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# An enigmatic specialized new eutherian mammal from the Late Cretaceous of Western Europe (Northern Pyrenees)

*Un nouveau mammifère euthérien spécialisé énigmatique du Crétacé supérieur d'Europe de l'Ouest (Pyrénées du Nord)*

Emmanuel Gheerbrant<sup>a\*</sup>, Dominique Teodori<sup>b</sup>

<sup>a</sup> UMR 7207, CR2P, Sorbonne Université, MNHN-UPMC-CNRS

<sup>b</sup> 8, impasse de San Marino 31140 Pechbonnieu (France)

\* corresponding author; email address: emmanuel.gheerbrant@mnhn.fr

## ABSTRACT

We report the discovery of a new Late Cretaceous eutherian mammal, *Azilestes ragei* n. g., n. sp. from the Mas-d'Azil northern Pyrenean site (France), which is among the largest known. It is only known from a broken lower jaw found in uppermost levels of the Grès de Labarre Formation (early Maastrichtian). Despite its poor preservation, it displays distinctive specialized features with respect to known Cretaceous eutherians. This includes a reduced premolar formula and shortened and robust jaw, an incipient hypolophid, and a cingular-like postcristid and hypoconulid. The phylogenetic analysis suggests indeed a possible stem relationship between *Azilestes* and some clades of herbivorous Cenozoic placentals, but with weak support. Several molar features reminiscent of the Zhelestidae, especially *Valentinella*, support instead that *Azilestes* is a basal eutherian showing early specialization in an herbivorous diet convergent with some crown placentals. Whatever the suprageneric position of *Azilestes*, which remains to be clarified with additional material, its discovery highlights a significant diversity of European Cretaceous eutherians in contrast to their very poor fossil record.

## RÉSUMÉ

Nous signalons la découverte au Mas-d'Azil (Pyrénées du Nord, France) d'un nouveau mammifère, *Azilestes ragei* n. g., n. sp., l'un des plus grands euthériens du Crétacé supérieur. Il est connu par un fragment de mâchoire inférieure provenant des niveaux supérieurs de la formation des Grès de Labarre (Maastrichtien). Malgré son mauvais état de conservation, ce spécimen présente des caractères remarquablement spécialisés qui le distinguent de l'ensemble des euthériens connus au Crétacé. Ce sont en particulier la rangée très réduite des prémolaires, une mandibule courte et robuste, un hypolophide naissant, et la postcristide et l'hypoconulide cingulaires. L'analyse phylogénétique favorise ainsi une possible parenté ancestrale d'*Azilestes* avec certains clades de placentaires herbivores du Cénozoïque, mais de façon mal soutenue. Plusieurs caractères des molaires d'*Azilestes* rappelant les Zhelestidae, particulièrement *Valentinella*, suggèrent qu'il s'agit en fait plutôt d'un euthérien basal précocement spécialisé dans un régime herbivore convergent avec les placentaires modernes. Quelle que soit la position supragénérique d'*Azilestes*, à clarifier avec plus de matériel, sa découverte met en lumière une diversité significative des euthériens du Crétacé européen malgré leur très pauvre registre fossile.

*Key words:* Mammalia, Eutheria, dental anatomy, France, Pyrenees, Mas-d'Azil, Cretaceous, Campano-Maastrichtian, Grès de Labarre.

*Mots-clefs :* Mammalia, Eutheria, anatomie dentaire, France, Pyrénées, Mas-d'Azil, Crétacé, Campano-Maastrichtien, Grès de Labarre.

## 1. Introduction

Mammals from the Latest Cretaceous remain poorly known, and have a very heterogeneous geographical fossil record. Within Laurasia, the fossil record of Europe is by far the most incomplete. Late Cretaceous European mammals are represented by three multituberculate genera of the endemic family Kogaionidae from Eastern Europe (e.g., Csiki et al., 2001, 2005, 2018; Codrea et al., 2002, 2014; Smith & Codrea, 2015) and a few therians from Western Europe, including the marsupial *Maastrichtidelphys* (Martin et al., 2005), and the four stem eutherian genera, *Labes*, *Lainodon*, *Valentinella* and *Mistralestes* (Ledoux et al., 1966; Pol et al., 1992; Gheerbrant and Astibia, 1994, 1999, 2012; Tabuce et al., 2004, 2013), all more or less confidently related to the family Zhelestidae (Gheerbrant and Astibia, 2012; Tabuce et al., 2013). The Late Cretaceous European eutherian mammals are only documented by isolated teeth and a few partial jaws from eight localities found in Southern France, Spain, and Portugal, which were part of the Ibero-Armorican Island in the European Archipelago (see Gheerbrant et Astibia, 2012; Tabuce et al., 2013; Csiki-Sava et al., 2015).

Fig 1 here

Here we report the discovery of a damaged dentary belonging to a new mammal from a vertebrate-bearing level of the Grès de Labarre Formation in the Plantaurel massif of Northern Pyrenees, near the Mas-d'Azil (Ariege Department, SW France) (Fig. 1). The specimen was found by surface prospecting outcrops of the Grès de Labarre levels, NE to the Mas-d'Azil. The vertebrate-bearing level is a fossiliferous hard sandstone (Fig. 2). It belongs to the upper unit of the Grès de Labarre which overlies the Marnes d'En Gauly. Structurally, the fossiliferous site is located in the Mas-d'Azil anticline from the Sub-Pyrenean zone that is bounded by the North Pyrenean frontal thrust to the South and by the Sub-Pyrenean frontal thrust to the North (Bilotte, 1985). The Sub-Pyrenean zone, which is made of several synclines and anticlines in the Plantaurel and Petites Pyrenees areas, corresponds to the external-most folds of the North Pyrenean domain. The Grès de Labarre Fm, together with the overlying "Marnes Rouges Inférieures" Fm (an eastern lateral equivalent of the Marnes d'Auzas Fm), comprises the last Cretaceous deposits of the Sub-Pyrenean zone in the Plantaurel massif.

The Grès de Labarre Fm corresponds to a poorly dated thick terrigenous Campano-Maastrichtian stratigraphic unit made of sandstones, shales, and clays that were deposited in fluvial and deltaic environments. Continental vertebrates were discovered in the Grès de Labarre Fm by the Abbé J.-J. Pouech in several localities (Pouech, 1859, 1881a,b; Buffetaut et al., 1991; Le Loeuff, 1991). The mammal specimen reported here was found in one rich Pouech's site known as the Capens locality (Pouech, 1881a; Le Loeuff, 1991). The vertebrate fauna from the Grès de Labarre Fm, which includes fishes, turtles, crocodylians and non-avian dinosaurs (skeletal remains and eggshell fragments), was described as one of the most diversified from Southern France (Buffetaut and Le Loeuff, 1991; Le Loeuff, 1991). It is found at the top of the Grès de Labarre Fm. In addition to vertebrates, Breton et al. (2013) reported the discovery of fossils micro-organisms (bacteria, spores and pollens) in amber from a clay level of the Grès de Labarre Fm. The Grès de Labarre Fm also yielded a palynoflora of Campanian age (Bilotte, 1985), although it is poorly constraining (Laurent et al., 2001) and it does not come from the area of the Mas-d'Azil. In the Mas-d'Azil area, the Grès de Labarre Fm overlies the Saint Cirac Marls which have yielded a Campanian phytoplankton and palynoflora (Bilotte, 1985). The Grès de Labarre Fm in the Mas-d'Azil area is indeed Campanian to early Maastrichtian, and the vertebrate level found at the top of the Formation is considered as Early Maastrichtian (Bilotte et al., 1983; Le Loeuff, 1991).

Fig 2 here

Additional information on the geological, stratigraphic, and paleoenvironmental contexts on the Grès de Labarre Fm and other late Cretaceous deposits of the sub-Pyrenean massifs of the Plantaurel and Petites Pyrenees are provided by Segura (1979), Bilotte (1985, 1990, 1991), Bilotte et al. (1983) and Lepicard (1985).

## 2. Materials and methods

CT scans: High-resolution computed microtomography ( $\mu$ CT) of the fragmentary left dentary, MNHN.F CTE215, were made at the AST-RX platform of the MNHN, Paris, using a GE Sensing and Inspection

Technologies phoenix|x-ray v|tome|x L240-180 CT scanner. Scan parameters: Voltage=100 kV; Current=260  $\mu$ A; Isotropic voxel size of 0.02641432 mm. Data were reconstructed using datos|x reconstruction software Phoenix|x-ray, release 2.0, and then exported as 16-bit TIFF stacks. We used tools in the software Mimics Innovation Suite (Materialise, Research Edition Release 21, <https://www.materialise.com/en/medical/software/mimics>) for the segmentation, analysis, visualisation of the image stacks.

For our cladistic analysis we used TNT 1.5. Traditional search (standard analysis) was made with 1000 replications and swapping algorithm TBR. Implied Weighting analysis was made with K=5 and TBR branch swapping. 10000 trees were retained in memory for the analyses.

We use the classical dental terminology for tribosphenic therian mammals (e.g., Van Valen 1966).

Abbreviations: MNHN.F CTE: collections of the Museum National d'Histoire Naturelle (Paleontology).

Measurements: L, H, W: length, height, and width. Measurements were taken with a Mitutoyo (QC200) measuring binocular.

### 3. Systematic palaeontology

Mammalia Linnaeus 1758

Eutheria Gill 1872

Family *incertae sedis* (?Zhelestidae)

*Azilestes ragei* n. g., n. sp. (Figs 3-7)

Fig 3 here

Derivatio nominis: *Azilestes*: Azil from the name of the type locality, Mas-d'Azil, and lestes, Greek, robber, pirate by allusion to the small size of many insectivore-like mammals from the Cretaceous and Paleogene; *ragei*: dedicated to Jean-Claude Rage as a tribute to his memory and to his major contribution on the study of Cretaceous European microvertebrates.

Holotype: MNHN.F CTE215, fragment of left dentary with damaged M<sub>1</sub> and M<sub>2</sub>.

Locality and age: Mas-d'Azil (Capens), Ariège, Plantaurel massif, Northern Pyrenees, France; upper part of the Formation des Grès de Labarre, early Maastrichtian.

Diagnosis: This species belongs to a tribosphenic therian mammal. Its molar morphology (e.g., hypoconulid and entoconid not twinned, paraconid much smaller than metaconid, trigonid compressed) differs from metatherians and marsupials, but indicates it belongs instead to a Cretaceous eutherian, and one of the largest known. The partial dental formula preserved in the holotype is C<sub>1</sub>, P<sub>4</sub>, P<sub>5</sub>, M<sub>1-2</sub> (incisors and last molar broken away). This species differs from all known Cretaceous eutherians by the following specialized traits: short and robust (deep) dentary; shortened anterior dentition lacking at least P<sub>1-3</sub> and any lower diastema, and with small single-rooted P<sub>4</sub>; mandibular symphysis extended close to P<sub>4</sub> level; hypoconulid and posteristid forming an isolated transverse cingular-like structure at the posterior part of the talonid; presence of an incipient but distinct hypolophid and a well-developed posterior fovea. The molars have a robust bunodont and grinding-crushing morphology that is associated with the presence of an interradicular crest and radicular grooves.

### 4. Description

Although damaged and incomplete, the specimen MNHN.F CTE215 is one of the most complete jaw remains of eutherian mammals reported from the late Cretaceous of Europe.

#### 4.1 Dentary (Figs. 3, 5)

MNHN.F CTE215 preserves only part of the mandibular corpus including the posterior part of the mandibular symphysis which extends far posteriorly, close to level of the unique P<sub>4</sub> alveolus. It is very short and robust. The mandibular corpus is dorso-ventrally high, and labially inflated. It is convex below the molars, but concave below the premolars (P<sub>4-5</sub>) and the symphysis. Its dorso-ventral depth rapidly decreases at the level of the symphysis. The posterior mental foramen is rather large and located ventro-labially below and between the two roots of P<sub>5</sub>, as in most Cretaceous eutherians.

Based on the CT scans, the mandibular canal was reconstructed as large and located directly ventral to the tooth roots (Fig. 5). Laterally, it extends on the labial side of the roots, but not on the lingual side. Its diameter is more or less constant up to P<sub>4</sub> level along preserved corpus length. Its cross-

section is typically dorso-ventrally flattened below the teeth, with a flat dorsal margin. Anteriorly, the mandibular canal divides in several small lateral branches (“lat br”, Fig. 5) labially to P<sub>5</sub> and P<sub>4</sub> (anterior) roots and lingually to the canine alveolus in the mandibular symphysis (Fig. 5 A-B; SI Figs. A1 and A2). The preserved anteriormost part of the mandibular canal is smaller in cross-section and dorso-labial to the canine alveolus (Fig. 5 B and G).

#### 4.2 Tooth row

The dentary MNHN.F CTE215 preserves two damaged molars, M<sub>1</sub> and M<sub>2</sub>, and four well-developed empty anterior alveoli, interpreted as corresponding to a two-rooted P<sub>5</sub>, and single-rooted P<sub>4</sub> and C<sub>1</sub> (Fig. 5-6 and see below). The anterior and posterior parts of the dentary are broken, so that M<sub>3</sub>, the canine and the incisors and their alveoli (except part of C<sub>1</sub> alveoli) are not preserved. There is no diastema. Anteriorly to the P<sub>4</sub> alveolus, there is only one very large alveolus, most probably for the canine (instead for an enlarged incisor, see below). It suggests a strongly reduced anterior cheek dentition in this species (only two premolars, P<sub>4</sub> being reduced), which is also supported by the position of the mandibular symphysis close to P<sub>4</sub>. Such a reduced tooth row is unique in stem eutherians. The dentary and its tooth-row curve lingually from the level of P<sub>4</sub>.

#### 4.3 Teeth (Figs. 3-6).

Canine - The CT scans and our 3 D reconstruction (Figs 5-7) show the occurrence one large anterior alveolus extending within the mandibular symphysis in its posterior part. It is identified as the alveolus for the lower canine because it has a size proportion and relative position to the symphysis known for this tooth in many Cretaceous eutherians. Enlarged lower incisors are known in a few Cretaceous eutherians such as zalambdalestids, but they also have a canine (e.g. Wible et al., 2004), and they have distinctive molar morphology. The alternative interpretation of the large anterior alveoli of MNHN.F CTE215 for the presence an enlarged incisor and the absence of a canine is unlikely for Cretaceous therians. Only the lower and posteriormost part of the large anterior alveolus is preserved (Fig. 5 D,G,H and Fig. 6). The alveolus is open anteriorly at the anterior part of specimen MNHN.F CTE215 where it is broken. Its orientation suggests a mesially inclined root within the dentary. A procumbent canine root is known in zhelestids such as *Parazhelestes* (Archibald and Averianov, 2012: figs. 15A, 22B). The alveolus size (3.3 x 2.7 mm at anterior preserved section, measured from the 3D digital model) indicates a large C<sub>1</sub>. Large to very large canine are known in eutherians such as the zhelestid *Eoungulatum* (Archibald and Averianov, 2012).

Premolars - The premolars are broken and are only represented by their alveoli (Fig. 5). Only three distinct alveoli anterior to M<sub>1</sub> are preserved in addition to the anteriormost large alveolus for the canine. They correspond to a two-rooted P<sub>5</sub> and a likely single-rooted P<sub>4</sub> (Figs. 5-6). Judging from the alveoli size, P<sub>5</sub> was a little smaller than M<sub>1</sub>, and P<sub>4</sub> was much smaller than P<sub>5</sub>. The P<sub>5</sub> alveoli are widely spaced and have a similar diameter. The alveolus of the single-rooted P<sub>4</sub> is half the size (diameter) of the anterior alveolus of P<sub>5</sub>. It is also significantly lingually shifted in the dentary with respect to the anterior root of P<sub>5</sub>, and it is located close to the mandibular symphysis. The anterior part of the dentary shows a small bony gap (hole) located lingually and in front of the P<sub>4</sub> alveolus (labelled “?” in figure 7) which could be interpreted as a small tooth alveolus, either for an anterior root of P<sub>4</sub> or a small P<sub>3</sub> (as seen in early eutherians such as zhelestids). In the tomographies this structure is seen as a darker (empty) space corresponding to small vertical cavity in the bone (Fig. 7). However, similar and probably homologous bone cavities of the same size are also found between the roots of p<sub>5</sub>, m<sub>1</sub> and m<sub>2</sub>, positioned lingually to the line of the alveoli (Fig. 7D-E). They correspond to bone vascularisation or pneumatization (air cells) rather than tooth alveoli. The CT scans do not show any trace of other alveoli anterior to P<sub>4</sub>, other than the very large and procumbent one for the canine. Actually, there is no space available for the anterior premolars (P<sub>1-3</sub>) between the alveoli of P<sub>4</sub> and C<sub>1</sub> (Figs. 5, 7). This evidence, together with the mandibular symphysis extending close to P<sub>4</sub> in MNHN.F CTE215, supports this as a natural condition representative of the species. As a result, the anterior cheek dentition of the Mas-d’Azil eutherian species is significantly and unexpectedly reduced, with only two premolars, one being reduced in size (single-rooted).

Fig 5 here

## Molars

Only  $M_1$  and  $M_2$  are preserved (the posterior molar,  $M_3$ , is broken). The molars are typically bunodont with inflated crown and cusps, and with large talonid and postfossid. They have two long separate roots that are wide transversely. There is typically a well-developed interradicular crest and a radicular groove on internal side of the root (Fig. 6), both for a firm bony anchorage of the tooth in the dentary. Interradicular crests are known in a few taxa of very different groups of mammals such as multituberculates, meridiolestidans, lipotyphlans (soricids and erinaceids) and rodents; however, the distribution of these roots features is poorly known in eutherians. The anterior root is smaller in diameter than the posterior one. The roots are robust and slightly dilated at their apex (Fig. 6). The ratio of the roots height to the crown height is 2.65 to 1.8.

Figs 6-7

$M_1$  (Figs. 3-4). The trigonid is broken but the talonid is well preserved. The trigonid occlusal outline is quadrate and it is wider than it is long (trigonid mesio-distally narrow). The trigonid width is about equal to that of the talonid. The talonid is high, especially labially below the hypoconid. It is long: longer than wide, and much longer than the trigonid. The postfossid is extended. The hypoflexid is wide and shallow. There is no trace of ectocingulid and mesoconid. The hypoconid is by far the largest talonid cusp. It might have been at least as large as the protoconid. It has a well-marked lingual wear facet which corresponds to the lingual phase grinding wear with the protocone (facet 9 of Crompton, 1971; facet 10 of Butler, 1952; hd-1 in fig. 2 of Schultz et al., 2018). This lingual phase wear facet is derived among stem eutherians that have mostly shearing teeth with restricted labial phase movements of mastication (Crompton, 1971; Crompton and Kielan-Jaworowska, 1978). The cristid obliqua is long and longitudinally oriented; it joins the trigonid in its labial mid-width. Its labial side shows a well-developed wear facet that extends low onto the hypoconid and displays subvertical striae for shearing with the postparacrista (facet 3 of Crompton, 1971; facet 6 of Butler, 1952; hd-mb in fig. 2 of Schultz et al., 2018). The wear facet posterior to the hypoconid, corresponding to shearing with premetacrista (facet 4 of Crompton, 1971; facet 7 of Butler, 1952; hd-d in Schultz et al., 2018), is comparatively much smaller. The posteristid is reduced (weak and short) on the distal flank of the hypoconid.

The hypoconulid has a distinctive ridge-like morphology instead of being cuspsate: together with the posteristid it forms a blunt cingular-like structure at the distal rim of the talonid (Fig. 4). This cingular-like posteristid-hypoconulid structure is isolated by notches from both the hypoconid and the entoconid. It is more inflated on its lingual side. As a result, the hypoconulid is closer to the entoconid than to the hypoconid. However, it is not twinned with entoconid. The entoconid is inflated, acute at apex (mesio-distally compressed) and slightly higher than the hypoconulid. It is far distal from the trigonid and aligned transversely with the hypoconid. The postfossid is opened disto-labially between the hypoconid and hypoconulid by a notch bearing a large wear facet, possibly corresponding to a lingual extension of facet 7 of Butler (1952). The transverse extension of the wear facet 7 is usually seen in lophodont mammals such as perissodactyls; it corresponds to a specialized transverse shearing with the metaloph. There is a faint but distinct transverse crest at the bottom of the postfossid that is extended between the hypoconid and the entoconid (Fig. 4); it is in the topographic position of the hypolophid and it delimits a posterior fovea. It has a tiny distal wear facet extending on the entoconid, which corresponds to facet 8 of Butler (1952) (ed-d in fig. 2 of Schultz et al., 2018), and to shearing with the hypocone. The mesio-lingual side of the entoconid is truncated by a wear facet (wear facet 9 of Butler, 1952; ed-m in Schultz et al., 2018), resulting from shearing with the protocone (distal side). The postfossid is closed lingually (no talonid notch). There is a distinct and inflated entoconulid. The crown is only moderately exodaenodont above the roots. Observations of the reconstructed 3D digital models of the teeth from CT scans shows the absence of postcingulid in  $M_1$  (see SI Fig. A1).

$M_2$  (Figs. 3-4). The crown of  $M_2$  is nearly entirely broken. It preserves only part of the metaconid and the entoconulid. The metaconid was as high as the hypoconulid of  $M_1$ . The occlusal outline of the trigonid is very narrow mesio-distally, and more so than in  $M_1$  (see Table 1). The 3D digital reconstruction from the CT scans supports the presence of a small paraconid in lingual position and closely appressed to the metaconid (Fig. 6A, SI Fig. A1). The tooth occlusal outline (Figs. 3-4) and the 3D models from CT scan indicate that  $M_2$  is slightly longer than  $M_1$ .

#### 4.4 *Dental occlusion and function*

Several features of lower molars of specimen MNHN.F CTE215 suggest occlusion with upper molars bearing a developed hypocone: the cingular-like postcrisid and hypoconulid, the hypolophid present and delimiting a posterior fovea, the postfossid opened between hypoconulid and hypoconid with a wear facet in between, and the likely presence of a wear facet 8 of Butler (1952). In particular, the hypolophid usually occludes in between the protocone and the hypocone, i.e. in the interloph. The bunodont molar construction, the large postfossid and hypoconid, the wear pattern including grinding wear facet 10 of Butler (1952), and the development of an interradicular crest and radicular grooves indicate strong power stroke and a developed crushing-grinding function, presumably corresponding to a (relatively hard) plant diet.

**Table 1.** Measurements of MNHN.F CTE215 (millimeters), holotype of *Azilestes ragei* n. g. , n. sp.**Tableau 1.** Dimensions de MNHN.F CTE215 (en millimètres), holotype de *Azilestes ragei* n. g. , n. sp.

	L	W	H
M <sub>1</sub>	4.1	?	?
M <sub>1</sub> trigonid	2.1	*2.68	
M <sub>1</sub> talonid	2.05	2.8	2.88
M <sub>2</sub>	4.25	?	?
M <sub>2</sub> trigonid	*1.45	*2.68	?
M <sub>2</sub> talonid	*2.45	?	?

L M <sub>1-2</sub>	7.81
L alveolus P <sub>5</sub>	4.3
L alveolus P <sub>4</sub>	1.7
H dentary below M <sub>2</sub>	6.53

## 5. Comparisons

### *Eutheria, Zhelestidae*

The tribosphenic pattern of the molars of specimen MNHN.F CTE215 indicates a therian mammal, although the reduced premolar formula of this species was previously unknown in Cretaceous metatherians and eutherians. The molar morphology of specimen MNHN.F CTE215, with among other features a small paraconid, a mesio-distally compressed trigonid, a hypoconulid not twinned to entoconid and the absence of ectocingulid and postcingulid, departs from marsupials and relates instead the Mas-d'Azil species to eutherian mammals. The likely presence of a hypocone (unknown in early metatherians) also relates MNHN.F CTE215 to eutherian mammals, although this is an inference from wear pattern and morphology of lower molars here. We assume indeed the presence of three molars as in the eutherian tooth formula in this species. Among Cretaceous eutherians, the molar morphology of specimen MNHN.F CTE215 is most closely reminiscent of the family Zhelestidae (Nessov et al., 1998; Archibald and Averianov, 2012). Significant shared features include the robust crown with bulbous cups and a large crushing-grinding hypoconid, the large talonid and postfossid, and the hypoconulid approximated to the entoconid. Strong and long molar roots are also found in the Zhelestidae. Some features are closer to the European zhelestid subfamily Lainodontinae (Gheerbrant and Astibia, 2012), than to the Asian Zhelestinae: the absence of postcingulid; the cristid obliqua labial to protoconid notch (shallow hypoflexid); the crown high labially below the hypoconid and slightly exodaenodont; the absence of ectocingulid; and the paraconid lingually set, close to the metaconid (located in lingual margin).

However, none of the described European zhelestid genera (*Lainodon*, *Labes*, and the possible genera *Valentinella* and *Mistralestes*) show close morphological affinities to MNHN.F CTE215. MNHN.F CTE215 is distinctive in having several remarkable features unknown in these genera or in other described zhelestids and other Cretaceous eutherians. These distinctive features include the following: the robust dentary (short, deep and convex mandibular body) with shortened anterior dentition lacking anterior premolars; the mandibular symphysis posteriorly extended close to P<sub>4</sub> level; the cingular-like morphology of the postcristid and hypoconulid (both forming a posterior ridge-like structure extended transversely) which is isolated by notches from hypoconid and entoconid; and the presence an incipient hypolophid in the postfossid as a weak but distinct transverse crest extended between the internal flanks of the hypoconid and the entoconid. These features are specialized and are identified as diagnostic of the new genus and species *Azilestes ragei* n. g., n. sp.

The closest zhelestid to *Azilestes* is *Valentinella vitrollense* described by Tabuce et al. (2004) from the Maastrichtian of southern France. This species based on poorly preserved material was considered as a *nomen dubium* by Archibald and Averianov (2012: 404). However, new material referred by Tabuce et al. (2013) supports the validity of this species. The most remarkable shared

feature of *Azilestes* and *Valentinella* is their large size. Both species are among the largest Cretaceous eutherians, and are much larger with respect to described zhelestids (see Nesson et al., 1998; Archibald et al., 2012; Tabuce et al., 2013). The few other known “large” Cretaceous eutherians are the North American species *Schowalteria clemensi* Fox and Naylor, 2003 (Taeniodonta), *Cimolestes magnus* Clemens and Russell, 1965 (Cimolestidae), and *Protungulatum combsi* Archibald et al., 2011 (?Arctocyonidae). However, by way of comparison *Azilestes* remains much smaller (three to four times smaller, based on tooth and lower jaw size) than the largest known Cretaceous mammal (the triconodont *Repenomamus giganticus* Hu et al., 2005). *Valentinella* has molars only a little smaller ( $M_1$  shorter by 17 %) than in *Azilestes*, whereas its mandibular body is a little deeper below  $M_2$  (by 36%). Other interesting shared traits of *Azilestes* and *Valentinella* include the bunodont crushing molar crown with bulbous cusps, the lingual hypoconulid, the  $M_2$  slightly longer than  $M_1$ , the paraconid lingual and close to the metaconid, and the last premolar ( $P_5$ ) slightly smaller than  $M_1$ . *Valentinella* also shares a robust and deep mandibular corpus that is convex ventrally, and the possible and noticeable presence of a molar radicular groove fitting with a bony septum (lamina) of the dentary (at least specimen UP-VLP-10-01, see fig. 3 in Tabuce et al., 2013). The likely presence of an hypocone in *Azilestes*, as inferred from the morphology and wear pattern of its lower molar (see above), would be a remarkable shared feature with *Valentinella* (Tabuce et al., 2013).

However, *Valentinella* differs from MNHN.F CTE215 by features such as the molar talonid shorter than the trigonid, especially in  $M_1$ , the hypoconid much smaller with a similar size to the entoconid ( $M_2$  observation in *Valentinella*), the deeper hypoflexid (and relatedly a cristid obliqua more oblique lingually), and the hypoconulid closer to the entoconid than in *Azilestes*. The penultimate premolar ( $P_4$ ) of *Valentinella* has two large roots, by contrast to *Azilestes*. In addition, *Azilestes* is distinctive in remarkable specialized (autapomorphic) traits mentioned above such as the shortened anterior dentition, including a small and single-rooted  $P_4$ . However, it should be stressed here that the comparison of *Valentinella* with *Azilestes* is limited because of the poor preservation of the former. Therefore, the comparison cannot be extended to other important features of *Azilestes*, especially the crown molar morphology.

Comparison with other European zhelestids (lainodontines) is more significant because of their better tooth preservation, and because it better helps to test the familial affinity. *Lainodon* (Gheerbrant and Astibia, 1994, 1999, 2012) and *Labes* (Pol et al., 1992; Martin et al., 2015) do not show any peculiar affinity to *Azilestes*. Besides their smaller size and absence of hypocone, they depart in the less bunodont crown and less bulbous cusps, the absence of entoconulid (inflated in *Azilestes*), and the shorter talonid. They also lack interradicular crests and radicular grooves, and dilated roots at apex. The latter root characters seem to depart from all known zhelestids, except possibly *Valentinella*. Nevertheless, it should be noted that one undetermined zhelestid species identified as *Lainodon* n. sp. (Gheerbrant and Astibia, 2012) has a large size close to *Azilestes*. It is known by a broken  $M_3$  (L1AT 18) that interestingly shares a long talonid, a labial cristid obliqua, and questionably an entoconulid. However, it differs by the fully twinned hypoconulid and entoconid and the root morphology (no interradicular crests and radicular grooves). *Azilestes* also differs by its specialized features (see diagnosis).

*Mistralestes arcensis* was described from the Campanian of the Aix en Provence Basin by Tabuce et al. (2013), based on a partial lower jaw preserving teeth interpreted as  $P_5$ ,  $M_{1-3}$ , although the alternative interpretation of these teeth as  $P_{4-5}$  and  $M_{1-2}$  cannot be fully rejected on the basis of available material. Despite several resemblances suggesting common zhelestid affinity such as a large talonid, a large hypoconid,  $M_2$  larger than  $M_1$ , the cristid obliqua very labial and the hypoflexid shallow, the hypoconulid close to entoconid (but not twinned), and the postcingulid absent, it is distinctive from *Azilestes*. *Mistralestes* actually departs more from *Azilestes* than *Valentinella* by both its small size ( $M_1$  55% shorter), and its less bunodont morphology. It also differs from *Azilestes* by the shallower mandibular corpus (60% of *Azilestes*), and the posterior mental foramen located more posteriorly - assuming the dental homologies of *Mistralestes* described by Tabuce et al. (2013). Other differences are the autapomorphic traits of *Azilestes* (see diagnosis).

*Gallolestes* from the Campanian of Baja California (Lillegraven, 1976) shares the bunodont construction with inflated cusps and the long talonid. It differs by the paraconid labial on M<sub>1</sub>, the narrow talonid, the smaller hypoconid, the presence of postcingulid and the cristid obliqua less labial. *Sheikhdzheilia* from the Cenomanian of Uzbekistan (Averianov and Archibald, 2005; Archibald and Averianov, 2012) departs from *Azilestes* by its molars less bunodont, its more oblique cristid obliqua and deeper hypoflexid, and its hypoconulid more central between hypoconid and entoconid. Molars of *Borisodon* from the Cenomanian of Uzbekistan (Archibald and Averianov, 2012) are also less bunodont, and have a more oblique cristid obliqua (joining the trigonid below protocristid notch) and deeper hypoflexid, and a more distally projected hypoconulid. *Paranyctooides* is distinct from *Azilestes* in many features, such as cusps and crown being less bunodont, the more oblique cristid obliqua and the deeper hypoflexid, the hypoconid being small and compressed mesio-distally, and the hypoconulid more central and distal.

#### *Zalambdalestidae*

The family Zalambdalestidae (including *Kulbeckia*, *Alymlestes*, *Zalambdalestes*, *Barunlestes*) shares with *Azilestes* an entoconid close to hypoconulid, as for the zhelestids. Zalambdalestids also share a large and elongated talonid. However, they have a less lingual paraconid, and distinctive insectivore-like teeth with sharp molar cusps and crests and high trigonid by contrast to the zhelestid-like bunodont and crushing-grinding morphology of *Azilestes*. Zalambdalestids also have a small canine and a large gliriforme-like anterior lower incisor.

#### “*Condylarthra*”

Among Cretaceous eutherians, the bunodont morphology of *Azilestes* is also found in “condylarths” such as *Protungulatum*, *Baiconodon*, *Oxyprimus*, and *Khamerungulatum*. However, none of these genera show peculiar morphological affinity. They differ especially in the less lingual hypoconulid and paraconid, the less compressed trigonid with more anterior paraconid, the less labial cristid obliqua and the noticeably smaller talonid.

#### *Discussion*

Among all known Cretaceous eutherians, the dental morphology of *Azilestes* displays closest affinity with the Zhelestidae, and especially with *Valentinella*. However, *Azilestes* shows remarkable specialized features that are unknown in Cretaceous eutherians, but are instead known in some herbivorous crown placental clades from the Cenozoic. These features include the robust, deep and short dentary, the reduced anterior dental formula (loss of anterior premolars and small P<sub>4</sub>), the mandibular symphysis posteriorly extended close to P<sub>4</sub> level, the presence of an incipient hypolophid and the cingular-like and transverse postcristid and hypoconulid. There are two possible phylogenetic interpretations of these specialized traits: 1) *Azilestes* belongs to an early and uniquely specialized new European stem eutherian lineage, possibly related to the Zhelestidae (and especially to *Valentinella*), 2) *Azilestes* is a stem group of some herbivorous crown placental clades.

## 6. Phylogenetic analysis

In order to investigate the relationships of *Azilestes*, we made a cladistic analysis with TNT 1.5 (Goloboff et al., 2008) based on the character matrix of Wible et al. (2009) that was modified and updated by Archibald and Averianov (2012) and Tabuce et al. (2013). This matrix, which is provided as supplementary information (SI File A.1), includes most known late Cretaceous eutherian taxa, and especially the European genera *Lainodon*, *Mistralestes*, and *Valentinella*. It however lacks *Labes*. A few corrections of the coding in this matrix were made before the analysis, mostly for *Valentinella*, for consistency with Tabuce et al.'s (2013) description. They include: character 98 (*Valentinella*, state 1 hypocone present, lower than protocone); character 115 (*Mistralestes*, state 3 or 4 cristid obliqua labially placed); character 125 (*Valentinella*, state 0 postcingulid unknown); character 130 (*Valentinella*, state 1 mandibular body deep and robust). The matrix includes three ordered features (24, 28, 60).

34 characters of *Azilestes* are coded in the matrix (see SI Text A.1). However, the matrix lacks some important features of *Azilestes* such as the cingular-like morphology of the hypoconulid and postcrisid, the small and single-rooted P<sub>4</sub>, and the presence of interradicular crest and radicular grooves. The distribution of some of these characters in Cretaceous eutherians, such as the tooth root morphology, remains poorly known (other states of *Azilestes* might be autapomorphic). We made several cladistic analyses that are summarized in Table 2. The MPTs found in our cladistic analyses recover two main topological hypotheses for *Azilestes* (Table 2, Fig. 8).

A stem Glires relationship (*Azilestes* (*Tribosphenomys*, *Paramys*)(*Rombomylus*(*Gomphos*, *Mimotona*))) is found in the 50% majority rule tree of Traditional (standard) Search analysis and in the consensus tree recovered from Implied Weighting analysis (Fig. 8B), either with ordered or non-ordered features; it is based on three homoplastic synapomorphies (character number in matrix): 2-3 (five postcanine teeth, i.e. loss of two teeth from the primitive eutherian tooth formula; RI= 70); 28-3 (premolar formula reduced to two teeth; RI= 67) and 130-1 (mandibular body deep and short; RI= 53). It is noted that characters 2-3 and 28-3 associated at this node are redundant because character 2 does not differentiate premolars and molars in the counting of the postcanine loci. When the character 2 is made inactive, the majority rule tree still recovers its stem glires position.

A sister-group relationship to *Valentinella* (clade (*Azilestes*, *Valentinella*)) when *Azilestes* is constrained to join the Zhelestidae (Fig. 8C); this clade is associated to a clade Lainodontinae (*Lainodon*(*Valentinella*, *Azilestes*)) in the Implied Weighting analysis. The clade (*Azilestes*, *Valentinella*) is based on only one homoplastic trait: 130-1 (RI= 53) mandibular body inflated (in addition to an homoplastic ambiguous synapomorphy optimised in *Valentinella*: 119-1, hypoconulid lingual). The clade Lainodontinae including *Azilestes* is supported by one homoplastic synapomorphy: 107-1 (RI= 40) paraconid on lingual margin.

The consensus tree of the standard analysis provides unresolved eutherian polytomy for the three European genera *Azilestes*, *Valentinella*, *Mistralestes* (Table 2, Fig. 8A). Actually, the cladistic analysis provides poorly constrained phylogenetic relationships for these genera with a few very homoplastic synapomorphies, low Bremer values, and several equally parsimonious topologies (Table 2, Fig. 8). A zhelestid relationship of *Azilestes* (Fig. 8C) - that is the best supported by our comparative anatomy study - requires only five additional steps than in standard analysis MPTs (tree length = 2354 steps). This hypothesis is *a priori* in conflict with some remarkable specializations of *Azilestes* that are unknown in Cretaceous eutherians. They are instead known in crown Placentalia as found in our unconstrained cladistic analyses, which recover a possible relationship with the Glires based on features related to the reduced dental formula. However, the relationship with the Glires remains weakly supported by a few homoplastic synapomorphies (some redundant). In particular, the reduction of the premolars number is most likely convergent with *Azilestes* because early anagalid glires have four premolars. *Azilestes* differs from glires by a large canine, the presence of a hypolophid and the cingular-like postcrisid. In addition, no specialized traits of the glires molar morphology (e.g., hypsodonty; Fostowicz-Frelik, 2017) are seen in *Azilestes*, and the anterior large alveolus seen in MNHN.F CTE215 does not extend far distally below premolars and molars as for the alveolus of the gliriform incisor. The presence of a hypolophid and the cingular-like morphology of the hypoconulid

Fig 8 here

and postcristid are instead noticeable shared derived features with lophodont ungulate-like crown placentals such as the Paenungulata, the Perissodactyla (Euungulata) and the Anthracobunia (Euungulata), although no relationship with paenungulate is found in our analysis (noting that Anthracobunia and Perissodactyla are not included in Wible et al.'s 2009 matrix). The strongly reduced anterior dentition (two premolars with a small single-rooted P<sub>4</sub>) seen *Azilestes* is also more specialized than in known early representatives of Perissodactyla, Anthracobunia, and Paenungulata, as for the Glires. This supports the convergence of *Azilestes* with these placental clades. In this respect and in agreement with our systematic comparisons, we conservatively assume a basal eutherian position of *Azilestes*, as a very specialized Cretaceous eutherian genus showing unexpected early convergences with some herbivorous crown placentals. It should be noted that within the Zhelestidae a sister group relationship of *Azilestes* and *Valentinella* is favoured by our analysis (Fig. 8C), in accordance with our morphological comparisons. The Zhelestidae relationship of *Azilestes* is the best supported among known stem eutherians, but it remains uncertain and requires further testing on additional fossil material.

Our cladistic analysis in the Implied Weighting option supports a zhelestid relationship for *Valentinella* (Fig. 8B), and it is the sister group of *Azilestes* in the constrained analysis (Fig. 8C). For *Mistralestes*, the analysis does not clearly support zhelestid relationship. The constrained analysis raises instead the hypothesis of a possible zalambdalestidan relationship of *Mistralestes* (Fig. 8C). This is in accordance with the alternative interpretation of the dental formula of the holotype of *Mistralestes* as P<sub>3-4</sub> and M<sub>1-2</sub>, and of a fully molariform P<sub>5</sub> which characterizes the zalambdalestids. However, this hypothesis would imply a P<sub>5</sub> even more molariform than in currently known zalambdalestids, with a very compressed trigonid. The relationship of *Mistralestes* needs to be checked, here again, on additional fossil material, and especially on the (unknown) upper teeth. The poorly constrained phylogenetic relationships of the Cretaceous European eutherians are linked to their still very incomplete documentation, limited to a few fragmentary jaws and isolated teeth that mostly belong to the lower dentition.

**Table 2.** Cladistic analysis with TNT 1.5 of the relationships of *Azilestes ragei* n. g., n. sp. Relationships of *Azilestes* and the European genera *Valentinella* and *Mistralestes* found in the strict consensus tree resulting from our six analyses, including “Traditional Search” analysis (1), Implied Weighting analysis (2), and analysis with *Azilestes* and *Valentinella* constrained within the Zhelestidae (3, 4). In analyses 3-4, the constrained clade includes *Azilestes*, *Valentinella*, *Borisodon*, *Eozhelestes*, *Sheikhdzheilia*, *Lainodon*, *Avitotherium*, *Gallolestes*, *Parazhelestes*, *Aspanlestes*, *Zhelestes*, *Eoungulatum*, *Alostera*. Br = Bremer support value. L = number of steps; RI and CI: retention and consistency index.

**Tableau 2.** Analyse cladistique des relations phylogénétiques d’*Azilestes ragei* n. g., n. sp. Relations phylogénétiques de *Azilestes*, *Valentinella* et *Mistralestes* trouvées dans l’arbre de consensus strict de nos six analyses : Recherche Traditionnelle (1), analyse en Pondération Successive (2), et analyse avec *Azilestes* et *Valentinella* contraints parmi les Zhelestidae (3, 4). Dans les analyses 3-4, le clade contraint inclut *Azilestes*, *Valentinella*, *Borisodon*, *Eozhelestes*, *Sheikhdzheilia*, *Lainodon*, *Avitotherium*, *Gallolestes*, *Parazhelestes*, *Aspanlestes*, *Zhelestes*, *Eoungulatum*, et *Alostera*. Br = Valeur de l’indice de Bremer. L = nombre de pas ; RI et CI : indice de rétention et de consistance.

Analysis	<i>Azilestes</i>	<i>Valentinella</i>	<i>Mistralestes</i>
1 <b>Fig. 8A</b> - Traditional search; characters ordered; 1080 trees. L= 2354; CI =24.6; RI=55.4	Eutherian polytomy; <b>Sister-group of Glires</b> in 50% majority rule tree.	Eutherian polytomy (incl. 50% majority rule tree)	Eutherian polytomy
2 <b>Fig. 8B</b> - Implied Weighting analysis (K=5); characters ordered. 9 trees; L= 2389; CI= 24.2; RI=54.5	<b>Sister-group of Glires</b> ( <i>Azilestes</i> ( <i>Paramys</i> , <i>Tribosphenomys</i> )( <i>Rhombomylus</i> ( <i>Mimotona</i> , <i>Gomphos</i> ))); Br=3	<b>Zhelestidae</b> ; Br=1	<b>Lipotyphla</b> : ( <i>Erinaceus</i> ( <i>Mistralestes</i> , <i>Eoryctes</i> )); Br=1
3 <b>Fig. 8C</b> - Traditional search; <i>Azilestes</i> and <i>Valentinella</i> constrained within Zhelestidae. 290 trees; L=2359; CI=24.5; RI=55.2	Clade ( <i>Azilestes</i> , <i>Valentinella</i> )	Clade ( <i>Azilestes</i> , <i>Valentinella</i> )	<b>Zalambdalestida</b> : ( <i>Zhangolestes</i> ( <i>Mistralestes</i> , <i>Alymestes</i> )( <i>Barunlestes</i> , <i>Zalambdalestes</i> )); Br= 1
4 Implied Weighting analysis (K=5); <i>Azilestes</i> and <i>Valentinella</i> constrained within Zhelestidae. 44 trees; L=2385; CI=24.3; RI=54.6	Clade Lainodontinae (polytomy <i>Azilestes</i> , <i>Valentinella</i> , <i>Lainodon</i> )	Clade Lainodontinae (polytomy <i>Azilestes</i> , <i>Valentinella</i> , <i>Lainodon</i> )	<b>Lipotyphla</b> ( <i>Erinaceus</i> ( <i>Mistralestes</i> , <i>Eoryctes</i> )); Br= 1

## 7. Conclusion

The new mammal *Azilestes ragei* n. g., n. sp., discovered in the Mas-d'Azil locality, is one of the largest known Cretaceous eutherians together with the other European species *Valentinella vitrollense*. Among Cretaceous eutherians, *Azilestes* is characterized by an original derived morphology with, in addition to bunodont cusps and crown, a shortened robust dentary with reduced premolar formula, the presence of a small hypolophid, and a cingular-like postcristid and entoconid. These traits are unknown in Cretaceous eutherians, even in *Valentinella* (except noticeably for the deep and robust dentary). The presence of a small hypolophid and a cingular-like postcristid and entoconid are instead molar features known in lophodont "ungulate" placental clades such as the Paenungulata and the Euungulata. Together with the molar wear pattern of *Azilestes*, they suggest the presence of a well-developed functional hypocone in upper molars. These traits are early specializations previously unknown in Cretaceous eutherians which obscure the relationships of *Azilestes*. However, besides these specializations the molar morphology of *Azilestes* is reminiscent of the Zhelestidae family among all known Cretaceous eutherians; this is illustrated by the robust and bunodont crown, the crushing-grinding functional pattern (morphology and wear pattern), the large talonid, postfossid and hypoconid, and the lingual paraconid and hypoconulid. Within the Zhelestidae, *Azilestes* displays much closer relationship with *Valentinella*. Shared derived traits include the large size, deep and robust dentary, presence of radicular grooves and the inferred occurrence of a hypocone in *Azilestes*. *Azilestes* is consequently conservatively considered here as a specialized basal eutherian of uncertain but possible zhelestid(?) affinity, that displays early convergences with some Cenozoic lophodont placental clades.

Whatever its phylogenetic relationships, *Azilestes* documents an interesting and somewhat unexpected taxonomic, morphological and functional diversity (in dental pattern) of the European Cretaceous eutherians. This is despite a still poor fossil record restricted to about 60 specimens (mostly isolated lower teeth) from nine localities, all from the Ibero-Armorican Island. This diversity is taxonomically exemplified by five known genera, representing as far as we know the radiation of a single family, although it remains the most uncertain for *Azilestes*. In any case, such a truncated picture of a significant diversity of early European eutherian mammals further underlines our poor knowledge of the Cretaceous European centre of evolution. In this context, *Azilestes ragei* from the Mas-d'Azil further confirms the promising potential of the field research in the Northern Pyrenees (Gheerbrant et al., 1995) within Southern Europe.

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## References

- Archibald, D. J., Averianov, A.O., 2012. Phylogenetic analysis, taxonomic revision, and dental ontogeny of the Cretaceous Zhelestidae (Mammalia: Eutheria). *Zool. J. Linn. Soc.* 164, 361–426.
- Averianov, A.O., Archibald, D., J., 2005. Mammals from the mid-Cretaceous Khodzhaikul Formation, Kyzylkum Desert, Uzbekistan. *Cret. Res.* 26, 593–608.
- Bilotte, M., 1985. Le Crétacé supérieur des plates-formes est-pyrénéennes, série. *Strata* 2, 5, pp. 1–438.
- Bilotte, M., 1990. Le Sénonien supérieur du bassin d'avant-pays sous-pyrénéen de l'Ariège et de la Haute-Garonne. *Strata*, 2, 13, 1-96.
- Bilotte, M., 1991. Séquences de dépôt et limites de bloc dans le Crétacé terminal et le Paléocène basal du bassin d'avant-pays sous-pyrénéen (Petites Pyrénées dômes annexes, France). *Bull. Centre Rech. Expl. -Prod. Elf Aquitaine*, 15, 2, 411-437.
- Bilotte, M., Tambareau, Y., Vilatte, J., 1983. Le Crétacé supérieur et la limite Crétacé-Tertiaire en faciès continental dans le versant Nord des Pyrénées. *Geol. Medit.* 10, 269-276.
- Breton, G., Bilotte, M., Eychenne, G., 2013. L'ambre campanien du Mas-d'Azil (Ariège, France) : gisement, micro-inclusions, taphonomie. *Ann. Pal.* 99, 4, 317-337.
- Buffetaut, E., Le Loeuff, J., 1991. Late Cretaceous dinosaur faunas of Europe: Some correlation problems. *Cret. Res.* 12, 159–176.
- Butler, P.M., 1952. The milk-molars of *Perissodactyla* with remarks on molar occlusion. *Proc. Zool. Soc. London B.* 777–817.
- Codrea, V., Smith, T., Dica, P., Folie, A., Garcia, G., Godefroit, P., Van Itterbeeck, J., 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Hațeg Basin (Romania). *C. R. Palevol* 1, 173–180. [https://doi.org/10.1016/S1631-0683\(02\)00021-0](https://doi.org/10.1016/S1631-0683(02)00021-0)
- Codrea, V.A., Solomon, A.A., Venczel, M., Smith, T., 2014. A new kogaionid multituberculate mammal from the Maastrichtian of the Transylvanian Basin, Romania. *C. R. Palevol* 13, 489–499.
- Crompton, A.W., 1971. The origin of the tribosphenic molar, in: *Early Mammals*, Suppl N°1, *Zool. J. Linn. Soc. Kermarck*, D.M. Kermarck, K.A., pp. 65–87.
- Crompton, A.W., Kielan-Jaworowska, Z., 1978. Molar structure and occlusion in Cretaceous therian mammals, in: Butler PM, Joysey, KA (Eds.), *Development, Function and Evolution of Teeth*. Academic Press, London, New-York, pp. 249–286.
- Csiki, Z., Grigorescu, D., 2001. Palaeobiogeographical implications of the fossil mammals from the Maastrichtian of the Hațeg Basin. *Act. Pal. Romaniae* 3, 87–95.
- Csiki, Z., Grigorescu, D., Rucklin M., 2005. A new multituberculate specimen from the Maastrichtian of Pui, Romania and reassessment of affinities of *Barbatodon*. *Act. Pal. Romaniae* 5, 73–86.
- Csiki-Sava, Z., Buffetaut, E., Ósi, A., Pereda-Suberbiola, X., Brusatte, S.L., 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *Zookeys* 469, 1–161.

- Csiki-Sava, Z., Vremir, M., Meng, J., Brusatte, S.L., Norell, M.A., 2018. Dome-headed, small-brained island mammal from the Late Cretaceous of Romania. *Proc Natl Acad Sci USA* 115, 4857–4862. <https://doi.org/10.1073/pnas.1801143115>
- Fostowicz-Frelik, Ł., 2017. Convergent and Parallel Evolution in Early Glires (Mammalia). In: Pontarotti, P. (Ed.), *Evolutionary Biology: Self/Nonself Evolution, Species and Complex Traits Evolution, Methods and Concepts*. Springer International Publishing, Cham, pp. 199–216.
- Gheerbrant, E., Astibia, H., 1994. Un nouveau mammifère du Maastrichtien de Laño (Pays Basque espagnol). *C. R. Acad. Sc.de Paris II*, 1125–1131.
- Gheerbrant, E., Abrial, C., Cappetta, H., 1997. Nouveaux sites à microvertébrés continentaux du Crétacé terminal des Petites Pyrénées (Haute-Garonne et Ariège, France). *Geobios* 30, 257–269.
- Gheerbrant, E., Astibia, H., 1999. The upper Cretaceous mammals from Laño (Spanish Basque Country). *Est. Mus. Cienc. Nat. de Alava* 14, 295–323.
- Gheerbrant, E., Astibia, H., 2012. Addition to the Late Cretaceous Laño mammal faunule (Spain), and to the knowledge of European “Zhelestidae” (*Lainodontinae* nov.). *Bull. Soc. Géol. Fr.* 183, 537–546. <https://doi.org/10.2113/gssgfbull.183.6.537>
- Goloboff, P.A., Farris, J.S., Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- Hu, Y., Meng, J., Wang, Y., Li, C., 2005. Large Mesozoic mammals fed on young dinosaurs. *Nature* 433, 149–152.
- Laurent, Y., Le Loeuff, J., Bilotte, M., Buffetaut, E., Odin, G.S., 2001. Campanian-Maastrichtian continental-marine connection at the Aquitaine-Pyrenees-Provence area (S France), in: Odin, Gilles S. (Ed.), *Developments in Palaeontology and Stratigraphy*. Elsevier, pp. 657–674.
- Le Loeuff, J., 1991. Les vertébrés maastrichtiens du Mas-d’Azil (Ariège, France): étude préliminaire de la collection Pouech. *Rev. Paléobiol.* 10(1), 61-67.
- Ledoux, J.-C., Hartenberger, J.-L., Michaux, J., Sudre, J., Thaler, L., 1966. Découverte d’un mammifère dans le Crétacé supérieur à Dinosaur de Champ-Garimond près de Fons (Gard). *C. R. Acad. Sc. Paris* 262, 1925–1928.
- Lepicard, B., 1985. Le Crétacé terminal et le Paléocène basal dans les Petites Pyrénées et les Dômes annexes. *Biostratigraphie – Sédimentologie. Strata série 2*, 4, 1-272.
- Lillegraven, A., J., 1976. A new genus of therian mammal from the late Cretaceous “El Gallo Formation”, Baja California, Mexico. *J. Pal.* 50, 437–443.
- Martin, J.E., Case, J.A., Jagt, J.W.M., Schulp, A.S., Mulder, E.W.A., 2005. A New European Marsupial Indicates a Late Cretaceous High-Latitude Transatlantic Dispersal Route. *J. Mam. Evol.* 12, 495–511. <https://doi.org/10.1007/s10914-005-7330-x>
- Martin, T., Buffetaut, E., Tong, H., 2015. A Late Cretaceous eutherian mammal from southwestern France. *Paläontol Zeit.* 89, 535–544. [10.1007/s12542-014-0231-7](https://doi.org/10.1007/s12542-014-0231-7)

- Nessov, L.A., Archibald, J. D., Kielan-Jaworowska, Z., 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. *Bull. Carn. Mus. Nat. Hist.* 34, 40–88.
- Pol, C., Buscalioni, A.D., Carbelleira, J., Frances, V., Martinez, L., N., Marandat, B., Moratalla, J.J., Sanz, J.L., Sige, B., Villatte, J., 1992. Reptiles and mammals from the late Cretaceous new locality (Burgos Province, Spain). *N. Jb. Geol. Paläont. Abh.* 184, 279–314.
- Pouech, J. J., 1859. Mémoire sur les terrains tertiaires de l'Ariège rapportés à une coupe transversale menée de Fossat à Aiilières, passant par le Mas-d'Azil, et projetée sur le méridien de ce lieu. *Bull. Soc. Géol. Fr.* 16, 381-411.
- Pouech, J. J., 1881a. Sur un nouveau gisement de reptiles fossiles de l'Ariège. *Bull. Soc. Géol. Fr.* 9, 15-16.
- Pouech, J. J., 1881b. Sur un ossement fossile supposé appartenir à un mammifère, trouvé dans les grés crétaqués du Mas d'Azil (Ariège). *Bull. Soc. Géol. Fr.* 9, 88-90.
- Segura, F., 1979. Etude géologique de la partie orientale des Petites Pyrénées -zones sous-pyrénéennes- (Ariège, Haute-Garonne). Thèse Doct. 3<sup>o</sup> cycle, Toulouse, 143 p., 35 fig., 8 pl.
- Schultz, J.A., Menz, U., Winkler, D.E., Schulz-Kornas, E., Engels, S., Kalthoff, D.C., von Koenigswald, W., Ruf, I., Kaiser, T.M., Kullmer, O., Südekum, K.-H., Martin, T., 2018. Modular Wear Facet Nomenclature for mammalian post-canine dentitions. *Hist. Biol.* 30, 30–41. <https://doi.org/10.1080/08912963.2017.1302442>
- Smith, T., Codrea, V., 2015. Red Iron-Pigmented Tooth Enamel in a Multituberculate Mammal from the Late Cretaceous Transylvanian “Hațeg Island.” *PLoS ONE* 10, e0132550. <https://doi.org/10.1371/journal.pone.0132550>
- Tabuce, R., Vianey-Liaud, M., Garcia, G., 2004. A eutherian mammal in the latest Cretaceous of Vitrolles, southern France. *Act. Pal. Pol.* 49, 347–356.
- Tabuce, R., Tortosa, T., Vianey-Liaud, M., Garcia, G., Lebrun, R., Godefroit, P., Dutour, Y., Berton, S., Valentin, X., Cheylan, G., 2013. New eutherian mammals from the Late Cretaceous of Aix-en-Provence Basin, south-eastern France. *Zool. J. Linn. Soc.* 169, 653–672. <https://onlinelibrary.wiley.com/doi/abs/10.1111/zoj.12074>
- Tambareau, Y., Crochet, B., Villatte, J., Deramond, J., 1995. Evolution tectono-sédimentaire du versant nord des Pyrénées centre-orientales au Paléocène et à l'Eocène inférieur. *Bull. Soc. Géol. Fr.* 166, 375-387.
- Van Valen, L., 1966. Deltatheridia, a new order of mammals. *Bull. Amer. Mus. Nat. Hist.* 132, 1–126.
- Wible, J.R., Novacek, J., M., Rougier, G.W., 2004. New data on the skull and dentition in the Mongolian Late Cretaceous eutherian mammal *Zalambdalestes*. *Bull. Amer. Mus. Nat. Hist.* 281, 1–144.
- Wible, J.R., Rougier, G.W., Novacek, M.J., Asher, R.J., 2009. The Eutherian Mammal *Maelestes gobiensis* from the Late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. *Bull. Amer. Mus. Nat. Hist.* 20, 1 – 123.



## Caption of figures

Fig. 1. Location of the Mas-d'Azil locality from the Campano-Maastrichtian Grès de Labarre formation that yielded the lower jaw MNHN.F CTE215 of *Azilestes ragei* n. g., n. sp. The specimen MNHN.F CTE215 comes from the upper-most levels of Grès de Labarre formation, that are dated early Maastrichtian. Geological map modified from Tambareau et al. (1995).

Fig. 1. Localisation du gisement du Mas-d'Azil de la Formation Campano-Maastrichtienne des Grès de Labarre, qui a livré la mâchoire inférieure MNHN.F CTE215 de *Azilestes ragei* n. g., n. sp. Le spécimen MNHN.F CTE215 provient des niveaux les plus hauts, datés du Maastrichtien inférieur, de la formation de Grès de Labarre. Carte géologique modifiée de Tambareau et al. (1995).

Fig. 2. Photograph of the early Maastrichtian fossiliferous level from the Grès de Labarre formation from which comes the lower jaw MNHN.F CTE215 of *Azilestes ragei* n. g., n. sp. The level consists in a hard sandstone yielding continental vertebrate remains.

Fig. 2. Photographie de l'horizon fossilifère du Maastrichtien inférieur de la formation de Grès de Labarre où a été trouvée la mâchoire inférieure MNHN.F CTE215 de *Azilestes ragei* n. g., n. sp. Ce niveau est formé d'un grès fortement induré riche en restes de vertébrés continentaux.

Fig. 3. *Azilestes ragei* n. g., n. sp., photography of the holotype MNHN.F CTE215, left lower jaw in lingual (A), labial (B) and occlusal (stereophotography) views (C). Abbreviations: al: alveolus; bs: bone septum inserting in the radicular groove of the P<sub>5</sub> (see bone septum and radicular grooves in M<sub>2</sub>, Fig. 5D-E); symp: mandibular symphysis.

Fig. 3. *Azilestes ragei* n. g., n. sp., photographie de l'holotype MNHN.F CTE215, mâchoire inférieure gauche en vue linguale (A), labiale (B) et occlusale (C : stéréophotographie). Abréviations : al : alvéole ; bs : septum osseux de la mandibule s'insérant dans le sillon radiculaire de P<sub>5</sub> (voir les septum osseux et sillon radiculaire sur M<sub>2</sub>, Fig 5D-E); symp : symphyse mandibulaire.

Fig 4. *Azilestes ragei* n. g., n. sp., detail of the molar morphology preserved in the holotype MNHN.F CTE215. A. Stereophotography of the M<sub>1</sub> in occlusal view (s.e.m. view); B. M<sub>1-2</sub>, in occlusal view (s.e.m. view); C-D. Detailed occlusal view of the M<sub>1</sub> with annotated morphological sketch. Abbreviations: hld + pcd : cingular-like hypoconulid and postcrisid; eld: entoconulid; hyphid: incipient hypolophid.

Fig 4. *Azilestes ragei* n. g., n. sp., détail de la morphologie des molaires conservées sur l'holotype MNHN.F CTE215. A. Stéréophotographie de M<sub>1</sub> en vue occlusale (vue m.e.b.) ; B. M<sub>1-2</sub>, en vue occlusale (vue m.e.b.) ; C-D. Détail de la vue occlusale de M<sub>1</sub> avec schéma morphologique annoté. Abréviations : hld + pcd : hypoconulide et postcriside cingulaires ; eld : entoconulide ; hyphid : hypolophide naissant.

Fig. 5. 3D digital model of the left lower jaw MNHN.F CTE215 of *Azilestes ragei* n. g., n. sp., from the CT scans. A. Labial view; B. Labial view, bone removed; C. Lingual view; D. Lingual view bone removed; E. Occlusal view. F. Occlusal view teeth removed; G. Antero-labial view; H. Anterior view. Teeth: pink. Alveoli: blue; bone: grey; mandibular and lateral canals: yellow. Abbreviations: al: alveolus; lat br (c): lateral branch of the mandibular canal of the canine; lat br (p): lateral branch of the mandibular canal of the premolars; ment can: mental canal; ment f: mental foramen; symph: mandibular symphysis.

Fig. 5. Modélisation 3D de la mâchoire inférieure gauche MNHN.F CTE215 d'*Azilestes ragei* n. g., n. sp., à partir des CT scans. A. Vue labiale ; B. Vue labiale, os enlevé ; C. Vue linguale ; D. Vue linguale, os enlevé ; E. Vue occlusale. F. Vue occlusale des alvéoles, dents enlevées ; G. Vue antéro-labiale ; H. Vue antérieure. Dents : roses. Alvéoles : bleues ; os : gris ; canaux mandibulaires et latéraux : jaunes. Abréviations : al : alvéole ; lat br (c) : branche latérale du canal mandibulaire de la canine ; lat br (p) : branche latérale du canal mandibulaire des prémolaires ; ment can : canal mandibulaire ; ment f : foramen mentonnier ; symphysis : symphyse mandibulaire.

Fig. 6. Reconstruction of the teeth and alveoli endocasts as virtually extracted from the CT scans of the type specimen MNHN.F CTE215 of *Azilestes ragei* n. g., n. sp. A. Lingual view; B. labial view; C, ventral view. Abbreviations: al: alveolus; inter-rad cr: interradicular crest; pad: paraconid; rad gr: radicular groove.

Fig. 6. Reconstitution des dents et des alvéoles, extraites virtuellement à partir des CT scans de l'holotype MNHN.F CTE215 de *Azilestes ragei* n. g., n. sp. A. Vue linguale ; B. Vue labiale ; C. Vue ventrale. Abréviations : al : alvéole ; inter-rad cr : crête inter-radulaire ; pad : paraconide ; rad gr : sillon radulaire.

Fig. 7. Microtomographic sections of the holotype MNHN.F CTE215 of *Azilestes ragei* n. g., n. sp. A-C. Longitudinal (sagittal) sections. D-E. Horizontal sections. Abbreviations: al: alveolus; mand can: mandibular canal; ment for/can: mental canal and foramen; rad gr: radicular groove (with interlocked interalveoli bony septum); symph: mandibular symphysis.

Fig. 7. Sections microtomographiques de l'holotype MNHN.F CTE215 d'*Azilestes ragei* n. g., n.sp. A-C. Coupes longitudinales (sagittales). D-E. Coupes horizontales. Abréviations : al : alvéole ; ment for/can : canal et foramen mentonniers ; rad gr : sillon radulaire (avec septum osseux inter-alvéolaire emboîté) ; symph : symphyse mandibulaire.

Fig. 8. Phylogenetic relationships of *Azilestes ragei* n. g., n. sp., MPTs recovered from the cladistic analysis with TNT1.5 (matrix of Tabuce et al., 2013 modified, and including 3 ordered character). **A.** Traditional (standard) search analysis (Table 1: analysis 1), strict consensus tree of 1080 MPTs; L= 2354; CI =24.6; RI=55.4. **B.** Implied Weighting search analysis (Table 1: analysis 2), strict consensus tree of 9 trees; L= 2389; CI= 24.2; RI=54.2. **C.** Traditional (standard) analysis with constrained clade Zhelestidae including *Azilestes* (Table 1: analysis 3); strict consensus tree of 290 trees; L=2359; CI=24.5; RI=55.2. The constrained clade in cladogram C includes *Azilestes*, *Valentinella*, *Eozhelestes*, *Sheikhdzheilia*, *Lainodon*, *Avitotherium*, *Gallolestes*, *Parazhelestes*, *Aspanlestes*, *Zhelestes*, *Eoungulatum*.

Fig. 8. Relations phylogénétiques d'*Azilestes ragei* n. g., n. sp., arbres les plus parcimonieux trouvés dans l'analyse cladistique avec TNT1.5 (matrice de Tabuce et al., 2013 modifiée, incluant 3 caractères ordonnés). **A.** Analyse en recherche Traditionnelle (standard) (Tableau 1 : analyse 1), strict consensus des 1080 arbres parcimonieux trouvés ; L= 2354 ; CI = 24,6 ; RI = 55,4. **B.** Analyse en recherche par Pondération Successive (Tableau 1 : analyse 2), consensus strict de 9 arbres ; L= 2389 ; CI= 24.2 ; RI=54.5. **C.** Analyse en recherche Standard avec clade des Zhelestidae contraint et comprenant *Azilestes* (Tableau 1 : analyse 3) ; consensus strict de 290 arbres ; L=2359 ; CI=24.5 ; RI=55.2. Le clade contraint du cladogramme C comprend *Azilestes*, *Valentinella*, *Eozhelestes*, *Sheikhdzheilia*, *Lainodon*, *Avitotherium*, *Gallolestes*, *Parazhelestes*, *Aspanlestes*, *Zhelestes*, *Eoungulatum*.

Table 1. Measurements of MNHN.F CTE215 (millimeters), holotype of *Azilestes ragei* n. g. , n. sp.  
Tableau 1. Dimensions de MNHN.F CTE215 (en millimètres), holotype de *Azilestes ragei* n. g. , n. sp.

Table 1. Cladistic analysis with TNT 1.5 of the relationships of *Azilestes ragei* n. g., n. sp. Relationships of *Azilestes* and the European genera *Valentinella* and *Mistralestes* found in the strict consensus tree resulting from our six analyses, including “Traditional Search” analysis (1), Implied Weighting analysis (2), and analysis with *Azilestes* and *Valentinella* constrained within the Zhelestidae (3, 4). In analyses 3-4, the constrained clade includes *Azilestes*, *Valentinella*, *Borisodon*, *Eozhelestes*, *Sheikhdzheilia*, *Lainodon*, *Avitotherium*, *Gallolestes*, *Parazhelestes*, *Aspanlestes*, *Zhelestes*, *Eoungulatum*, *Alostera*. Br = Bremer support value. L = number of steps; RI and CI: retention and consistency index.

Tableau 1. Analyse cladistique des relations phylogénétiques d'*Azilestes ragei* n. g., n. sp. Relations phylogénétiques de *Azilestes*, *Valentinella* et *Mistralestes* dans l'arbre de consensus strict trouvé dans nos six analyses, dont la recherche Traditionnelle (1), l'analyse en Pondération Successive (2), et l'analyse avec *Azilestes* et *Valentinella* contraints parmi les Zhelestidae (3, 4). Dans les analyses 3-4, le clade contraint inclut *Azilestes*, *Valentinella*, *Borisodon*, *Eozhelestes*, *Sheikhdzheilia*, *Lainodon*, *Avitotherium*, *Gallolestes*, *Parazhelestes*, *Aspanlestes*, *Zhelestes*, *Eoungulatum*, et *Alostera*. Br = Valeur de l'indice de Bremer. L = nombre de pas ; RI et CI : indice de rétention et de consistance.

### Appendices (Supplementary Information)

SI Fig. A.1. 3D reconstruction from CT scans of the lower jaw MNHN.F CTE215 of *Azilestes ragei* n. g., n. sp. with distinction (separate 3D models) of the teeth, alveoli, mandibular and lateral canals.

SI Fig. A.1. Reconstitution 3D à partir des CT scans de la mâchoire inférieure MNHN.F CTE215 d'*Azilestes ragei* n. g., n. sp., avec distinction (modèles 3D séparés) des dents, alvéoles, et canaux mandibulaires et branches latérales.

SI Fig. A.2. Video of the 3D reconstruction from CT scans of the lower jaw MNHN.F CTE215 of *Azilestes ragei* n. g., n. sp.

SI Fig. A.2. Enregistrement vidéo de la modélisation 3D à partir des CT scans de la mâchoire inférieure MNHN.F CTE215 d'*Azilestes ragei* n. g., n. sp.

SI Text A.1 List of characters coded in *Azilestes ragei* n. g., n. sp. (matrix of Wible et al. 2009)

SI Texte A.1 Liste des caractères codés chez *Azilestes ragei* n. g., n. sp. (matrice de Wible et al. 2009)

SI File A.1. Character matrix including *Azilestes ragei* used here, in the nexus format. Matrix of Wible et al. (2009) modified by Archibald and Averianov (2012) and Tabuce et al. (2013).

SI Fichier A.1. Matrice des caractères au format Nexus avec *Azilestes ragei*. Matrice originale de Wible et al. (2009) modifiée par Archibald and Averianov (2012) et Tabuce et al. (2013).







