Cainotheriidae (Mammalia, Artiodactyla) from Dams (Quercy, SW France): phylogenetic relationships and evolution around the Eocene–Oligocene transition (MP19–MP21)

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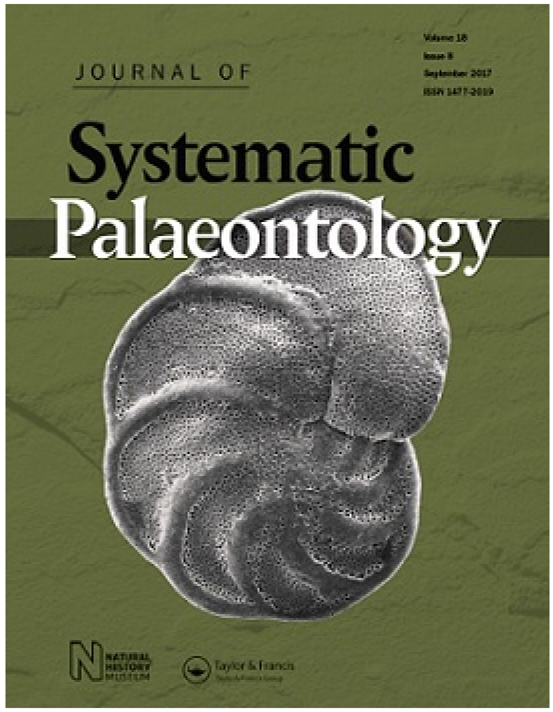

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Running title: Cainotheriidae from Dams, Quercy

Abstract:

Cainotheriids are a family of small artiodactyls, known in the fossil record from the late Eocene to the middle Miocene in Western Europe. Contrary to several European endemic ungulate groups that became extinct at the end of the Eocene or close to the Eocene-Oligocene transition (*Grande Coupure*), cainotheriids crossed this boundary and diversified during the Oligocene. The evolutionary history of cainotheriids around the Grande Coupure remains poorly documented and only a few works deal with the modalities of their evolution, notably because of the scarcity of available Eocene remains. A new fossiliferous karstic network named Dams was discovered during field prospections in the Quercy area (Tarn-et-Garonne, France).

It notably displays two infillings that yielded a great abundance of cainotheriid remains, namely DAM1 (MP19, late Eocene) and DAM3 (MP22, early Oligocene), bracketing the Eocene–Oligocene transition. A detailed study of cainotheriid mandibular and dental remains from these infillings reveals that only *Paroxacron valdense* occurs at DAM1, while five species are found in DAM3. The karstic network at Dams seemingly records a local taxonomic diversification of cainotheriids after the Grande Coupure, with Cainotheriinae being particularly successful. Our phylogenetic analysis, including cainotheriids from Dams, constitutes the first formal phylogeny of Cainotheriidae. Our results, based on mandibular and dental characters, allow for (i) clarifying relationships within Cainotheriidae (ii) erecting a new family Robiacinidae, as being the sister taxon to Cainotheriidae among Cainotherioidea and, more broadly, (iii) discussing the controversial position of Cainotheriidae within Artiodactyla, as being more closely related to Ruminantia than to Tylopoda.

Keywords: Grande Coupure, Quercy karstic infillings, Western Europe, deciduous dentition, morpho-anatomical phylogeny, faunal turnover.

Introduction

Cainotheriids are a family of small artiodactyls, known from the late Eocene to the middle Miocene in Western Europe (Blondel 2005). This family is composed of two sub-families and at least five genera (Blondel 2005): Oxacroninae Hürzeler, 1936, with *Oxacron* Fihol, 1884 and *Paroxacron* Hürzeler, 1936; and Cainotheriinae Camp & VanDerHoof, 1940, with *Plesiomeryx* Gervais, 1873, *Caenomeryx* Hürzeler, 1936, and *Cainotherium* Bravard, 1828. Their size range is variable, from small rabbit-sized species (e.g., *Oxacron*, *Paroxacron*) to a size slightly smaller than the extant tragulid ruminant *Tragulus javanicus* (Theodor 2010) (e.g., *Cainotherium*). Cainotheriids are characterised by brachydont selenodont molars. The upper molars bear five cusps arranged in a unique '*Cainotherium* plan' (Stehlin 1906), resulting from a posterior migration of the protocone (Erfurt & Métais 2007). Upper molars therefore have two anterior cusps (paracone and paraconule), and three posterior ones (metacone, metaconule, protocone).

Like many mammalian species, several European endemic ungulates became extinct at the end of the Eocene (Sudre & Legendre 1992; Blondel 2001), or close to the Eocene-Oligocene transition. This major mammalian faunal turnover, called the Grande Coupure (Stehlin 1910), is linked to climatic, geographic and oceanic circulation changes (Legendre 1987; Berggren & Prothero 1992; Akhmetiev & Beniamovski 2009). Unlike most other endemic artiodactyl taxa, cainotheriids crossed the Eocene-Oligocene boundary and diversified during the Oligocene (Blondel 2005). However, the evolutionary history of cainotheriids around this transition remains poorly documented and understood. Indeed, only few studies (Legendre 1980; Hooker & Weidmann 2000) are dedicated to Eocene cainotheriids and deal with the modalities of their evolution. This is primarily due to the apparent monotony of their dental characters and to the scarcity of cainotheriid remains documented in pre-Grande Coupure localities.

Knowledge of most cainotheriid genera (e.g *Oxacron*, *Plesiomeryx*, or *Caenomeryx*) principally relies on material collected from the Phosphorites karstic fillings from Quercy (southwestern France) during the last century (Blondel 2005). This fossiliferous area yielded an unparalleled fossil record with over 170 localities recording local faunal assemblages with a very short time intervall of ~1 million years or less (Aguilar *et al*. 1997, Escarguel *et al*. 2008), and a continuous record spanning the 38–26 Ma interval (late Eocene to late early Oligocene). In 2016, a new fossiliferous karstic network named "Dams" was discovered during field prospecting in the Quercy area (Tarn-et-Garonne, France). This karstic network was partly curated during the extensive phosphate exploitation in Quercy during the late 19th century. The Dams network however still houses a great quantity of clay infillings and preserves several fossiliferous channels distinct in age. Specifically, two fossiliferous infillings, named DAM1 and DAM3, yielded a great amount of cainotheriid remains. Thanks to a low-energy transport, osseous and dental material is particularly well preserved, and the smallest and most delicate dental elements are documented, including incisors and deciduous dentition. Biochronological dating of Dams fossiliferous infillings builds on their rodent assemblages; morphological analyses of their dental and cranial remains from Quercy localities have allowed for identification of several chronospecies (lineages), characterised by evolutionary changes in the dental features of related species (e.g. Schmidt-Kittler & Vianey-Liaud 1987; Vianey-Liaud 1974, 1976, 1979, 1998, 2015; Vianey-Liaud *et al*. 1995; Vianey-Liaud & Ringeade, 1993; Vianey-Liaud & Schmid 2009). They have proved to be reliable biochronological markers (e.g. Aguilar *et al*. 1997). Rodents, especially theridomorphs, are abundant in the Dams material. The assemblages found in the different Dams infillings indicate that they bracket the Eocene-Oligocene transition (see Material and Methods section for more details). Dams therefore provides an unprecedented window on cainotheriid evolution, before and after the Grande Coupure, i.e. a time interval experiencing a dramatic faunal turnover under drastic environmental changes.

This work builds principally on the exceptionally abundant cainotheriid material from DAM1 (MP19, pre-Grande Coupure) assigned here to the single species *Paroxacron valdense*. This material allows to revise and complete the diagnosis of this species and to describe for the first time the complete deciduous and permanent dentition of Cainotheriidae. Study of the less abundant, but more diverse post-Grande Coupure material of DAM3, allows for discussion the diversity dynamics of cainotheriids across the Eocene-Oligocene transition.

The phylogenetic position of Cainotheriidae within Artiodactyla remains an open question. They present a mosaic of plesiomorphic characters (unfused tarsals, complete digits II and V, complete dentition) and autapomorphies (selenodont molars with unique '*Cainotherium*' plan) (Theodor 2010), making their phylogenetic affinities difficult to assess. According to Romer (1966) Cainotheriidae would be placed within Tylopoda, together with Anoplotheriidae, Xiphodontidae, and Amphimerycidae. Webb & Taylor (1980) subsequently removed them from Tylopoda; while Gentry & Hooker (1988) supported placement of cainotheriids within Tylopoda in their 'preferred analysis' (manual, Gentry & Hooker 1988, fig. 9.8). However, the results of their formal analysis (using PAUP (Swofford 1984), Gentry & Hooker 1988, fig. 9.7) retrieved them in a much more basal position, outside of the "Selenodontia" clade (i.e., Tylopoda + Ruminantia). More recent phylogenetic analyses placed them either close to Tylopoda (Geisler & Uhen 2003, Geisler *et al*. 2007, Thewissen *et al*. 2007) or as an early offshoot of a wide clade including Ruminantia (Geisler & Uhen 2005; O'Leary & Gatesy 2007, Lihoreau *et al*. 2015). The revision of the dental nomenclature of cainotheriids performed in this work sets a sound basis for their inclusion in phylogenetic studies at the Artiodactyla level and identifies for the first time their closest relatives. Based on the abundant

Dams cainotheriid material, we here perform the first formal phylogenetic analysis of the family, in order to support the systematic framework and to discuss the phylogenetic affinities of Cainotheriidae.

Material and Methods

Material

In order to document and compare the exceptionally abundant cainotheriid dental remains from DAM1, we selected and measured 270 specimens. In addition to this material from DAM1, 152 specimens were also selected from the less abundant material of DAM3. The assignment of different species in DAM3 relies principally on morphological features of the premolars and size criterion. The attribution of several isolated specimens (mainly molars) remains uncertain. In this work we compare cainotheriid remains from Dams [DAM1 (MP19), DAM3 (MP22)] with material from other late Eocene and Oligocene fossiliferous localities of Quercy. All specimens from Dams are housed in the collection of Montpellier University, as other artiodactyl species used in this work, except for *Cainotherium laticurvatum* from the Museum d'Histoire naturelle de Toulouse. These taxa were scored through direct observation by RW. Only *Anoplotherium latipes*, *Parvitragulus priscus*, *Paratoceras coatesi*, and *Eotylopus reedi* were scored from the literature (see Phylogenetic analysis section).

The age of the material described here was determined using rodent species associations in the two loaclities DAM1 and DAM3. The assemblage documented in DAM1 consists in the co-occurrence of *Patriotheridomys altus* Vianey-Liaud, 1974 and *Suevosciurus* cf. *minimus* (Major 1873), pointing to a late Priabonian age. It corresponds to the Mammalian Paleogene (MP) reference level MP19. The specific diversity retrieved in DAM3 is higher with five associated taxa: *Sciuromys cayluxi* Schlosser, 1884; *Pseudoltinomys major* Vianey-Liaud, 1976; *Issiodoromys medius* Vianey-Liaud, 1976; *Blainvillimys gregarius* Schlosser, 1884; *Toeniodus curvistriatus* Pomel, 1853. This association points to MP22, coinciding with an early Rupelian age.

Methods

Measurements. Measurements (millimetres) were taken using a mesuroscope Nikon 10. The global surface of the tooth is expressed through: L, the maximal mesio-distal length; l, the maximal bucco-lingual dimension. The bucco-lingual aspect of the tooth is also expressed through two measurements: lp, maximal width of posterior lobe of the teeth; la, maximal width of anterior lobe. The height (h) corresponds to the maximal height of the crown. L3 and l3 respectively correspond to maximal length and width of the third lobe (distal) of the lower M3. Lam, corresponds to the maximal length of the third lobe of the lower DP4. Finally, some diastemata lengths or premolar rows have been estimated based on alveoli when one of the teeth was missing. The variability of dental measures is estimated by the variation coefficient (V).

Phylogenetic analysis. In order to discuss cainotheriid systematics and the position of Cainotheriidae within Artiodactyla, we performed a phylogenetic analysis including representatives of all cainotheriid genera, as well as representatives of Tylopoda, Ruminantia, and European endemic artiodactyl taxa and retrieved closely related to cainotheriids in previous studies. 23 artiodactyl species were included as operational terminal units among which eight constitute the ingroup Cainotheriiidae: *Paroxacron valdense*, *Paroxacron bergeri*, *Oxacron courtoisii*, *Plesiomeryx huerzeleri*, *Plesiomeryx cadurcensis*, *Caenomeryx procommunis*, *Caenomeryx filholi*, *Cainotherium laticurvatum*; thirteen species stand for the branching group (Antoine 2002, Orliac *et al*. 2010) which consists in members of Ruminantia (*Parvitragulus priscus*, *Lophiomeryx chalaniati*, *Archaeomeryx optatus*), Tylopoda (*Paratoceras coatesi*, *Eotylopus reedi*) and taxa of disputed phylogenetic position (*Robiacina minuta*, *Robiacina* *quercyi*, *Robiacina lavergnensis*, *Dacrytherium ovinum*, *Anoplotherium latipes*, *Mixtotherium cuspidatum*, *Amphimeryx murinus*, *Xiphodon castrense*); two species form the outgroup: *Eurodexis russelli* and *Dichobune leporina*. Dental characters (Dataset. S1) and taxa/characters matrix (Dataset. S2-3) provided in the Supplementary Online Material (S). 44 are original and 29 are based on or modified from previous analyses. Character coding is based on direct observations of specimens and on illustrations and descriptions from the literature: Stehlin (1908); Matthew & Reed (1910); Hürzeler (1936); Berger (1959); Emry (1978); Sudre (1978); Gentry & Hooker (1988); Erfurt & Métais (2007); Hooker (2007); Hooker & Weidmann (2000); Rincon *et al*. (2015). The matrix of characters was established with the software NDE 1.0 (Page 2001). Phylogenetic analysis was performed with PAUP* logicial version 4.0a161 (Swofford 2002), using a heuristic search (>12 taxa) with TBR algorithm, at 1000 repetitions (10 trees retained by repetition).

Dental nomenclature (Fig. 1-2)**.** The nomenclature of Boisserie *et al*. (2010) was used in this work to name crests/cristids. That of VanDerMade (1996, fig. 6) and Boivin *et al*. (2018) is used for deciduous dentition. The nomenclature of incisors was inspired from VanDerMade (1996, fig. 13). The justification of cusp/cuspids names is provided in the Discussion section.

Abbreviations

MX/: upper molars; M/X: lower molars; PX/: upper premolars; P/X: lower molars; DX: deciduous teeth; BSP: Bayerische Staatssammlung für Paläontologien, München, Germany; DAM1, DAM3: localities of Dams; MNHN: Muséum national d’histoire naturelle, Paris, France; NMB: Naturhistorisches Museum Basel, Switzerland.

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758

Order **Artiodactyla** Owen, 1848

Superfamily **Cainotherioidea** Camp & VanDerHoof, 1940

Emended Diagnosis. Small artiodactyls with large auditory bullae and large orbits. Paracone and metacone sub-equal on P3/; hypoconid small on P/2-P/3; postprotoconulid present. Mesoconid small to large on the lower molars; entoconid slightly more to more distal than the hypoconid. Protocone sub-central to distal on the upper molars and lingual with respect to the paraconule position on M3/.

Remarks. The justification for using the super-family Cainotherioidea is provided in the following section and ensues the results of phylogenetic analysis.

Family **Cainotheriidae** Camp & VanDerHoof, 1940

Emended Diagnosis. Cainotherioidea with a size ranging from small rabbit-sized species (e.g., *Oxacron*, *Paroxacron*) to slightly smaller than the extant tragulid ruminant *Tragulus javanicus* (e.g., *Cainotherium)*. Complete postorbital bar; enlarged bullae and orbits; morphology of the lower jaw variable within the family but tends to become massive and deepen posteriorly in some genera. Presence of diastemata within the premolar row in the Eocene species and tend to be reduced or lost (*Cainotherium*) in the Oligocene and Miocene forms. Lower incisors with two endocristulids; lower canine incisiform. Mesial premolars narrow; P/4 tends to be molarized; P1/ and P2/ without mesial lobe; P3/ triangular and labially concave, with a lingual cusp; P4/ subrectangular. Crowns of cheek teeth moderately high. Lower molars with a large medio-lingual metaconulid; entoconid very distal and close to hypoconulid; neotrigonid (Sudre 1977) present; absence of hypoconulid on M/1 and M/2. Upper molars sub-triangular to quadrangular with a W-shaped ectoloph and crescent-shaped lingual cusps; protocone disto-lingual and paraconule mesiolingual; postprotocrista long and distally orientated; postparacristula present; lack of preprotocrista and paraconule junction. Limbs tetradactyl with a reduction of lateral digits (II and V); forelimb shorter than hindlimb; tail long.

Subfamily **Oxacroninae** Hürzeler, 1936

Emended Diagnosis. Small cainotheriids, comprised around 400g (e. g. *Oxacron courtoisii*) – 900g (e. g. *Paroxacron bergeri*). Muzzle generally elongated and narrow; orbits large with respect to the small size of the skull; ethmoidal fissures absent. Diastemata present (except *P. bergeri*), between P/1-P/2, P/2-P/3 and P1/-P2/. Premolars narrow; postprotoconulid weak; protocone more mesial than paracone on P4/; P/1 biradiculate. Upper molars subtriangular to quandrangular (e. g. *P. bergeri*); styles without crest and mesostyle bounded (except *P. bergeri*); postparacristula relatively short.

Genus ***Paroxacron*** Hürzeler, 1936

Type species. *Paroxacron valdense* Stehlin, 1906 from Mormont Entreroches, Switzerland (MP19). Lectotype: right cranial fragment with P2/-M3/ (NMB Mt.230; Stehlin 1906),

Original Diagnosis. Oxacroninae with P1/, P/1, P2/ and P/2 elongated and premolariform, with a short diastema between P1/-P2/, P/1-P/2 and P/2-P/3 or no diastemata at all; anterior lobe of P3/ elongated; upper molars with mesostyle notch (Hürzeler 1936).

Paroxacron valdense (Stehlin, 1906)

(Fig. 2-7)

Synonymy: 1906 *Oxacron valdense* Stehlin; pp. 681–683, pl. 12:20, text-fig. 97.

1936 *Paroxacron valdense* (Stehlin); Hürzeler, pp. 105–106, fig. 72

1980 *Paroxacron* sp. Legendre, pp. 120–127, tab. 3–4.

Lectotype. A right cranial fragment with P2/-M3/ (NMB Mt.230; Stehlin, 1906), from Mormont Entreroches, Switzerland (MP19).

Emended Diagnosis. Species of *Paroxacron* with diastemata short or occasionally absent between P1/-P2/ and P/2-P/3, and very short to absent between P/1-P/2 and C-P/1; mandible with a gracile and relatively shallow horizontal ramus of constant height between the premolar area and the last molar; coronoid process of the mandible particulary high above the occlusal plane; mandibular condyle long medio-laterally and inclined medially in posterior view; angular apophysis not extended ventrally and stretched distally, with deeply concave dorsal outlines; shallow *incisura vasorum*.

Differential Diagnosis. *Paroxacron valdense* differs from Cainotheriinae by the presence of sub-triangular upper molars without crested styles, a shorter postparacristula, narrow premolars, a weaker postprotoconulid, a P/1 biradiculate, diastemata between P/2-P/3 and P1/-P2/, and a protocone more mesial than the paracone on P4/. It differs also from *Plesiomeryx* and *Caenomeryx* species by a smaller size (except *Ple. cadurcensis*), a small protocone and a longer mesial lobe on P3/, as well as the absence of a protocone on P2/. It diverges from *Cainotherium* by a smaller size, the absence of cingulum/id on premolars, a triangular P3/, and the presence of a valley between the entoconid and the mesoconid on lower molars. *Paroxacron valdense* differs from the other Oxacroninae *Oxacron courtoisii* by the presence of more elongate and premolariform premolars (P1 and P2), an elongate anterior lobe on the P3/ and a larger paroconule on the upper molars. Within *Paroxacron*, *Paroxacron valdense* distinguishes from P. *bergeri* by a smaller size, sub-triangular upper molars, looped mesostyle, and the presence of diastemata. Finally, *Paroxacron valdense* differs from *Paroxacron* sp. by a larger size, a M1/ more triangular and a shorter diastema between P/1-P/2.

New material from DAM1. DAM1: four left maxillary fragments with P2/-M3/ (DAM1 01-03, DAM1 07); two left maxillary fragments with P2/, P4/-M3/ (DAM1 04, DAM1 09); two left maxillary fragments with P3/-M3/ (DAM1 05-06); one right maxillary fragment with P1/-M3/ (DAM1 08); two left maxillary fragments with P4/-M3/ (DAM1 10, DAM1 13); two right maxillary fragments withs P4/-M3/ (DAM1 11, DAM1 14); one left maxillary fragments with P2/-M2/ (DAM1 12); two left maxillary fragments with P2/-P4/ (DAM1 15, DAM1 17); one right maxillary fragment with P3/-M2/ (DAM1 16); one left maxillary fragment with P2/-P3/ (DAM1 18); one left juvenile maxillary fragment with DP3/-M2/ (DAM1 19); one left mandibular fragment with P/2(partial)-M/3 (DAM1 20); one right mandibular fragment with P/2-M/3 (DAM1 21); two left mandibular fragments with P/1(partielle)-M/3 (DAM1 22-23); one right mandibular fragment with P/3-M/3 (DAM1 24); four left mandibular fragments with P/3-M/3 (DAM1 25-28); one left mandibular fragment with P/2, P/4-M/3 (DAM1 29); one left mandibular fragment with P/4-M/3 (DAM1 30); two right mandibular fragments with P/4M/3 (DAM1 31-32); one left mandibular fragmentt with P/3, M/1-M/3 (DAM1 33); one left mandibular fragment with P/1-M/1 (DAM1 34); one right mandibular fragment with P/2-M/1 (DAM1 35); one right mandibular fragment with P/2-M/2 (DAM1 36); one left mandibular fragment with P/1-P/4 (DAM1 37); one right mandibular fragment with P/2-P/4 (DAM1 38); six left P/1 (DAM1 39, DAM1 41-42, DAM1 44, DAM1 46, DAM1 48); seven right P/1 (DAM1 40, DAM1 43, DAM1 45, DAM1 47, DAM1 49-51); eight left P1/ (DAM1 52-57, DAM1 63, DAM1 65); seven right P1/ (DAM1 58-62, DAM1 64, 66); 23 left P3/ (DAM1 67, DAM1 69-71, DAM1 73-80, DAM1 85, DAM1 87-88, DAM1 90, DAM1 92-93, DAM1 95-96, DAM1 99-101); twelve right P3/ (DAM1 68, DAM1 72, DAM1 81-84, DAM1 86, DAM1 89, DAM1 91, DAM1 94, DAM1 97-98); eight right DP/4 (DAM1 102, DAM1 107-111, DAM1 113-114); seven left DP/4 (DAM1 103-106, DAM1 112, DAM1 115-116); six left DP/2-3 (DAM1 117-120, DAM1 122-123); three right DP/2-3 (DAM1 121, DAM1 124-125); five right DP/1 (DAM1 126-128, DAM1 130-131); two left DP/1 (DAM1 129, DAM1 132); six left DP4/ (DAM1 133-134, DAM1 140-141, DAM1 145, DAM1 147); nine right DP4/

(DAM1 135-139, DAM1 142-144, DAM1 146); six right DP3/ (DAM1 148, DAM1 151, DAM1 154-155, DAM1 158, DAM1 160); nine left DP3/ (DAM1 149-150, DAM1 152-153, DAM1 156-157, DAM1 159, DAM1 161-162); four right DP1-2/ (DAM1 163-165, DAM1 167); one left DP1-2/ (DAM1 166); seven right I/1 (DAM1 168, DAM1 170, DAM1 172, DAM1 174, 180-182); eight left I/1 (DAM1 169, DAM1 171, DAM1 173, DAM1 175-179); nine right I/2-3 (DAM1 183, DAM1 186-187, DAM1 189-191, DAM1 193, DAM1 196-197); six left I/2-3 (DAM1 184-185, DAM1 188, DAM1 192, DAM1 194-195); eleven right lower canines (DAM1 198-201, DAM1 204-206, DAM1 208-209, DAM1 211-212); four left lower canines (DAM1 202-203, DAM1 207, DAM1 210); six right I1/ (DAM1 213-214, DAM1 217-219, DAM1 221); four left I1/ (DAM1 215-216, DAM1 220, DAM1 222); ten right I2/ (DAM1 223-224, DAM1 227-230, DAM1 232, DAM1 234-235, DAM1 237); five left I2/ (DAM1 225-226, DAM1 231, DAM1 233, DAM1 236); seven left I3/ (DAM1 238, DAM1 242, DAM1 244-247, DAM1 251); eight right I3/ (DAM1 239-241, DAM1 243, DAM1 248-250, DAM1 252); eight right upper canines (DAM1 253-254, DAM1 258, DAM1 260, DAM1 262-264, DAM1 266); seven left upper canines (DAM1 255-257, DAM1 259, DAM1 261, DAM1 265, DAM1 267); one right mandibular fragment with M/3 (DAM1 268); two left P/3 (DAM1 269-270).

Description.

Lower dentition (Tab. S1; Fig. 2-3, 6). The lower incisors are characterised by dorso-ventrally straight crown and root.

I/1 (Fig. 2F, 6A) has a dorso-ventrally elongated and mesio-distally short crown. It is characterised by two endocristulids related to the pre-conulid and post-conulid, respectively; they form two pronounced lobes, surrounded by three fossids (pre, endo and post). The posterior lobe tends to be larger and more curved lingually than the anterior one. I/1 present also a small protoconid, weakly pronounced apical stylids, a post-fossid deeper than other fossids and wider than pre-fossid, the endofossid being the most important. They have an apical crest (mediocristid) connecting the two conulids slightly disto-lingually inclined, and a long and thin root. Morphological variation observed within the DAM1 sample (15 specimens) is negligible.

I/2-3 (Fig. 3K, 6B) are very similar morphologically. They differ from I/1 by a dorso-ventrally shorter crown, an anterior part of the tooth more mesially projected, and more pronounced lobes, with a posterior lobe more lingually directed than the anterior lobe. They also present a pre-stylid tending to be more pronounced than the postylid, bigger pre- and post-fossid, a more disto-lingually inclined crown, with a mediocristid strongly inclined disto-lingually, and a bulge at the base of mesial lobe. Morphological variation is rather small and concerns mainly the curvature of the crown (30 specimens).

Lower canine (Fig. 3L, 6C): The lower canine is incisiform. It is larger than the incisors and it differs from the latter teeth by a posterior part more mesially directed, a well-pronounced distal lobe and bigger than mesial lobe, a more marked prestylid, a bucco-lingually deep, and wide and mesio-distally short postfossid. It further differs from incisors by a mesio-distally deeper and larger endofossid, a mesio-distally elongated and dorso-ventrally short prefossid, a less disto-lingually inclined mediocristid. The lower canine also presents a bigger bulge at the base of the mesial lobe and a wider and longer root. Morphological variation is negligible and is focused on the post-fossid development (15 specimens).

P/1 and P/2 (Fig. 3A-B, 6D-E, 6L) are very similar morphologically and they essentially differ in size (Tab. S1) and root orientation. P/1 is short mesio-distally, with close oblique roots, whereas P/2 is longer with more remote roots. P/1 and P/2 are characterised by two main cuspids with a protoconid larger and higher than paraconid; a bending at the mesial margin of the tooth (postparacristid and preprotocristid junction), the postparacristid being disto-buccally directed and the preprotocristid mesio-buccally directed; a single and straight distal cristid disto-buccally orientated, connecting the protoconid to the distal margin of the tooth; a small accessory cusp at the back of the protoconid, called a postprotoconulid; a weak disto-lingual cingulid with a small distal stylid (distostylid); a disto-lingual fossid (endofossid). Inter-specimen variability mainly concerns the paraconid size. The bigger it is, the deeper the bending between protoconid and paraconid is. Some P/1 do not show this bending. Other variations are also observed as the distance between the roots, the size of the endofossid, the presence of an endoprotocristid, and the size of the postprotoconulid.

P/3 (Fig. 3C-D, 6L, 6N) is the longest premolar, and it may occasionally have a small root between the two main roots (Fig. 6M). Its morphology is very similar to that of P/1 and P/2, but it differs from the latter in its distal part by similarities with P/4. The postprotoconulid of P/3 is bigger and the distal cristid lingually curves on the distal margin of the tooth, and bears two small accessory cusps, called conulid 1 (end) and conulid 2. Mesially, the paraconid is also larger than on P/1-2. Marked morphological variations are observed on P/3s from DAM1: i) the distal cristid can be long to very short lingually, joining a small to absent conulid 1, ii) the depth and width of the endofossid vary, iii) a small distal and buccal cristid may be present, iv) the postprotoconulid is more or less large and may have a small endocristid disto-lingually curved, as on P/4.

P/4 (Fig. 3E-F, 6L, 6N) is shorter and more molariform than P/3 and it differs from it by the presence of three main cuspids with a large protoconid, a paraconid and a metaconid, the protoconid being more mesial than the metaconid. It also shows an anterior part (protoconid and paraconid) more lingually inclined, with a preprotocristid mesio-lingually orientated and a paracristid more lingually inclined. The entoconid and hypoconid are weakly pronounced, the latter having an extended prehypocristid. The postprotoconulid is smaller, with a more extended endocristid, and there are two posterior cristids on the protoconid and the metaconid, joining at the center of the tooth. P/4 further has disto-buccal and distal cingulids. Morphological variation only concerns the size of cristids and cingulids, and paracristid orientation. The endocristid of the postprotoconulid may in some specimens connect to an accessory cusp or link the metaconid.

M/1-2 (Fig. 3G-H, 6L, 6N) are very difficult to distinguish from each other. They are characterised by five main cusps with a high metaconid, a metaconulid mesio-lingually located and an entoconide disto-lingually. The entoconid has a loop-like shape, notably created by respectively distally convex and concave preentocristid and postentocristid. M/1-2 present also a small to absent lingual paraconid and an entoconid more distal than the hypoconid. The mesiodistal cristid (mediocristid) is short, connecting the premetacristulid and postmetacristid, and closing the transverse valley. There is a continuous cristid formed by a long prehypocristid and short premetacristulid; an accessory cusp is present on this last cristid, called a centroconulid, and bears a cristid (postendocentrocristulid) disto-lingually orientated. This set corresponds to the neotrigonid described by Sudre (1977). Finally, M/1-2 bear a major buccal cristid formed by the junction of the posthypocristid and postentocristid that is directly connected and a large distal cingulid. Morphological variation is negligible.

M/3 (Fig. 2C-D, 3I-J, 6L, 6N) exhibits the same pattern as M/1-2, differing from the latter in having a hypoconulid. This conulid connects the rest of the talonid by the prehypocristulid, which joins the postentocristid (short) and the posthypocristid (long). The hypoconulid and the entoconid are very close to one-another; the talonid is smaller than that of M/1-2. There are some variations between specimens (posthypocristulid sometimes present; roots are either fused or separate).

Upper dentition (Tab. S2; Fig. 2, 4, 7). The upper incisors are characterised by a spatulate-like crown (lingually concave) and an inclined root.

The I1/ (Fig. 2E, 7C) is a very simple tooth with a dorso-ventrally elongated crown. It is characterised by a mesio-distally symmetrical crown, with the apical portion of the tooth mesially convex. It bears two main cusps, with a small paracone and a metacone having respectively an endoparacrista and endometacrista, and small apical styles. The lingual surface bears a little mesial fossa (pre-fossa), a very tiny and lightly deep distal fossa (post-fossa), a mesio-distally large medial fossa (endo-fossa) and a lingual cingulum. The root is thin and short. Variation observed within our sample (11 specimens) is rather weak and concerns the mesial length of the paracone/parastyle portion of the tooth.

I2/ (Fig. 4K, 7B) is more complex and mesio-distally longer than I1/. It differs from the latter by a less spatulate-like and mesio-distally assymmetrical crown, a more mesially projected anterior part, more pronounced metacone and paracone (the latter being bigger), more marked styles, with a metastyle with a small bulge at its base. The pre-fossa and the post-fossa are mesio-distally wider and deeper, the endo-fossa is mesio-distally smaller. The apical crest connecting the paracone and the metastyle (postcrista) is inclined disto-lingually. The lingual cingulum is larger, and the root is longer and less arched than that of I1/. Morphological variation affects the size of cusps and styles and the degree of crests inclination (15 specimens).

I3/ (Fig. 4J, 7A) is mesio-distally shorter than I1/-2/. It differs from I2/ by a lower crown, a less mesially projected mesial part, a larger paracone giving the tooth a caniniform shape, a less dorso-ventrally extended metastyle and placed at the level of its bulge, at the base of the crown. The parastyle is more pronounced. The post-fossa is smaller but deeper, while the pre-fossa is larger, as wide as the central fossa. The post-fossa is strongly inclined distally. The precrista is more mesio-lingually inclined and the apical crest connecting the paracone and metacone (mediocrista) is more disto-lingually inclined. The root of I3/ is stockier than that of I2/. The morphological variation (15 specimens) is rather weak and similar to I2/. Some teeth present a strong mesial projection of their mesial part.

Upper canine (Fig. 4L, 7D) is taller and stockier than I3/. It differs from it by a more mesio-distally directed mesial part, larger paracone and metacone, more pronounced styles, the metastyle having a big basal bulge. The post-fossa is deeper, the pre-fossa is mesio-distally wider, and the endo-fossa is more compressed. The mesial fossa is thus more important than the endo-fossa. The mediocrista and postcrista are strongly disto-lingually inclined. The root of the upper canine is longer and very thick. Variation is mainly in metastyle and metacone development. Some teeth present an anterior part more mesially projected (15 specimens).

P1/ (Fig. 4A-B, 7I-J) is the smallest upper premolar. It is characterised by two medial main cusps, with a paracone larger and higher than the metacone, mesial (parastyle) and distal (metastyle) styles weaklier marked, the former being higher and more salient than the latter. The posterior part of P1/ is almost as wide as the anterior part. The paracristyla is mesio-lingually projected and the preparacrista slightly mesio-buccally orientated. There is a very small posterior fossa, and a weak lingual cingulum. The roots are close and oblique. The morphology of P1/ is highly variable: i) the general shape of the tooth can be elongated to very short, ii) the metacone varies also greatly in size from very small to as large as the paracone, iii) the paracristyla is variously mesio-lingually projected; a ectoprotocrista can be present, iv) the distance between the two roots varies in size.

P2/ (Fig. 4C-D, 7M) is mesiodistally longer than P1/, but quite similar in morphology. It differs from the latter by a smaller paracone, a parastyle more salient and individualised, a crest connecting the metacone to metastyle disto-buccally inclined, and the appearance of a lingual loop-like crest (postmetacristula), on the distal part of the tooth. The distal part of the tooth is enlarged, with a slightly bigger lingual cingulum. P2/ is more variable than P1/, especially in the distal part: i) a cingular cusp and an ectometacristyla can occur, ii) the postmetacristyla can be either long or short. Some teeth have a small root between the two main roots.

P3/ (Fig. 4E-F, 7M) differs morphologically from P1/-2/. It is subtriangular in shape and bears three roots. It is characterised by well-pronounced paracone, metacone and protocone, salient parastyle and metastyle, a very elongated mesial lobe (paracone and parastyle) and a crest connecting the metastyle to parastyle that is buccally concave. There are lingual and distal cingula. P3/ is highly variable: i) the protocone can be wide to mesio-distally compressed and it can be located in a distal to medial position, ii) mesial and disto-lingual (protocone) lobes can be variously elongated and wide, iii) the crests connecting the paracone and the parastyle (preparacrista and postparacristyla) can be more or less mesio-buccally inclined, iv) the crest formed by the junction of the postmetacrista and premetacristyla is variously inclined disto-buccally, v) an ectoprotocrista can be occasionally present, oriented towards the metacone, vi) cingulum can be variously expanded. The P3/ of this species therefore have a wide morphological diversity, ranging from a small, stocky and short tooth to an elongated and narrow tooth.

P4/ (Fig. 4G-H, 7M) is easily recognisable from other premolars by much shorter mesio-distal dimensions. It presents a paracone larger and higher than the mesial protocone, a small metacone, well individualised and salient parastyle and metastyle, medio-lingually bent. A crest connects the parastyle and the metastyle is buccally concave. An accessory cusp is present on the postprotocrista (conule 1), and it bears a crest extended buccally. The disto-lingual cingulum is large. Variations between specimens are important and mainly related to the cingulum development. The P4/ can vary from stocky and quadrangular to narrow and triangular.

Upper molars (Fig. 2A-B, 4I, 7M) are morphologically similar. They are characterised by the '*Cainotherium*' plan, composed of five main cusps (Stehlin, 1906). The paracone is mesio-buccal, the paraconule mesio-lingual, while the protocone is disto-lingual, located more mesially than the metacone and the metaconule. Upper molars present also well-pronounced styles, with a loop-like mesostyle; a short and continuous premetacristula; a preprotocrista tending to bind with the postparacristula; a preparacristula connecting the preparacristyla, and the postmetacristula joining the postmetacristyla; a mesial cingulum; a lingual cingulum symbolised by cingular cusps in front of (mediostyle) or behind the protocone (distostyle). The morphology of upper molars is highly variable: i) the crown shape can be triangular to rectangular (bucco-lingually), ii) the inclination of the crown is variously pronounced, with a small mesially and distally convex curvature, accompanied by a parastyle more or less buccal, iii) the preprotocrista can be long buccally in some teeth, iii) the distostyle is variously marked.

M2/ tends to be wider than the other two molars, whereas M1/ is the shortest. On M1/, the paraconule is more lingually located and the general outlines of the crown concurrently rectangular. However, because of important morphological variation, the distinction between M1/ and M2/ of our sample is essentially done by size criterion (Tab. S2).

M3/ further differs from other molars in having a more triangular shape, with a more buccal paraconule and a less prominent mediostyle. It has a paracone higher than the metacone in buccal view, unlike M1/ and M2/ where these two cusps are of equal height.

Lower deciduous teeth (Tab. S3; Fig. 5A-F, 6F-K). The lower deciduous teeth differ from the permanent ones by a lower and more mesio-distally elongated crown, with thinner enamel layer, and more individualised cuspids/stylids.

DP/1 (Fig. 5A-B, 6F-G) is very similar in morphology and variability to P/1. It differs from the latter in having a larger postprotoconulid, a cristid connecting the protoconid and postprotoconulid mesio-distally projected, a cristid joining the postprotoconulid and distal part of the tooth more disto-buccally oriented and curving lingually, a smaller lingual posterior fossid, spaced roots.

DP/2-3 (Fig. 5C-D, 6H-I) are morphologically similar to P/3 but they differ in their posterior part by pronounced hypoconid and entoconid; a larger conulid 2 with a small cristid lingually directed; a cristid descending from the postprotoconulid to the conulid 2 and joining the prehypocristid and postentocristid, strongly disto-buccally inclined; a disto-lingually inclined cristid starting from the postprotoconulid; a mesio-distal cristid connecting the protoconid and postprotoconulid. The morphological variation observed in our sample is low (nine specimens).

DP/4 (Fig. 5E-F, 6J-K) is very similar in morphology and variability to lower molars but it differs from them in the presence of a third lobe in its anterior part, consisting of a lingual primoconid and a buccal paraconid, the latter being little more mesial than the former. The talonid (posterior lobe) is larger than the mesial lobe. The postprimocristid is directed disto-lingually and joins the preprotocristid and premetacristid. There is a bucco-lingually inclined cristid formed by the junction of the endoprotocristid and ectometacristid, and a bucco-lingually inclined cristid originating from the hypoconid (endohypocristid). DP/4 bears an open transverse valley and an absent to weak mesial cingulid.

Upper deciduous teeth (Tab. S3; Fig. 5G-L, 7E-H, 7K-L). Compared to the permanent dentition, the upper deciduous teeth present the same general characteristics as the lower ones and they differ by a lower, narrower, and more mesio-distally elongated crown.

DP1-2/ (Fig. 5G-H, 7E-F) are premolariform and very close morphologically to P2/. However, they differ from P2/ in having a shorter postmetacristyla and in lacking a lingual cingular cusp. Morphological variation is negligible (five specimens).

DP3/ (Fig. 5I-J, 7G-H) is distally molarised and mesially premolarised. It is very similar to DP4/ and upper molars in its distal part and to DP1-2/ in its mesial part. However, DP3/ is shorter and wider than DP1/ and DP2/. It is characterised by a distal part with a metacone, metaconule and protocone, a mesial part with a big paracone, salient styles with posterior metastyle and mesostyle, as well as a highly mesially prominent anterior parastyle. The crown shows a significant distally concave curvature owing to a strong mesio-distally compressed protocone, splitting disto-buccal and disto-lingual parts. The anterior part of the tooth is very elongated and bucco-lingually compressed (paracone to parastyle). The paracristyla is mesio-buccally inclined, the ectoprotocrista binds with the premetacristula and the preprotocrista with the mediostyle. The distostyle is marked and the lingual cingulum is big. Morphological variation mainly affects the size of the protocone and the bucco-lingual compression of the distal part of the tooth (15 specimens).

DP4/ (Fig. 5K-L, 7K-L) morphologically resembles upper molars in its mesial half and DP3/ in its distal half. However, DP4/ is shorter and wider than the latter and it differs from other molars by its small size, and by a strong inclination of the crown, with a mesially convex and distally concave outline. Styles are also more salient and individualised, the parastyle being more buccal and metastyle strongly disto-buccally projected. The postprotocrista is more inclined disto-lingually. The distostyle is marked at the back of the protocone. DP4/ further differs from DP3/ by lack of a distal cingulum, presence of a lingual cingulum and a less marked mediostyle. Variation concerns size (Tab. S3) and the degree of inclination of the crown (15 specimens).

Diastemata/Mandible (Fig. 6L, 6N-R). Specimens are characterised by diastemata short or occasionally absent between P1/ and P2/, P/2 and P/3, and shorter or absent between P/1 and P/2 (Tab. S1; Fig. 6L, 6O). The posterior tip of the mandibular symphysis is located at the level of the distal margin of P/2 (Fig. 6L, 6N). Two mental foramina are constantly present on the horizontal ramus, one below the mesial part of P/2 and one below the mesial part of P/4 (Fig. 6O, 6R). The horizontal ramus is gracile, relatively shallow and its height is rather constant between the premolar area and the last molar. However, specimens show almost no variation. The mesial margin of the ascending ramus is wide at its root (Fig. 6O-P). The coronoid process is particulary high above the occlusal plane and its dorsal tip forms a sharp crest (6ig. 6P-Q). The condyle is narrow and convex mesio-distally (Fig. 6Q). In posterior view, the condyle is medio-laterally long and medially inclined. The masseteric fossa, in lateral view, is deep in its mesial portion. There is a wide mandibular foramen on the medial aspect of the ascending ramus base (Fig. 6P-Q). The mandibles are characterised by a very elongated angular apophysis, making a weak angle with ascending ramus. In lateral view, the dorsal outline of the angular process is deeply concave and it forms a pointed tip at the distal most part. The angular apophysis does not extend much ventrally beyond the level of the ventral margin of the horizontal ramus. Almost no variation is observed on the ventral extension of the angular process. The angular apophysis is mesially delimited by a shallow *incisura vasorum*.

Remarks. The cainotheriid material from DAM1 is referred here to *Paroxacron* based on the presence of i) small diastemata between P/1-P/2, P/2-P/3 and P1/-P2/, ii) premolariform P/1 and P/2, and iii) a P3/ with a long mesial lobe. Mandibular remains from DAM1 differ from those of *Paroxacron bergeri* in having a more elongated angular apophysis and a shorter angle with the ascending ramus, as well as a smaller and less marked *incisura vasorum* and the presence of diastemata. They also differ in the size and shape of their upper molars which have more triangular outlines, and smaller size.

The morphology of DAM1 specimens is compatible with the diagnosis of *Paroxacron valdense* as proposed by Stehlin (1906) and Hürzeler (1936). The maxilla Mt. 230 from Entreroches (Mormont, Switzerland), lectotype of the species, and the mandibles Mt. 232-233 from Cinq-Sous (Mormont, Switzerland) described by Stehlin (1906), as well as maxillae QS. 486 and the mandible QU. 32 from old Quercy collections described by Hürzeler (1936), are indeed morphologically and biometrically very similar. However, as mentioned by Hooker & Weidmann (2000) based on the new material from Eclepens C and Cinq-Sous (Mormont, Switzerland), some diagnostic characters like the diastemata length and the anterior premolar shape, present significant intraspecific variation. This variation is indeed also observed in DAM1 material (see description section above). However, specimens from Cinq-Sous and Eclepens C differ from those from Quercy and Entreroches by smaller dimensions of anterior premolars, by a P4/ and upper molars that are more triangular, producing a more primitive shape according to Hooker & Weidmann (2000). These differences may be related to the slightly older age of the first two sites (Hooker & Weidmann 2000). The differences observed between DAM1 material and *Paroxacron bergeri* and the similarities with *P. valdense* from the type locality of Entreroches allow the DAM1 specimens to be identified as *P. valdense*.

Legendre (1980) described two Oxacroninae species, attributed to *Oxacron courtoisii* and *Paroxacron* sp. in the late Priabonian locality of Escamps (MP19, Quercy). According to Legendre (1980), *Paroxacron* sp. from Escamps differs from *Paroxacron valdense* from Mormont in being slightly smaller and in having different mandible shape. However, we think that slight differences encountered with Mormont specimens, are attributable to intraspecific variation. Specimens from Escamps are here considered as conspecific with the DAM1 sample, based on biometrical and morphological characters (Tab. S1-S3; Legendre 1980, tab. 3-4), and are thus attributed to *Paroxacron valdense*. The comparison of DAM1 material with specimens referred to *Paroxacron* from Palembert (MP19) (Quercy locality, collection of Montpellier University) indicates that these specimens could also belong to *P. valdense*.

Paroxacron sp.

(Fig. 8)

New material from DAM3. Three left M3/ (DAM3 01-03); one right M2/ (DAM3 04); one left M2/ (DAM3 05); two right M1/ (DAM3 06-07); one left M1/ (DAM3 08); one right P4/ (DAM3 09); one right P1/ (DAM3 10); one right M/3 (DAM3 11); two right M/2 (DAM3 12, DAM3 14); one left M/2 (DAM3 13); two left M/1 (DAM3 15-16); one left DP/4 (DAM3 17); one right DP/4 (DAM3 18); one right P/2 (DAM3 19); one left P/1 (DAM3 20); one left mandibular fragment with M/2 (DAM3 21).

Description (Tab. S4-5; Fig. 8). The double-rooted P/1 and P/2 are premolariform, elongated and narrow (Fig. 8O-R). The paraconid and protoconid are weakly developed, their protoconid being the higher. The DP/4 present well individualised cusps, a mesial lobe smaller than the distal lobe (talonid) and no mesial cingulid (Fig. 8S-T).

P1/ is relatively elongated, premolariform, and double-rooted (Fig. 8M-N). The paracone is thicker than the weakly-marked parastyle and metastyle. P4/ is relatively narrow and triangular, with a large paracone distally located with respect to the protocone (Fig. 8A-B). Styles are salient and the disto-lingual cingulum is weak. Upper molars are subtriangular with a loop-like mesostyle (Fig. 8C-H).

Remarks. The presence of small teeth and double-rooted premolariform P/1 and P/2, elongated and narrow with weakly developed cusps, and a P4/ with a mesial protocone, allows to attribute these specimens to an unnamed species of *Paroxacron*, but which is different from either of the named ones. Specimens described by Blondel (2005) from Aubrelong 1, Ravet (MP21) and Plante 2 (MP22) of Quercy are similar to those of DAM3. However, dimensions are close to those of *Plesiomeryx cadurcensis*, and it is sometimes difficult to differentiate the two species on the basis of isolated upper and lower molars.

According to the description of Blondel (2005), *Paroxacron* sp. differs from *Paroxacron valdense* by an anterior lobe of the P3/ similar to that observed in *Plesiomeryx cadurcensis*, a more quandrangular M1/ and a longer diastema between P/1-P/2. The dimensions are also smaller, especially for upper premolars. Owing to the small available sample (with respect to DAM 1 material), it is not possible to test intraspecific variation accurately. Yet, morphological and metrical features of these Oligocene specimens are consistently distinct from those of DAM1. It is therefore possible to consider that the Aubrelong 1, Ravet, La Plante 2 and DAM3 sites include a younger species of *Paroxacron* which also differs from *Paroxacron bergeri* by its small size, its less quadrangular molars and the presence of a diastema between P/2-P/3. This species may be new.

Paroxacron bergeri Heissig, 1978

(Fig. 9)

Synonymy: 1959 cf. *Cainotherium*? *elongatum* Filhol (?Berger); Berger, p. 45, pl. 4, fig. 5.

1959 *Cainotherium*? n. sp.; Berger, p. 47, pl. 5, fig. 6–10.

Holotype. A right mandibular fragment I/3-M/3 (BSP 1879XV201), locality of Mouillac in Phosphorites of Quercy. The precise age and type locality are unknown (Old Quercy collections).

Diagnosis. Species of *Paroxacron* without a diastema between P/2-P/3. The edge of the mandible is more strongly bent than in *P. valdense*. The *angulus mandibulae* is short, high and angular. It is limited by a short but strong *incisura vasorum* anteriorly. P/3 and P/4 have a more complete talonid and the internal wall of the lower molars is higher than in *P. valdense* (Heissig 1978).

Differential Diagnosis. *Paroxacron bergeri* differs from Cainotheriinae species by the absence of crested styles on the upper molars, a shorter postparacristula, the presence of narrow premolars and a protocone more mesial than the paracone on P4/. It differs also from *Plesiomeryx* and *Caenomeryx* species by a small protocone and a longer mesial lobe on P3/, and the absence of diastemata and protocone on P2/. It distinguishes from *Cainotherium* by the absence of cingulum/id on premolars and a triangular P3/. *P. bergeri* diverges from the Oxacroninae *Oxacron courtoisii*, by a larger size, the presence of more elongate and premolariform premolars (P1 and P2), an elongate anterior lobe on the P3/, as well as a larger paroconule and pinched mesostyle on the upper molars. *P. bergeri* differs from *P. valdense* and *P*. sp. by a larger size, quadrangular upper molars, a pinched mesostyle and the absence of diastemata.

New material from DAM3. Two left M3/ (DAM3 22-23); one right M3/ (DAM3 24); two left M2/ (DAM3 25, DAM3 27); one right M2/ (DAM3 26); two left M1/ (DAM3 28-29); one left P4/ (DAM3 30); one right P3/ (DAM3 31); one left P2/ (DAM3 32); one right maxillary fragment with P1/ (DAM3 33).

Description (Tab. S6; Fig. 9). P1/ and P2/ are elongated and premolariform (Fig. 9I-L). The P3/ presents a well elongated anterior lobe, with salient parastyle and metastyle, and a pronounced protocone (Fig. 9M-N). The crest connecting these two styles is buccally concave, the disto-buccal lobe being very buccally inclined. The P4/ shows prominent paracone and mesial protocone, the paracone being higher (Fig. 9A-B). The parastyle and metastyle are well individualised and salient, and conule 1 presents an extended buccal crest. Upper molars are quadrangular with crested styles (Fig. 9C-H).

Remarks. The presence of quadrangular molars, a P3/ with a very elongated anterior lobe, a pronounced protocone and large size allow for referring these specimens to as *Paroxacron bergeri*. These teeth are similar in terms of size and morphology to *Paroxacron* cf. *bergeri* from Mas de Got (MP22), Pech Crabit, Roqueprune 2, and Mounayne (MP23) localities described by Blondel (2005). According to this author, some of these specimens are comparable in size to those referred to *P. huerzeleri* by Berger (1959), but they differ from the latter species by the morphology of the P2/ (smaller median cusp and presence of a lingual cingulum) and the P3/ (greater anterior lobe and smaller protocone). The same observations are performed in DAM3, and it is sometimes difficult to differenciate the two species on some isolated molars.

Subfamily **Cainotheriinae** Camp & VanDerHoof, 1940

Emended diagnosis. Small to large cainotheriids, comprised around 500g (e. g. *Plesiomeryx cadurcensis*) – 2,4 kg (e. g. *Cainotherium laticurvatum*). Muzzle elongated and narrow (e. g. *Plesiomeryx*) to short and wide (e. g. *Caenomeryx*); Orbits large; ethmoidal fissures present. Diastemata present (except *Cainotherium*), between P/1-P/2 and C-P1/. Premolars wide; postprotoconulid large; protocone at the same level than the paracone on P4/; P/1 uniradiculate. Upper molars quandrangular; styles crested and mesostyle pinched; postparacristula buccally long and joins the preprotocrista.

Genus ***Plesiomeryx*** Gervais, 1873

Plesiomeryx cadurcensis Gervais, 1873

(Fig. 10)

Holotype. Right mandibular P/2-M/3 (MNHN-QU 1772). Mouillac locality, Phosphorites of Quercy. The precise age and type locality are unknown (Old Quercy collections).

Diagnosis. Protocone and paraconule present (stage B, Hürzeler, 1936: 8). Long diastema between P1/ and C and between P/1 and P/2. P1/, P2/, P/2 and P/3 are short, P3/ with a strong lingual cone, P2/ with a weak lingual cone. The premaxilla reaches the frontal. The nasal is long, narrow and straight. The ethmoidal slit is falciform. The choanae are large. The horizontal portion of the lower jaw is slender (Hürzeler, 1936).

Differential Diagnosis. *Plesiomeryx cadurcensis* differs from Oxacroninae species by the presence of quadrangular upper molars with a pinched mesostyle (except *P. bergeri*) and crested styles, a longer postparacristula, larger premolars, a larger postprotoconulid, a P/1 uniradiculate, diastemata between P/1-P/2 and C-P1/, and a protocone at the same level than the paracone on P4/. It differs also from *Paroxacron* species by a shorter anterior lobe on the P3/ and a larger protocone on the P3/ and P2/. *Ple. cadurcensis* diverges from *Oxacron* by a larger protocone on the P3/ and P2/, as well as premolariform mesial premolars. *Ple. cadurcensis* diverges from *Cainotherium* by a smaller size, a smaller paraconule on the upper molars, the absence of cingulum/id on premolars, the presence of a triangular P3/, a larger protocone on the P3/ and P2/, a valley between the entoconid and the mesoconid on lower molars, and the presence of diastemata. It distinguishes from *Caenomeryx* species by a smaller size, a smaller protocone on the P3/ and P2/, a shorter mesial lobe on the P3/ and a smaller paraconule. Finally, *Ple. cadurcensis* differs from *Ple. huerzeleri* by a smaller size and a labial cone of the P/4 more distal than the lingual cone.

New material from DAM3. One left M3/ (DAM3 34); two right M3/ (DAM3 35-36); two left M2/ (DAM3 37, DAM3 40); three right M2/ (DAM3 38-39, DAM3 41); two right M1/ (DAM3 42, DAM3 44); one left M1/ (DAM3 43); one right DP4/ (DAM3 45); one left DP4/ (DAM3 46); one right P4/ (DAM3 47); one left P3/ (DAM3 48); one right P2/ (DAM3 49); one right P1/ (DAM3 50); one right maxillary fragment with P2/ (DAM3 51); two left M/3 (DAM3 52, DAM3 54); one right M/3 (DAM3 53); three right M/2 (DAM3 55, DAM3 57-58); two left M/2 (DAM3 56, DAM3 59); two left M/1 (DAM3 60, DAM3 62); three right M/1 (DAM3 61, DAM3 63-64); three right P/4 (DAM3 65, DAM3 67-68); one left P/4 (DAM3 66); four right P/3 (DAM3 69-70, DAM3 72, DAM3 74); two left P/3 (DAM3 71, DAM3 73); two left P/2 (DAM3 75, DAM3 76); one right P/2 (DAM3 77); one left mandibular fragment with M/1 (DAM3 78); one right mandibular fragment with P/3-P/4 (DAM3 79).

Description (Tab. S7-8; Fig. 10). P/1 is uniradiculate and probably premolariform (only alveoli are preserved). The diastema that separates P/1 from P/2 is short. The double-rooted P/2, P/3, and P/4 are short and wide (Fig. 10S-V). P/2 and P/3 present a strong protoconid. P/3 shows a short anterior lobe, a weak lingual cingulum, as well as an expansed distal cristid lingually curved. The protoconid of the P/4 is more mesial than the metaconid. The postprotoconulid is more or less large. The mandible bears a mandibular symphysis located on the distal margin of P/2 (Fig. 10U-V). A mental foramen is present, below the mesial part of P/2. The horizontal ramus is gracile and shallow.

P1/ is premolariform, short, wide, and biradicular (Fig. 10M-N). P2/ is more elongated and wider than P1/ (anterior lobe as wide as posterior lobe). It has a weakly pronounced protocone and a large paracone (Fig. 10O-P). P3/ is short with a well-developed protocone (Fig. 10A-B). The paracone and the protocone of P4/ seem to be median (in the same plan), but the only preserved tooth is strongly worn (Fig. 10C-D). Upper molars are quadrangular in occlusal view, with a pinched mesostyle, styles being very weakly crested, and a small paraconule (Fig.

10E-J). The DP4/ are similar to upper molars, but present an important mesially convexe curvature, with a mesially projected parastyle (Fig. 10Q-R).

Remarks. The presence of a uniradiculate and premolariform P/1, of a short diastema between P/1-P/2, of a strong protoconid on P/2 and P/3 (Blondel, 2005), and of upper molars with a small paraconule point to a representative of *Plesiomeryx*. Its small size and premolar morphology match those of *Plesiomeryx cadurcensis*, as described by Hürzeler (1936), Berger (1959), and Blondel (2005) from Aubrelong 1, Ravet (MP 21), Mas de Got, La Plante 2 (MP 22), Pech Crabit, Mounayne et Itardies (MP23, Quercy localities). Even if some isolated upper and lower molars are hardly distinguishable from those of *Paroxacron* sp. from DAM3, a slightly taller size, more quadrangular upper molars and a more pinched mesostyle in *P. cadurcensis* may allow to distinguish them.

Plesiomeryx huerzeleri Berger, 1959

(Fig. 11)

Synonymy: 1937 *Caenotherium gracile* Pomel; Dehm, p. 352.

Holotype. Skull BSP 1952 II 1149. Gaimersheim fissure filling (Germany) (MP28).

Diagnosis. Species of *Plesiomeryx* similar to *P. cadurcensis*, but larger. The fronto-nasal suture is short. The lingual cingulum of P/3 is missing. The lingual and labial cones of P/4 reach the same level (Berger 1959).

Differential Diagnosis. *Plesiomeryx huerzeleri* differs from other Cainotheriidae species in the same way as that is described for *Plesiomeryx cadurcensis*, but present a larger size than *Paroxacron valdense*, *Paroxacron*. sp. and *Oxacron courtoisii*. *Ple. huerzeleri* distinguishes from *Ple. cadurcensis* by a larger size, as well as the labial and lingual cones of the P4/ that reach at the same level.

New material from DAM3. Three right M3/ (DAM3 80-82); four right M2/ (DAM3 83-85, DAM3 88); two left M2/ (DAM3 86-87); three left M1/ (DAM3 89, DAM3 94-95); six right M1/ (DAM3 90-93, DAM3 96-97); two left P2/ (DAM3 98-99); one left P1/ (DAM3 100); one left maxillary fragment with P3/-P4/ (DAM3 101); two right M/3 (DAM3 102-103); two left M/3 (DAM3 104-105); two left M/2 (DAM3 106, DAM3 109); two right M/2 (DAM3 107-108); two left M/1 (DAM3 110-111); two right M/1 (DAM3 112-113); one left DP/4 (DAM3 114); three left DP/3 (DAM3 115-117); four right P/3 (DAM3 118-119, DAM3 121, DAM3 125); four left P/3 (DAM3 120, DAM3 122-124); one right P/2 (DAM3 126); one right P/1 (DAM3 127); one left mandibular fragment with P/4-P/3 (DAM3 128).

Description (Tab. S9-S10; Fig. 11). P/1 is uniradiculate and premolariform (Fig. 11S-T). A short diastema is present between P/1 and P/2 (Fig. 11W-X). The double-rooted P/2, P/3 and P/4 are short and wide (Fig. 11U-X). P/2 and P/3 present a strong protoconid. In lateral view, the protoconid of the P/4 is at the same level than the metaconid. The postprotoconulid is more or less pronounced. DP/4 and DP/3 are elongated, cusps being well individualised and cingulids absent (Fig. 11Y-B'). The mandible bears a mandibular symphysis located on the distal margin of P/2 (Fig. 11W-X). A mental foramen is present, below the mesial part of P/2. The horizontal ramus is relatively gracile on its mesial part.

P1/ and P2/ are short and wide with a large paracone (Fig. 11O-R). P2/ bears a weakly developed protocone. The triangular P3/ bears a strong protocone, and the parastyle and metastyle are not very prominent (Fig. 11A-B). The mesial lobe is quite short and the crest connecting the metastyle and parastyle is weakly buccally concave. P4/ is wide and rectangular in occlusal view, the paracone and the protocone being median. Upper molars are quadrangular with a small paraconule and a pinched mesostyle, styles being weakly crested (Fig. 11C-H).

Remarks. A larger size than in *Plesiomeryx cadurcensis*, a lack of lingual cingulum in P/3, and buccal and lingual cones at the same level in P/4, allow some specimens to be assigned to

Plesiomeryx huerzeleri. The morphology and size are very similar to those of Quercy specimens described by Blondel (2005) from Mas de Got, La Plante 2 (MP 22), Pech Crabit, Roqueprune 2 and Mounayne (MP 23). They are also similar to those specimens from Gaimersheim (MP28, Germany; Berger 1959, tab. 3, pl. 3; Bolliger 2013, fig. 3a). Some isolated upper molars are however hardly differentiated from those of *Paroxacron bergeri*. Slightly smaller size, a more quadrangular shape and a more pinched mesostyle in *Ple*. *huerzeleri* may allow them to be discriminated.

Genus ***Caenomeryx*** Hürzeler, 1936

Caenomeryx procommunis (Filhol, 1877)

Synonymy: 1877 *Cainotherium procommune* Filhol: 212, fig. 269–270.

1936 *Caenomeryx procommunis* (Filhol), Hürzeler, p. 100.

Holotype. Fragment of mandible bearing P/2-M/3 (Filhol collections, MNHNP). Precise age and type locality unknown (Old Quercy collections).

Emended Diagnosis. Upper molars are wider than long. Protocone and protoconule present (stage B, Hürzeler, 1936; p. 8). Diastema between P1/ and C is short. Diastema very short or missing between P/1 and P/2. Premolars reduced, P3/ with a strong lingual cone, P2/ with a weaker lingual cone, P1/ very small. The premaxilla does not reach the frontal. The wide nasal bones broaden behind the posterior extremities of the premaxilla. The ethmoidal gap is irregular, the choanae are large and the mandible is high, stocky and massive (Hürzeler, 1936). Remarks: According to our observations, the C-P1/ and P/1-P/2 diastemata are rather short than absent (*contra* the original diagnosis of Hürzeler (1936)).

Differential Diagnosis. *Caenomeryx procommunis* differs from Oxacroninae species by a larger size, the presence of quadrangular upper molars with a pinched mesostyle (except *P. bergeri*) and crested styles, a longer postparacristula, larger premolars, a larger postprotoconulid, a P/1 uniradiculate, diastemata between P/1-P/2 and C-P1/, and a protocone at the same level than the paracone on P4/. It differs also from *Paroxacron* species by a shorter anterior lobe on the P3/ and a larger protocone on the P3/ and P2/. *Cae. procommunis* diverges from *Oxacron* by the presence of a large protocone on the P3/ and P2/, and premolariform mesial premolars. *Cae. procommunis* distinguishes from *Cainotherium* by rectangular upper molars, the absence of important cingulum/id on premolars, the presence of a triangular P3/, a larger protocone on the P3/ and P2/, a valley between the entoconid and the mesoconid on lower molars, and the presence of diastemata. *Cae. procommunis* diverges from *Plesiomeryx* species by a larger size, a larger protocone on the P3/ and P2/, a longer mesial lobe on the P3/, a larger paraconule, smaller diastemata and more rectangular upper molars. Finally, *Cae. procommunis* differs from *Cae. filholi* by a longer mesial lobe on the P3/ and shorter diastemata.

Caenomeryx* cf. *procommunis (Filhol, 1877)

(Fig. 12)

New material from DAM3. One right M3/ (DAM3 129); two left M2/ (DAM3 130-131); one right M2/ (DAM3 132); two left M1/ (DAM3 133-134); one right P3/ (DAM3 135); four left M/3 (DAM3 136-139); one left M/2 (DAM3 140); one right M/1 (DAM3 141); one left M/1 (DAM3 142); one right P/4 (DAM3 143); one left P/4 (DAM3 144); two right DP/3 (DAM3 145-146); one right P/3 (DAM3 147); one left P/2 (DAM3 148); one left P/1 (DAM3 149); one right mandibular fragment with M/2 (DAM3 150); one left mandibular fragment with P/4-M/1 (DAM3 151); one right mandibular fragment with P/4-M/3 (DAM3 152).

Description (Tab. S11-S12; Fig. 12). P/1 is premolariform and single-rooted (Fig. 12M-N). P/2, P/3, and P/4 are short and wide (Fig. 12K-L, 12O-R). P/2 and P/3 present a pronounced paraconid; P/3 has a strong protoconid. DP/3 is elongated mesiodistally with a large mesial part (Fig. 12I-J). The mandible bears a mandibular symphysis located on the distal margin of P/2

(Fig. 12K-L). A mental foramen is present, below the distal part of P/4. The horizontal ramus is wide, dorso-ventrally extended and its height increase between the premolar area and the last molar.

The anterior lobe of the P3/ is relatively elongated mesio-distally and the crest connecting the parastyle and metastyle is buccally concave (Fig. 12A-B). The metastyle is well-marked and the protocone, althought broken away, seems to be strong. Upper molars are quadrangular in occlusal view (Fig. 12C-H). They are rather bucco-lingually elongated and they have a pinched mesostyle, styles being crested.

Remarks. The presence of large specimens, with a wide and tall corpus mandibulae, as well as short premolars with large cusps and rectangular upper molars (Hürzeler, 1936), suggests the occurrence of *Caenomeryx* within the DAM3 material. The morphology is similar to the undated specimens of the old Quercy collections attributed to *Caenomeryx procommunis* by Hürzeler (1936). It is also similar to the specimens later attributed to *Cae*. cf. *procommunis* by Blondel (2005) from Mas de Got (MP22), Pech Crabit, Itardies, Mounayne and Roqueprune 2 (MP23), and by Sudre (1995) from Le Garouillas (MP25). The dimension of DAM3 specimens are however a little smaller than previously described specimens from these localities. Moreover, it may be difficult to discriminate some isolated upper molars from those of *P. bergeri* and *Ple*. *huerzeleri*. In any case, a larger size, a more rectangular shape on the upper molars and a larger protocone on the premolars in *Caenomeryx* may allow to distinguish them.

Class **Mammalia** Linnaeus, 1758

Order **Artiodactyla** Owen, 1848

Superfamily **Cainotherioidea** Camp & VanDerHoof, 1940

Family **Robiacinidae**, fam. nov.

Type genus. *Robiacina* Sudre, 1969

Included genera. Type genus only.

Original Diagnosis. As for its type and only genus *Robiacina* (Sudre 1978).

Emended Diagnosis. Small Cainotherioidea similar in size to *Oxacron*. Skull globular in shape with a sub-spherical cerebral part and muzzle extremely short; very large orbits; lacrymal small; in the bottom of the orbital cavity, palatine does not contact the frontal, due to the great posterior development of the lacrimal; auditory bullae of large size, sub-spherical; ethmoid fissure absent. Lower and upper premolars short mesio-distally; diastemata absent to reduced; P/3 with a small medio-lingual cusp; P/1 and P/2 unicuspid. Lower molars with a pinched trigonid and a wide talonid; presence of a small to medium-sized metaconulid on the distal aspect of the metaconid; entoconid slightly more distal than the hypoconid; presence of a small hypoconulid on M/1-2 and a posthypocristulid on M/3. Upper molars subtriangular with five cusps and a central or slightly mesial protocone; metacone higher than the paracone; paraconule small; preparacrista short; preprotocrista linked to the paraconule; buccal wall of the paracone with or without a cingulum.

Remarks. The justification for the erection of the new family Robiacinidae is provided in the following section and ensues the results of phylogenetic analysis.

Results and Discussion

Dental nomenclature

Premolar and molar cusp/id patterns of Cainotheriidae differ from other Artiodactyla, which resulted in different dental nomenclatures for premolars and lower molars (Fig. 1A-E, I). According to Berthet (2003), the disto-lingual cusp of upper premolars corresponds to an hypocone while, according to Hürzeler (1936), Gentry & Hooker (1988), and Boisserie *et al.*

(2010), this cusp would correspond to the protocone instead. For lower premolars, these authors identify the mesial cuspid as the paraconid and the medio-lingual cuspid of P/4 as a metaconid. Berthet (2003) considers the mesial cuspid of lower premolars as a protoconulid, and the medio-lingual cuspid of P/4 an entoconid. Problems of identification of the cusps/ids also occur for the lower molars. According to Hürzeler (1936), the three lingual cuspids of lower molars correspond to: a mesial cuspid identified as a metaconid, and two distal ones, that would correspond to the entoconid and to the hypoconulid that would lie in a lingual position. According to Sudre (1977), the medio-lingual cuspid would not be an entoconid but a neoformation called the mesoconid. This mesoconid would originate from a duplication of the metaconid (Sudre 1977). Gentry & Hooker (1988) and Hooker & Weidmann (2000) identify the medio-lingual cuspid as a metastylid, originating from the cingulid. In this framework, the entoconid would also be placed distally.

We based our hypotheses of dental cusp(id) homologies of cainotheriids on the examination of: i) the genus *Robiacina* whose cranial features and dental pattern are very close to those of Eocene cainotheriids, and ii) the earliest documented cainotheriid, *Oxacron courtoisii* (Blondel 2005). According to Sudre (1969, 1977), *Robiacina* would be phylogenetically close to Cainotheriidae. Gentry & Hooker (1988) considered the genus as part of Cainotheriidae.

Concerning the premolars, the disto-lingual cusp of the upper premolars of *Oxacron* and *Robiacina* does not derive from the cingulum, and therefore is identified here as the protocone. For lower premolars, we consider that the medio-lingual cuspid of P/4 represent the metaconid and that the distal cuspid is the entoconid, by homology of position with lower molars. This corresponds to the nomenclature proposed by Gentry & Hooker (1988) and Boisserie *et al.* (2010).

For the lower molars, we identify the medio-lingual cuspid as a neoformed structure, in agreement with Sudre (1977), based on the presence of a small neoformed accessory cuspid at the base of the metaconid, in the lower molars of *Robiacina* (Fig. 1F, 1H). Indeed, the hypothesis of a duplication of the metaconid proposed by Sudre (1977) seem to be more parsimonious than a medio-lingual position of the entoconid and a concurrent lingual displacement of the hypoconulid as hypothesised by Hürzeler (1936). The latter hypothesis would imply a fusion/disappearance of the anterior and/or posterior crests of the talonid crescent, with a mesial migration of the entoconid and a lingual displacement of the hypoconulid. Moreover, according to this hypothesis, the entoconid would be located in front of the protocone during the occlusion with upper molars, contrary to most other artiodactyls (Sudre 1977). Finally, if Hürzeler's (1936) hypothesis is considered, with the hypoconulid in disto-lingual position on M/1 and M/2, what would then be the distalmost cuspid on the M/3? As concluded by Sudre (1977), the distalmost cuspid on M/3 is necessarily the hypoconulid. A hypoconulid is clearly visible on the M/1 and M/2 of *Robiacina*, positioned just distal to the entoconid (Fig. 1F). This disposition of the hypoconulid relative to the entoconid is also found on M/3 of Cainotheriidae, which lack a hypoconulid on M/1 and M/2. Finally, the hypothesis of a metastylid as medio-lingual cuspid, proposed by Gentry & Hooker (1988) and Hooker & Weidmann (2000), is here rejected as it does not originate from the cingulid, neither in *Robiacina*, nor in *Oxacron*. Contrary to Sudre (1977), we use the term 'metaconulid' instead of 'mesoconid', in order to homogenized with the nomenclatural system of Boisserie *et al*. (2010), and because mesoconid is used for another structure in other mammalian group (Klingener 1964; Skwara 1986; Hooker & Russell 2012).

Thus, according to the hypotheses of Sudre (1977; molars) and of Gentry & Hooker (1988) and Boisserie *et al*. (2010; premolars), the three lingual cuspids of lower molars would correspond to the metaconid (mesial), the metaconulid (medial, originates from metaconid duplication), and the entoconid (distal). The disto-lingual cusp of upper premolars is here identified as the protocone, and the mesial cuspid of lower premolars as the paraconid. The P/4 bears a metaconid (medio-lingual) and an entoconid (one distal).

Phylogenetic analysis

The heuristic search of the parsimony analysis retained a single parsimonious tree (L = 170, CI = 0.48, RI = 0.73; CI with only parsimony-informative characters = 0.46) (Fig. 13), reflecting a well-structured signal and relatively weakly homoplastic characters. Cainotheriidae are monophyletic and split into two subgroups, interpreted as subfamilies: Oxacroninae, with *Oxacron* and *Paroxacron*; and Cainotheriinae, with *Plesiomeryx*, *Caenomeryx*, and *Cainotherium*. Cainotheriidae, together with Mixtotheriidae, Anoplotheriidae and representatives of *Robiacina* form a clade, sister group to ruminants. Tylopoda split earlier in the tree, together with *Amphimeryx* and *Xiphodon*.

The monophyly of Cainotheriidae is supported by 13 non-ambiguous synapomorphies and a high Bremer index (IB = 7). They are characterised by the presence on their upper molars of a large parastyle similar to other styles (8^1; IR = 0.67), a disto-lingual protocone (11^2; IR = 0.94), a very strong dilambdodonty (20^1; IR = 0.88), a long (26^1; IR = 0.40) and distally orientated (27^1; IR = 1.00) postprotocrista, a postparacristula (29^1; IR = 0.86) and the lack of preprotocrista and paraconule junction (15^1; IR = 0.67); on their lower molars, they present a large (34^2; IR = 1.00) and individualised (35^0; IR = 1.00) metaconulid, a very distal entoconid and close to the hypoconulid (40^2; IR = 1.00), a neotrigonid (47^1; IR = 1.00), the absence of posthypocristulid (50^0; IR = 0.67) and hypoconulids on M/1 and M/2 (38^0; IR = 0.75). Cainotheriidae are composed of two clades: the Oxacroninae, characterised by the presence of styles without crests on upper molars (7^0; IR = 0.44), a protocone more mesial than the paracone on P4/ (56^1; IR= 0.50), as well as a biradiculate P/1 (70^1; IR = 1.00); Cainotheriinae, supported by the presence of a postparacristula buccally long joining the preprotocrista on upper molars (30^{1}; IR = 1.00)[30] and of a large postprotoconulid on lower premolars (69^{1}; IR = 1.00). They further differ from Oxacroninae by the presence of a uniradiculate P/1 (70^{0}; IR= 1.00) and large premolars (73^{1}; IR = 0.67), which represent plesiomorphic states of characters.

Within Oxacroninae, *Paroxacron* is paraphyletic. *Paroxacron bergeri* is excluded from the (*Paroxacron valdense*, *Oxacron courtoisii*) clade by the presence of quadrangular molars (31^{2}; IR = 0.60) with a pinched mesostyle (10^{1}; IR = 1.00) and the absence of diastemata between P1/-P2/ (5^{0}; IR = 0.50) and P/2-P/3 (6^{0}; IR = 0.33).

Within Cainotheriinae, *Cainotherium* is sister taxon to the clade (*Caenomeryx*, *Plesiomeryx*). *Cainotherium laticurvatum* is characterised by numerous autapomorphies, such as the absence of a valley between the entoconid and the metaconulid on lower molars (41^{0}; IR =0.78), the presence of a protocone at the same level (bucco-lingual axis) as the paraconule on the M3/ (17^{0}; IR= 0.50), the absence of a triangular P3/ (quandrangular shape) (61^{0}; IR = 0.50) and a wide cingulum/id on the premolars (72^{1}; IR = 0.50)[72]. The clade (*Caenomeryx*, *Plesiomeryx*) is supported by the presence of a protocone on P2/ (64^{1}; IR = 0.57) and diastemata between C-P1/ (3^{1}; IR=0.75) and P/1-P/2 (5^{1}; IR = 0.86).

Robiacina is sister taxon to the Cainotheriidae clade. This position is supported by the presence of a more distal (11 ;IR = 0.94) and lingual protocone (17^{1}; IR = 0.50) on upper molars and M3/, respectively, but also by sub-equal paracone and metacone on P3/ (60^{1}; IR = 1.00), the absence of protocone on P2/ (64^{0}; IR = 0.57), the presence of a small hypoconid on P/2-P/3 (67^{0}; IR = 0.75) and of a postprotoconulid on premolars (68^{1}; IR = 1.00). This result does not support the hypothesis of Sudre (1977) who placed *Robiacina* within Anoplotheriidae, close to Anoplotheriinae. Our results also slightly contrast with the hypothesis of Gentry & Hooker (1988) who placed *Robiacina* within Cainotheriidae. The clade composed of representatives of *Robiacina* is excluded from the Cainotheriidae clade by 13 unambiguous characters (see support of Cainotheriidae clade above) and it further differs from it by sharing three synapomorphies: sub-triangular upper molars (31^1; IR = 0.60), a small paraconule (14^0; IR = 0,43), and a short preparacrista (25^1; IR = 1,00). This marked morphological divergence between Cainotheriidae and the *Robiacina* clade leads us to recognise this clade as a new family, here named Robiacinidae. It would therefore constitute the closest family to Cainotheriidae, and forms with it the superfamily Cainotherioidea Camp & VanDerHoof, 1940.

Anoplotheriidae and Cainotherioidea form a clade (B) supported by the presence of a metaconulid (33^1; IR = 1.00), an entoconid positioned at the back of the hypoconid (40^1; IR = 1.00) and a valley between entoconid and metaconulid on the lower molars (41^1; IR = 0.78), as well as a connected paracone and metacone on P4/ (55^0; IR = 0.50). The Mixtotheriidae, Anoplotheriidae, and Cainotherioidea together form a clade (A) supported by the presence of a very large parastyle (8^0; IR = 0.67) and an absent to reduct postprotocrista (26^0; IR=0.40) on the upper molars, a 'loop-like' entoconid (39^1; IR = 1.00) on the lower molars, and the absence of a diastema between P/1-P/2 (5^0; IR = 0.86).

According to our results, Cainotherioidea, Anoplotheriidae and Mixtotheriidae are closer to Ruminantia than to Tylopoda. They share the presence of a protocone and a metaconule at the same level on M3/ (17^0; IR = 0.50), crested styles on P3/-P4/ (58^1; IR = 0.71), a large lingual cusp mesio-distally on P3/ (63^1; IR = 0.56), as well as a large hypoconid on P/3 and P/2 (67^1; IR = 0.75).

Impact on artiodactyl systematics

Cainotheriidae. According to our results (Fig. 13), *Paroxacron* is paraphyletic within Oxacroninae. Hooker & Weidmann (2000) proposed to synonymise the genera *Paroxacron* and *Oxacron*. However, *Oxacron* exhibits three autapomorphic characters: a short mesial lobe on the P3/ (62^0; IR = 0.25), a caniniform P/1 (71^0; IR= 0.50), and small paraconule (14^0; IR=0.43).

We therefore chose to maintain the genus *Oxacron*. *Paroxacron valdense* is the type species of *Paroxacron*. Our results raise the question of the erection of a new genus for the species *P. bergeri*. However, the latter has no dental autapomorphies based on our results. For the time being, based on dental data only, we therefore choose to keep *Paroxacron* as a paraphyletic assemblage.

Robiacinidae, fam. nov. Our results retrieve a monophyletic assemblage of *Robiacina* species. This clade appears as sister taxon to Cainotheriidae. This contrasts with the hypothesis of Hooker & Weidmann (2000), according to which *Robiacina lavergnensis* should be referred to *Mixtotherium*. Following these authors, *R. lavergnensis* shares many characters with the species of *Mixtotherium*: a short premetacristula, a pre-cingulum and crested styles on the upper molars; a prehypocristid fused with the postprotocristid, a basined hypoconulid in basin and a high crown on the lower molars, and a caniniform lower canine. However, we disagree on the coding of some of these characters for *Mixtotherium* by Hooker & Weidmann (2000). According to our observations, there is no basin on the hypoconulid, the premetacristula is long and the prehypocristid is unfused. Besides, the results of our phylogenetic analyses place *Robiacina* as sister taxon to Cainotheriidae, and far apart from *Mixtotherium*. The presence of crested styles in *Mixtotherium* and *R. lavergnensis* as mentioned by Hooker & Weidmann (2000) is here a symplesiomorphy. Contrary to Hooker & Weidmann (2000), we retain the binomen *Robiacina lavergnensis* instead of *Mixtotherium lavergnense*.

Cainotherioidea. We propose here to recognize the clade (Robiacinidae + Cainotheriidae) as defining the Cainotherioidea. The concept of this compound was defined by Simpson (1945) as single-family, then Hooker & Weidmann (2000) extended it by including the genera *Robiacina* and *Mixtotherium*. However, and according to our results, we propose here to exclude *Mixtotherium* from the Cainotherioidea.

Relationships of Cainotheriidae within Artiodactyla

The phylogenetic position of Cainotheriidae within Artiodactyla remains controversial. Gentry & Hooker (1988, fig. 9.8) supported the placement of cainotheriids within Tylopoda in their (informal) "preferred analysis", but retrieved them in a much more basal position, in their formal analysis (Gentry & Hooker 1988, fig. 9.7), i.e. outside of the "Selenodontia" clade (i.e., Tylopoda + Ruminantia). More recent phylogenetic analyses placed them either close to Tylopoda (e.g., Geisler & Uhen 2003, Geisler *et al*. 2007, Thewissen *et al*. 2007), or as an early offshoot of a wide clade including Ruminantia (e.g., Geisler & Uhen 2005; O'Leary & Gatesy 2007, Lihoreau *et al*. 2015). Our results are congruent with the previous studies that excluded Cainotheriidae from Tylopoda (Webb & Taylor 1980), and placed Cainotheriidae closer to Ruminantia (Geisler & Uhen 2005; O'Leary & Gatesy 2007; Lihoreau *et al*. 2015). Indeed, according to our sample, Cainotherioidea, Anoplotheriidae and Mixtotheriidae are sister group to Ruminantia. As far as direct relationships of Cainotherioidea are concerned, according to our results, Anoplotheriidae are their closest relatives.

It is worth noting that the nomenclature chosen here has an impact on the primary homology hypothesies underlaying the definition of phylogenetic characters. Indeed, the presence of a metaconulid (33) is retrieved as a synapormorphy of the Anoplotheriidae and Cainotherioidea clade (clade B in Figure 13, cf. below). If we consider an alternative primary homology hypothesis and identify the medio-lingual cuspid of the lower molars as a metastylid (following Gentry and Hooker, 1988 and Hooker and Weidmann, 2000), as for Mixotheriidae, coding of four characters (33 – 36) would be modified. However, the topology of the tree is not impacted by this new coding.

These relationships rely on dental characters only and it is necessary to extend the data matrix with mandibular, cranial and post-cranial characters, in order to test further the phylogenetic relationship of Cainotheriidae. These characters could bring additional support to clades with relatively low Bremer index.

Evolutionary history of Cainotheriidae around the Grande Coupure

Dams karstic network is a new exceptional fossiliferous compound locality documenting the evolutionary history of Cainotheriidae around the Grande Coupure (pre- and -post), through MP19 and MP22 fossiliferous infillings. The first documented representatives of Cainotheriidae are Oxacroninae (Fig. 14). They appear in the fossil record during the late Eocene between MP18-MP19 with two species, *Oxacron courtoisii* and *Paroxacron valdense* (Blondel 2005; Hooker & Weidmann 2000; Legendre 1980). Representatives of Cainotheriinae occur shortly after Oxacroninae, around MP19 with *Cainotherium commune*? (Blondel 2005). This diversity of Cainotheriidae during the late Eocene is not recorded at Dams, where only *Paroxacron valdense* is documented in DAM1 (MP19). However, Dams highlights a second, post-Grande Coupure, phase of diversification of Cainotheriidae, as suggested – based on other localities – by Blondel (2005), that took place at the beginning of the Oligocene. Indeed, at least five species are retrieved in DAM3 (MP22) and this specific diversity is also observed in other fossiliferous localities of Quercy such as Pech Crabit (six species) and Mas de Got (four species; Blondel 2005). The phase of diversification occurs mainly in Cainotheriinae, with the differentiation of five species belonging to *Plesiomeryx* (*Ple*. *cadurcensis* and *Ple*. *huerzeleri*), *Caenomeryx* (*Cae*. cf. *procommunis* and *Cae*. *filholi*) and *Cainotherium* (*Cainotherium* sp.) (Fig. 14). Among Oxacroninae, two new species also appear in the fossil record after the Grande Coupure: *Paroxacron* sp. and *Paroxacron bergeri*. The two subfamilies of Cainotheriidae thus survive to the Grande Coupure.

The Eocene-Oligocene transition further documents a body size increase in Cainotheriidae, as shown in *Plesiomeryx huerzeleri*, *Paroxacron bergeri* but also representatives of *Caenomeryx* and *Cainotherium* (see Tab. S1-S12). However, small species are still present after the Grande Coupure with *Paroxacron* sp. and *Plesiomeryx cadurcensis*. This reflects an increase in the size range of Cainotheriidae after the Grande Coupure, and thus likely an expansion in the occupation of different ecological niches. It is probable that the Cainotheriidae were quite generalist in terms of diet, and that they took the ecological niches released by endemic families of Europe which had became extinct at this transition, such as Xiphodontidae, Dacrytheriinae, or Mixtotheriidae (Blondel 2001).

The Grande Coupure coincides with a major mammalian faunal turnover concurrent to climatic, geographic, and oceanic circulation changes (Legendre 1987; Berggren & Prothero 1992; Akhmetiev & Beniamovski 2009). The increase of the chewing surface, with the appearance of more quadrangular molars, and the reduction of diastemata as observed in some species of Oligocene Cainotheriidae (notably in Dams) could be linked to changes in their diet (Fig. 14; Blondel 2001). Environmental changes were drastic during the concerned interval, with a shift from a rainforest under tropical/sub-tropical conditions to open environments under a much drier climate (Collinson 1992; Cavagnetto & Anadón 1996; Akhmetiev & Beniamovski 2009).

Conclusion

Dams is an exceptional fossil site that yields distinct deposits broadly bracketing the Grande Coupure. Cainotheriid remains are documented by thousands specimens and as such, they allow for in-depth insights into the history and systematics of this family. In the DAM1 deposits (MP19, late Eocene), a single species occurs: *Paroxacron valdense*. The DAM3 channel (MP22, early Oligocene) yields a higher taxonomic diversity with at least five species: *Paroxacron* sp., *Paroxacron bergeri*, *Plesiomeryx huerzeleri*, *Plesiomeryx cadurcensis*, and

Caenomeryx cf. *procommunis*. Dams localities highlight a phase of local diversification of cainotheriids by early Oligocene times, thus confirming the hypothesis of Blondel (2005). Among Cainotheriidae, this diversity increase mainly concerns Cainotheriinae. Yet, both Cainotheriinae and Oxacroninae survive to major environmental changes related to the Grande Coupure, contrary to many other European endemic artiodactyls.

Our phylogenetic analysis, including Dams taxa described in this work, constitutes the first formal phylogeny of Cainotheriidae. Our results, based on dental characters, allow for (i) clarifying relationships within Cainotheriidae, with Oxacroninae as sister group to Cainotheriinae, (ii) defining *Robiacina* (and the new family Robiacinidae) as being the sister taxon to Cainotheriidae among Cainotherioidea and, more broadly, (iii) discussing the controversial position of Cainotheriidae within Artiodactyla, as being more closely related to Ruminantia than to Tylopoda.

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Figure captions

Figure 1. Dental diagrams in occlusal view. P/4 of Cainotheriidae: **A**, Nomenclature of Berthet (2003); **B**, Nomenclature of Boisserie *et al*. (2010). M/1-M/2 of Cainotheriidae: **C**, Nomenclature of Hürzeler (1936); **D**, Nomenclature of Sudre (1977); **E**, Nomenclature of Gentry & Hooker (1988). M/1-M/2: **F**, *Robiacina*; **G**, *Dacrytherium*. M/3: **H**, *Robiacina*; **I**, Cainotheriidae. **Proto^{ulid}.**, protoconulid. For the rest of the legend, see Fig. 2.

Figure 2. Dental diagrams of the *Paroxacron valdense* dentition according to dental nomenclature of Boisserie *et al*. (2010). **A**, **B**, M1/-M2/; **C**, **D**, M/3; **E**, I1/; **F**, I/1. In occlusal view: **A**, **B**, **C**, **D**. In lingual view: **E**, **F**. Abbreviations: dist., distostyle; med., mediostyle; mes., mesostyle; met., metastyle; par., parastyle; **Meta.**, metacone; **Meta^{ul}.**, metaconule; **Para.**, paracone; **Para^{ul}.**, paraconule; **Proto.**, protocone; post^{ylid}., poststylid; pre^{ylid}., prestylid; **Centro^{ulid}.**, centroconulid; **Ento^{d}.**, entoconid; **Hypo^{d}.**, hypoconid; **Hypo^{ulid}.**, hypoconulid; **Meta^{d}.**, metaconid; **Meta^{ulid}.**, metaconulid; **Para^{d}.**, paraconid; **Post^{ulid}.**, postconulid; **Pre^{ulid}.**, preconulid; **Proto^{d}.**, protoconid; -c., -crista; -c^{ula}., -cristula; -c^{yla}., -cristyla ; -c^{id}., -cristid ; -c^{ulid}., -cristulid; -c^{ylid}., -cristylid; -f., fossa; -f^{id}., fossid. Full circles: cusp/style/conule/conulid; full lines: crest; dashed lines: valley/fosse; dotted lines: cingulum/cingulid; bold dashed lines: lobe contour; bold full lines: crown contour.

Figure 3. Dental diagrams of the permanent lower dentition of *Paroxacron valdense*. **A**, **B**, P/1-2; **C**, **D**, P/3; **E**, **F**, P/4; **G**, **H**, M/1-2; **I**, **J**, M/3; **K**, I/2-3; **L**, lower canine. In occlusal view: **A**, **C**, **E**, **G**, **I**. In lingual view: **B**, **D**, **F**, **K**, **L**. In buccal view: **H**, **J**. Scale 1mm. Abbreviations: **Postproto^{ulid}.**, postprotoconulid; disto^{ylid}., distostylid; co^{ulid} x., conulid x.

Figure 4. Dental diagrams of the permanent upper dentition of *Paroxacron valdense*. **A**, **B**, P1/; **C**, **D**, P2/; **E**, **F**, P3/; **G**, **H**, P4/; **I**, M1-2/; **J**, I3/; **K**, I2/; **L**, upper canine. In occlusal view: **A**, **C**, **E**, **G**. In lingual view: **B**, **D**, **F**, **H**, **I, J**, **K**, **L**. Scale 1mm. Abbreviations: co^{ul} x., conule x.

Figure 5. Dental diagrams of the deciduous dentition of *Paroxacron valdense*. **A**, **B**, DP/1; **C**, **D**, DP/2-3; **E**, **F**, DP/4; **G**, **H**, DP1-2/; **I**, **J**, DP3/; **K**, **L**, DP4/. In occlusal view: **A**, **C**, **E**, **G**, **I**, **K**. In lingual view: **B**, **D**, **H**, **J**, **L**. In buccal view: **F**. Scale 1 mm. Abbreviations: **Primo^{id}.**, primoconid.

Figure 6. Material of the lower dentition of *Paroxacron valdense*. **A**, right I/1 (DAM1 174); **B**, left I/2-3 (DAM1 194; mirror view); **C**, right lower canine (DAM1 199); **D**, **E**, right P/1 (DAM1 40); **F**, **G**, right DP/1 (DAM1 126); **H**, ; **I**, left DP/2-3 (DAM1 117); **J**, ; **K**, left DP/4 (DAM1 103); **L**, left mandibular fragment with P/1-M/3 (DAM1 22); **M**, left P/3 (DAM1 269); **N**, right mandibular fragment with P/2-

M/3 (DAM1 21); **O**, left mandibular fragment with P/1-M/3 (DAM1 22); **P**, **Q**, right mandibular fragment with M/3 (DAM1 268); **R**, right mandibular fragment with P/2-M/3 (DAM1 21). In lingual view: **A**, **B**, **C**, **E**, **G**, **I**, **Q**. In occlusal view: **D**, **F**, **H**, **J**, **L**, **N**. In buccal view: **K**, **M**, **O**, **P**, **R**. Scale 1 mm.

Figure 7. Material of the upper dentition of *Paroxacron valdense*. **A**, right I3/ (DAM1 252) ; **B**, right I2/ (DAM1 228); **C**, right I1/ (DAM1 213); **D**, left upper canine (DAM1 261); **E**, **F**, right DP1-2/ (DAM1 164); **G**, **H**, right DP3/ (DAM1 160); **I**, **J**, left P1/ (DAM1 66); **K**, **L**, right DP4/ (DAM1 144); **M**, right maxillary fragment with P1/-M3/ (DAM1 08). In lingual view: **A**, **B**, **C**, **D**, **F**, **H**, **I**, **L**. In occlusal view: **E**, **G**, **J**, **K**, **M**. Scale 1 mm.

Figure 8. Material of the *Paroxacron* sp. dentition. **A**, **B**, right P4/ (DAM3 09; mirror view); **C**, **D**, right M1/ (DAM1 06; mirror view); **E**, **F**, left M2/ (DAM3 04); **G**, **H**, left M3/ (DAM3 03); **I**, **J**, left M/2 (DAM3 21; mirror view); **K**, **L**, right M/3 (DAM3 11); **M**, **N**, right P1/ (DAM3 10; mirror view); **O**, **P**, right P/1 (DAM3 20; mirror view); **Q**, **R**, right P/2 (DAM3 19); **S**, **T**, left DP/4 (DAM3 17; mirror view); **U**, **V**, left M/1 (DAM3 16; mirror view). In occlusal view: **A**, **C**, **E**, **G**, **I**, **K**, **M**, **O**, **Q**, **S**, **U**. In lingual view: **B**, **D**, **F**, **H**, **N**, **P**, **R**. In buccal view: **J**, **L**, **T**, **V**.

Figure 9. Material of the *Paroxacron bergeri* dentition. **A**, **B**, left P4/ (DAM3 30); **C**, **D**, left M1/ (DAM3 29); **E**, **F**, right M2/ (DAM3 26; mirror view); **G**, **H**, right M3/ (DAM3 24; mirror view); **I**, **J**, left P1/ (DAM3 33); **K**, **L**, left P2/ (DAM3 32); **M**, **N**, right P3/ (DAM3 31; mirror view). In occlusal view: **A**, **C**, **E**, **G**, **I**, **K**, **M**. In lingual view: **B**, **D**, **F**, **H**, **J**, **L**, **N**.

Figure 10. Material of the *Plesiomeryx cadurcensis* dentition. **A**, **B**, right P3/ (DAM3 48; mirror view); **C**, **D**, right P4/ (DAM3 47; mirror view; **E**, **F**, right M1/ (DAM3 44; mirror view); **G**, **H**, left M2/ (DAM3 37); **I**, **J**, left M3/ (DAM3 34); **K**, **L**, left M/3 (DAM3 52; mirror view); **M**, **N**, right P1/ (DAM3 50; mirror view); **O**, **P**, right P2/ (DAM3 51; mirror view); **Q**, **R**, right DP4/ (DAM3 45; mirror view); **S**, **T**, right P/2 (DAM3 77); **U**, **V**, right mandibular fragment with P/3-P/4 (DAM3 79); **W**, **X**, right M/1

(DAM3 61); **Y**, **Z**, left M/2 (DAM3 56; mirror view). In occlusal view: **A**, **C**, **E**, **G**, **I**, **K**, **M**, **O**, **Q**, **S**, **U**, **W**, **Y**. In lingual view: **B**, **D**, **F**, **H**, **J**, **N**, **P**, **R**, **T**, **V**. In buccal view: **L**, **X**, **Z**.

Figure 11. Material of the *Plesiomeryx huerzeleri* dentition. **A**, **B**, left maxillary fragment with P3/-P4/ (DAM3 101); **C**, **D**, right M1/ (DAM3 88; mirror view); **E**, **F**, right M2/ (DAM3 83; mirror view); **G**, **H**, right M3/ (DAM3 81; mirror view); **I**, **J**, right M/1 (DAM3 111); **K**, **L**, right M/2 (DAM3 107); **M**, **N**, right M/3 (DAM3 103); **O**, **P**, left P1/ (DAM3 100); **Q**, **R**, left P2/ (DAM3 99); **S**, **T**, right P/1 (DAM3 127); **U**, **V**, right P/2 (DAM3 126); **W**, **X**, left mandibular fragment with P/4-P/3 (DAM3 128; mirror view); **Y**, **Z**, right DP/2-3 (DAM3 115); **A'**, **B'**, left DP/4 (DAM3 114; mirror view). In occlusal view: **A**, **C**, **E**, **G**, **I**, **K**, **M**, **O**, **Q**, **T**, **U**, **W**, **Y**, **A'**. In lingual view: **B**, **D**, **F**, **H**, **P**, **R**, **S**, **V**, **X**, **Z**. In buccal view: **J**, **L**, **N**, **B'**.

Figure 12. Material of the *Caenomeryx* cf. *procommunis* dentition. **A**, **B**, right P3/ (DAM3 135; mirror view); **C**, **D**, left M1/ (DAM3 133); **E**, **F**, right M2/ (DAM3 132; mirror view); **G**, **H**, right M3/ (DAM3 129; mirror view; **I**, **J**, right DP/2-3 (DAM3 145); **K**, **L**, right mandibular fragment with P/4-M/3 (DAM3 152); **M**, **N**, left P/1 (DAM3 149; mirror view); **O**, **P**, left P/2 (DAM3 148; mirror view); **Q**, **R**, right P3/ (DAM3 147). In occlusal view: **A**, **C**, **E**, **G**, **I**, **K**, **M**, **O**, **Q**. In lingual view: **B**, **D**, **F**, **H**, **J**, **N**, **P**, **R**. In buccal view: **L**.

Figure 13. Phylogeny of Cainotheriidae and their position within artiodactyls. Most parsimonious tree at 170 steps, with IC=0.48 and IR=0.73. The Bremer Index (IB) is indicated in bold at each node. **X** ● a - b: **X**, node number; a, number of synapomorphies; b, number of ambiguous characters (Acctran optimization).

Figure 14. Trends and stratigraphical extensions of cainotheriid species from Quercy, around the Grande Coupure (modified from Blondel (2005; fig. 5) on the stratigraphical position of *Paroxacron valdense* and *Paroxacron* sp., with the attribution of Escamps specimens to *Paroxacron valdense*).

Dotted-line: long diastemata, sub-triangular molars; simple line: diastemata reduction trend, quadrangular molars.

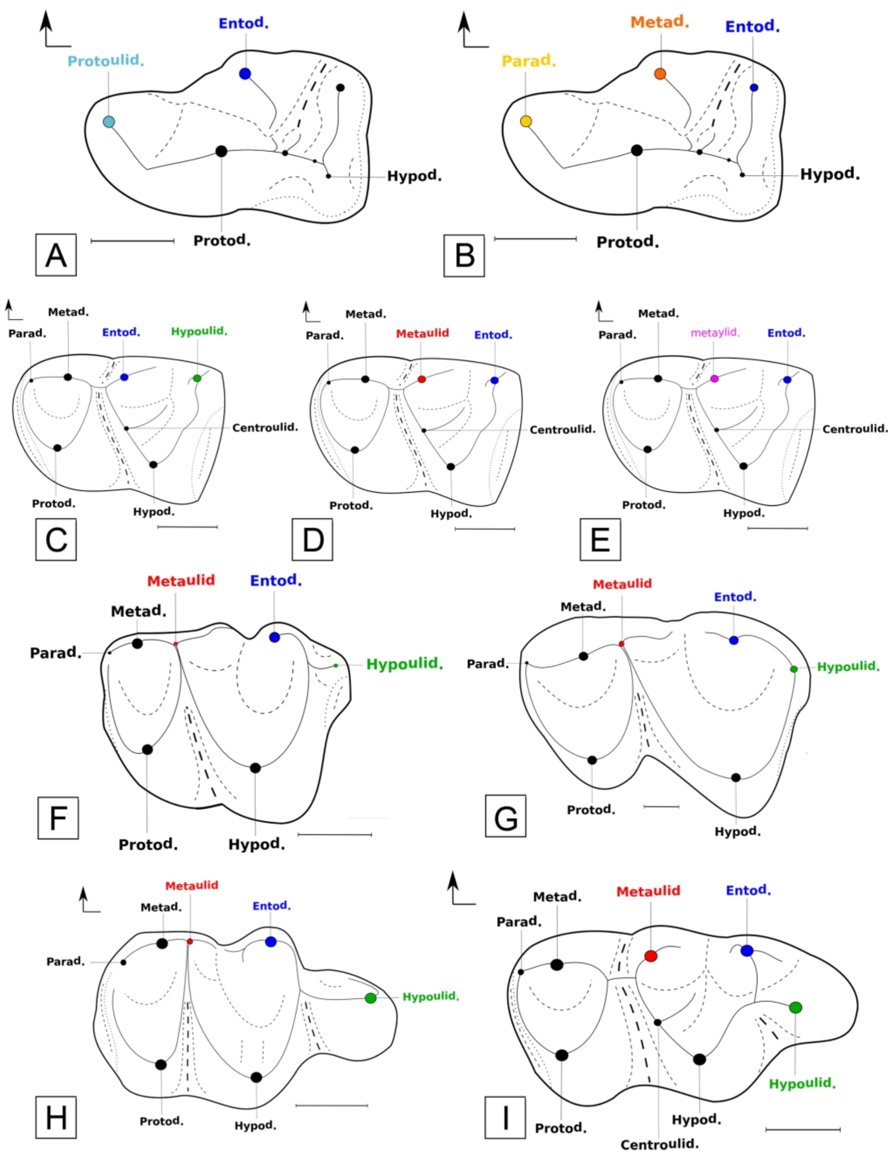

Figure 1. Dental diagrams in occlusal view. P/4 of Cainotheriidae: A, Nomenclature of Berthet (2003); B, Nomenclature of Boisserie et al. (2010). M/1-M/2 of Cainotheriidae: C, Nomenclature of Hürzeler (1936); D, Nomenclature of Sudre (1977); E, Nomenclature of Gentry & Hooker (1988). M/1-M/2: F, Robiacina; G, Dacrytherium. M/3: H, Robiacina; I, Cainotheriidae. Protoulid., protoconulid. For the rest of the legend, see Fig. 2.

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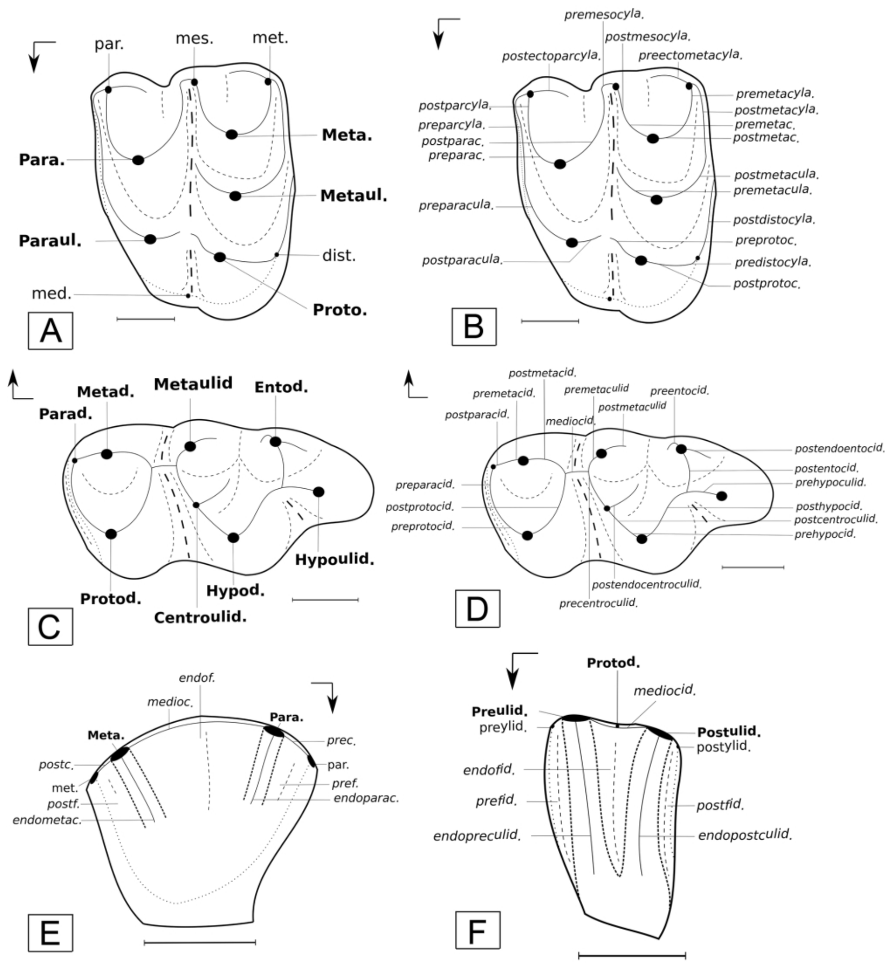

Figure 2. Dental diagrams of the Paroxacron valdense dentition according to dental nomenclature of Boisserie et al. (2010). A, B, M1/-M2/; C, D, M/3; E, I1/; F, I/1. In occlusal view: A, B, C, D. In lingual view: E, F. Abbreviations: dist., distostyle; med., mediostyle; mes., mesostyle; met., metastyle; par., parastyle; Meta., metacone; Metaul., metaconule; Para., paracone; Paraul., paraconule; Proto., protocone; postylid., poststylid; preylid., prestylid; Centroulid., centroconulid; Entod., entoconid; Hypod., hypoconid; Hypoulid., hypoconulid; Metad., metaconid; Metaulid., metaconulid; Parad., paraconid; Postulid., postconulid; Preulid., preconulid; Protod., protoconid; -c., -crista; -cula., -cristula; -cyla., -cristyla ; -cid., -cristid ; -culid., -cristulid; -cylid., -cristylid; -f., fossa; -fid., fossid. Full circles: cusp/style/conule/conulid; full lines: crest; dashed lines: valley/fosse; dotted lines: cingulum/cingulid; bold dashed lines: lobe contour; bold full lines: crown contour.

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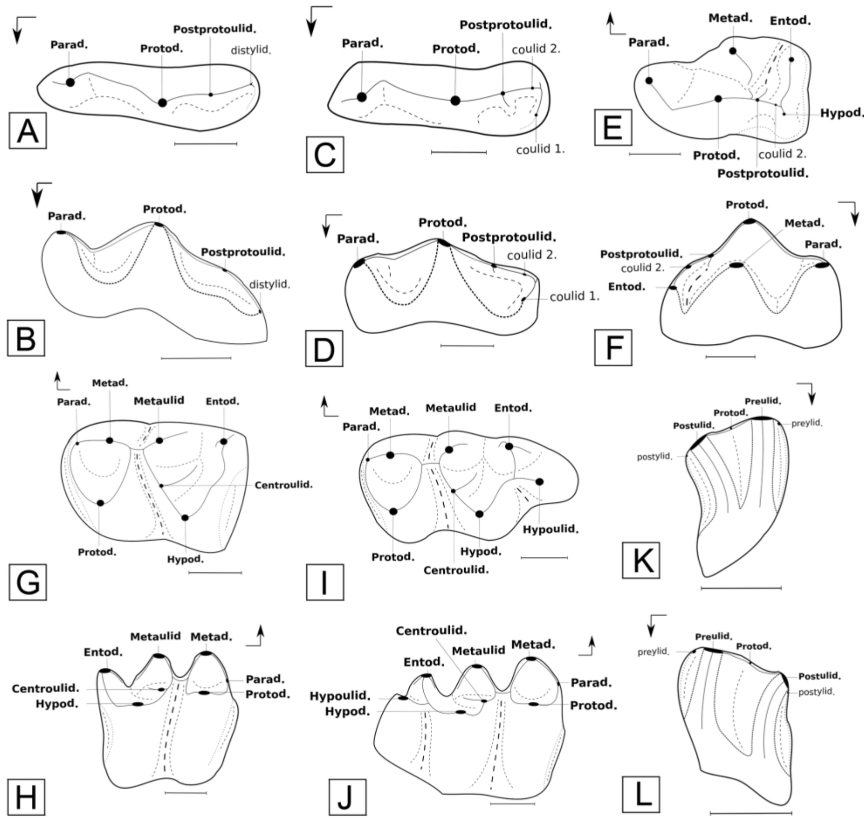

Figure 3. Dental diagrams of the permanent lower dentition of Paroxacron valdense. A, B, P/1-2; C, D, P/3; E, F, P/4; G, H, M/1-2; I, J, M/3; K, I/2-3; L, lower canine. In occlusal view: A, C, E, G, I. In lingual view: B, D, F, K, L. In buccal view: H, J. Scale 1mm. Abbreviations: Postprotoulid., postprotoconulid; distoylid., distostylid; coulid x., conulid x.

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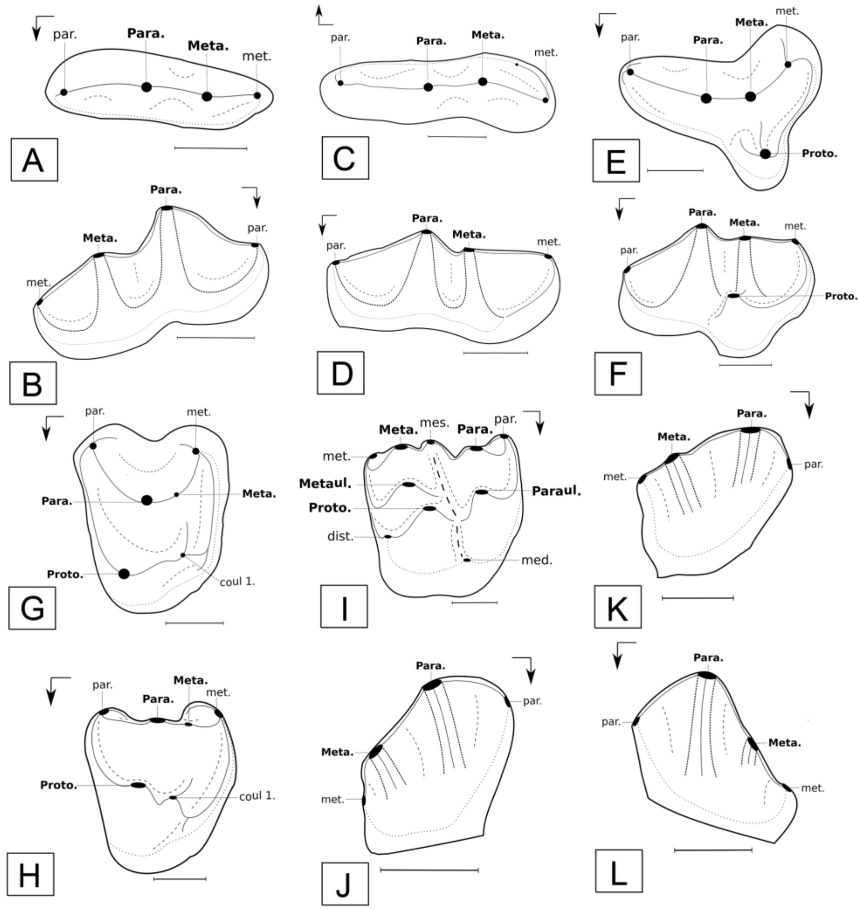

Figure 4. Dental diagrams of the permanent upper dentition of Paroxacron valdense. A, B, P1/; C, D, P2/; E, F, P3/; G, H, P4/; I, M1-2/; J, I3/; K, I2/; L, upper canine. In occlusal view: A, C, E, G. In lingual view: B, D, F, H, I, J, K, L. Scale 1mm. Abbreviations: coul x., conule x.

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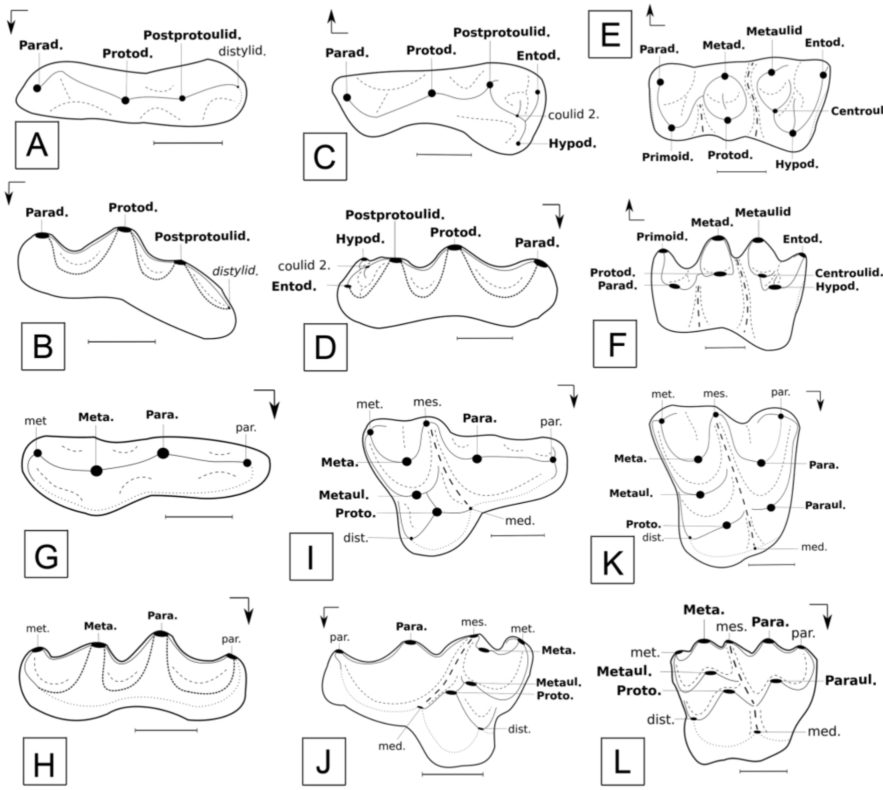

Figure 5. Dental diagrams of the deciduous dentition of Paroxacron valdense. A, B, DP/1; C, D, DP/2-3; E, F, DP/4; G, H, DP1-2/; I, J, DP3/; K, L, DP4/. In occlusal view: A, C, E, G, I, K. In lingual view: B, D, H, J, L. In buccal view: F. Scale 1 mm. Abbreviations: Primoid., primoconid.

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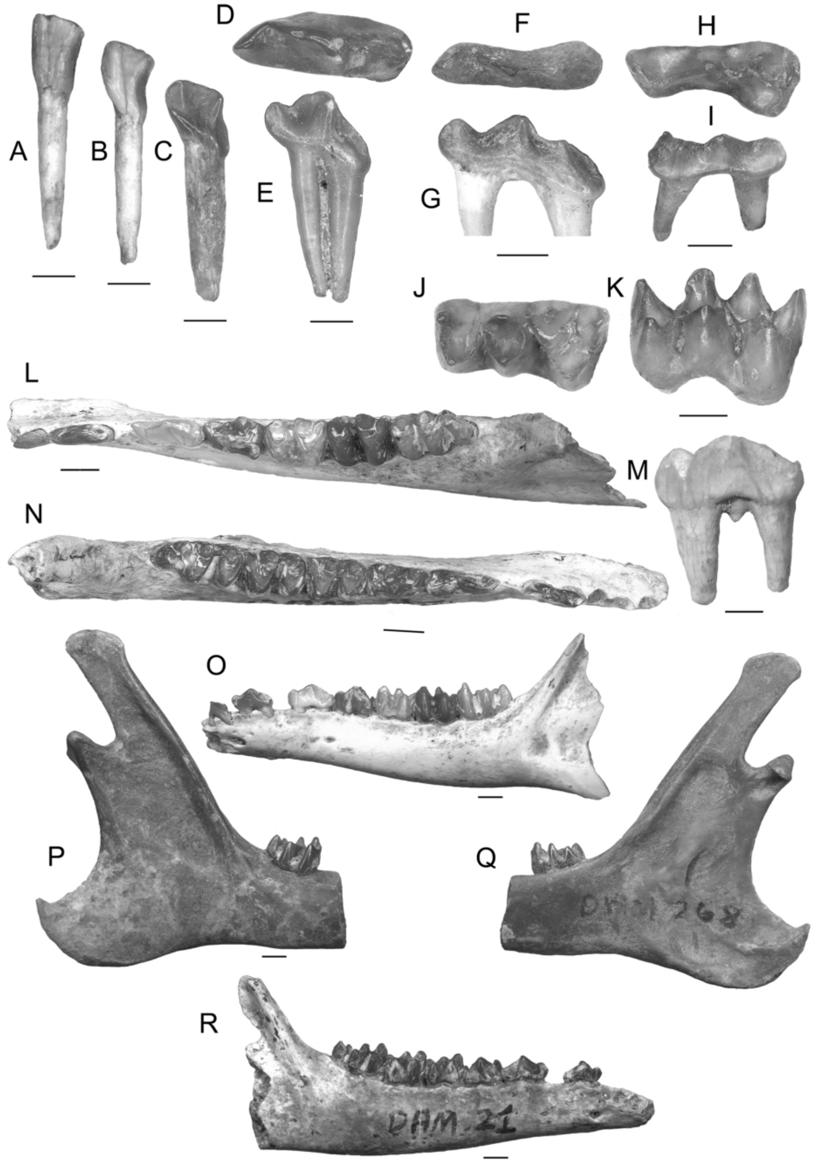

Figure 6. Material of the lower dentition of Paroxacron valdense. A, right I/1 (DAM1 174); B, left I/2-3 (DAM1 194; mirror view); C, right lower canine (DAM1 199); D, E, right P/1 (DAM1 40); F, G, right DP/1 (DAM1 126); H, ; I, left DP/2-3 (DAM1 117); J, ; K, left DP/4 (DAM1 103); L, left mandibular fragment with P/1-M/3 (DAM1 22); M, left P/3 (DAM1 269); N, right mandibular fragment with P/2-M/3 (DAM1 21); O, left mandibular fragment with P/1-M/3 (DAM1 22); P, Q, right mandibular fragment with M/3 (DAM1 268); R, right mandibular fragment with P/2-M/3 (DAM1 21). In lingual view: A, B, C, E, G, I, Q. In occlusal view: D, F, H, J, L, N. In buccal view: K, M, O, P, R. Scale 1 mm.

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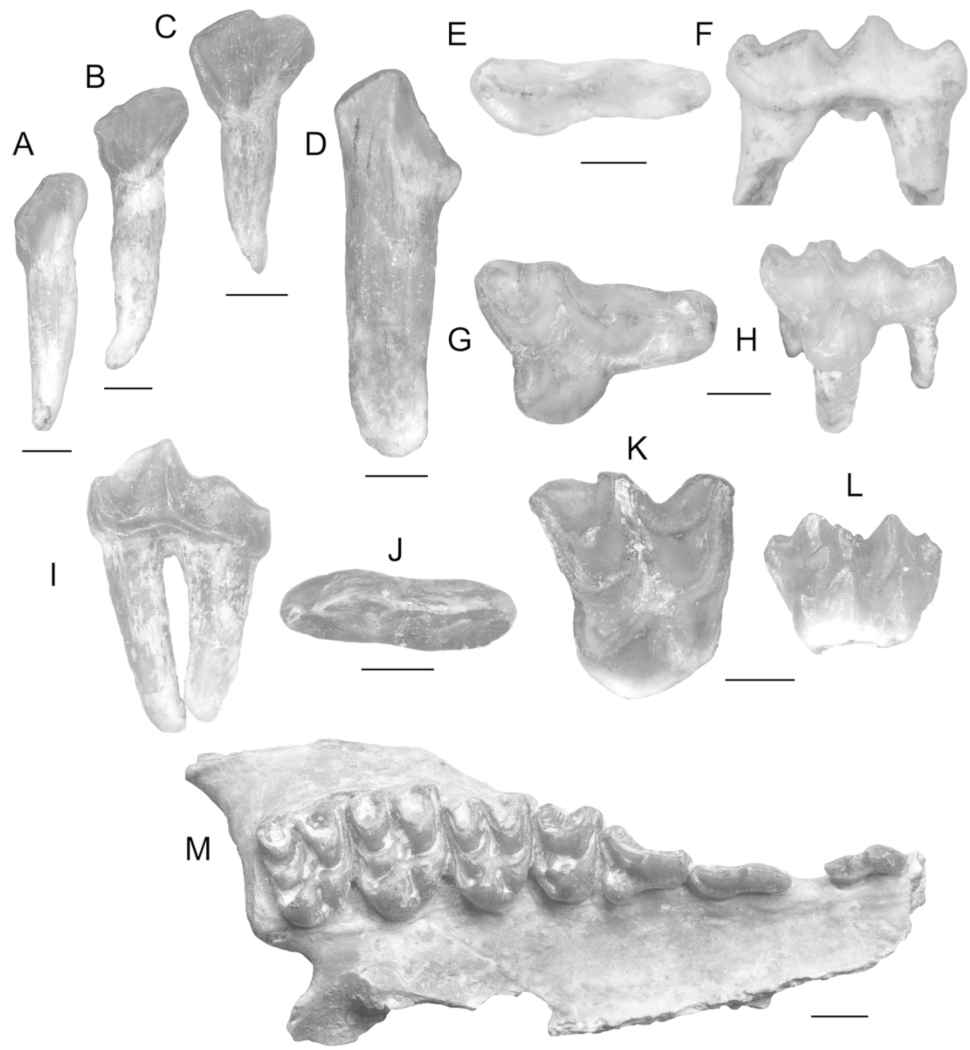

Figure 7. Material of the upper dentition of Paroxacron valdense. A, right I3/ (DAM1 252) ; B, right I2/ (DAM1 228); C, right I1/ (DAM1 213); D, left upper canine (DAM1 261); E, F, right DP1-2/ (DAM1 164); G, H, right DP3/ (DAM1 160); I, J, left P1/ (DAM1 66); K, L, right DP4/ (DAM1 144); M, right maxillary fragment with P1/-M3/ (DAM1 08). In lingual view: A, B, C, D, F, H, I, L. In occlusal view: E, G, J, K, M. Scale 1 mm.

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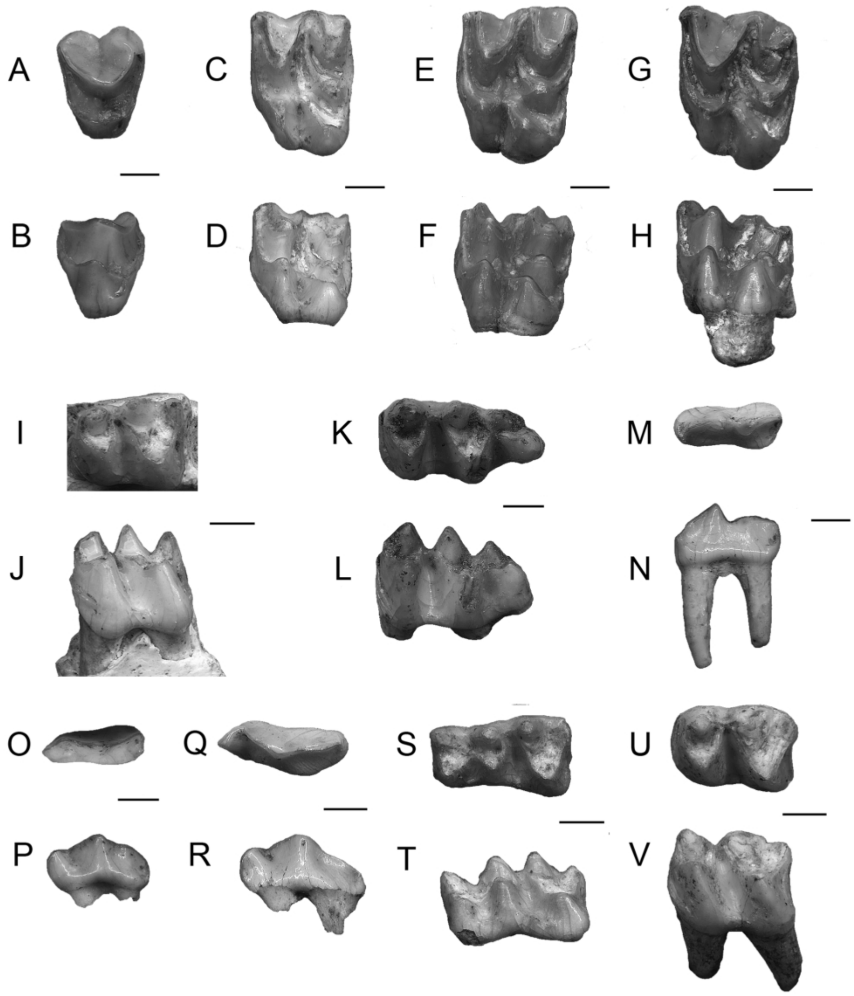

Figure 8. Material of the Paroxacron sp. dentition. A, B, right P4/ (DAM3 09; mirror view); C, D, right M1/ (DAM1 06; mirror view); E, F, left M2/ (DAM3 04); G, H, left M3/ (DAM3 03); I, J, left M/2 (DAM3 21; mirror view); K, L, right M/3 (DAM3 11); M, N, right P1/ (DAM3 10; mirror view); O, P, right P/1 (DAM3 20; mirror view); Q, R, right P/2 (DAM3 19); S, T, left DP/4 (DAM3 17; mirror view); U, V, left M/1 (DAM3 16; mirror view). In occlusal view: A, C, E, G, I, K, M, O, Q, S, U. In lingual view: B, D, F, H, N, P, R. In buccal view: J, L, T, V.

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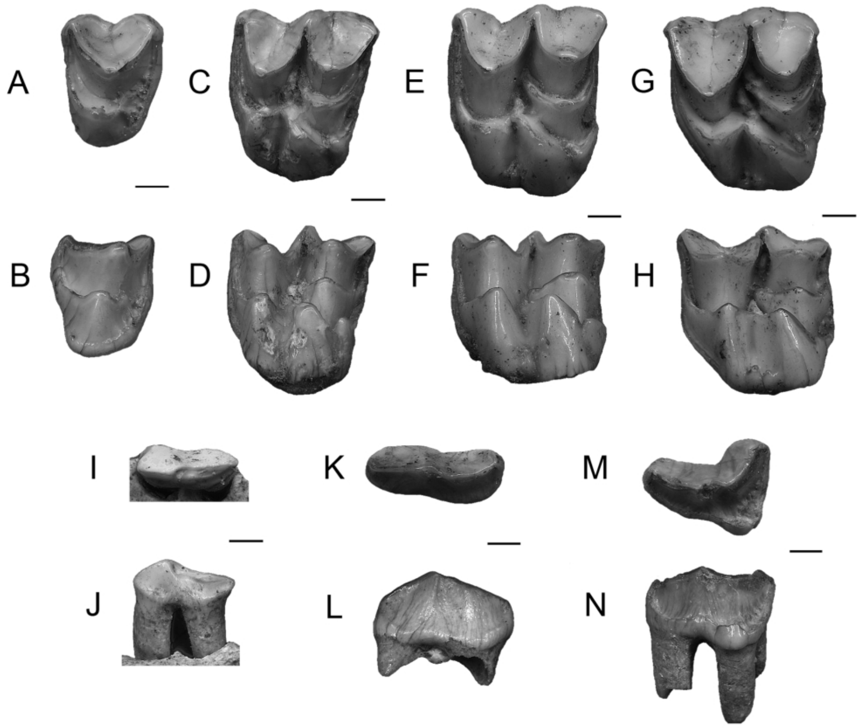

Figure 9. Material of the Paroxacron bergeri dentition. A, B, left P4/ (DAM3 30); C, D, left M1/ (DAM3 29); E, F, right M2/ (DAM3 26; mirror view); G, H, right M3/ (DAM3 24; mirror view); I, J, left P1/ (DAM3 33); K, L, left P2/ (DAM3 32); M, N, right P3/ (DAM3 31; mirror view). In occlusal view: A, C, E, G, I, K, M. In lingual view: B, D, F, H, J, L, N.

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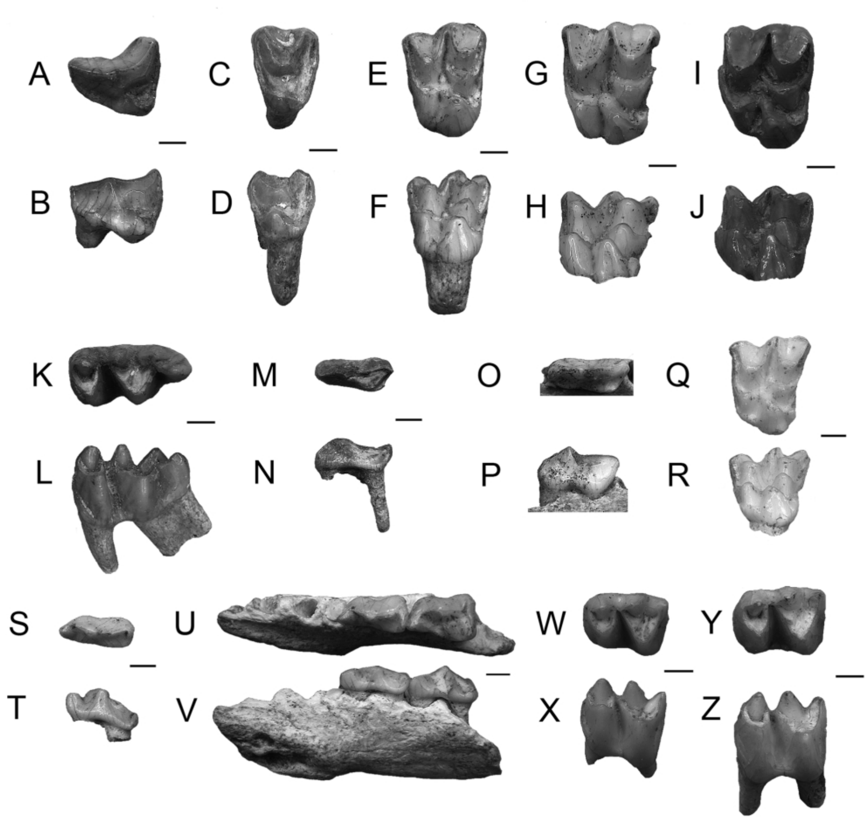

Figure 10. Material of the Plesiomeryx cadurcensis dentition. A, B, right P3/ (DAM3 48; mirror view); C, D, right P4/ (DAM3 47; mirror view; E, F, right M1/ (DAM3 44; mirror view); G, H, left M2/ (DAM3 37); I, J, left M3/ (DAM3 34); K, L, left M/3 (DAM3 52; mirror view); M, N, right P1/ (DAM3 50; mirror view); O, P, right P2/ (DAM3 51; mirror view); Q, R, right DP4/ (DAM3 45; mirror view); S, T, right P/2 (DAM3 77); U, V, right mandibular fragment with P/3-P/4 (DAM3 79); W, X, right M/1 (DAM3 61); Y, Z, left M/2 (DAM3 56; mirror view). In occlusal view: A, C, E, G, I, K, M, O, Q, S, U, W, Y. In lingual view: B, D, F, H, J, N, P, R, T, V. In buccal view: L, X, Z.

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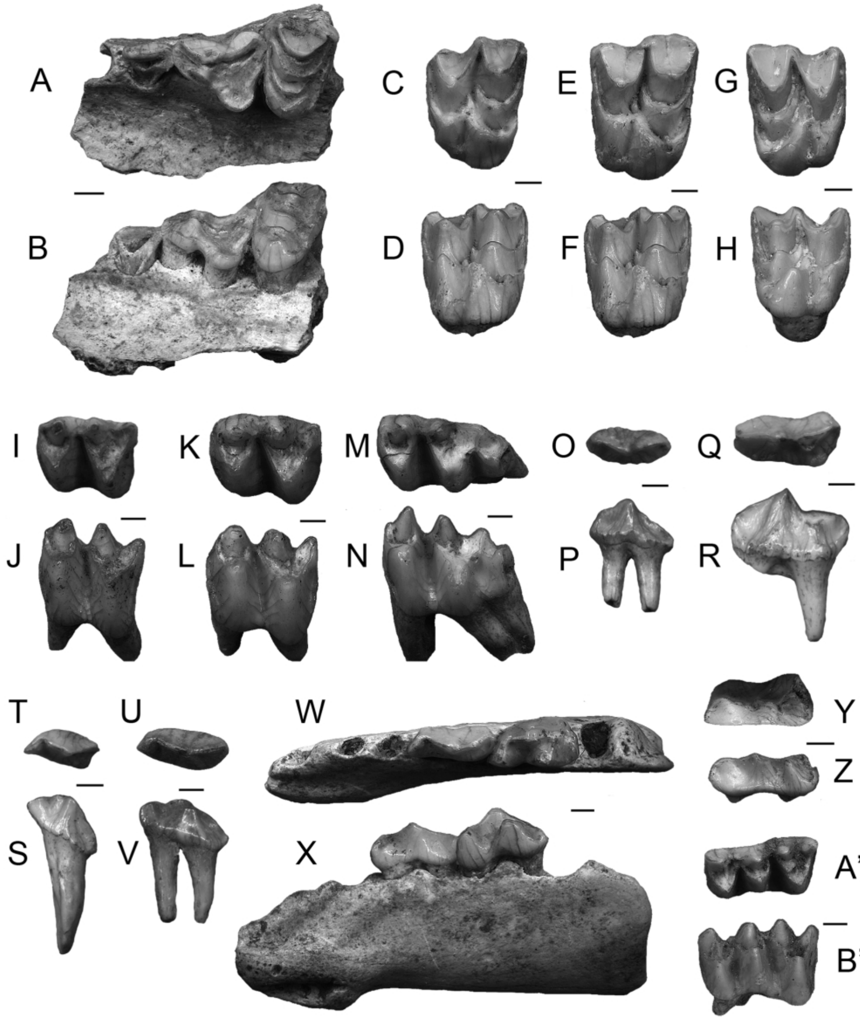

Figure 11. Material of the Plesiomeryx huerzeleri dentition. A, B, left maxillary fragment with P3/-P4/ (DAM3 101); C, D, right M1/ (DAM3 88; mirror view); E, F, right M2/ (DAM3 83; mirror view); G, H, right M3/ (DAM3 81; mirror view); I, J, right M/1 (DAM3 111); K, L, right M/2 (DAM3 107); M, N, right M/3 (DAM3 103); O, P, left P1/ (DAM3 100); Q, R, left P2/ (DAM3 99); S, T, right P/1 (DAM3 127); U, V, right P/2 (DAM3 126); W, X, left mandibular fragment with P/4-P/3 (DAM3 128; mirror view); Y, Z, right DP/2-3 (DAM3 115); A', B', left DP/4 (DAM3 114; mirror view). In occlusal view: A, C, E, G, I, K, M, O, Q, T, U, W, Y, A'. In lingual view: B, D, F, H, P, R, S, V, X, Z. In buccal view: J, L, N, B'.

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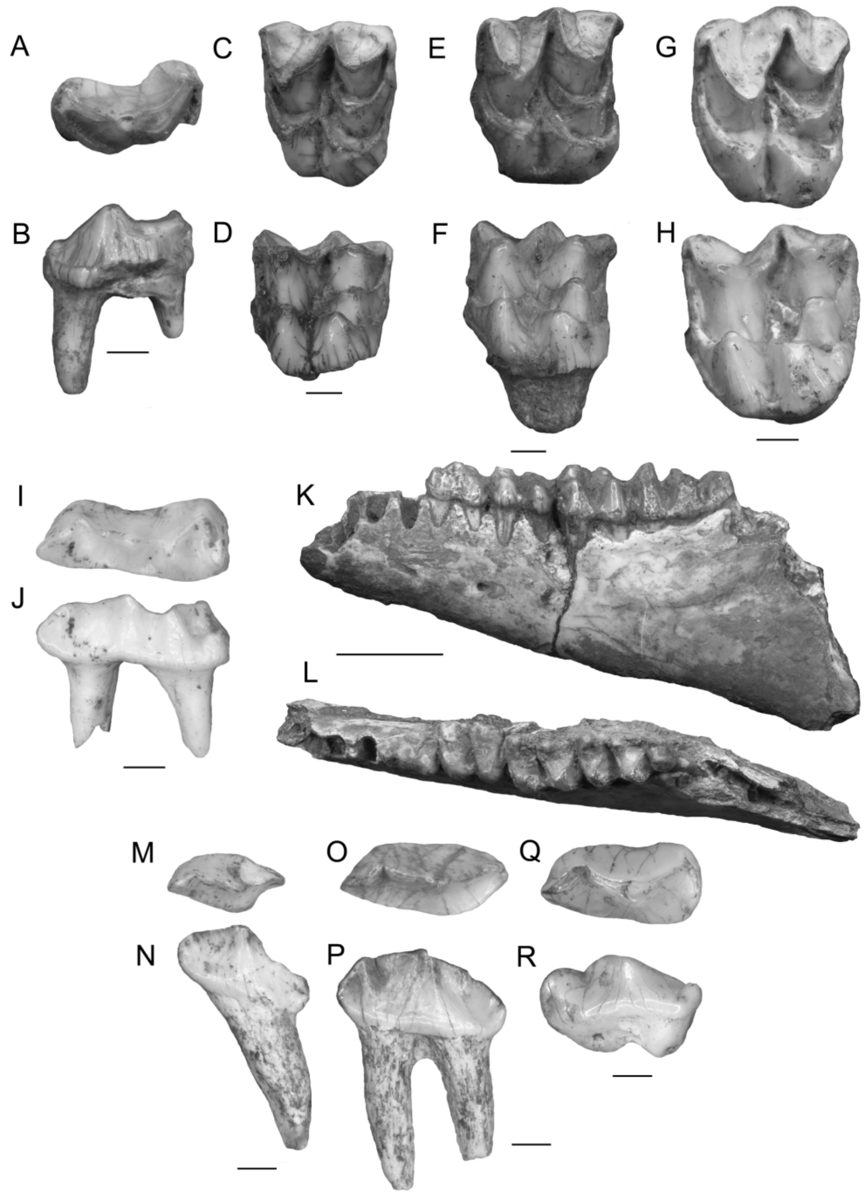

Figure 12. Material of the Caenomeryx procommunis dentition. A, B, right P3/ (DAM3 135; mirror view); C, D, left M1/ (DAM3 133); E, F, right M2/ (DAM3 132; mirror view); G, H, right M3/ (DAM3 129; mirror view; I, J, right DP/2-3 (DAM3 145); K, L, right mandibular fragment with P/4-M/3 (DAM3 152); M, N, left P/1 (DAM3 149; mirror view); O, P, left P/2 (DAM3 148; mirror view); Q, R, right P3/ (DAM3 147). In occlusal view: A, C, E, G, I, K, M, O, Q. In lingual view: B, D, F, H, J, N, P, R. In buccal view: L.

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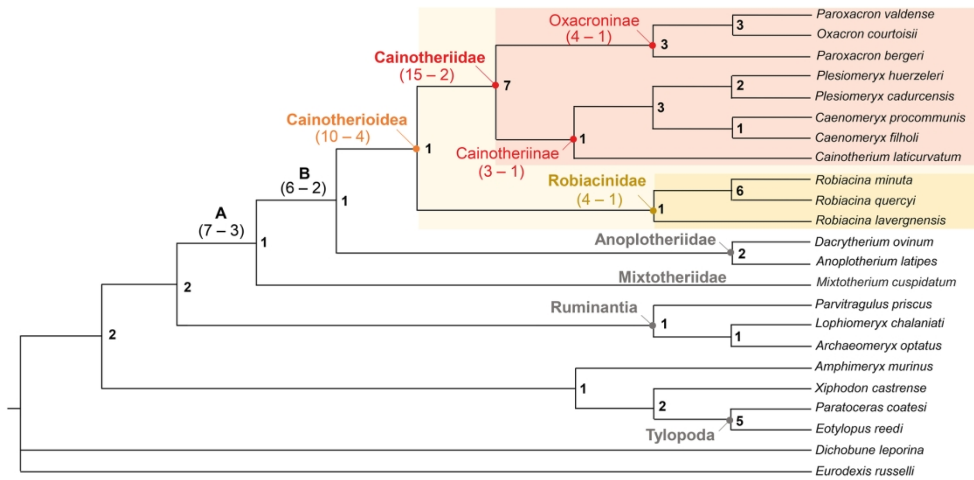

Figure 13. Phylogeny of Cainotheriidae and their position within artiodactyls. Most parsimonious tree at 170 steps, with IC=0.48 and IR=0.73. The Bremer Index (IB) is indicated in bold at each node. X a - b: X, node number; a, number of synapomorphies; b, number of ambiguous characters (Acctran optimization).

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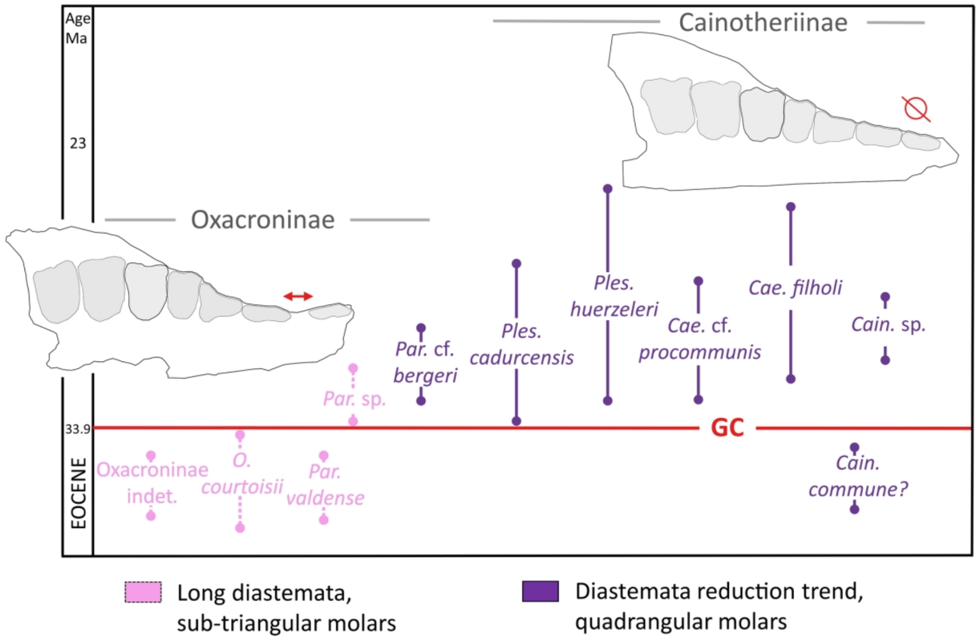

Figure 14. Trends and stratigraphical extensions of cainotheriid species from Quercy, around the Grande Coupure (modified from Blondel (2005; fig. 5) on the stratigraphical position of Paroxacron valdense and Paroxacron sp., with the attribution of Escamps specimens to Paroxacron valdense). Dotted-line: long diastemata, sub-triangular molars; simple line: diastemata reduction trend, quadrangular molars.

172x113mm (300 x 300 DPI)

Supplementary data: Cainotheriidae (Mammalia, Artiodactyla) from Dams (Quercy, SW France); phylogenetic relationships and evolution around the Eocene-Oligocene transition (MP19-MP21).

Dataset S1. Characters list

1. **Lower incisors.**
0. one endocristulid
1. two endocristulids

2. **Lower canine.** Hooker & Weidmann (2000)
0. caniniform
1. incisiform

3. **Diastema between C-P1/.**
0. absence
1. presence

4. **Diastema between P1/-P2/.**
0. absence
1. presence

5. **Diastema between P/1-P/2.**
0. absent to reduced
1. short to long

6. **Diastema between P/2-P/3.**
0. absent to reduced
1. short to long

7. **Upper M: styles, crests.** Hooker & Weidmann (2000)
0. absence
1. presence

8. **Upper M: parastyle, size.** Modified from Gentry & Hooker (1988)
0. very large, superior to other styles
1. large, like other styles

9. **Upper M: mesostyle.**
0. absence
1. presence

10. **Upper M: mesostyle, shape.** Gentry & Hooker (1988)
0. looped
1. pinched

11. **Upper M: position of the protocone (A).**
0. mesial
1. subcentral
2. distal

12. **M1/-M2/: hypocone.**
0. absence
1. presence

13. **Upper M: paraconule.** Modified from Gentry & Hooker (1988)
0. absence
1. presence

14. **Upper M: paraconule, size.** Modified from Gentry & Hooker (1988)
0. small
1. large

15. **Upper M: preprotocrista and paraconule, junction.**
0. absence
1. presence

16. **Upper M: metaconule, size.** Modified from Gentry & Hooker (1988)
0. small
1. large

17. **M3/: position of protocone relative to mesial or distal lingual cusp (bucco-lingual axis).** Modified from Hooker & Weidmann (2000)
Lingual code when protocone is significatively more lingual than the mesial or distal lingual cusp.
0. at the same level
1. protocone more lingual

18. **Upper M: cingulum surrounding the protocone (A).** Modified from Hooker & Weidmann (2000)
0. absent to very weak
1. weak
2. wide
3. very wide

19. **Upper M: dilambdodonty.**
0. absence
1. presence

20. **Upper M: dilambdodonty, type.** Modified from Hooker & Weidmann (2000)
0. strong, with crests weakly oblique and pronounced
1. very strong, with crests very oblique and pronounced

21. **Upper M: premetacristula.**
0. absence
1. presence

22. **Upper M: premetacristula, length.** Modified from Hooker & Weidmann (2000)
0. short
1. long, extend into the central valley

23. **Upper M: premetacristula, shape.** Modified from Hooker & Weidmann (2000)
0. continuous
1. discontinuous

24. **Upper M: postmetacristula and metastyle, junction.**
0. absence
1. presence

25. **Upper M: preparacrista, length.**
0. as long as the postparacrista
1. shorter than postparacrista

26. **Upper M: postprotocrista.**
0. absent to reduced
1. long

27. **Upper M: postprotocrista, direction.**
0. disto-buccally directed
1. distally directed

28. **Upper M: postprotocrista, bifurcation.**
0. absence
1. presence

29. **Upper M: postparacristula.**
0. absence
1. presence

30. **Upper M: postparacristula long and joins preprotocrista in the center of the tooth.** Modified from Erfurt & Métais (2007)
0. absence
1. presence

31. **Upper M: shape (A).** Modified from Erfurt & Métais (2007)
0. triangular
1. subtriangular
2. quadrangular

32. **Upper M: elongated bucco-lingually.**
0. absence
1. presence

33. **Lower M: metaconulid.**
0. absence
1. presence

34. **Lower M: metaconulid, size (A).**
0. small
1. medium
2. large (like other cuspids)

35. **Lower M: metaconulid and metaconid, linked.**
0. absence
1. presence

36. **Lower M: metastylid.** Gentry & Hooker (1988)
0. absence
1. presence

37. **M/3: hypoconulid in basin-shape.** Hooker & Weidmann (2000)
0. absence
1. presence

38. **M/1-M/2: hypoconulid.**
0. absence
1. presence

39. **Lower M: entoconid in 'loop-like'.**
In 'loop': postentocristid convex and preentocristid concave distally
0. absence
1. presence

40. **Lower M: entoconid and hypoconid, relative position (mesio-distal axis) (A).** Modified from Gentry & Hooker (1988)
0. opposed, to entoconid more mesial
1. entoconid slightly more distal
2. entoconid very distal

41. **Lower M: valley between entoconid and metaconid or metaconulid.**
0. absence
1. presence

42. **Lower M: paraconid.** Modified from Gentry & Hooker (1988)
0. absent to small
1. large

43. **Lower M: prehypocristid, fused (cusp or crest).**
0. absence
1. presence

44. **Lower M: prehypocristid (oblique cristid), junction with (NA).** Modified from Hooker & Weidmann (2000)
0. postprotocristid
1. metaconulid or metastylid
2. preentocristid

3. postprotocristid then preentocristid

45. Lower M: prehypocristid.
0. straight to convex buccally
1. concave buccallly

46. Lower M: postprotocristid and postmetacristid, fused.
0. absence
1. presence

47. Lower M: neotrigonid (Centroconulid + Postendocentrocristulid). Sudre (1977)
0. absence
1. presence

48. M/3: prehypocristulid, fused (cusp or crest).
0. absence
1. presence

49. M/3: prehypocristulid, junction with.
0. posthypocristid
1. posthypocristid and postentocristid

50. M/3: posthypocristulid.
0. absence
1. presence

51. M/3: posthypocristulid, inclined.
0. mesio-buccally
1. mesio-distally

52. Lower M: hypolophid. Gentry & Hooker (1988)
0. absence
1. presence

53. Lower M: straight buccal wall.
Straight buccal wall: buccal crests are aligned mesio-distally
0. absence
1. presence

54. P4/: metacone. Modified from Hooker & Weidmann (2000)
0. absence
1. presence

55. P4/: paracone et metacone, individualized. Modified from Hooker & Weidmann (2000)
0. absence
1. presence

56. P4/: paracone and protocone, level.
0. at the same level
1. protocone more mesial
2. paracone more mesial

57. P4/: postprotocrista. Modified from Gentry & Hooker (1988)
0. absent to reduced
1. long

58. P3/-P4/: styles, crests. Hooker & Weidmann (2000)
0. absence
1. presence

59. P3/: metacone.
0. absence
1. presence

60. P3/: metacone and paracone, relative size. Hooker & Weidmann (2000)
0. metacone smaller than paracone
1. metacone and paracone sub-equal

61. **P3/: triangular.**
0. absence
1. presence

62. **P3/: mesial lobe, very elongated.**
0. absence
1. presence

63. **P3/: protocone, mesio-distal width.** Modified from Hooker & Weidmann (2000)
0. small
1. large

64. **P2/: protocone.**
0. absence
1. presence

65. **P/3: metaconid (visible groove):** Modified from Gentry & Hooker (1988)
0. absence
1. presence

66. **P/3: entoconid.**
0. absence
1. presence

67. **P/2-P/3: hypoconid.**
0. absent to small
1. large

68. **Lower P : postprotoconulid.**
0. absence
1. presence

69. **Lower P : postprotoconulid, size.**
0. very small
1. small to large

70. **P/1: roots.**
0. uniradiculate
1. biradiculate

71. **P/1: shape.** Modified from Gentry & Hooker (1988)
0. caniniform
1. premolariform

72. **P: cingulum/id pronounced.**
0. absence
1. presence

73. **Lower P: large premolars with strong main cusp.**
0. absence
1. presence

(A) Ordered characters; (NA) Unordered characters

Dataset S2. Taxa/characters matrix from dental material (provided as .nex format)

#NEXUS

[File saved by NDE version 0.5.0, Sun Jan 13 10:07:54 2019]

```
BEGIN TAXA;
	DIMENSIONS NTAX=23;
	TAXLABELS
		'Paroxacron valdense'
		'Paroxacron bergeri'
		'Oxacron courtoisii'
		'Plesiomeryx huerzeleri'
		'Plesiomeryx cadurcensis'
		'Caenomeryx procommunis'
		'Caenomeryx filholi'
		'Cainotherium laticurvatum'
		'Robiacina minuta'
		'Robiacina quercyi'
		'Robiacina lavergnensis'
		'Dacrytherium ovinum'
		'Anoplotherium latipes'
		'Mixtotherium cuspidatum'
		'Parvitragulus priscus'
		'Lophiomeryx chalaniati'
		'Archaeomeryx optatus'
		'Amphimeryx murinus'
		'Xiphodon castrense'
		'Paratoceras coatesi '
		'Eotylopus reedi'
		'Dichobune leporina'
		'Eurodexis russelli'
		;
ENDBLOCK;

BEGIN CHARACTERS;
	DIMENSIONS NCHAR=73;
	FORMAT DATATYPE=STANDARD MISSING=? GAP=- SYMBOLS="0123";
	CHARLABELS
		[1] 'Lower incisors'
		[2] 'Lower canine'
		[3] 'Diastema between C-P1/'
		[4] 'Diastema between P1/-P2/'
		[5] 'Diastema between P/1-P/2'
		[6] 'Diastema between P/2-P/3'
		[7] 'Upper M: styles, crests'
		[8] 'Upper M: parastyle, size'
		[9] 'Upper M: mesostyle'
		[10] 'Upper M: mesostyle, shape'
		[11] 'Upper M: position of the protocone (A)'
		[12] 'M1/-M2/: hypocone'
		[13] 'Upper M: paraconule'
		[14] 'Upper M: paraconule, size'
		[15] 'Upper M: preprotocrista and paraconule, junction'
		[16] 'Upper M: metaconule, size'
		[17] 'M3/: position of protocone relative to mesial or distal lingual cusp (bucco-lingual axis)'
		[18] 'Upper M: cingulum surrounding the protocone (A)'
		[19] 'Upper M: dilambdodonty'
		[20] 'Upper M: dilambdodonty, type'
		[21] 'Upper M: premetacristula'
		[22] 'Upper M: premetacristula, length'
		[23] 'Upper M: premetacristula, shape'
		[24] 'Upper M: postmetacristula and metastyle, junction'
		[25] 'Upper M: preparacrista, length'
		[26] 'Upper M: postprotocrista'
		[27] 'Upper M: postprotocrista, direction'
		[28] 'Upper M: postprotocrista, bifurcation'
		[29] 'Upper M: postparacristula'
		[30] 'Upper M: postparacristula long and joins preprotocrista in the center of the tooth'
		[31] 'Upper M: shape (A)'
		[32] 'Upper M: elongated bucco-lingually'
		[33] 'Lower M: metaconulid'
		[34] 'Lower M: metaconulid, size (A)'
```

[35] 'Lower M: metaconulid and metaconid, linked'
[36] 'Lower M: metastylid'
[37] 'M/3: hypoconulid in basin-shape'
[38] 'M/1-M/2: hypoconulid'
[39] 'Lower M: entoconid in 'loop-like''
[40] 'Lower M: entoconid and hypoconid, relative position (mesio-distal axis) (A)'
[41] 'Lower M: valley between entoconid and metaconid or metaconulid'
[42] 'Lower M: paraconid'
[43] 'Lower M: prehypocristid, fused (cusp or crest)'
[44] 'Lower M: prehypocristid (oblique cristid), junction with (NA)'
[45] 'Lower M: prehypocristid'
[46] 'Lower M: postprotocristid and postmetacristid, fused'
[47] 'Lower M: neotrigonid (Centroconulid + Postendocentrocristulid)'
[48] 'M/3: prehypocristulid, fused (cusp or crest)'
[49] 'M/3: prehypocristulid, junction with'
[50] 'M/3: posthypocristulid'
[51] 'M/3: posthypocristulid, inclined'
[52] 'Lower M: hypolophid'
[53] 'Lower M: straight buccal wall'
[54] 'P4/: metacone'
[55] 'P4/: paracone et metacone, individualized'
[56] 'P4/: paracone and protocone, level'
[57] 'P4/: postprotocrista'
[58] 'P3/-P4/: styles, crests'
[59] 'P3/: metacone'
[60] 'P3/: metacone and paracone, relative size'
[61] 'P3/: triangular'
[62] 'P3/: mesial lobe, very elongated'
[63] 'P3/: protocone, mesio-distal width'
[64] 'P2/: protocone'
[65] 'P/3: metaconid (visible groove)'
[66] 'P/3: entoconid'
[67] 'P/2-P/3: hypoconid'
[68] 'Lower P : postprotoconulid'
[69] 'Lower P : postprotoconulid, size'
[70] 'P/1: roots'
[71] 'P/1: shape'
[72] 'P: cingulum/id pronounced'
[73] 'Lower P: large premolars with strong main cusp'
;
STATELABELS
1
'one endocristulid'
'two endocristulids',
2
caniniform
incisiform,
3
absence
presence,
4
absence
presence,
5
'absent to reduced'
'short to long',
6
'absent to reduced'
'short to long',
7
absence
presence,
8
'very large, superior to other styles'
'large, like other styles',
9
absence

presence,

10
looped
pinched,

11
mesial
subcentral
distal,

12
absence
presence,

13
absence
presence,

14
small
large,

15
absence
presence,

16
small
large,

17
'at the same level'
'protocone more lingual',

18
'absent to very weak'
'weak'
wide
'very wide',

19
absence
presence,

20
'strong, with crests weakly oblique and pronounced'
'very strong, with crests very oblique and pronounced',

21
absence
presence,

22
short
'long, extend into the central valley',

23
continuous
discontinuous,

24
absence
presence,

25
'as long as the postparacrista'
'shorter than postparacrista',

26
'absent to reduced'
long,

27
'disto-buccally directed'
'distally directed',

28
absence
presence,

29
absence
presence,

30
absence
presence,

31
triangular
subtriangular
quadrangular,

32
absence
presence,

33
absence
presence,

34
small
medium
'large (like other cuspids)',

35
absence
presence,

36
absence
presence,

37
absence
presence,

38
absence
presence,

39
absence
presence,

40
'opposed, to entoconid more mesial'
'entoconid slightly more distal'
'entoconid very distal',

41
absence
presence,

42
'absent to small'
large,

43
absence
presence,

44
postprotocristid
'metaconulid or metastylid'
preentocristid
'postprotocristid then preentocristid',

45
'straight to convex buccally'
'concave buccallly',

46
absence
presence,

47
absence
presence,

48
absence
presence,

49
'posthypocristid '
'posthypocristid and postentocristid',

50
absence
presence,

51
'mesio-buccally'

'mesio-distally',

52
absence
presence,

53
absence
presence,

54
absence
presence,

55
absence
presence,

56
'at the same level'
'protocone more mesial'
'paracone more mesial',

57
'absent to reduced'
long,

58
absence
presence,

59
absence
presence,

60
'metacone smaller than paracone'
'metacone and paracone sub-equal',

61
absence
presence,

62
absence
presence,

63
small
large,

64
absence
presence,

65
absence
presence,

66
absence
presence,

67
'absent to small'
'large',

68
absence
presence,

69
'very small'
'small to large',

70
uniradiclated
biradiculated,

71
caniniform
premolariform,

72
absence
presence,

73
absence

```
                            presence,
      ;
      MATRIX
'Paroxacron  valdense'          1101010110  2011011111  1001011010  1012000012  1011011110  -001011111
1100000101 100
'Paroxacron  bergeri'           ?100000111  2011011111  1001011010  201200???2  ?0????????  ??01011111
1100??0??1 100
'Oxacron  courtoisii'           1101010110  2010011111  1001011010  1012000012  1011011110  -001011111
1000000101 000
'Plesiomeryx  huerzeleri'       1110100111  2010011111  1001011011  2012000012  1011011110  -001001111
1011000110 101
'Plesiomeryx  cadurcensis'      ?110100111  2010011111  1001011011  2012000012  1011011110  -001001111
1011000110 101
'Caenomeryx procommunis'        1110101111 2011011111 1001011011 2112000012 1011011110 -001001111
1011000110 101
'Caenomeryx  filholi'           ??10101111  2011011111  1001011011  2112000012  1011011110  -001001111
1011000110 101
'Cainotherium  laticurvatum'    1100001111  2011010111  1001011011  2012000012  0011011110  -001001111
0000000110 111
'Robiacina  minuta'             ?1??010011  1010111010  111111000-  1010101111  1011010111  0001000011
100?100100 100
'Robiacina  quercyi'            ?100??1011  1010111010  111110-00-  1010101111  1011010111  0001000011
1000??0??? ?00
'Robiacina  lavergnensis'       ?0????1011  1010111210  100110-00-  1011101111  1010010111  0001011111
101?100??0 ?00
'Dacrytherium  ovinum'          0100001011  0011110210  100100-00-  2011101111  1011010111  0001001110
00111010-? 111
'Anoplotherium  latipes'        ??00001011  001111?210  100100-00-  201110??11  11110101??  ?001001110
00111010-? ?11
'Mixtotherium  cuspidatum'      ?000001011  0010110210  110100-00-  200--10110  000-110111  0001100110
10110010-? 101
'Parvitragulus priscus'     ????10110- 000--1000- 11010100-- 200--00000 0013010101 1011101110 101110?0-0
000
'Lophiomeryx chalaniati'    ????101111 000--10310 11010100-- 200--00100 0012010100 -000-01010 01111010-0
010
'Archaeomeryx optatus'      ?1--101111 000--10310 11010100-- 200--00?00 0012010101 0000-11110 1110?010-0
000
'Amphimeryx  murinus'           ??????0111  0011011211  1001010010  200--00100  000-110110  -00100101?
110????0-? ???
'Xiphodon castrense'        ?????01011 0011010210 1001010010 200--00000 00120100-1 001100101? 000?0100-
? ?10
'Paratoceras coatesi '      ????101111 000--1120- 10000100-- 200--00000 000-0000-1 0000-01010 00000100-0
011
'Eotylopus reedi'           0111100111 000--1110- 10000101-- 200--00000 000-0000-1 0000-01010 00100100-0
111
'Dichobune leporina'        ????11010- 011101130- 0--100-00- 200--0?100 1?0-010100 -101121??? ?????000-0
??0
'Eurodexis russelli'        ??????010- 101010130- 0--101000- 000--00100 010-010101 0000-0000- 100?????-?
???
      ;
ENDBLOCK;

BEGIN ASSUMPTIONS;
      OPTIONS DEFTYPE=UNORD POLYTCOUNT=MINSTEPS;
      TYPESET * default = ORD: 11 18 31 34 40;
ENDBLOCK;
```

Dataset S3. Apomorphy lists

```
   Branch                  Character                                              Steps     CI   Change
---------------------------------------------------------------------------------------------------------
```

node_36 --> node_37	7 (Upper M: styles, crests)	1	0.167	0 - -> 1
	9 (Upper M: mesostyle)	1	0.500	0 ==> 1
	18 (Upper M: cingulum surrounding the protoco)	1	0.375	3 ==> 2
	19 (Upper M: dilambdodonty)	1	0.333	0 ==> 1
	21 (Upper M: premetacristula)	1	1.000	0 ==> 1
	49 (M/3: prehypocristulid, junction with)	1	0.500	0 - -> 1
	59 (P3/: metacone)	1	1.000	0 - -> 1
node_37 --> node_38	15 (Upper M: preprotocrista and paraconule, j)	1	0.333	0 - -> 1
	17 (M3/: position of protocone relative to me)	1	0.250	1 ==> 0
	22 (Upper M: premetacristula, length)	1	0.333	0 - -> 1
	43 (Lower M: prehypocristid, fused (cusp or c)	1	0.333	0 - -> 1
	58 (P3/-P4/: styles, crests)	1	0.333	0 ==> 1
	63 (P3/: protocone, mesio-distal width)	1	0.200	0 ==> 1
	64 (P2/: protocone)	1	0.250	0 - -> 1
	65 (P/3: metaconid (visible groove))	1	0.333	0 - -> 1
	67 (P/2-P/3: hypoconid)	1	0.500	0 ==> 1
node_38 --> node_39	5 (Diastema between P/1-P/2)	1	0.500	1 ==> 0
	8 (Upper M: parastyle, size)	1	0.333	1 ==> 0
	26 (Upper M: postprotocrista)	1	0.250	1 ==> 0
	39 (Lower M: entoconid in ?loop-like?)	1	1.000	0 ==> 1
	44 (Lower M: prehypocristid (oblique cristid))	1	1.000	2 - -> 1
	71 (P/1: shape)	1	0.333	0 - -> 1
	73 (Lower P: large premolars with strong mai)	1	0.250	0 - -> 1
node_39 --> node_40	22 (Upper M: premetacristula, length)	1	0.333	1 - -> 0
	33 (Lower M: metaconulid)	1	1.000	0 ==>
1				
	37 (M/3: hypoconulid in basin-shape)	1	0.500	0 - -> 1
	40 (Lower M: entoconid and hypoconid, relativ)	1	1.000	0 ==> 1
	41 (Lower M: valley between entoconid and met)	1	0.333	0 ==> 1
	55 (P4/: paracone et metacone, individualized)	1	0.500	1 ==> 0
node_40 --> node_41	1 (Lower incisors)	1	1.000	0 - -> 1
	11 (Upper M: position of the protocone (A))	1	0.667	0 ==> 1
	17 (M3/: position of protocone relative to me)	1	0.250	0 ==> 1
	18 (Upper M: cingulum surrounding the protoco)	1	0.375	2 - -> 1
	60 (P3/: metacone and paracone, relative size)	1	1.000	0 ==> 1
	63 (P3/: protocone, mesio-distal width)	1	0.200	1 - -> 0
	64 (P2/: protocone)	1	0.250	1 ==> 0

	67 (P/2-P/3: hypoconid)	1	0.500	1 ==> 0
	68 (Lower P : postprotoconulid)	1	1.000	0 ==> 1
	73 (Lower P: large premolars with strong mai)	1	0.250	1 - -> 0
node_41 --> node_42	8 (Upper M: parastyle, size)	1	0.333	0 ==> 1
	11 (Upper M: position of the protocone (A))	1	0.667	1 ==> 2
	15 (Upper M: preprotocrista and paraconule, j)	1	0.333	1 ==> 0
	20 (Upper M: dilambdodonty, type)	1	0.500	0 ==> 1
	26 (Upper M: postprotocrista)	1	0.250	0 ==> 1
	27 (Upper M: postprotocrista, direction)	1	1.000	0 ==> 1
	29 (Upper M: postparacristula)	1	0.500	0 ==> 1
	34 (Lower M: metaconulid, size (A))	1	1.000	1 ==> 2
	35 (Lower M: metaconulid and metaconid, linked)	1	1.000	1 ==> 0
	37 (M/3: hypoconulid in basin-shape)	1	0.500	1 - -> 0
	38 (M/1-M/2: hypoconulid)	1	0.333	1 ==> 0
	40 (Lower M: entoconid and hypoconid, relativ)	1	1.000	1 ==> 2
	47 (Lower M: neotrigonid (Centroconulid + Pos)	1	1.000	0 ==> 1
	50 (M/3: posthypocristulid)	1	0.250	1 ==> 0
	65 (P/3: metaconid (visible groove))	1	0.333	1 - -> 0
node_42 --> node_43	7 (Upper M: styles, crests)	1	0.167	1 ==> 0
	56 (P4/: paracone and protocone, level)	1	0.500	0 ==> 1
	62 (P3/: mesial lobe, very elongated)	1	0.250	0 - -> 1
	70 (P/1: roots)	1	1.000	0 ==> 1
node_43 --> node_44	4 (Diastema between P1/-P2/)	1	0.500	0 ==> 1
	6 (Diastema between P/2-P/3)	1	0.333	0 ==> 1
	10 (Upper M: mesostyle, shape)	1	1.000	1 ==> 0
	31 (Upper M: shape (A))	1	0.500	2 ==> 1
node_44 --> O. courtoisii	14 (Upper M: paraconule, size)	1	0.200	1 ==> 0
	62 (P3/: mesial lobe, very elongated)	1	0.250	1 - -> 0
	71 (P/1: shape)	1	0.333	1 ==> 0
node_42 --> node_27	30 (Upper M: postparacristula long and joins)	1	1.000	0 ==> 1
	69 (Lower P : postprotoconulid, size)	1	1.000	0 ==> 1
	73 (Lower P: large premolars with strong mai)	1	0.250	0 - -> 1
node_27 --> node_26	3 (Diastema between C-P1/)	1	0.500	0 ==> 1
	5 (Diastema between P/1-P/2)	1	0.500	0 ==> 1
	63 (P3/: protocone, mesio-distal width)	1	0.200	0 - -> 1
	64 (P2/: protocone)	1	0.250	0 ==> 1

node_26 --> node_24	7 (Upper M: styles, crests)	1	0.167	1 ==> 0
	14 (Upper M: paraconule, size)	1	0.200	1 ==> 0
node_26 --> node_25	32 (Upper M: elongated bucco-lingually)	1	1.000	0 ==> 1
node_27 --> Cai. laticurvatum	17 (M3/: position of protocone relative to me)	1	0.250	1 ==> 0
	41 (Lower M: valley between entoconid and met)	1	0.333	1 ==> 0
	61 (P3/: triangular)	1	0.250	1 ==> 0
	72 (P: cingulum/id pronounced)	1	0.250	0 ==> 1
node_41 --> node_29	6 (Diastema between P/2-P/3)	1	0.333	0 - -> 1
	14 (Upper M: paraconule, size)	1	0.200	1 ==> 0
	25 (Upper M: preparacrista, length)	1	1.000	0 ==> 1
	31 (Upper M: shape (A))	1	0.500	2 ==> 1
node_29 --> node_28	18 (Upper M: cingulum surrounding the protoco)	1	0.375	1 ==> 0
	22 (Upper M: premetacristula, length)	1	0.333	0 ==> 1
	23 (Upper M: premetacristula, shape)	1	1.000	0 ==> 1
	34 (Lower M: metaconulid, size (A))	1	1.000	1 ==> 0
	57 (P4/: postprotocrista)	1	0.333	1 ==> 0
	58 (P3/-P4/: styles, crests)	1	0.333	1 ==> 0
node_28 --> R. minuta	7 (Upper M: styles, crests)	1	0.167	1 ==> 0
	26 (Upper M: postprotocrista)	1	0.250	0 ==> 1
node_29 --> R. lavergnensis	2 (Lower canine)	1	0.500	1 ==> 0
	18 (Upper M: cingulum surrounding the protoco)	1	0.375	1 - -> 2
	44 (Lower M: prehypocristid (oblique cristid))	1	1.000	1 ==> 0
	56 (P4/: paracone and protocone, level)	1	0.500	0 ==> 1
	63 (P3/: protocone, mesio-distal width)	1	0.200	0 - -> 1
node_40 --> node_30	61 (P3/: triangular)	1	0.250	1 ==> 0
	72 (P: cingulum/id pronounced)	1	0.250	0 ==> 1
node_30 --> A. latipes	42 (Lower M: paraconid)	1	0.500	0 ==> 1
node_39 --> M. cuspidatum	2 (Lower canine)	1	0.500	1 ==> 0
	14 (Upper M: paraconule, size)	1	0.200	1 ==> 0
	36 (Lower M: metastylid)	1	1.000	0 ==> 1
	43 (Lower M: prehypocristid, fused (cusp or c)	1	0.333	1 - -> 0
	45 (Lower M: prehypocristid)	1	0.500	0 ==> 1
	57 (P4/: postprotocrista)	1	0.333	1 ==> 0
	65 (P/3: metaconid (visible groove))	1	0.333	1 - -> 0
node_38 --> node_32	13 (Upper M: paraconule)	1	0.500	1 ==> 0
	49 (M/3: prehypocristulid, junction with)	1	0.500	1 - -> 0

node_32 --> P. priscus	9 (Upper M: mesostyle)	1	0.500	1 ==> 0
	18 (Upper M: cingulum surrounding the protoco)	2	0.375	2 ==> 0
	19 (Upper M: dilambdodonty)	1	0.333	1 ==> 0
	38 (M/1-M/2: hypoconulid)	1	0.333	1 ==> 0
	44 (Lower M: prehypocristid (oblique cristid))	1	1.000	2 ==> 3
	51 (M/3: posthypocristulid, inclined)	1	1.000	0 ==> 1
	53 (Lower M: straight buccal wall)	1	0.500	0 ==> 1
node_32 --> node_31	18 (Upper M: cingulum surrounding the protoco)	1	0.375	2 ==> 3
	54 (P4/: metacone)	1	0.333	1 ==> 0
	62 (P3/: mesial lobe, very elongated)	1	0.250	0 ==> 1
node_31 --> L. chalaniati	50 (M/3: posthypocristulid)	1	0.250	1 ==> 0
	58 (P3/-P4/: styles, crests)	1	0.333	1 ==> 0
	61 (P3/: triangular)	1	0.250	1 ==> 0
	72 (P: cingulum/id pronounced)	1	0.250	0 ==> 1
node_31 --> Arc. optatus	56 (P4/: paracone and protocone, level)	1	0.500	0 ==> 1
	64 (P2/: protocone)	1	0.250	1 ==> 0
node_37 --> node_35	3 (Diastema between C-P1/)	1	0.500	0 - -> 1
	4 (Diastema between P1/-P2/)	1	0.500	0 - -> 1
	29 (Upper M: postparacristula)	1	0.500	0 ==> 1
	55 (P4/: paracone et metacone, individualized)	1	0.500	1 ==> 0
	66 (P/3: entoconid)	1	1.000	0 - -> 1
	72 (P: cingulum/id pronounced)	1	0.250	0 - -> 1
node_35 --> Amp. murinus	7 (Upper M: styles, crests)	1	0.167	1 - -> 0
	20 (Upper M: dilambdodonty, type)	1	0.500	0 ==> 1
	45 (Lower M: prehypocristid)	1	0.500	0 ==> 1
	50 (M/3: posthypocristulid)	1	0.250	1 ==> 0
	62 (P3/: mesial lobe, very elongated)	1	0.250	0 ==> 1
node_35 --> node_34	38 (M/1-M/2: hypoconulid)	1	0.333	1 ==> 0
	48 (M/3: prehypocristulid, fused (cusp or cre)	1	1.000	1 ==> 0
	61 (P3/: triangular)	1	0.250	1 ==> 0
node_34 --> X. castrense	8 (Upper M: parastyle, size)	1	0.333	1 ==> 0
	17 (M3/: position of protocone relative to me)	1	0.250	1 ==> 0
	43 (Lower M: prehypocristid, fused (cusp or c)	1	0.333	0 ==> 1
	53 (Lower M: straight buccal wall)	1	0.500	0 ==> 1
node_34 --> node_33	13 (Upper M: paraconule)	1	0.500	1 ==> 0
	19 (Upper M: dilambdodonty)	1	0.333	1 ==> 0

	24 (Upper M: postmetacristula and metastyle,)	1	1.000	1 ==> 0
	46 (Lower M: postprotocristid and postmetacri)	1	1.000	1 ==> 0
	54 (P4/: metacone)	1	0.333	1 ==> 0
	73 (Lower P: large premolars with strong mai)	1	0.250	0 ==> 1
node_33 --> E. reedi	7 (Upper M: styles, crests)	1	0.167	1 - -> 0
	18 (Upper M: cingulum surrounding the protoco)	1	0.375	2 ==> 1
	28 (Upper M: postprotocrista, bifurcation)	1	1.000	0 ==> 1
	63 (P3/: protocone, mesio-distal width)	1	0.200	0 ==> 1
	71 (P/1: shape)	1	0.333	0 - -> 1
node_36 --> D. leporina	6 (Diastema between P/2-P/3)	1	0.333	0 - -> 1
	12 (M1/-M2/: hypocone)	1	1.000	0 ==> 1
	26 (Upper M: postprotocrista)	1	0.250	1 ==> 0
	41 (Lower M: valley between entoconid and met)	1	0.333	0 ==> 1
	50 (M/3: posthypocristulid)	1	0.250	1 ==> 0
	52 (Lower M: hypolophid)	1	1.000	0 ==> 1
	56 (P4/: paracone and protocone, level)	1	0.500	0 ==> 2
node_36 --> E. russelli	11 (Upper M: position of the protocone (A))	1	0.667	0 ==> 1
	14 (Upper M: paraconule, size)	1	0.200	1 ==> 0
	15 (Upper M: preprotocrista and paraconule, j)	1	0.333	0 - -> 1
	16 (Upper M: metaconule, size)	1	1.000	1 ==> 0
	31 (Upper M: shape (A))	2	0.500	2 ==> 0
	42 (Lower M: paraconid)	1	0.500	0 - -> 1
	54 (P4/: metacone)	1	0.333	1 ==> 0
	57 (P4/: postprotocrista)	1	0.333	1 ==> 0

Table S1. Measurements and statistical data of the permanent lower teeth of *Paroxacron valdense* of DAM1. N, number of specimens; L/lp/la/h/L3 and l3, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/Lp/la/h	LV	M ± SE	Σ	V
I/1	15	L	1.01-1.28	1.17 ± 0.02	0.08	6.93
		lp	0.70-0.95	0.82 ± 0.05	0.19	6.91
		h	1.43-2.07	1.84 ± 0.04	0.17	9.01
I/2-3	15	L	0.97-1.24	1.12 ± 0.02	0.07	6.54
		lp	0.72-0.90	0.81 ± 0.02	0.06	7.40

		h	1.73-2.00	1.84 ±0.02	0.08	4.17
Lower canine	15	L	1.26-1.98	1.46 ± 0.04	0.16	11.1
		lp	0.79-0.97	0.87 ± 0.01	0.04	5.08
		h	1.76-2.13	1.91 ± 0.03	0.11	5.96
P/1	15	L	2.35-3.17	2.83 ± 0.07	0.26	9.34
	16	lp	0.86-1.10	0.97 ± 0.02	0.08	7.90
		la	0.76-0.96	0.87 ± 0.02	0.06	7.01
		h	1.43-1.83	1.63 ± 0.03	0.12	7.09
P/2	10	L	3.10-3.58	3.32 ± 0.05	0.17	5.16
		lp	1.02-1.18	1.08 ± 0.01	0.04	4.00
		la	0.86-0.95	0.91 ± 0.01	0.04	4.23
		h	1.45-1.97	1.69 ± 0.05	0.16	9.29
P/3	17	L	3.48-4.05	3.76 ± 0.04	0.16	4.24
		lp	1.38-1.71	1.56 ± 0.02	0.10	6.50
		la	1.05-1.29	1.16 ± 0.02	0.07	5.69
		h	1.41-2.06	1.82 ± 0.04	0.18	9.80
P/4	18	L	2.92-3.42	3.14 ± 0.03	0.14	4.51
		lp	1.83-2.50	2.12 ± 0.04	0.18	8.42
		la	1.44-1.79	1.62 ± 0.03	0.11	6.64
		h	1.34-2.35	1.79 ± 0.07	0.29	16.20
M/1	17	L	2.96-3.40	3.15 ± 0.03	0.12	3.92
		lp	2.33-2.81	2.58 ± 0.03	0.14	5.53
		la	2.12-2.73	2.37 ± 0.04	0.15	6.50
		h	1.33-2.15	1.73 ± 0.05	0.22	12.49
M/2	15	L	3.19-3.51	3.34 ± 0.02	0.09	2.82
		lp	2.54-3.01	2.72 ± 0.04	0.14	5.18
		la	2.39-3.01	2.60 ± 0.04	0.17	6.68
		h	1.48-2.38	1.99 ± 0.07	0.26	13.01
M/3	15	L	4.35-4.77	4.51 ± 0.03	0.12	2.69
		lp	2.25-2.63	2.42 ± 0.03	0.12	5.06
		la	2.17-2.67	2.39 ± 0.04	0.16	6.56
		h	1.73-2.50	2.18 ± 0.06	0.24	11.16
		L3	1.02-1.43	1.22 ± 0.03	0.12	9.45
		l3	1.05-1.52	1.23 ± 0.03	0.12	9.87
M/1-M/3	14	L	10.62-11.39	10.97 ± 0.07	0.26	2.36
P/3-P/4	19	L	6.26-7.29	6.82 ± 0.06	0.26	3.80
P/2-P/4	10	L	10.32-11.61	11.06 ± 0.13	0.40	3.59
P/1-P/4	2	L	13.39-13.44	13.41		
Dia P/2-P/3	16	L	0.45-1.58	1.11 ± 0.08	0.33	30.00
Dia P/1-P/2	8	L	0.05-0.85	0.49 ± 0.06	0.21	42.81

Table S2. Measurements and statistical data of the permanent upper teeth of *Paroxacron valdense* of DAM1. N, number of specimens; L/lp/la/h, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/lp/la/h	LV	M ± SE	σ	V

I1/	10	L	1.73-2.03	1.92 ± 0.03	0.11	5.56
		lp	0.80-0.93	0.87 ± 0.01	0.04	4.97
		h	1.55-1.93	1.72 ± 0.05	0.15	8.53
I2/	15	L	1.53-1.90	1.74 ± 0.03	0.1	5.73
		lp	0.70-0.95	0.81 ± 0.02	0.07	8.71
		h	1.63-2.14	1.88 ± 0.03	0.13	6.86
I3/	15	L	1.45-1.75	1.56 ± 0.02	0.09	5.83
		lp	0.65-0.94	0.78 ± 0.02	0.07	8.65
		h	1.49-1.94	1.77 ± 0.04	0.14	8.21
Upper canine	15	L	1.56-2.00	1.75 ± 0.03	0.13	7.31
		lp	0.90-1.12	1.02 ± 0.02	0.06	6.23
		h	1.99-2.23	2.08 ± 0.02	0.07	3.56
P1/	16	L	2.67-3.54	3.08 ± 0.06	0.23	7.59
		lp	0.82-1.05	0.94 ± 0.01	0.07	5.98
		la	0.87-1.05	0.96 ± 0.01	0.05	5.26
		h	1.49-1.96	1.76 ± 0.03	0.13	7.56
P2/	11	L	3.46-4.15	3.75 ± 0.06	0.21	5.67
		lp	1.15-1.73	1.34 ± 0.05	0.18	13.2
		la	1.04-1.20	1.11 ± 0.02	0.06	5.49
		h	1.49-1.87	1.72 ± 0.04	0.14	8.03
P3/	12	L	3.21-3.86	3.53 ± 0.06	0.22	6.31
		lp	2.55-3.18	2.83 ± 0.05	0.17	6.17
		la	1.39-1.86	1.68 ± 0.04	0.14	8.09
		h	1.39-2.18	1.85 ± 0.07	0.23	12.2
P4/	17	L	2.39-2.78	2.55 ± 0.03	0.12	4.64
		lp	3.07-3.66	3.42 ± 0.04	0.15	4.46
		h	1.65-2.58	2.03 ± 0.06	0.24	11.92
M1/	15	L	2.94-3.46	3.24 ± 0.04	0.15	4.54
		lp	3.71-4.33	3.99 ± 0.05	0.20	4.92
		la	3.26-3.75	3.52 ± 0.04	0.14	4.11
		h	1.40-1.90	1.58 ± 0.03	0.13	8.53
M2/	15	L	3.34-3.74	3.55 ± 0.03	0.12	3.35
		lp	4.13-4.71	4.37 ± 0.04	0.16	3.60
		la	3.81-4.36	4.07 ± 0.05	0.18	4.40
		h	1.62-2.09	1.81 ± 0.04	0.16	8.78
M3/	13	L	3.13-3.65	3.37 ± 0.04	0.15	4.55
		lp	3.92-4.53	4.13 ± 0.04	0.16	3.76
		la	3.79-4.16	3.97 ± 0.03	0.12	3.05
		h	1.59-1.97	1.79 ± 0.04	0.13	7.14
M1/-M3/	13	L	9.08-10.57	9.89 ± 0.1	0.36	3.64
P3/-P4/	13	L	5.38-6.51	5.95 ± 0.09	0.33	5.48
P2/-P4/	10	L	8.95-10.44	9.62 ± 0.16	0.51	5.33
P1/-P4/	1	L		13.229		
Dia P1/-P2/	10	L	0-1.46	0.94 ± 0.13	0.41	43.17

Table S3. Measurements and statistical data of the deciduous upper and lower teeth of *Paroxacron valdense* of DAM1. N, number of specimens; L/lp/la/h and lam, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/lp/la/h	LV	M ± SE	σ	V
DP1-2/	5	L	3.56-3.80	3.66 ± 0.04	0.09	2.38
		lp	1.13-1.55	1.26 ± 0.08	0.17	13.61
		la	0.80-1.00	0.90 ± 0.04	0.08	8.90
		h	1.20-1.44	1.29 ± 0.04	0.09	6.90
DP3/	15	L	3.24-3.71	3.54 ± 0.04	0.15	4.16
		lp	2.14-2.73	2.49 ± 0.04	0.17	6.70
		la	1.23-1.54	1.40 ± 0.03	0.10	6.90
		h	1.10-1.43	1.28 ± 0.03	0.10	7.74
DP4/	15	L	2.87-3.14	3.02 ± 0.02	0.08	2.74
		lp	3.10-3.85	3.40 ± 0.05	0.20	5.84
		la	2.91-3.29	3.03 ± 0.03	0.13	4.22
		h	1.10-1.79	1.51 ± 0.05	0.18	11.77
DP/1	7	L	2.92-3.28	3.10 ± 0.05	0.13	4.33
		lp	0.78-0.94	0.87 ± 0.02	0.06	6.77
		la	0.71-0.94	0.84 ± 0.03	0.08	9.45
		h	1.07-1.35	1.24 ± 0.04	0.10	7.81
DP/2-3	9	L	3.11-3.87	3.66 ± 0.08	0.24	6.52
		lp	1.22-1.70	1.47 ± 0.05	0.14	9.17
		la	0.92-1.21	1.06 ± 0.03	0.10	9.61
		h	1.40-1.95	1.68 ± 0.07	0.20	11.88
DP/4	15	L	3.61-4.05	3.80 ± 0.03	0.12	3.19
		lp	1.90-2.22	2.08 ± 0.03	0.11	5.35
		la	1.57-1.76	1.62 ± 0.01	0.05	2.90
		h	1.42-2.15	1.73 ± 0.05	0.21	12.08
		lam	1.55-1.76	1.66 ± 0.02	0.07	4.50

Table S4. Measurements and statistical data of the upper teeth of *Paroxacron* sp. of DAM3. N, number of specimens; L/lp/la/h, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/lp/la/h	LV	M ± SE	σ	V
P1/	1	L		2.73		
		lp		1.17		
		la		1.01		
		h		1.56		
P4/	1	L		2.25		
		lp		2.85		
		h		1.93		
M1/	3	L	2.59-2.71	2.64 ± 0.04	0.06	2.42
		lp	3.47-3.70	3.61 ± 0.07	0.13	3.50
		la	3.05-3.58	3.39 ± 0.17	0.29	8.69
		h	1.08-1.36	1.23 ± 0.08	0.14	11.50
M2/	2	L	2.94-3.04	2.99 ± 0.05	0.07	2.48
		lp	3.94-3.95	3.94 ± 0.01	0.01	0.20
		la	3.26-3.67	3.46 ± 0.20	0.29	8.35

		h	1.62-1.68	1.65 ± 0.03	0.04	2.53
M3/	3	L	2.88-3.09	3.00 ± 0.06	0.10	3.44
		lp	3.58-3.92	3.76 ± 0.10	0.17	4.59
		la	3.49-3.61	3.53 ± 0.04	0.07	1.96
		h	1.30-1.75	1.52 ± 0.13	0.23	15.08

Table S5. Measurements and statistical data of the lower teeth of *Paroxacron* sp. of DAM3. N, number of specimens; L/lp/la/h/L3/l3 and lam, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	**L/Lp/la/h**	**LV**	**M ± SE**	**σ**	**V**
P/1	1	L		2.53		
		lp		1.00		
		la		0.79		
		h		1.54		
P/2	1	L		3.02		
		lp		1.15		
		la		1.00		
		h		1.39		
DP/4	2	L	3.16-3.25	3.21 ± 0.05	0.07	2.14
		lp	1.81-1.92	1.87 ± 0.05	0.08	4.13
		la	1.40-1.67	1.53 ± 0.13	0.19	12.26
		h	1.13-1.32	1.23 ± 0.09	0.13	10.74
		lam	1.41-1.65	1.53 ± 0.12	0.17	11.09
M/1	2	L	2.55-2.94	2.75 ± 0.20	0.28	10.06
		lp	1.86-2.09	1.98 ± 0.11	0.16	8.09
		la	1.71-1.95	1.83 ± 0.12	0.17	9.23
		h	1.03-1.37	1.20 ± 0.17	0.24	19.85
M/2	4	L	2.87-3.18	2.97 ± 0.07	0.14	4.83
		lp	2.01-2.25	2.17 ± 0.05	0.11	4.91
		la	1.88-2.11	1.99 ± 0.05	0.09	4.61
		h	1.36-1.92	1.68 ± 0.01	0.23	13.93
M/3	1	L		3.89		
		lp		2.04		
		la		1.96		
		h		2.22		
		L3		1.04		
		l3		1.34		

Table S6. Measurements and statistical data of the upper teeth of *Paroxacron bergeri* of DAM3. N, number of specimens; L/lp/la/h, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/lp/la/h	LV	M ± SE	σ	V
P1/	1	L		3.04		
		lp		1.25		
		la		1.33		
		h		1.06		
P2/	1	L		4.22		
		lp		1.63		
		la		1.52		
		h		2.48		
P3/	1	L		3.79		
		lp		2.84		
		la		2.01		
		h		2.08		
P4/	1	L		3.09		
		lp		3.98		
		h		2.36		
M1/	2	L	4.08-4.48	4.28 ± 0.20	0.28	6.64
		lp	4.85-5.11	4.98 ± 0.13	0.18	3.66
		la	4.55-4.81	4.68 ± 0.13	0.19	4.05
		h	1.68-2.45	2.07 ± 0.38	0.54	26.27
M2/	3	L	4.70-5.05	4.83 ± 0.11	0.19	4.00
		lp	5.14-5.69	5.50 ± 0.18	0.31	5.70
		la	4.67-5.44	5.13 ± 0.24	0.41	7.96
		h	2.25-2.78	2.59 ± 0.17	0.30	11.47
M3/	13	L	4.52-4.61	4.56 ± 0.03	0.05	1.06
		lp	5.06-5.63	5.40 ± 0.17	0.30	5.54
		la	4.98-5.32	5.17 ± 0.10	0.17	3.34
		h	1.95-2.75	2.38 ± 0.24	0.41	17.23

Table S7. Measurements and statistical data of the upper teeth of *Plesiomeryx cadurcensis* of DAM3. N, number of specimens; L/lp/la/h, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/lp/la/h	LV	M ± SE	σ	V
P1/	1	L		3.05		
		lp		1.28		
		la		1.07		
		h		1.25		
P2/	2	L	3.42-3.48	3.45 ± 0.03	0.04	1.15
		lp	1.48-1.69	1.59 ± 0.11	0.15	9.55
		la	1.26-1.33	1.29 ± 0.04	0.05	3.84
		h	1.52-1.69	1.60 ± 0.08	0.11	7.10
P3/	1	L		3.44		
		lp		2.94		
		la		1.81		
		h		1.54		
P4/	1	L		2.50		
		lp		3.25		

		h		1.44		
DP4/	2	L	3.01-3.07	3.04 ± 0.03	0.04	1.37
		lp	3.62-3.91	3.77 ± 0.15	0.21	5.51
		la	3.08-3.58	3.33 ± 0.25	0.35	10.64
		h	1.20-1.24	1.22 ± 0.02	0.03	2.66
M1/	3	L	3.08-3.34	3.22 ± 0.08	0.13	4.07
		lp	4.15-4.28	4.22 ± 0.04	0.06	1.50
		la	3.57-3.90	3.76 ± 0.10	0.17	4.62
		h	1.40-1.90	1.72 ± 0.10	0.17	9.89
M2/	5	L	3.51-3.78	3.61 ± 0.05	0.10	2.84
		lp	4.50-4.85	4.65 ± 0.06	0.14	3.04
		la	3.83-4.32	4.07 ± 0.10	0.22	5.52
		h	1.75-2.01	1.86 ± 0.05	0.10	5.49
M3/	3	L	3.14-3.69	3.45 ± 0.17	0.31	8.78
		lp	4.17-4.60	4.45 ± 0.14	0.25	5.57
		la	3.86-4.12	4.01 ± 0.08	0.14	3.50
		h	1.74-2.00	1.84 ± 0.08	0.14	7.62

Table S8. Measurements and statistical data of the lower teeth of *Plesiomeryx cadurcensis* of DAM3. N, number of specimens; L/lp/la/h/L3 and l3, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	**L/Lp/la/h**	**LV**	**M ± SE**	**Σ**	**V**
P/2	3	L	2.52-2.81	2.70 ± 0.09	0.16	5.80
		lp	1.07-1.29	1.16 ± 0.07	0.11	9.75
		la	0.93-1.03	0.97 ± 0.03	0.05	5.57
		h	1.46-1.77	1.61 ± 0.09	0.16	9.66
P/3	7	L	2.89-3.27	3.03 ± 0.05	0.14	4.50
		lp	1.35-1.61	1.49 ± 0.04	0.11	7.22
		la	1.00-1.35	1.21 ± 0.04	0.11	9.50
		h	1.60-2.13	1.79 ± 0.08	0.20	11.35
P/4	5	L	2.99-3.51	3.16 ± 0.09	0.20	6.46
		lp	1.85-2.03	1.96 ± 0.04	0.08	4.09
		la	1.51-1.76	1.60 ± 0.04	0.10	6.04
		h	1.50-2.58	1.88 ± 0.19	0.42	22.38
M/1	6	L	3.05-3.20	3.09 ± 0.02	0.06	1.85
		lp	2.24-2.57	2.37 ± 0.05	0.13	5.67
		la	1.89-2.41	2.13 ± 0.08	0.19	9.01
		h	1.40-2.08	1.79 ± 0.12	0.30	17.01
M/2	5	L	3.25-3.67	3.42 ± 0.08	0.17	5.08
		lp	2.47-2.89	2.64 ± 0.08	0.18	6.69
		la	2.14-2.59	2.42 ± 0.08	0.17	7.17
		h	1.79-2.29	1.98 ± 0.09	0.19	9.73
M/3	3	L	4.18-4.39	4.30 ± 0.06	0.11	2.52
		lp	2.14-2.28	2.21 ± 0.04	0.07	3.31
		la	2.13-2.25	2.19 ± 0.04	0.06	2.84
		h	1.89-2.29	2.14 ± 0.13	0.22	10.32

		L3	1.12-1.16	1.14 ± 0.01	0.02	2.05
		l3	1.26-1.65	1.44 ± 0.11	0.20	13.70
P/3-P/4	1	L		5.97		

Table S9. Measurements and statistical data of the upper teeth of *Plesiomeryx huerzeleri* of DAM3. N, number of specimens; L/lp/la/h, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	**L/lp/la/h**	**LV**	**M ± SE**	**σ**	**V**
P1/	1	L		3.23		
		lp		1.23		
		la		1.36		
		h		1.81		
P2/	2	L	4.24-4.46	4.35 ± 0.11	0.16	3.64
		lp	2.00-2.08	2.04 ± 0.04	0.06	2.85
		la	1.62-1.86	1.74 ± 0.12	0.17	9.60
		h	2.08-2.87	2.47 ± 0.39	0.55	22.42
P3/	1	L		4.08		
		lp		3.52		
		la		2.04		
		h		1.39		
P4/	1	L		3.25		
		lp		4.37		
		h		1.46		
M1/	9	L	3.75-4.06	3.92 ± 0.03	0.08	2.16
		lp	4.68-5.29	5.00 ± 0.07	0.20	4.00
		la	4.11-4.80	4.48 ± 0.07	0.22	4.99
		h	1.36-2.26	1.85 ± 0.09	0.27	14.75
M2/	6	L	3.95-4.49	4.23 ± 0.10	0.25	5.88
		lp	5.17-5.79	5.46 ± 0.10	0.24	4.39
		la	4.49-5.33	4.92 ± 0.12	0.30	6.01
		h	1.58-2.97	2.08 ± 0.21	0.52	24.87
M3/	13	L	4.15-4.25	4.20 ± 0.03	0.05	1.24
		lp	5.00-5.25	5.12 ± 0.07	0.13	2.48
		la	4.14-4.95	4.56 ± 0.24	0.41	8.95
		h	1.55-2.25	2.00 ± 0.22	0.39	19.46
P3/-P4/	1	L		7.14		

Table S10. Measurements and statistical data of the lower teeth of *Plesiomeryx huerzeleri* of DAM3. N, number of specimens; L/lp/la/h/L3/l3 and lam, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/Lp/la/h	LV	M ± SE	σ	V
P/1	1	L		2.77		
		lp		1.37		
		la		1.25		
		h		1.65		
P/2	1	L		3.41		
		lp		1.50		
		la		1.39		
		h		1.85		
P/3	9	L	3.51-4.17	3.84 ± 0.07	0.20	5.18
		lp	1.61-2.01	1.81 ± 0.05	0.14	7.61
		la	1.40-1.64	1.52 ± 0.03	0.09	6.18
		h	2.05-2.59	2.37 ± 0.06	0.17	7.06
DP/3	3	L	3.83-4.08	3.92 ± 0.08	0.14	3.53
		lp	1.77-1.91	1.85 ± 0.04	0.07	3.78
		la	1.45-1.66	1.53 ± 0.07	0.11	7.47
		h	1.29-2.01	1.66 ± 0.21	0.36	21.72
P/4	1	L		4.00		
		lp		2.34		
		la		2.12		
		h		2.31		
DP/4	1	L		4.92		
		lp		2.76		
		la		2.33		
		h		1.75		
		lam		2.35		
M/1	4	L	3.70-4.02	3.85 ± 0.07	0.13	3.48
		lp	2.73-3.09	2.89 ± 0.09	0.18	6.19
		la	2.49-2.93	2.66 ± 0.10	0.19	7.17
		h	1.60-2.19	1.96 ± 0.14	0.28	14.34
M/2	4	L	4.17-4.57	4.36 ± 0.08	0.17	3.87
		lp	3.12-3.20	3.16 ± 0.02	0.03	1.06
		la	2.90-3.00	2.95 ± 0.03	0.05	1.81
		h	2.16-2.84	2.35 ± 0.16	0.33	13.91
M/3	4	L	4.94-4.51	5.25 ± 0.12	0.23	4.46
		lp	2.60-2.80	2.70 ± 0.04	0.08	3.14
		la	2.57-2.76	2.67 ± 0.04	0.08	3.01
		h	1.38-2.44	2.02 ± 0.23	0.46	22.78
		L3	1.18-1.44	1.32 ± 0.06	0.12	8.81
		l3	1.62-1.92	1.77 ± 0.07	0.14	7.78
P/3-P/4	1	L		7.64		

Table S11. Measurements and statistical data of the upper teeth of *Caenomeryx* cf. *procommunis* of DAM3. N, number of specimens; L/lp/la/h, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/lp/la/h	LV	M ± SE	σ	V
P3/	1	L		3.46		
		lp				
		la		2.36		
		h		2.66		
M1/	2	L	4.80-5.13	4.96 ± 0.16	0.23	4.66
		lp	5.76-6.09	5.92 ± 0.17	0.23	3.94
		la	5.40-5.49	5.44 ± 0.04	0.06	1.16
		h	1.67-2.11	1.89 ± 0.22	0.31	16.59
M2/	3	L	5.07-5.35	5.18 ± 0.09	0.16	3.01
		lp	6.07-6.16	6.11 ± 0.03	0.05	0.73
		la	5.60-5.79	5.67 ± 0.06	0.11	1.87
		h	2.66-3.06	2.85 ± 0.11	0.20	6.96
M3/	1	L		4.83		
		lp		6.07		
		la		5.50		
		h		2.43		

Table S12. Measurements and statistical data of the lower teeth of *Caenomeryx* cf. *procommunis* of DAM3. N, number of specimens; L/lp/la/h/L3 and l3, see Methods; LV, limit values; M ± SE, Mean ± Standard Error; σ, standard deviation; V, coefficient of variation.

	N	L/Lp/la/h	LV	M ± SE	σ	V
P/1	1	L		3.19		
		lp		1.39		
		la		1.22		
		h		1.69		
P/2	1	L		4.21		
		lp		1.89		
		la		1.72		
		h		2.72		
P/3	1	L		4.02		
		lp		2.03		
		la		1.81		
		h		2.64		
DP/3	2	L	4.57-4.66	4.62 ± 0.04	0.06	1.32
		lp	1.82-1.90	1.86 ± 0.04	0.06	3.01
		la	1.64-1.69	1.66 ± 0.02	0.03	1.53
		h	1.82-2.23	2.03 ± 0.21	0.29	14.38
P/4	4	L	4.01-4.40	4.23 ± 0.08	0.17	3.93
		lp	2.79-3.13	2.92 ± 0.07	0.15	5.09
		la	1.95-2.49	2.20 ± 0.11	0.23	10.25
		h	1.66-3.47	2.37 ± 0.39	0.78	33.02
M/1	4	L	4.13-4.39	4.32 ± 0.06	0.13	2.91
		lp	3.23-3.84	3.57 ± 0.14	0.28	7.87
		la	3.15-3.66	3.40 ± 0.12	0.24	6.96

		h	1.36-2.80	2.05 ± 0.34	0.67	32.75
M/2	5	L	4.32-4.47	4.39 ± 0.03	0.06	1.30
		lp	3.23-3.68	3.44 ± 0.07	0.16	4.65
		la	3.08-3.66	3.30 ± 0.10	0.22	6.82
		h	2.17-2.80	2.50 ± 0.10	0.23	9.19
M/3	4	L	6.02-6.77	6.33 ± 0.18	0.35	5.54
		lp	2.79-3.41	3.13 ± 0.11	0.25	8.09
		la	2.90-3.35	3.15 ± 0.11	0.22	6.84
		h	2.34-3.44	3.03 ± 0.25	0.49	16.24
		L3	1.64-2.14	1.99 ± 0.09	0.21	10.42
		l3	2.04-2.27	2.16 ± 0.05	0.11	4.95
M/1-M/3	1	L		14.73		