

# The morphology of the upper molar roots does not provide evidence that *Palaeochoerus typus* belongs to the Suidae - relevance for the origin of the Suidae and the classification of the Suoidea

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## Abstract

The Suoidea are one of the main groups of ungulates and are unique in the way they are adapted to obtain subterranean food resources. They consist of the Suidae (pigs), Tayassuidae (peccaries) and a number of primitive species, most of which have been grouped under the names “Old World peccaries” or Palaeochoeridae. Recently it was argued that the family Suidae originated with *Palaeochoerus typus* in the Oligocene in Europe and that the name Palaeochoeridae cannot be used for “Old World peccaries”. Scrutiny of morphological features on which this is based shows that none supports the classification of *P. typus* in the Suidae. Particular attention is paid to the important character of lingual roots of the upper molars in *P. typus*, which were interpreted as being separate on the basis of a cast showing parts of the roots, but which are clearly seen to be fused in the original specimen. The view that the Suidae originated in Asia and dispersed into Europe at the beginning of the Miocene remains valid. Palaeochoeridae remains a valid name for a group of primitive Suoidea.

## Keywords

Palaeochoeridae, “Old World peccaries”, Suoidea, Biogeography.

## 1. INTRODUCTION

The question where the Suidae originated is subject to the content of the family. With time the delimitation of the Suidae became clearer. For a time it was the predominant view, that *Hyotherium* is the oldest pig known and that at the beginning of the Miocene it dispersed into Europe, presumably from Asia (Ginsburg, 1974; Van der Made, 1990, 1994, 2010; Hünemann, 1999). *Siamochoerus* and *Eocenchoerus* from the Eocene of Thailand and China have been presented as Suidae (Ducrocq *et al.*, 1998; Liu, 2001, 2003) but their affinities have been contested (Orliac *et al.*, 2010a). More recently, it has been suggested Suidae evolved from Doliochoeridae within Europe (Pickford, 2016, 2018) and that, based on the separate lingual roots of the upper molars, *Palaeochoerus typus* was the first suid. For over a century, the condition of the lingual roots of the upper molars has played in suoid classification. Figure 1 gives the taxa mentioned in the text and their classification according to different recent authors.

Originally Suidae included a large variety of primitive Artiodactyla. Stehlin (1899-1900, pp. 6, 469-470) was critical with Linnean systematics and used terms like “Suiden” and “Palaeochoeren” in an informal way. His “Suiden” is wider than Suoidea, but does not include all Suiformes. He noted that “Suiden” of the Eocene and Early Oligocene had upper molars with the lingual roots convergent and fused and that from the Late Oligocene onward, there were species which had them separate. The latter group are what we now call Suidae, but it should be noted that he also used Oligocene and Miocene in a different sense than we use it today. Stehlin noted that in the Earliest Miocene a third type occurred with divergent roots, connected with a thin lamella, which he compared to the skin between the fingers of a webbed foot (“Schwimmhaut zwischen zwei Fingern”). The lamella consists of dentine. Stehlin was not sure whether the maxilla from Saint Gérard-le-Puy, type specimen of *Palaeochoerus typus* Pomel, 1847, had separate or fused roots. He supposed them to be separate, despite describing another tooth from the same locality, which

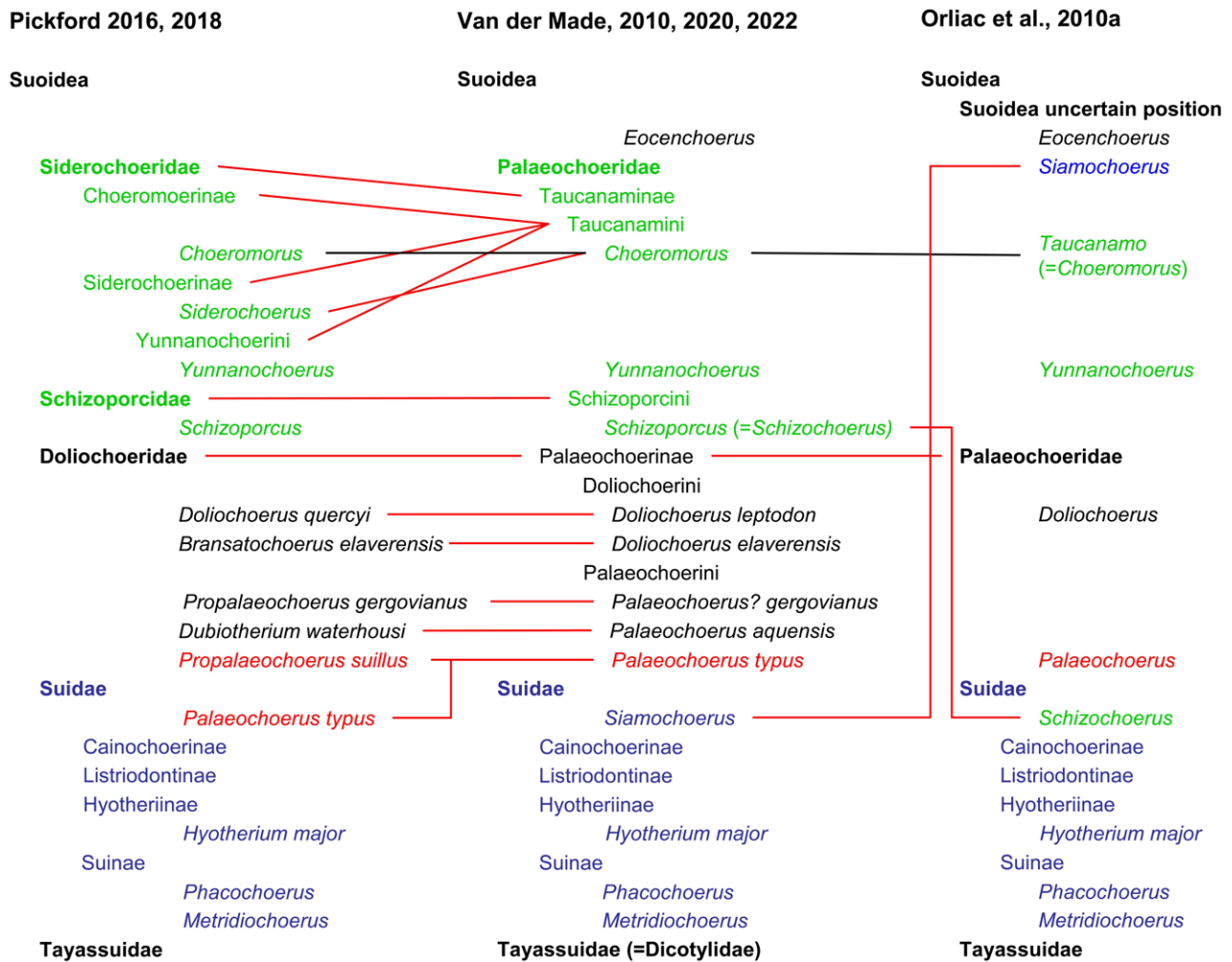


Fig. 1: The taxa mentioned in the text and their classification according to Orliac, Pickford and Van der Made. Based mainly on Orliac *et al.* (2010a), Van der Made (2010, 2020) and Pickford (2016, 2018). Orliac *et al.* (2010a) used Palaeochoeridae in their figure 4, but not in their table 1.

has them fused. In a broad sense, these three types of roots are now known to characterize the main groups of Suoidea.

Matthew (1924) named the Palaeochoerinae for the Oligocene Suoidea, while the more recent ones were placed in the Suinae and Dicotylinae and probably intended to place them all in the Suidae (seventh line from the bottom of p. 176), but erroneously put “Dicotylidae” (= Tayassuidae) (heading of the section). This recalls Stehlin’s (1899-1900) division and is an example of horizontal classification in the sense of Simpson (1945), based on general grade of evolution, rather than descent. Pearson (1927) studied the otic region of the skulls of the Suoidea and recognized two basic morphologies: of what we now call the Suidae and of the American peccaries, but she noted that the latter type is also found in the Old World. Simpson (1945) placed the latter in the Doliochoerinae, Tayassuidae. Much later, the informal names “Old World peccaries” or “Old World Tayassuidae” became in use.

Ginsburg (1974) revised the Doliochoerinae and included also *Palaeochoerus typus* and “*Doliochoerus quercyi aquensis*” in this subfamily within the Tayassuidae. Hellmund (1991) followed Ginsburg’s classification, but wrote in a footnote that an X-ray study showed the lingual roots in the upper molars of *Palaeochoerus typus* to be separate. However, he did not figure the X-ray photograph.

Much later, the Old World peccaries were considered to be a distinct family of the Suoidea and the name Palaeochoeridae Matthew, 1924 was applied to them (Van der Made, 1996). Six features were considered to be typical of this family, including the fused lingual roots of the upper molars. All known Suidae have separate lingual roots of the upper molars (Fig. 2.3), while the Palaeochoerini have divergent roots connected by a lamella (Fig. 2.1e) and other Palaeochoeridae (Doliochoerini and Taucanamini) have convergent fused roots (Fig. 2.2). Over twenty 20 European species and several more Asian ones were placed in seven to ten

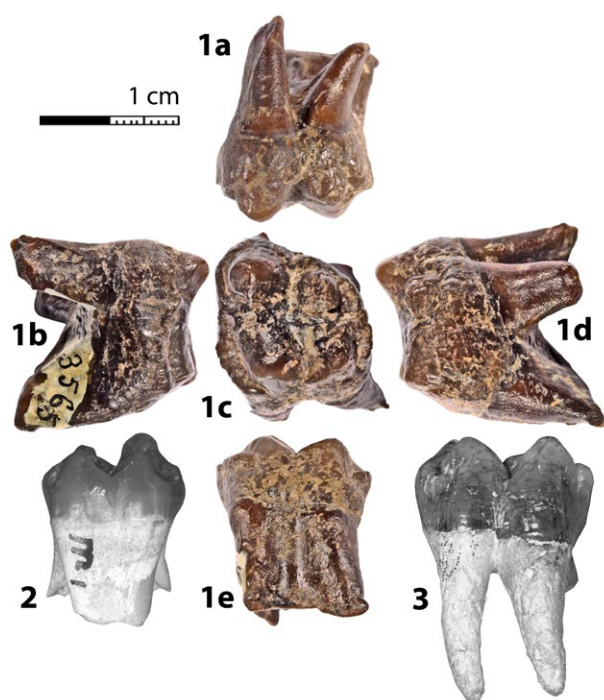


Fig. 2: 1) *Palaeochoerus typus* from Saint Gérard-le-Puy, MNHN SG3536 left M<sup>3</sup>: a) buccal, b) anterior, c) occlusal, d) posterior, and e) lingual views. 2) *Propalaeochoerus* sp. from Tomerdingen, SMNS 45020g right M<sup>1</sup>: lingual view. 3) *Hyotherium meissneri* from Hessler (FISF no number left M<sup>2</sup>: lingual view. In the buccal view 1a, the fused lingual roots are seen between the labial roots. In the lingual views 1 and 3, parts of the buccal roots are seen behind the lingual roots.

genera (e.g. Van der Made, 1997, 2010, 2020, 2022; Pickford, 2011, 2012).

Several cladograms or phylogenies were published, which included Old World peccaries (simplified versions in Fig. 3). In Liu's (2003) cladogram, including four genera, they would be paraphyletic. It was not specified which species and samples were studied. In the cladogram by Orliac *et al.* (2010a) *Palaeochoerus* + *Doliochoerus* formed a clade called Palaeochoeridae, but their relationship with other Old World peccaries and Suidae was not resolved (Fig. 3). Thus, this does not support a monophyletic Palaeochoeridae, including the other Old World peccaries, but does not contradict it either. In Pickford's (2016, fig. 198) cladogram, one species after the other of Old World peccaries and then Suidae branch off, most of the nodes being supported by a single feature. Up to *Dubiotherium* all are placed in a paraphyletic Doliochoeridae, and the rest, starting with *Palaeochoerus typus*, are placed in the Suidae. The decision to include *P. typus* in the Suidae and not *Dubiotherium* or *Doliochoerus* was completely subjective. Equally subjective was the decision to

not include *P. typus* in the "Doliochoeridae" and apply the name Palaeochoeridae to this group. The separate lingual roots in the upper molars were supposed to be a synapomorphy uniting *P. typus* to the Suidae, but was based on Hellmund's (1991) foot note.

In attempt to document the separate lingual roots in *P. typus*, Pickford (2018) described a cast of the upper molars of this species from Gondailly, which shows part of lingual roots, and stated again that the roots are separate. Based on this feature, Pickford (2018) proposed *P. typus* to be the first member of the Suidae, that the origin of this family is in Europe and not in Asia as generally believed. However, the fused condition of the lingual roots can unequivocally be observed in the original specimen from Gondailly and another specimen from St. Gérard-le-Puy, type locality of *P. typus*.

Given the importance that has been given to this feature and its implications, it is important that this error should be corrected. Otherwise, this error may compromise future research and lead to a sub-optimal use of funding.

## 2. MATERIAL

François Escuillié allowed me to study an upper tooth row, consisting of P<sup>3</sup> to M<sup>3</sup>, and the right and left mandibles, each with P<sub>4</sub> to M<sub>3</sub>, of *Palaeochoerus typus* from Gondailly. This was on 9-9-1992 in Lyon. He also gave me casts of these specimens. The casts are possibly of the same negatives as the casts described by Pickford (2018). I do not know where the originals are now. Specimens figured, studied or discussed are kept in the Muséum National d'Histoire Naturelle in Paris (SG3536), Staatliches Museum für Naturkunde in Stuttgart (45020g), Forschungsinstitut Senckenberg, Frankfurt (not numbered specimen from Hessler), Museum Guimet, Lyon (StG683) and the Faculté des Sciences of the Université Claude Bernard, Lyon (213863). The cast of the specimen from Gondailly figured here is kept in the Museo Nacional de Ciencias Naturales in Madrid under number MNCN-150.500.

## 3. DESCRIPTION OF THE LINGUAL ROOTS OF THE UPPER MOLARS OF PALAEOCHOERUS TYPUS

Figure 4 shows the original and cast of the upper tooth row from Gondailly. There must have been some air bubbles at the tips of the molar cusps when the cast was made; this is not wear. As Pickford (2018) noted it seems that the M<sup>2</sup> and M<sup>3</sup> changed positions. The lingual roots of the M<sup>1</sup> are hidden in the maxilla. The cast shows only about half of the lingual roots of the M<sup>2-3</sup>. Between them there is a depression, but it cannot be seen whether the bottom of this depression is a lamella, sediment or plasticine.

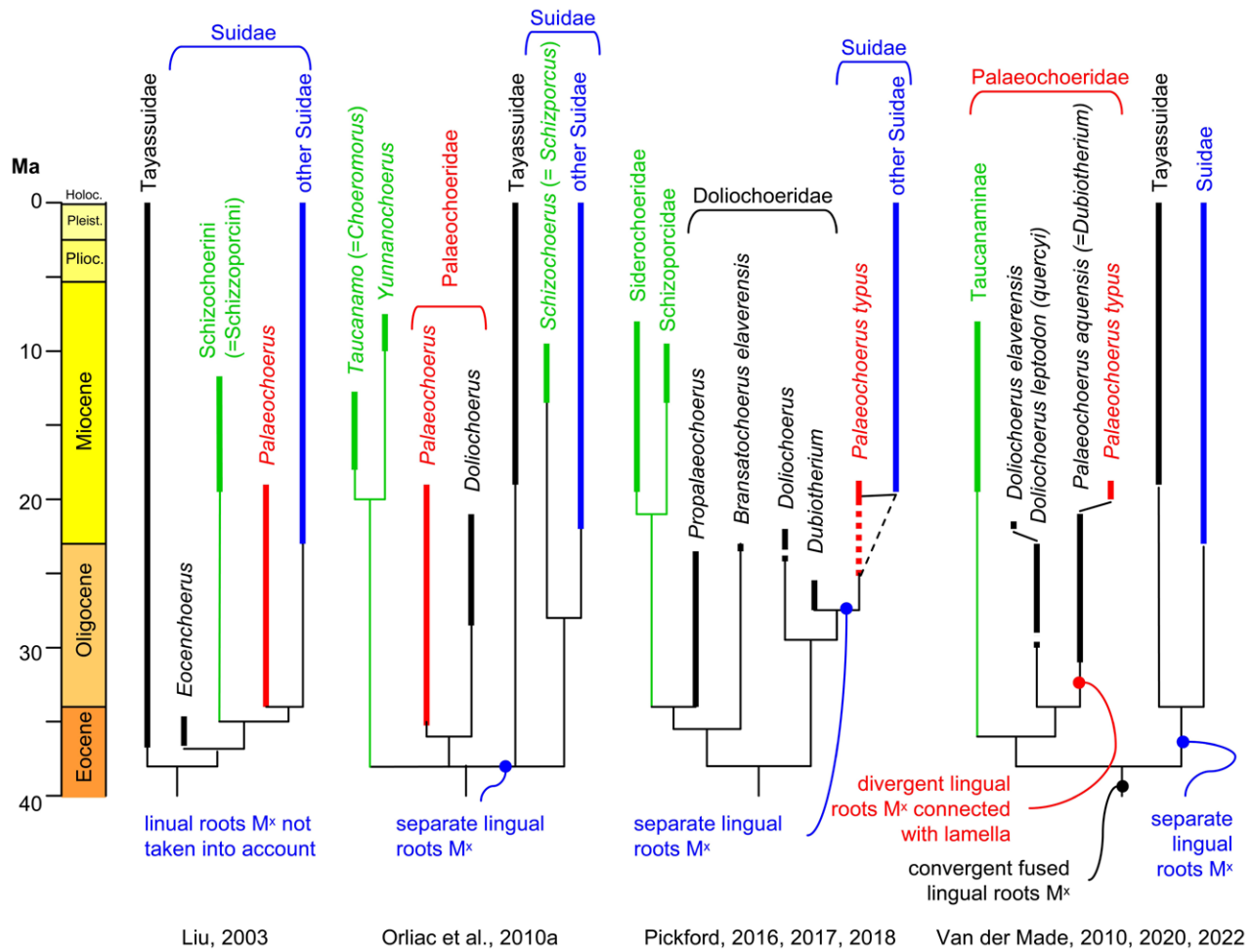


Fig. 3: Simplified phylogenies after different authors.

The original tooth row from Gondailly (Fig. 4.2), as studied by me, has the M<sup>2</sup> and M<sup>3</sup> changed as in the cast. The lingual roots of the M<sup>2-3</sup> can well be seen. In lingual view it can be observed that they are divergent, but connected. This is not sediment or plasticine, what we see. The plasticine is visible as a white material and there is no sediment adhering to the fossil. It is also not cementum; what we see is dentine. In occlusal view, a clear depression between the roots can be seen; it is moderate in the M<sup>3</sup> and very deep in the M<sup>2</sup>. The roots are connected by a thin lamella and are of the type compared by Stehlin (1899-1900) to a webbed foot.

Figure 2.1 shows an M<sup>3</sup> from Saint Gérard-le-Puy. It is the same specimen as discussed and figured by Stehlin (1899-1900, pp. 40-41, pl. 2 fig. 15), who noted already that the lingual roots are fused, but did not figure them. Here it is clearly visible that the roots are divergent but connected with a dentine lamella (Fig. 2.1e). They are not connected by cementum. There is a depression between the roots and in occlusal view (Fig. 4.2b) it can be seen that the depression is deep. This is common in the molars

with lingual roots that are connected by a thin dentine lamella.

It should be noted that in these specimens and others with divergent but connected roots, these roots are connected by a lamina. This is dentine, not cementum as stated by Pickford (2018, p. 528). In broken specimens the bone can be well seen and even the pulp cavities may extend some way into the lamina, becoming narrower and ending in a sharp point.

Figures 1/2 and 1/3 show the convergent fused roots, which occur in the Doliochoerini and Taucanaminae, and the divergent separate roots, which occur in the Suidae.

#### 4. DISCUSSION

##### 4.1. The correct data

Stehlin (1899-1900) and other authors after him gave importance to the roots of the molars in the Suidae. The fused lingual roots of the upper molars were among

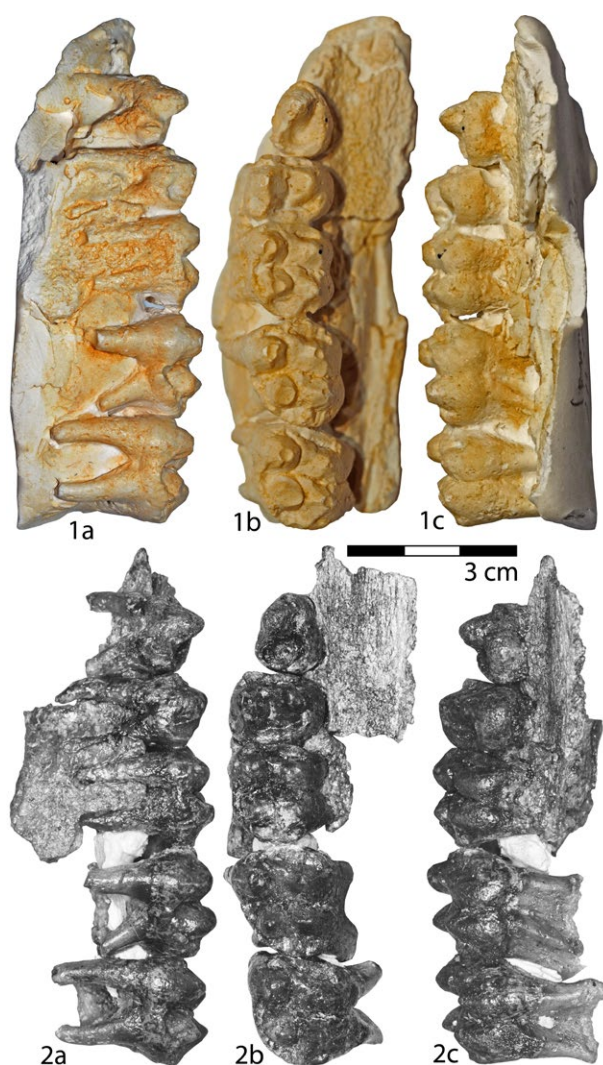


Fig. 4: *Palaeochoerus typus* from Gondailly, left P<sup>3</sup> - M<sup>3</sup>: 1) cast (MNCN-150.500), 2) original; a) buccal, b) occlusal, and c) lingual views.

the features used to typify the Palaeochoeridae, which includes the “Old World peccaries” (Van der Made, 1996). However, Pickford (2018) used the supposedly separate lingual roots in *Palaeochoerus typus* and some other features to support its inclusion in the Suidae. Let us first look at the data, then at the implications.

1) Pickford (2018) mentioned three specimens with separate lingual roots of the upper molars in *Palaeochoerus typus*, while others were not mentioned:

1A) On p. 526, *P. typus* from Gondailly is stated to have separate roots on the basis of a cast, which shows very little of the roots, while the original clearly contradicts this and shows the roots are connected by a lamella (Fig. 4.2c).

1B) On p. 527, Hellmund (1991) is cited for separate roots in this maxilla MGL StG683, who wrote that and X-ray study showed the roots to be separate, but

did not figure the X-ray photograph. A thin lamella may not have been detected. It might be possible to check the condition of the roots with a CT scan.

1C) On p. 525 it is said that the M<sup>1</sup> of another specimen from Saint-Gérard-le-Puy (FSL213863) has separate roots. It is also stated that a M<sup>3</sup> of *Propalaeochoerus suillus* was carefully selected to be similar and was mounted with plaster in the position of the M<sup>2</sup> and that removal of the plaster showed the roots of this tooth (p. 521). Page 523, fig. 3 shows that the right M<sup>1</sup> is in the maxilla, while the left M<sup>1</sup> has part of the maxilla on its lingual side, but that further lingually there is some plaster. No photographs of the roots of these molars were given. Since *Propalaeochoerus suillus* was considered to be a doliochoerid, it has to be assumed that the roots of the left M<sup>3</sup> were fused. Given the published information, it looks more like that the left M<sup>3</sup> belongs to the same individual as the rest and that it is the only tooth of which the roots are known and they are fused.

1D) Because of fused lingual molar roots and canine morphology, Pickford (2017, p. 31) recognized *Propalaeochoerus suillus* as different from *Palaeochoerus typus* and placed it in a different genus in the Doliochoeridae. Pomel (1854) named *Palaeochoerus suillus* on the basis of a skull from Langy, one of the localities of similar age near St. Gérard-le-Puy, which is a skull in the Natural History Museum in London with collection number 34961<sup>a</sup> (Filhol, 1880, p. 15; Lydekker, 1885). There is a hole in the palate next to the roots of the right M<sup>2</sup> and what can be seen of its roots is consistent with Pickford’s statement that the roots are fused. Filhol (1880), Lydekker (1885) and Hellmund (1992) considered the species a synonym of *P. typus* and I agree with them. This specimen is the male of *Palaeochoerus typus* and has a canine with a morphology that was one of the features used by Van der Made (1996) to characterize the Palaeochoeridae and a well developed *crista alveolaris*. Specimens MGL StG683 and FSL 213863 are females, have small alveolae for the canine and no *crista alveolaris*.

1E) An isolated tooth from Saint-Gérard-le-Puy has fused roots (Fig. 2.1e). Stehlin (1899-1900, pl. 2, fig. 15) considered it to belong to *Palaeochoerus typus* and this opinion seems to be correct.

In addition to the lingual roots of the molars (1), Pickford (2018) used four other features to place *P. typus* in the Suidae. Two were said to be described by Pickford (2016). These features are: 2) the anterior position of the zygomatic root, 3) the distance between the I<sup>3</sup> and the upper canine, and 4) the orientation of the canines, 5) rooting adaptations. The features are discussed below

2) *Palaeochoerus typus* was placed in the Suidae, because the posterior margin of the root of the zygomatic arc is at the level of the M<sup>2</sup>, while in *Doliochoerus* it is further back. However in the

holotype of *P. suillus*, included by Pickford in the Doliochoeridae, it is at the same place as in the type of *P. typus*. In all or nearly all other Suoidea, from which skulls are known, the root of the zygomatic arc is situated at the level of the M<sup>3</sup> or further back and in Suidae like the living wart hog *Phacochoerus* and its ancestor *Metridiochoerus* it is situated very far behind the M<sup>3</sup>. *Palaeochoerus typus* is in this respect the most primitive genus of the Suoidea of which skulls are known and, contrary to what Pickford (2018) pretends, the anterior position of the posterior margin of the zygomatic arc is not a valid argument to place this species in the Suidae.

- 3) *Palaeochoerus typus* was placed in the Suidae, because of the short space between the canine and I<sup>3</sup> in the two specimens from Saint Gérand-le-Puy (MGL StG 683 and FSL 213863). No measurements were given and no objective comparisons were made. This argument is a little surprising, since this space tends to be longer in the Suidae than in the Palaeochoeridae from which this feature is known. A short space is a primitive feature within the Suoidea and thus does not favor the inclusion of *Palaeochoerus* in the Suidae. It also should be noted that females tend to have this diastema smaller, because their lower canine is smaller than that of the males (Van der Made, 1991).
- 4) *Palaeochoerus typus* was placed in the Suidae, because the orientation of its canines was supposed to be less vertical, allowing for more lateral movement while chewing, while the Old World peccaries have lower molars with below each lobe fused lingual and labial roots and therefore narrow mandibles, indicating that chewing is more restricted to vertical movement, which is also seen in the shape of the glenoid. This is a complex way of reasoning and each part has to be correct for the argument to be valid. To start with, the two female specimens described as *P. typus* have no canines, but empty alveoli which do not allow to know precisely the orientation of the part of the canines outside the alveoli. Pickford placed the male specimen with a canine (the type of *P. suillus*) in the Doliochoeridae, implying that the canine orientation in this specimen should be more vertical. Nothing has been done to quantify or visualize the supposed difference. That fused roots in the lower molars mean less lateral movement while chewing, could be true, but has to be documented and proven. The chewing movements could be demonstrated with the directions of wear striae. In any case, Pickford (2018) did not figure, describe or mention any lower molar of *P. typus* with separate roots below each lobe. So this remains purely hypothetical. The glenoid may provide information on chewing movements, but the only specimen which preserves this part is the holotype of *P. suillus* and is placed in the family that Pickford supposes

to have mainly vertical chewing movements. In all cases, proof is lacking because the relevant parts are not preserved, or because the fossils are assigned to a different species, supposedly with the opposite character state.

- 5) *Palaeochoerus typus* was placed in the Suidae, because it was supposed to be a good roter.
- 5A) An indication for rooting was taken to be its strong narial musculature as indicated by the areas of origin of the narial musculature. For instance, a deep preorbital fossa is indicative of a strong *levator rostri* muscle (Ewer, 1958). It was stated that none of the doliochoerid specimens examined showed indications of strong narial musculature. It was not indicated which skulls these are, but we may infer that the type skull of *P. suillus* was considered to have no indications of strong rhinarial musculature. Most of the species of Old World peccaries are not known by skulls that preserve the area of the origin of the narial musculature, while skulls of nearly all species of *Choeromorus* are known that preserve this area, but always it is badly crushed or broken and the feature cannot be studied. However, the type skull of *Doliochoerus quercyi* has the fossas where these muscles originate better visible than in the skull of *P. typus* that was figured to show these features. The living *Phacochoerus* has very shallow fossas for the rhinarial musculature. Nevertheless, during the dry periods it relies on rooting and is capable to break the hard dry soil to do so. So shallow fossas for the rhinarial musculature may be indicative of a different rooting adaptation, not necessarily the absence of rooting.
- 5B) Another rooting adaptation was the supposed keen sense of smell, as indicated by the elongate snout. In fact, a long snout in itself is a rooting adaptation. In Suidae, the snout is long because: the palate moved to the front, there are long diastemata, and the premaxilla is elongate with elongated incisors, notably the I<sup>2</sup>. An anterior position of the palate relative to brain case contributes to a longer snout. If the snout is long, the teeth are situated more anteriorly relative to the posterior margin of the root of the zygomatic arc. However, Pickford (2018) placed *P. typus* in the Suidae precisely because this is not the case (feature 2). Long diastemata contribute to a long snout. The only diastema of *P. typus* is between the canine and third incisor and the species was placed in the Suidae, because it is so short (feature 3). Also the premaxilla was not elongated. The snout of *P. typus* was short, not long.

To summarize, of the five features used in support of placing *Palaeochoerus typus* in the Suidae: all these features are contradicted if *P. suillus* is a synonym of *P. typus*, as believed by most palaeontologists who studied its type specimen, features 1, 2 and 3 are contradicted by other data, features 1, 3, 4 and 5 are not or not sufficiently

documented, and data are lacking on features 4 and 5. These characters do not support the inclusion of *P. typus* in the Suidae.

#### 4.2. Taxonomic implications

Whether *Palaeochoerus typus* belongs to the Suidae or to the “Old World peccaries” has implications for the classification of the Suoidea. Pickford (2018, p. 527) stated that “The main problem with basing a family name on *Palaeochoerus* is that “it can be argued that the genus belongs to the Suidae”. This statement ignores the historic element of taxonomic classification and the principle of priority (ICZN, 1999): the valid name of a taxon is the oldest available name applied to it. After names have been given, there is no free choice of what would be the most appropriate one. In this particular case, we should not choose a different name, but resolve the question on the affinities of *Palaeochoerus* in the most objective possible way.

Pickford (2016, fig. 198) published a cladogram, which shows the Doliochoeridae as paraphyletic, one genus branching off after the other, while the next branches are *Palaeochoerus* and then *Hyotherium* and other true Suidae. In this cladogram *Palaeochoerus* was included in the Suidae, while it equally well could be included in the paraphyletic Doliochoeridae. This is entirely subjective. Parting from the basis that *Palaeochoerus typus* belongs to the Suidae, the name Palaeochoeridae would not be an appropriate name for the Old World peccaries and another name is needed. In various places Pickford (2017) cited cladograms by Liu (2003) and Orliac *et al.* (2010a) to argue for splitting the Palaeochoeridae up in more families and raised Doliochoeridae and Schizoporcidae to family rank and introduced the new names Siderochoeridae, Siderochoerinae and Choeromoerinae. However, several of these names should not be used because of the rules of the International Code of Zoological Nomenclature (ICZN, 1999).

Pickford (2017) named the Siderochoeridae and classified *Yunnanochoerus* as Siderochoeridae subfamily indet. However, Pickford (2011) named the tribe Yunnanochoerini. A family group name is valid at any family group level with the original author and year of publication (ICZN, 1999, article 36.1). This implies that Yunnanochoeridae Pickford, 2011 has priority over Siderochoeridae Pickford, 2017.

The name *Taucanamo* Simpson, 1945 was in use for a long time, but Pickford (2012) pointed out that this is a junior synonym of *Choeromorus*. *Taucanamo* is the type genus of the Taucanamini Van der Made, 1997. However, family group names based on a genus name that is a junior synonym remain valid (ICZN, 1999, article 40.1). As a consequence, Taucanamidae would be a senior synonym of Siderochoeridae Pickford, 2017, if these suids would be considered to be a different family

from the Palaeochoeridae, and Taucanamini is a senior synonym of the Choeromorinae Pickford, 2017.

Simpson’s (1945, pp. 17, 23) observations on classification remain valid: it should not be subject to “the caprices of shifting theory and individual opinion” and that “specialists on particular groups almost always have a tendency to exaggerate ranks within their specialty” and give “family rank to what should be called genera, generic rank to species, etc.”. It should be noted that Pickford’s Siderochoeridae correspond to Taucanamini and Doliochoeridae to Palaeochoerinae (within Palaeochoeridae) as applied by me (Van der Made, 2010) and that the inclusion of *Palaeochoerus* in the Suidae is totally subjective. The Palaeochoeridae could be considered as horizontal classification (in the sense of Simpson, 1945) or a stem group, and the cladograms by Orliac *et al.* (2010a, b) can be interpreted in this way. However, there are shared derived features indicating that at least a large part of this group is monophyletic (Van der Made, 2020). Discussion on the “Old World peccaries” will continue, but should be based on observed and documented character states, not on inferred characters.

#### 4.3. Biogeographic implications

A biogeographic implication of a supposed lineage starting with a European species of the Doliochoeridae evolving during the Late Oligocene into *Palaeochoerus typus* and later into *Hyotherium* (Pickford, 2018) would be that the Suidae originated in Europe and did not arrive there by dispersal from Asia.

This is not an entirely new hypothesis. Pomel (1847) named *Palaeochoerus typus* and *P. major* and placed both in the same genus, while the latter now is placed in *Hyotherium* (Ginsburg, 1974; Van der Made, 1990, 1994, 2010; Hellmund, 1991; Pickford, 2016). For a long time, the name *Palaeochoerus* has been applied to older species of *Hyotherium* (see review by Van der Made, 1994) and for over a century many considered *Hyotherium* to be a descendant of *Palaeochoerus* (the citations by Hellmund, 1992, p. 37 are not exhaustive). Possibly the most recent and explicit is the hypothesis by Ginsburg (1980, p. 869), that *Hyotherium* might be a descendant of *Palaeochoerus gergovianus* (Doliochoerinae) and that the suids from Gibel and Grépiac (France) were intermediate between them. This is similar to Pickford’s (2018) proposal and should have been discussed.

By contrast, it has been suggested that the earliest Suidae have ages that far predate *Palaeochoerus typus*. Ducrocq *et al.* (1998) and Liu (2001, 2003) assigned material from the Eocene of Thailand and China to the Suidae, but the affinities of these species have been contested (Orliac *et al.*, 2010a). Orliac *et al.* (2010b) assigned some specimens from the middle of the Oligocene of Pakistan to *Hyotherium* sp. These papers should have been discussed, or mentioned at least, by Pickford (2018).

If the Suidae are considered to have originated with *Palaeochoerus typus* and *Hyotherium*, the latter would be a very primitive suid. This is a traditional view, but is not in accordance with morphology. A discussion on this is beyond the scope of this paper, but the cladogram by Orliac *et al.* (2010a) shows the Listriodontinae and Cainochoerinae in a much more basal position than the Hyotheriinae and this coincides with my data and interpretation.

An additional difficulty with Pickford's hypothesis is that *Hyotherium* first appeared in MN1 (Ginsburg, 1980; Van der Made, 1990, 1994, 2010; Hellmund, 1991) and that *P. typus* is mainly known from St. Gérard-le-Puy, Langy and Gondailly, early Miocene localities (MN2), but that for *P. typus* being ancestral to *Hyotherium*, it should be older. Pickford (2018) assigned part of the fossils from Gunzenheim (Late Oligocene, MP28) to *P. typus*. This material was previously assigned to *P. typus* (Dehm, 1935) or to *Propalaeochoerus gergovianus* (Hellmund, 1992). The redescription of this material is very short and for a secure identification of the specimens as *P. typus* not only similarities with *P. typus* should be indicated, but also differences with *P. gergovianus*. This has not been done.

Apart from these omissions and difficulties, the data do not support placing *P. typus* in the Suidae and thus also not that the Suidae originated with this species and in Europe. Moreover, other data suggest that *P. typus* does not belong to the Suidae. The upper canine of the male *P. typus* (= *P. suillus*) is flattened and has anterior and posterior enamel bands (Pickford, 2017), while the male Suidae have wider canines with a wide lingual third enamel band (Van der Made, 1996). It is likely that both types evolved independently from canines without enamel bands extending from the crown towards the base of the tooth. This feature and others suggest that *P. typus* and the Palaeochoeridae have nothing to do with the origin of the Suidae: the divergent roots connected with a lamella in the Palaeochoerini and the divergent separate roots in the Suidae are a parallelism. The most likely scenario is that the Palaeochoeridae split off from other Suoidea in Asia and dispersed several times into Europe, at the beginning of the Oligocene (Palaeochoerinae), and during the Miocene (*Choeromorus* and *Schizoporcus*, Taucanaminae), while the other branch of Suoidea gave rise to the Suidae, which dispersed numerous times into Europe starting with *Hyotherium* at the beginning of the Miocene, and the Tayassuidae, which dispersed to America.

#### 4. CONCLUSIONS

The revision of several morphological characters of *Palaeochoerus typus*, used by Pickford (2018) to place this genus in the Suidae, leads to the following conclusions:

- These features do not support including *P. typus* in the Suidae.
- As a consequence, the Suidae did not originate with *Palaeochoerus typus* from the Doliochoerini in Europe.
- These features do not support excluding *P. typus* from the Palaeochoeridae and do not inhibit the use of the name Palaeochoeridae for the Old World peccaries.
- The hypothesis is proposed here that the Palaeochoeridae originated not later than the earliest Oligocene, while the Suidae and Tayassuidae evolved separately from the Palaeochoeridae.

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