

***Bransatochoerus* (Suoidea: Mammalia) from the late Oligocene of Coderet (Bransat, Allier, France): osteology, diet and growth variables**

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Abstract

Excavations at Coderet (Massif Central, France) yielded a comprehensive sample of small and medium-sized mammalian species. Because of its rich and diverse mammalian fauna the locality was selected as the last representative of the European Palaeogene mammalian biozonation levels, MP 30.

Cranial and post-cranial elements of Suoidea are abundant at Coderet. They pertain to a genus *Bransatochoerus*, with affinities to *Propalaeochoerus* and *Doliochoerus* but closer to *Doliochoerus* in the morphology of its neurocranium and closer to Suidae in its dentition, especially the M3 and m3. The post-cranial remains throw light on the locomotion of the species; among the peculiarities of its skeleton are the presence of five digits in the manus and spatulate terminal phalanges in the manus and pes, indicating a digging behaviour.

Keywords

Coderet, *Bransatochoerus*, Doliochoeridae, Suoidea, pentadactyl, body weight, sexual dimorphism.

1. INTRODUCTION

During the Oligocene and Early Miocene a rift – called Limagne – developed in the French Massif Central which was characterized by rapid subsidence in which accumulated terrestrial deposits which have yielded mammalian fossils from numerous localities. Some localities contain rich and diverse faunas and have been selected as reference levels (niveaux repères) for the European Standard Mammal Biozonation: Coderet (Allier) is the reference locality for MP 30 (uppermost stage of the Palaeogene Period) and Montaigu-le-Blin (Allier) is the reference fauna for MN 2 (Neogene levels being quoted as MN). But, at different levels in the rift infilling, mammal localities, even though poorer than these two sites, make it possible to follow faunal evolution in the region, particularly spanning the Oligocene-Miocene boundary (Hugueney *et al.*, 2003).

2. GEOLOGICAL CONTEXT

The locality Coderet (Commune de Bransat, Allier; coordinates x: 668.450, y: 146.130, altitude: 330 m) is

situated in the North-Western Limagne (Fig. 1) at the point of contact between the crystalline rocks to the West and Tertiary freshwater deposits to the East separated by the main rift border fault which is oriented more or less North-South.

Late Oligocene Limagne sediments comprise lacustrine and fluvial deposits that are generally rich in fossils, not only in species but also in individuals. The Coderet fauna in particular has yielded 20 families of mammals (not counting the Chiroptera and Carnivora) and 44 species, 24 of them rodents. Cenogram analyses, which correlate the variation in body size distribution and species richness of the fauna with environmental gradients, indicates that the assemblage from Coderet could correspond to relatively humid, warm and forested conditions (Legendre, 1989; Comte, 2000).

Poorer faunas have also been described in the region, including the Gannat fauna (Allier) which comprises 13 families, 16 species and only five species of rodents. Similar patterns of distribution are recognized in other Limagne localities: La Roche-Blanche/Gergovie (Puy-de-Dôme) and Cluzel (Allier), which correlate with other European localities such as Rottenbuch 8 (Germany) and Boudry 2 (Switzerland). The age of all these

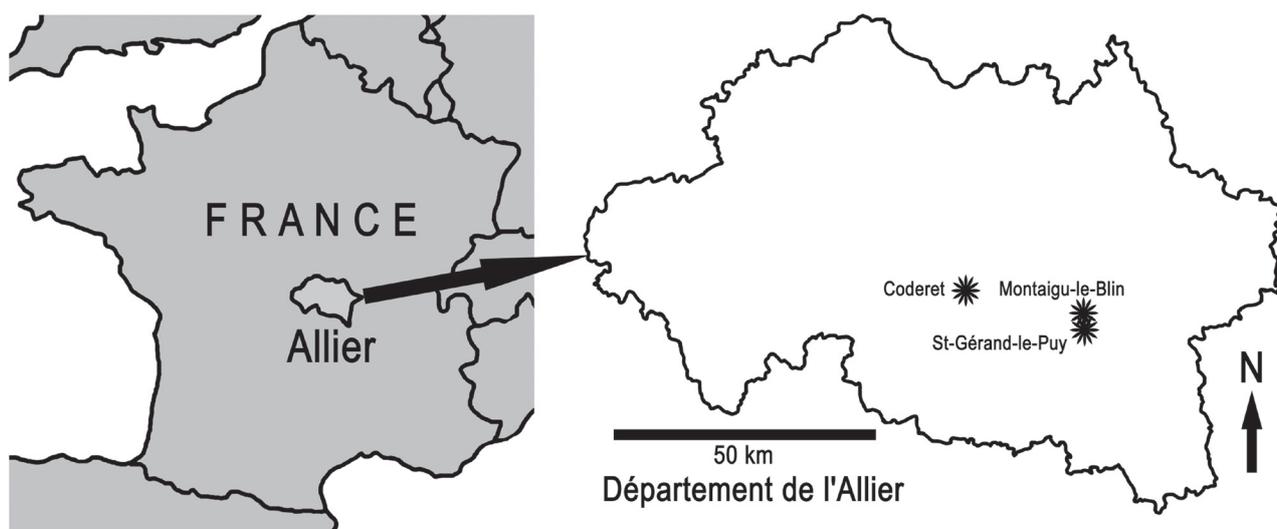


Fig. 1: Locality map, fossiliferous deposits in the Département of Allier, central France. Coderet is the type locality (niveau repère) of European Mammal Biozone MP 30 (latest Oligocene), Montaigu-le-Blin is the type locality of zone MN 2 (Early Miocene). St-Gérard-le-Puy correlates to MN 2a.

localities, as indicated by the evolutionary degree of their rodents, is approximately the same and slightly younger than Coderet; they are ascribed to MN 1. The Billy-Crechy section (Allier; Hugueney *et al.*, 2003), which documents the Oligo-Miocene transition, possesses a variety of rodent taxa in the Late Oligocene beds but the order experienced a drastic reduction in diversity at the beginning of the Neogene. The faunas of these basal Miocene levels are dominated by eomyids and glirids, and sometimes zapodids.

In the younger Montaigu-le-Blin fauna, representative of the Early Miocene (base of MN 2 = MN 2a), the species richness is greater: it consists of 18 families, 33 species but only 11 rodent taxa, which represents 1/3 of the species – versus more than 50% at Coderet. The faunal community indicates an open tropical landscape.

Drastic faunal changes took place at the MP 30 / MN 1 boundary – even if some immigrations and disappearances occurred during the Late Oligocene (MP 29 - MP 30) –:

- the entire family Theridomyidae, endemic to the European Eocene and Oligocene, disappeared as did the last creodont of the genus *Hyaenodon* Laizer & Parieu, 1838, and the Artiodactyla *Microbunodon* Depéret, 1908, and *Anthracotherium* Cuvier, 1822.
- the genus *Cainotherium* Bravard, 1828, became the unique representative of its family (Bravard, 1835) as did *Amphiperatherium* Filhol, 1879, for Didelphidae. Among rodent genera, the eomyid *Eomys* Schlosser, 1884, the cricetid *Adelomyarion* Hugueney, 1969, the glirid *Gliravus* Schaub (in Stehlin & Schaub, 1951), and the castorid *Rhizospalax* Miller & Gidley, 1919, did not cross this boundary.

However, lineages that persisted developed new and more derived species: all the Oligocene species of

Plesiosminthus Viret, 1925, disappeared and were replaced by a unique new species, *Plesiosminthus myarion* Schaub, 1930.

The pattern of faunal changes observed in Limagne is repeated over much of Europe, from which we conclude that the general persistence of Late Oligocene lineages makes it possible to interpret European earliest Miocene faunas as impoverished Oligocene assemblages.

Legendre (1987, 1989) showed that local extinctions in mammal faunas can be correlated with successive temperature decreases within oceans and that the most noticeable effect of a temperature drop is a decrease in the number of species of which the body weight is less than 500 g, which is the case for most of the Oligocene rodents. So the change between Late Oligocene and Early Miocene faunas could perhaps be interpreted as being caused by one, or perhaps several, successive temperature changes accompanied by increases in seasonality (Hugueney, 1984; Comte, 2000).

A similar result could be obtained by evoking changes in aridity but, in the case of Limagne, the presence of lakes prevents the attribution of these faunal changes to very dry conditions.

Evidence concerning Northern Limagne faunal evolution ends with the Montaigu-le-Blin deposits due to the filling up of the rift.

3. HISTORY OF THE LOCALITY

The locality of Coderet was discovered by J. Viret who, as early as 1925, described new rodents from it. Collections were made on a regular basis until 1939, the fossils being curated at the University of Lyon

(FSL). More or less simultaneously H. Helbing from Basel (Switzerland) excavated the locality so that a lot of material is curated in the Basel collections, among which are some suoids, including evidence of the first metacarpal (Stehlin, 1929). At the time of these preliminary excavations the fossiliferous deposits were not completely exposed but were obstructed by large blocks of rock, meaning that it was only possible to collect from sediments exposed below the blocks or from the extensive scree deposit beneath. By 1962, when M.H. started her excavations, these blocks had fallen, exposing the previously inaccessible deposits (Fig. 2). The fresh outcrops revealed that in the succession, there were three marly levels of slightly different colours. The three levels were excavated in detail which demonstrated that mammals were present in all of them, the lower level (grey marls) being less rich than the other two horizons. The superposed brown to red marls were richer in fossils and suoids were particularly concentrated in this level. The upper level of green to rust-coloured marls was rich in teeth and bones of small mammals, especially small rodents. Usually only disarticulated specimens were found, but several associated skeletal elements of suoids were excavated, some in anatomical connection, even though crushed by sediment compaction.

The Coderet quarry exploited fresh-water, poorly stratified rocks with concretionary nodules and blocks that yield continental and freshwater molluscs; *Caseolus ramondi* Brongniart, 1810, a helicid snail characteristic of the Upper Oligocene is found not only in the calcareous rocks but also in the fossiliferous marls.

Fossiliferous marly layers or lenses of various dimensions are intercalated; these marly deposits are not the result of karstic dissolution but evidence the inflow of small rivers reworking the surrounding deposits (Viret, 1928b, 1929).

4. MATERIAL AND METHODS

The fossil material from Coderet curated in Laboratoire de Géologie de Lyon, Université Claude Bernard – Lyon 1 (numbered FSL) corresponds to the collections made by J. Viret, and to fossils recovered from sediments excavated by M. Huguency from 1963 to 1965 (ten tons) and regular smaller samples made later. Larger bones had been crushed by the weight of the overlying sediments and were consolidated in situ prior to removal; two skulls were subsequently placed on a plaster support by J. Battetta, preparator at the Lyon Museum.

The precise location of fossils within the locality grid was noted directly on the fossils whenever possible (Huguency, 1969).

Abbreviations

FSL: Faculty of Science, University of Lyon (now Laboratoire de Géologie, Université Claude Bernard – Lyon 1).



Fig. 2: View of the outcrops of freshwater sands, silts, clays and marls at Coderet, France, in 1962, type locality (localité repère) of Palaeogene Mammal Zone MP 30.

MC: metacarpal

MNHN: Muséum National d'Histoire Naturelle, Paris

MN: Mammal Neogene

MP: Mammal Palaeogene

MNI: Minimum Number of Individuals (not to be confused with MN 1)

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

P/p: upper/lower premolars

M/m: upper/lower molars

5. SYSTEMATIC DESCRIPTION

Superfamily Suoidea Cope, 1887

Family Doliochoeridae Simpson, 1945

Genus *Bransatochoerus* Pickford, 2016

***Bransatochoerus elaverensis* (Viret, 1928)**

- 1928a. *Palaeochoerus meissneri* von Meyer, mutation *elaverensis* nob. Viret, p. 1311.
- 1928b. *Palaeochoerus meissneri* von Meyer, mutation *elaverensis* nob. Viret, pp. 245-252, fig. 26-27, pl. 31, fig. 1-12.
1929. *Palaeochoerus meissneri* von Meyer, mutation *elaverensis* nob. Viret, pp. 245-252, fig. 26-27, pl. 31, fig. 1-12.
1929. *Propalaeochoerus elaverensis* (Viret).– Stehlin, pp. 621-625, fig. 12-13.
1971. *Propalaeochoerus elaverensis* (Viret).– Bouvrain, p. 7 (unpublished thesis)

NB: the last page of Viret's thesis, submitted in May 1928, shows the printing date 1928. The follow-up publication in the *Annales de l'Université de Lyon* was printed in 1929.

Original diagnosis of the species: Déjà de la taille du *P. meissneri* von Meyer, 1850, en diffère par des caractères plus primitifs de la dentition et de la patte qui le rapprochent du *Propalaeochoerus* de Stehlin. "Already the same size as *P. meissneri* von Meyer, it differs from it by more primitive characteristics of the teeth and feet which approach it to Stehlin's (1899-1900) *Propalaeochoerus*" (from Viret, 1928a).

Emended diagnosis (1): Forme de la taille du *P. meissneri*, en différant par quelques caractères un peu plus primitifs. Ici les molaires supérieures ont deux racines externes bien séparées et deux racines internes encore rattachées l'une à l'autre sur toute leur longueur. Quant aux molaires inférieures elles possèdent une racine antérieure et une postérieure, racines plates sans doute, mais où la tendance au dédoublement est à peine sensible. Canine supérieure remarquablement plate... la base de la couronne passe à la racine sans rétrécissement notable. Le collet est dépourvu de toute tubérosité (from Viret, 1928b, 1929).

Emended diagnosis (2): Species larger than *Doliochoerus quercyi* Filhol, 1882, with tendency for the M3 to possess enlarged posterior cingula, rarely forming a distinct hypoconule. Length of M1-M3, 40-42 mm, distal epiphyses of metapodials with low ridge dorsally, sharp, prominent, ventrally; third phalanges with expanded and flattened distal part (from Pickford, 2016).

Lectotype: FSL 97728, left M3 figured by Viret (1928b, plate 31, fig. 11) (nominated by Bouvrain, 1971). Figured by Pickford (2016, fig. 164 A).

Osteology

Viret (1929, figs 26 and 27) illustrated (in mirror image as left complexes) and interpreted the right carpal and tarsal complexes and their corresponding metapodials of what he called *Palaeochoerus meissneri* (sic) mut. *elaverensis*. He stressed that the MC III does not make contact with the trapezoid, unlike the situation in *Sus* Linnæus, 1758, and the magnum is quite reduced. He also pointed out that the lateral metapodials were solidly fixed to the median ones and did not show any tendency to splay outwards or backwards, unlike in *Sus* in which they do. Our own observations confirm this morphology. Stehlin (1929) studying the Coderet collection in Basel, recognized a first metacarpal in the forefoot of "*Propalaeochoerus*", described and figured it extensively and noticed that it was the youngest known artiodactyl with five digits in the manus. Pickford (2016) however, has shown that Early and Middle Miocene Siderochoeridae also possessed pentadactyl forefeet, thereby considerably extending the record of this primitive condition of the manus of artiodactyls.

Pickford (2016) described many of the suoid specimens from Coderet, but additional observations and comments can be made. The skull material is crushed, which renders interpretation difficult (Figs 3, 4). The orbit is positioned above the M2-M3, there are short diastemata between the canine and P1 and the P1 to P2 and there is a shallow

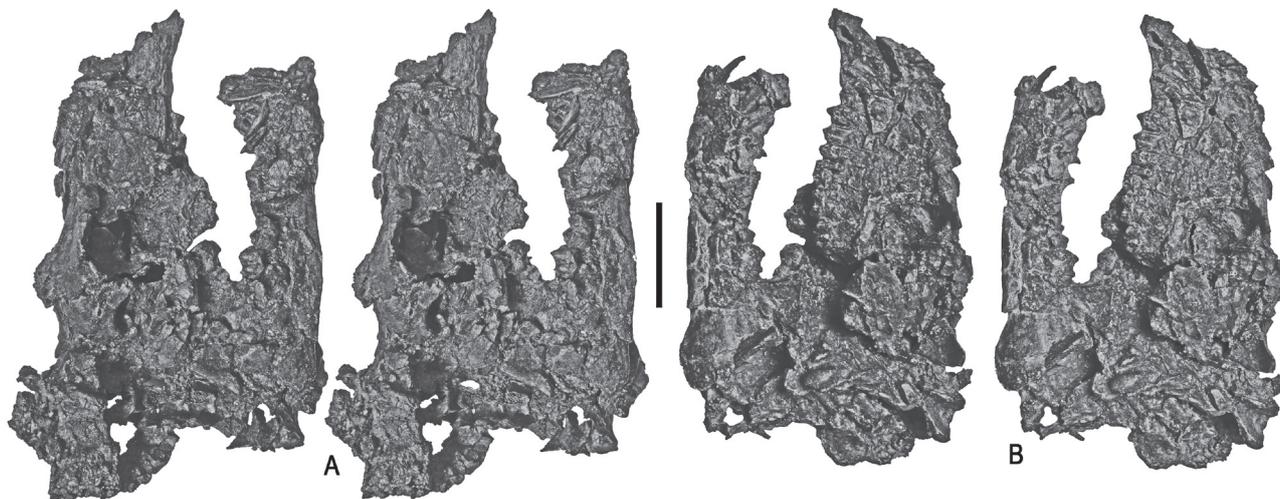


Fig. 3: FSL 99321, crushed cranium and cervical vertebrae of *Bransatochoerus elaverensis* from Coderet. A) stereo right lateral view, B) stereo left lateral view (scale: 5 cm).

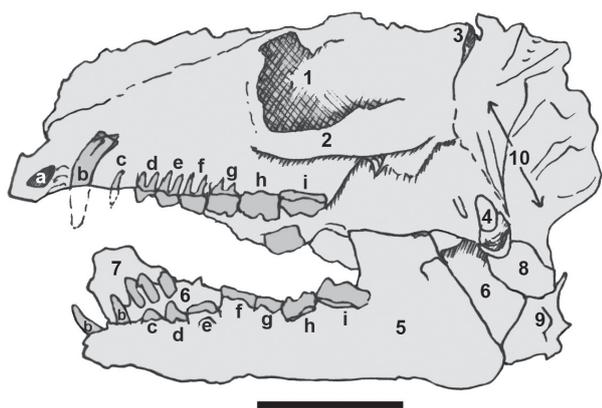


Fig. 4: Interpretation of FSL 99321, left lateral view of crushed skull, mandible and cervical vertebrae of *Bransatochoerus elaverensis* from Coderet. (1: orbit, 2: zygomatic arch, 3: nuchal crest, 4: occipital condyles, 5: left mandible, 6: right mandible, 7: fragment of right maxilla containing anterior premolars, 8: atlas, 9: axis, 10: crushed cervical vertebrae) (a: I3 alveolus, b: upper and lower canines, c: P1 and p1, d: P2 and p2, e: P3 and p3, f: P4 and p4, g: M1 and m1, h: M2 and m2, i: M3 and m3) (scale: 5 cm).

canine niche between the upper canine and I3. The neurocranium is shorter than the splanchnocranium, the part behind the leading edge of the orbit being somewhat shorter than the part in front of it.

The post-cranial material is generally preserved as isolated bones and fragments. Viret (1928b, 1929) already described and illustrated the wrist and ankle complexes of this species. We here concentrate on parts of the skeleton not previously mentioned in detail.

The ulna of *Bransatochoerus* does not possess a curved groove on the lateral side parallel to the sigmoid articulation (Figs 5, 6), a significant difference from the ulnae of Siderochoeridae which possess this groove (Pickford, 2017). In the Siderochoeridae, this groove accepts the lateral pillar of the humerus in the fully extended position, thereby augmenting the stabilisation of the elbow joint. In the extant Collared Peccary, *Pecari tajacu* (Linnæus, 1758) the sigmoid articular surface is subdivided into two parts, a small lateral facet separated from the main facet by a capacious depression in the body of the ulna. Neither the Doliochoeridae nor the Siderochoeridae show a similar fossa subdividing the sigmoid articular facet.



Fig. 5: Left elbow joint of *Bransatochoerus elaverensis* in fully flexed (A) and fully extended (B) positions to show the extent of movement possible at the joint (scale: 5 cm).

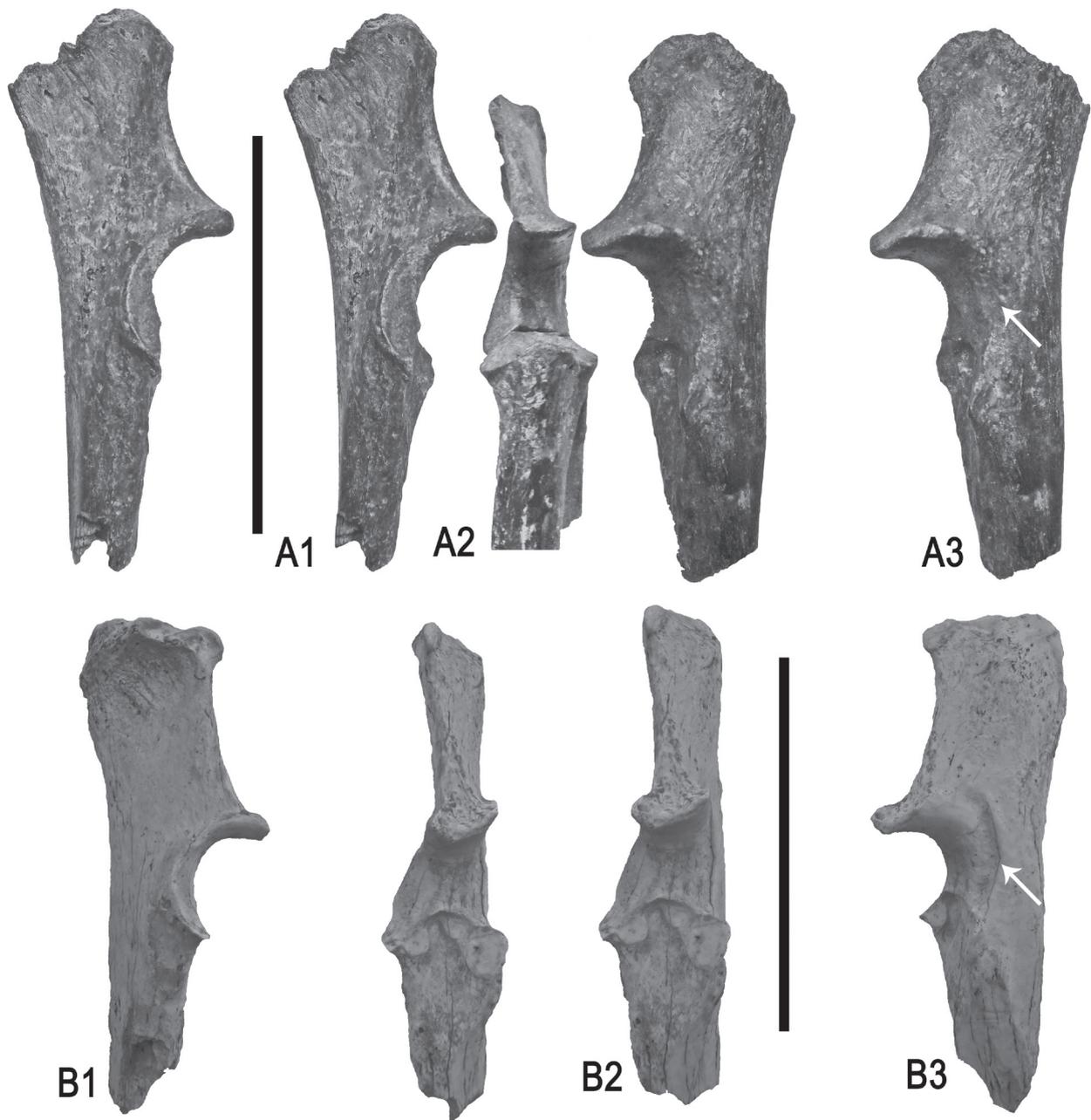


Fig. 6: Comparison of left proximal ulnae of (A) *Bransatochoerus elaverensis* from Coderet, France, and (B) *Choeromorus petersbuchensis* Pickford (2017) from Petersbuch 108, Germany. A1: stereo medial view, A2: cranial view, A3: stereo lateral view, B1: medial view, B2: stereo cranial view, B3: lateral view (white arrows show the curved groove concentric to the sigmoid articular surface in (B) and its absence in (A) (scale: 5 cm).

Restudy of the Lyon Coderet collection led to the recognition of a first metacarpal (as in Basel collection), which makes it possible to reconstitute the forefoot of *Bransatochoerus* as pentadactyl (Fig. 7), like the forefeet of Siderochoeridae (Pickford, 2017).

Functional significance of terminal phalangeal morphology

The terminal phalanges of *Bransatochoerus elaverensis* have a spatulate distal part (Fig. 8), thereby resembling

the phalanges of digging mammals such as *Orycteropus afer* (Pallas, 1766) (the aardvark, or antbear of Africa). This evidence suggests that the feet of *Bransatochoerus* were adapted for digging, but it is not known whether digging was undertaken to access food items buried in the soil, or whether they excavated burrows in which they sheltered and gave birth, like the collared peccary (*Pecari tajacu*) does, or both.

The fact that several of the Coderet suoid specimens comprise associated skeletal elements, sometimes in

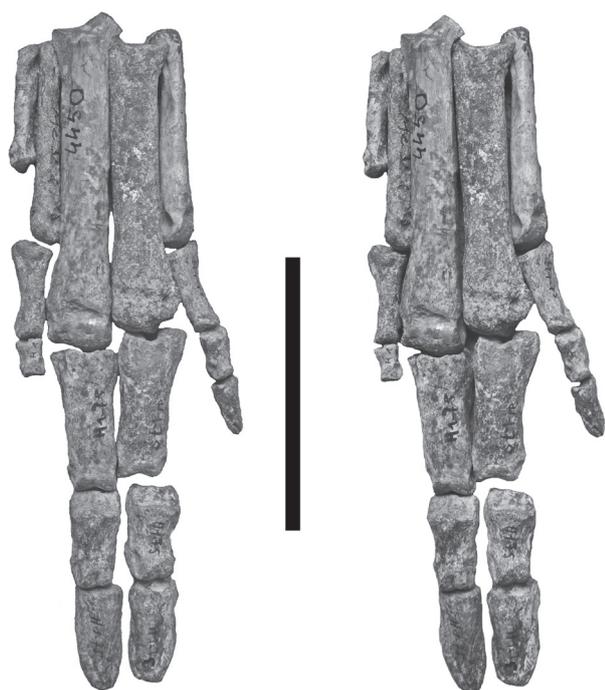


Fig. 7: An essay at reconstituting the left forefoot of *Bransatochoerus elaverensis* using diverse isolated bones from Coderet. Stereo dorsal view of ensemble. Note the presence of the MC I (scale: 5 cm).

connection, even though crushed, plus the fact that skeletal elements of infants, juveniles, sub-adults, mature adults and senile individuals were found in close proximity suggest that they could have died within burrows, and were not greatly disturbed post-mortem, other than by sediment compaction processes. This scenario agrees with the behaviour of extant peccaries which live in herds and which retire to self-dug burrows when they are not actively searching for food or doing other above-ground activities.

Skeletal preservation and Minimum Number of Individuals (MNI)

The skeletal remains of *Bransatochoerus elaverensis* are unevenly preserved, with some bones being more common than others. The greatest number of specimens is represented by the talus, of which there are 32 (18 right, 14 left). The next best represented bone is the calcaneum with 25 specimens (15 left, 10 right), and then some of the teeth, among which the I1 is the commonest (16 left, 9 right) to which may be added the DI1 (6 left, 2 right). There are very few vertebrae preserved but, of the vertebral column, the cervical vertebrae are the best preserved with the atlas and the axis being rare but well preserved, and the posterior cervical vertebrae rarer and generally poorly preserved. Thoracic, lumbar and caudal vertebrae are rare and poorly preserved, and the ribs almost non-existent (one specimen only retaining the articular parts). The scapula, humerus and femur are



Fig. 8: *Bransatochoerus elaverensis* phalanges. A) composite median phalangeal row, stereo dorsal views, B) FSL 99407, terminal phalanx (B1: dorsal view, B2: interior view, B3: volar/plantar view, B4: external view, B5: proximal view, B6: distal view (scale: 10 mm).

represented only by incomplete fragments, but the radius and tibia are known from a few complete specimens. The carpals and tarsals, metapodials and phalanges are well represented and generally well preserved. Cranial material is invariably crushed but two specimens preserve enough information to yield approximate measurements of cranial length and breadth and details concerning the position of the orbit relative to the tooth row, and the height of the mandibular condyle above the occlusal surface of the cheek teeth, and the position of the posterior nares relative to the tooth rows.

We calculate that the minimum number of adult and sub-adult individuals is 18 on the basis of the talus. If we add infants to this quantity, known principally on the basis of their deciduous teeth (minimum number of six individuals) then the global MNI would be greater, possibly as many as 22 individuals, if none of the left I1s represent the same individuals as the left dI1s. In any case the MNI at Coderet is greater than 18 and probably fewer than 23.

It is possible to propose a reconstruction of the skeleton of *Bransatochoerus elaverensis*, with the proviso that the proportions of the vertebral column and the upper segments of the limbs are poorly constrained, and the shape of the cranium is somewhat hypothetical (Fig. 9). From this it is then possible to estimate the body weight of the species.

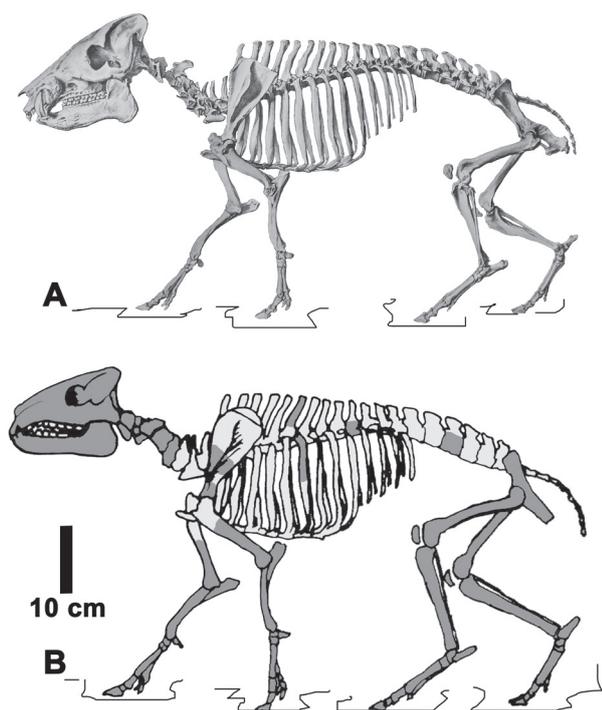


Fig. 9: Essay at reconstitution of the skeleton of *Bransatochoerus elaverensis* (B) compared with that of the extant Collared Peccary, *Pecari tajacu* (A) (historical drawing from De Blainville, 1847, reversed). *Bransatochoerus* is on average ca 131% of the size of *Pecari tajacu*, but its skull is somewhat smaller and its hind legs relatively longer than the front ones. The light coloured parts (vertebral column, scapula and ribs) of the fossil are largely hypothetical. The dark parts are represented by fossils (scale: 10 cm).

Sexual bimodality

In *Bransatochoerus elaverensis*, there does not appear to be a significant difference between the body dimensions of males and females. The talus, of which there are 31 specimens which can be measured (one is too broken to measure) shows a unimodal distribution with a low number of relatively small specimens which are interpreted as juvenile individuals (Table 1). Even if males could have been, on average, larger than females, the pattern of distribution in bivariate plots of the cloud of points of the talar dimensions, suggests that the difference, if there were any, was less than 10%, with the expectation that some females would have been larger than some of the males.

Sexual dimorphism

In *Bransatochoerus elaverensis*, males tend to have slightly larger canines than females (Pickford, 2016). However, the shape of the teeth appears to be similar in the two sexes and some specimens which are not completely erupted could have been incorrectly sexed.

Dental eruption sequence and diet

In the suoid sample from Coderet, there are infant, juvenile, young adult, mature adult and senile specimens. It is thus possible to deduce many details concerning the dental eruption sequence and hints as to the diet.

Age class comparisons are made with *Sus scrofa* (miniature domestic pigs: Clawn strain, Ide *et al.*, 2013; wild boar, Lemoine *et al.*, 2014). Whilst *Bransatochoerus* had a different growth trajectory from *Sus scrofa*, and somewhat different eruption order of the teeth, the pig data provide a base line for comparison.

Specimen FSL 99328 is an infant left mandible containing the di3, the deciduous canine, and d2, d3 and d4 in occlusion (Fig. 10). The incomplete germ of the m1 is still in its crypt. There is no sign of a p1 in this individual, but it could be hidden inside the mandible. This observation suggests either that the p1 does not have a deciduous precursor, in agreement with the finding of Ide *et al.* (2013) for the Miniature Pig, or that what we call the “p1” is a late-forming d1 which is not shed later in life. The dc and the d2 are separated from each other by a diastema, and the rear margin of the symphysis is beneath the front of the d2. This individual corresponds to a 5 month old piglet (Ide *et al.*, 2013).

FSL 99324 is a right mandible fragment containing the lightly worn d4, the fully formed m1 crown with minor root formation in crypto, and the incompletely formed germ of the m2 at the base of the ascending ramus (Fig. 10). Crushing has twisted the m2 crown such that the occlusal surface is oriented almost vertically and faces buccally. This individual is slightly older than FSL 99328 (more worn d4) corresponding to a 6 month old piglet (Ide *et al.*, 2013).

Specimen FSL 99329 is a crushed left mandible with symphysis (Fig. 10). Bone has flaked off the lingual side of the jaw exposing the permanent premolars in their crypts beneath the deciduous teeth. In this jaw the i1-i3 and m1 are fully erupted and in occlusion, while the d2, d3 and d4 are still in situ in the jaw, with the fully developed crowns (without roots) of the p2-p4 beneath them, all three teeth at the same level in the mandible. The m2 has erupted almost to the occlusal surface but has not yet occluded with the upper molar, and the rootless crown of the m3 is still in its crypt beneath the ascending ramus. The canines are incompletely erupted. The p1 is in occlusion and has a prominent root. This individual corresponds in its development to an 11 month old piglet (Ide *et al.*, 2013).

FSL 99330 is a young adult right mandible and the rear part of the left ramus (Fig. 11). All the deciduous teeth have been shed, but the m3 has not yet fully erupted, although the apices of the cusps are almost at the occlusal surface. The m1 is moderately deeply worn, whereas all the other teeth are only lightly worn, save for the m3 which has not yet entered into occlusion. The rear of the symphysis is beneath the p2, and the erupted canine and p1 have largely filled what used to be the diastema between it and

Table 1: Measurements (in mm) of the tali of *Bransatochoerus elaverensis* from Coderet, France (lt: left, rt: right). (NB: Specimens 99468aa and 99468ab have the ancient numbers 4456 and 4468 written on them).

Catalogue	Bone	External length	Internal length	Proximal breadth	Distal breadth
FSL 99468aa (4456)	Talus rt	29.9	27.1	14.5	16.4
FSL 99468ab (4468)	Talus rt	30.3	27.2	14.3	15.7
FSL 99417	Talus lt	30.9	29.4	14.5	15.6
FSL 99465	Talus rt	--	--	14.6	--
FSL 99468	Talus lt	--	--	14.0	--
FSL 99468a	Talus lt	28.9	26.4	12.8	13.7
FSL 99468b	Talus rt	--	27.6	--	14.7
FSL 99468c	Talus rt	31.3	28.5	14.1	16.2
FSL 99468d	Talus rt	27.7	--	12.8	--
FSL 99468e	Talus lt	31.6	29.0	14.3	15.6
FSL 99468f	Talus rt	30.8	26.5	13.5	15.1
FSL 99468g	Talus rt	30.9	28.8	13.7	14.9
FSL 99468h	Talus rt	32.8	29.4	14.8	17.2
FSL 99468i	Talus rt	29.6	27.0	13.8	15.8
FSL 99468j	Talus rt	29.3	26.5	14.2	15.2
FSL 99468k	Talus lt	29.7	26.7	13.0	15.3
FSL 99468l	Talus lt	30.2	27.2	13.4	15.0
FSL 99468m	Talus rt	31.6	29.7	14.5	15.7
FSL 99468n	Talus lt	--	27.7	15.1	--
FSL 99468o	Talus rt	--	--	13.4	--
FSL 99468p	Talus lt	29.6	27.2	13.7	14.3
FSL 99468q	Talus rt	28.5	26.0	13.3	14.4
FSL 99468r	Talus lt	31.0	29.1	14.4	15.4
FSL 99468s	Talus rt	30.3	27.1	13.6	15.4
FSL 99468t	Talus rt	31.2	28.8	13.7	15.5
FSL 99468u	Talus lt	31.5	29.9	14.0	15.7
FSL 99468v	Talus lt	29.0	--	14.5	--
FSL 99468w	Talus rt	29.1	26.4	12.5	14.5
FSL 99468x	Talus rt	--	26.4	--	15.3
FSL 99468y	Talus lt	--	28.0	--	15.3
FSL 99468z	Talus lt	--	--	--	15.4

the p2 in the infant mandible. This specimen corresponds to a young adult pig, possibly equivalent in development to an 18 month old.

FSL 99327 is a senile right mandible (Fig. 11) which could represent the same individual as the partial skull, FSL 99320. The m2 is deeply worn with the occlusal surface represented by a single dentine lake surrounded by a thin remnant of enamel. The roots of this tooth are fused into a pillar, almost like teeth of the Aardvark, *Orycteropus* Geoffroy, 1796, and in this respect it recalls the doliochoerid *Lorancahyus* Pickford & Morales,

1998. The p4 in this specimen is also deeply worn, yet the p1 is almost unworn. Despite the heavy wear in these molars and p4, their occlusal surfaces are still in the same plane as that of the other teeth, indicating that the tooth does not cease erupting when the crown is fully erupted, but continues erupting as the crown is worn away. This is essentially similar to the hypsorrhizic molars described in the geologically younger genus *Lorancahyus* (MN 2). This individual corresponds to a pig which is older than 8 years (Lemoine *et al.*, 2014).

Bransatochoerus elaverensis is unusual among suoids

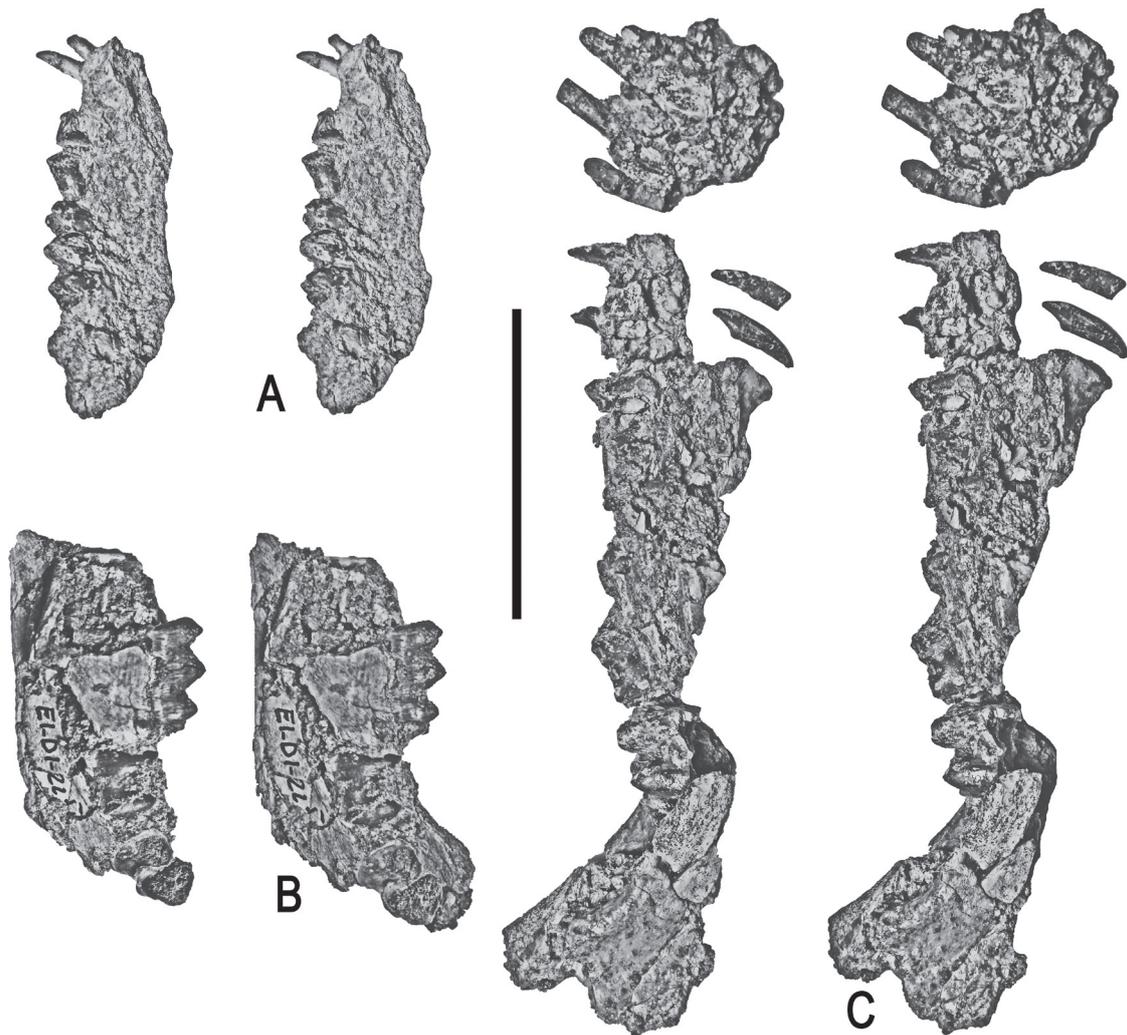


Fig. 10: Lower jaws of *Bransatochoerus elaverensis* from Coderet, France. A) stereo lingual view of FSL 99328, infant left mandible containing di3, dc1, d2, d3, d4 and germ of m1 in crypt; B) stereo lingual view of FSL 99324, baby right mandible with lightly worn d4, m1 and m2 in crypt; C) stereo lingual view of FSL 99329, juvenile symphysis and left mandible with permanent incisors, p1, d2-d4 and m1 in occlusion, p2-p4 and m2-m3 partly erupted (scale: 5 cm).

(especially the pig *Sus scrofa*) in that the m1 is fully erupted and in moderate wear before the permanent premolars erupt. The lower incisor row also erupts early, with the permanent incisors in occlusion well before the shedding of the milk molars.

The impression obtained from the study of the dental eruption sequence and wear pattern of the teeth of *Bransatochoerus*, is that it was likely ingesting abrasive or durable food items (or food to which abrasive particles were attached) from a very young age, and that in order to obtain and process the food, it required a strong and resistant incisor battery well before the sub-adult stage was attained, and that chewing durable or abrasive food went hand-in-hand with precocious eruption of the first permanent molars, leaving the deciduous premolars relatively unworn in between. By the young adult stage, the permanent premolars are fully erupted but the anterior

ones remain relatively unworn, the p1 almost untouched, whereas the p4 is deeply worn with fused roots, the m1 is worn to a stub, but with its occlusal surface still in the same plane as that of the other cheek teeth, the m2 moderately worn, and the m3 not fully erupted.

In the senile stage, the p4 is deeply worn, the m1 and m2 are worn to featureless stubs, but their occlusal surfaces are still at the same level as the occlusal plane, yet the p1 is relatively fresh with little apical wear having occurred.

Body weight estimate

Adult Collared Peccaries (*Pecari tajacu*) weigh between 14 and 31 kg (22.5 +/- 8.5 kg) (Bodmer & Sowls, 1993; Nowak, 1991; Schmidt, 1990; Wilson & Reeder, 1993). Schwarm *et al.* (2009) give the body weight of *Pecari tajacu* as 18 +/- 5 kg.

In most measurements, the skeleton of *Bransatochoerus*

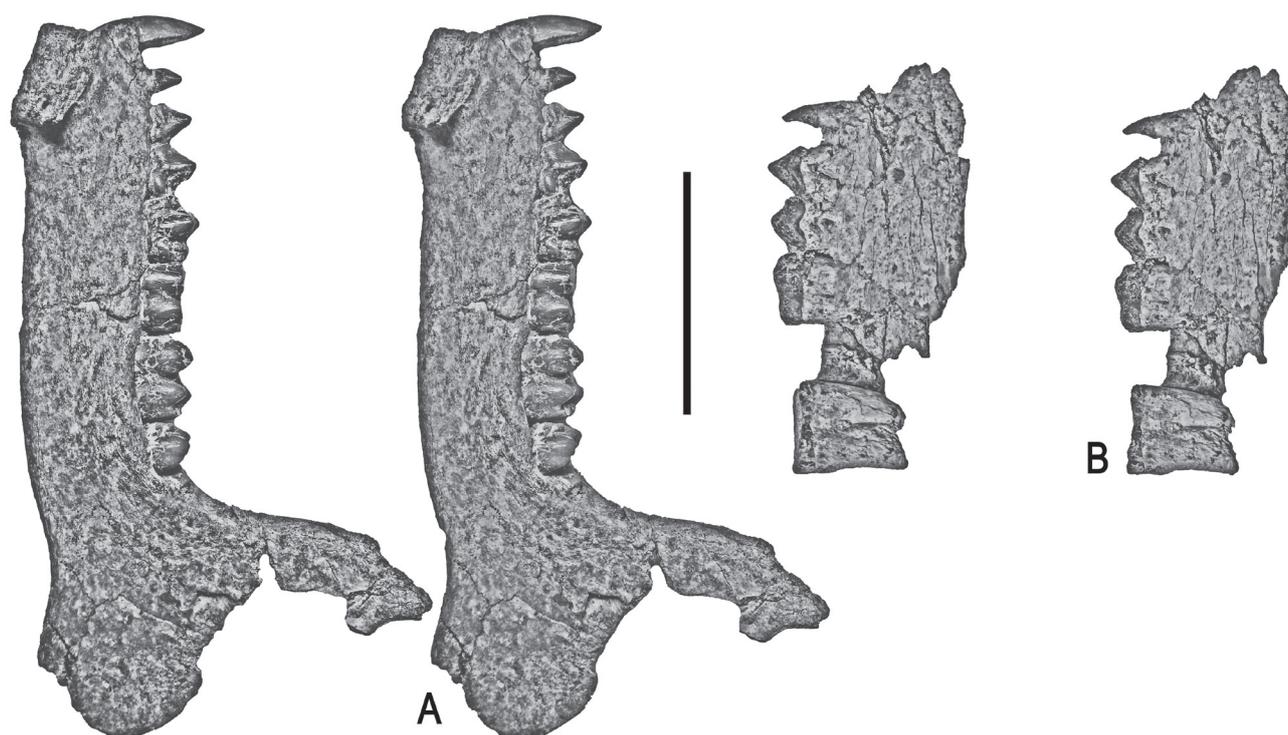


Fig. 11: Lower jaws of *Bransatochoerus elaverensis* from Coderet, France. A) stereo lingual view of FSL 99330, young adult right mandible containing c1-m2 in occlusion m3 partly erupted; B) stereo buccal view of FSL 99327, senile right mandible with p1-p4, m2 (note the pillar-like root mass of the m2, the crown of which has all but been eradicated by wear (scale: 5 cm).

elaverensis is larger than a specimen of *Pecari tajacu* housed in the MNHN (1898-309, 19871). On average, the lengths of the long bones of *Bransatochoerus* are 131% of the length of the same bones in the measured specimen of *Pecari tajacu*.

The lower jaw of *Bransatochoerus*, in contrast, has the same length as that of the peccary, suggesting that its head was relatively smaller than that of the peccary.

If we assume that the few measurable bones of *Bransatochoerus elaverensis* are close to the mean of the species, it is calculated that its body weight would have been about 50 +/- 19 kg, using the body weight of 22.5 +/- 8.5 kg for the extant taxon. If the body weight of the Collared Peccary given by Schwarm *et al.* (2009) forms the basis for calculation, then the figure for *Bransatochoerus* would be correspondingly lower.

6. DISCUSSION AND CONCLUSIONS

Coderet, a latest Oligocene fossiliferous locality in the Limagne Rift, France, yielded abundant fossils which provide a rare opportunity to reconstitute the skeleton and some of the life history variables and possible behaviour of a peccary-like suoid, *Bransatochoerus elaverensis*, defined at the site by Viret (1928b). The fossiliferous locality of Tomerdingen, Germany, rich in remains of *Doliochoerus pusillus* (Ginsburg, 1974) is

another such locality (Hellmund & Heizmann, 2011). Sansan, France, has also yielded some post-cranial remains of *Choeromorus lemuroides* (Pickford, 2017). In general however, remains of suids and doliochoerids from European sites are scattered and isolated, making it difficult to obtain sufficient elements to reconstruct the skeleton, and from that basis to estimate body weight and other information about the skeletal adaptations of the taxa (Pickford, 2016, 2017).

We here provide a reconstruction of the skeleton of *Bransatochoerus elaverensis*, which shows that the species was about 131% the size of the extant Collared Peccary, *Pecari tajacu*. From this basis we estimate that the Coderet suoid probably weighed about 50 kg +/- 19 kg. The sample of skeletal remains from Coderet includes the first metacarpal, the manus of the species being pentadactyl as was already demonstrated by Stehlin (1929). The third phalanges of *Bransatochoerus elaverensis* have spatulate distal parts suggesting that the species habitually dug in the ground.

The sample of suoid bones from Coderet indicates that there was not a high degree of sexual dimensional bimodality in *Bransatochoerus elaverensis*, and that even the dentition was not greatly dimorphic. Thus, it is concluded that males and females were about the same size.

The presence of upper and lower jaws of diverse ontogenetic ages permits elucidation of several details

of the dental eruption sequence of *Bransatochoerus*. Permanent incisors and the m1 erupt early, while the d2-d4 are still in use. The p1 in contrast, erupts well after the deciduous molars, suggesting that it is likely to be a permanent tooth that does not have a deciduous precursor. The p4 and permanent molars develop pillar-like root masses which continue to erupt even when the crown is completely worn away, maintaining the occlusal surface of the teeth at the general level of the occlusal plane. This morphology indicates that *Bransatochoerus* was ingesting either coriaceous food, or food that had abrasive particles adhering to it.

The finding of articulated skeletal elements indicates minimal post-mortem disturbance of the cadavres, the main damage being due to sediment compaction processes. The fact that several individuals of diverse ontogenetic ages were found close together indicates the possibility that the individuals were in a burrow at the time that they died, protected from the attention of predators and scavengers.

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REFERENCES

- Bodmer R. E. & Sowls L. K. 1993. The Collared Peccary (*Tayassu tajacu*). In: Oliver W. L. R. (Ed.), *Pigs, Peccaries and Hippos: Status Survey and Action Plan*. IUCN, Gland, Switzerland: 7-12.
- Bouvrain G. 1971. *Contribution à l'étude des Suidés de l'Aquitainien*. PhD Thesis, Université Paris VI, Paris, 80 pp., 8 pls.
- Bravard A. 1828. *Monographie de la montagne de Perrier, près d'Issoire (Puy-de-Dôme), et de deux espèces du genre Felis découvertes dans l'une de ses couches d'alluvion*. Dufour & D'Ocagne, Paris, 147 pp.
- Bravard A. 1835. *Monographie du Cainotherium, nouveau genre fossile de la famille des Pachydermes, trouvé dans les terrains tertiaires d'eau douce du département du Puy-de-Dôme*. Levrault, Paris, 35 pp.
- Brongniart A. 1810. Sur des terrains qui paraissent avoir été formés sous l'eau douce. *Annales du Muséum d'Histoire Naturelle*, 15: 357-405.
- Comte B. 2000. Rythme et modalités de l'évolution chez les rongeurs à la fin de l'Oligocène, leurs relations avec les changements de l'environnement. *Palaeovertebrata*, 29 (2-4): 83-360.
- Cope E. D. 1887. The classification and phylogeny of the Artiodactyla. *Proceedings of the American Philosophical Society*, 24: 377-400.
- Cuvier G. 1822. *Recherches sur les ossemens fossiles où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces*. Tome 3, G. Dufour et E. D'Ocagne, Paris, 412 pp., 80 pls.
- De Blainville H.M.D. 1847. *Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie et à la géologie. Sur les Hippopotames (Buffon) (Hippopotamus L.) et les Cochons (Buffon) (Sus L.)*. Tome Quatrième, Atlas. J.B. Baillièere et Fils, Paris, 248 pp.
- Depéret C. 1908. L'histoire géologique et la phylogénie des Anthracothéridés. *Comptes rendus de l'Académie des Sciences*, 146(4): 158-162.
- Filhol H. 1879. Etude des mammifères fossiles de Saint-Gérand-le-Puy. *Annales des sciences géologiques*, 10: 1-253.
- Filhol H. 1882. Observations relatives à un groupe de Suidés dont la dentition possède quelques caractères simiens. *Comptes rendus hebdomadaires de l'Académie des Sciences*, 94(18): 1258-1260.
- Goeffroy E. 1796. Extrait d'un mémoire sur le *Myrmecophaga capensis*, Gme. *Bulletin de la Société philomathique*, 50: 1-2.
- Ginsburg L. 1974. Les Tayassuidés des Phosphorites du Quercy. *Palaeovertebrata*, 6: 55-85.
- Hellmund M. & Heizmann E. J. P. 2011. Vergleichende osteologische Untersuchungen am postcranialen Skelett von *Propalaeochoerus pusillus* (Suoidea) aus der untermiozänen Karstspaltenfüllung Tomerdingen (SW-Deutschland). *Hallesches Jahrbuch für Geowissenschaften*, 32: 171-190.
- Huguene M. 1969. Les Rongeurs (Mammalia) de l'Oligocène supérieur de Coderet-Bransat (Allier). *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, 34: 1-227.
- Huguene M. 1984. Evolution du paléoenvironnement dans le Tertiaire de Limagne (Massif Central, France) à partir des faunes de mammifères. In: Paléoécologie, Congrès international Lyon 1983. *Geobios, Mémoire Spécial*, 8: 385-391.
- Huguene M., Berthet D., Bodergat A. M., Escuillié F., Mourer-Chauviré C. & Watinne A. 2003. La limite Oligocène-Miocène en Limagne: changements fauniques chez les mammifères, oiseaux et ostracodes des différents niveaux de Billy-Créchy (Allier, France). *Geobios*, 36: 719-731.
- Ide Y., Nakahara T., Nasu M., Matsunaga S., Iwanaga T., Tominaga N. & Tamaki Y. 2013. Postnatal mandibular cheek tooth development in the Miniature Pig based on two-dimensional and three-dimensional X-Ray analyses. *The Anatomical Record*, 296: 1247-1254.
- Laizer L. de & de Parieu J. 1838. Description et détermination d'une mâchoire fossile appartenant à un mammifère jusqu'à présent inconnu, *Hyaenodon leptorhynchus*. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences*, 7(8): 442.
- Legendre S. 1987. Mammalian faunas as palaeotemperature indicators: concordance between oceanic and terrestrial palaeontological evidence. *Evolutionary Theory*, 8: 77-86.
- Legendre S. 1989. Les communautés de mammifères du Paléogène d'Europe occidentale: structure, milieu et évolution. *Münchner Geowissenschaftliche Abhandlungen, A*, 16: 1-110.

- Lemoine X., Zeder M. A., Bishop K. J. & Rufolo S. J. 2014. A new system for computing dentition-based age profiles in *Sus scrofa*. *Journal of Archaeological Science*, 47: 179-193.
- Linnæus C. 1758. *Systema Naturae, Ed. X. (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis). Editio decima, reformata*. Tomus 1: Laurentius Salvius, Holmiae, 824 pp.
- Miller G. S. & Gidley J. W. 1919. A new rodent from the Upper Oligocene of France. *Bulletin of the American Museum of Natural History*, 41: 595-601.
- Nowak R. M. (Ed.) 1991. *Walker's Mammals of the World (Fifth Edition)*. The Johns Hopkins University Press, volume 1, pp. i-xlvi + 1-642 + xlix-lxiii, volume 2, pp. i-xiii + 643-1629.
- Pallas P.S. 1766. *Miscellanea zoologica*. P. van Cleef, La Haye, 224 pp.
- Pickford M. 2016. Revision of European Hyotheriinae (Suidae) and Doliochoeridae (Mammalia), *Münchner Geowissenschaftliche Abhandlungen*, A 44: 1-270.
- Pickford, M. 2017. Revision of "peccary-like" Suoidea (Artiodactyla: Mammalia) from the Neogene of the Old World. *Münchner Geowissenschaftliche Abhandlungen*, A 46: 1-144.
- Pickford M. & Morales J. 1998. A tubulidentate suiform lineage (Tayassuidae, Mammalia) from the Early Miocene of Spain. *Comptes rendus de l'Académie des Sciences*, 327: 285-290.
- Schaub S. 1930. Fossile Sicistinae. *Eclogae Geologicae Helvetiae*, 23(2): 616-636.
- Schlosser M. 1884. Die Nager des europäischen Tertiärs: nebst Betrachtungen über die Organisation und die geschichtliche Entwicklung der Nager überhaupt. *Palaeontographica*, 31: 19-162.
- Schmidt C.R. 1990. Peccaries. In: Parker S. P. (Ed.), *Grzimek's Encyclopedia of Mammals*. McGraw-Hill, New York, Volume 5: 48-55.
- Schwarm A., Ortmann S., Rietschel W., Kühne R., Wibbelt G. & Clauss M. 2009. Function, size and form of the gastrointestinal tract of the collared *Pecari tajacu* (Linnæus 1758) and white-lipped peccary *Tayassu pecari* (Link 1795). *European Journal of Wildlife Research*, 56(4): 569-576.
- Simpson G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85: 1-350.
- Stehlin H. G. 1899-1900. Über die Geschichte des Suiden Gebisses. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 26/27: 1-527.
- Stehlin H. G. 1929. Artiodactylen mit fünffingriger Vorderextremität aus dem europäischen Oligocän. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 40(2): 599-625.
- Stehlin H. G. & Schaub S. 1951. Die Trigonodontie der simplicidentaten Nager. *Schweizerischen Paläontologische Abhandlungen*, 67: 1-385.
- Viret J. 1925. Sur la faune de rongeurs de Saint-Gérard-le-Puy (Allier). *Comptes rendus des séances de l'Académie des Sciences*, 181(10): 337-339.
- Viret J. 1928a. Sur la faune oligocène de Coderet près Branssat (Allier). *Comptes rendus des séances de l'Académie des Sciences*, 186(19): 1309-1311.
- Viret J. 1928b. *Les faunes de mammifères de l'Oligocène supérieur de la Limagne bourbonnaise*. Thèse Doctorat ès Sciences naturelles, Lyon, 328 pp., 32 fig., 32 pl.
- Viret J. 1929. Les faunes de mammifères de l'Oligocène supérieur de la Limagne bourbonnaise. *Annales de l'Université de Lyon, Nouvelle Série I, Sciences et Médecine*, 47: 1-328.
- Von Meyer H. 1829. Letter. *Zeitschrift für Mineralogie*, 1: 150-152.
- Von Meyer H. 1850. Der Schädel des *Hyotherium meissneri* aus dem Tertiärkalke des Salzbachthales bei Wiesbaden. *Jahrbücher des Nassauischen Vereins für Naturkunde*, 6: 116-125.
- Wilson D. E. & D. M. Reeder (Eds) 1993. *Mammal Species of the World: A Taxonomic and Geographic Reference (Second Edition)*. Smithsonian Institution Press, Washington D.C., xviii + 1206 pp.

