

A eutherian mammal in the latest Cretaceous of Vitrolles, southern France

RODOLPHE TABUCE, MONIQUE VIANEY-LIAUD, and GÉRALDINE GARCIA



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In Europe, the fossil record of the eutherian mammals is very scanty for the Late Cretaceous, as only two genera, documented by isolated teeth, are presently recorded in France and in Spain. Both genera, *Labes* and *Lainodon*, are considered to be representatives of the “zhelestids”, a paraphyletic unit regarded as being at the origin of Cenozoic ungulates within the Ungulatomorpha clade. We here describe *Valentinella vitrollense* gen. et sp. nov. from Vitrolles la Plaine (Maastrichtian, southern France). This species, represented by fragmentary remains of lower and upper dentitions, is tentatively assigned to the “zhelestids” according to the hypoconulid-entoconid twinning and the antero-posteriorly short trigonid on m1–3. The occlusal surfaces are obliterated by dental attrition, but *Valentinella* could be an evolved “zhelestid”, more derived than *Labes* and *Lainodon* by its fully compressed trigonid. *Valentinella* is similar to *Gallolestes* by other derived characters such as a crushing specialization of the teeth, associated with a probably molariform p4 (or dp4) and slightly reduced m3. The enamel microstructure, showing a radial prismatic pattern combined with a reduced interprismatic matrix, in which cristallites are oriented at about 45° to the prisms axes, appears compatible with the ancestral morphotype for all ungulates; although no synapomorphy can be proposed for the ungulatomorphs.

Key words: Mammalia, Eutheria, “Zhelestidae”, enamel microstructure, Cretaceous, France.

Rodolphe Tabuce [rtabuce@isem.univ-montp2.fr], Monique Vianey-Liaud [movianey@isem.univ-montp2.fr], Laboratoire de Paléontologie, Institut des Sciences de l'Evolution, cc064, Université Montpellier II, place Eugène Bataillon, 34095 Montpellier cedex 05, France;

Géraldine Garcia [geraldine.garcia@univ-poitiers.fr], Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Faculté des Sciences Fondamentales et Appliquées, Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers cedex, France.

Introduction

According to present paleontological knowledge, the Late Cretaceous is a key period for the evolution of placental mammals, as the first representatives of the extant supraordinal groups originated at that time (McKenna and Bell 1997; Archibald et al. 2001). In Europe, Late Cretaceous mammalian history is poorly understood because of the paucity of continental deposits yielding mammals. Thus, the fossil record in this area is very scarce in contrast to other holartic provinces (e.g., western North America, Gobi Desert, and Uzbekistan in Asia). Only a few localities are known, all of them located in the Iberian-Armorican and Transylvanian islands that made up part of the European Archipelago (Rage 2002): Champ-Garimond (Campanian, France) (e.g., Sigé et al. 1997), La Neuve (Campanian, France) (Garcia et al. 2000), Laño (?Campanian, Spain) (e.g., Gheerbrant and Astibia 1999), Taveiro (Late Campanian or Maastrichtian, Portugal) (Antunes et al. 1986), Peyrecave (Maastrichtian, France) (Gheerbrant et al. 1997), Quintanilla del Coco (Maastrichtian, Spain) (Pol et al. 1992), Pui (Maastrichtian, Romania) (e.g., Rădulescu and Samson 1997), Totești-Baraj (Maastrichtian, Romania) (Codrea et al. 2002), and Nălaț-Vad (Maastrichtian, Romania) (Smith et al. 2002).

The eutherian mammals recovered from these sites are still poorly documented, they are only known by fragmentary or isolated complete teeth. Eutherians are undoubtedly documented only in Champ-Garimond, Taveiro, Laño, and Quintanilla del Coco.

During excavations of dinosaur bones and eggshells in an Upper Cretaceous locality near Vitrolles (southern France) (Garcia 1998; Garcia and Vianey-Liaud 2001), three worn and crushed mammalian specimens have been recovered. The mammalian specimens are in association with other vertebrate remains, some ratite eggshells, and typical Rognacian molluscs (*Lychnus matheroni*) (Garcia et al. in preparation). The Rognacian is a regional stratigraphic unit correlated with the upper Campanian plus Maastrichtian by the magnetostratigraphy and the dinosaur eggshells distribution (Garcia and Vianey-Liaud 2001). The occurrence of dinosaur egg clutches, belonging to the *Megaloolithus mamillare* oospecies, restricts the age of the site to the Maastrichtian. Besides, the position of the locality, below the Rognac Limestone, suggests an early Maastrichtian age for Vitrolles la Plaine (Table 1, Fig. 1).

The mammalian specimens belong to a new eutherian genus that seems to be related to the “zhelestids”. This paraphyletic family is considered as closely related to Cenozoic

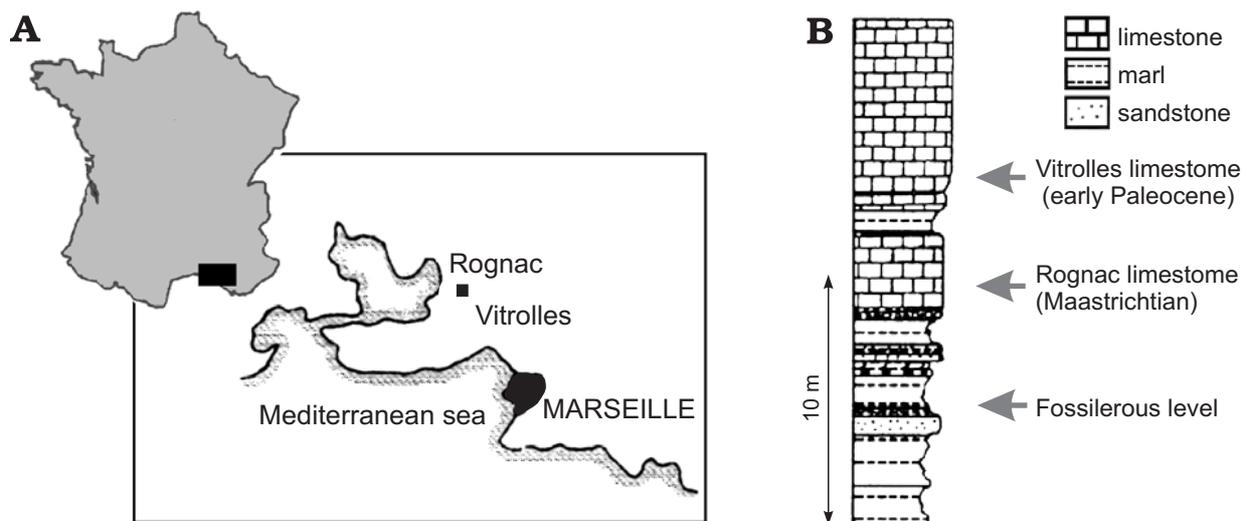


Fig. 1. A. Location of the Vitrolles la Plaine site (Arc Basin, Bouches-du-Rhône, southern France). B. Stratigraphic section through the fossiliferous layers.

archaic and modern ungulates within the Ungulatomorpha clade (Archibald 1996; Nessov et al. 1998; Archibald et al. 2001). The new genus here described is therefore a putative critical representative of one of the very few superordinal groupings of modern mammals known before the Cretaceous-Paleogene boundary.

Storage.—The specimens described in this paper are housed in the collections of the Institut des Sciences de l'Évolution, Université Montpellier II (France) with the abbreviation ISEM/VLP; the second part of the abbreviation refers to Vitrolles la Plaine.

Table 1. Faunal list from the Vitrolles la Plaine site (Maastrichtian, southern France).

Bony fish
Ginglymodi
Lepisosteidae indet.
Teleostei
Sparidae indet.
Squamates
Squamata indet.
Turtles
Pleurodira
Bothremyidae
cf. <i>Polysternon</i>
Crocodylians
Eusuchia
Alligatoroidea
cf. <i>Musturzabalsuchus</i>
Dinosaurs
Saurischia
Theropoda indet.
Sauropoda
Titanosauridae indet.
Mammals
Eutheria
<i>Valentinella vitrollense</i> gen. et sp. nov.

Systematics

Class Mammalia Linnaeus, 1758

Infraclass Eutheria Gill, 1872

Supergrandorder cf. Ungulatomorpha Archibald, 1996

Family cf. “Zhelestidae” Nessov, 1985

Genus *Valentinella* nov.

Type species: *Valentinella vitrollense* sp. nov.

Known range: Maastrichtian, Arc Basin, southern France.

Diagnosis.—That of the type species.

Etymology.—Dedicated to Xavier Valentin (University of Poitiers, France), who discovered the specimens.

Valentinella vitrollense sp. nov.

Figs. 2, 3.

Holotype: ISEM/VLP-2, damaged right dentary with p3–m3.

Referred material.—ISEM/VLP-4: fissured fragment of a right dentary with a damaged ?p4, associated with two very fragmentary adjacent teeth. ISEM/VLP-3: a fractured maxillary fragment with roots of right and left canines and a right ?P2.

Diagnosis.—*Valentinella* presents the classic “zhelestid” features: the teeth are characterized by developed crushing function, the paraconid is lingually or sublingually positioned with a clear appression to the metaconid, the entoconid and the hypoconulid are twinned, and the talonid is expanded labiolingually. *Valentinella* differs from the Asian “zhelestids” by the molarization of the ultimate premolar, and is distinct from *Avitotherium* and *Gallolestes* by its simple, bulbous p3 and by its larger metaconid and entoconid on lower molars, respectively. *Valentinella* differs from *Labes* and *Lainodon* in having a mesio-distally compressed trigonid.

Etymology.—From Vitrolles, name of the town near the fossiliferous site.

Measurements.—(in mm): ISEM/VLP-2: p3 (L = 2.3; W = 1.5); p4 (or dp4) (L = 2.3; W = 2); m1 (L = 3.4; W = 2.35; Ltri = 2; Ltal = 1.4; Wtri = 2; Wtal = 2.35); m2 (L > 3.5; W = 2.9); m3 (L = 3.1; W > 2). ISEM/VLP-4: ?p4 (Ltri = 1.5; Ltal = 1.2; Wtri = 1.35; Wtal = 1.9). ISEM/VLP-3: right canine (H > 2.5; diameter of the root = 1.7); left canine (H > 2.3; diameter of the root = 1.6); ?P2 (L = 2.5; W = 2.0)

Description.—During diagenesis and compaction of the sediment, the teeth were distorted along parallel cracks caused by plant roots, and/or between talonids and trigonids, and between teeth. These movements have produced oblique deformations.

On ISEM/VLP-2 (Fig. 2), the dentary is almost an outline of a jaw fissured in the marl, while both dentine and enamel are rather better conserved. The five teeth exhibit two robust roots.

The occlusal outline of the p3 is oval. This is the only well-preserved tooth. The crown has a single, large, bulbous cusp (protoconid). Distally there is a small, low cingulid and a distinct concavity between the disto-lingual flank of the protoconid and the distal heel. On the distal side of the protoconid, although this cusp is damaged, it appears that no crest is present; the distal side appears swollen.

The p4 (or dp4?) is smaller than the molars, and the wear pattern suggests that it is either a molarized premolar or a deciduous premolar; according to its small mesio-distal dimension, we favor a p4 status for this tooth. Taking into account the crushing, the only morphological traits of the crown that can be described are the labially rounded sides of both protoconid and hypoconid. The labial position of the protoconid suggests the presence of a distinct metaconid.

On m1, we can distinguish the protoconid and the hypoconid. The trigonid is badly damaged lingually. The cusps show considerable dental attrition; dentine is well exposed in both the distal part of the trigonid and the whole talonid. The worn occlusal surfaces are flat and the trigonid and talonid are of the same height. On the labial side, an incipient exaenodonty can be seen. The talonid appears to be shorter and wider than the trigonid. The quadrate shape of the mesial part of the crown suggests that the paraconid—if it is present—is not mesially projected but strongly appressed to the metaconid. This trait, which is also found in m2–m3, will need to be verified on unworn specimens.

The m2 is longer and wider than the m1. Its trigonid is very worn and damaged. On the talonid, three cusps can be identified with some difficulty. The hypoconid is not larger than the entoconid; and according to their rounded bases these cusps were likely more bulbous than sharp. A fragment of the hypoconulid is preserved disto-labially to the entoconid and is positioned near it (“twinning”).

The m3 is shorter and appears to be narrower than the two other molars. Only the labial half of the crown is not

crushed. The tooth is strongly worn, suggesting, like the occlusal surfaces observed in m1–2, a developed crushing function of the teeth during dental attrition. On the talonid, which is shorter than the trigonid, the remaining area of the postcristid does not suggest a strong distal development of a hypoconulid.

ISEM/VLP-4 is a very damaged specimen which displays fragments of both ?p3 and ?m1, plus a better preserved ?p4. Only the lingual wall of the ?p3 is preserved, the length of this tooth being superior to 1.5 mm, as roughly estimated from the two roots. The mesio-distal axis of the ?p4 shows a 90° labial rotation relative to the ?p3. The tooth is probably two-rooted, although the roots are not well-preserved on the specimen. The crown appears to be high (about 2 mm, on the disto-lingual side), but because of poor enamel preservation, it is difficult to identify the position of the neck. On the occlusal surface, the morphology is badly preserved, the talonid seems shorter and wider than the trigonid. As for the posterior tooth, the ?m1, only fragments of enamel remain.

On ISEM/VLP-3 (Fig. 3), a fragment of bone bears two parallel and elongated vestiges of dentine and enamel. We tentatively interpret these dental remains as right and left upper canines. Distally, some fragments of the maxilla are preserved; they are followed by a two-rooted tooth, that could be P2. This unicuspid upper premolar is the best preserved tooth of the material studied here. The paracone is centrally positioned and laterally narrow; this cusp exhibits a sharp mesial crest, is slightly expanded on its lingual margin, but does not bear an incipient protocone. The mesial root strongly slants distally before joining the crown.

Comparisons and discussion.—The large and three-cusped talonid of *Valentinella* suggests a therian, and the entoconid-hypoconulid twinning is evocative of the metatherians. Considering the dental formula of the lower jaw ISEM/VLP-2, however, with only three molars bearing a reduced paraconid, we conclude that *Valentinella* is certainly a eutherian. Some Late Cretaceous eutherians resemble our specimens in their wear pattern; it is particularly true for *Gypsonictops* (see Lillegraven 1969: 52), which also exhibits a reduced paraconid. This genus clearly differs from *Valentinella* in having a very reduced p2, a premolariform p3 with a bicuspidate talonid, a true molariform p4 and by a non-reduced m3. Moreover, as in most Late Cretaceous eutherian mammals, *Gypsonictops* has a more centrally positioned hypoconulid on the postcristid. According to Setoguchi et al. (1999), the entoconid-hypoconulid twinning (observed in *Valentinella*) is typical of the families Zalambdalestidae and “Zhelestidae”. In the zalambdalestids, Archibald and Averianov (2003) argued however that, at least in *Kulbeckia*, the entoconid and hypoconulid are very close to each other, but not twinned.

Within the zalambdalestids, the Mongolian *Zalambdalestes* and *Barunlestes* (Kielan-Jaworowska 1969; Kielan-Jaworowska and Trofimov 1980) also share with *Valentinella* a reduced m3; but they differ by a vestigial P2, a longer

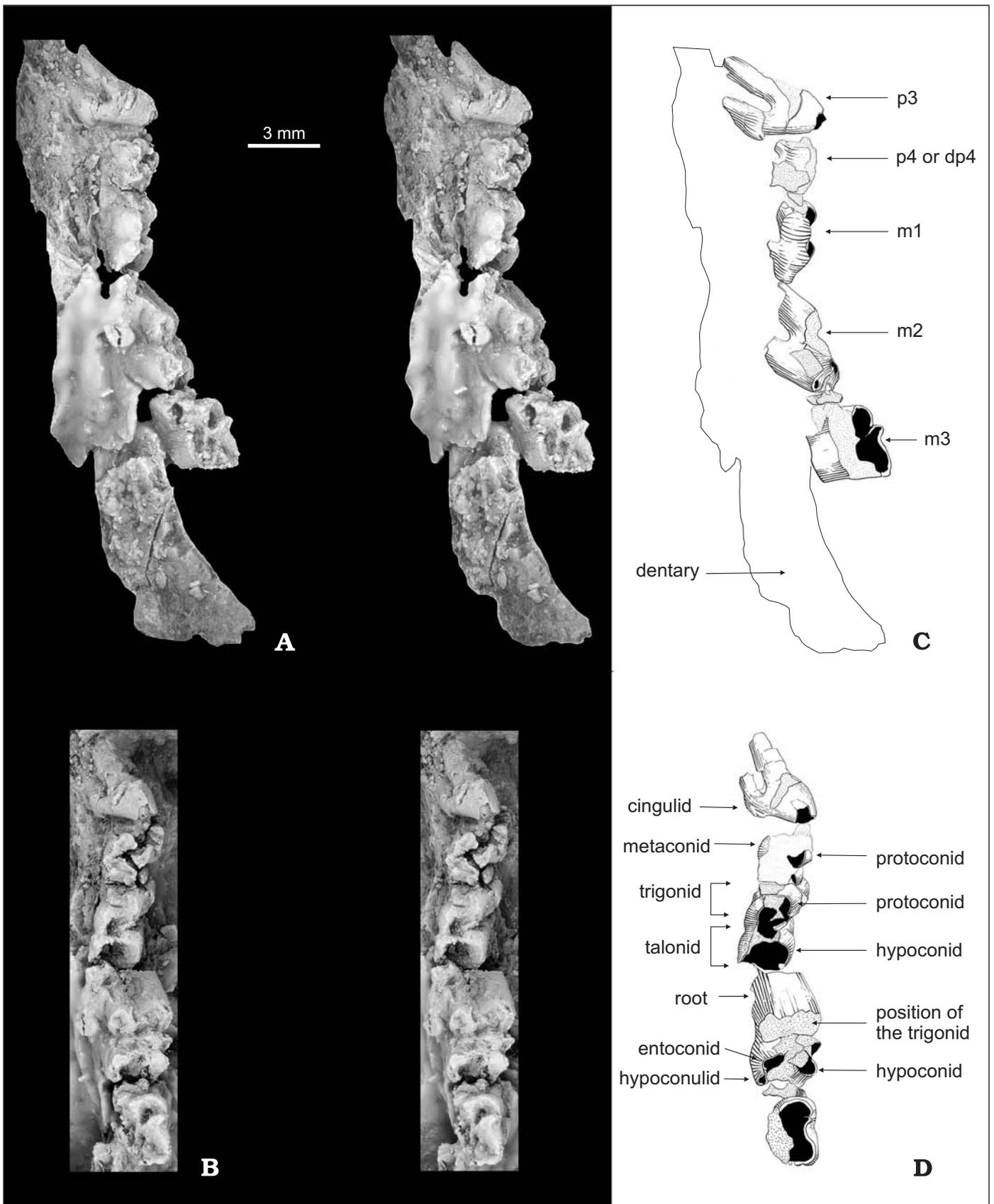


Fig. 2. *Valentinella vitrollense* gen. et sp. nov., stereophotographs and explanatory drawings of ISEM/VLP-2 (holotype) in lingual (A, C) and occlusal (B, D) views.

p4, and less swollen cusps on molars. *Kulbeckia*, the oldest known zalambdalestid, is more evocative of our specimens in the short molariform p4 and by the sub-rectangular occlusal pattern of the teeth. *Kulbeckia*, however, has a long m3 and a very small P2.

According to the diagnosis of the Ungulatomorpha (“zhelestids” plus ungulates) (Archibald 1996; Nessov et al. 1998), *Valentinella* is more reminiscent of this supergrand-order by 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. The wear pattern, typical of a crushing function of the teeth, and their relatively large size are also characters of genera included in the “zhelestids”.

The dental formula of the Asian Turonian–Coniacian representatives of this paraphyletic family is characterized by the occurrence of five premolars. Nessov et al. (1998) have equivocally suggested that the small premolar at position three (p3 or permanent dp2) is lost in more derived “zhelestids”. If we admit this assumption, the p3–4 of *Valentinella* must be compared respectively with the p4–5 of *Aspanlestes* and *Sorlestes*, the only known primitive “zhelestids” documented by their lower premolars. These genera differ from *Valentinella* by their long, labio-lingually compressed, and premolariform p5 without metaconid; the p4 of *Aspanlestes* is more evocative of the p3 of ISEM/VLP-2 by its mesial protoconid and by the small distal heel without cusp, but clearly differs by a sharp cristid running from the apex of the protoconid to the distal margin of the tooth. As for the anterior upper teeth, ISEM/VLP-3 can be compared only with the holotype of *Zhelestes temirkazyk*. In this species, the large canine alveolus suggests that this tooth is longer and more acute than in *Valentinella*; the two-rooted unicuspidate P2 are more similar by an asymmetrical profile, showing a small mesial shelf, whereas the distal side is steeper. Thus, the main difference between *Valentinella* and the Asian “zhelestids” concern the molarization of the ultimate premolar, this character is derived and can be explained by the chronological gap between both groups.

According to Nessov et al. (1998), *Gallolestes*, *Alostera*, and *Avitotherium* are the North American Late Cretaceous representatives of the “zhelestids”; these genera share with *Valentinella* the “zhelestid” molars traits listed above. The p3 of *Avitotherium* (Ciffelli 1990) obviously differs by its more slender protoconid, which bears both mesial and distal cristids. Moreover a lingual cingulid is present in *Avitotherium*, and the talonid is broad with two well-defined cusps enclosing a small talonid basin. As for the p3 of *Gallolestes*, only the distal part of the crown is known (Lillegraven 1976) and the simplicity of the construction evokes the p3 of *Valentinella*. Both genera are also similar in that the molariform p4 bears a distinct metaconid and two strongly developed roots. Butler (1977, 1990) suggested that the fourth premolar of *Gallolestes* is a

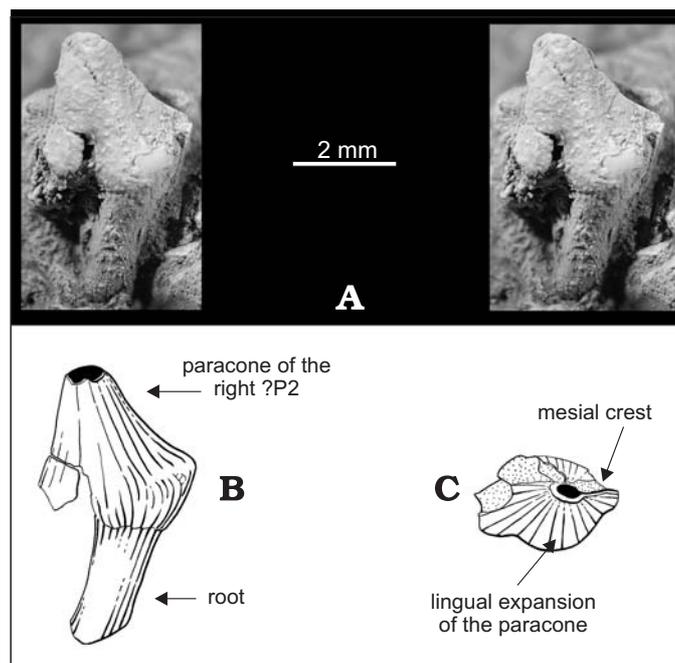


Fig. 3. *Valentinella vitrollense* gen. et sp. nov., stereophotographs and explanatory drawings of ISEM/VLP-3 (right ?P2) in lingual (A, B) and occlusal (C) views.

dp4 (see also Nessov et al. 1998); in the same way we also do not exclude a dp4 status for the ultimate premolar of *Valentinella* on ISEM/VLP-2. The molars are also similar in the reduction of the m3, their strong roots, their quadrate mesial occlusal outline, and by their robust aspect with rather bulbously-constructed cusps. *Gallolestes* differs in its smaller metaconid and entoconid relative to protoconid and hypoconid respectively.

The Late Cretaceous European genera *Lainodon* from Laño and *Labes* from Champ-Garimond and Quintanilla del Coco have been related to “zhelestids” by Gheerbrant and Astibia (1994, 1999). After that, Nessov et al. (1998) included these genera in the definition of the “zhelestids”. Morphologically, *Lainodon* and *Labes* share with *Valentinella* the “zhelestid” characters, and a robust general morphology including massive bunodont cusps and strong roots, an incipient exaenodonty, and similar dimensions as well (*Valentinella* being slightly bigger). All the characters listed by Gheerbrant and Astibia (1999) to differentiate *Lainodon* from *Labes* cannot be observed on our specimens. With caution, the shorter talonid of *Valentinella* seems to indicate more affinities with *Lainodon*. *Lainodon* and *Labes* differ from *Valentinella* in having a more anteriorly positioned paraconid and by an hypoconulid stronger and more distally positioned on lower molars. A p2? or p3?, tentatively referred to *Lainodon* by Gheerbrant and Astibia (1999), is distinct to the p3 of *Valentinella* by its less robust morphology (not bulbous), its narrower occlusal outline, and by the occurrence of a crest on the distal flank of the protoconid.

Recently, Averianov et al. (2003) advocated a “zhelestid” status for the alleged marsupial from the Cretaceous of Madagascar described by Krause (2001). This fragmentary lower molar does not permit close comparisons with *Valentinella*. The greater trigonid angle of the Malagasy form (a primitive trait also observed in *Labes*, *Lainodon* and in both early metatherians and eutherians) suggests that *Valentinella* is more reminiscent of the older Asian “zhelestids” in this character.

To conclude, *Valentinella* is a eutherian, and could be a derived “zhelestid”, characterized by a probable molariform p4 (or dp4) and a slightly reduced m3; it could be therefore compared with some early “condylarths”. The crushing specialization, the entoconid-hypoconulid twinning, and the bulbous protoconid on p3 evoke the Mioclaenidae. The genera *Promioclaenus*, *Mioclaenus* and some species of *Tiucloaenus* present in particular a slightly to considerably reduced m3. Moreover, as *Valentinella*, *Mioclaenus* and *Tiucloaenus robustus* are also characterized by obsolete to absent ectoconulid (Archibald 1998; de Muizon and Cifelli 2000). *Valentinella* is nevertheless distinct from mioclaenids by its molariform p4 (or dp4). In order to discuss the systematic position of *Valentinella*, notably its relationships with the “condylarths”, we carried out the analysis of the enamel microstructure of *Valentinella*.

Enamel microstructure of *Valentinella*

Method.—Enamel is particularly useful in investigations of fossil specimens because its highly mineralized composition is virtually unaltered by the process of fossilization; and despite the poor preservation of the material studied here, the enamel microstructures are reasonably well-preserved. The enamel specimens consist of very small fragments from these molariform teeth. The fragments were imbedded in polyester resin and sectioned vertically and horizontally. After grinding, polishing (with frequent checking under a dissecting microscope), and slight etching during 30 sec. with 37% phosphoric acid to make morphological details visible, the specimens were successively rinsed with 10% ammonia and distilled water. After air drying, samples were sputter-coated with platinum and examined under a JEOL SEM at magnifications between x500 and x15000. The terminology used here for describing enamel follows Koenigswald and Sander (1997).

Description.—On vertical plane section of p4 (or dp4) (ISEM/VLP-2), the enamel layer (100 μm of thickness) appears divided into two parts (Fig. 4): (1) in the outer part (14–21 μm), we note a prismless enamel with incremental lines; (2) in the thick inner part, a radial prismatic enamel occurs with prisms directed away radially with a minor inclination; near the enamel dentine junction, the prisms are less in-

dividualized. The diameter of the prisms on p4 is around 3–4 μm . The interprismatic matrix (IPM) is poorly preserved, but the cristallite orientation of this IPM appears not to be parallel to the prism long axes.

On a nearly vertical plane section of ?p4 (ISEM/VLP-4), the enamel presents the same organization with a thin enamel layer (140 μm) showing a prismless outer part (26 μm) and radial organization of prisms in the inner layer (114 μm). In this section, the IPM is clearly observable, and the cristallite orientation of this IPM is about 40–45° to the prism long axes.

On a horizontal plane section of m1 (ISEM/VLP-2), the prisms, viewed roughly perpendicular to their long axes, are closely packed, and circular to hexagonal in cross section, clearly not arc-shaped. The arrangement of prisms seems to be erratic. The prisms are large (6–8 μm in diameter) with a central depression. The latter could have been a preparing artifact, as acid preferentially attacks the ends of cristallites faster than their long sides; however as holes are visible on the entire section, we interpret this structure as natural. Reif (1974) and Sahni and Koenigswald (1997) observed the same depressions in hexagonal prisms in carnivores and extant dolphin respectively. Sahni and Koenigswald (1997) regarded these structures as a result of incomplete mineralization restricted to the area where prisms disappear in the IPM; and they suggested that the hexagons represent the area of one ameloblast and the central depression may represent the trace of Tomes’ process.

Discussion.—The prismatic structure of the enamel confirms the mammalian status of *Valentinella*. In fact, a consensus now exists that no reptiles have true prismatic enamel. An exception is known for the extant agamid lizard *Uromastix* where, however, the prisms are obviously not homologous to those of mammals (see Wood and Stern 1997). According to the more recent advances (Sander 1997; Wood et al. 1999), synapsid reptiles and some Mesozoic mammals (e.g., *Morganucodon*, Haramiyidae, Kuehneotheriidae) exhibit the synapsid columnar enamel (or SCE), where columnar units are oriented parallel to one another and perpendicular to the outer enamel surface. In the clade Mammalia *sensu stricto*, the appearance of a prism sheath transforms SCE into a plesiomorphic prismatic enamel (or PPE). The PPE is characterized by at least five (presumably independent) characters sets (Wood et al. 1999; Wood 2000) among these: the occurrence of a thick prismless outer layer, of a strong prism seam that bisects part of the prism within the sheath, and of prisms usually separated by broad areas of IPM. Lastly, essentially within Theria, a derived prismatic enamel is commonly observed, which could be defined by a considerable density of well arranged prisms separated by a small amount of IPM. Primitively, in PPE and in derived prismatic enamel as well, the prisms are directed away radially from the enamel-dentine junction (or EDJ) to the outer enamel surface without a decussating pattern, and their cross-sections are arc-shaped.

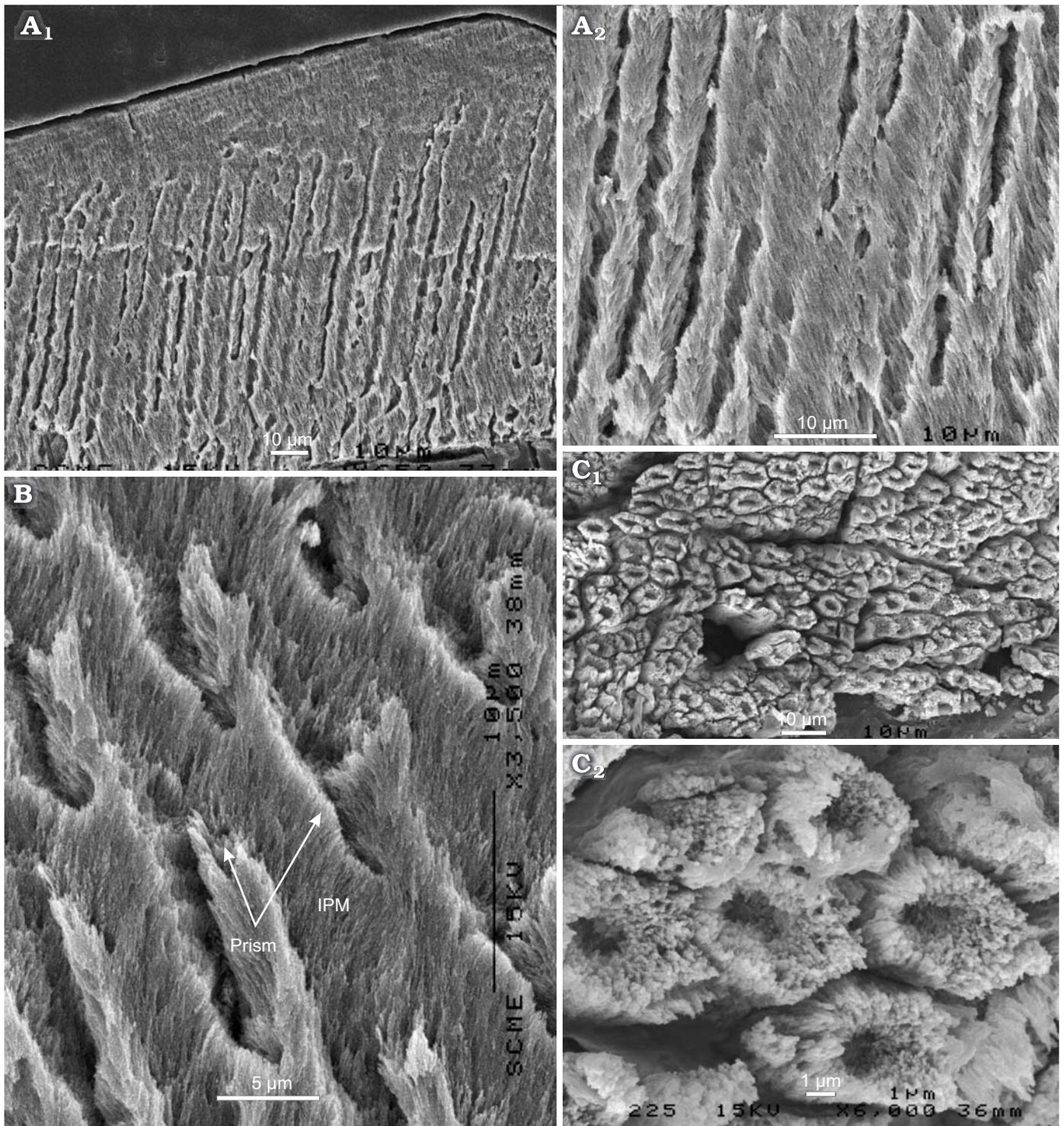


Fig. 4. Enamel microstructure of *Valentinella vitrollense* gen. et sp. nov. (SEM micrographs). **A.** The p4 or dp4 of the holotype, ISEM/VLP-2; A₁, vertical plane section showing outer prismless enamel and inner radial enamel; A₂, detail of A₁ in the radial enamel; IPM is badly preserved in this section. **B.** Rather vertical plane section through ?p4, ISEM/VLP-4; IPM is better preserved and clearly appears not parallel to the prisms. The cristallites of the IPM are at angle with prisms long axes (40–45°). **C.** the m1, ISEM/VLP-2; C₁, horizontal plane section, note the large diameter of prisms in this view (see text). Prisms are numerous and well packed with irregular arrangement; their cross-section vary from hexagonal to rounded aspect. The hole in center of prisms could correspond to the vanishing of Tomes' process according to Sanhi and Koenigswald (1997); C₂, detail of C₁, in this area the prisms show a clear rounded cross-section.

At first glance the apparent lack of arrangement of prisms in *Valentinella* could suggest a PPE. Moreover, the

large size of the prisms on m1 is reminiscent of the so-called “gigantoprismatic” enamel of the cimolodontan multi-

tuberculates (e.g., Carlson and Krause 1985; Fosse et al. 1985; Clemens 1997; see also Luo et al. 2002). In the “gigantoprismatic” enamel, however, the prisms are arcuate in outline, relatively fewer, and more widely spaced than in *Valentinella*. Anyway, the macromorphology of *Valentinella* is clearly different from that of the multi-tuberculates.

In fact, the enamel of *Valentinella* is obviously a derived prismatic form (in relation to the PPE) by the density of prisms, the reduction of the IPM, the thin prismless outer layer, and by the absence of a seam. A more important character is the circular, closed cross-section of the prisms. According to Dumont (1996), primitive eutherians such as Dormaalidae, Leptictidae, and “Palaeoryctidae” exhibit arc-shaped prisms, while modern or specialized forms are more characterized by closed prisms. The derived macromorphology (herbivorous?) seen in *Valentinella* is congruent with this result. As noted above, one of the most striking characteristics of the enamel of *Valentinella* concerns the large prisms on m1; actually in most extinct and extant eutherians, the prism diameter is smaller, between 3–4 μm (Dumont 1996). This trait is not unique. Some prisms, as large as those seen in *Valentinella*, have been observed in certain primitive Glires (cf. Mimotonidae) (Martin 1999), Carnivora (*Canis lupus*) (Stephen 1997), archaeocetes (Sahni and Koenigswald 1997), and “condylarths” (*Peripitychus coarctatus*) (Stephen 1999). In the same way, it is interesting to note that the rounded to hexagonal outline of the cross section of the prisms in *Valentinella*, is also present in most Carnivora and some “condylarths”: *Chriacus*, *Mioclaenus*, *Pachyaena*, and *Hyopsodus* (Stephen 1997, 1999). These taxa are not primitive “condylarths”, and except *Hyopsodus*, they obviously differ from *Valentinella* by the occurrence of a more complex Schmelzmuster (poorly to highly developed Hunter-Schreger bands, i.e. the prisms decussate in layers).

Primitive “condylarths”, such as *Protungulatum* and *Molinodus*, are more evocative of *Valentinella* by their radial prisms (Stephen 1999; Koenigswald 1997a). Because the radial enamel is the most primitive enamel type among placental mammals (e.g., Proteutheria, Lipotyphla, Plesiadapiformes), it cannot be used to support a close phylogenetic relationship (Koenigswald 1997b). Nevertheless, *Valentinella* and “condylarths” show a shared derived character: the same angle between the cristallites of the IPM and prisms long axes (40–45°). This character, although homoplastic (it occurs in Lipotyphla for example), could be a synapomorphy, as initially the cristallites of the IPM and prisms are parallel in the radial enamel (Koenigswald 1997b). As in Marsupialia (Koenigswald 1995), the crossing of IPM and prisms was later achieved in Placentalia during the Late Cretaceous; whereas lineages such as some carnivorans retained the primitive condition with parallel IPM and prisms.

Therefore, if *Valentinella* is a “zhelestid”, its enamel microstructure does not contradict and seems additionally to

give some arguments in favor of phylogenetic relationships between “condylarths” and “zhelestids”. These enamel evidences are tenuous, subsequent studies on unequivocal “zhelestids” are needed.

Conclusion

In southern France, the continental Late Cretaceous deposits are widely exposed. Nevertheless, in spite of numerous intensive research for forty years, the eutherian fossil record was restricted to the two lower molars of *Labes* from the Campanian of Champ Garimond. This locality plus Laño and Quintanilla del Coco in Spain, and Taveiro in Portugal have yielded isolated teeth that represented all our knowledge of the European Late Cretaceous eutherians. The discovery of the Maastrichtian *Valentinella*, especially represented by a fragmentary lower jaw bearing p3–m3, is thus of critical importance. Only three molars with a reduced paraconid indicate a eutherian status for *Valentinella*. This genus could be a derived “zhelestid” characterized by a molariform p4 (or dp4) and a slightly reduced m3. Because *Valentinella* is very poorly preserved, it does not shed new light on “zhelestid”– “condylarth” relationships, except that its enamel microstructure is congruent with a possible relationship of these taxa. The phylogenetic position of *Valentinella* remains uncertain, but it appears that this genus could be a “zhelestid”.

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References

- Antunes, M.T., Sigogneau-Russell, D., and Russell, D.E. 1986. Sur quelques dents de mammifères du Crétacé supérieur de Taveiro, Portugal (note préliminaire). *Comptes Rendus de l'Académie des Sciences, Paris* 303: 1247–1250.
- Archibald, J.D. 1996. Fossil evidence for a Late Cretaceous origin of “hoofed” mammals. *Science* 272: 1150–1153.
- Archibald, J.D. 1998. Archaic ungulates (“Condylarthra”). In: C.M. Janis, K.M. Scott, and L.L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America*, 292–329. Cambridge University Press, Cambridge.
- Archibald, J.D. and Averianov, A.O. 2003. The Late Cretaceous placental mammal *Kulbeckia*. *Journal of Vertebrate Paleontology* 23: 404–419.
- Archibald, J.D., Averianov, A.O., and Ekdale, E.G. 2001. Late Cretaceous

- relatives of rabbits, rodents, and other extant eutherian mammals. *Nature* 414: 62–65.
- Averianov, A. O., Archibald, J.D., and Martin, T. 2003. Placental nature of the alleged marsupial from the Cretaceous of Madagascar. *Acta Palaeontologica Polonica* 48: 149–151.
- Butler, P.M. 1977. Evolutionary radiation of the cheek teeth of Cretaceous placentals. *Acta Palaeontologica Polonica* 22: 241–271.
- Butler, P.M. 1990. Early trends in the evolution of tribosphenic molars. *Biological Reviews of the Cambridge Philosophical Society* 65: 529–552.
- Carlson, S.J. and Krause, D.W. 1985. Enamel ultrastructure of multituberculate mammals: an investigation of variability. *Contributions from the Museum of Paleontology. The University of Michigan* 27: 1–50.
- Cifelli, R. 1990. Cretaceous mammals of Southern Utah. IV. Eutherian mammals from the Wahweap (Aquilan) and Kaiparowits (Judithian) formations. *Journal of Vertebrate Paleontology* 10: 346–360.
- Clemens, W.A. 1997. Characterization of enamel microstructure terminology and application of the origins of prismatic structures in systematic analyses. In: W. von Koenigswald and P.M. Sander (eds.), *Tooth Enamel Microstructure*, 85–112. Balkema, Rotterdam.
- Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., Godefroid, P., and Van Itterbeeck, J. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Hațeg Basin (Romania). *Comptes Rendus Palevol* 1: 173–180.
- Dumont, E.R. 1996. Enamel prism morphology in molar teeth of small eutherian mammals. *Scanning Microscopy* 10: 349–370.
- Fosse, G., Kielan-Jaworowska, Z., and Skaale, S.G. 1985. The microstructure of tooth enamel in multituberculate mammals. *Palaeontology* 28: 438–449.
- Garcia, G. 1998. *Les coquilles d'œufs de dinosaures du Crétacé supérieur du sud de la France: diversité, paléobiologie, biochronologie et paléoenvironnements*. 152 pp. (unpublished). Ph.D. Dissertation, University Montpellier 2, Montpellier.
- Garcia, G. and Vianey-Liaud, M. 2001. Dinosaur eggshells as new biochronological markers in Late Cretaceous continental deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology* 169: 153–164.
- Garcia, G., Duffaud, S., Feist, M., Marandat, B., Tambareau, Y., Villatte, J. and Sigé, B. 2000. La Neuve, gisement à plantes, invertébrés et vertébrés du Bégudien (Sénonien supérieur continental) du Bassin d'Aix-en-Provence. *Géodiversitas* 22: 325–348.
- Gill, T. 1872. On the characteristics of the primary groups of the class of mammals. *Proceedings of the American Association for the Advancement of Science*, 284–306. Twentieth Meeting, held at Indianapolis, Indiana, August, 1871.
- Gheerbrant, E. and Astibia, H. 1994. Un nouveau mammifère du Maastrichtien de Laño (Pays Basque espagnol). *Comptes Rendus de l'Académie des Sciences, Paris, Série II*, 318: 1125–1131.
- Gheerbrant, E. and Astibia, H. 1999. The Upper Cretaceous mammals from Laño (Spanish Basque Country). *Estudios del Museo de Ciencias naturales de Alava* 14: 295–323.
- Gheerbrant, E., Abrial, C., and Cappetta, H. 1997. Nouveaux sites à microvertébrés continentaux du Crétacé terminal des petites Pyrénées (Haute-Garonne et Ariège, France). *Géobios M.S.* 20: 257–269.
- Kielan-Jaworowska, Z. 1969. Preliminary data on the Upper Cretaceous eutherian mammals from Bayn Dzak, Gobi Desert. *Palaeontologia Polonica* 19: 171–191.
- Kielan-Jaworowska, Z. and Trofimov, B.A. 1980. Cranial morphology of the Cretaceous eutherian mammal *Barunlestes*. *Acta Palaeontologica Polonica* 25: 167–185.
- Koenigswald, W., von. 1995. Enamel differentiation in myoxid incisors and their systematic significance. *Hystrix* 6: 99–107.
- Koenigswald, W., von. 1997a. Brief survey of enamel diversity at the schmelzmuster level in Cenozoic placental mammals. In: W. von Koenigswald and P.M. Sander (eds.), *Tooth Enamel Microstructure*, 137–161. Balkema, Rotterdam.
- Koenigswald, W., von. 1997b. Evolutionary trends in the differentiation of mammalian enamel ultrastructure. In: W. von Koenigswald and P.M. Sander (eds.), *Tooth Enamel Microstructure*, 203–235. Balkema, Rotterdam.
- Koenigswald, W., von. and Sander, P.M. 1997. *Tooth Enamel Microstructure*. 280 pp. Balkema, Rotterdam.
- Krause, D.W. 2001. Fossil molar from a Madagascar marsupial. *Nature* 412: 497–498.
- Lillegraven, J.A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *The University of Kansas Paleontological Contributions* 50: 1–122.
- Lillegraven, J.A. 1976. A new genus of therian mammal from the Late Cretaceous “El Gallo Formation”, Baja California, Mexico. *Journal of Paleontology* 50: 437–443.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.
- Luo, Z., Kielan-Jaworowska, Z., and Cifelli, R. 2002. In quest for phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* 47: 1–78.
- Martin, T. 1999. Phylogenetic implications of Glires (Euryomyliidae, Mimotonidae, Rodentia, Lagomorpha) incisor enamel microstructure. *Mitteilungen des Museums für Naturkunde Berlin, Zoologische Reihe* 75: 257–273.
- McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.
- Muizon, C., de and Cifelli, R. 2000. The “condylarths” (archaic Ungulata, Mammalia) from the early Paleocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. *Géodiversitas* 22: 47–150.
- Nessov, L.A. 1985. New mammals of the Cretaceous of Kyzylkum [in Russian]. *Vestnik Leningradskogo Universiteta Serii 7*: 8–18.
- Nessov, L.A., Archibald, J.D., and Kielan-Jaworowska, Z. 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. *Bulletin of Carnegie Museum of Natural History* 34: 40–88.
- Pol, C., Buscalioni, A.D., Carballeira, J., Francés, V., Lopez-Martinez, N., Marandat, B., Moratalla, J.J., Sanz, J.L., Sigé, B., and Villatte, J. 1992. Reptiles and mammals from the Late Cretaceous new locality Quintanilla del Coco (Burgos Province, Spain). *Neues Jahrbuch für Geologie und Paläontologie* 184: 279–314.
- Rădulescu, C. and Samson, P. 1997. Late Cretaceous Multituberculata from Hațeg Basin (Romania). *Sargetia* 17: 247–255.
- Rage, J.-C. 2002. The continental Late Cretaceous of Europe: toward a better understanding. *Comptes Rendus Palevol* 1: 257–258.
- Reif, W.-E. 1974. REM-Beobachtung am Schmelz eines rezenten und eines fossilen Caniden. *Biomínéralisation* 7: 56–68.
- Sahni, A. and Koenigswald, W., von. 1997. The enamel structure of some fossil and recent whales. In: W. von Koenigswald and P. M. Sander (eds.), *Tooth Enamel Microstructure*, 177–191. Balkema, Rotterdam.
- Sander, P.M. 1997. Non-mammalian synapsid enamel and the origin of mammalian enamel prisms: the bottom-up perspective. In: W. von Koenigswald and P.M. Sander (eds.), *Tooth Enamel Microstructure*, 41–62. Balkema, Rotterdam.
- Setoguchi, T., Tsubamoto, T., Hanamura, H., and Hachiya, K. 1999. An early Late Cretaceous mammal from Japan, with reconsideration of the evolution of tribosphenic molars. *Paleontological Research* 3: 18–28.

- Sigé, B., Buscalioni, A.D., Duffaud, S., Gayer, M., Orth, B., Rage, J.-C., and Sanz, J.L. 1997. Etat des données sur le gisement crétacé supérieur continental de Champ-Garimond (Gard, Sud de la France). *Münchner Geowissenschaftliche Abhandlungen* 34: 111–130.
- Smith, T., Codrea, V., Săsăran, E., Van Itterbeeck, J., Bultynck, P., Csiki, Z., Dica, P., Fărcaș, C., Folie, A., Garcia, G., and Godefroid, P. 2002. A new exceptional vertebrate site from the Late Cretaceous of the Hațeg Basin (Romania). *Studia Universitatis Babeș-Bolyai, Geologia* Special Issue 1: 321–330.
- Stephen, C. 1997. Differentiations of Hunter-Schreger bands of carnivores. In: W. von Koenigswald and P.M. Sander (eds.), *Tooth Enamel Microstructure*, 123–136. Balkema, Rotterdam.
- Stephen, C. 1999. The enamel of Creodonts, Arctocyonidae, and Mesonychidae (Mammalia), with special reference to the appearance of Hunter-Schreger-Bands. *Paläontologische Zeitschrift* 71: 291–303.
- Wood, C.B. 2000. Tooth enamel microstructure in *Deltatherium* (Metatheria, Late Cretaceous of Mongolia), with comparison to some other Mesozoic mammals. *Journal of the Paleontological Society of Korea, Special Publication* 4: 127–152.
- Wood, C.B. and Stern, D.N. 1997. The earliest prisms in mammalian and reptilian enamel. In: W. von Koenigswald and P.M. Sander (eds.), *Tooth Enamel Microstructure*, 63–83. Balkema, Rotterdam.
- Wood, C.B., Dumont, E.R., and Crompton, A.W. 1999. New studies of enamel microstructure in Mesozoic mammals: a review of enamel prisms as a mammalian synapomorphy. *Journal of Mammalian Evolution* 6: 177–213.