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A stagodontid mammal from the mid-Cretaceous of France confirms the Euramerican distribution of early marsupialiforms

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ABSTRACT

The global palaeobiogeography of early marsupialiform mammals is still poorly understood due to a meagre fossil record outside western North America. Here, two isolated teeth of a marsupialiform mammal from the lowermost Upper Cretaceous (lower Cenomanian) of southwestern France are described and referred to Stagodontidae, a dentally specialized group whose unambiguous members are so far known exclusively from the Upper Cretaceous of North America. The occurrence of stagodontids in Europe represents additional evidence of faunal exchanges between the two landmasses during the latest Albian–early Cenomanian

interval, around 100 million years ago, and shows that early (mid-Cretaceous) marsupialiforms were more widely distributed than previously thought.

Keywords:

Metatheria, fossil teeth, Cenomanian, Europe, palaeobiogeography

1. Introduction

The fossil record seems to indicate that marsupia. form metatherians originated and first diversified in North America in the mid-Creater ous (Albian–Cenomanian) (Williamson et al., 2014). Furthermore, some intercontinental dispersal events may have existed during this time interval, as suggested by the only wid-Cretaceous occurrence of this mammalian group outside North America (i.e. *Arcantiodally hys marchandi* from the Cenomanian of France; Vullo et al., 2009). Thus, Vullo et al. (2009) noted the potential value of the Cenomanian vertebrate-bearing localities way a southwestern France in the understanding of early marsupialiform evolutio, and palaeobiogeography.

Here we report a second marsupialiform occurrence from the Cenomanian of France, based on a previously described premolar (Néraudeau et al., 2005), which is here reassessed, and a recently discovered upper molariform fragment from the same locality (Les Renardières quarry). These two specimens, here regarded as conspecific, show a suite of features present in stagodontids, a family of durophagous marsupialiforms so far unambiguously known only from the Upper Cretaceous (Cenomanian–Maastrichtian) of North America (Kielan-Jaworowska et al., 2004; Williamson et al., 2014; Wilson et al., 2016; Cohen, 2018; Eldridge

et al., 2019) and possibly from the Eocene of Brazil (Carneiro and Oliveira, 2017). This new stagodontid occurrence represents further evidence for dispersal of early marsupialiforms between North America and the European archipelago, thus supporting the hypothesis that episodic faunal links persisted long after the separation of the two continents.

2. Geological setting

The two isolated teeth described here come from the Le; Renardières quarry at Tonnay-Charente (about 10 km east of Rochefort, Chaunte Maritime Department, SW France; GPS 45°58'1.7"N, 0°49'47.5"W), which is r ow closed and refilled (Néraudeau et al., 2005) (Fig. 1). Uppermost Albian (subunit A1 to Lowermost Cenomanian (subunits A2 and B1) beds were exposed in this locality. $T_{1,2} \circ 20$ -m-thick section represents a transgressive sequence; clays and sands of subunits A1 and A2 were accumulated in estuarine environments, whereas beds of the orbunit B1 were deposited in shallow marginal marine environments (Néraudeau et al., 2005). Vertebrate microremains (isolated teeth, bones and scales) were intensively collected from a ~0.7-m-thick layer of shelly clayey sand located in the middle part of the sucurit B1 (bed B1s) (Néraudeau et al., 2005) (Fig. 1). The invertebrate fauna includes large benthic foraminifers (Orbitolina concava), oysters (Rhynchostreon suborbiculatum), crustaceans and echinoderms (Néraudeau et al., 2005). The rich and diverse vertebrate fauna is dominated by coastal marine species such as elasmobranchs (e.g. Tribodus morlati, Haimirichia amonensis), actinopterygian fishes (e.g. pycnodontids) and the primitive snake Simoliophis rochebrunei. Terrestrial species are relatively common, including mostly turtles, crocodyliforms, dinosaurs, and pterosaurs (Néraudeau et al., 2005; Vullo and Néraudeau, 2008); mammals are known only by the two teeth described here.

3. Systematic palaeontology

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

Marsupialiformes Vullo et al., 2009

Stagodontidae Marsh, 1889

Stagodontidae indet.

3.1. Specimens

MNHN CCH5, right third lowe. premolar; MNHN CCH6, right anterior upper molar fragment. Specimens catalogued in the planmal collection from the Cenomanian of Charentes (CCH), Muséum national d'Hieroire naturelle (MNHN), Paris.

3.2. Locality and horizon

Les Renardières quarry near Lussant (northern Aquitaine Basin, SW France), middle part of subunit B1 (bed B1s), lower Cenomanian.

3.3. Description

MNHN CCH 5 is interpreted as a right third lower premolar (Rp3) (Fig. 2A–E). This two-rooted premolariform tooth has a robust, inflated crown. The crown is longer (3.22 mm)

than wide (1.79 mm). The protoconid is flanked anterolingually by a poorly defined cuspule (paraconid), and posteriorly by a relatively well-developed basined heel. Faint ridges are present anteriorly from the apex of the protoconid to the small cuspule, and posteriorly from the apex of the protoconid to the anterolabial part of the talonid. The posterior region of the talonid shows a well-developed cusp (hypoconulid), which is linked to the base of the protoconid by a low, blunt labial crest. The lingual and posterior surfaces of the protoconid show a slightly rugose enamel. The protoconid shows a large subhorizontal apical wear facet indicating significant abrasion. Smaller oblique attritional wear facet s are also present posterolabial to the apex of the protoconid and on the labia? sixte of the hypoconulid. Just below the crown, the distal root is larger in cross section u. an the mesial root.

MNHN CCH6 is a right anterior upper molar fragment (RM1 or 2?), consisting of the posterolabial part of the crown (preserved/esti. ateu anteroposterior length: 1.59/~2.10 mm; preserved/estimated labiolingual width: 1.2 /~2.30 mm) (Fig. 2F–I, Fig. 3A). This tooth fragment shows the metacone, the posterolabial slope of the paracone, and the posterior half of the stylar shelf (bearing the stylar upps C and D, and the postmetacrista). The labial margin of the crown is broke: at the level of the ectoflexus. No roots are preserved. This tooth shows a brachyodont and outpodont morphology, with low and blunt cusps. The stylar shelf is relatively wide. The well- leveloped metastylar lobe is rounded and projects labially in occlusal view. An ectoflexus is present and seems to have been relatively deep. The base paracone is slightly more labially placed than the base of the metacone. The labial face of the metacone, the paracone and the metacone may have been subequal in basal anteroposterior length. Cusp D is inflated, with no labiolingual compression; it is larger and taller than cusp C. The small, low stylar cusp C is labiolingually oriented, showing a comma-shaped apical wear facet. Cusp C is shifted lingually, with a short accessory crest approaching the deepest

point of the centrocrista; thus, in occlusal view, cusp C is well separated from the labial edge of the crown, being placed anterolingually to cusp D and lingually to the ectoflexus. In labial view, the paracone and the metacone are well separated by a broad, U-shaped valley. In its deepest region, the centrocrista is slightly deflected labially in occlusal view, corresponding to an incipient dilambdodont pattern (see Butler, 1996); it approaches the stylar shelf and almost contacts the lingual base of the stylar cusp C. This incipient dilambdodont morphology indicates a well-developed shearing function with the crest of the hypoconid; this shearing function is actually marked by a well-developed wear facet on the metacone. A blunt transverse crest descends along the lingual "ace of the cusp D and terminates at the base of the metacone. The postmetacrista is transverse (i.e. labiolingually oriented). It bears a few cuspules, including a very small cusp "c" (also designated as "metacrista cusp"; see Crompton, 1971; Kielar -a. w/rowska and Dashzeveg, 1989) close to the metacone. There is no metacingulum.

3.4. Comparisons

The preserved portio. of MNHN CCH6 shows a relatively broad stylar shelf with well-developed stylar cospect and D, and a relatively short postmetacrista. This is consistent with an assignment to Marsupialiformes, i.e. non-deltatheroidan metatherians (Kielan-Jaworowska et al., 2004; Vullo et al., 2009; Williamson et al., 2014). Among Cretaceous metatherians, upper molars of deltatheroidans show little or no development of stylar cusps and have a distal stylar shelf more transversely developed, characterized by a long and salient postmetacrista (Kielan-Jaworowska et al., 2004). In Cretaceous eutherians, upper molars have a narrower stylar shelf and are characterized by a strong reduction or loss of stylar cusps (Kielan-Jaworowska et al., 2004). These dental features can be clearly observed in the zhelestids (e.g. *Labes* and *Lainodon*) from the Campanian–Maastrichtian of France and Spain

(Gheerbrant and Astibia, 2012; Martin et al., 2015), which represent the only eutherian group so far identified in the Upper Cretaceous of Europe.

Among comparable mid-Cretaceous taxa (including both Tribosphenida incertae sedis and Marsupialiformes), the Les Renardières marsupialiform is most similar to Pariadens (Eaton, 1993) in being relatively large and in having paracone and metacone well separated by a broad U-shaped valley, strong stylar cusps C and D, a labiolingualy oriented cusp C approaching the deepest point of the centrocrista, and presence of a few cuspules (including a small cusp "c") on the postmetacrista; however, *Pariadens* is 'arg, r and has a more oblique postmetacrista (Fig. 3B). Arcantiodelphys is significantly smaller and has stylar cusps C and D that are less developed (Vullo et al., 2009). Dakota ien: is well distinct, with 1) D. morrowi having a less rounded metastylar lobe, a less developed ecoflexus, and a stylar cusp C in a more labial position (Eaton, 1993); and 2) D. Partrutus having closely spaced paracone and metacone, a V-shaped centrocrista in labia. view, and stylar cusps C and D less developed (Cifelli et al., 2016). Eoalphadon has atvia" cusps C and D that are less developed and a postmetacrista that is more straight and oblique (Eaton, 1993, 2009); other "alphadontids" such as *Protalphadon* (Eaton, 19,3) and *Varalphadon* (Carneiro, 2018) have upper molars more compressed anteror oscentroly, a V-shaped centrocrista in labial view, and a stylar cusp C weakly developed or at sent. Sinbadelphys and Adelodelphys are significantly smaller and have upper molars more compressed anteroposteriorly, with slender paracone and metacone, and stylar cusp C and D absent (Cifelli, 2004). Culicolestes has upper molars with paracone and metacone well joined, a wide stylar shelf, and a stylar cusp C in labial position, distantly located from the paracone and metacone (Cifelli, 2004). Kokopellia has upper molars devoid of stylar cusps C and D (Cifelli and de Muizon, 1997).

Mid-Cretaceous (Albian–Cenomanian) metatherians and eutherians generally have relatively slender, not enlarged premolariform teeth, clearly different from MNHN CCH5

(Kielan-Jaworowska et al., 2004). For instance, in the few Cenomanian marsupialiforms for which posterior lower premolars are known (e.g. *Kokopellia* [Cifelli, 1993; Cifelli and de Muizon, 1997] and *Eoalphadon* [Eaton, 1993, 2009]), these teeth are smaller, not inflated, and markedly less robust than MNHN CCH5. Unfortunately, the premolars of *Pariadens* are unknown to date.

4. Discussion

Stagodontidae have long been thought to be reduced to the uppermost Cretaceous (Santonian-Maastrichtian) of North America, represented here by Eodelphis and Didelphodon (Fox, 1981; Fox and Naylor, 2006). Another genus, Pariadens, from the Cenomanian of Utah, was described as a possible primitive staged ontid (Cifelli and Eaton, 1987; Eaton, 1993; Cifelli, 2004); subsequent studies have el her refuted (e.g. Fox and Naylor, 2006; Williamson et al., 2014; Scott and Fox, 2015) or supported (e.g. Kielan-Jaworowska et al., 2004; Averianov et al., 2010; Williamson et al., 2012; Bi et al., 2015; Rougier et al., 2015; Wilson et al., 2016; Carneiro, 2018) dris contative assignment. Recently, Cohen (2018) has described two unequivocal stagodo. tids, Fumodelphodon and Hoodootherium, from the Turonian of Utah, and confirmed the placement of Pariadens within Stagodontidae. We follow here Cohen's (2018) conclusions in considering Pariadens as the earliest and less derived member of Stagodontidae. Finally, *Eobrasilia* is an enigmatic specialized marsupialiform from the Eocene of Brazil that shows stagodontid-like dental features, including an enlarged and inflated third lower premolar. Previously described as a didelphid (Simpson, 1947; Marshall, 1984), Eobrasilia was later recognized as sister taxon to Didelphodon in some phylogenetic analyses (Ladevèze and de Muizon, 2010; Carneiro and Oliveira, 2017). Carneiro and

Oliveira (2017) formally included *Eobrasilia* in Stagodontidae and provided an emended diagnosis for the family, but this assignment has recently been challenged (Eldridge et al., 2019).

The two mammalian teeth from the Les Renardières quarry are interpreted as belonging to the same marsupialiform species, as suggested by their compatible size and overall robust construction with low and inflated cusps. The Les Renardières marsupialiform is referred to Stagodontidae on the basis of a combination of several features, including (1) relatively large size compared with other Cretaceous marsupir fito ms; (2) enlarged and inflated third lower premolar with heavy apical wear facet, indicative of a possible crushing function and abrasive diet; (3) upper molars with a labor neurally oriented and lingually shifted stylar cusp C; and (4) absence of a metacingulum. This suite of characters is present in the typical stagodontid *Eodelphis*, although in his genus the C region of the stylar shelf bears a variable number of irregular cuspules rau. r than a true cusp C (Fox, 1981; Fox and Naylor, 2006; Scott and Fox, 2015). Furthermore, the size difference observed between MNHN CCH5 and MNHN CCH6 is consistent v iti, that reported between the enlarged p3 and the relatively small M1 of Eodelphis (Fox, 1981: Scott and Fox, 2015). The three Cenomanian–Turonian stagodontid genera (i.e. Fan. dens, Fumodelphodon, and Hoodootherium) are less well documented (Cifelli, 1990: Eaton, 1993; Cohen, 2018), but the available material shows similarities with the teeth from Les Renardières. The p3 of *Hoodootherium* bears a heavily worn protoconid; it is inflated and has a small posterior heel (Cifelli, 1990; Cohen, 2018). The p3 of *Fumodelphodon* is enlarged and bulbous, and the only molariform tooth (deciduous P3) known for this genus has a labiolingually oriented stylar cusp C (Cohen, 2018). Although premolars are unknown for Pariadens, this large genus has upper molars with no metacingulum and in which stylar cusp C can be labiolingually oriented (Eaton, 1993). Interestingly, the Les Renardières form supports the assignment of Pariadens to

Stagodontidae in having both a *Pariadens*-like upper molar morphology and a third lower premolar with stagodontid features.

The discovery of a stagodontid in the Cenomanian of Western Europe is consistent with the known stratigraphical range of the family in North America and reveals that an intercontinental dispersal event occurred early in the evolutionary history of this group of specialized marsupialiforms, around 100 million years ago. In North America, Cenomanian marsupialiforms are almost exclusively known from the western part of the continent (Laramidia) (Kielan-Jaworowska et al., 2004; Williamson et $\epsilon_{1,2}$, 2014), since their presence in the eastern part (Appalachia) is based only on a single toot 1 (lo wer molar) from the Woodbine Formation of Texas (Jacobs and Winkler, 1998). The cio, ely related genera *Dakotadens* from Utah (Eaton, 1993; Cifelli et al., 2016) and Arcantiouelphys from France (Vullo et al., 2009), together with the Woodbine taxon, indicate th. ⁺ faunal exchanges may have occurred between Laramidia and the European archipelago (, Appalachia and Greenland; see Fig. 1C) during the latest Albian–early Cenomanian Jow sca level stand, as previously suggested for other vertebrate groups such as early hadronauromorph dinosaurs (Head, 1998; Vullo et al., 2007; Csiki-Sava et al., 2015). Similari, stagodontids may have dispersed between western North America and Europe around the Albian–Cenomanian boundary. This hypothesis would be consistent with the presenve of a relictual member of this group in the Campanian of New Jersey (Grandstaff et al., 2000; Denton and O'Neill, 2010). If confirmed, the Appalachian occurrence of a stagodontid said to be more advanced than Pariadens but less derived than Eodelphis and Didelphodon (Denton and O'Neill, 2010) may result from an Albian-Cenomanian dispersal followed by a post-Cenomanian geographical isolation (subsequent to global sea-level rise) and local evolution.

Recently, *Arcantiodelphys* was considered as a plesiomorphic (non-metatherian) tribosphenidan (Eaton and Cifelli, 2013), and *Sinodelphys* from the Lower Cretaceous

(Barremian) of China, originally described as the oldest metatherian (Luo et al., 2003), was reinterpreted as a eutherian (Bi et al., 2018). Consequently, Bi et al. (2018) did not take into account these two European and Asiatic taxa in their palaeobiogeographical conclusions and argued that the early evolutionary history of metatherians took place exclusively in North America, during the Albian–Cenomanian interval. In this context, the discovery of a marsupialiform more advanced than *Arcantiodelphys* in the Cenomanian of France is of considerable importance. Our finding demonstrates that early marsupialiforms were definitely present in the mid-Cretaceous of Europe, thus confirming that their palaeogeographical distribution was wider than previously thought.

5. Conclusions

As underlined in previous studies, the mid-Cretaceous vertebrate-bearing localities of the northern Aquitaine Basin (SW Trance) offer unique opportunity to document and understand the distribution of each marsupialiform mammals outside North America. The present study provides evidence indicating that unequivocal marsupialiforms were present in the European archipelage as early as the Cenomanian. The Les Renardières mammal, more derived than *Arcantiodelphys* from the same area, is referred to Stagodontidae based on its dental features; although it may represent a new taxon, we prefer to leave it in open nomenclature (Stagodontidae indet.) pending further discoveries. This is the first report of Stagodontidae in Europe. Furthermore, the Les Renardières stagodontid is one of the oldest known members of the group, together with *Pariadens* from the Cenomanian of Utah. This suggests that early stagodontids were widely distributed from western North America (Laramidia) to the European archipelago.

Declaration of competing interest

The authors declare no competing interests.

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Fig. 1. A, Locations of the two Cenomanian mammal-bearing localities of the northern Aquitaine Basin (Rochefort area, Charente-Maritime department, SW France): Les Renardières quarry at Tonnay-Charente (present study; dark grey star) and Font-de-Benon quarry at Archingeay-Les Nouillers (type and only locality of *Arcantiodelphys marchandi*; light grey star). B) Generalized section of the lowermost Cenomanian of the Rochefort area, showing the stratigraphical positions of the Les Renardières stagodontid (dark grey silhouette) and *Arcantiodelphys marchandi* (light grey silhouette). C) Early Cenomanian global palaeogeography showing the location of the Aquitaine Basin, Western Europe (black star).

Abbreviations: Af, Africa; Ap, Appalachia (eastern North America); As, Asia; Eu, European archipelago; La, Laramidia (western North America); SA, South America.

Fig. 2. Indeterminate stagodontid marsupialiform from the lower Cenomanian (Upper Cretaceous) of the Les Renardières quarry, southwestern France. A–E, MNHN CCH5, right lower premolar (Rp3) in labial (A), lingual (B), occlusal (C), anterior (D) and posterior (E) views. F–I, MNHN CCH6, right upper molar (RM1 or 2?) fragment in labial (F), lingual (G), occlusal (H, stereopair) and posterior (I) views. Scale bars equal 1.1m.

Fig. 3. Interpretative line drawing of upper molar fragment (MNHN CCH6) of the Les
Renardières stagodontid (A) and comparison with complete upper molar (Museum of
Northern Arizona V5843; mirror image) of *Pariaaens kirklandi* from the Cenomanian of Utah
(B), in occlusal view (after Eaton, 1993). So ale bars equal 1 mm.

Highlights

- Two marsupialiform teeth itom the mid-Cretaceous of France are described.
- Both specimens are conspecific and referred to an indeterminate stagodontid.
- This is the first occurre, ce of this North American group in Europe.
- Early marsupial in the subset of between Laramidia and the European archipelago.





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