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The oldest modern therian mammal from Europe and its bearing on stem marsupial paleobiogeography

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We report the discovery of mammalian tribosphenic teeth from the basal Cenomanian of southwestern France that we refer to a new primitive marsupial-like form identified as a basal taxon of Marsupialiformes, a new clade recognized here to include the crown group Marsupialia and primitive stem lineages more closely related to Marsupialia than to Deltatheroidea. *Arcantiodelphys marchandi* gen et sp nov. shares several significant marsupial-like features (*s.l.*) with marsupialiform taxa known from the North American Mid-Cretaceous. Among marsupialiforms, it shows a closer resemblance to *Dakotadens*. This resemblance, which is plesiomorphic within “tribotherians,” makes *Arcantiodelphys* one of the most archaic known Marsupialiformes. Moreover, *Arcantiodelphys* is characterized by an original and precocious crushing specialization. Both the plesiomorphic and autapomorphic characteristics of *Arcantiodelphys* among Marsupialiformes might be explained by an Eastern origin from Asian stem metatherians, with some in situ European evolution. In addition, the presence of a mammal with North American affinities in western Europe during the early Late Cretaceous provides further evidence of a large Euramerican biogeographical province at this age or slightly before. Concerning the paleobiogeographical history of the first stem marsupialiforms during the Albian–Cenomanian interval, 2 possible dispersal routes from an Asian metatherian ancestry can be proposed: Asia to Europe via North America and Asia to North America via Europe. The main significance of the Archingeay-Les Nouillers mammal discovery is that it indicates that the beginning of the stem marsupialiforms history involved not only North America but also Europe, and that this early history in Europe remains virtually unknown.

Cretaceous | mammals | Marsupialiformes nov.

The early evolution of modern therians (i.e., metatherian and eutherian boreosphenidan mammals) is documented mainly in North America and Asia, where numerous rich Mid-Cretaceous microvertebrate localities are known. In Europe, there is a major gap in the mammal fossil record for the Late Cretaceous, especially for the totally blank Aptian–Santonian interval (1). New Cenomanian localities in western France (Charentes) have yielded some rich coastal assemblages, including continental vertebrates (2, 3). Some rare, indeterminate mammal teeth were reported from Charentes (3, 4), attesting to the presence of this group in the terrestrial ecosystems of the Mid-Cretaceous European archipelago. The present study describes a new mammal from basal Cenomanian deposits of the Font-de-Benon quarry, at Archingeay-Les Nouillers, Charentes (Fig. S1). The new mammal material reported here includes 4 marsupial-like tribosphenic fragmentary teeth, which provide information on the early European boreosphenids. The earliest therian mammals [boreosphenidans *sensu* Luo et al. (5)] from Europe are *Aegialodon* and *Tribactonodon* from the Early Cretaceous of England (6, 7). The mammal from Archingeay-Les Nouillers is the oldest modern therian known so far in Europe,

that is, the oldest European representative of the clade including metatherians and eutherians.

Systematic Paleontology. Boreosphenida Luo, Cifelli, and Kielan-Jaworowska, 2001; Metatheria Huxley, 1880; Marsupialiformes supercohort nov.; Family indet.; *Arcantiodelphys marchandi* gen et sp nov.

Comments. Marsupialiformes [= Marsupialia *sensu* Kielan-Jaworowska et al. (1)] is erected to account for the crown group Marsupialia (extant marsupials and related extinct fossil taxa) plus all stem marsupialiform taxa that are more closely related to them, as their sister taxa, than to Deltatheroidea and basal Metatheria. Basal marsupialiforms, such as the North American taxa from the Early/Late Cretaceous (8), include the stem groups of the crown marsupials. Basal marsupialiforms include primitive Cretaceous taxa previously gathered in the paraphyletic taxon “Ameridelphia” (1, 8). Metatheria includes Marsupialiformes and Deltatheroidea (presumed sister groups), plus basal metatherians, such as *Sinodelphys*.

Holotype. The holotype MNHN CCH4 is as follows: Right upper (anterior?) molar, possibly an anterior one, with mesial part broken; Charentes Cenomanian collections of the Muséum national d'Histoire naturelle (MNHN CCH) in Paris (Fig. 1). Hypodigm: Holotype MNHN CCH4; MNHN CCH1, trigonid of left lower molar, M₁; MNHN CCH2, talonid of right lower molar; MNHN CCH3, trigonid of right lower molar, M₂ or more posterior molar.

Etymology. The generic name is based on *Arcantius* (Latin), the name of the Gallo-Roman domain from which the village of Archingeay developed, and *delphys* (Greek), the term used for marsupials. The specific name is dedicated to Joseph Marchand, who sorted part of the material and discovered the holotype, and to the Marchand family, owner of the Font-de-Benon quarry.

Locality and Horizon. The hypodigm was collected in the Font-de-Benon quarry, Archingeay-Les Nouillers, Charente-Maritime, southwestern France, Cenomanian. The horizon corresponds to the sand at the base of the unit B (subunit B1; level B1cs), which is early Cenomanian in age (9).

Diagnosis. Tribosphenic mammal with marsupialiform characters: Paraconid enlarged (but smaller than metaconid) and lingual (posterior molars), hypoconulid lingual and approxi-

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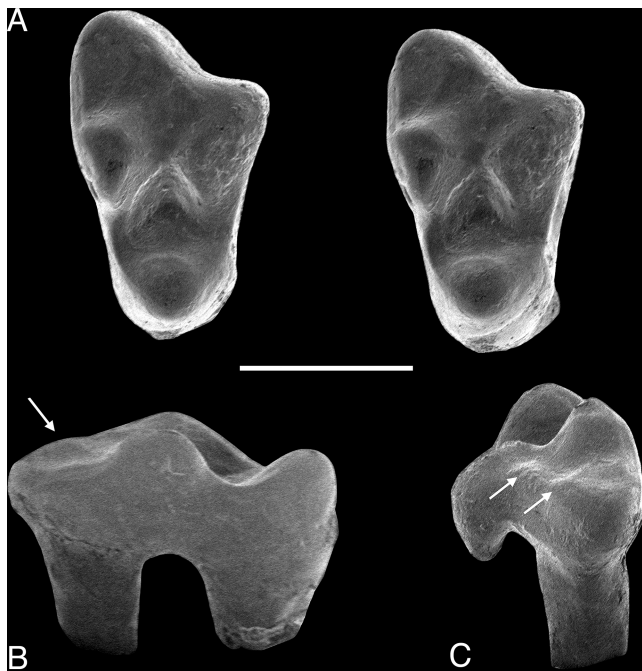


Fig. 1. *A. marchandi* gen et sp nov., holotype, MNHN CCH4, anterior(?) right upper molar in occlusal (A) (stereophotography), distal (B), and labial (C) views; SEM photographs. Arrows indicate stylar cusps C and D. (Scale bar: 1 mm.)

mated to entoconid (but not twinned), well-developed entoconid, paracone and metacone of similar size and well separated, wide stylar shelf, stylar cusps D and C present (but small), protocone well developed (uncompressed), no lingual cingulum. Molar morphology is similar to that of the earliest North American basal marsupialiforms, such as *Dakotadens*, *Iugomortiferum*, *Adelodelphys*, *Synbadelphys*, and *Pariadens* (8, 10–12). It especially shares the robust construction (i.e., low and bulbous cusps, low trigonid, wide talonid, large protocone) and wear pattern, indicating an early specialized crushing function, with *Dakotadens* and *Iugomortiferum*. It differs from the Cretaceous stem marsupialiforms (except *Dakotadens*) in primitive features, such as absence of postcingulid, a postprotocrista that does not extend labially at the posterior base of the metacone (no metacingulum and no double-rank postvallum–prevallid shearing), absence of conules (traces in *Dakotadens*) and their internal crest, and absence of a carnassial notch on the postmetacrista. *Iugomortiferum* differs in these traits (although conules are reduced), and in a less lingual, less inflated, and more anterior protocone; a cristid obliqua more lingual on the trigonid; and a twinned hypoconulid and entoconid. It differs from *Dakotadens* in the following traits: more inflated cusps, absence of conules, approximated but not twinned hypoconulid and entoconid (separated by a small distolingual notch), more lingual and more inflated protocone, more inflated protoconid, less distal metaconid, more compressed hypoconid, and smaller hypoconulid with respect to the entoconid. It is among the smallest known marsupialiforms, with *Adelodelphys* and *Synbadelphys*.

Dimensions: Upper molar CCH4: Minimal estimated length, >1.14 mm; width, 1.86 mm (protocone length, 0.7 mm). Lower molars: See Table 1.

Description and Comparisons. CCH4 (Fig. 1 and Fig. 2 D and F) is a 3-rooted upper molariform tooth. The paracone and parastylar area are broken and missing. The prominent metastylar lobe and asymmetric ectoflexus suggest an anterior molar. The tooth is characterized by a robust and bunodont morphology, with low

Table 1. Dimensions of the lower teeth of *A. marchandi* gen et sp nov. (in mm)

	L trigonid	W trigonid	L talonid	W talonid
CCH1, M ₁₇	1.3	1.15		
CCH2, M ₁ or M ₂ or M ₃			≥0.95	1.3
CCH3, M ₂ or M ₃ or M ₄	1.2	1.25		

and inflated cusps and crests. The occlusal outline seems short and wide, but this might be unreliable because of the broken mesial part of the crown (including the paracone). The metastylar lobe is well developed, with long and predominantly transversal postmetacrista and a wide stylar shelf labial to the metacone. The ectoflexus is deep and asymmetric, with a wider metastylar area according our comparative reconstruction. The ectocingulum and stylar cusps are worn, but cusps D and C are distinctly inflated. A slight but distinct oblique crest links cusp D to the base of the metacone. The postmetacrista is robust and has no carnassial notch. The paracone is broken but apparently is similar in size to the metacone or even slightly larger, judging from its greater lingual extension. Paracone and metacone are more compressed mesiodistally than labiolingually. These are well separated, but not deeply. The conules are absent, as are their internal crests. The postprotocrista links the lingual flank of the metacone, so that there is no metacingulum. The protofossa (trigon basin) is large and nearly as long as it is wide. The protocone is remarkably well developed, both longitudinally and transversely. Its labial flank is inflated at the apex, lingual to the paracone–metacone notch, and slightly procumbent. There are no lingual cingula.

CCH1 (Figs. 2A and S2A–D) is a trigonid of a tribosphenic left lower molar. It preserves only the most anterior part of the talonid. CCH1 is identified as an M₁, based on its mesiodistally expanded trigonid and its paraconid shifted mesially. The trigonid is low and displays a robust and bunodont morphology; the cusps are inflated, low, and bulbous, and the wear is dominated by abrasion. Only the most distal part of the precingulid is preserved. The occlusal outline is triangular, with a very trans-

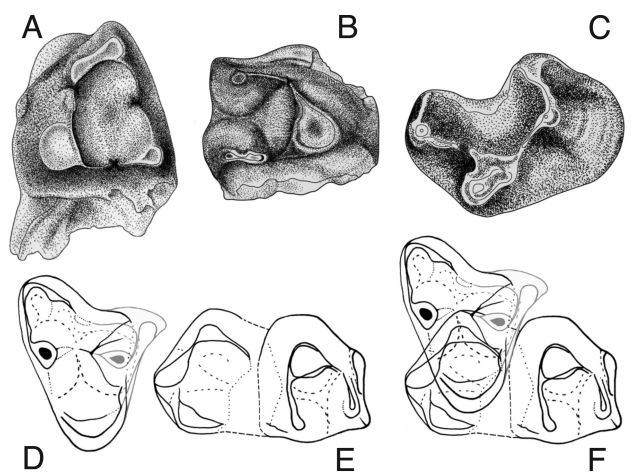


Fig. 2. Drawings and reconstruction of the teeth of *A. marchandi* gen et sp nov. (A) MNHN CCH1, trigonid of left lower molar, M₁, in occlusal view. (B) MNHN CCH3, trigonid of right lower molar, M₂₇, M₃₇, or M₄₇, in occlusal view. (C) MNHN CCH2, talonid of right lower molar, in occlusal view. (D–F) Tentative reconstruction (occlusal views) of upper (D) and lower molars (E), and of their occlusal sketch (F). (D) is based on the holotype CCH4 and anterior molars of *Adelodelphys* (for parastylar area). (E) is based on CCH2 (talonid) and CCH3 (trigonid). (Scale bars: 1 mm.)

verse protocristid and a paraconid that is well shifted mesially. The trigonid crests show wide notches, but not carnassial notches. The paraconid is well developed, nearly as large and high as the metaconid. It is located lingually; its mesiolingual flank is very convex and salient mesially above the root (paraconid keel). The paraconid and metaconid are linked lingually by a small crest (premetacristid), which closes the trigonid basin lingually. The protoconid apex is truncated by the abrasion. It is slightly elongated mesiodistally. The trigonid basin is large and extended mesiodistally (longer than it is wide). The mesial flank of the protoconid is slightly inflated labially toward the paraconid, close to the paracristid notch. Judging from the preserved part of the cristid obliqua, the talonid is wider than the trigonid. The cristid obliqua abuts noticeably labially against the trigonid, between the protoconid apex and the protocristid notch; consequently, the hypoflexid is shallow. A postmetacristid is present at the base of the metaconid. The ectocingulid is absent.

CCH2 (Figs. 2 *C*, *E*, and *F*) is the talonid of an unidentified left lower tribosphenic molar, but not of the most distal one, as illustrated by the hypoconulid morphology. Although the base of the crown is broken, it probably was low. In an occlusal view, this talonid is short and wide. The postcingulid is absent. The hypoconulid is shifted lingually, but is not twinned with the entoconid. The 2 cusps are separated by a deep notch, which is distinct in a distolingual view of the postcristid. As a result, the hypoconulid is salient distolingually. Because of the strong abrasion of the hypoconulid with respect to the entoconid, the 2 cusps appear less well approximated than they probably were. The cristid obliqua is slightly more lingual mesially than on CCH1, and the hypoflexid seems deeper.

CCH3 (Fig. 2 *B*, *E*, and *F* and Fig. S2 *E* and *F*), is the trigonid of a right lower molar similar in size to CCH1. It belongs to a more posterior molar ($M_{2?}$, $M_{3?}$, or $M_{4?}$) than CCH1, based on its more mesiodistally compressed trigonid and more lingual paraconid. The trigonid is low. The paraconid is only slightly smaller than the metaconid and slightly more labial. Its mesiolingual flank is strongly salient mesially, forming a prominent vertical mesiolingual “keel” that is somewhat inflated or crested. The protoconid apex is even more truncated by abrasion than in CCH1. The trigonid basin is opened lingually, with no trace of a lingual crest as seen in CCH1. The precingulid, although damaged, is well developed mesiodistally. The protocristid is very transverse. It bears a deeper notch than the paracristid. The postmetacristid is well developed. The cristid obliqua abuts labially against the trigonid, as in CCH1.

Wear is illustrated by attrition facets resulting from the labial phase [nomenclature of Crompton (13)] and by apical abrasion. CCH1 shows a small shearing wear facet 2 (postvallum–prevallid shearing facet) on the mesial flank of the paraconid and apical abrasion of the paraconid and protoconid. The shearing wear facet 1 is not distinct. CCH2 shows strong apical abrasion of the hypoconulid. On the internal flank of the entoconid is a well-developed wear facet 6, resulting from the postprotocrista of opposite upper molar. On CCH3, the shearing wear facet 2 is extended on the mesial flank of the protoconid. The wear facet 1 (prevallum–postvallid shearing facet) is distinct on the labial margin of the distal flank of the protoconid. There is also a well-developed wear facet 5 on the postmetacristid. Abrasion is well developed at the protoconid apex and slight on the protocristid. On CCH4, abrasion strongly affects the apices of the protocone, metacone, and postmetacrista. A triangular wear facet 9 is distinct in the lingual flank of the protocone, denoting a developed crushing-grinding function. Other wear facets are indistinct.

The 4 mammal specimens from Archingeay-Les Nouillers present close morphological affinities, suggesting that they belong to the same mammal species. In particular, they share an overall robust construction with low and inflated cusps, a similar

wear pattern with developed abrasion, and are comparable in size. The affinity of the tribosphenic upper and lower molars from Archingeay-Les Nouillers is illustrated by their resemblance in robust general morphology and related crushing (horizontal) wear pattern, the absence of carnassial notches, and overall consistent occlusal relative pattern, as illustrated by their occlusal relationship (Fig. 2*F*). The occlusal relationship shows a slight size difference (CCH4 is slightly smaller), but this is within the range of the intraspecific variation. Keep in mind that this specific association is based on very fragmentary material and needs to be confirmed by additional material, including more complete teeth and tooth rows. In the meantime, our interpretation, based on anatomical data, is considered the most consistent.

The Archingeay-Les Nouillers material documents the typical tribosphenic molar pattern of therian mammals. These molars have a remarkably robust construction, with low and bulbous cusps, a low trigonid, a wide talonid, broad protofossa, and a large and inflated protocone. Together with the developed abrasion and the grinding wear facet 9 on the holotype, this suggests an early therian species with developed crushing diet. The Archingeay-Les Nouillers material belongs to a new therian mammal, *Arcantiodelphys marchandi* gen et sp nov., which is characterized by an original association of features that are summarized and compared in Tables S1 and S2. These features also are included in the character list used for the phylogenetic analysis (see *SI Appendix*).

Among all known Cretaceous tribosphenic mammals, *A. marchandi* most closely recalls the most primitive known marsupialiforms and some peculiar “tribotherians” (i.e., stem boreosphenidans). It differs from primitive eutherians in the enlarged and lingually placed paraconid, the paraconid keel, the similarly sized and well-separated paracone and metacone, and the occurrence of styler cusps D and C. It differs from the deltatheroidans (Metatheria) in the large talonid and protocone, the narrower styler shelf, the shorter postmetacrista, and the smaller paraconid and paracristid.

Among all Cretaceous therians, *A. marchandi* most closely resembles *Dakotadens*, which was initially described as an indeterminate “tribotherian” with marsupial-like features (12), and which was recently referred to Marsupialia (= Marsupialiformes here) by Kielan-Jaworowska et al. (1). It is noteworthy that *Dakotadens* is of contemporaneous Cenomanian age with *A. marchandi*, as is *Pariadens*. *A. marchandi* also closely resembles several other early North American stem marsupialiforms, previously classified as “Ameridelphia” (8). Its marsupial-like features (*sensu lato*, i.e., marsupialiform features) are the similarly sized and well-separated paracone and metacone [character K10 (1–2)], the wide styler shelf [K3 (0)], the occurrence of styler cusps D and C [K6 (1) and K7 (1)] (although small on known material), the well-developed (uncompressed) protocone [K4 (1)], the hypoconulid lingually approximated (but not connate) to entoconid [K (1)], the large and lingual paraconid [K21 (1), 22 (1)], the low trigonid [K17 (1)], the wide talonid [K30 (2)], the large entoconid [K32 (3)], and the cristid obliqua, which joins the trigonid labially, below the protoconid [K27 (2)] and defines a shallow hypoflexid [K28 (2)]. Other features known mostly in basal stem marsupialiforms are the low and bulbous cusps [K1 (2)], the low protoconid [K23 (1)], the distinct postmetacristid [K29 (0)], the mesiolingual flank of the paraconid and prominent above the root [K19 (0)], the weak ectocingulum and styler cusps D and C, and the wide styler shelf with a long and transverse postmetacrista [K12 (1)] (but less developed than in deltatheroidans). The small size also is reminiscent of the smallest known Cretaceous marsupialiforms, such as *Sinbadelphys* and *Adelodelphys*. The paraconid keel [K19 (0)] might be primitive, corresponding to a probable trace of the eupantotherian and “tribotherian” cusp e. Features 6 (1), 10 (1–2), 12 (0), 21 (0), 22

(0), and 29 (0) (see *SI Appendix*) also are found in “tribotherians” and might be primitive. However, most of these traits—especially the large (but smaller than the metaconid) and lingual paraconid—are also reminiscent of marsupialiforms. Features 4 (1), 27 (2), 28 (2), 30 (2), 31 (1), and 32 (3) (see *SI Appendix*) are the most significant derived marsupialiform features of *A. marchandi*.

It is noteworthy that several of the derived features shared with stem marsupialiforms are remarkably poorly developed in *Arcantiodelphys*. This is especially true for the paraconid development and the hypoconulid–entoconid relationship. Several other remarkable features shared with *Dakotadens* are unknown in other stem marsupialiforms, including *Kokopellia*, the oldest known one (14, 15): the absence of the postcingulid [K34 (0)] and of the conules [K8 (0)] and their internal crests, the postprotocrista that does not extend labially at the base of the metacone [K9 (0)], and the protocone that is poorly shifted mesially [K14 (0)]. These characteristics of *Arcantiodelphys* are known in “tribotherians” and most likely correspond to symplesiomorphies retained in some of the most basal Marsupialiformes. *Dakotadens* was not formally included in “Marsupialia” (i.e., Marsupialiformes) by its author mainly because of some of these features, especially the absence of the postcingulid (12). However, in *A. marchandi* these primitive traits are associated with a suite of other features that are more common in early stem marsupialiforms than in any other early tribosphenic mammals. We also should emphasize that deltatheroidan metatherians lack the postcingulid and the labial extension of the postprotocrista, and also have a less mesially shifted protocone than in marsupialiforms. Overall, the morphology of *A. marchandi*, although still poorly known, clearly suggests an archaic stem Marsupialiformes. The species might belong to one of the most primitive marsupialiform metatherians known (Fig. 3A). It is even more primitive than the earlier *Kokopellia* in some remarkable traits [K8 (0), 9 (0), 14 (0), 34 (0)], although it also shows some specialized features in relation to it, such as the more lingual hypoconulid and the robust crushing molars that have a large and inflated protocone that displays wear facet 9.

Among primitive marsupialiforms, *A. marchandi* is characterized by an overall striking robust molar construction, with low and bulbous cusps, a large and inflated protocone, low trigonid and protoconid, a large hypoconid, and a wide talonid with a large basin. This construction indicates a predominantly crushing function, as also illustrated by the wear pattern with developed apical abrasion of the cusps (especially the protoconid and protocone). This construction also is known in *Dakotadens* and *Iugomortiferum*, but in a less advanced way, and most probably as a parallelism. Crushing molars with developed “horizontal wear” (abrasion) is considered by Fox and Naylor (16) to be a distinctive feature of early “marsupials” (i.e., stem marsupialiforms) with respect to other therian mammals. In *A. marchandi*, the crushing function associated with a large and inflated protocone with wear facet 9 is a noteworthy early specialization, possibly corresponding to an autapomorphy of the European lineage illustrated by *Arcantiodelphys*.

A cladistic analysis of the few known features of *A. marchandi* using the TNT program (17) was developed to test and formalize the position of *A. marchandi* within and among marsupialiforms (see *SI Appendix*). The analysis includes only characters observed in *Arcantiodelphys*, that is, 36 molar features, with 4 additional key characters (K37–40) related to the dental formula, which are diagnostic of the major therian clades (Eutheria, Metatheria, Deltatheroidea, and Marsupialiformes). The exact analysis confirms the relationships of *Arcantiodelphys* to marsupialiforms; however, it yields unusual results with respect to previous studies, such as a basal stem therian position of the Deltatheroidea versus the Metatheria (i.e., sister group of *Sinodelphys* + Marsupialiformes) and the derived position of primitive bun-

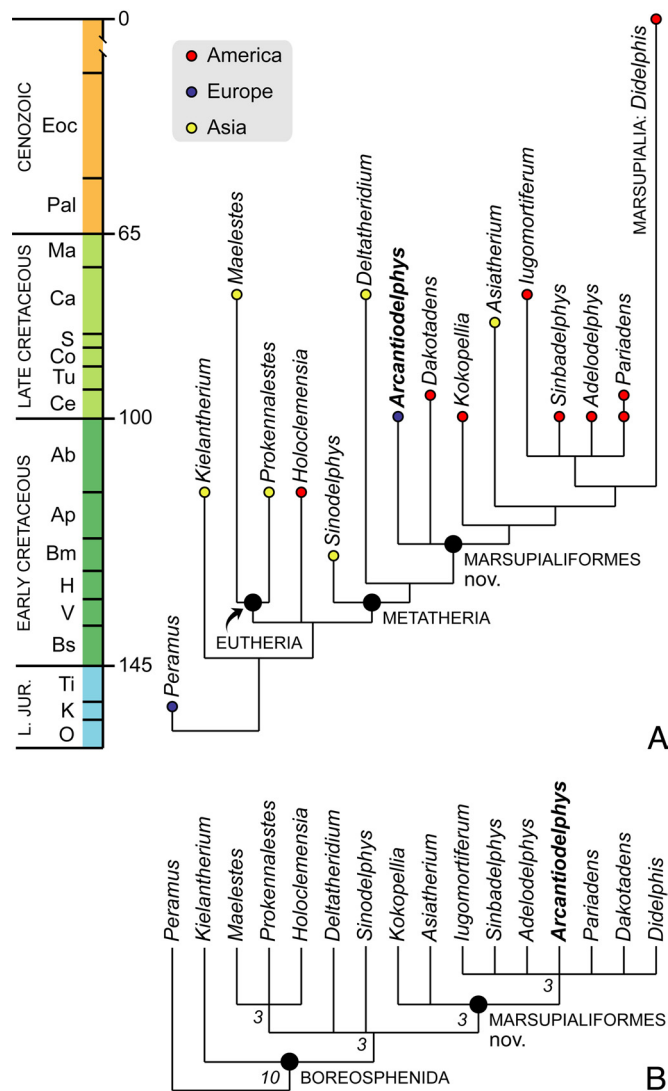


Fig. 3. Hypotheses on the phylogenetic relationships of *A. marchandi* gen et sp nov. (A) Schematic representation of the phylogenetic relationships (stratigraphically calibrated) of *A. marchandi* among other early therians and metatherians as hypothesized from the present study and comparisons. (B) Results of the parsimony analysis: cladistic relationships of *A. marchandi* among selected non-marsupialiform and marsupialiform taxa. (See *SI Appendix* for the complete analysis.) A single cladogram (RI: 56.1; CI: 71.5) was obtained from the exact analysis (implicit enumeration) with the TNT program (16) based on 36 molar characters plus 4 major diagnostic characters among tribosphenidans, related to the dental formula (see *SI Appendix*). Only the nodes with a Bremer support value ≥ 3 are reported and retained here from the consensus tree. Other nodes are fragile and do not fit previous analysis (e.g., *Deltatheridium* and *Sinodelphys* relative position; see text); they require further testing with additional data on *Arcantiodelphys*.

odont taxa such as *Dakotadens* and *Arcantiodelphys*, which are closer to *Didelphis* (i.e., to crown Marsupialia) than to the base of the Marsupialiformes. The stem therian position of the Deltatheroidea (based on, e.g., the central position of the hypoconulid) was previously suggested in the parsimony analysis of Cifelli (18), which also was based on molar features, which led the author to question their relationships with Marsupialia (Marsupialiformes here). The convergence of our results with Cifelli’s analysis is unexpected, given our addition of the recently discovered major taxa, such as *Sinodelphys*, *Asiatherium*, and *Kokopellia*. The derived position of *Dakotadens* and *Arcantiodelphys* is mainly the result of noticeably and unlikely reversions

favored by the parsimony analysis, such as the lingual postprotocrista, the absence of conules, the central protocone, and the absence of the postcingulid. Other shared features known in *Dakotadens* and *Arcantiodelphys*, as well as in *Iugomortiferum* (e.g., bunodonty, low protoconid, extended abrasion), are probably convergent.

Calculation of the Bremer support value (as well as the bootstrap value) shows that in fact only 3 nodes are well supported and reliable in this tree (Fig. 3B), among which are the Marsupialiformes, including *Arcantiodelphys*. Otherwise, it shows that several important points are poorly resolved in the parsimony analysis, including the relationships of *Arcantiodelphys* among Marsupialiformes and the relationships of basal taxa to Marsupialiformes, with the polytomy including especially Marsupialiformes, Eutheria, and *Holoclemensia*. These limitations of our analysis are probably linked to our poor knowledge of *Arcantiodelphys*, on which it is focused (e.g., mostly molar characters).

Conclusions

Implications for Marsupial and Marsupialiform Origin and Paleobiogeography. The new mammal from Archingeay-Les Nouillers is the first fossil discovery that fills the huge gap in the fossil record of the Mid-Cretaceous of Europe (1). *A. marchandi* is the oldest known European representative of the metatherian–eutherian clade. It also is the oldest known European stem marsupialiform and one of the oldest known Marsupialiformes. The only known older stem marsupialiform is *Kokopellia* from the Early Cretaceous (latest Albian). *Sinodelphys* from the Early Cretaceous (Barremian) of China is a much more primitive and basal metatherian that predates the deltatheroidan divergence (19). Moreover, *A. marchandi* is one of the most primitive stem marsupialiforms known so far (Fig. 3A), although its primitive features are interpreted as reversals in the parsimony analysis. It is most closely reminiscent of its subcontemporaneous *Dakotadens*, with which it shares such plesiomorphic characteristics as absence of the postcingulid, a central protocone, and a postprotocrista restricted lingually to the metacone, as well as the derived and probably convergent robust crushing molars.

The Archingeay-Les Nouillers discovery sheds new light on an unknown early center of the marsupialiform evolution, the Cretaceous of Europe. The only other known stem marsupialiform described in the Late Cretaceous of Europe is *Maastrichtidelphys* from the Maastrichtian of the Netherlands, an advanced form related to herpetotheriids (20). This family is considered the sister group of Marsupialia and thus would include the most derived stem marsupialiforms (21). *A. marchandi* fills a major gap in our knowledge of the early evolution of marsupialiforms in Europe. The discovery in southwest France (Charentes) of a new mammal most closely related to early North American stem marsupialiforms provides the first mammalian evidence of the wide Euramerican paleobiogeographical province (*s.l.*) in the Mid-Cretaceous. The early Euramerican continental province is well supported by affinities of other vertebrate taxa. Among dinosaurs, the early Cenomanian deposits of Charentes have yielded teeth of *Probractrosaurus*-grade iguanodontians (similar to *Protodadon* and *Eolambia*), nodosaurids, brachiosaurids, and troodontids (22). All of these forms are well represented in the North American Cenomanian assemblages, particularly in the Mussentuchit local fauna (upper Cedar Mountain Formation, Utah) (23, 24). The same observation can be made concerning the crocodyliform taxa, with atoposaurids, cf. bernissartiids, goniopholidids, and pholidosaurids occurring in both Utah and Charentes localities. Some of these dinosaurian and crocodyliform taxa also are present together with an indeterminate stem marsupialiform in the Woodbine Formation of Texas (25, 26), which also shares numerous coastal selachians with Charentes (27).

The discovery of *A. marchandi* shows that Europe was an

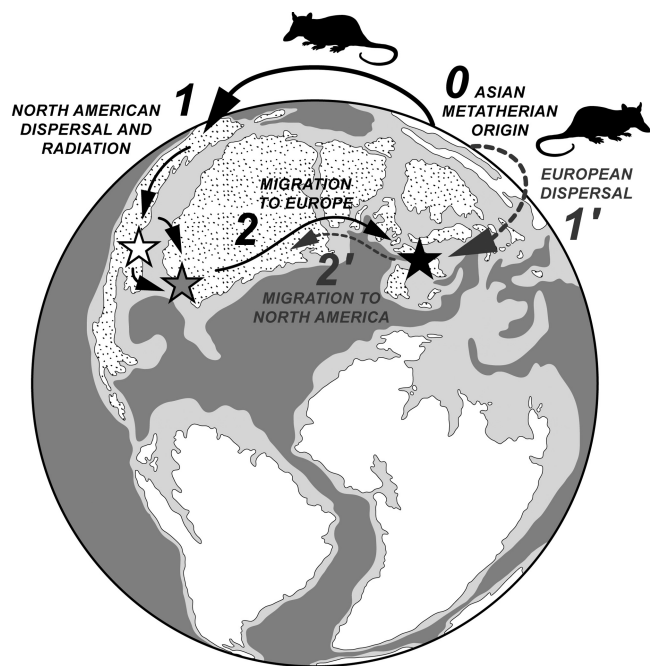


Fig. 4. Two possible scenarios for the early paleobiogeographical history of Marsupialiformes. 0, Marsupialiformes originated from an Asian Early Cretaceous metatherian stem group. 1, They reached North America via Beringia before the Albian–Cenomanian where they underwent the Late Cretaceous diversification. 2, This was followed by a dispersal from North America to Europe that occurred around Albian–Cenomanian boundary, explaining the origin of *Arcantiodelphys marchandi*. Hypothesis 1–2 is supported by the distribution of early Marsupialiformes in the western part of North America. Alternative hypothesis 1'–2': The metatherian stem group of Marsupialiformes dispersed from Asia to North America via Europe, which is supported by the primitive features of the Charentes taxon *A. marchandi*. The Cenomanian marsupialiforms occurrences of the Euramerican biogeographical province (dashed area) discussed in the present study are represented by stars (black star, Charentes, France; gray star, Woodbine Formation, Texas; white star, upper Cedar Mountain and Dakota Formations, Utah).

important area in the basal radiation of marsupialiforms, and closely fits with the current models of metatherian and marsupial paleobiogeographical history, which assume an early dispersal from a Laurasian and most likely an Asian center of origin (metatherian ancestry) to the modern Australian center of diversification, via the North and South American early centers of radiation (19, 28). Affinities of the Archingeay-Les Nouillers species suggest that the marsupialiform initial center of radiation involved a wide Euramerican continental province.

Although metatherians seem to have originated in Asia (e.g., *Sinodelphys*, deltatheroidans), the paleobiogeographical history and origin of the Cretaceous European and Euramerican marsupialiforms—and of the therians in general—remains mostly unresolved. Direct dispersals from Asia to North America are illustrated by several vertebrate taxa (29), some of which colonized Europe from North America, especially in the Late Cretaceous (20). But this does not exclude direct early dispersals from Asia to Europe, especially because the Ouralian seaway (Turgai strait) developed later, in the Turonian. Indeed, a Cretaceous dispersal from Asia explains the origin of the European zhelestids, *Gobiconodon*, kogaionids, amphilestines, and *Probractrosaurus*-grade iguanodontians (29–32). A comparison with Cretaceous North American marsupialiforms suggests that *A. marchandi* is a very primitive stem marsupialiform, despite the (unlikely) reversals implied by our parsimony analysis. Our view of the primitiveness of *Arcantiodelphys* would favor

an Asian origin and a trans-Ouralian dispersal (vs. a North American origin and a North Atlantic dispersal) (Fig. 4).

It is noteworthy that basal marsupialiforms have a distribution on both sides of the Western Interior Seaway since the Cenomanian (1, 10, 26), suggesting that the latter was not a major barrier to the dispersal of some of the North American and Euramerican Cenomanian taxa (Fig. 4 and Table S3). This also is true for the other European taxa with Euramerican affinities reported above. However, most of the described basal marsupialiforms, including the oldest known form (i.e., *Kokopellia*), occur in the western part of North America (Table S3). If this North American fossil record is representative, it might be the best evidence for an Eastern dispersal of the Marsupialiformes from their Asian metatherian stem group, and accordingly for a North American origin of *Arcantiodelphys*. However, in our view, the origin of the primitive Euramerican Marsupialiformes remains a wide-open question, especially because of the major gaps in the European Cretaceous. New fossil discoveries might further highlight the paleobiogeographical significance of both the primitive and autapomorphic states of *Arcantiodelphys* among marsupialiforms.

The Archingeay-Les Nouillers discovery demonstrates that the beginning of the Marsupialiformes' history also involved Europe, and that the European part of this history remains widely enigmatic. Current data cannot exclude any paleo-

geographical scenario (especially with respect to the involved dispersal route) in the American marsupialiform colonization. Given the scarcity of the Cretaceous mammal record of Europe, any new discovery in the Mid-Cretaceous of western France is likely to provide key data of early marsupialiform phylogeny and paleobiogeography.

Materials and Methods

The early Cenomanian deposits of Charentes, in the northern margin of the Aquitaine Basin (southwestern France), display estuarine to shallow coastal facies corresponding to lithostratigraphic units A2 and B1–3 defined by Néraudeau et al. (9). The vertebrate-bearing layer of the Font-de-Benon quarry corresponds to the shelly sand at the base of the unit B1. It is earliest Cenomanian in age, according to the presence of the benthic foraminifera *Orbitolina concava* (33, 34) (Fig. S1). Intensive sediment screen-washing of about 5 tons of matrix between 2003 and 2005 allowed the collection of a rich vertebrate assemblage, including sharks and rays, bony fishes, frogs, turtles, crocodyliforms, theropod dinosaurs, pterosaurs, snakes, and mammals (2, 22, 33, 35). The sedimentology, paleontology, and paleoenvironment have been described in detail by Vullo et al. (34). See *SI Appendix* for the character descriptions and the cladistic analysis with the TNT program (17).

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