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

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We report here the discovery of mammalian tribosphenic teeth from the basal Cenomanian of SW 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 closer resemblances to *Dakotadens*. These resemblances, which are plesiomorphic within “tribotherians”, make *Arcantiodelphys* one of the most archaic known Marsupialiformes. *Arcantiodelphys* is moreover characterized by an original and precocious crushing specialization. Both the plesiomorphic and autapomorphic character states 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, two possible dispersal routes can now be proposed from an Asian metatherian ancestry: (H1) Asia to Europe via North America, or (H2) Asia to North America via Europe. The main significance of the Archingeay-Les Nouillers mammal discovery is 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.

mammals | Marsupialiformes nov. | Cretaceous | Europe | paleobiogeography

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The early evolution of modern therians (i.e., metatherian and eutherian boreosphenidan mammals) is mainly documented in North America and Asia, where numerous rich mid-Cretaceous microvertebrate localities are known. In Europe, a major gap occurs in the mammal fossil record for the Late Cretaceous, and 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 briefly 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 (SI Fig. 1). The new mammal material reported here includes four 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, i.e. the oldest European representative of the clade including metatherians and eutherians.

Systematic Paleontology. 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 (e.g., ref. 8) includes the stem groups of the crown marsupials. Basal marsupialiforms include primitive Cretaceous taxa previously gathered in the paraphyletic taxon “Ameridelphia” (e.g., refs. 1 and 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), Paris, France (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), name of the gallo-roman domain from which the village of Archingeay developed, and *delphys* (Greek), 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 “Font-de-Benon” quarry, Archingeay-Les Nouillers, Charente-Maritime, SW 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, approximated to

entoconid (but not twinned), well developed entoconid, paracone and metacone of similar size and well separated, wide styler shelf, styler cusps D and C present (but small), protocone well developed (uncompressed), no lingual cingulum. Molar morphology similar to earliest North American basal marsupialiforms such as *Dakotadens*, *Iugomortiferum*, *Adelodelphys*, *Synbadelphys*, and *Pariadens* (8, 10–12). It shares especially with *Dakotadens* and *Iugomortiferum* the robust construction (cusps low and bulbous, low trigonid, wide talonid, large protocone), and the wear pattern, indicating an early specialized crushing function. Differs from Cretaceous stem marsupialiforms, except *Dakotadens*, in primitive features such as the absence of postcingulid, the postprotocrista which 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 carnassial notch on the postmetacrista. *Iugomortiferum* differs in these traits (although conules are reduced), and in the protocone less lingual, less inflated, and more anterior, the cristid obliqua more lingual on the trigonid, and the hypoconulid and entoconid twinned. Differs from *Dakotadens* in the following traits: more inflated cusps, absence of conules, hypoconulid and entoconid approximated but not twinned (separated by a small disto-lingual notch), protocone more lingual and more inflated, protoconid more inflated, metaconid less distal, hypoconid more compressed, hypoconulid smaller with respect to the entoconid. This is among the smallest known marsupialiforms with *Adelodelphys* and *Synbadelphys*. Dimensions: upper molar CCH4: Minimal Estimated Length > 1.14 mm; width = 1.86 mm (length of the protocone = 0.7 mm); lower molars: see Table 1.

Description and Comparisons. CCH4 (Fig. 1, SI Fig. 3 A and C), is a three-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 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 styler shelf labial to the metacone. The ectoflexus is deep and asymmetric with wider metastylar area according our comparative reconstruction. The ectocingulum and styler cusps are worn, but the cusps D and C are distinctly inflated. A slight but distinct oblique crest links the cusp D to the base of the metacone. The postmetacrista is robust, and bears no carnassial notch. The paracone is broken, but is apparently 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 wide. The protocone is remarkably well developed, both longitudinally and transversely. Its labial flank is inflated at the apex. It is lingual to the paracone–metacone notch, and slightly procumbent. There are no lingual cingula.

CCH1 (Fig. 2 A, SI Fig. 2A–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 transverse protocristid and a paraconid 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 mesiodistally extended (longer than wide). The mesial flank of the protoconid is slightly inflated labially toward the paraconid, close to the paracristid notch. Judged 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. The hypoflexid is consequently shallow. A postmetacristid is present at the base of the metaconid. The ectocingulid is absent.

CCH2 (Fig. 2C, SI Fig. 3 B and C) is the talonid of an unidentified left lower tribosphenic molar, but not of the most distal as illustrated by the hypoconulid morphology. Although the base of the crown is broken, it was probably low. In occlusal view, this talonid is short and wide. The postcingulid is absent. The hypoconulid is shifted lingually, but it is not twinned with the entoconid. The two cusps are separated by a deep notch, which is distinct in 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 two cusps seem less approximated than they probably were. The cristid obliqua is slightly more lingual mesially than on CCH1, and the hypoflexid seems deeper.

CCH3 (Fig. 2B, SI Figs. 2 E and F, 3 B and C) 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 trigonid being more compressed mesiodistally and its paraconid more lingual. 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”, 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 lingual crest as seen in CCH1. The precingulid, although damaged was 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 protoconid apex, and slight on the protocristid. On CCH4, abrasion strongly affects apices of protocone, metacone, and postmetacrista. A triangular wear facet 9 is distinct in the lingual flank of the protocone, denoting developed crushing-grinding function. Other wear facets are indistinct.

The four mammal specimens from Archingeay-Les Nouillers present close morphological affinities suggesting that they belong to the same mammal species. Especially, they share an overall robust construction with low and inflated cusps, a similar wear pattern with developed abrasion and are comparable in size. Affinity of the tribosphenic upper and lower molars from Archingeay-Les Nouillers is illustrated by resemblance in robust general morphology and related crushing (horizontal) wear pattern, in the absence of carnassial notches, and by their overall consistent occlusal relative pattern as illustrated by their occlusal

relationship (SI Fig. 3C). The occlusal relationship shows slight size difference (CCH4 is slightly smaller), but it remains in the range of the intraspecific variation. However, it is noteworthy 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 regarded as 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, low trigonid and wide talonid, broad protofossa and large and inflated protocone. Together with the developed abrasion, and development of 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 SI Tables 1–2. These features are also included in the character list used for the phylogenetic analysis (SI Text).

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

Among all Cretaceous therians, *Arcantiodelphys 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 *Arcantiodelphys marchandi*, as is *Pariadens*. *Arcantiodelphys marchandi* also closely resembles several other early North American stem marsupialiforms, previously classified as “Ameridelphia” (e.g., ref. 8). Its marsupial-like features (*sensu lato*, i.e., marsupialiform features) are the paracone and metacone of similar size and well separated [character K10(1-2)], the wide stylar shelf [K3(0)] and occurrence of stylar cusps D and C [K6(1)-K7(1)] (although small on known material), the well developed (uncompressed) protocone [K4(1)], the hypoconulid lingual 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 mostly known 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 inflated and prominent above the root [K19(0)], the weak ectocingulum and stylar cusps D and C, the wide stylar shelf bearing a long and transverse postmetacrista [K12(1)] (but which is less developed than in deltatheroidans). The small size also reminds one 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), 29(0) (see SI Text) are also found in “tribotherians” and might be primitive. However, most of these traits—and especially the paraconid large (but smaller than metaconid) and lingual—are also reminiscent of marsupialiforms. Features 4(1), 27(2), 28(2), 30(2), 31(1), 32(3) (see SI Text) are the most significant, derived, marsupialiform features of *Arcantiodelphys 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 relation. Several other remarkable features shared with *Dakotadens* are unknown in other stem marsupialiforms, including in *Kokopellia* which is 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 which does not extend labially at the base of the metacone [K9(0)], and the protocone poorly shifted mesially [K14(0)]. These character states of *Arcantiodelphys* are known in “tribotherians” and most probably 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, such as especially the absence of the postcingulid (12). However, these primitive traits are associated in *Arcantiodelphys marchandi*, with a suite of other features that are more common in early stem marsupialiforms than in any other early tribosphenic mammals. We should also emphasize that deltatheroidan metatherians lack the postcingulid and the labial extension of the postprotocrista, and also retain a less mesially shifted protocone than in marsupialiforms. As a whole, the morphology of *Arcantiodelphys 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 which bear especially a large and inflated protocone, that additionally displays a wear facet 9.

Among primitive marsupialiforms, *Arcantiodelphys marchandi* is characterized by an overall striking robust molar construction, with low and bulbous cusps, large and inflated protocone, low trigonid and protoconid, large hypoconid and wide talonid bearing large basin. It indicates a predominantly crushing function, which is also illustrated by the wear pattern with developed apical abrasion of the cusps (especially protoconid and protocone). This construction is also known in *Dakotadens* and *Iugomortiferum*, but in a less advanced way, and most probably as a parallelism. Crushing molar with developed “horizontal wear” (abrasion) is considered by Fox and Naylor (16) as a distinctive feature of early “marsupials” (i.e., stem marsupialiforms) with respect to other therian mammals. In *Arcantiodelphys marchandi*, the crushing function associated to a large and inflated protocone bearing a 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 *Arcantiodelphys marchandi*, with the program TNT (17) was developed in order to test and formalize the position *Arcantiodelphys marchandi* with and among marsupialiforms (see *SI Text*). The analysis only includes characters observed in *Arcantiodelphys*, i.e. 36 molar features, with four additional key characters (K37-40) related to the dental formula, which are diagnostic of the major therian clades (Eutheria, Metatheria, Deltatheroidea, 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 Metatheria (i.e., sister group of *Sinodelphys* + Marsupialiformes), and the derived position of primitive bunodont 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 for instance on the central position of the hypoconulid) was already suggested in the parsimony analysis of Cifelli (18), also 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 (18) 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 favoured by the parsimony analysis, such as the postprotocrista lingual, the absence of conules, the protocone central, and the absence of postcingulid. Other shared features known in *Dakotadens* and *Arcantiodelphys*, and also *Iugomortiferum* (e.g., bunodonty, low protoconid, extended abrasion) are probably convergent.

Calculation of the Bremer support value (as well as bootstrap value) shows in fact that only three nodes are well supported and reliable in this tree (Fig. 3B), among which the Marsupialiformes including *Arcantiodelphys*. Otherwise, it shows that several important points are poorly resolved in the parsimony analysis: 1) relationships of *Arcantiodelphys* among Marsupialiformes; and 2) 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 within the huge gap in the fossil record of mid-Cretaceous of Europe (e.g., ref. 1). *Arcantiodelphys marchandi* is the oldest known European representative of the metatherian–eutherian clade. It is also the oldest known European stem marsupialiform, and one of the oldest known Marsupialiformes. The only older stem marsupialiform known 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, *Arcantiodelphys marchandi* is one of the most primitive stem marsupialiform known so far (Fig. 3A; although its primitive features are interpreted as reversals in the parsimony analysis). It is most closely reminiscent of its sub-contemporaneous *Dakotadens*, with which it shares plesiomorphic character states such as the absence of the postcingulid, the protocone central and the postprotocrista restricted lingually to the metacone, but also 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 has been regarded as the sister group of Marsupialia and would therefore include the most derived stem marsupialiforms (21). *Arcantiodelphys marchandi* emphasizes a major gap in our knowledge of the early evolution of marsupialiforms in Europe. The discovery in SW France (Charentes) of a new mammal most closely related to early North American stem marsupialiforms provides the first mammalian evidence for 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 *Probactrosaurus*-grade iguanodontians (similar to *Protohadros* and *Eolambia*), nodosaurids, brachiosaurids, and troodontids (22). All these forms are well represented in the North American Cenomanian assemblages, in particular 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 are also 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 *Arcantiodelphys marchandi* shows that Europe was an important area in the basal radiation of marsupialiforms, and fits well the current models of metatherian and marsupial paleobiogeographical history which assume an early dispersal from a Laurasian and most probably an Asian center of origin (metatherian ancestry) to the modern Australian center of diversification, via the North and South American early centers of radiation (e.g., refs. 19 and 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 (e.g., ref. 29), some of which colonized Europe from North America, especially in the Late Cretaceous (e.g., ref. 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. A Cretaceous dispersal from Asia explains indeed the origin of the European zhelestids, *Gobiconodon*, kogaionids, amphilestines, and *Probactrosaurus*-grade iguanodontians (29–32). Comparison with Cretaceous North American marsupialiforms suggests that *Arcantiodelphys marchandi* is a very primitive stem marsupialiform, despite the (unlikely) reversals implied by our parsimony analysis. Our view of the primitiveness of *Arcantiodelphys* would favour an Asian origin and a trans-Ouralian dispersal (*versus* 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 (see Fig. 4 and SI Table 3). This is also 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 (see SI Table 3). 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, the origin of the primitive Euramerican Marsupialiformes remains, in our view, a widely open question, especially because of the major gaps in the European Cretaceous. New fossil discoveries might further enlighten the paleobiogeographical significance of both the primitive and autapomorphic state of *Arcantiodelphys* among marsupialiforms.

The Archingeay-Les Nouillers discovery shows 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 paleobiogeographical 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 to our knowledge of early marsupialiform phylogeny and paleobiogeography.

Materiel and Methods

The early Cenomanian deposits of Charentes, in the northern margin of the Aquitaine Basin (SW France), display estuarine to shallow coastal facies corresponding the lithostratigraphic

units A2, 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) (SI Fig. 1). Intensive sediment screen-washing of about 5 tons of matrix, from 2003 to 2005, allowed to collect 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 are described in detail in Vullo *et al.* (34). Supporting Information includes the character description and the cladistic analysis with TNT program (17).

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Figure Legends

Fig. 1. *Arcantiodelphys 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: stylar cusps C and D. (Scale bar: 1 mm.)

Fig. 2. Drawings and reconstruction of the teeth of *Arcantiodelphys 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, M_{2?}, M_{3?} or M_{4?}, in occlusal view. (C) MNHN CCH2, talonid of right lower molar in occlusal and distal views. Tentative reconstruction (occlusal views) of upper (D) and lower molars (E), and of their occlusal sketch (F). D: based on the holotype CCH4 and anterior molars of *Adelodelphys* (for parastylar area); E: based on CCH2 (talonid) and CCH3 (trigonid). (Scale bars: 1 mm.)

Fig. 3. Hypotheses on the phylogenetic relationships of *Arcantiodelphys marchandi* gen et sp nov. (A) Schematic representation of the phylogenetic relationships (stratigraphically calibrated) of *Arcantiodelphys marchandi* gen et sp nov. among other early therians and metatherians as hypothesized from the present study and comparisons. (B) Results of the parsimony analysis: cladistic relationships of *Arcantiodelphys marchandi* gen et sp nov. among selected non-marsupialiform and marsupialiform taxa (see *SI Text* for the complete analysis). A single cladogram (RI: 56.1; CI: 71.5) was obtained from the exact analysis (implicit enumeration) with TNT program (16) based on 36 molar characters plus four major diagnostic characters among tribosphenidans, related to the dental formula (see *SI Text*). Only the nodes with 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 need to be further tested with additional data on *Arcantiodelphys*.

Fig. 4. Possible scenario on 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 *Arcantiodelphys 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; grey star: Woodbine Formation, Texas; white star: upper Cedar Mountain and Dakota formations, Utah).

Table Legends

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