</i>
<i>C. primus</i>	Petersbuch 2/3	CRW		
<i>C. primus</i>	Petersbuch 7	CRW		
<i>C. primus</i>	Artenay	MNHN	Mayet 1908	<i>Choerotherium pygmaeum</i>
<i>C. primus</i>	Buñol	MPV	Van der Made et al. 1998	<i>Taucanamo</i> aff. <i>sansaniense</i>
<i>C. primus</i>	Bézian	MNHN cast	Ginsburg & Bulot 1987	
<i>C. primus</i>	Els Casots	IPS	Pickford & Moyà Solà 1994	<i>Taucanamo pygmaeum</i>
<i>C. primus</i>	Montréal = Béon 1	MHNT	Orliac et al. 2006	<i>Taucanamo grandaevus</i>
<i>C. lemuroides</i>	Lavardens	MHNT		
<i>C. lemuroides?</i>	Mala Miliva	RGF	Petroniević 1967	<i>T. sansaniense</i>
<i>C. ?lemuroides</i>	Thannhausen	BSP	Pickford 2017	<i>Pecarichoerus inonuensis</i>
<i>C. lemuroides</i>	Petersbuch 68	CRW	Pickford 2017	<i>Choeromorus petersbuchensis</i>
<i>C. lemuroides</i>	Castelnau d'Arbieu	BSP	Pickford 2017	<i>Pecarichoerus inonuensis</i>
<i>C. lemuroides</i>	Sansan	MNHN, NHM, BSP, MHNT, IPS, NMB	Filhol 1891 Pickford 2012 Pickford 2017	<i>Choeromorus sansaniensis</i> , <i>Choerotherium mamillatum</i> <i>Choeromorus mamilatus</i> <i>Choeromorus lemuroides</i>
<i>C. lemuroides</i>	Gračanica	NHMW	this paper	<i>C. lemuroides</i>
<i>C. lemuroides</i>	Göriach	SLJG	Thenius 1956	<i>T. pygmaeum</i>
<i>C. lemuroides</i>	Petersbuch 31	CRW	Pickford 2017	<i>C. petersbuchensis</i>
<i>C. inonuensis</i>	Petersbuch 39	CRW	Pickford 2017	<i>C. petersbuchensis</i>
<i>C. inonuensis</i>	Petersbuch 108		Pickford 2017	<i>C. petersbuchensis</i>
<i>C. inonuensis</i>	Prebreza	RGF, NHMB	Pavlović 1969	<i>T. sansaniense</i>
<i>C. inonuensis</i>	Inönü 1	MTA	Pickford & Ertürk 1979	<i>Taucanamo inönüensis</i>
<i>C. inonuensis</i>	Paşalar	PDTFAU	Fortelius & Bernor 1990	<i>Taucanamo inonuensis</i>
<i>C. inonuensis</i>	Derching	NMA		
<i>C. grandaevus</i>	Çandır	PDTFAU	Van der Made 2003, Pl. 2, figs h-l	<i>Schizochocerus anatoliensis?</i>
<i>C. grandaevus</i>	Steinheim	SMNS	Chen 1984	<i>T. pygmaeum</i>
<i>C. grandaevus</i>	La Grive oc	UCBL, MGL	Van der Made 1996	<i>T. grandaevum</i>
<i>C. grandaevus</i>	La Grive L7	UCBL		
<i>C. grandaevus</i>	Przeworno 2	ISEAK	Kubiak 1981	<i>T. sansaniense</i> (in part)

<i>C. grandaevus</i>	Anwil	IPS cast	Engesser 1972	<i>T. pygmaeum</i>
	Petersbuch 35	CRW		
<i>C. ? orientalis</i>	Chinji Fm	AMNH	Colbert 1933a	<i>Pecarichoerus orientalis</i>
<i>C. ? orientalis</i>	Kanatti Chak 7	BSP	Pickford 2011, 2017	<i>P. orientalis</i>
<i>S. muenzenbergensis</i>	Sandelzhausen	BSP	Van der Made 2010	<i>S. muenzenbergensis</i>
			Zdarsky 1909	<i>Choerotherium sansaniense</i>
<i>S. muenzenbergensis</i>	Münzenberg	SLJG	Thenius 1956	<i>T. sansaniense</i>
<i>S. muenzenbergensis</i>	Neudorf Spalte	NHMW, IPUW	Zapfe 1983	<i>Palaeochoerus (Aureliachoerus) aurelianensis</i>
<i>S. muenzenbergensis</i>	Petersbuch 54	CRW		
<i>B. lockharti</i>	Gerlenhofen	SMNS	Dehm 1934	<i>Listriodon lockharti</i>
<i>B. lockharti</i>	Langenau I	SMNS	Van der Made 1996	<i>Bunolistriodon lockharti</i>
<i>B. lockharti</i>	Pellécabus	NMB	Roman & Viret 1934	<i>L. lockharti</i>
<i>B. lockharti</i>	Antonios		Koufos 2007	<i>B. lockharti</i>
<i>B. lockharti</i>	Montréal-du-Gers	MHNT	Orliac 2006	<i>Eurolistriodon tenarezensis</i>
<i>B. lockharti</i>	Engelswies	NMB	Stehlin 1899-1900	<i>L. lockharti</i>
<i>B. lockharti</i>	La Romieu	UCBL	Roman & Viret 1934	<i>L. lockharti</i>
<i>B. lockharti</i>	Chevilly	MNHN	Mayet 1908	<i>L. lockharti</i>
<i>B. lockharti</i>	Buñol	IVAU, MPV	Van der Made et al. 1998	<i>B. lockharti</i>
<i>B. lockharti</i>	Córcoles	UCM	Van der Made 1996	<i>B. lockharti</i>
			Golpe-Posse 1972	<i>Palaeochoerus giganteus</i>
<i>B. lockharti</i>	Can Canals	IPS	Pickford & Moyà Solà 1995	<i>Eurolistriodon lockharti</i>
			Orliac 2007	<i>E. tenarezensis</i>
<i>B. lockharti</i>	Baigneaux-en-Beauce	NMB	Van der Made 1996	<i>B. lockharti</i>
<i>B. lockharti</i>	Pontlevoy	MNHN	Stehlin 1925	<i>L. lockharti</i>
<i>B. lockharti</i>	Tavers	COBO	Van der Made 1996	<i>B. lockharti</i>
<i>B. lockharti</i>	Ravensburg	NMB	Van der Made 1996	<i>B. lockharti</i>
<i>B. adelli</i>	La Artesilla	MPZ	Azanza et al. 1993	<i>Bunolistriodon aff. latidens</i>
<i>B. adelli</i>	Els Casots	IPS	Pickford & Moyà Solà 1995	<i>Eurolistriodon adelli</i>
<i>B. adelli</i>	Córcoles	UCM	Van der Made 1996	<i>Bunolistriodon adelli</i>
<i>B. adelli</i>	La Retama	MNCN	Pickford & Morales 2003	<i>Listriodon retamaensis</i>
<i>B. adelli</i>	Munébrega I	IVAU	Van der Made 1996	<i>B. adelli</i>
<i>B. adelli</i>	Munébrega III	IVAU	Van der Made 1996	<i>B. adelli</i>
<i>B. adelli</i>	Munébrega AB	IVAU	Van der Made 1996	<i>B. adelli</i>
<i>B. adelli</i>	Armantès I	IVAU	Van der Made 1996	<i>B. adelli</i>
<i>B. adelli</i>	Mahou	MNCN	Pickford 2016b	<i>L. retamaensis</i>
<i>B. adelli</i>	Los Nogales	MNCN	Pickford 2016b	<i>L. retamaensis</i>
<i>B. adelli</i>	Barajas 17	MNCN	Pickford 2016b	<i>L. retamaensis</i>
<i>B. adelli</i>	Estación Imperial	MNCN	Pickford 2016b	<i>L. retamaensis</i>

<i>B. adelli</i>	Olival da Susana	CEPUNL	Antunes & Estravis 1986	<i>B. lockharti</i>
<i>B. adelli</i>	Lisbon Vb	CEPUNL	Antunes & Estravis 1986	<i>B. lockharti</i>
<i>B. adelli</i>	Carpetana	MNCN	Pickford 2016b	<i>L. retamaensis</i>
<i>B. adelli?</i>	Chios		Paraskevaidis 1940	<i>Listriodon (n.sp.?) lockharti</i> Pomel var. <i>Michali</i> n. var.
<i>B. latidens</i>	Mala Miliva	RGF	Petronievic 1967	<i>L. lockharti</i>
			Biedermann 1873	<i>Sus latidens</i>
<i>B. latidens</i>	Veltheim	NSSW	Stehlin 1899-1900	<i>Listriodon latidens</i>
			Van der Made 1996	<i>Bunolistriodon latidens</i>
<i>B. latidens</i>	Prebreza	RGF, MNHB	Pavlović 1969	<i>Listriodon michali</i>
<i>B. latidens</i>	Gračanica	NHMW	this paper	<i>B. latidens</i>
<i>B. m. meidamon</i>	Paşalar	PDTFAU, PIMUZ	Fortelius et al. 1996b	<i>Bunolistriodon meidamon</i>
			Van der Made 1996	
<i>B. meidamon ultimus</i>	Çandır	MTA, PIMUZ	Van der Made 1996	<i>B. meidamon</i>
			Van der Made 2003	<i>B. meidamon ultimus</i>
			Bernor et al. 2004	<i>Conohyus olujici</i>
<i>P. steinheimensis olujici</i>	Lučane			
<i>P. steinheimensis</i>	Manchones I	IVAU		
<i>P. steinheimensis</i>	La Grive	MGL	Depéret 1887	<i>Sus aff. steinheimensis</i>
		MGL	Depéret 1892	<i>Hyotherium soemmeringi</i> , v. Meyer Race <i>Grivense</i> , Depéret
<i>P. steinheimensis</i>	Steinheim	SMNS, NMB	Fraas 1882	<i>Chaeropotamus Steinheimensis</i>
			Chen 1984	<i>Conohyus steinheimensis</i>
<i>P. steinheimensis</i>	Can Admiral	IPS	Golpe-Posse 1972	<i>H. soemmeringi</i>
<i>P. steinheimensis</i>	Kaisersteinbruch	NHMW		
<i>P. steinheimensis</i>	San Quirze	MLGSB		
<i>P. steinheimensis</i>	Castell de Barberà	IPS	Golpe-Posse 1972	<i>H. soemmeringi</i>
<i>P. steinheimensis</i>	Wissberg	NMM	Hünemann 1968	
<i>P. huenermanni</i>	Rudabánya	HGSB	Fortelius et al. 2005	<i>Parachleuastochoerus kretzoi</i>
<i>P. huenermanni</i>	Can Ponsic I	IPS		
<i>P. crusafonti</i>	Can Llobateres	IPS	Pickford 1981	<i>Parachleuastochoerus crusafonti</i>
		IM, GSP, MNHI,	Pilgrim 1926	
<i>R. sindiensis</i>	Pakistan / India	AMNH, BSP, FISF,	Colbert 1933b, 1935	<i>Conohyus sindiensis</i>
		NMB, IVAU	Pickford 1988	
<i>R. sindiensis</i>	Bâlâ	MTA	Pickford & Ertürk 1979	<i>Conohyus simorrensis</i>
<i>R. sindiensis</i>	Mala Miliva	RGF	Petroniević 1967	<i>C. simorrensis</i>
<i>R. sindiensis</i>	Petrovac	RGF	Laskarev 1937	<i>Hyotherium soemmeringi</i> var. <i>media</i>
			De Blainville 1839-1864	<i>Sus choerotherium</i>
<i>R. sindiensis</i>	Sansan		Ginsburg 1977	<i>Conohyus simorrensis</i>
			Pickford 2012	tetraconodont, <i>C. simorrensis</i>
<i>R. sindiensis</i>	Somosaguas	UCM	Van der Made & Salesa 2004	<i>C. simorrensis</i>
			Pickford & Laurent 2014	<i>Retroporcus complutensis</i>
<i>R. sindiensis?</i>	Montejo de la Vega	MNCN	Mazo et al. 1999	<i>C. simorrensis</i>
<i>C. simorrensis?</i>	Puente de Vallecas	MNCN, MSI	Golpe-Posse 1972	<i>Hyotherium soemmeringi matritensis</i>

			Morales & Soria 1984, pl3 fig 4	<i>B. lockharti</i>
			Pickford & Laurent 2014	<i>R. matritensis</i>
<i>C. simorrensis</i>	Gračanica	NHMW	this paper	<i>C. simorrensis</i>
			Thenius 1956	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Göriach	SLJG	Van der Made 1989	<i>C. simorrensis goeriachensis</i>
			Van der Made 1998	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Rosenthal	SLJG	Van der Made 1989, 1998	<i>C. simorrensis</i>
<i>C. simorrensis</i>	St. Oswald	SLJG	Van der Made 1989, 1998	<i>C. simorrensis</i>
			Thenius 1956	
<i>C. simorrensis</i>	Au	SLJG	Van der Made 1989, 1998	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Simorre	MNHN	Pickford & Laurent 2014	<i>C. simorrensis</i> & <i>R. matritensis</i>
<i>C. simorrensis</i>	Villefranche d'Astarac	MNHN	Pickford & Laurent 2014	<i>C. simorrensis</i> & <i>R. matritensis</i>
<i>C. simorrensis</i>	Alhambra	MNCN	Van der Made & Morales 2003	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Paşalar	PDTFAU	Fortelius & Bernor 1990	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Carpetana	MNCN	Pickford 2013	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Elgg	NMB	Kaup 1859	<i>Sus abnormis</i>
			Stehlin 1899-1900	<i>Hyotherium simorrense</i>
<i>C. simorrensis</i>	Kleinhadersdorf	NHMW	Van der Made & Ribot 1999	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Kleineisenbach	BSP		
<i>C. simorrensis</i>	Tutzing	NMB	Stehlin 1899-1900	<i>Hyotherium simorrense</i>
<i>C. simorrensis</i>	Urlau	NMB	Stehlin 1899-1900	<i>H. simorrense</i>
<i>C. simorrensis</i>	Pischelsberg	BSP		
<i>C. simorrensis</i>	Pitten	IPUW		
<i>C. simorrensis</i>	Le Fousseret	MNHN, MGPIUSB	Pickford & Laurent 2014	<i>C. simorrensis</i>
<i>C. simorrensis</i>	Mira	IPS	Golpe-Posse 1972	<i>Conohyus melendezi</i>
<i>C. simorrensis</i>	El Buste	MPZ	Azanza Asensio 1986	<i>Conohyus ebroensis</i>
			Pickford & Laurent 2014	<i>Conohyus doati</i>
<i>C. simorrensis</i>	Fonte do Pinheiro	NHML	Roman 1907	<i>H. simorrense doati</i>

Suppl.-Tab. 3

The acronyms, which are used to indicate in which institutes fossils were studied, or where they are kept presently.

Acronym	collection
AMNH	American Museum of Natural History, New York
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, München
CEPUNL	Centro de Estratigrafia e Paleobiologia da Universidade Nove de Lisboa (Lisbon)
COBO	Collection Olivier Bardot, Orléans
CRW	Collection M. Rummel, Weissenburg
CS	Collection U. Schmidt
FISF	Forschungsinstitut Senckenberg, Frankfurt
GSP	Geological Survey of Pakistan, Islamabad
IGF	Istituto di Geologia, now Museo di Storia Naturale, Firenze (Florence)
IM	Indian Museum, Calcutta
IPS	Instituto de Paleontología, Sabadell
IPUW	Institut für Paläontologie der Universität, Wien (Vienna)
IVAU	Instituut Voor Aardwetenschappen, Utrecht
ISEAK	Institute of Systematics and Evolution of Animals, Kraków
MGPUSB	Museo di Geologia e Paleontologia, Università degli Studi di Bologna
MHNT	Muséum d'Histoire Naturelle, Toulouse
MLGSB	Museu i Laboratori de Geologia del Seminari, Barcelona
MNB	Museum für Naturkunde, Berlin
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Muséum National d'Histoire Naturelle, Paris
MPV	Museo Paleontológico de Valencia
MPZ	Museo Paleontológico de la Universidad de Zaragoza
MTA	Maden Tetkik ve Arama, Ankara
MGL	Muséum Guimet, Lyon
MSI	Museo de San Isidro, Madrid
NBC	Naturalis Biodiversity Center, Leiden
NHM	Natural History Museum, London
NHMB	Natural-Historical Museum, Belgrade

NHML	Natural-Historical Museum, Lisbon
NMA	Naturmuseum, Augsburg
NMB	Naturhistorisches Museum, Basel
NMM	Naturhistorisches Museum, Mainz
NHMW	Naturhistorisches Museum, Wien (Vienna)
NSSW	Naturwissenschaftliche Sammlungen der Stadt Winterthur
PMNHI	Pakistan Natural History Museum, Islamabad
PDTCAU	Paleoantropoloji, Dil ve Tarih Cografya Facultesi, Ankara Universitesi (palaeoantropology section, university of Ankara)
PIMUZ	Paläontologisches Institut und Museum der Universität, Zürich
RGF	Institute for Regional Geology and Paleontology, Faculty of Mining and Geology, University of Belgrade
SLJG	Steiermärkisches Landesmuseum Joanneum, Graz
SMNS	Staatliches Museum für Naturkunde, Stuttgart
UCBL	Université Claude Bernard, Lyon
UCM	Universidad Complutense, Madrid

Suppl.-Tab. 4

The ages of the localities. The reference is to papers which either supplied information on the assignation to MN unit, local biozone, paleomagnetism, or which described or listed the fauna, which here is used to assign the locality to a MN unit or biozone, or which provided the numerical age for a biozone.

Locality	MN	Local	Paleomag	interpreted / indicated age (Ma)	Reference
Petersbuch 62, 29	3			>16.8	Pickford 2017
Petersbuch 2	4	B		16.8-16.5	Daams & Freudenthal 1990; Van der Meulen et al. 2012
Grimmelfinger	4	Grimmelfingen Beds		17.5-17.3	Reichenbacher et al. 2013
Langenau I	4b	BM, Kirchberg Beds		17.1	Reichenbacher et al. 2013
Gerlenhofen	4b	BM, Upper Kirchberg Beds		16.8-16.5	Rössner 2017
Gerlenhofen	4/5	BM/OSM transition			Sach & Heizmann 2001
Artenay	4a	(B)		16.8-16.5	Mein 1977; Van der Meulen et al. 2012; Van Dam et al. 2006
Pellécahus	4a	3 Pellécahus Limestone			Ginsburg 1971
Montréal du Gers	4	Lower Lectoure Limestone (?)		16.8-16.5	Bulot et al. 2006; Van Dam et al. 2006
Antonios	5				Koufos 2006
Münzenberg (Leoben)	5	Karpatian		17.25-16.4	Mottl 1970; De Bruijn et al. 1992; Steininger 1999
Seegraben (Leoben)	5	Karpatian		17.25-16.4	Mottl 1970; De Bruijn et al. 1992; Steininger 1999
Bézian	4b / 4	Lower Lectoure Limestone			Ginsburg & Bulot 1987
Engelswies	5	OSM, anterior to Ries-Impakt; top Kirchberg Beds		>14.88 / ≈16.6	Heizmann & Begun 2001 Reichenbacher et al. 2013
La Romieu	4a	4 Lower Lectoure Limestone			Ginsburg 1971; Mein 1977
Baigneaux-en-Beauce	4 / 4b				Mein 1977 / Ginsburg 1990
La Artesilla	4	Ca	C5Br	16.49	Van der Meulen et al. 2012
Els Casots	4	Ca		16.0	Casnovas-Villar et al. 2011; Agustí & Moyà Solà 1991
Buñol	4	Ca		16.6-15.9	Van Dam et al. 2006
Córcoles	4	C		16.6-15.9	Daams et al. 1998; Van Dam et al. 2006
Lisbon Va	4/ 4a	Lisbon Va			Mein 1977; De Bruijn et al. 1992
Can Canals		Cb		16.6-15.9	Agustí et al. 1984; Van Dam et al. 2006
Chios	5				Mein 1990
Chios-Thymiana	lower 5		C5Br	15.974-15.160	Kondopoulou et al 1993; Koufos 2006
La Retama	4	Db		15.8-15.6	Hernández-Bailarín et al. 2017; Van Dam et al. 2006

Chevilly	4/5				
Munébrega I		Db		15.8-15.6	Daams et al. 1977
Munébrega III		Db		15.8-15.6	Daams et al. 1977
Munébrega AB		Db		15.8-15.6	Daams et al. 1977
Armantes I		Db	C5Br (base)	≈15.9	Daams et al. 1999b; Hilgen et al. 2012
Tavers	5	above marine M Miocene		<15.97	Ginsburg 1990; Hilgen et al. 2012
Pontlevoy	5	above marine M Miocene		<15.97	Mein 1977; Reichenbacher et al. 1998; Hilgen et al. 2012
Sandelzhausen	5	OSM C+D	C5Cn.1n-1r/2n-2r	16.47-16.27	Moser et al. 2009
		OSM C+D		15.2	Reichenbacher et al. 2013
Sandelzhausen		Db	5Bn.2n	15.8-15.6	Van Dam et al. 2006
Mahou		Dc		15.6-14.8	
Los Nogales		Dc		15.6-14.8	Hernández-Bailarín & Peláez-Campomanes 2017
Estación Imperial		Dc		15.6-14.8	Hernández-Bailarín & Peláez-Campomanes 2017
Barajas 17		Dc		15.6-14.8	
Quinta da Farinheira		Lisbon Vb			Antunes & Estravís 1986
Olival da Susana	5	Lisbon Vb			Antunes & Estravís 1986; Mein 1977; De Bruijn et al. 1992
Lisbon Vb		between zones N8 and N9		16.5-14.24	Antunes 1984
Lisbon Vb lower		Db		15.91-14.75	Mein 2000
Lisbon Vb upper		Dc		15.6-14.75	Mein 2000
Lavardens		7 Auch Limestone			Ginsburg 1971
Mala Miliva	5	Badenien			Mein 1977; De Bruijn et al. 1992; Rabeder 1978
Veltheim	5				
		below <i>FAD Illyricocongeria frici</i>		>15.5 Ma	Mandic et al. 2011, 2016
Gračanica			base C5Bn.1r	≈15.0	De Leeuw et al. 2010
Lučane				14.05-13.363	this paper
Gračanica	6				
		interfingering with			
Sankt Oswald	5	"Lagenid zone"		>14.2	Rabeder 1978; Harzhauser et al. 2002
Montejo de la Vega	5	E		14.1-13.8	Mazo et al. 1998
Somosaguas		E		14.1-13.8	Hernández-Bailarín & Peláez-Campomanes 2017
Puente de Vallecas	5	E		14.1-13.8	De Bruin et al. 1992
Georgensgmünd	6				De Bruijn et al. 1992
Georgensgmünd	5				Van der Made 1996; Ginsburg 1999; Berger 2010
Thannhausen		Middle OSM, above		14.88-14.55	Heissig 1989; Moser et al. 2009

		Ries-Impakt			
Stätzling	6				De Bruijn et al. 1992
Castelnau d'Arbieu	5	8 Lower Astarac Limestone			Ginsburg 1971
Göriach		Badenian		15.97-12.8	Mottl 1970; Hilgen et al. 2012
Rosenthal		Badenian		15.97-12.8	Mottl 1970; Hilgen et al. 2012
Au		Badenian		15.97-12.8	Mottl 1970; Hilgen et al. 2012
Neudorf Spalte	6	Lower Badenian		<15.97	Steininger et al. 1996; Hilgen et al. 2012
Ravensburg	5 / 6	OSM			Van der Made 1996; Salvador et al. 2015
Rümikon	6	OSM F	C5ADn	14.6-14.2	Kälin & Kempf, 09; Moser et al. 2009
Sansan	6	9 Sansan Limestone			Mein 1977; Ginsburg 1971
Sansan			C5Bn.2n	15.16-15.03	Sen 1997
Sansan			C5ABn	13.6	Daams et al. 1999b
Petersbuch 31	6				Pickford. 2017
Petersbuch 39	6				Pickford. 2017
Petersbuch 108	6				Pickford. 2017
Inönü 1	6		C5Br	<15.2±0.3 15.2±0.3	Kappelman et al. 1996 Steininger et al. 1996
Prebreza	6				De Bruijn et al. 1992
Carpetana		F		13.8-13.6	Hernández-Bailarín & Peláez-Campomanes 2017
Paracuellos 5		F		13.8-13.6	Van Dam et al. 2006
			C5ABr upper	13.7	Hernández-Bailarín & Peláez-Campomanes 2017
Alhambra				13.8-13.6	Van Dam et al. 2006; Montes et al. 2006
		F			Hernández-Bailarín & Peláez-Campomanes 2017
Elgg	5/6				Van Dam et al. 2006
Paşalar	6				
Simorre-Rajégats		10 Monlezun Limestone			De Bruijn et al. 1992
Kleinhadersdorf	6				Ginsburg 1971
Çandır	6				De Bruijn et al. 1992
Çandır			C5ACn / C5Abn	14.1 / 13.5	De Bruijn et al. 1992
			C5Cn.1r / C5Cn.2r	16.5 / 16.3	2 best fits - Krijgsman 2003
		same lithostratigraphic level			alternative fits - Krijgsman 2003
Arroyo del Val I-VI		as Manchones I			Daams et al. 1977
Manchones I	6	G2		13.25	Daams et al. 1999
Paracuellos 3	6	G2		13.4-12.8	Hernández-Bailarín & Peláez-Campomanes 2017
			C5Ar.1n/2n	12.8	Montes et al. 2006

Can Admiral	6			Agustí et al. 1984; De Bruijn et al. 1992
Sarıçay		later Çandır -Faunengruppe		Becker-Platen et al. 1975
Simorre-le Seignou	7+8	12 Astarac Limestone		Ginsburg 1971; De Bruijn et al. 1992
Villefranche d'Astarac		12 Astarac Limestone		Ginsburg 1971
Steinheim	7+8			De Bruijn et al. 1992
La Grive	7+8			De Bruijn et al. 1992
Anwil	7+8	Anwil	13.8-13.2	Kálin & Kempf 2009
Kleineisenbach	7+8			De Bruijn et al. 1992
San Quirze	7+8			De Bruijn et al. 1992
Castell de Barberà	8			Mein 1977; Agustí et al. 1984
	9			De Bruijn et al. 1992
Wissberg	8			
Le Fousseret	8	13 Fousseret Molasse		Ginsburg 1971
Mira	8			Van der Made 1989
El Buste	8			
St. Gaudens-Valentine	8 / 7+8		14	Ginsburg 1971; Mein 1975a; De Bruijn et al. 1992
Fonte do Pinheiro	9			
Rudabánya	9			De Bruijn et al. 1992
Can Ponsic I	9 upper	<i>Cricetulodon</i> zone		Agustí et al. 1984
Can Llobateres	9 upper	<i>Cricetulodon</i> zone		Agustí et al. 1984

Suppl.-Tab. 5

The measurements (in mm) of the lectotype of *Conohyus simorreensis* (PAL2011.0.84.1 and PAL2011.0.84.3) and other specimens of the same species from Villefranche d'Astarac.

				DAP	DTa	DTp	DTpp	Ta
		d	M ₂	21.0	15,2	15,5		1,4
		d	M ₁	18.4	13.6	14.0		0.7
MHNT	PAL2011.0.84.1	d	P ₄	17.9	13.0	15.0		
		d	P ₃	21.9	11.7	14.6		
		d	P ₂	>17.6	7.0	8.0		
		s	M ₃	28.1	16.3	14.5	11.9	2.1
MHNT	PAL2011.0.84.2	s	M ₂	20.4	15.4	15.5		1.6
		s	M ₁	19.4	13.3	14.1		0.9
		s	P ₄	18.3	13.0	14.9		
MHNT	PAL2011.0.84.3	s	M ₃	29.0	17.0	14.1	11.9	1.9
		s	P ₄	18.7	12.3	14.7		
MHNT	PAL2012.0.197	s	P ₃	22.6	10.8	14.4		
		s	P ₂	19.1	6.7	7.7		
MHNT	PAL2012.0.195	d	M ₁	20,5	13,6	--		
MNHN	VAS16	s	M ₃	26.9	16.2	13.7	9.7	2.0
MNHN	Cast	s	P ₃	22.4	11.3	14.5		
		s	P ₂	19.1	6.6	7.5		
MNHN	Cast	d	P ₃	>17.1	12.5	17.7		
		d	P ₂	19.1	6.7	7.8		
		d	M ₃	≈23.5	--	16.1	10.6	
MHNT	PAL2012.0.194	d	M ₂	19.1	18.9	--		
		d	P ₄	13.9		17.9		
MHNT	PAL2012.0.198	d	M ₂	19.9	17.6	18.8		
		d	P ₄	13.7		18.8		
MHNT	PAL2012.0.196	d	P ₃	>17.6	12.5	18.1		
		d	P ₂	19.0	6.7	7.8		
MHNT	PAL2012.0.197	d	D ₄	15.5	12.9	13.0		