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New eutherian mammals from the Late Cretaceous of Aix-en-Provence Basin, south-eastern France

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In Europe, the fossil record of Late Cretaceous eutherian mammals is very poor, being limited to only three genera (*Labes*, *Lainodon*, and *Valentinella*). *Labes* and *Lainodon* are well-supported members of Zhelestidae, a stem eutherian clade, whereas *Valentinella* is more problematic, being recently considered as a *nomen dubium*. Based on X-ray computed microtomography scan analysis of the holotype and thanks to the discovery of new specimens from the type locality (Vitrolles-La Plaine, south-eastern France, late Maastrichtian), we reassessed *Valentinella*. This genus is unique by the association of an enlarged and rounded jaw angle with an assumed relatively elevated angular process, a bulbous protoconid and an unbasined heel on p4, a p5 with a wide molariform talonid and a hypoflexid, a robust molar morphology with a potential specialized crushing-grinding function (bulbously constructed cusps, large talonid, and horizontal apical wear facet of the hypocone), a somewhat reduced m3 relative to m2, a premolariform ?P3 or ?P4 lacking a metacone, and a relatively large hypocone on upper molars. These characters reinstate *Valentinella* as a valid genus. We also describe ***Mistralestes arcensis*** **gen.** et **sp. nov.** from a newly discovered locality (La Cairanne-Highway, south-eastern France, late Campanian). *Mistralestes* is defined by a robust premolariform p5 with no cingulid, paraconid, or metaconid; molars with a transverse protocristid, a gradual compression of the trigonid from m1 to m3, and paracristid and protocristid probably confluent on m3. Based on comparisons and phylogenetic analyses, *Valentinella* and *Mistralestes* may belong to Zhelestidae but this systematic attribution remains poorly supported.

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ADDITIONAL KEYWORDS: Campanian – dental anatomy – Europe – Maastrichtian – phylogeny – Zhelestidae.

INTRODUCTION

During the Late Cretaceous, the European Archipelago (Dercourt *et al.*, 2000) was a crossroads for tetrapod migrations amongst Asia, North America, and Africa. The palaeobiogeographical affinities of the Late Cretaceous European tetrapods are consequently complex; the continental fauna includes rare taxa of African affinities, together with endemic and mainly Asiamerican taxa, amongst them few mammals (e.g. Le Loeuff, 1991; Pereda-Suberbiola,

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2009). In the current state of our knowledge, only five sites have yielded irrefutable eutherian mammals. All are situated in the Iberian-Armorican Island that was part of the European Archipelago. For several decades, the only therian mammal known from the Late Cretaceous of Europe was the ‘Champ-Garimond tooth’ from the eponymous Campanian locality in southern France (Ledoux *et al*., 1966). Early on, several authors recognized this specimen as a eutherian (Clemens, 1968; McKenna, 1969; Butler, 1977). Despite intensive screen-washing efforts, only one additional tooth was discovered from that locality (Sigé *et al*., 1997); the two lower molars from Champ-Garimond constitute the hypodigm of *Labes garimondi*. This species was described by Pol *et al*. (1992) after the discovery of a closely related species, *Labes quintanillensis*, in the Quintanilla del Coco locality (Maastrichtian, Spain). Concomitantly, two other sites were discovered in the Iberian Peninsula: Taveiro (late Campanian or Maastrichtian, Portugal; Antunes, Sigogneau-Russell & Russell, 1986) and Laño (late Campanian or early Maastrichtian, Spain; Astibia *et al*., 1990). Laño is today the richest known locality for eutherians in the Late Cretaceous of Europe, with 20 isolated teeth that belong to the genus *Lainodon* (Gheerbrant & Astibia, 1999, 2012). The most recently discovered site is Vitrolles-La Plaine in the Aix-en-Provence Basin (Maastrichtian, south-eastern France), which has yielded *Valentinella*, the third known Late Cretaceous eutherian genus from Europe (Tabuce, Vianey-Liaud & Garcia, 2004). With the exception of a few fragmentary dental specimens of uncertain eutherian affinities from Taveiro and Quintanilla del Coco, all dental remains discovered in the various European Late Cretaceous localities therefore belong to only three genera, namely *Labes*, *Lainodon*, and *Valentinella*.

Labes and *Lainodon* are currently regarded as founder members of Lainodontinae (Gheerbrant & Astibia, 2012), a subfamily of Zhelestidae. The third known genus, *Valentinella*, was also cautiously referred to the zhelestid family by Tabuce *et al*. (2004), and its referral to lainodontines is considered as questionable (Gheerbrant & Astibia, 2012). Zhelestids are eutherian mammals known from the Cenomanian to Maastrichtian in Asia, Europe, North America, and Madagascar. Initially regarded as the sister-group of all Cenozoic ungulates (e.g. Archibald, 1996), zhelestids are today considered as a stem eutherian clade (Wible *et al*., 2009; Archibald & Averianov, 2012). As for the European representatives of this family, *Labes* and *Lainodon* retain some dental characters that are viewed as ancestral for zhelestids, suggesting a Cenomanian migration of zhelestids from Asia to Europe (Archibald & Averianov, 2012; Gheerbrant & Astibia, 2012). The systematic position of *Valentinella* is more problematic. In their recent monograph of zhelestids, Archibald & Averianov (2012) considered this genus as a *nomen dubium*, according to the lack of diagnostic features on the holotype.

To obtain a more reliable documentation of *Valentinella* in its type-locality, some of us (X. V., G. G., M. V.-L., P. G., and R. T.) have conducted several excavations at Vitrolles-La Plaine (Aix-en-Provence Basin) since 2007 (Valentin *et al*., 2012). In this paper, we describe two newly discovered specimens, a dentary fragment with roots of three molars, and a fragment of an upper molar. This latter specimen provides for the first time information on the upper molar morphology of a European Cretaceous eutherian. Furthermore, *Valentinella vitrollense* is reassessed through X-ray computed microtomography (μCT) imaging of the holotype. We also describe a new eutherian mammal from the newly discovered locality of La Cairanne-Highway (Aix-en-Provence Basin). The holotype and unique specimen is a relatively well-preserved dentary fragment with preserved p5 to m3 and roots of p4. This specimen, discovered by some of us (T. T., Y. D., S. B., and G. C.), is the most complete eutherian mammal from the Late Cretaceous of Europe described so far.

MATERIAL AND METHODS

UM-VLP-2 and MHNAix-PV.2008.1.1 were scanned with Skyscan 1076 μCT and Scanco μCT80 microtomographic scanners, respectively. The 3D rendering and 2D slices were reconstructed using AVIZO (Visualization Sciences Group, VSG) and VGStudio MAX (VolumeGraphicsGmbH). The 3D segmentations were performed using AVIZO (VSG). Specimens were also figured using Leica LAS multifocus image fusion. According to French legislation, all necessary permits were obtained for the described field studies from the relevant authorities, namely the Mayor of the City of Vitrolles (Vitrolles-La Plaine site) and the ESCOTA Society (VINCI Group) (La Cairanne-Highway site).

ANATOMICAL AND MEASUREMENT ABBREVIATIONS

P/p, upper and lower premolars; M/m, upper and lower molars; H, height; L, length; Ta, talonid; Tr, trigonid; W, width.

INSTITUTIONAL ABBREVIATIONS

UM-VLP, Université de Montpellier, France, Vitrolles-La Plaine collection; UP-VLP, Université de Poitiers, France, Vitrolles-La Plaine collection; MHNAix-PV, Muséum d’Histoire Naturelle d’Aix-en-Provence, France; UCMP, Museum of Paleontology, University of California, Berkeley, USA; AMNH, American Museum of Natural History, New York, USA; L1AT, Laño collection, Museo de Ciencias Naturales de Alava, Spain; CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia.

GEOLOGICAL SETTING AND DATING

The sites of Vitrolles-La Plaine (city of Vitrolles) and La Cairanne-Highway (village of Rousset), separated by 29 km, are respectively located in the western and eastern parts of the Aix-en-Provence Basin (Bouches-du-Rhône Department, south-eastern France; Fig. 1). They are situated in an argillite formation characterized by fluviatile deposits and lacustrine beds (historically named Lower 'Argiles et Grès à Reptiles' Formation or Lower 'Argiles Rutilantes' Formation) dated from the Lower Rognacian, a local continental stage. It has been equivocally proposed to be equivalent to the late Campanian–Maastrichtian period or to the Maastrichtian (Babinot & Durand, 1980; Babinot *et al.*, 1983; Garcia & Vianey-Liaud, 2001; Cojan & Moreau, 2006).

La Cairanne-Highway is a new site discovered in 2006 during the course of works undertaken to open new lanes along the A8 highway. Excavations were conducted by the Natural History Museum of Aix-en-Provence (MHNAix). The locality is situated in floodplain deposits characterized by a succession of fluvial beds rich in bioclastic elements in a red clayey formation (Fig. 2). The geological section is situated about 300 m to the west of the historic La Cairanne-Rousset Erben section, with which it is partially correlated (Ashraf & Erben, 1986; Garcia & Vianey-Liaud, 2001). The type horizon of the new genus and species is a greenish sandstone lens of 1 m in length and 20 cm thickness. A diverse dinosaur fauna was recovered, mainly documented by teeth of Nodosauridae, Rhabdodontidae, Titanosauria, and Dromaeosauridae. Some rhabdodontid postcranial elements were also collected and include a partial sacrum, a chevron, and isolated ossified tendons. This fossiliferous lens is located 2 m above layers bearing *in situ* clutches of dinosaurs attributed to *Megaloolithus aureliensis* and *Cairanoolithus dughii* oospecies, and below the 30-m-thick argillite deposit. Overlying sandstone channels contain rolled bones and isolated eggshells. The correlated sandstone and clayey layers of the La Cairanne-Rousset Erben section have yielded various eggshells (including *M. aureliensis*, *Megaloolithus siruguei*, *Prismatoolithus tenuis*, and a ratite morphotype) and clutches of *Megaloolithus microtuberculata* and *Ca. dughii* a few metres above the new locality. The uppermost channels at the Rousset village contain pisoliths and bivalves

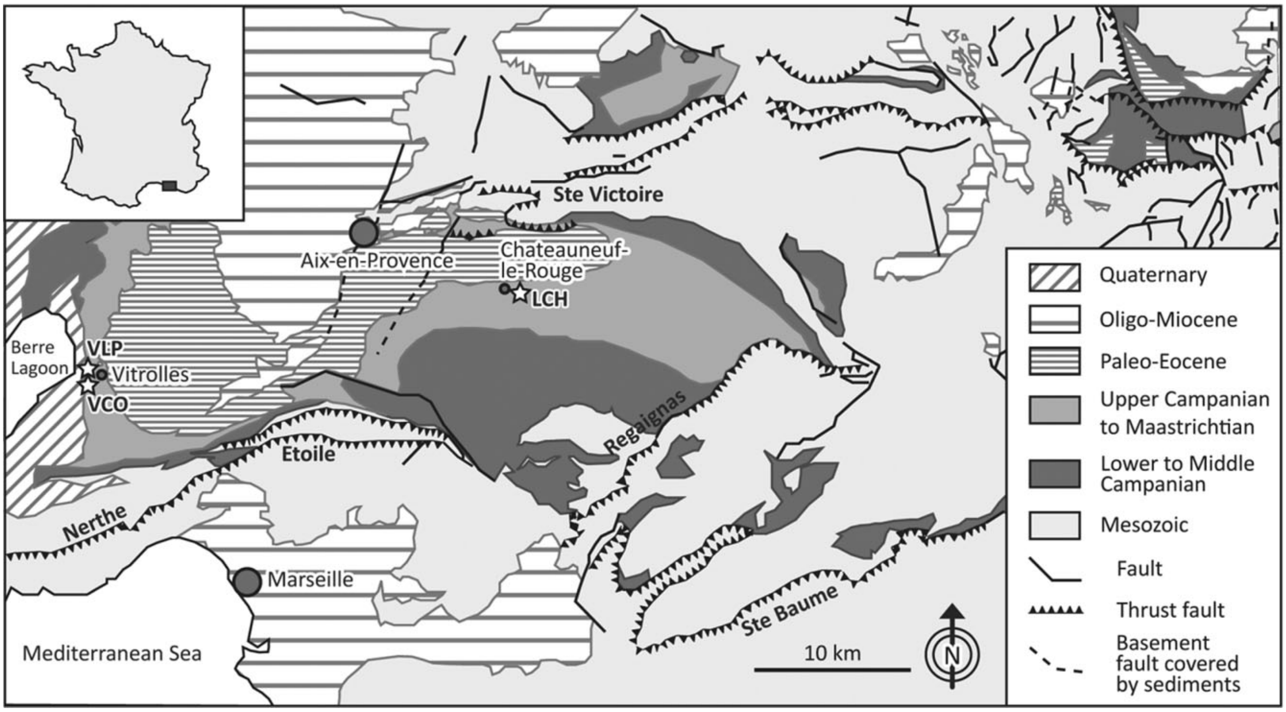

Figure 1. Geological map and location of the Late Cretaceous sites Vitrolles-La Plaine (VLP), Vitrolles Couperigne (VCO) and La Cairanne Highway (LCH) in the Aix-en-Provence Basin.

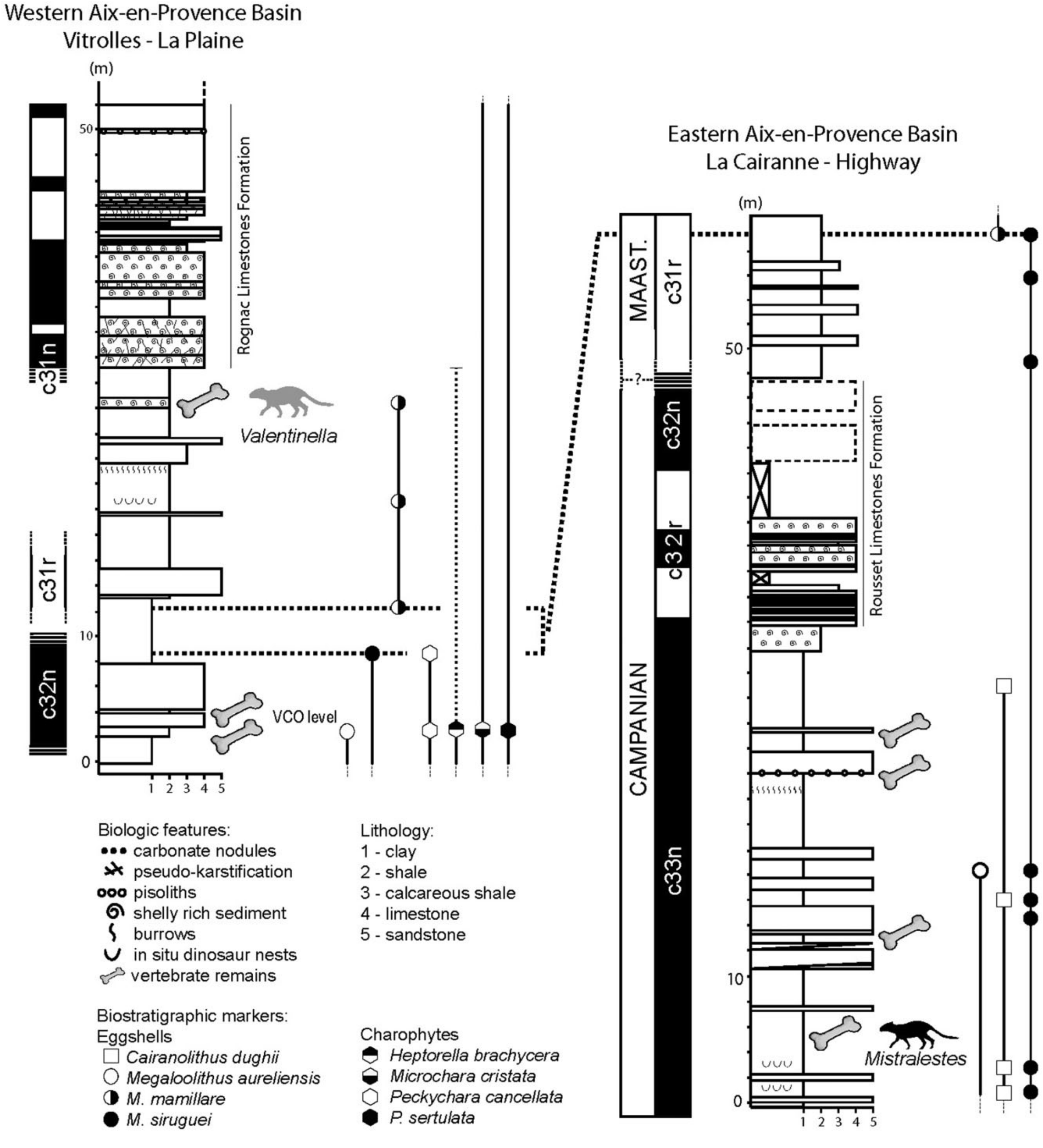

Figure 2. Lithological logs and biochronological/magnetostratigraphical correlations of the Vitrolles-La Plaine and La Cairanne Highway sections. MAAST., Maastrichtian.

(*Unio cuvieri*), which are not present in the overlying lake deposits. This latter formation is composed of grey marls and then by white to grey compact limestone layers, locally named the Rousset Limestone Formation. With a total thickness of 20 m, these lake deposits are very rich in gastropods (dominated by *Bauxia disjuncta* and *Cyclophorus heliciformis*).

The Vitrolles-La Plaine locality was discovered in 1997 and several excavation campaigns were conducted by the University of Poitiers in collaboration with the University of Montpellier 2 and the Royal Belgian Institute of Natural Sciences (Garcia, 1998; Vianey-Liaud & Garcia, 2000; Garcia & Vianey-Liaud, 2001; Tabuce *et al*., 2004; Valentin *et al*., 2012). The Vitrolles-La Plaine site is located in lake deposits, just below an important series of limestone layers, both constituting the basis of the Rognac Limestone Formation (Fig. 2). The geological section is situated about 1 km northwards and stratigraphically 25 m above another vertebrate locality, Vitrolles-Couperigne, known for the discoveries of partial skeletons of the ornithopod dinosaur *Rhabdodon* (Garcia *et al*., 1999). The positions of the Vitrolles localities in the general stratigraphy of the western Aix-en-Provence Basin are well known thanks to various geological sections and drills made in different locations of the Rognacian deposits (Garcia & Vianey-Liaud, 2001; Cojan & Moreau, 2006). The type horizon of *Valentinella* is composed of greyish and shelly marls, very rich in vertebrate remains including bony fishes, squamates, cryptodyran chelonians, Alligatoridae, and dinosaurs (basal Iguanodontia, Hadrosauridae, Neoceratosauria, Coelurosauria, and Titanosauria; Valentin *et al*., 2012). Also recovered were some eggshells (*Megaloolithus mamillare* and prismatic, geckonoid, and ratite morphotypes), charophytes (*Peckichara sertulata*) and the typical Rognacian gastropods *Lychnus matheroni* and *Pyrgulifera armata.*

Stratigraphical correlations between the La Cairanne-Highway and Vitrolles-La Plaine localities are imprecise because of important lateral variations in the thickness of the studied geological sections and of their lithology from west to east and south to north, depending on the structural constraints of the basin and the general tectonics. Magnetostratigraphical correlations have been performed for the last 30 years, but data are only known from limited geological sections and, often remain missing, incomplete, or undetermined in key horizons (Hansen, Gwodz & Rasmussen, 1989; Krumsiek & Hahn, 1989; Galbrun, 1997; Cojan & Moreau, 2006). This difficulty notably arises in the western and eastern-most parts of the basin. Finally, biostratigraphical correlations are strongly limited by the difficulties in matching the classical continental biomarkers (charophytes, ostracods, pollen), which are rarely collected or discovered.

In order to propose an independent approach, the abundant dinosaur eggshells were used as biostratigraphical markers. The successions of the various ootaxa have been studied on the basis of numerous *in situ* eggshells and clutches present in various sections from the western and eastern parts of the Aix-en-Provence Basin (e.g. Garcia, 1998; Vianey-Liaud & Garcia, 2000), showing the identical successions of dinosaur ootaxa. Their associations, as well as their first and last occurrences, led to the establishment of an oostratigraphical scale (Garcia & Vianey-Liaud, 2001). From the La Cairanne-Highway section (supplemented by the La Cairanne-Erben, Rousset, and La Bégude sections; see Garcia & Vianey-Liaud, 2001; Cojan & Moreau, 2006), the ootaxa discovered in the type horizon of the new genus and species belong to *M. aureliensis*, *M. siruguei*, and *Ca. dughii*. The last occurrences of *M. aureliensis* and *Ca. dughii* are situated in the overlying argilites, at about 20 m and a few metres below the Rousset Limestone Formation, respectively. *Megaloolithus siruguei* disappears a few metres above the last calcareous levels of the Rousset Limestone Formation, whereas *M. mamillare* appears in the overlaying horizons. Thus, the type horizon for the new genus and species is located about 30 m below this lacustrine formation. In the western Aix-en-Provence Basin, in the Vitrolles-La Plaine section (supplemented by the Vitrolles-Couperigne and Vitrolles-Eurocopter sections, and drills data; see Garcia & Vianey-Liaud, 2001), the same succession is documented, namely *M. aureliensis*, *M. siruguei*, and *M. mamillare*. More precisely, *M. aureliensis* occurs at Vitrolles-Couperigne (VCO level, Fig. 1). *Megaloolithus siruguei* first occurs between both sites. Finally, the *Valentinella* type horizon is situated in a level that has yielded *M. mamillare* (Fig. 2).

Therefore, on the basis of the oostratigraphy (notably by the occurrence of *M. aureliensis*), we can roughly correlate Vitrolles-Couperigne (VCO level) with the base of the section of La Cairanne-Highway. More precisely, the presence of some charophytes at Vitrolles-Couperigne allows us to constrain the dating to the *Peckichara cancellata* biozone, chron 32r-32n (Riveline, 1986). Another correlation point between the eastern and western Aix-en-Provence Basin is provided by the replacement of *M. siruguei* with *M. mamillare*. According to recent studies conducted in the continental Tremp Formation, in Spain, the *M. siruguei*–*M. mamillare* replacement occurs around the reversal of chrons 31r-31n, in the Late Maastrichtian, around 68.5 Mya (Vila *et al*., 2011).

To conclude, Vitrolles-La Plaine which has yielded *Valentinella* is confirmed to be late Maastrichtian in age, posterior to reversal chron 31r-31n, and located about 15 m above the *M. siruguei*–*M. mamillare* replacement. By contrast, the new genus and species from La Cairanne-Highway is definitely late Campanian in age (chron 33n) with its type horizon situated about 65 m below this ootaxa replacement. However, we note that, relative to the Rousset Limestone, the Campanian/Maastrichtian boundary is not precisely situated in the eastern part of Aix-en-Provence (Fig. 2).

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

INFRACLASS EUTHERIA GILL, 1872

FAMILY ?ZHELESTIDAE NESOV 1985

VALENTINELLA VITROLLENSE TABUCE, VIANEY-LIAUD & GARCIA, 2004

Holotype: UM-VLP-2, damaged right dentary with p4-m3.

Referred material: UP-VLP-10-01, a left dentary fragment with roots of m1–m3; UM-VLP-4, a dentary with remnants of right and left molariform teeth; UM-VLP-3, fragment of a probable right P^X; UP-VLP-07-04, fragment of a left upper molar.

Remarks: Despite the poor preservation of all these specimens, their attribution to *Valentinella vitrollense* is supported by their large size. Lower molars of *Valentinella* are at least twice as large as those of most Late Cretaceous eutherian mammals (Asioryctitheria, Zalambdalestidae, Zhelestidae, *Gypsonictops*, *Deccanolestes*, *Kharmerungulatum*) and similar in size to those of *Cimolestes stirtoni*, which is, along with two larger species, *Cimolestes magnus* and *Protungulatum coombsi*, one of the largest Late Cretaceous eutherian mammals. Additionally, all specimens described herein were found concentrated in the same excavation area (Valentin *et al*., 2012).

Revised diagnosis: Valentinella differs from all the other Late Cretaceous eutherian mammals by a unique combination of characters: the jaw angle is elongated with a convex ventral border indicative of a relatively elevated angular process; simple and bulbous p4; p5 with a hypoflexid and a molarifom talonid; robust lower molars with labiolingually expanded talonid; labially inclined protocone with a long lingual slope; and development of an incipient hypocone on the cingulum.

Measurements (in mm): UM-VLP-2 (p4: L = 3.11, W = 1.91; p5: L > 3.2, W = 2.77, LTa = 1.5; m1: L = 4.04, W = 2.8, LTa = 2.45; m3: L = 3.48, W > 2.33); UM-VLP-3 (Px: L ≥ 3.33, W > 2.71).

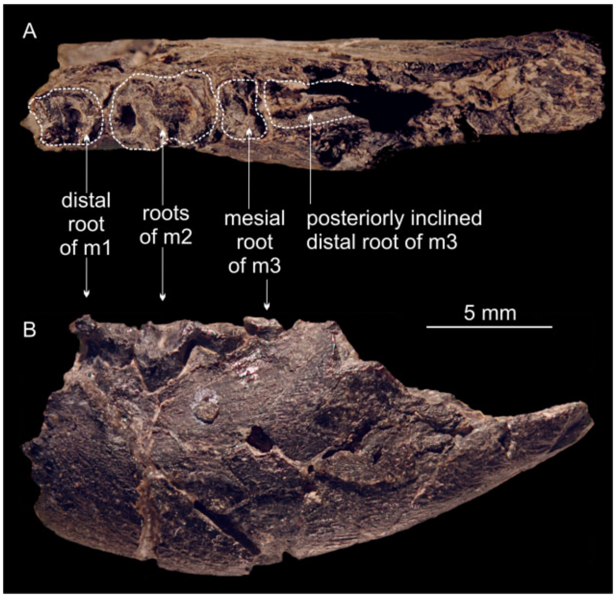

Figure 3. *Valentinella vitrollense* from Vitrolles-La Plaine, UP-VLP-10-01, left dentary fragment with roots of m1–m3. A, occlusal; B, labial views. Note the posteriorly inclined distal root of m3, mesially indented by a thin bony lamina.

Description: The newly discovered dentary fragment UP-VLP-10-01, although having only preserved roots and/or alveoli of m1–m3, is informative in showing a robust and deep mandibular body (8.95 mm below m2). Ventrodistally to the m3, the mandibular body displays the ventral extremity of a blunt coronoid crest (Fig. 3). The close proximity between this structure and the posteriorly inclined large distal root of m3 (mesially indented by a thin bony lamina) indicates that the retromolar space was reduced or even absent. The mandibular ramus is ventrodistally elongated behind m3 and has a very ventral convex border. This morphology indicates the occurrence of a rounded angle with the development of a relatively elevated angular process (near the alveolar margin). On the holotype UM-VLP-2, the mandibular body revealed by 3D reconstruction is too severely crushed and displaced labially to be described; only the mandibular canal is preserved (Fig. 4).

The holotype has two premolars and three molars; all teeth are damaged, with the exception of the relatively well-preserved penultimate premolar (Figs 5, 6). The premolars are numbered as p4 and p5 based on a growing consensus that the primitive dental formula of early eutherians and placentals comprises five premolars (Cifelli, 2000; Wible *et al*., 2009; Archibald & Averianov, 2012). The two-rooted p4, oval in occlusal outline, is a simple tooth dominated by a large and bulbous protoconid; distally, there is a low, small unbasined heel with a small cingular cusp. The p5, more poorly preserved, is longer than p4 and shorter than m1. There are two labial and one lingual patches of enamel and a remnant of the hypoflexid. Enamel elements on the distal wall of the trigonid indicate also that the talonid has a similar length as the trigonid. The talonid is however narrower compared with the

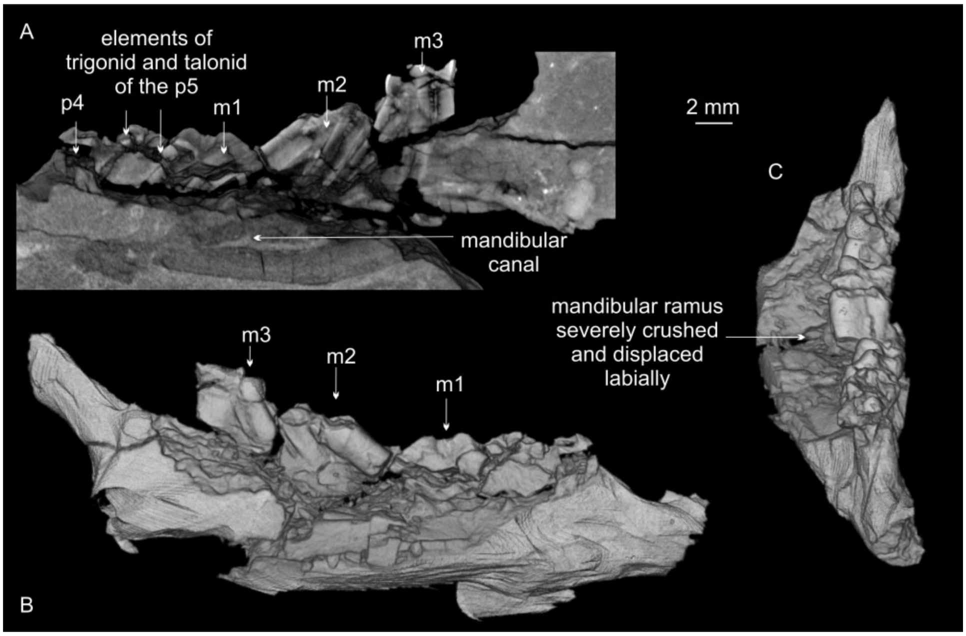

Figure 4. *Valentinella vitrollense* from Vitrolles-La Plaine, holotype UM-VLP-2, right dentary with p4–m3. A, two-dimensional virtual slice images acquired by X-ray computed microtomography (µCT); three-dimensional reconstruction using µCT scan images; B, labial; C, mesial views.

trigonid. The hypoconulid is distolingually displaced. The potential presence of a metaconid, proposed by Tabuce *et al*. (2004) based on the believed labial position of the protoconid, is possibly an erroneous interpretation as most of the crown is missing. However, the hypothesis that, as seen in p4, the trigonid was unicuspid with a large and bulbous protoconid is unlikely regarding the molariform and basined talonid. The combination of a single-cusped bulbous trigonid and a basined talonid is indeed unknown in Cretaceous or Palaeogene eutherians. As a result, the trigonid of p5 was certainly molariform, with three cusps.

The molars are preserved on the holotype as well as on UM-VLP-4, which was initially interpreted as bearing ?p4–?m2 by Tabuce *et al*. (2004). Subsequent preparation of this specimen revealed that this dentary fragment has poorly preserved right and left teeth. On the labial side of the talonid of a molariform tooth, a small portion of wrinkled enamel is preserved. On the holotype, characters of the molars are also mainly obliterated by wear and distortions caused by tectonic deformation. These distortions are obvious in µCT reconstructions (Fig. 4); the trigonids are distally and vertically shifted relative to the talonids. As a result, we cannot define exactly the height and degree of compression of the trigonid (i.e. the position of the paraconid relative to the metaconid). Likewise, we cannot determine whether the hypoconulid is twinned with the entoconid or more centrally positioned on the postcristid. On the labial side of m1, some enamel remnants can be distinguished on both the protoconid and the hypoconid. The base of both of these cusps is bulbously constructed. The hypoflexid is also preserved and appears relatively deep. All the cusps show considerable attrition; dentine is well exposed in both the distal part of the trigonid and the whole talonid. The worn occlusal surfaces are flat, so the trigonid and talonid appear to be the same height. A wear facet on the labial side of the hypoconid is still visible. The talonid appears shorter and wider than the trigonid. The m2 is so crushed and worn that no unquestionable morphological observations can be made. Judging from the robustness of their roots (also obvious on UP-VLP-10-01), it seems that the relative molar size is m1 < m2 > m3. Only the labial half of m3 is not crushed. Like the occlusal surface of m1, m3 is strongly worn, suggesting a crushing function of the molars during dental attrition. On the talonid, which is shorter than the trigonid, the remaining area of the postcristid does not suggest any strong distal development of a hypoconulid.

The upper dentition is represented by two specimens. UM-VLP-3 is a two-rooted tooth that could be, according to its size, a P3 or a P4 (Fig. 7A, B). This premolar was initially thought to be preserved along with possible remnants of canines on a maxillary (Tabuce *et al*., 2004). However, a better a preparation of the specimen and µCT-scan analysis indicate that

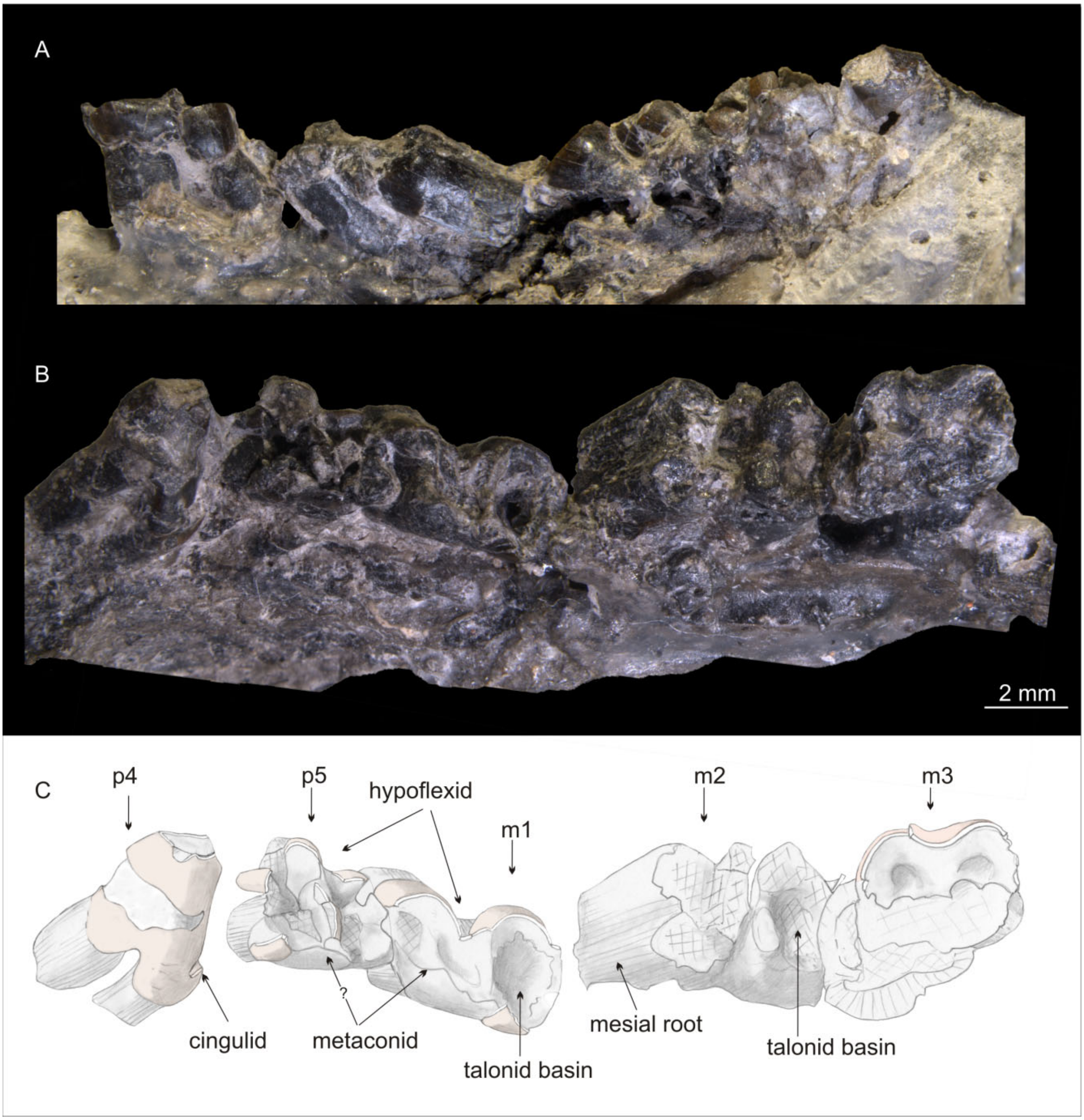

Figure 5. *Valentinella vitrollense* from Vitrolles-La Plaine, holotype UM-VLP-2, right dentary with p4–m3. A, labial; B, occlusal views; C, interpretative drawing in occlusal view, salmon-coloured areas indicate preserved patches of enamel.

both the supposed maxillary and canines are merely isolated fragments of bone without an obvious direct relationship with the premolar. On the latter, the main cusp is attributed to the paracone as it is centrally positioned above the two roots. The central position of the paracone, relative to the roots, also suggests that there is no metacone. The paracone is laterally narrow and slightly expanded along its lingual margin, but, as the crown is broken lingually, the presence or absence of a small protocone is unknown. The paracone exhibits a sharp distal crest ending in the incipient metastyle; there is no labial cingulum. The second specimen, UP-VLP-07-04, is a fragmentary left upper molar, with only the distolingual part of the crown preserved (Fig. 7C, D). This fragment displays the hypocone and part of the

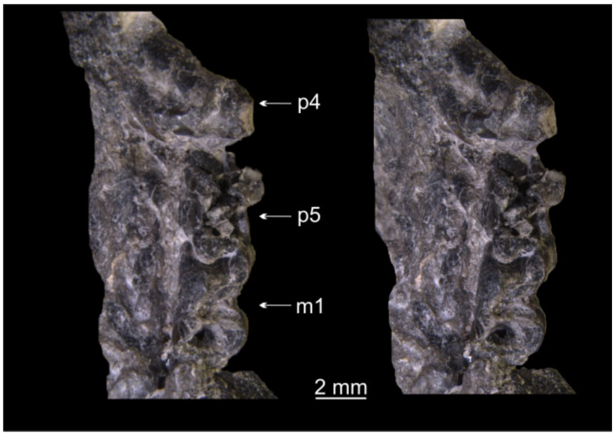

Figure 6. *Valentinella vitrollense* from Vitrolles-La Plaine, holotype UM-VLP-2, occlusal stereoview of p4–m1.

protocone. Although the protocone is too fragmentary to estimate its height and size, this cusp appears somewhat mesiodistally inflated, inclined labially and has a long lingual slope. The hypocone is an incipient cusp resulting in elevation of the lingual end of the postcingulum. The hypocone is affected to a minor degree by occlusal wear.

Comparisons and discussion: The holotype of *Valentinella* is regarded as having two premolars (p4 and p5) and three molars. However, considering that the p4 is a simple premolariform premolar and that the p5 is interpreted as a molariform tooth, a combination that is not characteristic of eutherians, two other alternative interpretations of the dental formula of the holotype need to be discussed: p4-dp5-m1-m2-m3 or alternatively p3-m1-m2-m3-m4. The first hypothesis, which claims the presence of a dp5 on the holotype, appears unlikely as it would imply that this deciduous last premolar is retained in old adults (the m3 is very worn on the holotype). In addition, μCT-scan analysis indicates that there is no trace of p5 beneath the presumed deciduous tooth. The second interpretation, the presence of four molars, would imply that *Valentinella* is a metatherian, an assumption that is clearly also refutable considering the presence of a hypocone on the distal cingulum of the upper molar UP-VLP-07-04 and the morphology of the dentary UP-VLP-10-01, which does not indicate the presence of a medial inflected angle. As a result, our identification of the preserved loci in the holotype of *Valentinella* (p4-p5-m1-m2-m3) appears to be the most logical hypothesis. Finally, the lack of gradual molarization of the premolars (combination of a simple p4 with a molariform p5) in *Valentinella* can be observed in other Late Cretaceous eutherians (e.g. *Zalambdalestes*).

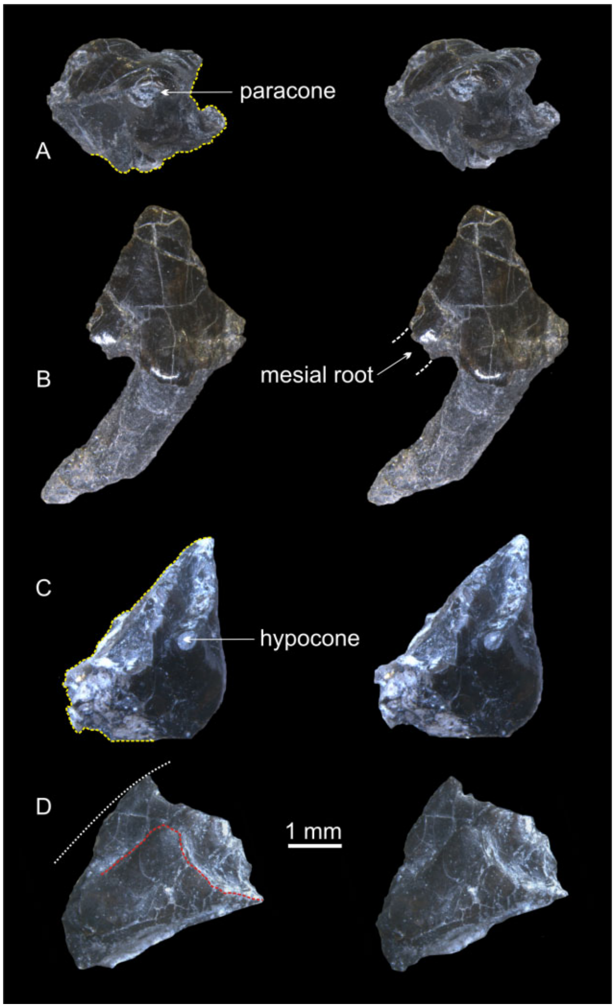

Figure 7. *Valentinella vitrollense* from Vitrolles-La Plaine. UM-VLP-3, probable right ?P3 or ?P4; A, occlusal; B, labial stereoviews. UP-VLP-07-04, fragment of a left upper molar; C, occlusal; D, distal stereoviews. Yellow, white, and red dotted lines indicate, respectively, the broken parts of the crown, the slope of the protocone, and the lingual slope of the hypocone on the postcingulum.

Valentinella was initially compared to both Zhelestidae and some ‘condylarths’, based on the robust dental morphology of the holotype with specialized crushing-grinding function as illustrated by its bulbously constructed cusps that are severely worn horizontally (see Tabuce *et al.*, 2004). *Valentinella* was subsequently regarded as closely related to the zhelestids because of ‘the lingual or sublingual position of the paraconid with a clear appression to the metaconid, the entoconid and the hypoconulid twinned, the expanded talonid, and by the indication of a quite similar height of both trigonid and talonid’ (Tabuce *et al.*, 2004: 352). However, based on both μCT analysis and an advanced preparation of the holotype, it appears that it is not possible to determine confidently the position of the paraconid and hypoconulid relative to the metaconid and entoconid, respectively. Therefore, we refute our initial assumption that *Valentinella* is partly diagnosed by an appression of the trigonid and an entoconid twinned with hypoconulid. Similarly, Archibald & Averianov (2012) recently considered *V. vitrollense* as a *nomen dubium* because of the putative lack of diagnostic features on the holotype.

However, we estimate that some characters on the *Valentinella* hypodigm are relevant to maintain this genus as a valid taxon. Firstly, *Valentinella* is characterized by a robust dental morphology with specialized crushing-grinding function as illustrated by the horizontal apical wear facet of the hypocone and by the bulbously constructed cusps of the holotype that are severely worn horizontally. *Valentinella* is also characterized by the rounded and enlarged angle of its lower jaw with an assumed relatively elevated angular process, a bulbous protoconid and an unbasined heel on p4, a molariform p5 having a wide talonid and a hypoflexid, a large talonid on the molars, a somewhat reduced m3 relative to m2, a premolariform ?P3 or ?P4 lacking a metacone. Finally, the upper molar exhibits few, but important, characters such as the long lingual slope of the labially inclined protocone and the development of an incipient hypocone.

These characters on the upper molar are important to compare *Valentinella*. Amongst zhelestids, a swollen and lingually elevated postcingulum, without true hypocone, developed as a distinct cusp, is present only in the Zhelestinae *Aspanlestes aptap*, *Parazhelestes robustus*, and *Eoungulatum kudukensis*. A developed hypocone, as observed in *Valentinella*, has not been described in zhelestids so far. Amongst other Cretaceous mammals, the postcingulum is slightly enlarged in the asioryctitherian *Kennalestes* and the cimolestids *Batodon* and *Maelestes*, but a hypocone is not developed. The only known Cretaceous mammal in which a hypocone is incipiently developed as in *Valentinella* is *Gypsonictops*. A lingually high postcingulum with a hypocone shelf showing both a lingual slope and an occlusal wear facet is present in some M2 of this North American genus (AMNH 21984; Clemens, 1973: 20). However, the hypocone of *Gypsonictops* is less developed in occlusal view than in *Valentinella*. The lower dentition of *Gypsonictops* and *Valentinella* share the molarization of p5. *Gypsonictops* has however a more molarized p4 with constantly present paraconid and metaconid, and a basined talonid.

Amongst latest Cretaceous–early Palaeocene mammals, Luo (1991) observed a morphocline on the lingual part of the upper molars. This morphocline arises with the cimolestid *Procerberus*, in which the postcingulum is low lingually and the protocone has a short lingual slope. In the asioryctitherian *Kennalestes*, the postcingulum rises lingually but does not present a lingual slope. The next grade is exemplified by the leptictid *Gypsonictops* (or to a lesser degree by the zhelestids and the plesiadapiform *Purgatorius*), in which a small lingual slope of the postcingulum occurs and the lingual slope of the protocone is longer. The ultimate grade is represented by *Protungulatum*, in which a true incipient hypocone occurs and the lingual slope of the protocone is very long relative to the tooth size.

Along with *Valentinella*, the first mammals that developed an incipient hypocone are therefore taxa that have been included within the nebulous paraphyletic ‘condylarths’ (*Protungulatum* included). Whether these ‘condylarth’ lineages occurred in the latest Cretaceous or just after the Cretaceous/Tertiary (K/T) boundary is still a matter of debate (Archibald *et al.*, 2011). In the current state of our knowledge, the first ascertained latest Cretaceous ‘condylarth’ species are *Protungulatum coombsi* from Montana, USA (Archibald *et al.*, 2011) and *Kharmerungulatum vanvaleni* from India (Prasad *et al.*, 2007). The presence or absence of a hypocone on the upper molars of these species could not be determined as they are only known by an upper premolar and a lower molar, respectively. The earliest North American ‘condylarths’ with a developed hypocone are members of various genera that appeared during the earliest Palaeocene (Puercan 1, NALMA), namely the ?arctocyonid *Protungulatum*, the arctocyonids *Oxyprimus* and *Baiconodon*, and several periptychids such as *Mimatuta* and *Oxyacodon* (Archibald, 1982; Lofgren *et al.*, 2004).

The hypocone of *Valentinella* therefore appears to be a significant character because it limits the comparisons to just a few genera. However, from a phylogenetic point of view, there is no clear evidence that this character supports ‘condylarth’ affinities for *Valentinella*. Indeed, the hypocone convergently evolved more than 20 times amongst placentals during the Cenozoic (Hunter & Jernvall, 1995), and the same is probably true for the latest Mesozoic (the pre-hypocone grade seen in *Gypsonictops* and zhelestids supports this hypothesis, see above). Further detailed comparisons between *Valentinella* and earliest ‘condylarths’ are limited because of the poor preservation of the lower dentition of the former. *Valentinella* resembles *Mimatuta* in having a molariform p5 with talonid and trigonid of equal width, and a long, basined talonid; but it differs by the reduced m3 relative to m2. This character also distinguishes *Valentinella* from *Protungulatum*, *Oxyprimus*, *Baiconodon*, and *Oxyacodon*. However, some genera from the Puercan 2, such as *Mimotricentes*, *Litomylus*, and *Eoconodon*, are characterized by a reduced m3 as in *Valentinella*. However, considering that these taxa belong to various families (namely the arctocyonids, hyopsodontids, and triisodontids, respectively), the reduction of m3 is a probable homoplastic trait amongst 'condylarths'. Some Puercan 'condylarths', such as *Protungulatum donnae* (UCMP 121782, the holotype of *Protungulatum* '*mckeeveri*') and *Eoconodon coryphaeus* (AMNH 16329), also resemble *Valentinella* by their elongated mandibular ramus with a rounded angle and an elevated angular process. Finally, based on enamel microstructure, Tabuce *et al*. (2004) observed several characters that could indicate 'condylarth' affinities for *Valentinella*: closely packed prisms, with a circular cross-section, and a large size (6–8 μm in diameter), single-layered Schmelzmuster with radial enamel, reduction of the IPM (interprismatic matrix), and a similar angle between the crystallites of the IPM and prism's long axes (40–45°). Interestingly, *Protungulatum* shares with *Valentinella* the three latter traits, the two latter being derived amongst eutherians.

Based on enamel microstructure alone, comparisons between *Valentinella* and zhelestids are unfortunately impossible because enamel microstructure of the latter was neither described, nor illustrated. A study of the enamel microstructure of stem eutherians is clearly needed. In any case, *Valentinella* differs from all zhelestids by being twice as large in size, an enlargement of the angle of the jaw with a higher elevated angular process, a more bulbous protoconid on p4, and a more advanced condition of the hypocone (see above). Besides these differences, *Valentinella* shares with zhelestids a submolariform p5 having a wide talonid (*Paranyctoides*, the supposed sister-taxon of zhelestids, presents a less molarized p5), a robust molar morphology with potential specialized crushing-grinding function (bulbously constructed cusps of the holotype that are severely worn horizontally, horizontal apical wear facet of the hypocone, and large talonid), a somewhat reduced m3 relative to m2 (*Aspanlestes*, *Parazhelestes*, *Zhalmouzia*, but not *Borisodon*), simple ?P3 or ?P4 lacking a metacone.

MISTRALESTES GEN. NOV.

Type species: Mistralestes arcensis sp. nov., late Campanian, Aix-en-Provence Basin, south-eastern France.

Diagnosis: As for the type-species.

Etymology: From *Mistral* (name of the strong wind affecting south-eastern France), which signifies 'the master' in Provençal, a language spoken in southern France; and the Greek *lestes*, robber, pirate.

MISTRALESTES ARCENSIS SP. NOV.

(FIGS 8–10)

Holotype: MHNAix-PV.2008.1.1, right dentary fragment with p5 to m3 and roots of p4.

Type locality: La Cairanne-Highway (village of Rousset, Aix-en-Provence Basin, Bouches-du-Rhône, France), Upper Campanian.

Etymology: From the coastal river Arc, which flows south of the La Cairanne-Highway locality.

Diagnosis: Mistralestes differs from other known Late Cretaceous eutherian mammals by the unique combination of the following characters: a robust premolariform p5 without cingulid, paraconid, or metaconid; a gradual compression of the trigonid from m1 to m3; a transverse protocristid; and a paracristid probably fused with the protocristid on m3.

Measurements (in mm): MHNAix-PV.2008.1.1 (p5: L = 2.24, W = 1.16, LTr = 1.40; m1: L = 2.30, LTr = 1.05, WTr = 1.38, WTa = 1.34; m2: L = 2.84, LTr = 1.47, WTr = 1.75, WTa = 1.64; m3: L ≥ 2.30, LTr = 1.15, WTr > 1.54, WTa ≥ 1.42).

Description: The horizontal ramus of the dentary is robust but moderately deep (height = 3.9 mm under m2). A virtual deconstruction and reconstruction of the holotype, using 3D μCT scan data (Figs 9, 10), allowed us to replace manually some parts of the specimen such as the trigonid of m2 and the anteriormost part of the dentary. Four teeth are preserved, the first one is premolariform and the other three are molariform. According to our interpretation, MHNAix-PV.2008.1.1 contains p5 to m3 (see below). A bony sulcus on the dentary extends ventrolingually from the mesial root of p4 to the mesial root of p5; this sulcus does not correspond to the mesial end of the mandibular symphysis but to an artefact of preservation (the bone being clearly altered dorsally to this sulcus). The dentary has two mental foramina. The mesial one is located ventral to the mesial root of p4. The second one is situated beneath the distal root of m1 (the position of these mental foramina is discussed below). The dentary is labiolingually enlarged at the level of m3. The μCT scan data show that the roots of p4 are smaller and shorter than those of p5, suggesting that p4 was somewhat reduced (Fig. 9). The p5 is as long as m1. The m2 is larger than m1, and also probably than m3. From p4 to m2, both roots have a similar morphology; the anterior root is

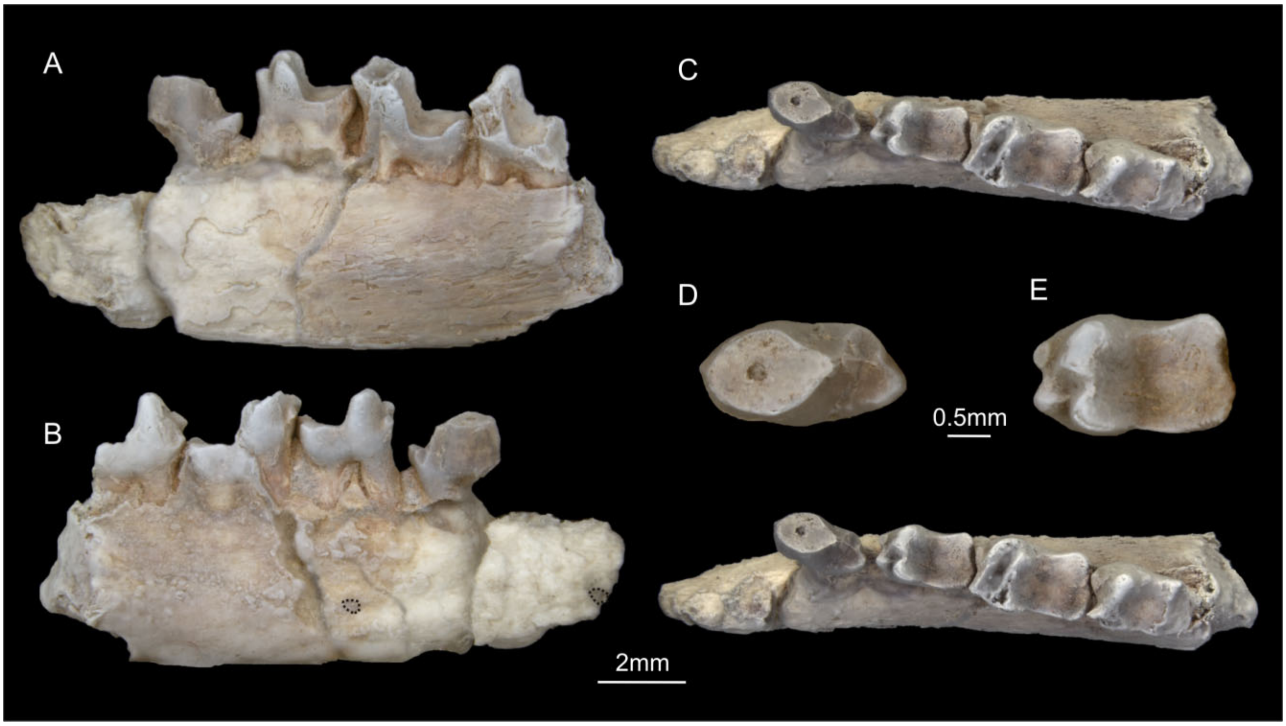

Figure 8. ***Mistralestes arcensis* gen.** et **sp. nov.** from La Cairanne Highway, holotype MHNAix-PV.2008.1.1, right dentary fragment with p5 to m3 and roots of p4. A, lingual; B, labial; C, occlusal (stereoscopic) views; mental foramina are highlighted by black dotted lines; D, p5; E, m1 in occlusal view.

shorter and less robust than the posterior one. In contrast, the anterior root of m3 is longer and more robust than the posterior root.

The p5 is a robust premolariform tooth without a cingulid (Fig. 8D); the protoconid is the dominant cusp and is apically truncated by breakage. A weak paracristid is faintly visible; this cristid does not reach the mesial base of the crown. There is no trace of a swelling of the crown in either the metaconid or paraconid regions. The talonid is nearly as wide as the protoconid and long (about one third of the total mesiodistal length of the tooth). The cristid obliqua is long and very robust; it reaches the distal flank of the protoconid. The hypoconid is partly broken in its mesiolabial part, labially offset from the protoconid, and connected to a tiny cuspid (incipient hypoconulid?). This cuspid is distally protruding and has a short lingual cristid that partially closes the talonid basin.

The m1 is the best preserved molar (Figs 8E–10). The trigonid is less than twice as high as the talonid and has bulbously constructed cusps. The paraconid is cuspate and rounded; it is located only slightly labial to the metaconid. The base of the paraconid is high on the crown. There is a prominent cingulid cuspule f (see Kielan-Jaworowska, Cifelli & Luo, 2004), mesial to the protoconid. This cuspule f is joined to the paracristid notch by a short crest. The protoconid is larger than the metaconid; both cusps are transversally aligned relative to the long axis of the crown. Although the height of the protoconid and metaconid cannot be accurately estimated because they are worn, the protoconid was surely the highest cusp of the trigonid. The paracristid is rectilinear from the protoconid to the paraconid (not L-shaped). The protocristid notch is narrow and rather shallow. The distal flank of the trigonid has a concave vertical wear surface. A short postmetacristid is visible. On the talonid, the cusps and crest are largely obliterated by wear. However, the cusps were evidently peripheral and the hypoconid was certainly the most voluminous cusp on the talonid. The orientation of the cristid obliqua cannot be adequately determined. The lack of a labial valley in the hypoflexid area may suggest that the cristid obliqua was labially orientated. The talonid is longer than and as wide as the trigonid. Lingually to the hypoconid, the distal outline of the crown is concave; this concavity receives the cuspule f of the m2. Judging from this concavity, the entoconid and hypoconulid, which are not clearly visible on the distolingual border of the crown, were probably quite close or even twinned, and distally salient relative to the hypoconid. There is no postcingulid.

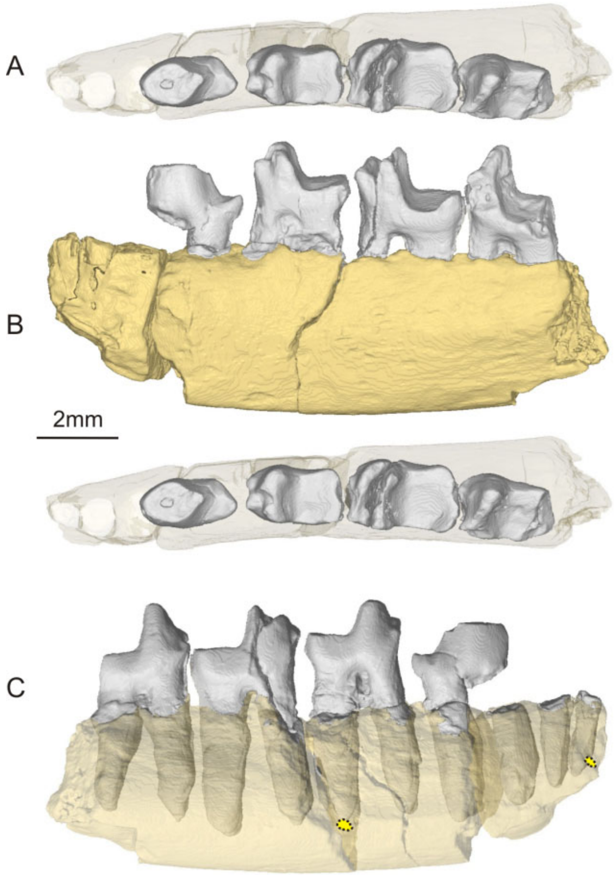

Figure 9. ***Mistralestes arcensis*** **gen.** et **sp. nov.** from La Cairanne Highway, reconstruction of the holotype MHNAix-PV.2008.1.1, using three-dimensional X-ray computed microtomography scan images. A, occlusal (stereoscopic); B, lingual; C, labial views; mental foramina are highlighted by black dotted lines and yellow circles.

The m2 is rather similar to the m1; m2 differs from it in being longer and larger, in having a more crestiform cuspule f, and a paraconid more tightly appressed to the metaconid (Fig. 10). During the preparation of the specimen, the trigonid was broken and improperly glued, so it appears higher than that of m1 (Fig. 8A, B). The μCT-scan reconstruction (Fig. 9B, C) exemplifies that the height of the trigonid relative to the talonid is similar in both m1 and m2. On m2, the apices of the closely approximated entoconid and hypoconulid are still visible despite extensive wear (Fig. 10).

Although its distal part is broken off, m3 seems shorter than but as wide as the m2 (Fig 10). The lingual margins of the paraconid, metaconid, and talonid are broken off. The apex of the protoconid is unworn; distolabial to this cusp, a small ectostylid is present. By comparison with the two other molars, the paracristid and the protocristid are probably confluent, the protoconid is more mesiodistally pinched, and the cuspule f appears smaller in labial view but remains mesiodistally extended. The cristid obliqua is labial and short; there is no hypoflexid. The distal part of the crown suggests that the talonid was more elongated relative to the trigonid.

Comparisons and discussion: The first question is to determine whether p5-m3 or p4-m2 (with p5 or dp5) is preserved in the holotype of *Mistralestes*. The higher degree of molarization of the three posterior teeth, relative to the premolariform aspect of the first tooth, speaks for the first hypothesis. However, the slight reduction of the second tooth, relative to the third one, may alternatively suggest that these teeth are p5 (or dp5) and m1, respectively. Moreover, the position of the posterior-most mental foramen under the distal root of the second tooth also favours the hypothesis that this tooth is p5 (or dp5). In most Cretaceous eutherians, the posterior-most mental foramen is indeed under the ultimate premolar, rarely at the mesial root of m1. Consequently, the holotype of *Mistralestes* may preserve p4–m2 (with p5 or dp5) instead of p5-m3. This uncertainty can be partly resolved using our *μ*CT analysis. Our reconstruction reveals that (1) there is no developing premolar beneath the erupted teeth; (2) there is no trace of a root for a supplementary tooth distal to the ultimate preserved molar; and (3) the distal root of the last preserved molar is shorter and slightly compressed laterally and more posteriorly inclined than that of the other molars, suggesting that this last preserved molar is the ultimate locus of the tooth row. These data support the hypothesis that *Mistralestes* is documented by p5–m3. As for the position of the posterior-most mental foramen under the distal root of m1, which may appear problematic, we do not attach decisive importance to this character as it is well known that the position and number of mental foramina is variable amongst mammals. For example, amongst zhelestids, the anterior foramen is under i1, i2, or the canine and the posterior foramen between p4 and p5. A third foramen can be present under p1. In the zalambdalestoid *Bobolestes*, the posterior mental foramen is under the posterior root of p4, or between p4 and p5. A third small mental foramen can be also present under the anterior root of m1. As a consequence, we cannot exclude the possibility that the posterior-most mental foramen in *Mistralestes* is a supernumerary one and that another foramen was present under the p5 where the dentary is broken. Finally, the reduction of the m1 relative to the m2, although not characteristic of most early eutherians, occurs in numerous taxa, including the earliest ‘condylarths’ (e.g. *Protungulatum, Baiconodon, Oxyprimus*) (see also Halliday & Goswami, 2013).

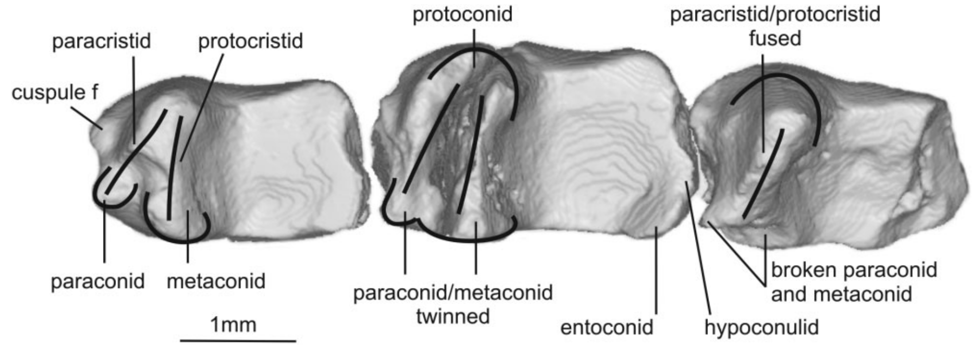

Figure 10. ***Mistralestes arcensis*** **gen.** et **sp. nov.** from La Cairanne Highway, reconstruction of the holotype MHNAix-PV.2008.1.1, using three-dimensional X-ray computed microtomography scan images, in occlusal view showing the main structures of the molars, notably the gradual compression of the trigonid from m1 to m3.

Hence, we are confident that the holotype of *Mistralestes* preserves p5–m3. Consequently, the absence of m4 from the dental formula, together with the reduction and labial position of the paraconid relative to the metaconid and the lack of a prominent vertical keel on the mesiolingual edge of the paraconid, strongly indicate that *Mistralestes* is not a metatherian but a eutherian mammal.

Amongst Late Cretaceous eutherian mammals, *Mistralestes* superficially resembles Zalambdalestidae. They share lower molars with a mesiodistally compressed trigonid, a relatively low trigonid, and a large and wide talonid. Zalambdalestids however are distinct from *Mistralestes* by the increase in height of the talonid from m1 to m3, their less bulbously constructed cusps, and their high-crowned, large, molariform ultimate premolar (with paraconid and metaconid well developed).

Mistralestes is peculiar because of its simple p5 without a cingulid, paraconid, or metaconid. Other unusual characters of *Mistralestes* are, at least on m3, the apparent lack of a hypoflexid and the labial orientation of the cristid obliqua, the lingually displaced hypoconid, and the gradual compression of the trigonid from m1 to m3. These traits excludes any relationships with the vast majority of Late Cretaceous to early Palaeogene eutherians described so far (Asioryctheria, Cimolestidae, plesiadapiforms, 'condylarths', *Gypsonyctops*, *Deccanolestes*).

Comparisons with Late Cretaceous eutherians from Europe are limited to *Valentinella*, *Labes*, and *Lainodon*. *Valentinella* and *Mistralestes* share a robust dental morphology and a reduced m3. However, *Mistralestes* differs from *Valentinella* by being half the size, and considering the smaller size of the roots of its p4, we can easily suppose that *Mistralestes* has a relatively smaller p4 than *Valentinella*. *Valentinella* also differs from *Mistralestes* by a molarized p5 with a hypoflexid and a talonid as wide as the trigonid.

Labes and *Lainodon* share with *Mistralestes* numerous characters that are also diagnostic features of zhelestids, suggesting that *Mistralestes* could be a zhelestid. According to Gheerbrant & Astibia (2012), these characters include a robust dental morphology with specialized crushing-grinding function, as illustrated by their basally inflated cusps, a horizontal wear pattern, lower molars with low trigonid, a paraconid more or less lingually located, a large and wide talonid, and a hypoconulid more or less appressed to the entoconid. Further similarities between Lainodontinae and *Mistralestes* include the lack of a postcingulid, the protoconid being taller than the metaconid, and the occurrence of both a postmetacristid and robust cuspule f.

Labes is known by *Lab. quintanillensis* from Quintanilla del Coco (Burgos Province, Spain) and by *Lab. garimondi* from Champ-Garimond (Languedoc-Roussillon Province, France) (Pol *et al*., 1992). These two species are documented by noncomparable material, *Lab. garimondi* by two m1 or 2 and *Lab. quintanillensis* by only one m3. Pol *et al*. (1992) and then Archibald & Averianov (2012) argued that these two species essentially differ by their size, *Lab. quintanillensis* being the smaller. The m1–2 of *Lab. garimondi* is intermediate in size between the m1 and the m2 of *Mistralestes*. Moreover, in addition to the zhelestid characters listed above, *Mistralestes* evokes *Labes* by a transverse protocristid (metaconid and protoconid set at the same transversal level). However, contrary to *Labes*, which is characterized by a trigonid on m3 that is moderately compressed mesiodistally, *Mistralestes* has a fully compressed trigonid on m2–3. *Labes* also differs from *Mistralestes* by a deeper hypoflexid, a wider and deeper V-shaped protocristid and, on m3, by a more centrally positioned hypoconulid and the fusion of the two roots.

Lainodon is known by at least three species: *Lainodon orueetxebarriai*, *Lainodon ragei*, and *Lainodon* sp.

from Laño (Spain), as well as by *Lainodon* sp. from Taveiro (Portugal), which may be conspecific with *Lai. ragei* (Gheerbrant & Astibia, 2012). The only known lower premolar of *Lainodon* that allows comparisons with *Mistralestes* is the p4 or p5 L1AT 20 attributed to *Lai.* cf. *orueetxebarriai*. It shares with *Mistralestes* a similar size, the robustness of the structures, the lack of a distinct cingulid, the crown dominated by a large and high protoconid without a metaconid, the long and robust cristid obliqua that rises high and labially on the trigonid, and the small but complex talonid with an enclosed basin, and a distally salient (and laterally compressed) hypoconulid. However, *Mistralestes* differs by a talonid as large as the protoconid and the absence of a postmetacristid, which is continuous with the entocristid in *Lainodon*. The lower molars of *Lainodon* are only known by two well-preserved probable m1 (L1AT 14 and L1AT 6), a damaged and worn putative m2 (L1AT 1), and a few fragmentary trigonids and talonids. The m1 of *Lai. ragei* is comparable in size with that of *Mistralestes*, whereas it is much larger in *Lai. orueetxebarriai*. Unfortunately, further comparisons in teeth dimensions are not possible with *Lai. ragei* because of the lack of both m2 and m3 in this species. In *Lai. orueetxebarriai*, the m1 is as large as the m2, whereas the m1 is significantly smaller than the m2 in *Mistralestes*. *Mistralestes* also differs from *Lai. orueetxebarriai* (specimen L1AT 1) by a lower horizontal ramus. Comparisons are impossible for m2, because it is damaged in the only *Lai. orueetxebarriai* specimen. The m1 of *Lai. orueetxebarriai* also differs by slightly stronger bunodonty, a mesially canted trigonid bearing a larger protoconid relative to the metaconid, the presence of a paraconid along its lingual margin, the distal position of the metaconid (protocristid oblique), a more developed postmetacristid, a shorter talonid, and the lower crown base below the hypoconid.

Labes and *Lainodon* were recently gathered in their own subfamily by Gheerbrant & Astibia (2012), whereas Archibald & Averianov (2012) regarded these two genera as Zhelestidae incertae sedis along with *Sheikhdzheilia* (Uzbekistan; early Cenomanian), *Borisodon* (Kazakhstan; early Turonian), *Gallolestes* (Mexico and Texas, USA; Campanian), and *Avitotherium* (Utah and Montana, USA; Campanian).

Amongst these genera, *Mistralestes* shares with *Sheikhdzheilia* the lack of a metaconid on p5, a protoconid taller than the metaconid (as in *Labes* and *Lainodon*), and the absence of a postcingulid on the molars. However, *Mistralestes* differs from *Sheikhdzheilia* by numerous characters, including a p5 without precingulid, lingual cingulid, or paraconid; a transverse protocristid, a more closed trigonid with gradual appression of the paraconid and metaconid; and a labially orientated cristid obliqua on the molars. *Mistralestes* differs from *Avitotherium* by the same characters. *Mistralestes* more closely resembles *Borisodon* and *Gallolestes* by its transverse protocristid between the protoconid and the metaconid. However, it differs from them by the gradual appression of the paraconids and metaconids from m1 to m3, the labial orientation of the cristid obliqua, and the lack of both postcingulid and hypoflexid (at least on m3). On p5, *Mistralestes* and *Borisodon* share the absence of a metaconid, but *Borisodon* differs by a longer talonid, a complete lingual cingulid, and a less robust, distinctly curved, and hook-like protoconid, with its apex pointed distally. *Borisodon* has a faint Meckelian groove, which is clearly lacking in *Mistralestes*. *Mistralestes* also differs from *Borisodon* by the m1 being much smaller than the m2.

The other Zhelestidae, which are grouped within the subfamily Zhelestinae, belong to the genera *Zhelestes*, *Aspanlestes*, *Parazhelestes*, and *Eoungulatum* from the Turonian to ?Coniacian of Uzbekistan. Compared with the other zheslestids, these genera are more reminiscent of *Mistralestes* by the significant reduction of m3 and the apparent mesiodistal constriction of the trigonid. The wear pattern of the talonid seen in *Mistralestes* also evokes that of zhelestines (i.e. CCMGE 36/12000, the holotype of *Parazhelestes mynbulakensis*). However, p5 of the zhelestines is molariform with a separate metaconid and a cuspate paraconid (crestiform or absent in *Zhelestes*), and the metaconid of the molars is as high and as wide as the protoconid. More importantly, the mesiodistal constriction of the trigonid of m1 to m3 of zhelestids is mainly due to the reduced and crestiform aspect of the paraconid from m1 to m3 and the L-shaped aspect of the paracristid. In *Mistralestes*, the paracristid is rectilinear in m1–2 (certainly fused with the protocristid on m3) and the paraconid is twinned with the metaconid on m2 (and also probably on m3).

PHYLOGENETIC ANALYSIS

Although it is worn and damaged, the material attributed to *Mistralestes* and *Valentinella* preserves a list of characters sufficient to include these two genera in a phylogenetic analysis dealing with the suprafamilial relationships amongst early eutherians. For this purpose, we used the data matrix of Wible *et al*. (2009), which was recently updated by Archibald & Averianov (2012) by the addition of additional Cretaceous eutherians. *Mistralestes* and more particularly *Valentinella* introduce further missing data into the matrix, but not more than some already included taxa (e.g. *Lainodon*). Data were managed using the NEXUS data editor v. 0.5.0 (see Appendix) and phylogenetic reconstruction was performed with PAUP v. 4.0b10 following the character/taxon assumptions indicated by Wible *et al*. (2009).

The analysis generated 80 878 equally most parsimonious trees of 2363 steps each (consistency index = 0.2539; retention index = 0.5531). Although the strict consensus tree is globally unresolved (Fig. 11A), some clades appear monophyletic in most of the equally most parsimonious trees (Fig. 11B). For example, *Valentinella* is included in 99.6% of these 80 878 trees within the Zhelestidae + *Paranyctoides* + *Alostera* clade. The 0.4% of alternative topologies exclude *Sheikhdzheilia* and/or *Lainodon* and/or *Alostera* from this clade. As a result, *Valentinella* is always included in the core-zhelestid clade and appears far from *Protungulatum* and *Oxyprimus*, suggesting that the observed similarities between *Valentinella* and these early 'condylarths' are the result of convergence. In 91% of the 80 878 equally most parsimonious trees *Mistralestes* is included within a large clade that gathers Placentalia *s.l.*, Leptictidae, Zalamdalestidae, *Deccanolestes*, and Asioryctitheria. The relationships within this clade are quite similar to those of Wible *et al*. (2009) and Archibald & Averianov (2012). However, the precise position of *Mistralestes* remains problematic and unresolved. It is related either to Zalamdalestidae (23.4%), or to Placentalia *s.s.* (*Purgatorius*, *Protungulatum*, and *Oxyprimus* excluded) (57%), or to Placentalia *s.l.* + Leptictidae (62%).

In a second analysis, characters were a posteriori reweighted according to their rescaled consistency index, as a means of reducing the misleading effect of homoplasy. This analysis resulted in 151 equally most parsimonious trees. The strict consensus tree (Fig. 11C) is well resolved and very similar to the majority-rule consensus tree of the first unweighted analysis. Although the position of *Valentinella* within zhelestids (plus *Paranyctoides*) remains unresolved, *Mistralestes* appears robustly nested within zhelestids as the sister-taxon of the Zhelestineae + *Avitotherium* clade. The position of *Mistralestes* is thus remarkably dissimilar between the two analyses. The clade that gathers *Mistralestes* with Zhelestinae and *Avitotherium* is however supported by only one unambiguous synapomorphy: an anteroposteriorly compressed trigonid (angle less than 35°; character 111, 1 = = > 2). The larger clade that embraces *Mistralestes* and *Valentinella* within the zhelestids (plus *Paranyctoides*) is supported by three unambiguous synapomorphies of the lower molars: the talonid is subequal to or wider than the trigonid (character 119, 1 = = > 2), the hypoconulid is closely approximated to the entoconid (character 120, 1 = = > 3), and the entoconid is subequal to or larger than the hypoconid and/or the hypoconulid (character 122, 1 = = > 2). However, considering on the one hand that the two latter characters are unknown in *Valentinella*, and on the other the fluctuating position of *Mistralestes* between the unweighted and the reweighted analysis, we consider that the phylogenetic position of both *Mistralestes* and *Valentinella* remains unclear. Pending more data, we place both genera in ?Zhelestidae.

CONCLUSION

Valentinella and *Mistralestes* significantly improve our knowledge of the European eutherian mammals in documenting morphologies previously unknown in the Late Cretaceous fossil record of Europe. Unfortunately, their dental remains are somewhat worn and damaged; cusps and crest of the talonids are especially obliterated by wear. Hence, even though there are indications that they might belong to Zhelestidae, they are currently insufficiently documented to be clearly placed within the phylogeny of eutherians. In this context, recent field and laboratory studies of mammals have consistently indicated that amongst all species of eutherians currently known from the Cretaceous, none are included in the Placentalia (Wible *et al*., 2009; Goswami *et al*., 2011; Archibald & Averianov, 2012; O'Leary *et al*., 2013). This growing consensus amongst palaeontologists is mainly based on the fossil record of North America and Asia and, unfortunately, less is known on the European and Gondwanan continents; around 5% of the Cretaceous fossil mammal localities are documented there (Kielan-Jaworowska *et al*., 2004). In this respect, despite active field efforts, the lack of any data in the Late Cretaceous of Africa so far is a key problem regarding the origin of Placentalia. Whereas molecular phylogeneticists argue for a basal position of the native African placentals (the so-called Afrotheria) in the molecular tree of placental mammals, nothing is known about the history of African eutherians before the Late Palaeocene. As a consequence, pending the discovery of Cretaceous eutherians in Africa, all palaeobiogeographical scenarios for the place and date of origin of Placentalia remain conjectural. Unlike eutherian mammals, other vertebrates are known in the Late Cretaceous of Africa. The palaeogeographical distribution of abelisauroid theropods, titanosaurid sauropods, madtsoiid snakes, bothremydid turtles, and possibly sebecosuchian crocodyliforms (Curry Rogers, 2005; Pereda-Suberbiola, 2009) suggests that several African clades reached southern insular Europe during the Campanian and Maastrichtian via the Mediterranean Tethyan sill (Alboran and Apulian routes) (Rage, 2002; Gheerbrant & Rage, 2006; Ezcurra & Agnolin, 2012). These taxa constitute the basic pattern of the 'Eurogondwanan fauna'

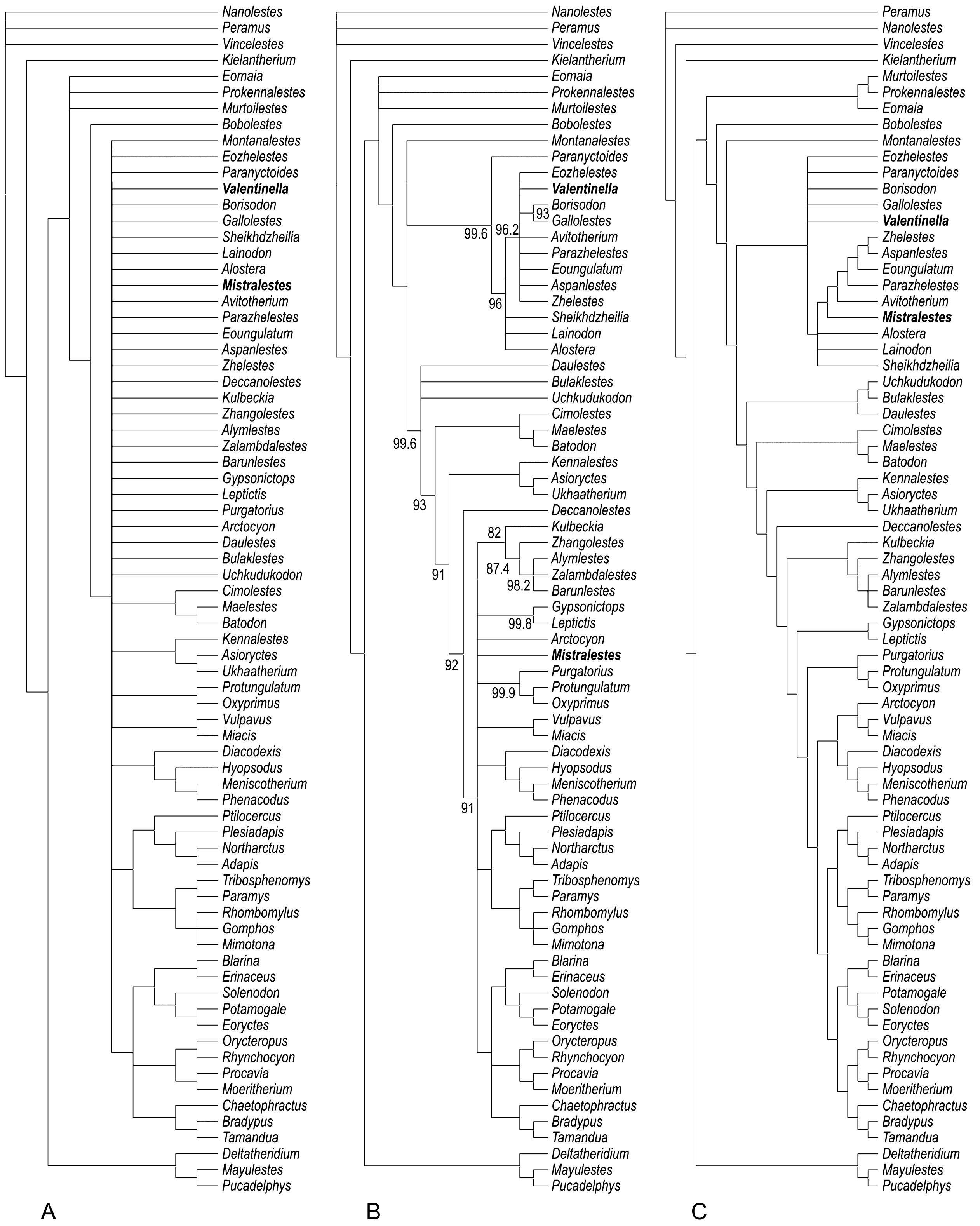

Figure 11. Phylogenetic analyses of Cretaceous eutherians based on the data set of Wible *et al.* (2009), as modified by Archibald & Averianov (2012), including *Valentinella* and ***Mistralestes* gen. nov.** A, strict consensus of 80 878 equally most parsimonious trees; B, 80% majority-rule tree; C, strict consensus of 151 equally most parsimonious trees (characters reweighted a posteriori according to their rescaled consistency index).

(Le Loeuff, 1991). Consequently, if Placentalia were present in Africa during the mid-Cretaceous as molecular clock estimates claim, we cannot a priori reject the possibility that they also emigrated towards southern Europe during the Campano-Maastrichtian. This hypothesis, although speculative, is highly promising and Europe provides an excellent opportunity to test the Cretaceous origin of Placentalia. This allows the promising hypothesis that the Late Cretaceous beds of Europe may yield evidence of totally unsuspected branches of the basal radiation of placental mammals.

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APPENDIX

Character scores for *Valentinella vitrollense* and *Mistralestes arcensis* gen. et sp. nov., based on the matrix of Wible *et al*. (2009):

MISTRALESTES ARCENSIS

00???????? ?????????? ?????????? ?????????? ?????????? ????001100 100??????? ?????????? ?????????? ?????????? ?????00000 201012122(23) ?1?00010?3 0????????? ?????????? ???1?????? ????????

VALENTINELLA VITROLLENSE

00???????? ?????????? ?????????? 1????????? ?????????? ?000??0?0? 100??????? ?????????? ?????????? ????????0? ?????????? ????1???2? ?????11??? 0????????? ?0???0???? ????????