New Dryolestidan Mammal from the Hauterivian—Barremian Transition of the Iberian Peninsula

Authors: Gloria Cuenca-Bescós, Ainara Badiola, José I. Canudo, José M. Gasca, and Miguel Moreno-Azanza

Source: Acta Palaeontologica Polonica, 56(2) : 257-267

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.0157
New dryolestidan mammal from the Hauterivian–Barremian transition of the Iberian Peninsula

GLORIA CUENCA-BESCÓS, AINARA BADIOLA, JOSÉ I. CANUDO, JOSÉ M. GASCA, and MIGUEL MORENO-AZANZA

Introduction

The Stem clade Cladotheria are important and diversified Mesozoic mammals that comprise several groups of pretribosphenic mammals, the dryolestoids, the amphitheriids, Vincelestes, and the zatherians, including Zatheria and “peramurans” (Kielan-Jaworowska et al. 2004). The Stem Cladotheria represent the intermediate grade between the plesiomorphic “symmetroodontans”, with a reversed-triangle molar pattern like Spalacotherium and their kin, and the apomorphic tribosphenic mammals, with the triangle-molar pattern of metatherians and eutheriens (Kielan-Jaworowska et al. 2004). The molars of Stem Cladotheria share with symmetroodontans the reversed-triangle molar pattern, though the upper molars are wider than the lower ones, having a third (lingual) root and the labial stylar cusps being more elaborate. The last upper premolars may be molariform in some groups, though they have only two roots.

The stem cladotherians are known from the Middle Jurassic on (Kirtlington, Forest Marble Formation in Britain; Guimarota Mine in Portugal; Morrison Formation in the USA). They survive throughout the Cretaceous: in the Early Cretaceous of Europe (Spain, Britain) and Morocco, Mongolia, South America, and possibly Australia, and in the Late Cretaceous of Argentina and possibly North America (Henkel and Krebs 1969; Freeman 1979; Prothero 1981; Bonaparte 1990, 1994, 1996, 2002; Krebs 1993; Canudo and Cuenca-Bescós 1996; Martin 1999; Sigogneau-Russell 1999; Kielan-Jaworowska et al. 2004). The Early Cretaceous Stem Cladotheria from the Iberian Peninsula are represented by Dryolestida and peramurans from the provinces of Teruel (Galve) and Cuenca (Uña) in the Iberian Range in central and north-eastern Spain (Henkel and Krebs 1969; Krebs 1993; Canudo and Cuenca-Bescós 1996; Martin 1998) (Fig. 1).

More than a hundred Late Jurassic (Tithonian) and Early Cretaceous (Hauterivian–Barremian) vertebrate-fossil-bearing beds are present in the Galve syncline, around the village of Galve (Teruel), which are included in four formations of the Galve sub-basin (Ruiz-Omeñaca et al. 2004), that forms part of the Maestrazgo Basin (Fig. 1). The known stem cladotherians from Galve are from two localities of the El Castellar Formation and one from the Camarillas Formation. The upper layers of the El Castellar Formation are terminal Hauterivian-basal Barremian in age. The fossil mammalian remains were found in two different localities of the El Castellar Formation: Galve Th, and Pelejón 2. The third...
mammalian site of Galve is Poca, in the upper layers of the Camarillas Formation. The mammals described are the dryolestid *Crusafonia cuencana* Henkel and Krebs, 1969 at the sites of Galve Th and Pelejón 2, and the peramurid dryolestid *Pocamus pepelui* at the sites of Galve Th and Pelejón 2, and the peramurid dryolestid the Camarillas Formation. The mammals described are the

![Geographical and geological setting of Galve](image)

**Fig. 1.** Geographical and geological setting of Galve (Teruel, Spain). **A.** Simplified geological map of the Iberian Peninsula. **B.** Palaeogeographic sub-basins within the Maestrazgo Basin and active faults during Early Cretaceous sedimentation, modified from Salas et al. (2001), and the palaeogeographical—and geographical—relationship with the Uña area (Cuenca, Spain). **C.** Litho- and chronostratigraphy of the Mesozoic mammal record from the areas of Galve and Uña. Abbreviations: Ga, Galve; Mo, Morella; Ol, Oliete; Pa, Las Parras; Pe, Perelló; Pg, Peñagolosa; Sa, Salzedella.

Geographic and geological setting

The localities of Galve are situated in the geographic domain of the Central Iberian Range, in the province of Teruel in the NE of Spain (Fig. 1). The new mammalian tooth was found in the locality of Cuesta Corrales 2. The site is 1.5 km east of the village of Galve, on the eastern flank of the Galve syncline (Fig. 2).

The Galve syncline is situated to the west of the Galve sub-basin, which together with six other sub-basins comprises the Maestrazgo Basin (Salas et al. 2001; Liesa et al. 2006). The Galve sub-basin is NNW-SSE oriented, and is 40 km long and 20 km wide (Fig. 1B). It was formed as a consequence of the Jurassic–Cretaceous extensional deformation of the Iberian rift (Liesa et al. 2006). In the Galve sub-basin, marine, continental and transitional sediments outcrop from the Kimmeridgian (Late Jurassic) to the early Aptian (Díaz Molina and Yébenes 1987). Sites of Mesozoic vertebrates from the Galve syncline are distributed throughout the stratigraphic sequence. The geological units that are richest in vertebrates are the Villar del Arzobispo Formation (late Tithonian–early Berriasian), the El Castellar Formation (terminal Hauertrivian–basal Barremian), and the Camarillas Formation (early Barremian) (Sanz et al. 1987; Estes and Sanchiz 1982; Díaz Molina and Yébenes 1987; Ruiz-Omeñaca et al. 2004; Canudo et al. 2006; Badiola et al. 2009) (Figs. 1C, 2).

The El Castellar Formation represents the first synrift unit included in the Wealden facies of the Galve sub-basin. It lies above an unconformity on the Villar del Arzobispo Formation, and there is a stratigraphic gap that extends from the Berriasian to the upper Hauertrivian (Díaz Molina and Yébenes 1987; Liesa et al. 2006; Meléndez et al. 2009). The El Castellar Formation has a thickness of roughly 100 m, with two clearly differentiated parts: a lower part (80 m) con-
sisting of lutites, sandstones, conglomerates and alluvial, palustrine and lacustrine limestones, which represent alluvial, palustrine and lacustrine subenvironments; and an upper part comprising some 20 m of alternating marls and limestones typical of a lacustrine system in phases of expansion and retraction (Meléndez et al. 2009). In this upper part are the sites, from south to north, of Pelejón 2, Piélagos 0, Cuesta Corrales 2, and Colladico Blanco (Fig. 2).

Cuesta Corrales 2 (CC 2) is a fossil-bearing level that has a depth of roughly four metres and displays great lateral continuity. CC 2 is an accumulation site for microvertebrate remains and eggshell fragments. In the microscopic fraction
it was possible to recover isolated teeth from Osteichthyes, Chondrichthyes and neosuchian crocodiles, as well as fragmentary remains of amphibians and squamates and a tooth under study in this paper. In addition, charophytes and ostracods are present in abundance, while freshwater gastropods are scarcer. The most abundant fossil remains are eggshells. CC 2 is the type locality of the ootaxon Macroolithus turolensis Amo Sanjuan, Canudo, and Cuenca-Bescós, 2000. Moreover, eggshell fragments from the oofamilies Prismatoolithidae, Elongatoolithidae and Krokoolithidae have been identified (Amo Sanjuán et al. 2000; this work).

The stratigraphic position of CC 2 is close to that of other sites from the top of the El Castellar Formation, such as Colladico Blanco and Pelejón 2 (Estes and Sanchez 1982; Krebs 1985; Hahn and Hahn 1992; Ruiz-Omeñaca et al. 2004). The upper part of the El Castellar Formation is dated by the charophyte association corresponding to the Triquetra Biozone, Triquetra Subzone, as terminal Hauterivian–basal Barremian (Schudack 1989; Riveline et al. 1996; Martin-Closas 2000). Above the El Castellar Formation is the Camarillas Formation with the mammal sites, Yacimiento Herrero at its base and Poca towards the top (Canudo and Cuenca-Bescós 1996; Ruiz-Omeñaca et al. 2004) (Fig. 2).

Material and methods

Approximately 200 kg of sediments were collected from the CC 2 site. The sediments were sieved down to a mesh size of 0.5 mm. The residues were picked with the help of a binocular microscope. Among the fossils of other small vertebrates and eggshell fragments, a mammalian tooth was found.

Here we follow the Linnaean classification and anatomical terminology of stem cladotherian mammals proposed by Kielan-Jaworowska et al. (2004) with some modifications by Martin (1999), Sigogneau-Russell (1999), and this work. Measurements are given in mm.

Systematic palaeontology

Order Dryolestida Prothero, 1981

Genus Crusafontia Henkel and Krebs, 1969

_Type species:_ Crusafontia cuencana Henkel and Krebs, 1969, Uña, Cuenca, Late Barremian.

_Crusafontia amoae_ sp. nov.

Fig. 3.

Fig. 3. Dryolestidan mammal Crusafontia amoae sp. nov., MPZ CC2-1 M4 or M5, holotype, from the site of Cuesta Corrales 2, Colladico Blanco level, El Castellar Formation, Galve, Teruel, Spain in, occlusal (A), mesial (B), labial (C), distal (D), and lingual (E) views. The schematic drawing of C. amoae, in the box in the lower left-hand corner shows the main anatomical elements of the occlusal surface of a dryolestidan.
**Etymology**

The name is dedicated to our late colleague Olga Amo, who studied the vertebrate eggshells remains of the site CC2.

**Holotype**

Upper left molar MPZ CC2−1.

**Type locality and horizon**

Cuesta Corrales 2, Terminal Hauterivian–basal Barremian.

**Stratigraphic and geographic range**

Terminal Hauterivian –early Barremian, Galve, Teruel, Spain.

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**Material**

Two upper molars: the holotype, one upper left molar, MPZ CC2-1, probably M4 or M5, described here. One upper right molar, MPZ Galve P-2 H4, from the site of Pelejón 2, probably M6 or M7, collected by José M. Herrero; described as *Crusafontia cuencana* and figured in Krebs (1993: fig. 2). Both sites lie in the upper part of the El Castellar Formation (Fig. 2). Here we tentatively assign the

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doi:10.4202/app.2009.0157
lower molar MPZ Galve Y H2 described as *Crusafontia cuencana* and figured in Krebs (1993: fig. 6). The “Y” site is probably the Yacimiento Herrero site, in the lowermost part of the Camarillas Formation, early Barremian (Fig. 2). The discussion (below) of the upper molar described by Krebs (1993) is based solely on his descriptions.

**Diagnosis.**—Large-sized species of *Crusafontia* with upper molars characterized by their mesio-labially enlarged parasyile with a large mesial wear facet that runs from the tip of the stylocone to the base of the parastyle, the ample ectoflexus on their labial border, their continuous metacrista with a deep notch, and the pointed mesio-lingual slope of the paracrista.

**Differential diagnosis.**—*Crusafontia amoae* sp. nov. differs from *Crusafontia cuencana* by its larger size, the high, mesially protruding and rounded parastyle (as in *Comotherium*) in relation to the stylocone, the larger mesial wear facet, the pointed and more linguially placed slope of the paracone (as in *Comotherium*, unlike *Crusafontia cuencana* and other Dryolestida) directed to the mesio-lingual corner, the wider ectoflexus (as a measure of the distance between the stylocone and the metastyle), the presence of cusp C, the larger and distinct metacone, and the presence of a notch in the metastyle (Fig. 3C). There is a tiny cusp “C” in the distolabial indentation or ectoflexus on the labial face. The lingual side is dominated by a lofty paracone, which is the highest cusp of the tooth (Fig. 3B, D, E). On the labial side there are three cusps: from mesial to distal, the parastyle, stylocone, and metastyle (Fig. 3C). There is a tiny cusp “C” in the distolabial corner. In the posterior crest, or metacrista, a distinct metacone is separated from the paracone by a notch, a character best displayed in distal view (Fig. 3D). The paracone is large, and slightly less elevated compared with the stylocone; the parastyle region is enlarged, forming a parastylar wing. There are two transversal crests, the paracrista and the metastyle. The paracrista joins the paracone with the stylocone. The metacrista joins the paracone, metacone and cusp “C”. In the trigon basin there are no traces of a median stylar cusp and median ridge, nor is there a swelling in the middle; on the contrary, its bottom is uniformly basined.

Upper right molar MPZ Galve P-2 H4, probably M6 or M7, described by Krebs (1993: 238–241, fig. 2). It is similar, in its size and heart-shaped morphology in occlusal view (Fig. 4), to the molar from CC 2. The ample ectoflexus that separates the stylocone and the metastyle is similar in the two teeth, especially when viewed in labial view (Fig. 3C and Krebs 1993: fig. 2).

**The upper molars of *Crusafontia***

The upper molars of *Crusafontia amoae* sp. nov. have the typical morphology of upper molars of Dryolestida in that they have a triangular outline in occlusal view, a labio-lingually expanded occlusal surface, a large paracone, three well-developed stylar cusps, and two more or less complete transverse ridges, the paracrista and metacrista. *Crusafontia*

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**Table 1. Stem Cladotheria taxa mentioned in this work.**

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Geographic situation</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Leonardus cuspidotus</em> Bonaparte, 1990</td>
<td>Los Alamos Fm., Argentina</td>
<td>Campanian</td>
</tr>
<tr>
<td><em>Crusafontia cuencana</em> Henkel and Krebs, 1969</td>
<td>Uña, Colladico Blanco, Spain</td>
<td>late Barremian</td>
</tr>
<tr>
<td><em>Pocamus pepelai</em> Canudo and Cuena-Bescós, 1996</td>
<td>Poca, Camarillas Fm., Spain</td>
<td>early Barremian</td>
</tr>
<tr>
<td><em>Crusafontia amoae</em> sp. nov.</td>
<td>Caesta Corrales 2, Pelejón 2, Castellar Fm.; Yacimiento Herrero, Camarillas Fm., Spain</td>
<td>late Hauterivian–early Barremian</td>
</tr>
<tr>
<td><em>Afriquiamus nessovi</em> Sogigneau-Russell, 1999</td>
<td>Aounoual, Morocco</td>
<td>Berriasian?</td>
</tr>
<tr>
<td><em>Donodon perscriptoris</em> Sogigneau-Russell, 1991</td>
<td>Aounoual, Morocco</td>
<td>Berriasian?</td>
</tr>
<tr>
<td><em>Laolestes andresi</em> Martin, 1997</td>
<td>Porto Pinheiro, Portugal</td>
<td>Jurassic–Cretaceous boundary</td>
</tr>
<tr>
<td><em>Portopinheirodon asymmetricalis</em> Martin, 1999</td>
<td>Porto Pinheiro, Portugal</td>
<td>Jurassic–Cretaceous boundary</td>
</tr>
<tr>
<td><em>Peramus teneirostris</em> Owen, 1871</td>
<td>Lulworth Beds, Durlston Bay, UK</td>
<td>Tithonian–Berriasian</td>
</tr>
<tr>
<td><em>Laolestes (= Melanodon) goodrichi</em> (Simpson, 1929)</td>
<td>Morrison Fm., USA</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Dryolestes (= Herpetaius) priscus</em> Marsh, 1878</td>
<td>Morrison Fm., USA</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Dryolestes leiriensis</em> Martin, 1999</td>
<td>Guimarota, Portugal</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Krebsotherium lastianicum</em> Martin, 1999</td>
<td>Guimarota, Portugal</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Comotherium richi</em> Prothero, 1981</td>
<td>Morrison Fm., USA</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Drescatherium acutum</em> Krebs, 1998</td>
<td>Guimarota, Portugal</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Euthlastus cordiformis</em> Simpson, 1927</td>
<td>Morrison Fm., USA</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Henkelotherium guimarotae</em> Krebs, 1991</td>
<td>Guimarota, Portugal</td>
<td>Kimmeridgian</td>
</tr>
<tr>
<td><em>Tathiodon agilis</em> Simpson, 1927</td>
<td>Morrison Fm., USA</td>
<td>Kimmeridgian</td>
</tr>
</tbody>
</table>
cuencana is the closest species to it, morphologically, geographically and biostratigraphically speaking. The latter species of dryolestid was described by Henkel and Krebs (1969) on the basis of two fragmentary lower jaws from the late Barremian locality of Uña (province of Cuenca). No upper dentition was described at the time, though there is a mention of three upper molars in the list provided by Krebs (1985). In this work Krebs (1985) does not describe, measure or draw the upper molars. Nearly 25 years after the original description, Krebs (1993) studied new specimens which he referred to C. cuencana: isolated upper molars from Uña and Galve (MPZ Uña 28, L, 0.85; W, 1.03; H, 1.82, and MPZ Galve P-2 H4, L, 0.64; W, 1.08; H, 1.44), together with a collection of mostly corroded and fragmented upper molars from Uña.

We have included MPZ CC2-1 and the molar MPZ Galve P-2 H4 in a new species of Crusafontia because of their general morphological resemblance to those assigned to C. cuencana, though we have put them in a distinct species for a number of reasons. The main differences were set out in the differential diagnosis; morphological characters of the upper molars of Crusafontia and related genera will be discussed below.

A discussion of the characters of the lower molars of Crusafontia cuencana is beyond the scope of the present work, mainly because we do not yet have lower teeth of C. amoae for comparison. What is more, chronostratigraphically there is an important difference between the level of Colladico Blanco, which is early Barremian in age, and the level of the locality of Uña, in the La Huérguina Formation, which is late Barremian in age (Fig. 1), as a consequence of which the two species are separated by nearly two million years, following the Geologic Time Scale by Gradstein et al. (2004). Below we analyse in detail the main differences and/or similarities among the upper molar characters in Dryolestida, with a view to discussing the taxonomy of Crusafontia amoae sp. nov. The diagnostic anatomical characters of the upper molars of Dryolestida have been discussed by several authors (see Table 1 for a complete list of the stem cladotherians with their authors, locality and ages, quoted in the present work). Here we summarize the characters established by Prothero (1981), Sigogneau-Russell (1991, 1999), Krebs (1993, 1998), Martin (1997, 1998, 1999), Kielan-Jaworowska et al. (2004), and our own observations (Figs. 4–6).

Size.—Usually Dryolestida are tiny mammals. Dryolestes leiriensis is one of the largest dryolestids (Martin 1999). Crusafontia amoae sp. nov. is a small dryolestidan (see Figs. 4, 5 for comparisons), though slightly larger than C. cuencana.

Molar outline.—The outline of the molars in occlusal view varies from triangular to rectangular. Upper molars of Crusafontia are more triangular in occlusal view than in most genera of other Dryolestida; this character is similar to the upper molars of Portopinheirodon, Comotherium, Euthlastus, Laolestes goodrichi, and Tathiodon. The new species C. amoae shares with these genera the triangular outline, although its paraesthesia projects more mesially, as in Comotherium. It differs from the latter in having a complete metaconid and a less-developed metacone. The main differences between C. cuencana and C. amoae in this character are that the new species C. amoae presents a pointed lingual side and the paracone is narrower mesio-lingually, while in C. cuencana the lingual side is rounded. This character is constant in the molar series of Dryolestida (see Prothero 1981; Martin 1999).

Ectoflexus.—The stylocone and the metastyle, on the labial side, are separated by a labial indention or ectoflexus that may be present or absent. The ectoflexus of Crusafontia amoae sp. nov. is wider than that in C. cuencana, Portopinheirodon, Comotherium, and Euthlastus. The ectoflexus is absent in D. leiriensis (Martin 1999). In labial views the stylocone and metastyle of C. amoae are more separated than in C. cuencana (Fig. 3C).

Mesiodistal compression of the trigon.—The trigon varies between not being compressed and being compressed mesiodistally, in relation to the total length of the tooth. It is a measure of the tooth length in relation with the tooth width. The presence of a trigon basin and the corresponding development of a paracrista and metaconid appear in the stem Cladotheria. The mesiodistal compression is characteristic of some dryolestids, such as Dryolestes, Comotherium, and Leonardus cuspidatus. The species Crusafontia cuencana has a trigon that is not compressed, while C. amoae sp. nov. presents a strong mesiodistal compression.

Lingual margin.—The paracone region may be round or more acute. Crusafontia amoae sp. nov. is more acute lingually than C. cuencana. Other Dryolestida species, represented by more than one molar in more or less complete series, such as

doi:10.4202/app.2009.0157

Fig. 5. Stem Cladotheria measurements of upper premolars (P) and molars (M). Pocamus is represented by a P5. The grouping to the left of Peramus tenuirostris are the anterior premolars, P2 and P3, while the second grouping represents the posterior most premolars P4 and P5. Drescheratherium acutum is represented by molars.
Krebsotherium lusitanicum, Dryolestes leiriensis, Comotherium richi, and Drescheratherium acutum, present a uniform type of lingual margin, either pointed or rounded, but never mixed. Therefore we classify the Galve upper molar MPZ P-2 H4 from Krebs (1993) together with the new tooth described here as belonging to the new species Crusafontia amoae, differing from Crusafontia cuencana (Uña upper molar, MPZ Uña 28) in their acute lingual side.

**Development of the paracrista.**—The paracrista may be strong or weak. Here we consider the paracrista to be the crest or ridge joining the paracone with the stylocone. In Crusafontia it is complete and strong, as usually the case in Dryolestida. Portopinheirodon and Laolestes goodrichi have a unique character in that they have a double paracrista, lacking the median crest described in Martin (1999).

**Development of the metacrista.**—It may be strong or weak. A strong and continuous metacrista runs from the paracone to the metastyle, also joining the metastyle and cusp “C” in the majority of Dryolestida, except e.g., Dryolestes, Comotherium, and Laolestes goodrichi, in which the metacrista is discontinuous. The metacrista is more continuous in C. cuencana than in C. amoae sp. nov., where a notch slightly separates the paracone from the metastyle.

**Development of the paracone.**—The paracone may be higher than, or subequal to, the stylar cusps. Crusafontia cuencana has a higher paracone, in relation to the stylar cusps, than Crusafontia amoae sp. nov.

**Development of the paracrista.**—It may be strongly or weakly hooked and interlocked with the preceding metastyle. Since the fossil from CC 2 is an isolated molar it is impossible to see the hooked and interlocked with the preceding metastyle. Since the Development of the parastyle Crusafontia amoae, differing from Crusafontia cuencana (Uña upper molar, MPZ Uña 28) in their acute lingual side.

**Development of the paracrista.**—The paracone may be higher than, or subequal to, the stylar cusps. Crusafontia cuencana has a higher paracone, in relation to the stylar cusps, than Crusafontia amoae sp. nov.

**Position of the paracone.**—The paracone may be labial or lingual to the stylocone. Laolestes goodrichi, Dryolestes, and Comotherium have the paracone labial to the stylocone, while in Crusafontia and Euthlastus it is lingual to the stylocone.

**Development of the stylocone.**—It may be strong or weak. The stylocone is more prominent in dryolestids than in paurodontids. Crusafontia cuencana and the new species from CC 2 have weak stylar and metacone cusps.

**Position of the stylocone.**—In some dryolestids the stylocone varies from being more anterior, in the parastylar region, to slightly more medial. Crusafontia amoae sp. nov. shares with Comotherium an anterior position of the stylocone. In Crusafontia cuencana it is nearly medial.

**Presence-absence of the metacone.**—The metacone may be absent or present. The metacone is well developed in the upper molars of Crusafontia amoae sp. nov. but weak in C. cuencana.

**Presence-absence of the metastyle.**—The metastyle may be absent or present. It is very independent in Comotherium, Dryolestes, and the South American dryolestids. In Crusafontia this stylocusp is well developed and independent too, although it is more isolated in C. cuencana than in C. amoae sp. nov. In Krebsotherium the metastyle varies in size and position from the first molar to the M8.

**Presence-absence of cusp “C”.**—Cusp “C” is present in the new species Crusafontia amoae and absent in Crusafontia cuencana. It is also present in Comotherium, Euthlastus, Henkelotherium, and probably Krebsotherium.

**Basal cingulum.**—Upper molars of Dryolestida lack a labial cingulum. Only Donodon presents a basal cingulum on the lingual side of the molar (Sigogneau-Russell 1991: fig. 3). However, the upper premolars do have a basal cingulum, well developed on the labial side, e.g., P4 of Dryolestes leiriensis. Interestingly, the dP3–dP4 of Dryolestes leiriensis lack a basal cingulum.

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**The upper premolars of Crusafontia**

Martin (1998) described premolars of several stem Cladotheria as belonging to Crusafontia cuencana. He had isolated teeth from the lower dentition from Uña, and lower and upper dentition from Galve. In this work the author proposed that a tooth from Pocamus pepelui, described by Canudo and Cuenca-Bescós (1996) as a peramurid, was an upper premolar (P4) of Crusafontia cuencana. Here we examine this synonymy, in view of the descriptions of deciduous premolars and premolars of stem Cladotheria provided by Clemens and Mills (1971), Prothero (1981), Martin (1997, 1998, 1999), Sigogneau-Russell (1999), and Kielen-Jaworowska et al. (2004) as well as our own research into the dentition of Dryolestida.

In his introduction to the description of the upper premolars of Crusafontia cuencana, Martin (1998) outlines the main features of the upper premolars of dryolestids: they are four in number, and they all have two roots; P1 and P2 are small, while P3 and P4 are large; the anterior and posterior stylar cusps give P3 and P4 a symmetrical appearance; the paracone is lingual; there is a shallow ectoflexus in P4 (the indentation in the middle of the labial side according to Martin 1998); the anterior and posterior accessory cuspules, parastyle and metastyle, are present though minute; the premolars are longer than broad. He did not mention the metacone in this general introduction, although in the description of the right upper premolar specimen (Galve Th 23) the author did mention a tiny wear facet or a primordial metacone.

The molar of Pocamus pepelui bears a prominent metacone (see discussion below). According to Martin (1998), the swelling distal to the paracone and in the posterior cutting edge (the metacrista in this work) is in just the right place for the metacone. Martin here points to the fact that in the same area a minute wear facet is present in the upper P4 of Crusafontia from Galve (Galve Th 23, Martin 1998: fig. 7). Here we
disagree with this observation because Martin in his fig. 7
blows up the supposed metacone, while in the photograph in
fig. 6 it is nearly invisible (Martin 1998: figs. 6, 7). Moreover,
when the author refers to the Guimarota Dryolestidae he de−
clares that such a swelling at the posterior cutting edge of P4 is
a variable character, and gives the example of the holotype of a
new species of Dryolestes from Guimarota, referring to his
subsequent work (Martin 1999). We do not doubt the variabil−
ity in the development of the metacone in the upper molars of
dryolestids, although the comparison is incorrect because the
holotype of the only new species of Dryolestes, D. leiriensis,
described by Martin (1999) in Guimarota, is a lower jaw with
the canine, the four premolars and the eight molars, and in this
specimen the metaconid is indeed present in p4. Yet we see
from the figures that the cusp in the position of the metacone is
present in the P4 of D. leiriensis (Martin 1999: fig. 15), though
the presence of a metacone in the upper premolars of the spe−
cies is not mentioned in the text, or in his cladistic analysis
(Martin 1999: 83).

In our earlier description of Pocamus pepelui, we de−
scribed the metacone as an incipient protocone, and cusp “C”
as the metacone. Here we emend this error, which was first
observed by Martin (1998: 127), and confirm that the two
cusps distal to the paracone are the metacone and cusp “C”,
and that the small cusp labial to cusp “C” is the metastyle
(metaconid cusp in Martin 1998).

However, we do not agree with the designation of the
tooth from Pocamus pepelui as an upper premolar of Crusa−
fontia cuencana. The upper premolars of Dryolestida are
symmetrical, with the paracone being in the middle of the
tooth, or slightly distal, while the tooth from Pocamus as well
as the upper premolars MPZ Galve Th 20 and MPZ Galve Th
23 have the paracone in an anterior or mesial position, being
asymmetrical in labial and lingual views. The descriptions of
the upper premolars in Peramus (Clemens and Mills 1971;
Kielan-Jaworowska et al. 2004) coincide, though in Peramus
the paracone of P4 is slightly less anterior than in P5. The P5
of Peramus has minute, parastylar cusps similar to the tooth
of Pocamus pepelui, originally described as the last premolar
P5 or the first molar M1 in Canudo and Cuenca-Bescós
(1996) (Fig. 6).

The ectoflexus in the upper premolars is present in some
dryolestidans such as Krebsotherium though the feature is
absent in general in premolar dentitions. The ectoflexus of
peramurans is a well-known character, less developed in the
upper premolars than in the upper molars (Sigogneau-Rus−
sell 1999), though always present. The P4 of MPZ Galve Th
23 and Pocamus have a shallow though distinct ectoflexus
(Fig. 6). The basal cingulum is present in some upper pre−
molars of Dryolestida as described above, though never in
the uppers of peramurans.

To conclude, both the premolars assigned to Crusafontia

DOI: 10.4202/app.2009.0157
cuencana by Martin (1998) as well as the previously described premolar assigned to Pocamus pepelui are here assigned to P. pepelui, tentatively classified as stem Cladotheria, superorder Zatheria incertae sedis.

Conclusions

One of the richest and most diverse levels in mammals from the Early Cretaceous of the Iberian Peninsula is the upper part of the El Castellar Formation, terminal Hauерtian–basal Barremian in age. Several sites from this level are known in Galve (Colladico Blanco, Pelejón 2 and Cuesta Corrales 2). This paper includes description of a new species of Dryolestida, Crusafontia amoae, on the basis of two isolated upper molars: one M4 or M5 from the site of CC 2, and the M6 or M7 from the site of Pelejón 2 studied by Krebs (1993) and originally assigned by this author to the species Crusafontia cuencana, the closest species to it in morphological, geographical and biostratigraphical terms. The main differences between C. cuencana and C. amoae sp. nov. are: the larger size of C. amoae, its mesially protruding and rounded parastyle in relation to the stylocone, the larger mesial wear facet on the parastyle, the pointed and more lingually placed slope of the paracone, the wider ectoflexus, and the presence of a notch in the metastylocone in distal view. Also notable is that the geological age of the two species differs by at least two million years.

The premolars assigned to Crusafontia cuencana by Martin (1998) as well as the previously described premolar assigned to Pocamus pepelui are here assigned to P. pepelui, tentatively classified as stem Cladotheria, superorder Zatheria incertae sedis.

As such, the stem cladotherian record from the Early Cretaceous of the Iberian Peninsula is composed of at least three different taxa: two species of Crusafontia, the known C. cuencana and C. amoae sp. nov described here, and Pocamus pepelui, each from a different stratigraphic level and age.

Acknowledgements

Rupert Glasgow (Zaragoza, Spain) revised and improved the English version of the text. The manuscript has been greatly improved thanks to the skilful work of the reviewers, Guillermo Rougier (University of Louisville, Louisville, USA), José Ignacio Ruiz Omeñaca (Museo Jurasico de Asturias, Colunga, Spain), and the editor Richard Cifelli (University of Oklahoma, Norman, USA). This paper forms part of the projects CGL2007-62469, CGL2010-16447, subsidized by the Ministry of Science and Innovation of Spain, the European Regional Development Fund, the Government of Aragon (“Grupos Consolidados” and “Dirección General de Patrimonio Cultural”). AB acknowledges support from the Programa Juan de la Cierva of the Ministry of Education and Science. JMG and MM are supported by the grants of the Diputación General de Aragón.

References


doi:10.4202/app.2009.0157