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A new Late Triassic (Rhaetian or Late Norian) Mammaliaformes fossil locality: Avillers (Vosges, France)

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Abstract
We report the occurrence of two taxa of Late Triassic (Rhaetian or Late Norian) cynodonts, dromatheriid *Pseudotriconodon* cf. *wildi* and mammaliaform *Morganucodon peyeri* from the new locality of Avillers (Vosges, northeastern France). The discovery increases our knowledge of the presence of early mammals in northeastern France (previously limited to Saint-Nicolas-de-Port and Varangéville) and northwestern Europe.

Keywords
Cynodonta, Mammaliaformes, Dromatheriidae, Morganucodontidae, Triassic, Rhaetian.

INTRODUCTION

The fossil record of early mammaliamorphs in northwestern Europe is limited. We here present a new fossil site from the eastern margin of the Paris Basin, where sediments of Rhaetian or Late Norian (Late Triassic) age crop out in an elongate range between Thionville and Vittel, and beyond (Rauscher *et al*., 1995, fig. 9, p. 179). In this area, the quarries of Saint-Nicolas-de-Port and Rosières-aux-Salines (or shortly SNP and RAS) in the Meurthe-et-Moselle department, France, situated some 10 km SE of Nancy, are well known for their rich vertebrate fauna including therapsids and mammaliaforms (Cuny & Ramboer, 1991; Godefroit & Sigogneau-Russell, 1999; Debuysschere *et al*., 2014; Debuysschere, 2015, 2016, 2017). Roughly one thousand mammaliaform teeth have been found there in addition to other material (Debuysschere, 2015, p. 515). The age of the material is here tentatively considered to be Rhaetian (c. 208.05-201.36 Ma; Galbrun *et al.,* 2020), although no absolute dating has so far been performed, and a possible Late Norian age cannot be explicitly excluded (Godefroit & Battail, 1997). We therefore use the term Rhaetian with some caution, as we also did for the age of the recently described Late Triassic material from Winterswijk, The Netherlands (De Lange *et al*., 2023).

Several other localities in the larger area have also yielded mammaliaform remains: Varangéville (Meurthe-et-Moselle), not far from SNP/RAS (Godefroit, 1997), Rinckebierg (Medernach), Luxemburg (Cuny *et al*., 1995; Delsate, 1999), Syren, Luxemburg (Godefroit *et al*., 1998; Delsate, 2000), Habay-la-Vieille and Attert in the Province of Luxemburg, Southern Belgium (Fuffin *et al.,* 1983; Godefroit, 1999; Delsate, 1994, 1995), and Hallau, canton Schaffhausen, Switzerland (Clemens, 1980). Reconstructions based on the faunal composition of the samples suggest a coastal or deltaic paleoenvironment, probably deposited during a transgressive phase (the 'Rhaetian' transgression; Rauscher *et al*., 1995; Godefroit, 1997).

Here, we present the third locality from northeastern France in addition to the SNP/RAS and Varangéville localities where teeth of mammaliaforms are found: Avillers (Fig. 1). Although so far only two teeth have

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Fig. 1. A. Map of the surroundings of Mirecourt (Vosges, France); red star indicates the position of the Avillers site. B. The trench of Avillers in 2023; dimensions of the first author for scale.

been recognized, one of a cynodont and one of a derived mammaliaform, the discovery increases our knowledge of the early mammalian presence in northwestern Europe. Several small fossiliferous outcrops of Late Triassic age have been discovered during the last decade, some 38 km in a southerly direction from SNP/RAS, in the eastern surroundings of Mirecourt (department of Vosges, France). The sediments are considered to belong to what is regionally known as the 'Grès et schistes à *Avicula contorta*', or GSAC (see Rauscher *et al*., 1995 for details on the regional stratigraphy of the eastern part of the Paris Basin). One of these GSAC sites is the Avillers outcrop, located in an abandoned sand quarry which extends over about one hundred metres, but is now overgrown by secondary forest. This quarry was not indicated on the geological map (Minoux, 1978), which did not indicate GSAC at this point but instead the underlying formation known as 'Marnes irisées supérieures' (Upper iridescent marls). The locality was shown to the first author in 2012 by the mayor of Avillers, Mr Denis Bastien. A small-scale excavation has been carried out here since 2018, resulting in the discovery of mostly (and as yet undescribed) marine vertebrate fossils. The discovery of two teeth of early mammaliaforms enhanced the importance of the Avillers locality. They were found in the lower two metres of the working face of the presently excavated trench which is at least 7 m high. The contact of the GSAC sands with the underlying 'Marnes irisées supérieures' has so far not been recognized. A larger-scale excavation and an in-depth description of the full vertebrate fossil association are planned for the near future.

MATERIAL AND METHODS

Taxa recognized from the site so far comprise chondrichthyan teeth and dermal denticles, actinopterygian teeth and some scales, dipnoi dental ridges and scales, a labyrinthodont tooth, some possibly sphenodont jaw fragments and a possibly salientian jaw fragment. These fossils are awaiting further study. The preservation quality is good, though fragmentary. The presence of well-preserved terrestrial, aquatic and marine fossils indicates the proximity of the Avillers site to the land during Rhaetian times.

Here, we focus on two teeth of cynodont and mammaliaform origin from the Avillers site. The material was collected by the first author and is stored in the collection of the Department of Earth Sciences, Utrecht University, the Netherlands. Measurements were taken and drawings were made by the last author using a Wild M5 binocular microscope fitted with a drawing prism.

Order Therapsida Broom, 1905
Infraorder Cynodontia Owen, 1861
Family Dromatheriidae Gill, 1872
Genus *Pseudotriconodon* Hahn, Lepage & Wouters, 1984

Type species: *Pseudotriconodon wildi* Hahn, Lepage & Wouters, 1984

Original generic diagnosis (after Hahn *et al*., 1984; translated from the original German): Dromatheriid genus characterized by long and slender teeth, buccal and lingual sides are parallel, length of teeth 1.0-1.5 mm, width about 0.5 mm. Crown with one major cusp and one to two mesial and one to three distal cuspules; all cusps arranged in a longitudinal row, with sharp anterior and posterior cutting edges. Height of the main cusp 1.0 to 1.5 mm, cuspules at most half as tall. Absence of cingulids, neither on the lingual nor the buccal sides. Enamel surface smooth. Root about 1.25 times as high as long and about 1.5 times as high as the crown; semi-elliptical in side [lateral] view and either undivided, seemingly divided near the pulpa or divided near the root apex. Root and crown are not separate; absence of a ridge or a furrow at the transition between root and crown.
Revised generic diagnosis (according to Godefroit & Battail, 1997): "Crown of postcanine teeth tricuspid to pentacuspid and very narrow (ratio "length/width" of the crown 2.4 to 4.2); labial [buccal] and lingual sides of the crown nearly parallel. Cutting edge perfectly straight. Base of the crown not constricted. Root semi-elliptical in outline, about 1.5 times as high as the crown; tip of the root sometimes divided by a short furrow; pulpal canal small, elliptical in shape and sometimes double."

Pseudotriconodon cf. *P. wildi* Hahn, Lepage & Wouters, 1984

Fig. 2, 1a-c

Specific diagnosis (after Godefroit & Battail, 1997): length of the crown of post-canine teeth 0.9 to 3.1 mm; width of the crown of postcanine teeth 0.35 to 0.95 mm.
Measurements: The fragmentary tooth AV-001 has a mediodistal length of 1.42 mm and a width of 0.66 mm, of which measurements the width is not dependent on the absence of part of the tooth; these sizes evidently fit within the wide range mentioned in the diagnosis.
Description: A tetracuspid crown, probably a right lower, with smooth buccal and lingual faces and without a cingulid, except for a small and inconspicuous section situated buccally below the posteriormost accessory cuspule. Part of tooth AV-001 appears to be missing; the breakage margin is rounded by abrasion and not clearly demarcated. The missing part most probably consisted of a small single accessory cusp. The main cusp is the highest and shows slight wear on its buccal side. The first accessory cusp is cone-shaped, the smaller second one is crescent-shaped in occlusal view.

The outline in lateral view resembles specimen IRSNB 28114/766 depicted by Godefroit & Battail (1997, fig. 4O), but this specimen is probably also missing one accessory cusp; the authors do not provide its measurements. If indeed a small accessory cusp is missing in our specimen too, it is originally quite similar to specimen IRSNB 28114/994 (Godefroit & Battail, 1997, fig. 4W). This specimen has (according to Godefroit & Battail, 1997, table 1) a length of ?1.8 mm, a width of 0.65 mm and thus a L/W ratio of ?2.77. It is thus somewhat longer than the tooth described here but it has a similar width. Godefroit & Battail (1997) distinguish six categories of teeth, based on the number of accessory cuspules. With the attribution of their tooth IRSNB 28114/994 to Group II, having 1 anterior and 2 posterior accessory cuspules, our specimen could also belong to this category.

There are two minor differences between tooth AV-001 and the material described by Godefroit & Battail (1997). First, we observe a small buccal cingulid below the posteriormost accessory cuspule. Both the original diagnosis and Godefroit & Battail (1997) indicate the absence of a cingulids. Also, this last accessory cuspule is crescent-shaped in occlusal view and not conical or triangular. Because of these differences in the morphology of this cuspule, the taxonomic implications of which we cannot yet ascertain, we here tentatively restrict ourselves to a confer (cf.) identification: *Pseudotriconodon* cf. *P. wildi*.

Infraorder Cynodontia Owen, 1861
Clade Mammaliaformes Rowe, 1988
Order Morganucodonta Kermack, Musset & Rigney, 1973
Family Morganucodontidae Kühne, 1958
Genus *Morganucodon* Kühne, 1949
Type species: *Morganucodon watsoni* Kühne, 1949

***Morganucodon peyeri* Clemens, 1980**
Fig. 2, 2a-c

Diagnosis (Clemens, 1980): "A small morganucodontid with molariform teeth smaller than those of

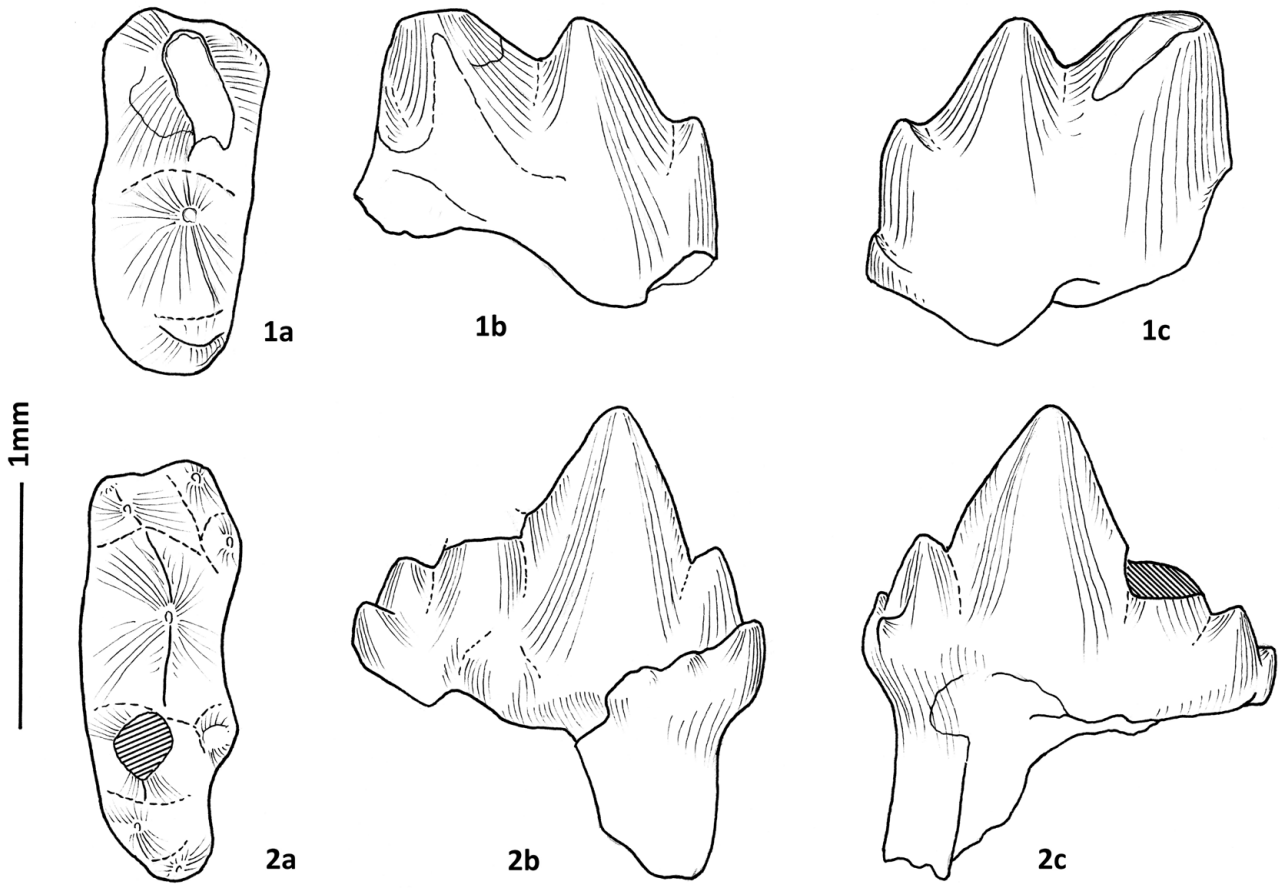

Fig. 2. *Pseudotriconodon* cf. *P. wildi*, Avillers. Right lower molariform tooth, AV-001. 1a, occlusal view, anterior up; 1b, lingual view; 1c, buccal view. The largest cusp is slightly worn.
Morganucodon peyeri, Avillers. Left lower molariform tooth, AV-002. 2a, occlusal view, anterior up; 2b lingual view; 2c buccal view. Hatching = broken cusp.

Morganucodon oehleri but approximately the same size as those of *M. watsoni*, however, their crowns appear to be relatively narrower than those of the latter species. Buccal and lingual cingula of upper molariforms tend to be more weakly developed than those of *M. watsoni* and *M. oehleri* and the buccal more frequently interrupted across the base of the principal cusp. Resembling *M. watsoni*, but not *M. oehleri*, the lingual cingulum of the lower molars is relatively well developed. Possibly the presence of a large, anterolingual cingular cusp, almost as large as the anterior accessory cusp, might separate *M. peyeri* from the other species. No evidence of buccal cingula, present on a very few molars of *M. watsoni* (Parrington, 1971) and on some of the few described molars of *M. oehleri* (Mills, 1971), has been found in the small sample of *M. peyeri*."

Description: Our tooth (AV-002) is a left molar, most possibly m2 or perhaps m3. There are four cusps on the central ridge; the major cusp is the second one from anterior; the apex of the third one is broken. The tooth thus resembles the left molar of *M. peyeri* depicted by Debuysschere *et al*. (2014: fig. 4A, p. 831) which also has the apex of its third cusp broken off. Both the posteriormost and anteriormost cusps are bordered on their lingual sides by a cingulid, the cingulid below the anteriormost cusp being larger and bearing two very small accessory cuspules. A rather indistinct boss is present below the third cusp on its lingual side.

Measurements: Molar AV-002 has a length of 1.72 mm and a width of 0.65 mm. Clemens (1980) mentions a length of 1.65 and a width of 0.62 mm for the holotype lower molariform of *M. peyeri*; Debuysschere *et al*. (2014) provide measurements of two specimens, respectively L = 1.73, W = 0.62 and L = 1.67, W = 0.59. These published sizes do not significantly differ from the ones of our specimen.

CONCLUSION

The presence of dromatheriid and morganucodontid cynodont material in Avillers forms an interesting addition to the known hypodigm of Late Triassic cynodonts from northeastern France and adjacent regions, such as Saint-Nicolas-de-Port and Varangéville near Nancy (Meurthe-et-Moselle, France) and neighbouring countries. The discovery increases our knowledge of the presence of dromatheriid and morganucodontid cynodonts in northwestern Europe. More extensive excavations in Avillers are planned in the nearby future.

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