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New dryolestidan mammal from the Hauterivian–Barremian transition of the Iberian Peninsula

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Crusafontia amoae sp. nov. (Dryolestida, Stem Cladotheria) is represented by two isolated upper molars (M4 or M5 and M6 or M7) from the terminal Hauterivian–basal Barremian (Early Cretaceous) of the El Castellar Formation (Galve, Spain). The molars have a deep ectoflexus, a distinct metacone, a continuous metacrista, and an antero-lingually placed paracone. They differ from the molars of the other species of the genus, *Crusafontia cuencana*, by their larger size, by their outsized parastyle, by the pointed lingual slope of the paracone, their more symmetrical appearance with a deep ectoflexus in occlusal view, and the well-developed metacone. Revision of three isolated teeth previously attributed to *Crusafontia cuencana* suggests that instead of being upper premolars belonging to *Crusafontia cuencana* they in fact belong to *Pocamus pepelui*, of the stem cladotherian superorder Zatheria, probably “peramuran”. As such, the stem Cladotheria record from the Early Cretaceous of the Iberian Peninsula is composed of two dryolestids (*Crusafontia amoae* and *Crusafontia cuencana*) and one zatherian (*Pocamus pepelui*).

Key words: Mammalia, Cladotheria, Dryolestida, *Crusafontia*, systematics, Cretaceous, Iberian Peninsula.

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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 “symmetrodontans”, with a reversed-triangle molar pattern like *Spalacotherium* and their kin, and the apomorphic tribosphenic mammals, with the triangle-molar pattern of metatherians and eutherians (Kielan-Jaworowska et al. 2004). The molars of Stem Cladotheria share with symmetrodontans the reversed-triangle molar pattern, though the upper molars are wider than the lower ones, having a third (lingual) root and the labial styler 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; Guimarães 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

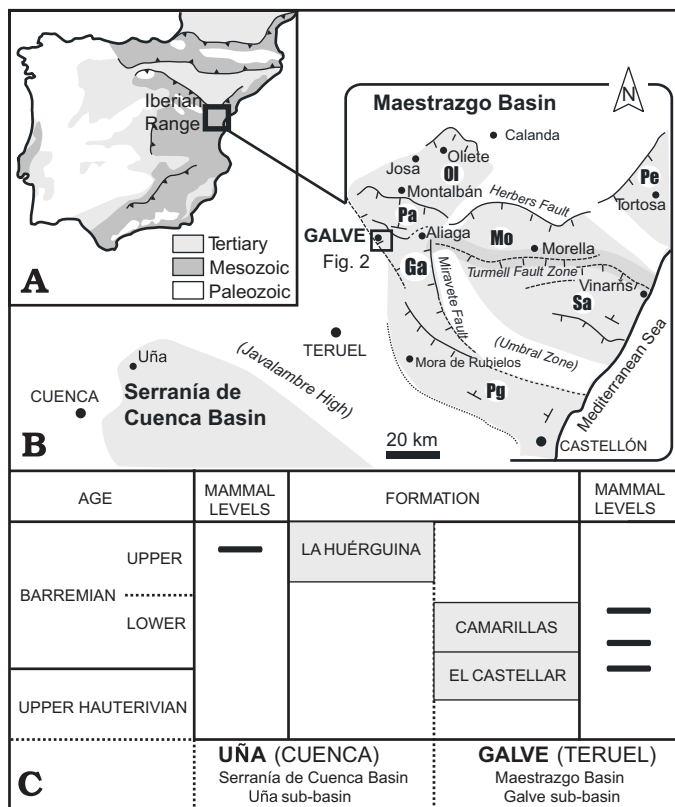


Fig. 1. Geographical and geological setting of Galve (Teruel, Spain). **A.** Simplified geological map of the Iberian Peninsula. **B.** Palaeogeographic sub-basins within the Maestrazgo Basin and active faults during Early Cretaceous sedimentation, modified from Salas et al. (2001), and the palaeogeographical—and 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.

mammalian site of Galve is Poca, in the upper layers of the Camarillas Formation. The mammals described are the dryolestid *Crusafontia cuencana* Henkel and Krebs, 1969 at the sites of Galve Th and Pelejón 2, and the peramurid *Pocamus pepelui* Canudo and Cuenca-Bescós, 1996 at the site of Poca. The species *Crusafontia cuencana* was first discovered and described by Henkel and Krebs (1969) in the late Barremian site of Uña in the province of Cuenca (La Huérguina Limestone Formation, the Serranía de Cuenca Basin; see Buscalioni et al. 2008 for a bibliography). Between the terminal Hauterivian–basal Barremian of the El Castellar and Camarillas formations, and the late Barremian of the La Huérguina Formation, there is a span of around 2 Ma.

Multituberculate and “symmetrodontan” mammals have also been described from the Galve area (Crusafont-Pairó and Adrover 1966; Crusafont and Gibert 1976; Hahn and Hahn 1992, 2002; Canudo and Cuenca-Bescós 1996; Badiola et al. 2009, 2011). The only species of Early Cretaceous Iberian “symmetrodontan” mammal, *Spalacotherium henkeli* Krebs, 1985, was found at the site of Colladico Blanco

(Krebs 1985) in the upper levels of the El Castellar Formation, terminal Hauterivian–basal Barremian in age (Canudo and Cuenca-Bescós 1996). Near the Galve syncline in the province of Teruel, other Mesozoic mammals have been described (Cuenca-Bescós and Canudo 2003; Badiola et al. 2008).

Recently, a new dryolestid upper tooth has been found in the El Castellar Formation. In this paper, it is assigned to a new species of *Crusafontia*. The aim of this paper is twofold, on the one hand a description of this new species of Dryolestida from the Hauterivian–Barremian transition of the Galve area, and on the other hand a revision of the premolars of stem cladotherians, especially those assigned to *Crusafontia cuencana* from several localities of the Early Cretaceous of Galve.

Institutional abbreviation.—MPZ, Museo de Paleontología de la Universidad de Zaragoza.

Other abbreviation.—CC 2, Cuesta Corrales 2.

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 Hauterivian–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 syn-rift 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 Hauterivian (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-

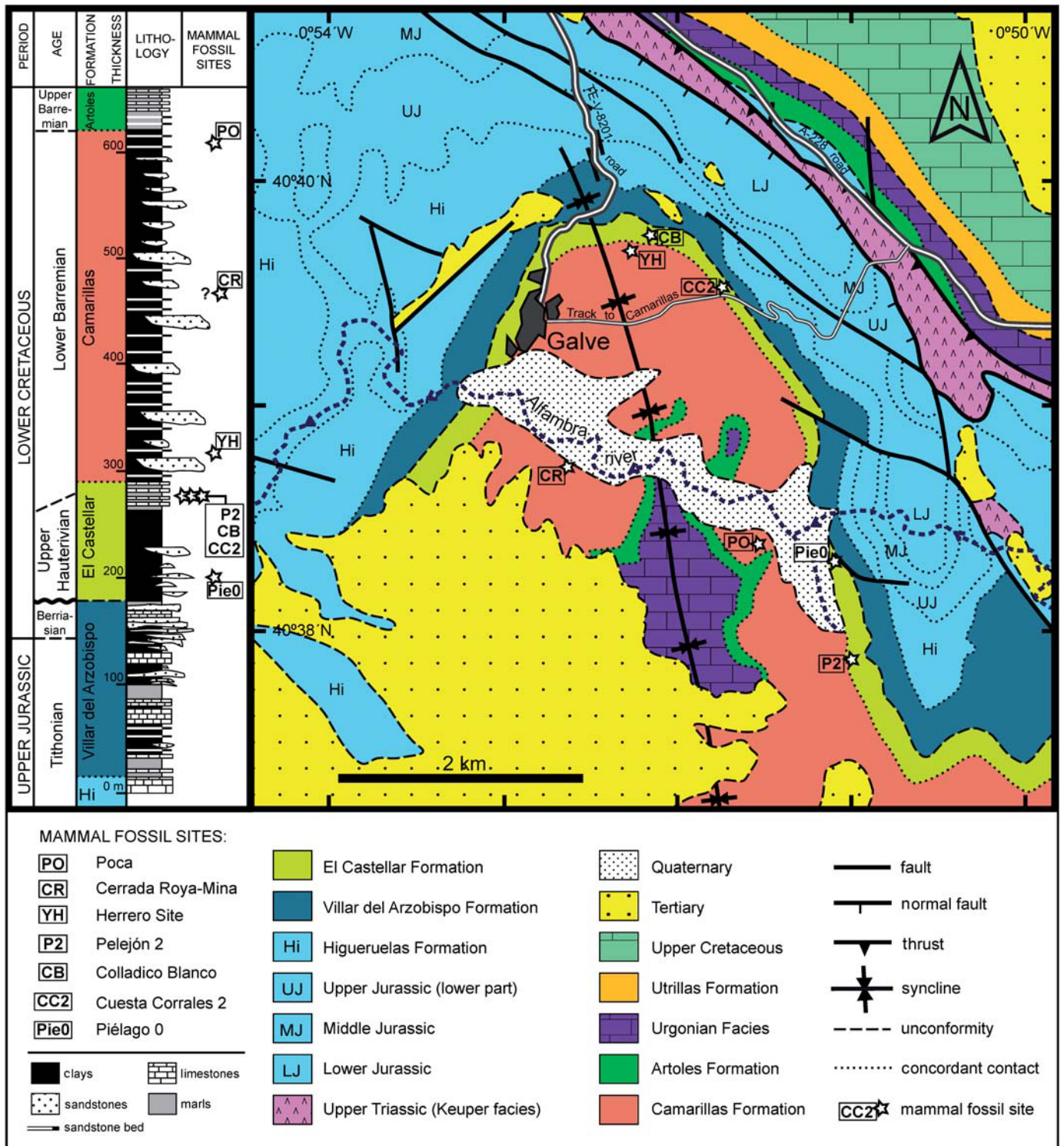


Fig. 2. Geological setting of the Mesozoic mammal fossil sites from the Galve area. Stratigraphy of the Wealden facies and geological mapping of the Galve syncline (modified from Díaz Molina and Yébenes 1987).

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, Piélago 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 Prismoolithidae, 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 Sanchiz 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; Martín-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 amoa sp. nov.

Fig. 3.

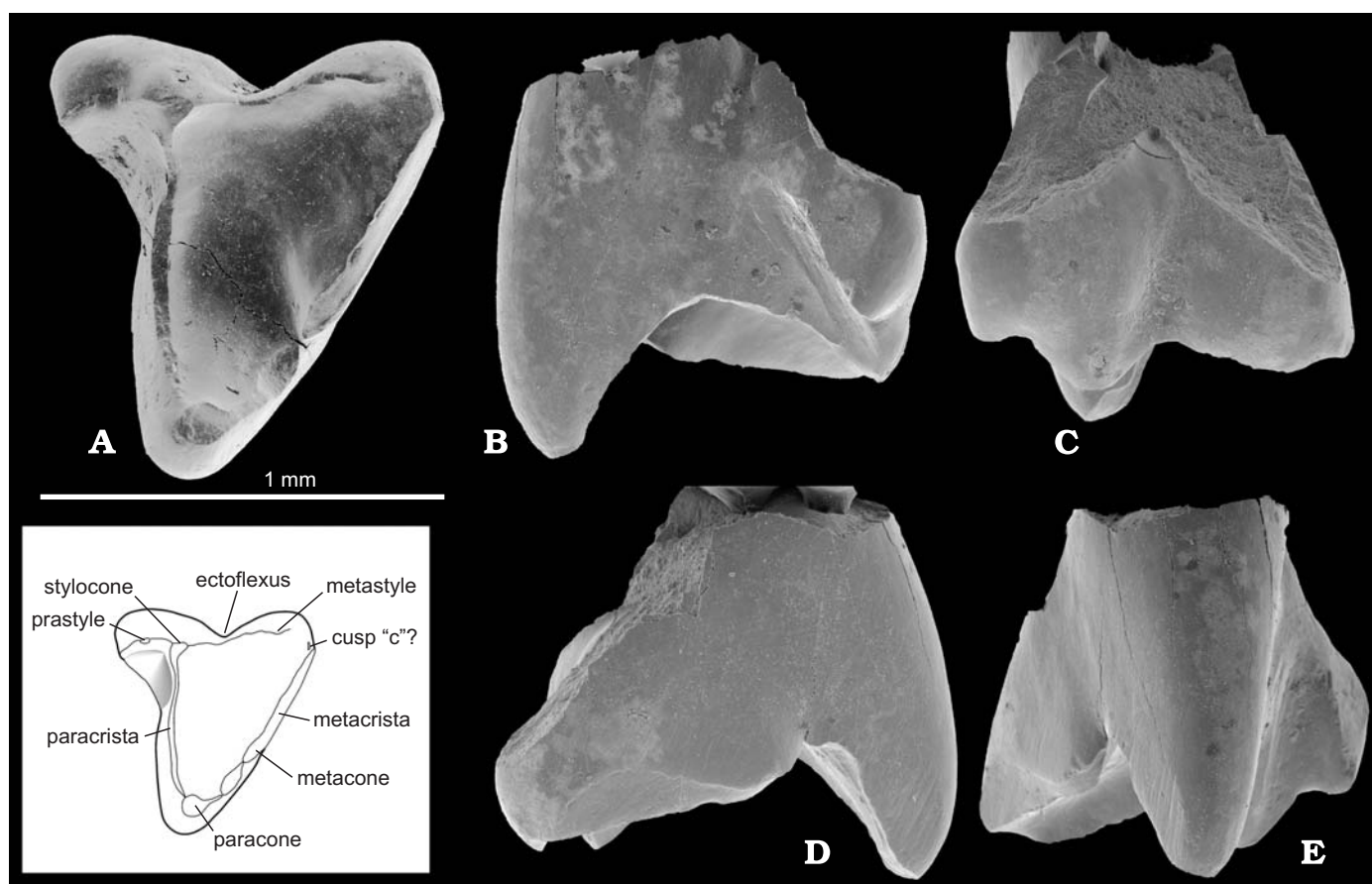


Fig. 3. Dryolestidan mammal *Crusafontia amoa* sp. nov., MPZ CC2-1 M4 or M5, holotype, from the site of Cuesta Corrales 2, Colladico Blanco level, El Castellar Formation, Galve, Teruel, Spain in, occlusal (A), mesial (B), labial (C), distal (D), and lingual (E) views. The schematic drawing of *C. amoa*,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

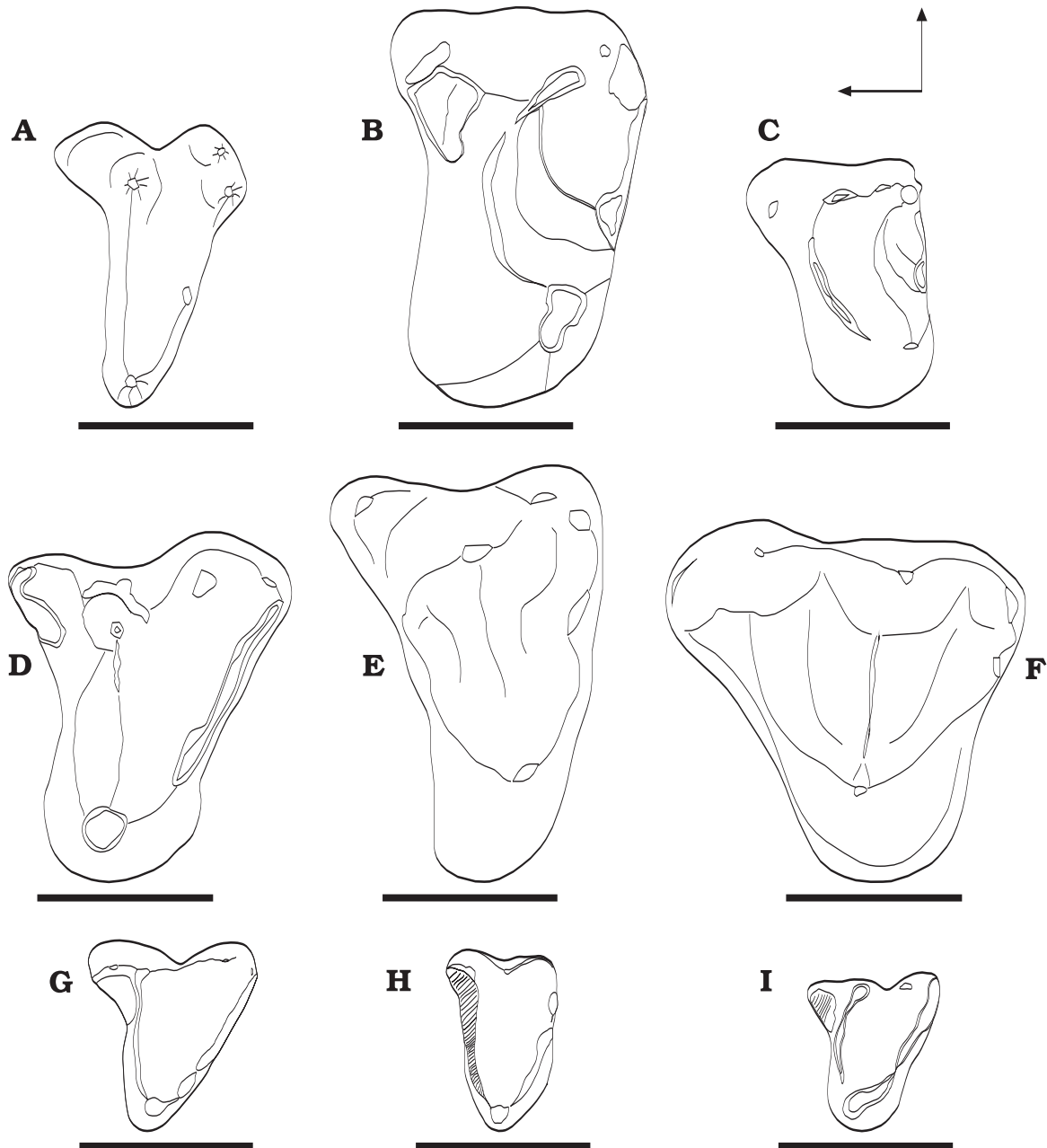


Fig. 4. Drawings of Dryolestida left upper-molar, modified from the original descriptions. A–C, Kimmeridgian; D–F, Tithonian–Berriasian; G–H, early Barremian; I, late Barremian. **A.** Left M4 or M5 of *Comotherium richi* Prothero, 1981, from the Upper Jurassic Morrison Formation, Como Bluff locality, Wyoming, USA. **B.** Right M5, reversed, of *Dryolestes leiriensis* Martin, 1999, from Guimarota, Portugal. **C.** Left M6 of *Krebsotherium lusitanicum* Martin, 1999, from Guimarota, Portugal. **D.** Right M4 or M 6 (reversed) of *Portopinheirodon asymmetricus* Martin, 1999, Porto Pinheiro, Lourinha, Portugal. **E.** Right M5 (reversed) of *Laolestes andresi* Martin, 1999, from Porto Pinheiro, Lourinha, Portugal. **F.** Right upper molar of *Donodon perscriptoris* Sigogneau-Russell, 1991, Anoual, Morocco. **G.** Left M4 or M 5 of *Crusafontia amoae* sp. nov., holotype, Cuesta Corrales 2, El Castellar Formation, Galve, Teruel, Spain. **H.** Right M6 or M 7 (reversed) of *Crusafontia amoae* sp. nov., first described as upper molar of *Crusafontia cuencana* by Krebs (1993), P-2 H4 Pelejón 2, Galve, Teruel, Spain. **I.** Left M2 or M3, of *Crusafontia cuencana* Henkel and Krebs, 1969, Uña, La Huérguina Formation, Cuenca, Spain, (from Krebs 1993). Scale bars 1 mm.

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.

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

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 parasyle 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 paracone.

Differential diagnosis.—*Crusafontia amoa* 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 linguallly 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 metacrista in distal view. As in *Comotherium richi* and *Crusafontia cuencana*, no cusps or ridges are found in the trigon basin, unlike other Dryolestida.

Description.—MPZ CC2-1 is an upper left molar (L, 0.98; W, 1.11; H, 0.91), probably a M4 or M5 in position in view of its well-developed parastylar region. We rule out the possibility of it being a premolar or a deciduous tooth because it is enlarged labio-lingually and because of the presence of a lingual root (though broken). The molar is triangular in occlusal view, with rounded corners and with a narrower, pointed lingual part (Fig. 3A). There is a conspicuous medial

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 parastyle is large, and slightly less elevated compared with the stylocone; the parastylar region is enlarged, forming a parastylar wing. There are two transversal crests, the paracrista and the metacrista. 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 amoa* 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*

Table 1. Stem Cladotheria taxa mentioned in this work.

Taxa	Geographic situation	Age
<i>Leonardus cuspidatus</i> Bonaparte, 1990	Los Alamitos Fm., Argentina	Campanian
<i>Crusafontia cuencana</i> Henkel and Krebs, 1969	Uña, Colladico Blanco, Spain	late Barremian
<i>Pocamus pepelui</i> Canudo and Cuenca-Bescós, 1996	Poca, Camarillas Fm., Spain	early Barremian
<i>Crusafontia amoa</i> sp. nov.	Cuesta Corrales 2, Pelejón 2, Castellar Fm.; Yacimiento Herrero, Camarillas Fm., Spain	late Hauterivian–early Barremian
<i>Afriquiamus nessovi</i> Sigogneau-Russell, 1999	Annoual, Morocco	Berriasian?
<i>Donodon perscriptoris</i> Sigogneau-Russell, 1991	Annoual, Morocco	Berriasian?
<i>Laolestes andresi</i> Martin, 1997	Porto Pinheiro, Portugal	Jurassic–Cretaceous boundary
<i>Portopinheirodon asymmetricus</i> Martin, 1999	Porto Pinheiro, Portugal	Jurassic–Cretaceous boundary
<i>Peramus tenuirostris</i> Owen, 1871	Lulworth Beds, Durlston Bay, UK	Tithonian–Berriasian
<i>Laolestes</i> (= <i>Melanodon</i>) <i>goodrichi</i> (Simpson, 1929)	Morrison Fm., USA	Kimmeridgian
<i>Dryolestes</i> (= <i>Herpetairus</i>) <i>priscus</i> Marsh, 1878	Morrison Fm., USA	Kimmeridgian
<i>Dryolestes leiriensis</i> Martin, 1999	Guimarota, Portugal	Kimmeridgian
<i>Krebsotherium lusitanicum</i> Martin, 1999	Guimarota, Portugal	Kimmeridgian
<i>Comotherium richi</i> Prothero, 1981	Morrison Fm., USA	Kimmeridgian
<i>Drescheratherium acutum</i> Krebs, 1998	Guimarota, Portugal	Kimmeridgian
<i>Euthlastus cordiformis</i> Simpson, 1927	Morrison Fm., USA	Kimmeridgian
<i>Henkelotherium guimarotae</i> Krebs, 1991	Guimarota, Portugal	Kimmeridgian
<i>Tathiodon agilis</i> Simpson, 1927	Morrison Fm., USA	Kimmeridgian

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 dryolestidans (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

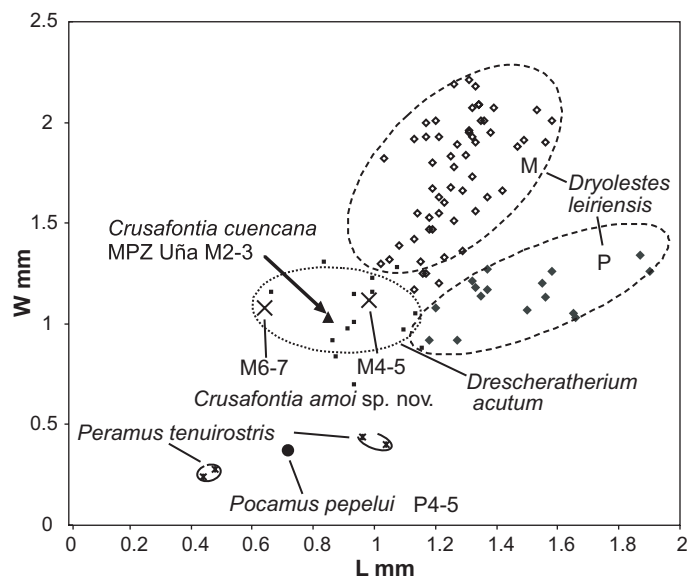


Fig. 5. Stem Cladotheria measurements of upper premolars (P) and molars (M). *Pocamus* is represented by a P5. The grouping to the left of *Peramus tenuirostris* are the anterior premolars, P2 and P3, while the second grouping represent the posterior most premolars P4 and P5. *Drescheratherium acutum* is represented by molars.

parastyle projects more mesially, as in *Comotherium*. It differs from the latter in having a complete metacrista 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 indentation 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 metacrista 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 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

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 amoe*, 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 metacone 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. amoe* sp. nov., where a notch slightly separates the paracone from the metacone.

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 amoe* sp. nov.

Development of the parastyle.—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 degree of interlocking. The parastyle is quite hooked, as in *Comotherium*. The upper molar of *Crusafontia* from Uña has a slightly weaker parastyle. The South American dryolestids and *Laolestes* have very reduced parastyles or no parastyle at all.

Position of the parastyle.—The parastyle may be labial or lingual to the stylocone. *Laolestes goodrichi*, *Dryolestes*, and *Comotherium* have the parastyle 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 amoe* 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 amoe* 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 *Crusa-*

fontia this stylar cusp is well developed and independent too, although it is more isolated in *C. cuencana* than in *C. amoe* 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 amoe* 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.

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 Kielan-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

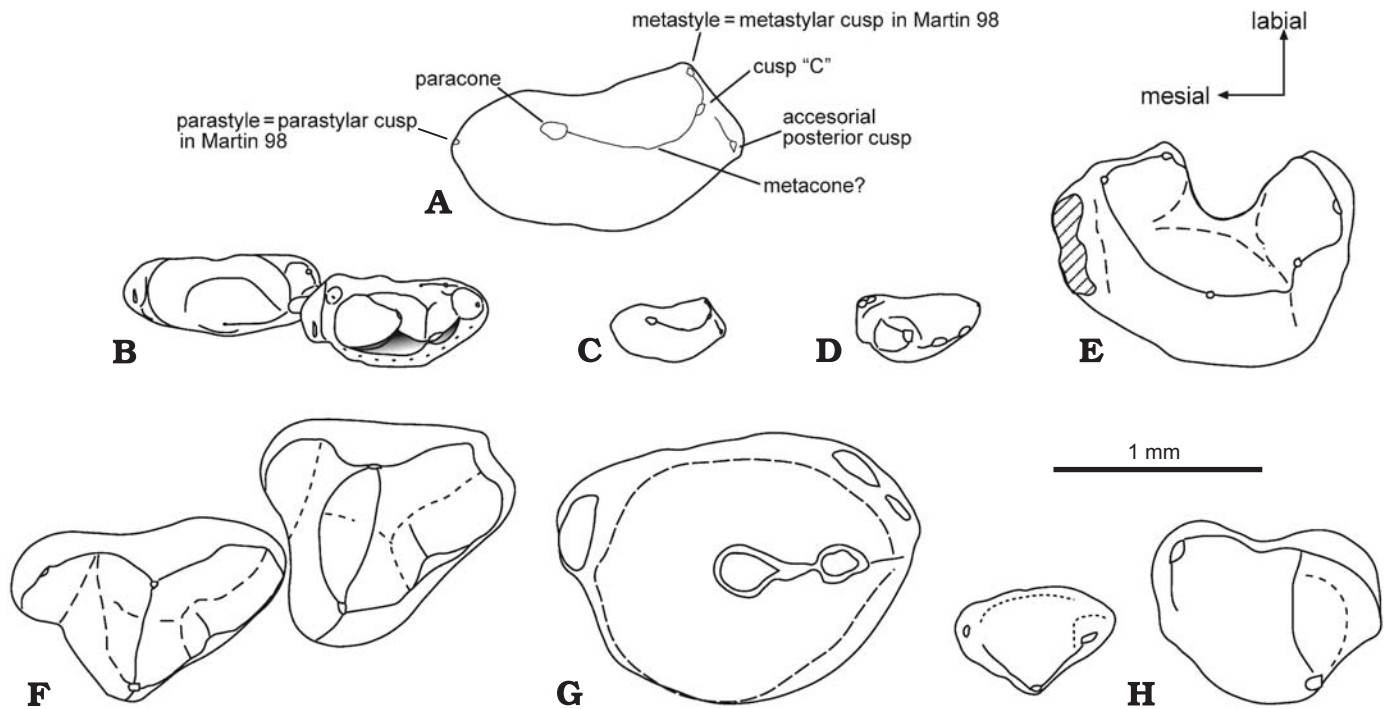


Fig. 6. Drawings of premolars modified and assigned to dryolestids in Martin (1998). **A.** Nomenclature of the “peramuran” premolars. **B.** Left P4 and P5 of *Peramus tenuirostris* modified after Clemens and Mills (1971). **C.** Right P4 here assigned to *Pocamus pepelui* Galve Th 23, reversed, modified after Martin (1998). **D.** Right P5 of *Pocamus pepelui* (holotype) from Poca, modified after Canudo and Cuenca-Bescós (1996). **E.** Left upper molar of *Afriquiamus nessovi*, modified after Sigogneau-Russell (1999). **F–H.** Deciduous premolars (dP) and premolars of Dryolestida for comparison with those of “Peramurans”. **F.** Right dP3–4 of *Dryolestes leiriensis* (reversed) modified after Martin (1997, 1999). **G.** Right P4 of *Dryolestes leiriensis* (reversed) modified after Martin (1999). **H.** Left P3 and P4 of *Krebsotherium lusitanicum* modified after Martin (1999). Note that the molars are all drawn with the mesial side to the left; thus some are reversed drawings.

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 declares 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 variability 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 species is not mentioned in the text, or in his cladistic analysis (Martin 1999: 83).

In our earlier description of *Pocamus pepelui*, we described 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 (metastylar cusp in Martin 1998).

However, we do not agree with the designation of the tooth from *Pocamus pepelui* as an upper premolar of *Crusafontia 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-Russell 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 premolars of Dryolestida as described above, though never in the uppers of peramurans.

To conclude, both 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.

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 Hauterivian–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 metacrista 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.

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