

New data on Early Miocene *Palaeochoerus typus* and the origins of the family Suidae (Mammalia)

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Abstract

Fossils from St-Gérard-le-Puy, France, include the remains of a primitive suid which indicates that the family Suidae probably evolved in southwestern Europe. In the long history of study of suoids from Europe, specimens of suids and doliochoerids have frequently been mixed together. The various hypodigms of *Palaeochoerus typus* are no exception – a maxilla of a suid and a mandible of a doliochoerid were attributed to it by several authors, a mixture which influenced many interpretations of the fossils. One reconstructed specimen described herein is a chimera of specimens from two different families. Such admixture has caused a huge amount of confusion. This contribution examines the suoids from the type locality of *Palaeochoerus typus* (St-Gérard-le-Puy) in an attempt to throw light on its taxonomy and systematics. It is demonstrated that it is a suid, and that conclusions that it was an Old World Peccary were based on some characters gleaned from doliochoerid fossils mis-identified as *Palaeochoerus*. The available fossil evidence indicates that the family Suidae probably originated in Europe rather than being an immigrant from Asia, but it does not completely resolve the issues of precisely when the transition occurred (between MP 28 and MN 1-2) and from which precursor (*Doliochoerus*, *Bransatochoerus*, *Propalaeochoerus*, *Dubiotherium* or another form).

Keywords

Palaeochoerus, Suidae, Doliochoeridae, Miocene, Europe, Evolution.

1. INTRODUCTION

For a century and a half there has been a great deal of debate about the taxonomic and systematic affinities of the genus *Palaeochoerus* Pomel, 1847. There are several reasons for this, the main one being that the various hypodigms of successive authors comprised mixed samples containing remains of two or more genera belonging to two families of suoids. Such admixture of specimens seems to have resulted from the desire by fossil collectors to possess imposing or impressive fossils, there being several examples of reconstructions of specimens combining remains of different taxa.

As originally conceived, the genus *Palaeochoerus* was based on specimens of two species of different dimensions, *Palaeochoerus typus* Pomel, 1847, and *Palaeochoerus major* Pomel, 1847, the latter of which was eventually transferred to a different genus, *Hyootherium* Von Meyer, 1834. The original diagnosis of the genus thus comprised features from two taxa. To complicate matters, *Palaeochoerus typus* was subsequently diagnosed on the basis of a maxilla and mandible from St-Gérard-le-Puy, the latter of which, for a long time, was thought to belong to the same individual as the maxilla (Filhol, 1881;

Viret, 1929). However, the mandible does not belong to the same individual as the maxilla – it is appreciably smaller, having the dimensions appropriate for the small doliochoerid from the same locality, *Propalaeochoerus suillus* (Pomel, 1853). Thus the emended diagnosis of *P. typus* combined characters from two taxa from two different families of suoids (Pickford, 2016b).

Re-examination of a snout of *P. typus* from St-Gérard-le-Puy, and of an upper cheek tooth row from Gondailly (3 km north-north-east of St-Gérard) (Fig. 1) throws light on the affinities of *P. typus*, revealing that it is a suid rather than a peccary-like suoid. Some teeth from Gunzenheim, Germany are included. The aim of this paper is to describe and interpret the fossils from St-Gérard-le-Puy, Gondailly and Gunzenheim, with a view to clarifying the taxonomy and systematics of the genus. It is shown that *P. typus* had the facial morphology of a rooster, and is thus more closely related to Suidae than to Doliochoeridae or any other family of Suoidea.

The new data indicate that the Suidae may well have originated within Europe from a doliochoerid precursor, rather than evolving elsewhere (Asia is usually cited) and then dispersing to Europe as fully derived Suidae.

2. LOCATION OF ST-GÉRAND-LE-PUY

St-Gérand-le-Puy is in the Département de l'Allier, in the Auvergne Region, north-north-east of Clermont-Ferrand and north-west of Lyon (Fig. 1). There are several other fossiliferous localities in the vicinity (Gondailly, Montaigu-le-Blin, Langy, Servilly, Treteau) and it is not impossible that there has been some misattribution of fossils to localities, especially in collections made before 1900. Most of the fossiliferous deposits in this region of the Puys comprise indurated marl and/or travertine/tufa rich in land and freshwater snails.

Other suoids from, and age of, St-Gérand-le-Puy

There are four species of suoids described from St-Gérand-le-Puy. The most commonly preserved in collections is *Hyotherium major* Pomel, 1847. The other three taxa are rare, and comprise the primitive suid *P. typus*, and two doliochoerids, *Propalaeochoerus suillus* and *Lorancayus hypsorhizus* Pickford & Morales, 1998 (Pickford, 2011). As an assemblage, these taxa indicate correlation to MN 2 in the European Land Mammal Zonation of which Montaigu-le-Blin is the type locality (niveau répère).

3. MATERIAL AND METHODS

Original fossils and casts preserved in the Faculty of Science, University of Lyon (now Laboratoire de Géologie, University Claude Bernard - Lyon 1), and the Centre de Conservation et d'Etude des Collections du Musée des Confluences, Lyon (CCECL) were studied.

Other material from St-Gérand-le-Puy is preserved in the Natural History Museum, London (NHMUK), the Muséum national d'Histoire naturelle, Paris (MNHN), the SNSB-BSPG (Munich) and the Naturhistorisches Museum Basel (NHMB). The focus of this article is a snout curated at the FSL and a cast of an upper tooth row in the same institution (the current location of the original fossil is not known: it is possibly housed in the Natural History Museum, Toulouse).

For details of dental nomenclature, figure preparation and measuring techniques, refer to Pickford (2016a).

Abbreviations

FSL: Faculty of Science, University Claude Bernard - Lyon 1.

MNHN: Muséum National d'Histoire Naturelle, Paris

MN: Mammal Neogene

MP: Mammal Palaeogene

For teeth the following abbreviations are employed (see Pickford, 2016 for dental nomenclature)

C/c: upper/lower canine

D/d: upper/lower deciduous cheek teeth

I/i: upper/lower incisor

M/m: upper/lower molars

4. A NOTE ON FOSSIL CHIMERA

Palaeontologists usually endeavour to avoid mixing their fossil samples. Nevertheless, there have been many instances in which fossils attributed to a single taxon belong in reality to two or more species. It is rarer for fossils attributed to a single individual to be interpreted as

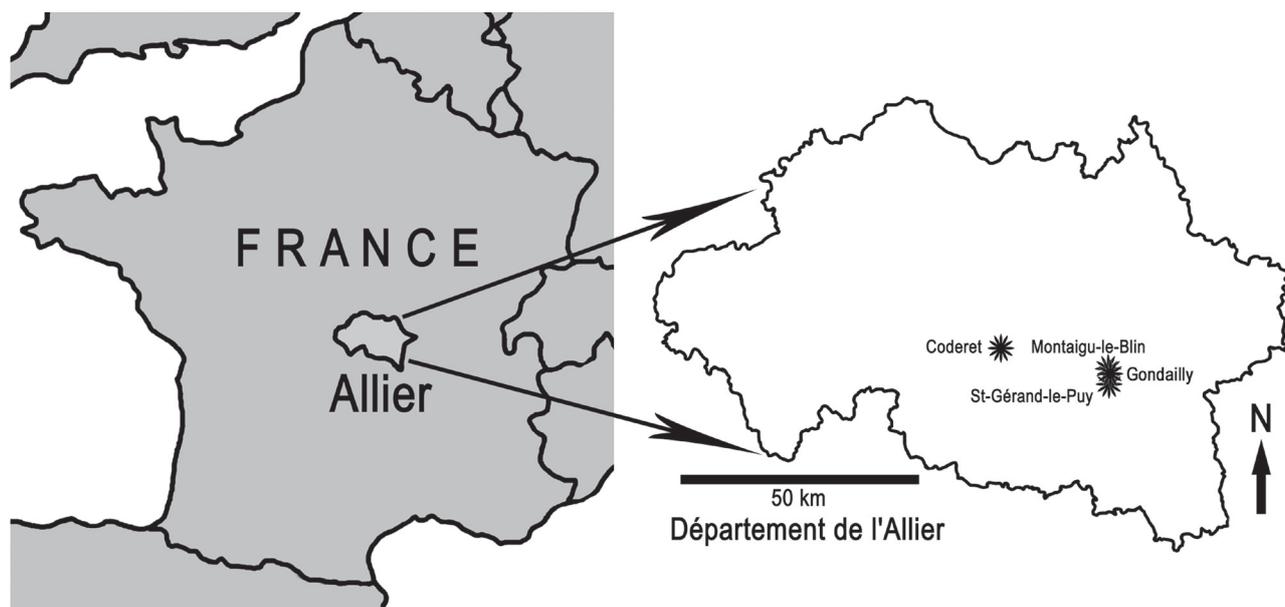


Fig. 1: Location of the late Oligocene locality of Coderet (type locality of MP 30) and Early Miocene localities of St-Gérand-le-Puy (MN 2) and Montaigu-le-Blin (type locality of MN 2) between which is Gondailly.

belonging to two taxa, yet there are some cases where this happened. Among the Rhinocerotidae, a skull published as *Aceratherium grandincisivum* by Kaup (1832, 1834) was reconstructed from parts of two different taxa, an acerathere and a brachypothere (Giaourtsakis & Heissig, 2004). Later, a composite skull was reconstructed from pieces of several individuals, casts made and sent to several international establishments where it was used as a reference by many authors, none of whom realized that it contained parts of at least two genera of rhinocerotids. Over the years this caused a vast amount of confusion, affecting nearly one thousand scientific papers. Another of Kaup's taxa, *Cynochoerus zieglerei*, Kaup, 1859, was a chimera, the type specimen being a mixture of an amphicyonid canine and a suoid upper molar, but this taxon resulted in less confusion because the admixture was so evident (Stehlin, 1899-1900; Pickford, 2016b).

The snout of *P. typus*, which is the subject of this study, has been reconstructed from two fragments, one of which belongs to a different taxon (Viret, 1929). Not only is the tooth in the position of the right M2 an upper third molar as shown by the root orientation (the disto-buccal root slants to the rear), but also, it belongs to a doliochoerid, probably *Propalaeochoerus suillus*. For a long time, the type specimen of *P. typus* (a maxilla) was said to belong to the same individual as a mandible (Viret, 1929) yet the lower jaw is too small to belong to the same individual as the maxilla, the length of the cheek tooth row, p1-m3, in the mandible being appreciably less than that of the length of P1-M2 in the maxilla. Close examination of the lower jaw reveals it does not represent the same taxon (it belongs to *Pr. suillus*), yet mandibular characters observed in this mandible were eventually included in the diagnosis of the species and the genus by Viret (1929). Needless to say, such admixtures cause immense confusion, and can be extremely difficult to detect.

The snout of *Palaeochoerus* studied herein was expertly reconstructed with Plaster-of-Paris which, on the left side had been delicately sculpted to show details of the palatine groove and the palatine foramen, and then painted to resemble the rest of the specimen, such that at first site few people would realise that parts of it were false. The doliochoerid tooth in the position of the left M2 was carefully selected to have a similar degree of wear to that of the genuine tooth on the opposite side of the jaw, and the roots were hidden under plaster. Had it not been for the presence of minor differences in the positions of the anterior accessory cusplet and the depth of the crown, the chimera would not have been suspected. As it happens, the minor difference in the position of the anterior accessory cusplet of the teeth on the two sides of the snout led to the realisation that the tooth in the position of the left M2 was in reality an M3 of another taxon. Removal of plaster from the roots on the buccal side confirmed that the tooth is a third molar and must have been added to the snout in error. A neurocranium with the same catalogue number as the snout, probably does not belong to the same individual.

The cast of the upper tooth row from Gondailly described below, consists of a maxilla fragment containing three teeth (P3-M1) accompanied by two isolated teeth (M2 and M3) set in plasticine behind. These two isolated molars probably do belong to the same individual, but in the cast they have been transposed. Needless to point out that measurements taken on this cast without realising that the M2 and M3 are in the wrong positions, would lead to imprecision in any metric analyses that flowed from the measurements.

5. SYSTEMATIC DESCRIPTION

Family Suidae Gray, 1821

Genus *Palaeochoerus* Pomel, 1847

Original diagnosis: «Tetradactyle ... dont les molaires, au nombre de sept au maxillaire, se composent de trois mâchelières à quatre gros tubercules coniques simples, les intérieurs étant un peu dilatés transversalement et ayant une lame qui se porte devant le tubercule opposé. Cette lame est double dans le postérieur et enveloppe complètement le cône externe postérieur; aucune partie ne présente les tubercules et petits mamelons des dents analogues dans les cochons; les avant-molaires se compliquent de plus en plus de la première biradiculée, et probablement comprimée et tranchante, à la quatrième à trois tubercules, deux externes conjoints, l'interne en forme de crête en croissant et limitant en arrière une petite fosse. Ces dents se trouvent contiguës entre elles et avec la canine, dont l'alvéole est ovale presque elliptique, et assez bien développée. Les alvéoles des trois incisives sont presque disposées sur le prolongement du bord alvéolaire des molaires, ce qui indique un museau très étroit; les dents étaient sans doute obliques en avant, et la première paire était aussi grosse, dans sa partie radiculaire du moins, que la canine; la troisième était la plus petite» (from Pomel, 1847) (NB: This diagnosis combines characters from the genus *Hyotherium* (those of the lower dentition) and *Palaeochoerus* (those based on the maxilla).

Emended diagnosis (1): «Même formule dentaire que *Sus* 3.1.4.3/3.1.4.3. La dentition forme encore une série presque continue où les canines sont développées en défenses encore peu puissantes. Les molaires supérieures ont des racines internes séparées, ce qui est un caractère d'évolution chez les Suidés, et distingue ce genre du g. *Propalaeochoerus* (sic) Stehlin (1899-1900) des Phosphorites. *Palaeochoerus* (sic) diffère du genre miocène *Hyotherium* par ses prémolaires plus courtes, moins comprimées latéralement, par ses molaires en général moins compliquées de verrucosités, et surtout (Stehlin, 1899-1900) par la canine inférieure du mâle, offrant une tendance à l'hypsodontie, mais non franchement hypsodonte comme chez cette forme plus récente. La canine supérieure, dont l'évolution est bien

plus lente est encore pourvue d'une couronne courte. Le crâne se distingue de celui du Sanglier par sa forme plus courte, que compense le plus grand volume de sa boîte crânienne» (from Viret, 1929).

Emended diagnosis (2): „In den Dimensionen (L/B) nahezu den stärksten Individuen von *Propalaeochoerus gergovianus* (Croizet, 1846) bzw. Einem durchschnittlichen Exemplar von *Hyotherium meissneri* (v. Meyer, 1829) entsprechend; *Propalaeochoerus paronae* Dal Piaz, 1930, und *Propalaeochoerus pusillus* Ginsburg, 1974, deutlich an Grösse übertreffend. Innenwurzeln an den Molaren sup. gesspalten, übrige Bezahnung morphologisch derjenigen von *Propalaeochoerus gergovianus* bzw. *Propalaeochoerus pusillus*“ (from Hellmund, 1992).

Type species: *Palaeochoerus typus* Pomel, 1847

Species *Palaeochoerus typus* Pomel, 1847

Lectotype: CCECL STG 683+684, left maxilla containing P3-M2 and alveoli of I1-I3, C1 and P1-P2. The

lectotype of *P. typus* was described recently by Pickford (2016) but is illustrated again for ease of reference (Fig. 2).

Original diagnosis: «Plus petite (que *Palaeochoerus major*) dont la même dent (P4) n'a qu'un tubercule externe à peine bifurqué» (from Pomel, 1847).

Emended diagnosis (1): «Espèce de petite taille, aux caractères assez archaïques, chez qui les prémolaires sont serrés en une rangée continue. En général, p4 montre en avant du tubercule principal un denticule bien net, haut placé. M3 n'est pas encore pourvue d'un talon différencié» (from Viret, 1929). NB: the character of the p4 is from a doliochoerid mandible belonging to *Propalaeochoerus suillus*.

Emended diagnosis (2): Lingual roots in upper molars separated from each other, presence of fossae on the face of the maxilla for the snout musculature (dilatator naris lateralis, depressor rostri, levator rostri), palatine foramen enters maxilla at the front of M2, with a small posterior branch entering the palate in line with the middle of M2; upper incisor alveolar process bends ventrally such that the incisor battery is appreciably lower than the occlusal

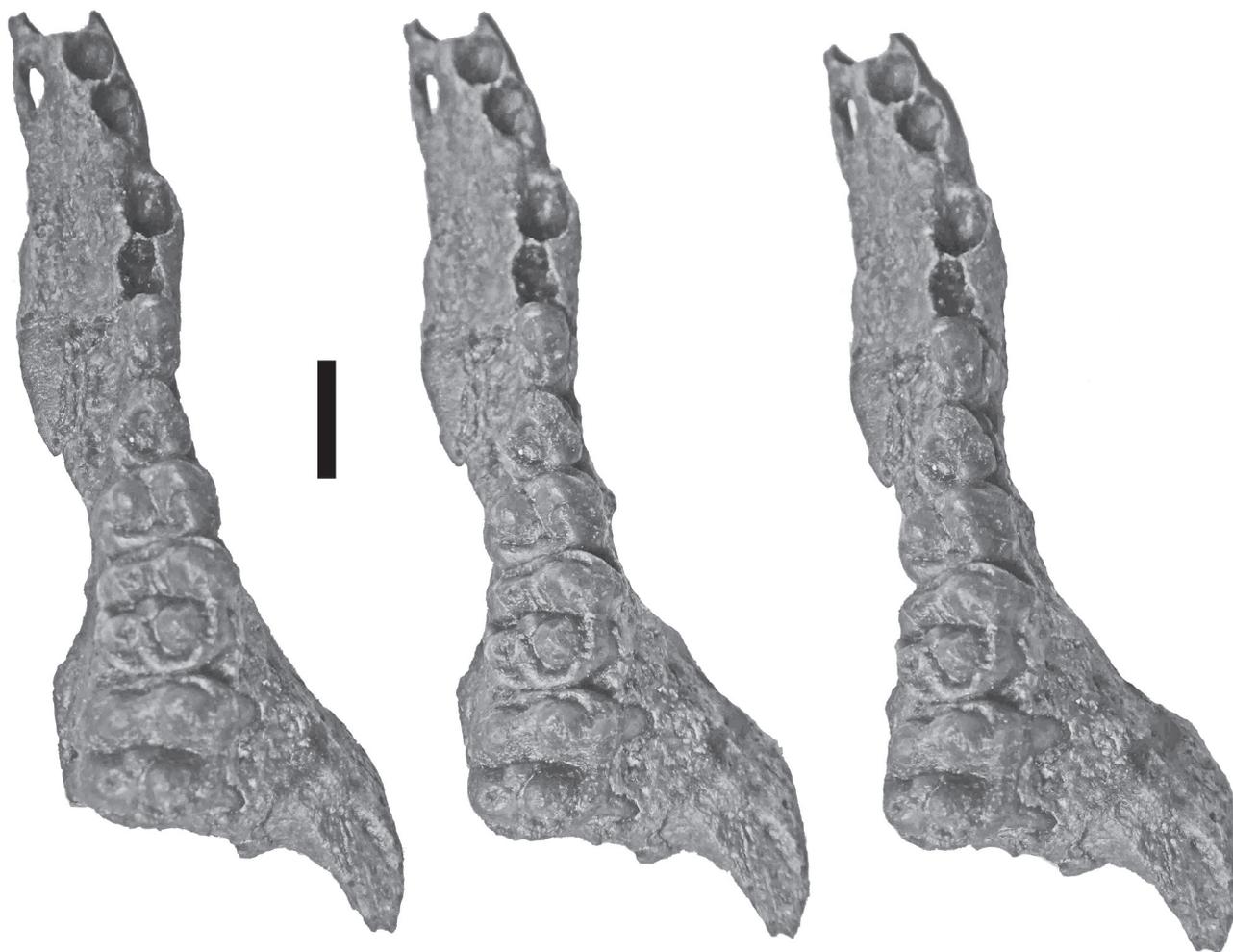


Fig. 2: CCECL 683+684, lectotype maxilla of *Palaeochoerus typus* from St-Gérard-le-Puy, France (MN 2), stereo occlusal views (scale: 10 mm).

surface of the molar row; maxillary recess at the level of the distal loph of M2; facial crest above the M1; posterior nares open immediately behind the M3s; orbit above the molar row; lacrymal foramen above M1 (this paper).

Type locality and Age: St-Gérard-le-Puy, France, MN 2 (Early Miocene).

Description of St-Gérard-le-Puy material: FSL 213863, a suoid snout from St-Gérard-le-Puy, was described by Viret (1929, pl. 18, fig. 1) who illustrated

only the right side in occlusal view. The specimen is important because it can be compared with the lectotype of *P. typus*, which it closely resembles it, but being substantially more complete it yields a great deal of additional information concerning the splanchnocranium of the species which throws light on its taxonomic affinities within the Suoidea.

The fossil under study (Fig. 3) comprises the snout of a juvenile in which the P3, P4 and M3 are still in their

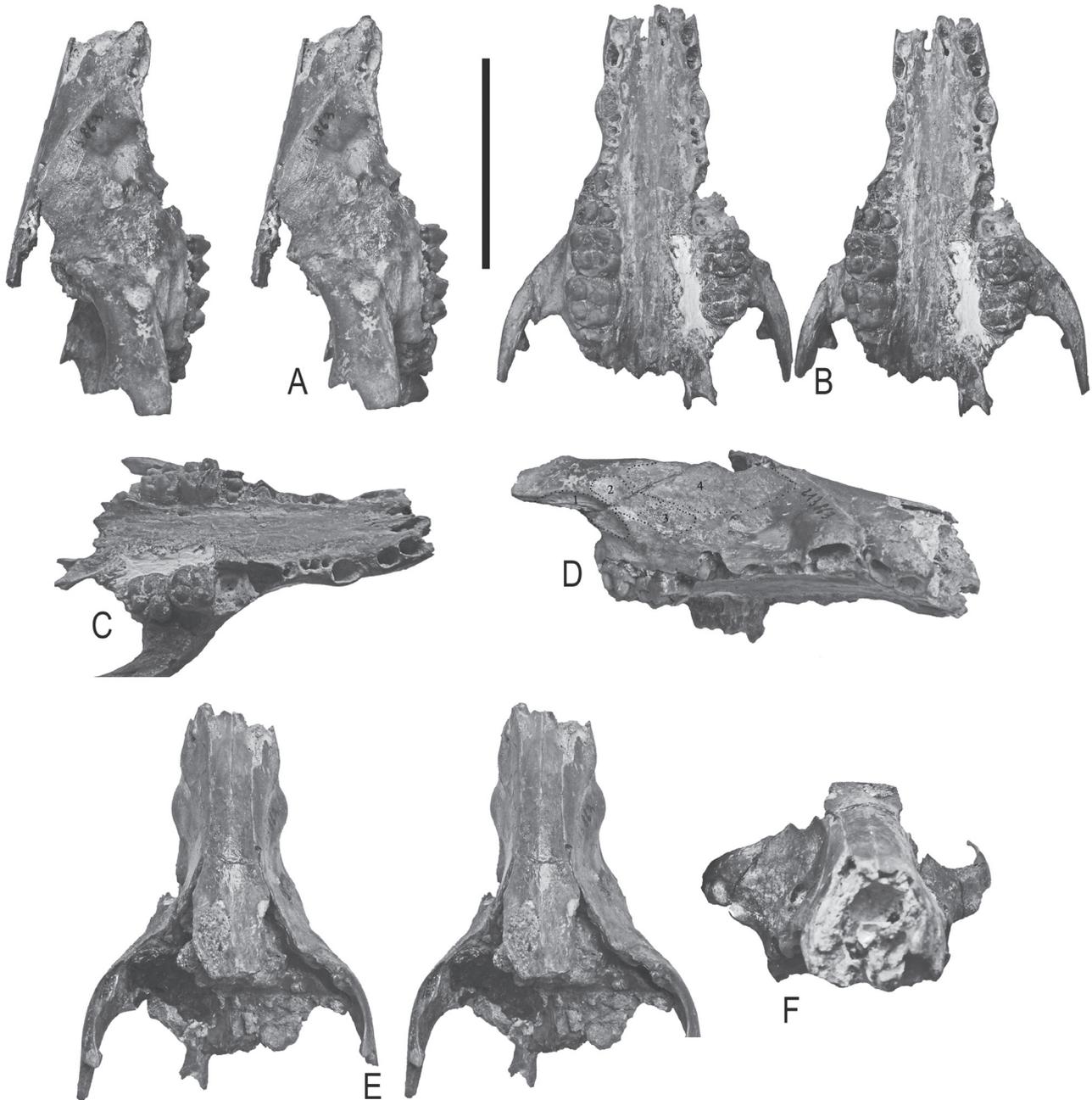


Fig. 3: FSL 213863, splanchnocranium of *Palaeochoerus typus* from St-Gérard-le-Puy, France. A) stereo right lateral view, B) stereo palatal view (note that the tooth in the position of the left M2 is an M3 of *Propalaeochoerus suillus* that was erroneously added to the specimen), C) oblique palatal view to highlight the palatine groove and the palatine foramina, D) oblique view of right side to highlight the lateral position of the canine alveolus and the small pre-canine concavity, E) stereo dorsal view, F) anterior view (scale: 5 cm).

crypts, the M1 is lightly worn, and the M2 almost fully erupted, but with no wear facets. The tooth in the position of the left M2 is not only an M3, but is also from a different individual from another family of suoids, the morphology of the crown indicating that it belongs to *Propalaeochoerus suillus*. In particular, the position of the anterior accessory cusplet between the protocone and paracone, is like that in the holotype of the latter species from St-Gérard-le-Puy (Pickford, 2016b). In *P. typus*, the anterior accessory cusplet is mesial to the protocone and paracone. The presence of a tiny talonal bulge at the lingual end of the distal cingulum indicates that this tooth is probably an M3, an observation borne out by the orientation of the disto-buccal root which slants distally. This tooth is set in Plaster-of-Paris and resin and was evidently added to the snout in error.

In lateral view, the facial crest is positioned above the middle of M1. It separates a lower fossa on the ventral surface of the zygomatic process of the maxilla, which is the surface of attachment of the masseter muscle, from a shallow but mesio-distally long fossa developed on the lateral surface of the zygomatic process extending anteriorly as far as the level of the P4. This fossa represents the origins of the dilatator naris lateralis and depressor rostri muscles (Ewer, 1958, 1970). Above it there is an expansive but shallow depression beneath the anterior margin of the orbit which extends anteriorly as far as the level of the infra-orbital foramen and upwards to a low, but sharp crest just beneath the contact between the maxilla and the nasal bones. This large but shallow fossa is the origin of the levator rostri musculature. The presence of these fossae indicate that *P. typus* was probably an active rooter, using a mobile nasal disc for foraging in soil and leaf litter. None of the doliochoerid fossils examined possesses indications of a rooting function in their facial architecture, and from this it is concluded that *Palaeochoerus* is to be classified as a suid rather than in a different family along with *Doliochoerus* Filhol, 1882, or *Choeromorus* Gervais, 1850.

The infra-orbital foramen is large and is accompanied below by a small accessory foramen. The foramen lies above the front of P4 and the depression in front of it extends a short way anteriorly, ending above the front of the P3. The conformation of this fossa in *Palaeochoerus* is completely different from the elongated deep facial fossa that occurs in the peccary-like suoid, *Choeromorus* (Pickford, 2012).

The lacrymal foramen is at the leading edge of the orbit above the M1. The orbit is located above the molar row, and the post-orbital process of the zygomatic arch sweeps upwards at the level of the M3.

The canine jugum forms a low swelling on the side of the maxilla and slopes upwards and backwards towards the point where the premaxilla, maxilla and nasals form a triple junction of sutures. The nasal bones are long and almost flat, extending at least as far back as the leading edge of the orbit where they are broken off.

There is a short gap between the alveoli of the I3 and the canine, which forms a shallow concavity (but not a niche) for acceptance of the lower canine when the jaws are closed.

The alveolar process of the premaxilla bends ventrally such that the incisors are appreciably lower than the occlusal surface of the cheek teeth. There is a large offset between the canine alveolus and that for the I3.

In palatal view, the palatine groove is observed to run from the large incisive foramina backwards close to the lingual margin of the alveolar process of the maxilla, entering the palate at the level of the front of M2. A short accessory extension of the groove continues distally and enters the palate at the level of the mesial loph of the M2. The incisive foramina are elongated, extending from the rear of the alveolus of the I2 anteriorly as far as the middle of the alveolus of the I1.

The two canines are steeply inserted in the jaw, but they are not vertical. Instead they diverge at an angle of about 15° from the sagittal plane. The alveolus of the P1 is inside the line of the canine alveolus, tucked into its disto-lingual corner. The alveoli for the D2-D4 diverge slightly from each other from front to back.

The posterior nares are located slightly beyond the rear of the M3s, and are accompanied by well-developed pterygoid flanges either side. The maxillary recess is positioned in line with the distal loph of the M2. The ventral surface of the zygomatic process of the maxilla shows a roughened fossa which extends from the facial crest where it is broad, backwards as far as the rear of the orbit where it is narrow. This is the masseter scar.

In dorsal view, one observes parts of two shallow grooves in the nasal bones, which fade out anteriorly before reaching the hind extremity of the premaxillae. These grooves would have extended backwards to enter the frontal bones at the supra-orbital foramina.

The snout in front of the infra-orbital foramen is narrow (the palate is 25 mm broad just behind the canine alveoli), broadening posteriorly (72 mm at the post-orbital processes of the zygomatic arch).

In anterior view, the section of the snout is trapezoidal, narrow at the nasals which are almost flat (the nasals are 11 mm broad above the canine alveoli) and the maxilla broadens palatwards (24 mm broad just in front of the canine alveoli).

Dentition: The dental formula is three incisors, one canine, four premolars and three molars. There is a short diastema between the I3 and the upper canine. Otherwise the teeth are close to each other. Measurements are provided in Table 1.

The P3 is partly hidden in its crypt. It has a tall pointed buccal cusp with a sharp post-crista which swells basally to form a low tubercle. The distal cingulum extends lingually to wall off a shallow disto-lingual fovea.

The P4 is also in its crypt. It has a tall pointed buccal cusp (paracone) and a smaller, lower, lingual cusp (protocone). There is an anterior accessory cusplet in the midline of

the tooth blocking the mesial fovea that separates the protocone from the paracone. The post-paracrista ends basally at a low tubercle, which joins the distal cingulum. There is a bulge in the distal cingulum which is linked to the post-protocrista, thereby blocking the rear of the mesial fovea.

The M1 has four main cusps accompanied by anterior, median and posterior accessory cusplets in the midline of the crown. The anterior and median accessory cusplets are joined to the lingual cusps (protocone, hypocone) by their pre-cristae and the posterior accessory cusplet is joined to the hypocone via the post-hypocrista. The mesial cingulum is broad and lies in front of the anterior accessory cusplet. The distal cingulum is strong, and extends along the buccal side of the metacone, fading out on the lateral surface of the paracone. The lingual roots have a deep groove between them, signifying that they are separated, unlike the strongly fused lingual roots of doliochoerid upper molars.

The M2 is similar in morphology to the M1 but is larger. What can be seen of the M3 in its crypt shows that it is like the M2, but has a swollen cingular cusplet lingually forming a small talon in line with the hypocone and protocone.

The tooth in the position of the left M2 in this skull is in fact an M3 of a doliochoerid. This is revealed by the fact that the anterior accessory cusplet is reduced in stature and is posed between the protocone and paracone, not in front of these cusps, the median transverse valley is narrow, the tooth crown is deep and the disto-buccal root slants distally. This tooth is compatible in dimensions and morphology to specimens of *Propalaeochoerus suillus*.

Description of Gondailly material: The deposits at Gondailly (MN 2), 3 km north-north-east of St-Gérard-le-Puy, yielded a lightly worn cheek tooth row of a suid (Fig. 4, Table 1). The P3-M2 are similar in morphology to those in the type specimen of *P. typus*. The Gondailly specimen has the M3, which is missing in the holotype.

Table 1: Measurements (in mm) of the teeth of *Palaeochoerus typus* from St-Gérard-le-Puy and Gondailly. NB: in the snout FSL 213863 the left M3 (marked with a star) is in the position of the M2 and is from a different species of suoid, *Propalaeochoerus suillus*. CCECL StG 683 is the lectotype maxilla of *Palaeochoerus typus* (lt – left, rt – right).

Catalogue N°	Tooth	Length	Breadth
FSL 213863	M1 lt	10.6	10.5
FSL 213863	M1 rt	11.0	11.4
FSL 213863	M2 rt	11.8	12.2
FSL 213863*	M3 lt*	11.0	11.5
FSL 213863	M3 rt	--	12.0
CCECL StG 683	P2 lt	8.7	5.0
CCECL StG 683	P3 lt	9.3	7.7
CCECL StG 683	P4 lt	8.5	11.8
CCECL StG 683	M1 lt	10.8	12.0
CCECL StG 683	M2 lt	11.9	13.1
FSL Coll CL FD	P4 lt	8.0	10.4
FSL Gondailly (cast)	P3 rt	8.5	7.2
FSL Gondailly (cast)	P4 rt	8.6	10.6
FSL Gondailly (cast)	M1 rt	11.0	10.5
FSL Gondailly (cast)	M2 rt	11.5	12.0
FSL Gondailly (cast)	M3 rt	12.3	11.8

The cast of this specimen housed by the FSL reveals that the M2 and M3 were transposed prior to casting. This is shown by the distal slant of the posterior roots in the M3 and the more vertical roots in the M2. The tiny talon in the M3 is slightly to the lingual side of the midline of the crown.

The P3 has a main cusp with blunt pre- and post-crista, a low tubercle at the end of the post-crista, and a well-developed posterior and lingual cingulum forming the rim of a disto-lingual basin. The P4 has a single large

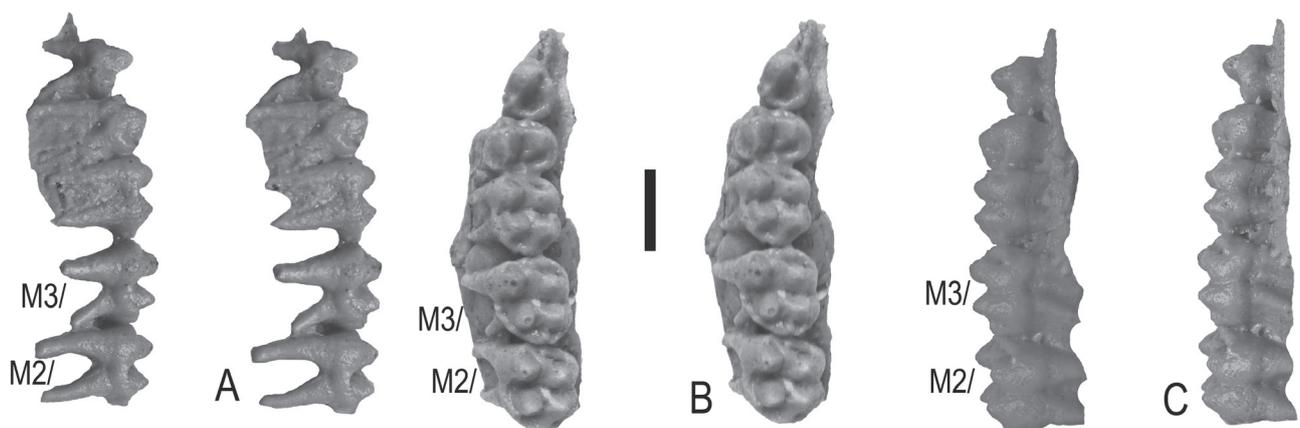


Fig. 4: FSL Gondailly, cast of right upper cheek teeth (P3-M3). A) stereo buccal view, B) stereo occlusal view, C) stereo lingual view (scale: 10 mm). NB: The M2 and M3 were inadvertently transposed in the reconstruction prior to casting.

buccal cusp and a prominent protocone on the lingual side. There are broad mesial and distal cingula. The M1 has four main cusps and in the mid-line there are anterior, median and posterior accessory cusplets. These cusplets are linked to the lingual cusps by the pre- and post-cristae of the protocone and hypocone. There is a distal cingulum that extends along the buccal side of the tooth as far as the paracone where it fades out. The lingual roots are separated from each other. The M2 is similar in morphology to the M1 but is slightly larger. It also has separated lingual roots. The M3 is like the M2 but is slightly narrower than it, and the posterior accessory cusplet is more in line with the protocone and hypocone, thereby forming a tiny talon. The metacone is slightly reduced which makes the distal loph narrower than the mesial one, and which imparts a rounded appearance to the disto-buccal part of the crown. The roots of the M3 are not as tall as those of the M2 and the distal ones slant to the rear.

Description of Gunzenheim (Germany) material: The karst infilling at Gunzenheim (48°46'38"N: 10°46'43"E) yielded a small collection of diminutive suoids comprising 28 teeth, which were attributed to *P. typus* by Dehm (1935) (Table 2). The fossils were redescribed by Mayr (1968) and Hellmund (1992) who identified them as *Pr. gergovianus*. Re-examination of the specimens in the SNSB-BSPG reveal that both taxa are present in the sample (Figs 5-7). The P2 and P3 from the site are like those in the lectotype of *P. typus*, and the specimen from Gondailly, in particular by the presence of a capacious disto-lingual fossa rimmed by the distal cingulum. Indeed, Hellmund (1992) considered that the P2 was a P3 because of this feature, which is better developed in suids than in doliochoerids. The P4 and some upper molars from the site belong to a slightly larger species akin to *Propalaeochoerus gergovianus*. The collection also contains a lower third incisor which is similar to the specimen from Quercy described by Deschaseaux (1959) as *Doliochoerus quercyi*, but which is in fact a specimen of *Pr. gergovianus* (Pickford, 2016b). Finally some isolated lower premolars and molars probably belong to *P. typus*, the premolars in particular having a narrower trigonid part than is usual in *Propalaeochoerus* Stehlin, 1899-1900.

6. DISCUSSION

The Gunzenheim suoids are here interpreted to belong to two taxa, a suid, *P. typus*, and a doliochoerid, *Pr. gergovianus*. The Gunzenheim deposits have traditionally been correlated to MP 27 (de Bonis & Guinot, 1987) or MP 28 (Hellmund, 1992) but, if the identifications of the suoids are correct, they could be somewhat younger, more or less the same age as St-Gérard-le-Puy (MN 1-2) which contains both of these

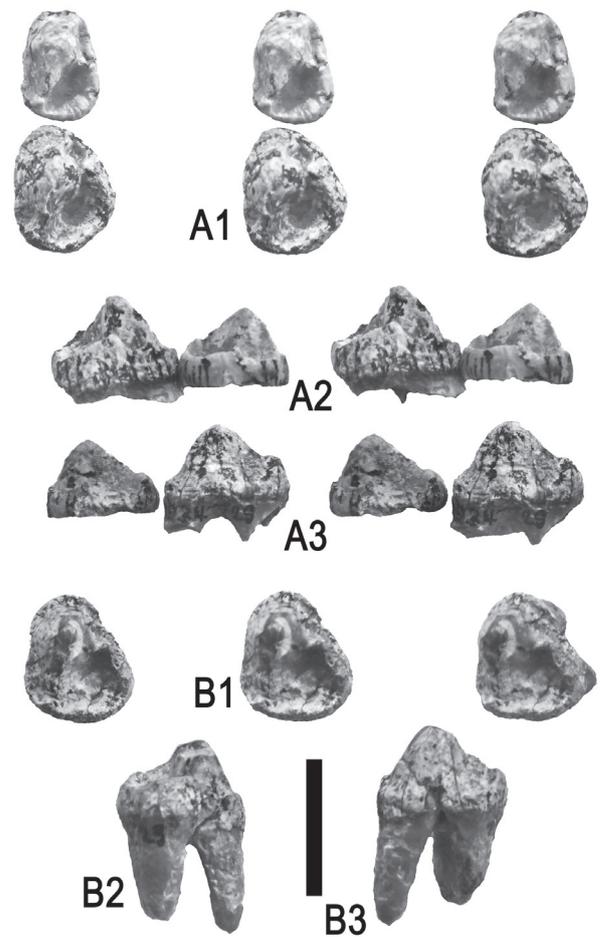


Fig. 5: Upper premolars of *Palaeochoerus typus* from Gunzenheim, Germany. A) SNSB-BSPG 1934 V 29, right P2-P3, (A1 – stereo triplet occlusal view, A2 – stereo lingual view, A3 – stereo buccal view); B) SNSB-BSPG 1934 V 29, right P4 (B1 – stereo triplet occlusal view, B2 – lingual view, B3 – buccal view) (scale: 10 mm).

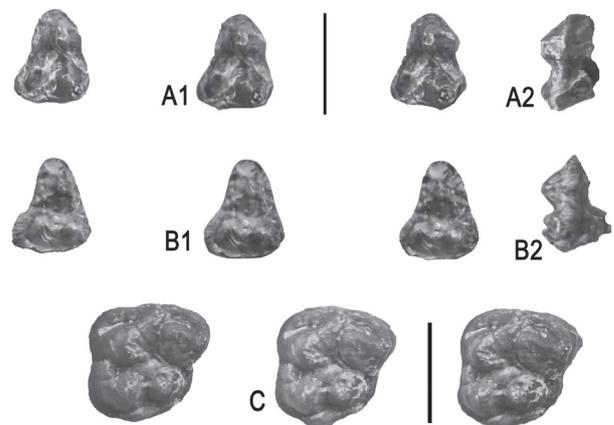


Fig. 6: Upper cheek teeth from Gunzenheim, Germany, attributed to *Palaeochoerus typus*. A-B) SNSB-BSPG 1934 V 31, left D3s, in (1) stereo occlusal and (2) buccal views; C) SNSB-BSPG 1934 V 29, left M3, stereo triplet occlusal view (scales: 10 mm).

Table 2: Measurements (in mm) of suoid teeth from Gunzenheim, Germany. (*P.* = *Palaeochoerus*, *Pr* = *Propalaeochoerus*, BLB – Bucco-lingual breadth, MDL – Mesio-distal length, lt = left, rt = right).

Catalogue	Tooth	MDL	BLB	Taxon	Data source and comments
SNSB-BSPG 1934 V 31	D3 lt	9.8	8.0	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 9.75 x 8
SNSB-BSPG 1934 V 31	D3 lt	9.3	7.2	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 9.2 x 7.2
SNSB-BSPG 1934 V 29	M3 lt	12.0	12.4	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 12.6 x 12.2
SNSB-BSPG 1934 V 29	P2 rt	8.1	5.8	<i>P. typus</i>	own, 2016. Hellmund, 1992 as 8.3 x 6.3, P3
SNSB-BSPG 1934 V 29	P3 rt	9.4	7.8	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 9.5 x 7.8
SNSB-BSPG 1934 V 29	P3 rt	9.6	7.2	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 9.4 x 7.25
SNSB-BSPG 1934 V 32	m2 rt	12.8	9.3	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 12.7 x 9.2
SNSB-BSPG 1934 V 32	m3 rt	18	9.5	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 18.2 x 9.5
SNSB-BSPG 1934 V 33	p4 lt	10.2	6.0	<i>P. typus</i>	Hellmund, 1992
SNSB-BSPG 1934 V 33	p4 lt	10.5	6.0	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 10.5 x 6.1
SNSB-BSPG 1934 V 33	p4 lt	10.5	6.1	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 10.6 x 6
SNSB-BSPG 1934 V 33	p4 rt	9.8	5.9	<i>P. typus</i>	own, 2016; Hellmund, 1992 as 10.5 x 6.2
SNSB-BSPG 1934 V 33	p4 rt	10.4	6.3	<i>P. typus</i>	Hellmund, 1992
SNSB-BSPG 1934 V 34	i1 rt	4.0	5.7	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 34	i3 lt	7.0	4.0	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 30	I1 rt	11.0	7.1	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 30	I1 rt	9.0	6.0	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 30	I1 rt	10.0	6.8	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 30	I1 rt	11.0	7.0	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 33	m1 lt	11.5	7.5	<i>Pr. gergovianus</i>	own, 2016; Hellmund, 1992 as 11.8 x 7.5
SNSB-BSPG 1934 V 33	m1 rt	11.8	8.1	<i>Pr. gergovianus</i>	own, 2016; Hellmund, 1992 as 11.9 x 8.1
SNSB-BSPG 1934 V 27	M1 lt	11.0	11.9	<i>Pr. gergovianus</i>	own, 2016. Hellmund, 1992 as 10.65 x 11.9
SNSB-BSPG 1934 V 27	M2 lt	11.9	13.2	<i>Pr. gergovianus</i>	own, 2016; Hellmund, 1992 as 12.1 x 13.35
SNSB-BSPG 1934 V 27	M3 lt	13.0	12.5	<i>Pr. gergovianus</i>	own, 2016; Hellmund, 1992 as 13.55 x 12.7
SNSB-BSPG 1934 V 29	M2 rt	12.5	13.7	<i>Pr. gergovianus</i>	own, 2016; Hellmund, 1992 as 11.5 x 11.7
SNSB-BSPG 1934 V 29	M3 rt	12.1	13.9	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 33	M1 rt germ	12.0	11.8	<i>Pr. gergovianus</i>	own, 2016
SNSB-BSPG 1934 V 26	P4 rt	9.4	12.3	<i>Pr. gergovianus</i>	own, 2016

taxa. Alternatively the deposits at the site could have accumulated at different times.

Taxonomic and systematic affinities of *Palaeochoerus*

There has been extended debate about the affinities of *Palaeochoerus*, with opposing views that it is either a suid (see review in Pickford, 2016b) or an Old World Peccary (Van der Made, 1998). The admixture of fossils from diverse taxa caused a huge amount of confusion, and logically matured with the proposal to resurrect the family Palaeochoeridae (Matthew, 1924) by Van der Made (1998, 2010) for what were often referred to in the literature as the Old World Tayassuidae (or Old World Peccaries; Pickford, 1993), or Ächten Schweinen (Stehlin, 1902) distinct from the Suidae. Pickford (2016b) showed however, that the lectotype maxilla of *Palaeochoerus typus* possesses several suid-like features and is divergent from those of Old World Peccaries, whereas the mandible long associated with it (Viret,

1929) belongs to *Pr. suillus* which is a member of the latter group, here called the Doliochoeridae.

There are problems with the resurrection of the family name Palaeochoeridae. The first, and least troublesome, is that the family name was erected by Stehlin (1909) (and mentioned by Zdarsky, 1909), fifteen years before Matthew (1924) did the same thing for a radically different suite of genera. The main problem with basing a family name on *Palaeochoerus* is that the lectotype of the type species of the genus possesses a suite of suid-like features, as shown by Viret (1929) and Hellmund (1992) (separated lingual roots in the upper molars) and Pickford (2016b) (several osteological features of the maxilla). The skull described herein is much more complete than the lectotype, but in the parts that can be compared the two specimens are closely similar, not only morphologically, but also metrically. There can be little doubt that FSL 213863 represents *P. typus*.

The snout yields significant evidence that links the genus

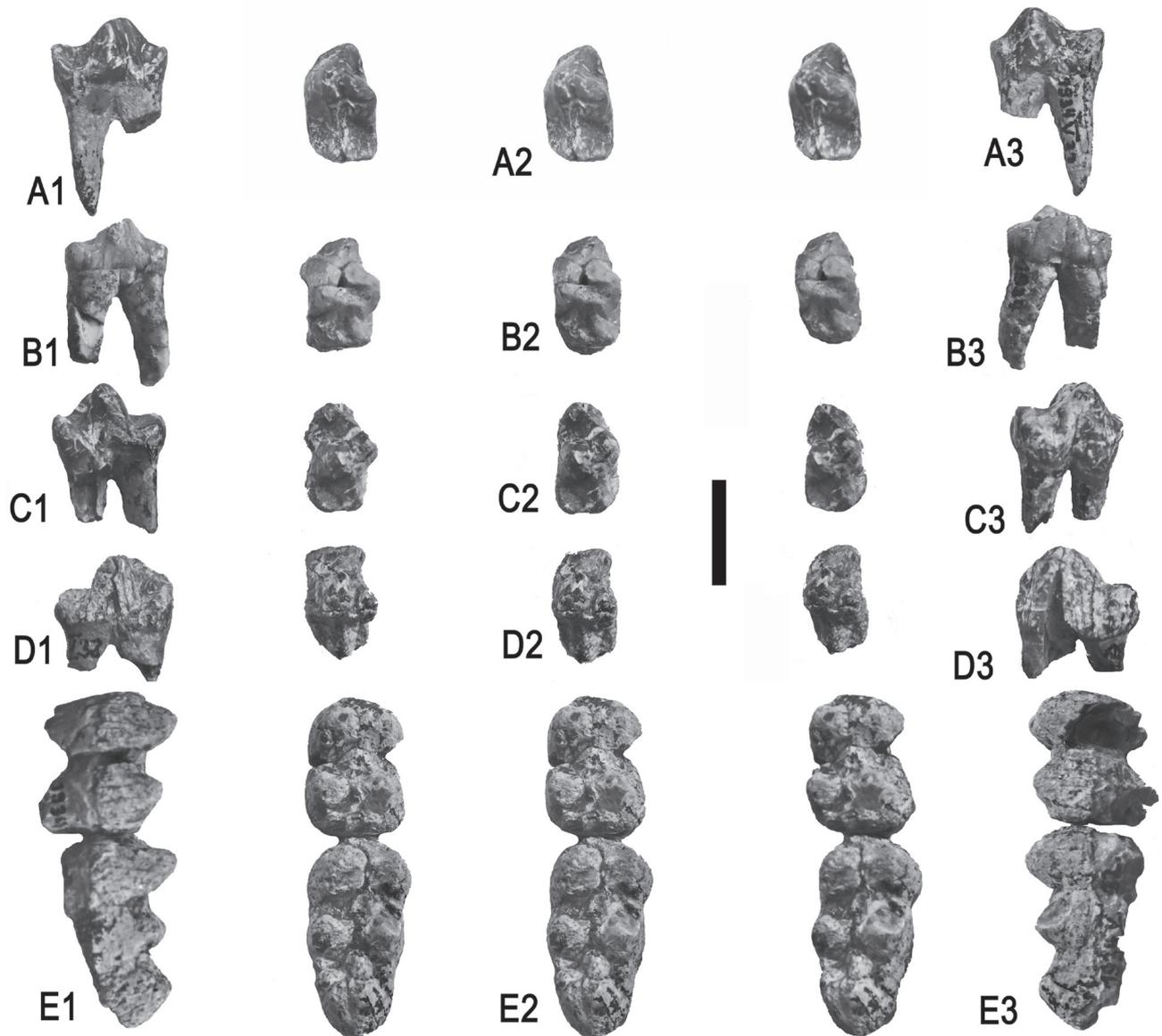


Fig. 7: Lower cheek teeth from Gunzenheim, Germany, attributed to *Palaeochoerus typus*. A-D) SNSB-BSPG 1934 V 33, p4s in (1) lingual, (2) stereo occlusal and (3) buccal views, (A – left p4, B – left p4, C – right p4, D – left p4) E) SNSB-BSPG 1934 V 32, right m2-m3 (E1 – lingual, E2 – stereo occlusal, E3 – buccal view) (scale: 10 mm).

Palaeochoerus to the Suidae rather than to the Old World Peccaries. The most parlant is the presence of fossae in the pre-orbital region which are homologous to the fossae present in other suids, in which the origins of the snout musculature are located (Fig. 8). Thus, there is a large but shallow fossa for the levator rostri muscles, and small fossae lower down close to the zygomatic process of the maxilla, where the dilatator naris lateralis and depressor rostri muscles originate. There can be little doubt that this morphology signifies that *P. typus* was a roter, using its mobile, well-muscled snout disc to forage for food in soil and leaf litter.

A further line of argument about the affinities of *Palaeochoerus* comes from the radicular morphology of the cheek teeth. Suids have the roots somewhat splayed

out from one another, with the lingual roots of the upper molars separated from each other, and the lingual and buccal roots of the lower molars separated from each other. In doliochoerids in contrast, the lingual roots of the upper molars are joined to each other by a lamella of cementum, and the buccal and lingual roots of the lower molars are close together and joined by a transverse lamella of cementum. Thus doliochoerids possess more slender mandibles than suids, in which the buccal and lingual roots of the lower molars are more splayed apart. These differences in radicular morphology reflect differences in chewing motions. In doliochoerids, the glenoid fossa is blocked behind by a post-glenoid process and the vertically oriented canines prevent significant side-to-side movements of the front of the jaw when

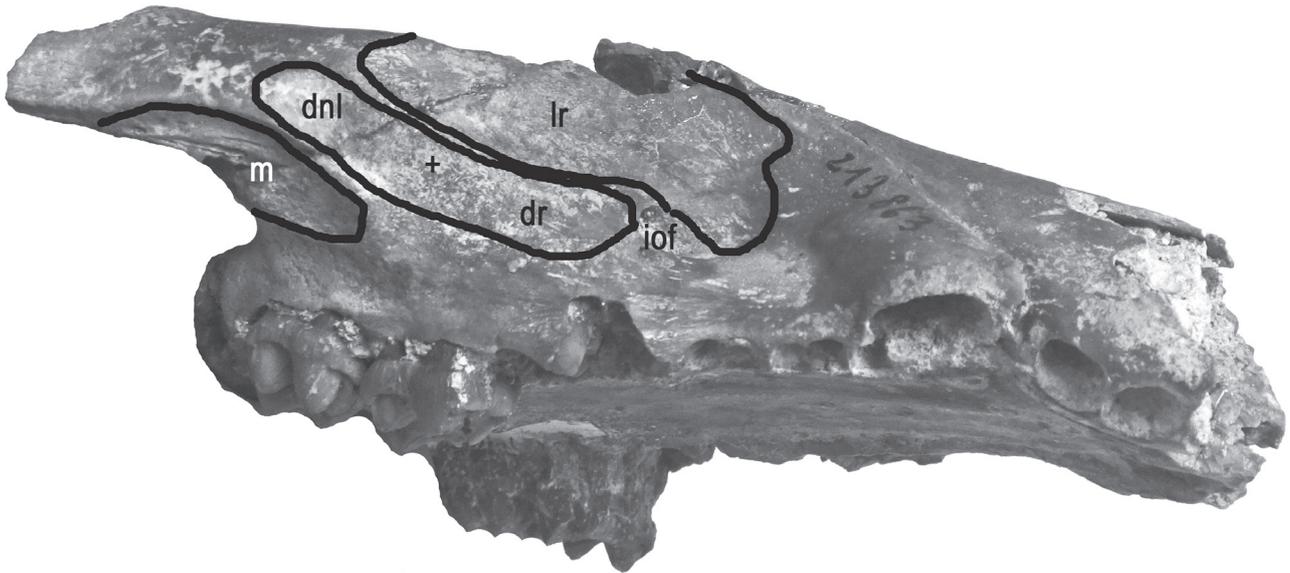


Fig. 8: Oblique view of the right side of the splanchnocranium of *Palaeochoerus typus* from St-Gérard-le-Puy, France, with the rhinarial muscle origins outlined (dnl - dilatator naris lateralis, dr - depressor rostri, iof - infra-orbital foramen, lr - levator rostri, m - masseter origin). Note the marked downward bend of the incisor alveolar process relative to the cheek tooth row, and the lateral position of the canine alveolus.

the molars are in occlusion (Pearson, 1927). Thus the forces of mastication are essentially vertical, with little if any lateral component. In suids in contrast, the glenoid fossa is not well constrained behind, and the upper and lower canines are splayed outwards, a combination which permits side-to-side movements of the jaw even when the molars are in occlusion. Thus, in suids, the chewing forces have an important lateral component, and this is reflected in the more splayed out orientation of their lower molar roots which thereby require a thicker mandible. Since *Palaeochoerus* has separated roots in the upper molars, and its canines are somewhat divergent from the vertical, it follows that it groups with Suidae rather than with Doliochoeridae.

Behavioural implications

Rooting in extant suids is comprised of four main components: (a) “whole-head” movements which push the snout into the ground and move it backwards, forwards and sideways, often done while (b) walking slowly forwards, producing a ploughing action, which leaves irregular furrows in the soil (Fig. 9), accompanied by (c) finer scale snout disc movements which churn the soil loosened by the whole-head movements, and associated with (d) a highly developed sense of smell for detecting edible items hidden in the soil. The whole-head movements are produced by well-developed nuchal muscles inserted into the back of the skull, driven by thick necks and heavy shoulders. The snout disc movements are produced by the levator rostri, dilatator naris lateralis and depressor rostri muscles, which twist and turn the snout disc in various directions in search of underground

food items such as tubers, corms, fungi, insects and small vertebrates and invertebrates. All this is linked to a highly developed sense of smell which detects the underground food items which are hidden from view. The elongated snout of *Palaeochoerus typus* indicates the likelihood that it had a well-developed sense of smell.

Origins of the family Suidae

Some authors (Ginsburg, 1974) considered that the family Suidae evolved outside Europe (south-east Asia) and dispersed into Europe at the beginning of the Neogene. The new interpretation of the fossils from Gunzenheim, Gondailly and St-Gérard-le-Puy indicates an alternative scenario. Whilst it is reasonably well established that Suoidea were absent from Europe during the Eocene and that one or two genera of the Superfamily dispersed to Europe from Asia at, or soon after, the Grande Coupure (Stehlin, 1909; Hellmund, 1992), it now appears likely that, having arrived in the continent, the suoids radiated within Europe giving rise to several lineages with diverse adaptations – Doliochoeridae, Sanitheriidae and Suidae, each of which radiated in its turn. It is clear from a study of the fossil faunas from the Far East (Indo-Pakistan-Myanmar and China) that during the Neogene there was semi-permanent dispersal of mammals between the Far East on the one hand, and Europe on the other, and the suoids were no exception. Yet the earliest suids known from Indo-Pakistan and China are not as primitive as *P. typus*, as shown by their longer snouts with rather long diastemata between the canines and the anterior premolars. Thus the evidence yielded by the cranial remains of *P. typus* shifts the focus of suid origins away



Fig. 9: Stony soil ploughed up by Bush Pigs, *Potamochoerus porcus* (Linnæus, 1758) on the flanks of Napak Volcano at Akisim, Uganda. The ploughing was achieved with the snout disc using “whole-head” movements while walking slowly forwards, accompanied by finer snout disc movements which explore the disturbed soil in search of edible items, detected by the well-developed sense of smell that these suids possess.

from an imprecise region in the Far East towards Europe, in particular it south-western parts.

If Gunzenheim correlates to MP 28, then it is concluded that the origin of the family Suidae dates from about MP 27-28, but if the deposits which yielded *Palaeochoerus* are younger, then the time of origin of the family would be correspondingly younger, but in any case prior to or within MN 1-2, to which the sites of St-Gérard-le-Puy and Gondailly correlate.

7. CONCLUSIONS

A snout of *P. typus* housed in the FSL (Viret, 1929) reveals significant evidence concerning the affinities of this poorly understood suoid. The presence of facial fossae in which the rhinarial musculature originates, indicate that *Palaeochoerus* was an active rooter, and thus falls into the definition of the family Suidae rather than in the non-suid

suoids (peccary-like suoids). Previous interpretations of the genus were often based on an admixture of suid-like and peccary-like suoids.

The presence of *P. typus* in France and Germany in deposits ranging in age from MP 28 to MN 1-2, well before their earliest records in Africa and the Far East, indicates that the family Suidae likely originated in Europe, probably descending from the family Doliochoeridae. The main distinguishing features are the inferred rooting habit and dentognathic changes related to a better-developed side-to-side chewing motion of the jaws in suids, compared to the lack of rooting habit and chewing restricted to vertical movements of the jaws in doliochoerids.

ACKNOWLEDGEMENTS

I thank the editors for the opportunity to publish this paper in the Claude Guérin Memorial Volume. Claude and I

wrote several papers together on perissodactyls of Africa, and he wrote several other papers on fossils that I collected at various sites. We worked together harmoniously and it was always a pleasure to discuss palaeontology with him. His knowledge was encyclopaedic, and his mind was open to new ideas and interpretations.

Thanks to Reinhard Ziegler and Manuela Aiglstorfer (SMNS), Madelaine Böhme and Ingmar Werneberg (GPIT), Gertrud Rössner (BSPG), Didier Berthet, David Besson and François Vigouroux (CCECL), Loïc Costeur (NHMB), Heinz Furrer (PIMUZ), Irene Zorn (GBW), Ursula Göhlich (NHMW), Christine Argot (MNHN), Pip Brewer and Roula Pappa (NHMUK), Emmanuel Robert and Abel Prieur (FSL), Oliver Sandrock (HLMD), Fritz Geller-Grimm and Felix Richter (MUWI), Ottmar Kullmer, Rainer Brocke and Gunnar Riedel (SMF), Karl Rauscher (IPUW), Eberhard Frey and Wolfgang Munk (SMNK), Michael Rummel (NMA), Michael Gross (LMJG), Herbert Lutz (NHMM), Kirsten Grimm (Johannes-Gutenberg-Universität, Mainz), Salvador Moya-Sola (IPS), Jorge Morales (MNCN) and Andreas Wilts (FFS) for permitting me to study fossils in their care. Thanks also to Philip Havlik (GPIT), Ursula Leppig (GPIFB), and Maria Haas and Ernst Schmotz (FFS) for help in the collections. Ursula Menkveld-Gfeller and Bernhard Hostettler (NMB) kindly provided access to the fossils in their care. Especial thanks to M. Hugueney and L. de Bonis, for providing access to fossils from Coderet, Laugnac and Paulhiac, which were crucial to advancing the research programme, and to the referees S. Ducrocq and S. Sen for their useful comments to improve this article.

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