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

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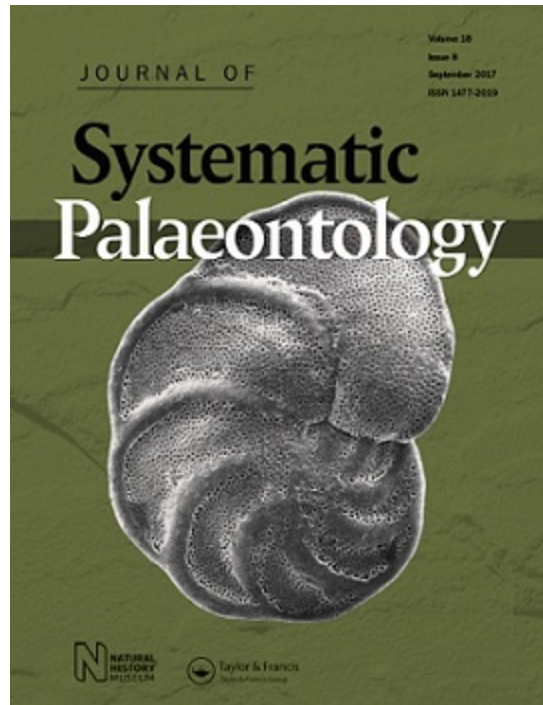
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**Cainotheriidae (Mammalia, Artiodactyla) from Dams (Quercy, SW France); phylogenetic relationships and evolution around the Eocene-Oligocene transition (MP19-MP21).**

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nexus_matrix_Cainotheriidae.nex	

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1  
2  
3 1 **Title: Cainotheriidae (Mammalia, Artiodactyla) from Dams (Quercy, SW France);**  
4  
5 2 **phylogenetic relationships and evolution around the Eocene-Oligocene transition**  
6  
7  
8 3 **(MP19-MP21).**

9  
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31 14  
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33 15 **Running title: Cainotheriidae from Dams, Quercy**

34  
35 16  
36  
37 17 **Abstract:**

38  
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40 18  
41  
42 19 Cainotheriids are a family of small artiodactyls, known in the fossil record from the late  
43  
44 20 Eocene to the middle Miocene in Western Europe. Contrary to several European endemic  
45  
46 21 ungulate groups that became extinct at the end of the Eocene or close to the Eocene-Oligocene  
47  
48 22 transition (*Grande Coupure*), cainotheriids crossed this boundary and diversified during the  
49  
50 23 Oligocene. The evolutionary history of cainotheriids around the Grande Coupure remains  
51  
52 24 poorly documented and only a few works deal with the modalities of their evolution, notably  
53  
54 25 because of the scarcity of available Eocene remains. A new fossiliferous karstic network named  
55  
56 26 Dams was discovered during field prospections in the Quercy area (Tarn-et-Garonne, France).

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2  
3 1 It notably displays two infillings that yielded a great abundance of cainotheriid remains, namely  
4  
5 2 DAM1 (MP19, late Eocene) and DAM3 (MP22, early Oligocene), bracketing the Eocene–  
6  
7 3 Oligocene transition. A detailed study of cainotheriid mandibular and dental remains from these  
8  
9 4 infillings reveals that only *Paroxacron valdense* occurs at DAM1, while five species are found  
10  
11 5 in DAM3. The karstic network at Dams seemingly records a local taxonomic diversification of  
12  
13 6 cainotheriids after the Grande Coupure, with Cainotheriinae being particularly successful. Our  
14  
15 7 phylogenetic analysis, including cainotheriids from Dams, constitutes the first formal  
16  
17 8 phylogeny of Cainotheriidae. Our results, based on mandibular and dental characters, allow for  
18  
19 9 (i) clarifying relationships within Cainotheriidae (ii) erecting a new family Robiacinidae, as  
20  
21 10 being the sister taxon to Cainotheriidae among Cainotherioidea and, more broadly, (iii)  
22  
23 11 discussing the controversial position of Cainotheriidae within Artiodactyla, as being more  
24  
25 12 closely related to Ruminantia than to Tylopoda.  
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33 14 **Keywords: Grande Coupure, Quercy karstic infillings, Western Europe, deciduous**  
34  
35 15 **dentition, morpho-anatomical phylogeny, faunal turnover.**  
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## 1 Introduction

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8 Cainotheriids are a family of small artiodactyls, known from the late Eocene to the  
9  
10 middle Miocene in Western Europe (Blondel 2005). This family is composed of two sub-  
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12 families and at least five genera (Blondel 2005): Oxacroninae Hürzeler, 1936, with *Oxacron*  
13  
14 Fihol, 1884 and *Paroxacron* Hürzeler, 1936; and Cainotheriinae Camp & VanDerHoof, 1940,  
15  
16 with *Plesiomeryx* Gervais, 1873, *Caenomeryx* Hürzeler, 1936, and *Cainotherium* Bravard,  
17  
18 1828. Their size range is variable, from small rabbit-sized species (e.g., *Oxacron*, *Paroxacron*)  
19  
20 to a size slightly smaller than the extant tragulid ruminant *Tragulus javanicus* (Theodor 2010)  
21  
22 (e.g., *Cainotherium*). Cainotheriids are characterised by brachydont selenodont molars. The  
23  
24 upper molars bear five cusps arranged in a unique ‘*Cainotherium* plan’ (Stehlin 1906), resulting  
25  
26 from a posterior migration of the protocone (Erfurt & Métais 2007). Upper molars therefore  
27  
28 have two anterior cusps (paracone and paraconule), and three posterior ones (metacone,  
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30 metaconule, protocone).  
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36 Like many mammalian species, several European endemic ungulates became extinct at  
37  
38 the end of the Eocene (Sudre & Legendre 1992; Blondel 2001), or close to the Eocene-  
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40 Oligocene transition. This major mammalian faunal turnover, called the Grande Coupure  
41  
42 (Stehlin 1910), is linked to climatic, geographic and oceanic circulation changes (Legendre  
43  
44 1987; Berggren & Prothero 1992; Akhmetiev & Beniamovski 2009). Unlike most other  
45  
46 endemic artiodactyl taxa, cainotheriids crossed the Eocene-Oligocene boundary and diversified  
47  
48 during the Oligocene (Blondel 2005). However, the evolutionary history of cainotheriids  
49  
50 around this transition remains poorly documented and understood. Indeed, only few studies  
51  
52 (Legendre 1980; Hooker & Weidmann 2000) are dedicated to Eocene cainotheriids and deal  
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54 with the modalities of their evolution. This is primarily due to the apparent monotony of their  
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1 dental characters and to the scarcity of cainotheriid remains documented in pre-Grande Coupure  
2 localities.

3 Knowledge of most cainotheriid genera (e.g. *Oxacron*, *Plesiomeryx*, or *Caenomeryx*)  
4 principally relies on material collected from the Phosphorites karstic fillings from Quercy  
5 (southwestern France) during the last century (Blondel 2005). This fossiliferous area yielded  
6 an unparalleled fossil record with over 170 localities recording local faunal assemblages with a  
7 very short time interval of ~1 million years or less (Aguilar *et al.* 1997, Escarguel *et al.* 2008),  
8 and a continuous record spanning the 38–26 Ma interval (late Eocene to late early Oligocene).  
9 In 2016, a new fossiliferous karstic network named “Dams” was discovered during field  
10 prospecting in the Quercy area (Tarn-et-Garonne, France). This karstic network was partly  
11 curated during the extensive phosphate exploitation in Quercy during the late 19<sup>th</sup> century. The  
12 Dams network however still houses a great quantity of clay infillings and preserves several  
13 fossiliferous channels distinct in age. Specifically, two fossiliferous infillings, named DAM1  
14 and DAM3, yielded a great amount of cainotheriid remains. Thanks to a low-energy transport,  
15 osseous and dental material is particularly well preserved, and the smallest and most delicate  
16 dental elements are documented, including incisors and deciduous dentition. Biochronological  
17 dating of Dams fossiliferous infillings builds on their rodent assemblages; morphological  
18 analyses of their dental and cranial remains from Quercy localities have allowed for  
19 identification of several chronospecies (lineages), characterised by evolutionary changes in the  
20 dental features of related species (e.g. Schmidt-Kittler & Vianey-Liaud 1987; Vianey-Liaud  
21 1974, 1976, 1979, 1998, 2015; Vianey-Liaud *et al.* 1995; Vianey-Liaud & Ringeade, 1993;  
22 Vianey-Liaud & Schmid 2009). They have proved to be reliable biochronological markers (e.g.  
23 Aguilar *et al.* 1997). Rodents, especially theridomorphs, are abundant in the Dams material.  
24 The assemblages found in the different Dams infillings indicate that they bracket the Eocene-  
25 Oligocene transition (see Material and Methods section for more details). Dams therefore

1 provides an unprecedented window on cainotheriid evolution, before and after the Grande  
2 Coupure, i.e. a time interval experiencing a dramatic faunal turnover under drastic  
3 environmental changes.

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

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

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

## 4 5 **Material and Methods**

### 6 7 **Material**

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

20 The age of the material described here was determined using rodent species associations  
21 in the two localities DAM1 and DAM3. The assemblage documented in DAM1 consists in the  
22 co-occurrence of *Patriotheridomys altus* Vianey-Liaud, 1974 and *Suevosciurus cf. minimus*  
23 (Major 1873), pointing to a late Priabonian age. It corresponds to the Mammalian Paleogene  
24 (MP) reference level MP19. The specific diversity retrieved in DAM3 is higher with five  
25 associated taxa: *Sciurromys cayluxi* Schlosser, 1884; *Pseudoltinomys major* Vianey-Liaud,



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3 1 1976; *Issiodoromys medius* Vianey-Liaud, 1976; *Blainvillimys gregarius* Schlosser, 1884;  
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5 2 *Toeniodus curvistriatus* Pomel, 1853. This association points to MP22, coinciding with an early  
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7 Rupelian age.  
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## 11 5 **Methods**

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15 6 **Measurements.** Measurements (millimetres) were taken using a mesuroscope Nikon 10. The  
16  
17 global surface of the tooth is expressed through: L, the maximal mesio-distal length; l, the  
18  
19 maximal bucco-lingual dimension. The bucco-lingual aspect of the tooth is also expressed  
20  
21 through two measurements: lp, maximal width of posterior lobe of the teeth; la, maximal width  
22  
23 of anterior lobe. The height (h) corresponds to the maximal height of the crown. L3 and l3  
24  
25 respectively correspond to maximal length and width of the third lobe (distal) of the lower M3.  
26  
27 Lam, corresponds to the maximal length of the third lobe of the lower DP4. Finally, some  
28  
29 diastemata lengths or premolar rows have been estimated based on alveoli when one of the teeth  
30  
31 was missing. The variability of dental measures is estimated by the variation coefficient (V).  
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36 15 **Phylogenetic analysis.** In order to discuss cainotheriid systematics and the position of  
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38 Cainotheriidae within Artiodactyla, we performed a phylogenetic analysis including  
39  
40 representatives of all cainotheriid genera, as well as representatives of Tylopoda, Ruminantia,  
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42 and European endemic artiodactyl taxa and retrieved closely related to cainotheriids in previous  
43  
44 studies. 23 artiodactyl species were included as operational terminal units among which eight  
45  
46 constitute the ingroup Cainotheriidae: *Paroxacron valdense*, *Paroxacron bergeri*, *Oxacron*  
47  
48 *courtoisii*, *Plesiomeryx huerzeleri*, *Plesiomeryx cadurcensis*, *Caenomeryx procommunis*,  
49  
50 *Caenomeryx filholi*, *Cainotherium laticurvatum*; thirteen species stand for the branching group  
51  
52 (Antoine 2002, Orliac *et al.* 2010) which consists in members of Ruminantia (*Parvitragus*  
53  
54 *priscus*, *Lophiomeryx chalaniati*, *Archaeomeryx optatus*), Tylopoda (*Paratoceras coatesi*,  
55  
56 *Eotylopus reedi*) and taxa of disputed phylogenetic position (*Robiacina minuta*, *Robiacina*  
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3 1 *quercyi*, *Robiacina lavergnensis*, *Dacrytherium ovinum*, *Anoplotherium latipes*, *Mixtotherium*  
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5 2 *cuspidatum*, *Amphimeryx murinus*, *Xiphodon castrense*); two species form the outgroup:  
6  
7 3 *Eurodexis russelli* and *Dichobune leporina*. Dental characters (Dataset. S1) and taxa/characters  
8  
9 4 matrix (Dataset. S2-3) provided in the Supplementary Online Material (S). 44 are original and  
10  
11 5 29 are based on or modified from previous analyses. Character coding is based on direct  
12  
13 6 observations of specimens and on illustrations and descriptions from the literature: Stehlin  
14  
15 7 (1908); Matthew & Reed (1910); Hürzeler (1936); Berger (1959); Emry (1978); Sudre (1978);  
16  
17 8 Gentry & Hooker (1988); Erfurt & Métais (2007); Hooker (2007); Hooker & Weidmann  
18  
19 9 (2000); Rincon *et al.* (2015). The matrix of characters was established with the software NDE  
20  
21 10 1.0 (Page 2001). Phylogenetic analysis was performed with PAUP\* logical version 4.0a161  
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23 11 (Swofford 2002), using a heuristic search (>12 taxa) with TBR algorithm, at 1000 repetitions  
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25 12 (10 trees retained by repetition).

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31 13 **Dental nomenclature** (Fig. 1-2). The nomenclature of Boisserie *et al.* (2010) was used in this  
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33 14 work to name crests/cristids. That of VanDerMade (1996, fig. 6) and Boivin *et al.* (2018) is  
34  
35 15 used for deciduous dentition. The nomenclature of incisors was inspired from VanDerMade  
36  
37 16 (1996, fig. 13). The justification of cusp/cuspids names is provided in the Discussion section.  
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### 43 **Abbreviations**

44  
45 19 MX/: upper molars; M/X: lower molars; PX/: upper premolars; P/X: lower molars; DX:  
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47 20 deciduous teeth; BSP: Bayerische Staatssammlung für Paläontologien, München, Germany;  
48  
49 21 DAM1, DAM3: localities of Dams; MNHN: Muséum national d'histoire naturelle, Paris,  
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51 22 France; NMB: Naturhistorisches Museum Basel, Switzerland.  
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3 **Systematic palaeontology**  
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8 3 Class **Mammalia** Linnaeus, 1758  
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10 4 Order **Artiodactyla** Owen, 1848  
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12 5 Superfamily **Cainotherioidea** Camp & VanDerHoof, 1940  
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14

15 6 **Emended Diagnosis.** Small artiodactyls with large auditory bullae and large orbits. Paracone  
16 and metacone sub-equal on P3/; hypoconid small on P2-P3; postprotoconulid present.  
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18 8 Mesoconid small to large on the lower molars; entoconid slightly more to more distal than the  
19 hypoconid. Protocone sub-central to distal on the upper molars and lingual with respect to the  
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22 9  
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25 10 paraconule position on M3/.

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28 11 **Remarks.** The justification for using the super-family Cainotherioidea is provided in the  
29 following section and ensues the results of phylogenetic analysis.  
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33 13 Family **Cainotheriidae** Camp & VanDerHoof, 1940  
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35

36 14 **Emended Diagnosis.** Cainotherioidea with a size ranging from small rabbit-sized species (e.g.,  
37 *Oxacron*, *Paroxacron*) to slightly smaller than the extant tragulid ruminant *Tragulus javanicus*  
38 (e.g., *Cainotherium*). Complete postorbital bar; enlarged bullae and orbits; morphology of the  
39  
40  
41 16 lower jaw variable within the family but tends to become massive and deepen posteriorly in  
42  
43 17 some genera. Presence of diastemata within the premolar row in the Eocene species and tend to  
44  
45 18 be reduced or lost (*Cainotherium*) in the Oligocene and Miocene forms. Lower incisors with  
46  
47 19 two endocristulids; lower canine incisiform. Mesial premolars narrow; P4/ tends to be  
48  
49 20 molarized; P1/ and P2/ without mesial lobe; P3/ triangular and labially concave, with a lingual  
50  
51 21 cusp; P4/ subrectangular. Crowns of cheek teeth moderately high. Lower molars with a large  
52  
53 22 medio-lingual metaconulid; entoconid very distal and close to hypoconulid; neotrigonid (Sudre  
54  
55 23 1977) present; absence of hypoconulid on M/1 and M/2. Upper molars sub-triangular to  
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1 quadrangular with a W-shaped ectoloph and crescent-shaped lingual cusps; protocone disto-  
 2 lingual and paraconule mesiolingual; postprotocrista long and distally orientated;  
 3 postparacristula present; lack of preprotocrista and paraconule junction. Limbs tetradactyl with  
 4 a reduction of lateral digits (II and V); forelimb shorter than hindlimb; tail long.

5 Subfamily **Oxacroninae** Hürzeler, 1936

6 **Emended Diagnosis.** Small cainotheriids, comprised around 400g (e. g. *Oxacron courtoisii*) –  
 7 900g (e. g. *Paroxacron bergeri*). Muzzle generally elongated and narrow; orbits large with  
 8 respect to the small size of the skull; ethmoidal fissures absent. Diastemata present (except *P.*  
 9 *bergeri*), between P1/P2, P2/P3 and P1/P2/. Premolars narrow; postprotoconulid weak;  
 10 protocone more mesial than paracone on P4/; P1 biradicate. Upper molars subtriangular to  
 11 quadrangular (e. g. *P. bergeri*); styles without crest and mesostyle bounded (except *P.*  
 12 *bergeri*); postparacristula relatively short.

13 Genus **Paroxacron** Hürzeler, 1936

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

16 **Original Diagnosis.** Oxacroninae with P1/, P1, P2/ and P2 elongated and premolariform, with  
 17 a short diastema between P1/P2/, P1/P2 and P2/P3 or no diastemata at all; anterior lobe of  
 18 P3/ elongated; upper molars with mesostyle notch (Hürzeler 1936).

19 ***Paroxacron valdense*** (Stehlin, 1906)

20 (Fig. 2-7)

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

22 1936 *Paroxacron valdense* (Stehlin); Hürzeler, pp. 105–106, fig. 72

23 1980 *Paroxacron* sp. Legendre, pp. 120–127, tab. 3–4.

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2  
3 1 **Lectotype.** A right cranial fragment with P2/-M3/ (NMB Mt.230; Stehlin, 1906), from  
4  
5 2 Mormont Entreroches, Switzerland (MP19).  
6  
7

8 3 **Emended Diagnosis.** Species of *Paroxacron* with diastemata short or occasionally absent  
9  
10 4 between P1/-P2/ and P2-P/3, and very short to absent between P/1-P/2 and C-P/1; mandible  
11  
12 5 with a gracile and relatively shallow horizontal ramus of constant height between the premolar  
13  
14 6 area and the last molar; coronoid process of the mandible particularly high above the occlusal  
15  
16 7 plane; mandibular condyle long medio-laterally and inclined medially in posterior view;  
17  
18 8 angular apophysis not extended ventrally and stretched distally, with deeply concave dorsal  
19  
20 9 outlines; shallow *incisura vasorum*.  
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25 10 **Differential Diagnosis.** *Paroxacron valdense* differs from Cainotheriinae by the presence of  
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27 11 sub-triangular upper molars without crested styles, a shorter postparacristula, narrow premolars,  
28  
29 12 a weaker postprotoconulid, a P/1 biradicate, diastemata between P/2-P/3 and P1/-P2/, and a  
30  
31 13 protocone more mesial than the paracone on P4/. It differs also from *Plesiomeryx* and  
32  
33 14 *Caenomeryx* species by a smaller size (except *Ple. cadurcensis*), a small protocone and a longer  
34  
35 15 mesial lobe on P3/, as well as the absence of a protocone on P2/. It diverges from *Cainotherium*  
36  
37 16 by a smaller size, the absence of cingulum/id on premolars, a triangular P3/, and the presence  
38  
39 17 of a valley between the entoconid and the mesoconid on lower molars. *Paroxacron valdense*  
40  
41 18 differs from the other Oxacroninae *Oxacron courtoisii* by the presence of more elongate and  
42  
43 19 premolariform premolars (P1 and P2), an elongate anterior lobe on the P3/ and a larger  
44  
45 20 paroconule on the upper molars. Within *Paroxacron*, *Paroxacron valdense* distinguishes from  
46  
47 21 *P. bergeri* by a smaller size, sub-triangular upper molars, looped mesostyle, and the presence  
48  
49 22 of diastemata. Finally, *Paroxacron valdense* differs from *Paroxacron* sp. by a larger size, a M1/  
50  
51 23 more triangular and a shorter diastema between P/1-P/2.  
52  
53  
54  
55  
56  
57

58 24 **New material from DAM1.** DAM1: four left maxillary fragments with P2/-M3/ (DAM1 01-  
59  
60 25 03, DAM1 07); two left maxillary fragments with P2/, P4/-M3/ (DAM1 04, DAM1 09); two

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

1 (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).

## 17 **Description.**

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

19 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

1 (mediocristid) connecting the two conulids slightly disto-lingually inclined, and a long and thin  
2 root. Morphological variation observed within the DAM1 sample (15 specimens) is negligible.

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

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

18 P/1 and P/2 (Fig. 3A-B, 6D-E, 6L) are very similar morphologically and they essentially  
19 differ in size (Tab. S1) and root orientation. P/1 is short mesio-distally, with close oblique roots,  
20 whereas P/2 is longer with more remote roots. P/1 and P/2 are characterised by two main cuspids  
21 with a protoconid larger and higher than paraconid; a bending at the mesial margin of the tooth  
22 (postparacristid and preprotocristid junction), the postparacristid being disto-buccally directed  
23 and the preprotocristid mesio-buccally directed; a single and straight distal cristid disto-  
24 buccally orientated, connecting the protoconid to the distal margin of the tooth; a small  
25 accessory cusp at the back of the protoconid, called a postprotoconulid; a weak disto-lingual



1  
2  
3 1 cingulid with a small distal styloid (distostyloid); a disto-lingual fossid (endofossid). Inter-  
4  
5 2 specimen variability mainly concerns the paraconid size. The bigger it is, the deeper the bending  
6  
7 3 between protoconid and paraconid is. Some P/1 do not show this bending. Other variations are  
8  
9 4 also observed as the distance between the roots, the size of the endofossid, the presence of an  
10  
11 5 endoprotocristid, and the size of the postprotoconulid.  
12  
13

14 6 P/3 (Fig. 3C-D, 6L, 6N) is the longest premolar, and it may occasionally have a small  
15  
16 7 root between the two main roots (Fig. 6M). Its morphology is very similar to that of P/1 and  
17  
18 8 P/2, but it differs from the latter in its distal part by similarities with P/4. The postprotoconulid  
19  
20 9 of P/3 is bigger and the distal cristid lingually curves on the distal margin of the tooth, and bears  
21  
22 10 two small accessory cusps, called conulid 1 (end) and conulid 2. Mesially, the paraconid is also  
23  
24 11 larger than on P/1-2. Marked morphological variations are observed on P/3s from DAM1: i) the  
25  
26 12 distal cristid can be long to very short lingually, joining a small to absent conulid 1, ii) the depth  
27  
28 13 and width of the endofossid vary, iii) a small distal and buccal cristid may be present, iv) the  
29  
30 14 postprotoconulid is more or less large and may have a small endocristid disto-lingually curved,  
31  
32 15 as on P/4.  
33  
34  
35  
36

37 16 P/4 (Fig. 3E-F, 6L, 6N) is shorter and more molariform than P/3 and it differs from it  
38  
39 17 by the presence of three main cuspids with a large protoconid, a paraconid and a metaconid, the  
40  
41 18 protoconid being more mesial than the metaconid. It also shows an anterior part (protoconid  
42  
43 19 and paraconid) more lingually inclined, with a preprotocristid mesio-lingually orientated and a  
44  
45 20 paracristid more lingually inclined. The entoconid and hypoconid are weakly pronounced, the  
46  
47 21 latter having an extended prehypocristid. The postprotoconulid is smaller, with a more extended  
48  
49 22 endocristid, and there are two posterior cristids on the protoconid and the metaconid, joining at  
50  
51 23 the center of the tooth. P/4 further has disto-buccal and distal cingulids. Morphological variation  
52  
53 24 only concerns the size of cristids and cingulids, and paracristid orientation. The endocristid of  
54  
55  
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2  
3 1 the postprotoconulid may in some specimens connect to an accessory cusp or link the  
4  
5 2 metaconid.  
6

7  
8 3 M/1-2 (Fig. 3G-H, 6L, 6N) are very difficult to distinguish from each other. They are  
9  
10 4 characterised by five main cusps with a high metaconid, a metaconulid mesio-lingually located  
11  
12 5 and an entoconide disto-lingually. The entoconid has a loop-like shape, notably created by  
13  
14 6 respectively distally convex and concave preentocristid and postentocristid. M/1-2 present also  
15  
16 7 a small to absent lingual paraconid and an entoconid more distal than the hypoconid. The  
17  
18 8 mesiodistal cristid (mediocristid) is short, connecting the premetacristulid and postmetacristid,  
19  
20 9 and closing the transverse valley. There is a continuous cristid formed by a long prehypocristid  
21  
22 10 and short premetacristulid; an accessory cusp is present on this last cristid, called a  
23  
24 11 centroconulid, and bears a cristid (postendocentrocristulid) disto-lingually orientated. This set  
25  
26 12 corresponds to the neotrigonid described by Sudre (1977). Finally, M/1-2 bear a major buccal  
27  
28 13 cristid formed by the junction of the posthypocristid and postentocristid that is directly  
29  
30 14 connected and a large distal cingulid. Morphological variation is negligible.  
31  
32  
33  
34

35 15 M/3 (Fig. 2C-D, 3I-J, 6L, 6N) exhibits the same pattern as M/1-2, differing from the  
36  
37 16 latter in having a hypoconulid. This conulid connects the rest of the talonid by the  
38  
39 17 prehypocristulid, which joins the postentocristid (short) and the posthypocristid (long). The  
40  
41 18 hypoconulid and the entoconid are very close to one-another; the talonid is smaller than that of  
42  
43 19 M/1-2. There are some variations between specimens (posthypocristulid sometimes present;  
44  
45 20 roots are either fused or separate).  
46  
47  
48  
49

50 21 **Upper dentition (Tab. S2; Fig. 2, 4, 7).** The upper incisors are characterised by a  
51  
52 22 spatulate-like crown (lingually concave) and an inclined root.  
53

54 23 The I1/ (Fig. 2E, 7C) is a very simple tooth with a dorso-ventrally elongated crown. It  
55  
56 24 is characterised by a mesio-distally symmetrical crown, with the apical portion of the tooth  
57  
58 25 mesially convex. It bears two main cusps, with a small paracone and a metacone having  
59  
60

1  
2  
3 1 respectively an endoparacrista and endometacrista, and small apical styles. The lingual surface  
4  
5 2 bears a little mesial fossa (pre-fossa), a very tiny and lightly deep distal fossa (post-fossa), a  
6  
7 3 mesio-distally large medial fossa (endo-fossa) and a lingual cingulum. The root is thin and  
8  
9 4 short. Variation observed within our sample (11 specimens) is rather weak and concerns the  
10  
11 5 mesial length of the paracone/parastyle portion of the tooth.  
12  
13

14 6 I2/ (Fig. 4K, 7B) is more complex and mesio-distally longer than I1/. It differs from the  
15  
16 7 latter by a less spatulate-like and mesio-distally asymmetrical crown, a more mesially  
17  
18 8 projected anterior part, more pronounced metacone and paracone (the latter being bigger), more  
19  
20 9 marked styles, with a metastyle with a small bulge at its base. The pre-fossa and the post-fossa  
21  
22 10 are mesio-distally wider and deeper, the endo-fossa is mesio-distally smaller. The apical crest  
23  
24 11 connecting the paracone and the metastyle (postcrista) is inclined disto-lingually. The lingual  
25  
26 12 cingulum is larger, and the root is longer and less arched than that of I1/. Morphological  
27  
28 13 variation affects the size of cusps and styles and the degree of crests inclination (15 specimens).  
29  
30  
31

32 14 I3/ (Fig. 4J, 7A) is mesio-distally shorter than I1/-2/. It differs from I2/ by a lower crown,  
33  
34 15 a less mesially projected mesial part, a larger paracone giving the tooth a caniniform shape, a  
35  
36 16 less dorso-ventrally extended metastyle and placed at the level of its bulge, at the base of the  
37  
38 17 crown. The parastyle is more pronounced. The post-fossa is smaller but deeper, while the pre-  
39  
40 18 fossa is larger, as wide as the central fossa. The post-fossa is strongly inclined distally. The  
41  
42 19 precrista is more mesio-lingually inclined and the apical crest connecting the paracone and  
43  
44 20 metacone (mediocrista) is more disto-lingually inclined. The root of I3/ is stockier than that of  
45  
46 21 I2/. The morphological variation (15 specimens) is rather weak and similar to I2/. Some teeth  
47  
48 22 present a strong mesial projection of their mesial part.  
49  
50  
51

52 23 Upper canine (Fig. 4L, 7D) is taller and stockier than I3/. It differs from it by a more  
53  
54 24 mesio-distally directed mesial part, larger paracone and metacone, more pronounced styles, the  
55  
56 25 metastyle having a big basal bulge. The post-fossa is deeper, the pre-fossa is mesio-distally  
57  
58  
59  
60

1 wider, and the endo-fossa is more compressed. The mesial fossa is thus more important than  
2 the endo-fossa. The mediocrista and postcrista are strongly disto-lingually inclined. The root of  
3 the upper canine is longer and very thick. Variation is mainly in metastyle and metacone  
4 development. Some teeth present an anterior part more mesially projected (15 specimens).

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

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

23 P3/ (Fig. 4E-F, 7M) differs morphologically from P1/-2/. It is subtriangular in shape and  
24 bears three roots. It is characterised by well-pronounced paracone, metacone and protocone,  
25 salient parastyle and metastyle, a very elongated mesial lobe (paracone and parastyle) and a

1  
2  
3 1 crest connecting the metastyle to parastyle that is buccally concave. There are lingual and distal  
4  
5 2 cingula. P3/ is highly variable: i) the protocone can be wide to mesio-distally compressed and  
6  
7 3 it can be located in a distal to medial position, ii) mesial and disto-lingual (protocone) lobes can  
8  
9  
10 4 be variously elongated and wide, iii) the crests connecting the paracone and the parastyle  
11  
12 5 (preparacrista and postparacristyla) can be more or less mesio-buccally inclined, iv) the crest  
13  
14 6 formed by the junction of the postmetacrista and premetacristyla is variously inclined disto-  
15  
16 7 buccally, v) an ectoprotocrista can be occasionally present, oriented towards the metacone, vi)  
17  
18 8 cingulum can be variously expanded. The P3/ of this species therefore have a wide  
19  
20 9 morphological diversity, ranging from a small, stocky and short tooth to an elongated and  
21  
22 10 narrow tooth.

23  
24  
25  
26 11 P4/ (Fig. 4G-H, 7M) is easily recognisable from other premolars by much shorter mesio-  
27  
28 12 distal dimensions. It presents a paracone larger and higher than the mesial protocone, a small  
29  
30 13 metacone, well individualised and salient parastyle and metastyle, medio-lingually bent. A crest  
31  
32 14 connects the parastyle and the metastyle is buccally concave. An accessory cusp is present on  
33  
34 15 the postprotocrista (conule 1), and it bears a crest extended buccally. The disto-lingual cingulum  
35  
36 16 is large. Variations between specimens are important and mainly related to the cingulum  
37  
38 17 development. The P4/ can vary from stocky and quadrangular to narrow and triangular.

39  
40  
41  
42 18 Upper molars (Fig. 2A-B, 4I, 7M) are morphologically similar. They are characterised  
43  
44 19 by the '*Cainotherium*' plan, composed of five main cusps (Stehlin, 1906). The paracone is  
45  
46 20 mesio-buccal, the paraconule mesio-lingual, while the protocone is disto-lingual, located more  
47  
48 21 mesially than the metacone and the metaconule. Upper molars present also well-pronounced  
49  
50 22 styles, with a loop-like mesostyle; a short and continuous premetacristula; a preprotocrista  
51  
52 23 tending to bind with the postparacristula; a preparacristula connecting the preparacristyla, and  
53  
54 24 the postmetacristula joining the postmetacristyla; a mesial cingulum; a lingual cingulum  
55  
56 25 symbolised by cingular cusps in front of (mediostyle) or behind the protocone (distostyle). The  
57  
58  
59  
60

1 morphology of upper molars is highly variable: i) the crown shape can be triangular to  
2 rectangular (bucco-lingually), ii) the inclination of the crown is variously pronounced, with a  
3 small mesially and distally convex curvature, accompanied by a parastyle more or less buccal,  
4 iii) the preprotocrista can be long buccally in some teeth, iii) the distostyle is variously marked.

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

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

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

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

20 DP/2-3 (Fig. 5C-D, 6H-I) are morphologically similar to P/3 but they differ in their  
21 posterior part by pronounced hypoconid and entoconid; a larger conulid 2 with a small cristid  
22 lingually directed; a cristid descending from the postprotoconulid to the conulid 2 and joining  
23 the prehypocristid and postentocristid, strongly disto-buccally inclined; a disto-lingually  
24 inclined cristid starting from the postprotoconulid; a mesio-distal cristid connecting the

1  
2  
3 1 protoconid and postprotoconulid. The morphological variation observed in our sample is low  
4  
5 2 (nine specimens).

6  
7 3 DP/4 (Fig. 5E-F, 6J-K) is very similar in morphology and variability to lower molars  
8  
9 4 but it differs from them in the presence of a third lobe in its anterior part, consisting of a lingual  
10  
11 5 primoconid and a buccal paraconid, the latter being little more mesial than the former. The  
12  
13 6 talonid (posterior lobe) is larger than the mesial lobe. The postprimocristid is directed disto-  
14  
15 7 lingually and joins the preprotocristid and premetacristid. There is a bucco-lingually inclined  
16  
17 8 cristid formed by the junction of the endoprotocristid and ectometacristid, and a bucco-lingually  
18  
19 9 inclined cristid originating from the hypoconid (endohypocristid). DP/4 bears an open  
20  
21 10 transverse valley and an absent to weak mesial cingulid.

22  
23  
24  
25  
26  
27 11 **Upper deciduous teeth (Tab. S3; Fig. 5G-L, 7E-H, 7K-L).** Compared to the  
28  
29 12 permanent dentition, the upper deciduous teeth present the same general characteristics as the  
30  
31 13 lower ones and they differ by a lower, narrower, and more mesio-distally elongated crown.

32  
33 14 DP1-2/ (Fig. 5G-H, 7E-F) are premolariform and very close morphologically to P2/.  
34  
35 15 However, they differ from P2/ in having a shorter postmetacristyla and in lacking a lingual  
36  
37 16 cingular cusp. Morphological variation is negligible (five specimens).

38  
39  
40 17 DP3/ (Fig. 5I-J, 7G-H) is distally molarised and mesially premolarised. It is very similar  
41  
42 18 to DP4/ and upper molars in its distal part and to DP1-2/ in its mesial part. However, DP3/ is  
43  
44 19 shorter and wider than DP1/ and DP2/. It is characterised by a distal part with a metacone,  
45  
46 20 metaconule and protocone, a mesial part with a big paracone, salient styles with posterior  
47  
48 21 metastyle and mesostyle, as well as a highly mesially prominent anterior parastyle. The crown  
49  
50 22 shows a significant distally concave curvature owing to a strong mesio-distally compressed  
51  
52 23 protocone, splitting disto-buccal and disto-lingual parts. The anterior part of the tooth is very  
53  
54 24 elongated and bucco-lingually compressed (paracone to parastyle). The paracrystyla is mesio-  
55  
56 25 buccally inclined, the ectoprotocrista binds with the premetacristula and the preprotocrista with  
57  
58  
59  
60

1 the mediostyle. The distostyle is marked and the lingual cingulum is big. Morphological  
2 variation mainly affects the size of the protocone and the bucco-lingual compression of the  
3 distal part of the tooth (15 specimens).

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

13 **Diastemata/Mandible (Fig. 6L, 6N-R).** Specimens are characterised by diastemata  
14 short or occasionally absent between P1/ and P2/, P2/ and P3/, and shorter or absent between  
15 P1/ and P2/ (Tab. S1; Fig. 6L, 6O). The posterior tip of the mandibular symphysis is located at  
16 the level of the distal margin of P2/ (Fig. 6L, 6N). Two mental foramina are constantly present  
17 on the horizontal ramus, one below the mesial part of P2/ and one below the mesial part of P4/  
18 (Fig. 6O, 6R). The horizontal ramus is gracile, relatively shallow and its height is rather constant  
19 between the premolar area and the last molar. However, specimens show almost no variation.  
20 The mesial margin of the ascending ramus is wide at its root (Fig. 6O-P). The coronoid process  
21 is particularly high above the occlusal plane and its dorsal tip forms a sharp crest (Fig. 6P-Q).  
22 The condyle is narrow and convex mesio-distally (Fig. 6Q). In posterior view, the condyle is  
23 medio-laterally long and medially inclined. The masseteric fossa, in lateral view, is deep in its  
24 mesial portion. There is a wide mandibular foramen on the medial aspect of the ascending ramus  
25 base (Fig. 6P-Q). The mandibles are characterised by a very elongated angular apophysis,



1  
2  
3 1 making a weak angle with ascending ramus. In lateral view, the dorsal outline of the angular  
4  
5 2 process is deeply concave and it forms a pointed tip at the distal most part. The angular  
6  
7 3 apophysis does not extend much ventrally beyond the level of the ventral margin of the  
8  
9 4 horizontal ramus. Almost no variation is observed on the ventral extension of the angular  
10  
11 5 process. The angular apophysis is mesially delimited by a shallow *incisura vasorum*.

12  
13  
14  
15 6 **Remarks.** The cainotheriid material from DAM1 is referred here to *Paroxacron* based on the  
16  
17 7 presence of i) small diastemata between P/1-P/2, P/2-P/3 and P1/-P2/, ii) premolariform P/1  
18  
19 8 and P/2, and iii) a P3/ with a long mesial lobe. Mandibular remains from DAM1 differ from  
20  
21 9 those of *Paroxacron bergeri* in having a more elongated angular apophysis and a shorter angle  
22  
23 10 with the ascending ramus, as well as a smaller and less marked *incisura vasorum* and the  
24  
25 11 presence of diastemata. They also differ in the size and shape of their upper molars which have  
26  
27 12 more triangular outlines, and smaller size.

28  
29  
30  
31 13 The morphology of DAM1 specimens is compatible with the diagnosis of *Paroxacron*  
32  
33 14 *valdense* as proposed by Stehlin (1906) and Hürzeler (1936). The maxilla Mt. 230 from  
34  
35 15 Enteroches (Mormont, Switzerland), lectotype of the species, and the mandibles Mt. 232-233  
36  
37 16 from Cinq-Sous (Mormont, Switzerland) described by Stehlin (1906), as well as maxillae QS.  
38  
39 17 486 and the mandible QU. 32 from old Quercy collections described by Hürzeler (1936), are  
40  
41 18 indeed morphologically and biometrically very similar. However, as mentioned by Hooker &  
42  
43 19 Weidmann (2000) based on the new material from Eclepens C and Cinq-Sous (Mormont,  
44  
45 20 Switzerland), some diagnostic characters like the diastemata length and the anterior premolar  
46  
47 21 shape, present significant intraspecific variation. This variation is indeed also observed in  
48  
49 22 DAM1 material (see description section above). However, specimens from Cinq-Sous and  
50  
51 23 Eclepens C differ from those from Quercy and Enteroches by smaller dimensions of anterior  
52  
53 24 premolars, by a P4/ and upper molars that are more triangular, producing a more primitive shape  
54  
55 25 according to Hooker & Weidmann (2000). These differences may be related to the slightly older  
56  
57  
58  
59  
60

1 age of the first two sites (Hooker & Weidmann 2000). The differences observed between  
 2 DAM1 material and *Paroxacron bergeri* and the similarities with *P. valdense* from the type  
 3 locality of Entreroches allow the DAM1 specimens to be identified as *P. valdense*.

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

#### 14 *Paroxacron* sp.

15 (Fig. 8)

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

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

1  
2  
3 1 P1/ is relatively elongated, premolariform, and double-rooted (Fig. 8M-N). The  
4  
5 2 paracone is thicker than the weakly-marked parastyle and metastyle. P4/ is relatively narrow  
6  
7 3 and triangular, with a large paracone distally located with respect to the protocone (Fig. 8A-B).  
8  
9 4 Styles are salient and the disto-lingual cingulum is weak. Upper molars are subtriangular with  
10  
11 5 a loop-like mesostyle (Fig. 8C-H).  
12  
13

14  
15 6 **Remarks.** The presence of small teeth and double-rooted premolariform P/1 and P/2, elongated  
16  
17 7 and narrow with weakly developed cusps, and a P4/ with a mesial protocone, allows to attribute  
18  
19 8 these specimens to an unnamed species of *Paroxacron*, but which is different from either of the  
20  
21 9 named ones. Specimens described by Blondel (2005) from Aubrelong 1, Ravet (MP21) and  
22  
23 10 Plante 2 (MP22) of Quercy are similar to those of DAM3. However, dimensions are close to  
24  
25 11 those of *Plesiomeryx cadurcensis*, and it is sometimes difficult to differentiate the two species  
26  
27 12 on the basis of isolated upper and lower molars.  
28  
29

30  
31 13 According to the description of Blondel (2005), *Paroxacron* sp. differs from  
32  
33 14 *Paroxacron valdense* by an anterior lobe of the P3/ similar to that observed in *Plesiomeryx*  
34  
35 15 *cadurcensis*, a more quadrangular M1/ and a longer diastema between P/1-P/2. The  
36  
37 16 dimensions are also smaller, especially for upper premolars. Owing to the small available  
38  
39 17 sample (with respect to DAM 1 material), it is not possible to test intraspecific variation  
40  
41 18 accurately. Yet, morphological and metrical features of these Oligocene specimens are  
42  
43 19 consistently distinct from those of DAM1. It is therefore possible to consider that the Aubrelong  
44  
45 20 1, Ravet, La Plante 2 and DAM3 sites include a younger species of *Paroxacron* which also  
46  
47 21 differs from *Paroxacron bergeri* by its small size, its less quadrangular molars and the presence  
48  
49 22 of a diastema between P/2-P/3. This species may be new.  
50  
51  
52  
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54

55 23 *Paroxacron bergeri* Heissig, 1978

56  
57 24 (Fig. 9)

58  
59 25 Synonymy: 1959 cf. *Cainotherium? elongatum* Filhol (?Berger); Berger, p. 45, pl. 4, fig. 5.

1  
2  
3 1 1959 *Cainotherium?* n. sp.; Berger, p. 47, pl. 5, fig. 6–10.  
4  
5

6 2 **Holotype.** A right mandibular fragment I/3-M/3 (BSP 1879XV201), locality of Mouillac in  
7  
8 3 Phosphorites of Quercy. The precise age and type locality are unknown (Old Quercy  
9  
10 4 collections).  
11  
12

13 5 **Diagnosis.** Species of *Paroxacron* without a diastema between P/2-P/3. The edge of the  
14  
15 6 mandible is more strongly bent than in *P. valdense*. The *angulus mandibulae* is short, high and  
16  
17 7 angular. It is limited by a short but strong *incisura vasorum* anteriorly. P/3 and P/4 have a more  
18  
19 8 complete talonid and the internal wall of the lower molars is higher than in *P. valdense* (Heissig  
20  
21 9 1978).  
22  
23  
24  
25

26 10 **Differential Diagnosis.** *Paroxacron bergeri* differs from Cainotheriinae species by the absence  
27  
28 11 of crested styles on the upper molars, a shorter postparacristula, the presence of narrow  
29  
30 12 premolars and a protocone more mesial than the paracone on P4/. It differs also from  
31  
32 13 *Plesiomeryx* and *Caenomeryx* species by a small protocone and a longer mesial lobe on P3/,  
33  
34 14 and the absence of diastemata and protocone on P2/. It distinguishes from *Cainotherium* by the  
35  
36 15 absence of cingulum/id on premolars and a triangular P3/. *P. bergeri* diverges from the  
37  
38 16 Oxacroninae *Oxacron courtoisii*, by a larger size, the presence of more elongate and  
39  
40 17 premolariform premolars (P1 and P2), an elongate anterior lobe on the P3/, as well as a larger  
41  
42 18 paroconule and pinched mesostyle on the upper molars. *P. bergeri* differs from *P. valdense* and  
43  
44 19 *P. sp.* by a larger size, quadrangular upper molars, a pinched mesostyle and the absence of  
45  
46 20 diastemata.  
47  
48  
49  
50

51 21 **New material from DAM3.** Two left M3/ (DAM3 22-23); one right M3/ (DAM3 24); two left  
52  
53 22 M2/ (DAM3 25, DAM3 27); one right M2/ (DAM3 26); two left M1/ (DAM3 28-29); one left  
54  
55 23 P4/ (DAM3 30); one right P3/ (DAM3 31); one left P2/ (DAM3 32); one right maxillary  
56  
57 24 fragment with P1/ (DAM3 33).  
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1 **Description (Tab. S6; Fig. 9).** P1/ and P2/ are elongated and premolariform (Fig. 9I-L). The  
 2 P3/ presents a well elongated anterior lobe, with salient parastyle and metastyle, and a  
 3 pronounced protocone (Fig. 9M-N). The crest connecting these two styles is buccally concave,  
 4 the disto-buccal lobe being very buccally inclined. The P4/ shows prominent paracone and  
 5 mesial protocone, the paracone being higher (Fig. 9A-B). The parastyle and metastyle are well  
 6 individualised and salient, and conule 1 presents an extended buccal crest. Upper molars are  
 7 quadrangular with crested styles (Fig. 9C-H).

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

#### 17 Subfamily **Cainotheriinae** Camp & VanDerHoof, 1940

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

1  
2  
3 1 Genus *Plesiomeryx* Gervais, 1873  
4

5 2 *Plesiomeryx cadurcensis* Gervais, 1873  
6

7 3 (Fig. 10)  
8  
9

10 4 **Holotype.** Right mandibular P/2-M/3 (MNHN-QU 1772). Mouillac locality, Phosphorites of  
11  
12 Quercy. The precise age and type locality are unknown (Old Quercy collections).  
13  
14

15 6 **Diagnosis.** Protocone and paraconule present (stage B, Hürzeler, 1936: 8). Long diastema  
16  
17 between P1/ and C and between P/1 and P/2. P1/, P2/, P/2 and P/3 are short, P3/ with a strong  
18  
19 lingual cone, P2/ with a weak lingual cone. The premaxilla reaches the frontal. The nasal is  
20  
21 long, narrow and straight. The ethmoidal slit is falciform. The choanae are large. The horizontal  
22  
23 portion of the lower jaw is slender (Hürzeler, 1936).  
24  
25  
26  
27

28 11 **Differential Diagnosis.** *Plesiomeryx cadurcensis* differs from Oxacroninae species by the  
29  
30 presence of quadrangular upper molars with a pinched mesostyle (except *P. bergeri*) and crested  
31  
32 styles, a longer postparacristula, larger premolars, a larger postprotoconulid, a P/1  
33  
34 uniradicate, diastemata between P/1-P/2 and C-P1/, and a protocone at the same level than  
35  
36 the paracone on P4/. It differs also from *Paroxacron* species by a shorter anterior lobe on the  
37  
38 P3/ and a larger protocone on the P3/ and P2/. *Ple. cadurcensis* diverges from *Oxacron* by a  
39  
40 larger protocone on the P3/ and P2/, as well as premolariform mesial premolars. *Ple.*  
41  
42 *cadurcensis* diverges from *Cainotherium* by a smaller size, a smaller paraconule on the upper  
43  
44 molars, the absence of cingulum/id on premolars, the presence of a triangular P3/, a larger  
45  
46 protocone on the P3/ and P2/, a valley between the entoconid and the mesoconid on lower  
47  
48 molars, and the presence of diastemata. It distinguishes from *Caenomeryx* species by a smaller  
49  
50 size, a smaller protocone on the P3/ and P2/, a shorter mesial lobe on the P3/ and a smaller  
51  
52 paraconule. Finally, *Ple. cadurcensis* differs from *Ple. huerzeleri* by a smaller size and a labial  
53  
54 cone of the P/4 more distal than the lingual cone.  
55  
56  
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1 **New material from DAM3.** One left M3/ (DAM3 34); two right M3/ (DAM3 35-36); two left  
 2 M2/ (DAM3 37, DAM3 40); three right M2/ (DAM3 38-39, DAM3 41); two right M1/ (DAM3  
 3 42, DAM3 44); one left M1/ (DAM3 43); one right DP4/ (DAM3 45); one left DP4/ (DAM3  
 4 46); one right P4/ (DAM3 47); one left P3/ (DAM3 48); one right P2/ (DAM3 49); one right  
 5 P1/ (DAM3 50); one right maxillary fragment with P2/ (DAM3 51); two left M/3 (DAM3 52,  
 6 DAM3 54); one right M/3 (DAM3 53); three right M/2 (DAM3 55, DAM3 57-58); two left  
 7 M/2 (DAM3 56, DAM3 59); two left M/1 (DAM3 60, DAM3 62); three right M/1 (DAM3 61,  
 8 DAM3 63-64); three right P/4 (DAM3 65, DAM3 67-68); one left P/4 (DAM3 66); four right  
 9 P/3 (DAM3 69-70, DAM3 72, DAM3 74); two left P/3 (DAM3 71, DAM3 73); two left P/2  
 10 (DAM3 75, DAM3 76); one right P/2 (DAM3 77); one left mandibular fragment with M/1  
 11 (DAM3 78); one right mandibular fragment with P/3-P/4 (DAM3 79).

12 **Description (Tab. S7-8; Fig. 10).** P/1 is uniradicate and probably premolariform (only  
 13 alveoli are preserved). The diastema that separates P/1 from P/2 is short. The double-rooted  
 14 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  
 15 shows a short anterior lobe, a weak lingual cingulum, as well as an expanded distal cristid  
 16 lingually curved. The protoconid of the P/4 is more mesial than the metaconid. The  
 17 postprotoconulid is more or less large. The mandible bears a mandibular symphysis located on  
 18 the distal margin of P/2 (Fig. 10U-V). A mental foramen is present, below the mesial part of  
 19 P/2. The horizontal ramus is gracile and shallow.

20 P/1 is premolariform, short, wide, and biradicular (Fig. 10M-N). P/2 is more elongated  
 21 and wider than P/1 (anterior lobe as wide as posterior lobe). It has a weakly pronounced  
 22 protocone and a large paracone (Fig. 10O-P). P/3 is short with a well-developed protocone (Fig.  
 23 10A-B). The paracone and the protocone of P/4 seem to be median (in the same plan), but the  
 24 only preserved tooth is strongly worn (Fig. 10C-D). Upper molars are quadrangular in occlusal  
 25 view, with a pinched mesostyle, styles being very weakly crested, and a small paraconule (Fig.

1 10E-J). The DP4/ are similar to upper molars, but present an important mesially convexe  
2 curvature, with a mesially projected parastyle (Fig. 10Q-R).

3 **Remarks.** The presence of a uniradicate and premolariform P/1, of a short diastema between  
4 P/1-P/2, of a strong protoconid on P/2 and P/3 (Blondel, 2005), and of upper molars with a  
5 small paraconule point to a representative of *Plesiomeryx*. Its small size and premolar  
6 morphology match those of *Plesiomeryx cadurcensis*, as described by Hürzeler (1936), Berger  
7 (1959), and Blondel (2005) from Aubrelong 1, Ravet (MP 21), Mas de Got, La Plante 2 (MP  
8 22), Pech Crabit, Mounayne et Itardies (MP23, Quercy localities). Even if some isolated upper  
9 and lower molars are hardly distinguishable from those of *Paroxacron* sp. from DAM3, a  
10 slightly taller size, more quadrangular upper molars and a more pinched mesostyle in *P.*  
11 *cadurcensis* may allow to distinguish them.

12 *Plesiomeryx huerzeleri* Berger, 1959

13 (Fig. 11)

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

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

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

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



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

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

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

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

1  
2  
3 1 *Plesiomeryx huerzeleri*. The morphology and size are very similar to those of Quercy specimens  
4 described by Blondel (2005) from Mas de Got, La Plante 2 (MP 22), Pech Crabit, Roqueprune  
5 2 and Mounayne (MP 23). They are also similar to those specimens from Gaimersheim (MP28,  
6 Germany; Berger 1959, tab. 3, pl. 3; Bolliger 2013, fig. 3a). Some isolated upper molars are  
7 however hardly differentiated from those of *Paroxacron bergeri*. Slightly smaller size, a more  
8 quadrangular shape and a more pinched mesostyle in *Ple. huerzeleri* may allow them to be  
9 discriminated.

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19  
20 8 Genus *Caenomeryx* Hürzeler, 1936

21  
22 9 *Caenomeryx procommunis* (Filhol, 1877)

23  
24  
25 10 Synonymy: 1877 *Cainotherium procommune* Filhol: 212, fig. 269–270.

26  
27 11 1936 *Caenomeryx procommunis* (Filhol), Hürzeler, p. 100.

28  
29  
30 12 **Holotype.** Fragment of mandible bearing P/2-M/3 (Filhol collections, MNHNP). Precise age  
31 and type locality unknown (Old Quercy collections).

32  
33  
34 14 **Emended Diagnosis.** Upper molars are wider than long. Protocone and protoconule present  
35 (stage B, Hürzeler, 1936; p. 8). Diastema between P1/ and C is short. Diastema very short or  
36 missing between P/1 and P/2. Premolars reduced, P3/ with a strong lingual cone, P2/ with a  
37 weaker lingual cone, P1/ very small. The premaxilla does not reach the frontal. The wide nasal  
38 bones broaden behind the posterior extremities of the premaxilla. The ethmoidal gap is  
39 irregular, the choanae are large and the mandible is high, stocky and massive (Hürzeler, 1936).  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49 20 Remarks: According to our observations, the C-P1/ and P/1-P/2 diastemata are rather short than  
50 absent (*contra* the original diagnosis of Hürzeler (1936)).

51  
52  
53  
54 22 **Differential Diagnosis.** *Caenomeryx procommunis* differs from Oxacroninae species by a  
55 larger size, the presence of quadrangular upper molars with a pinched mesostyle (except *P.*  
56  
57  
58  
59 24 *bergeri*) and crested styles, a longer postparacristula, larger premolars, a larger

1 postprotoconulid, a P/1 uniradicate, diastemata between P/1-P/2 and C-P1/, and a protocone  
 2 at the same level than the paracone on P4/. It differs also from *Paroxacron* species by a shorter  
 3 anterior lobe on the P3/ and a larger protocone on the P3/ and P2/. *Cae. procommunis* diverges  
 4 from *Oxacron* by the presence of a large protocone on the P3/ and P2/, and premolariform  
 5 mesial premolars. *Cae. procommunis* distinguishes from *Cainotherium* by rectangular upper  
 6 molars, the absence of important cingulum/id on premolars, the presence of a triangular P3/, a  
 7 larger protocone on the P3/ and P2/, a valley between the entoconid and the mesoconid on lower  
 8 molars, and the presence of diastemata. *Cae. procommunis* diverges from *Plesiomeryx* species  
 9 by a larger size, a larger protocone on the P3/ and P2/, a longer mesial lobe on the P3/, a larger  
 10 paraconule, smaller diastemata and more rectangular upper molars. Finally, *Cae. procommunis*  
 11 differs from *Cae. filholi* by a longer mesial lobe on the P3/ and shorter diastemata.

12 ***Caenomeryx cf. procommunis* (Filhol, 1877)**

13 (Fig. 12)

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

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

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

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

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

20 Class **Mammalia** Linnaeus, 1758

21 Order **Artiodactyla** Owen, 1848

22 Superfamily **Cainotherioidea** Camp & VanDerHoof, 1940

23 Family **Robiacinidae**, fam. nov.

24 **Type genus.** *Robiacina* Sudre, 1969

1  
2  
3 1 **Included genera.** Type genus only.  
4

5  
6 2 **Original Diagnosis.** As for its type and only genus *Robiacina* (Sudre 1978).  
7

8  
9 3 **Emended Diagnosis.** Small Cainotherioidea similar in size to *Oxacron*. Skull globular in shape  
10  
11 4 with a sub-spherical cerebral part and muzzle extremely short; very large orbits; lacrymal small;  
12  
13 5 in the bottom of the orbital cavity, palatine does not contact the frontal, due to the great posterior  
14  
15 6 development of the lacrimal; auditory bullae of large size, sub-spherical; ethmoid fissure absent.  
16  
17 7 Lower and upper premolars short mesio-distally; diastemata absent to reduced; P/3 with a small  
18  
19 8 medio-lingual cusp; P/1 and P/2 unicuspid. Lower molars with a pinched trigonid and a wide  
20  
21 9 talonid; presence of a small to medium-sized metaconulid on the distal aspect of the metaconid;  
22  
23 10 entoconid slightly more distal than the hypoconid; presence of a small hypoconulid on M/1-2  
24  
25 11 and a posthypocristulid on M/3. Upper molars subtriangular with five cusps and a central or  
26  
27 12 slightly mesial protocone; metacone higher than the paracone; paraconule small; preparacrista  
28  
29 13 short; preprotocrista linked to the paraconule; buccal wall of the paracone with or without a  
30  
31 14 cingulum.  
32  
33  
34  
35  
36

37 15 **Remarks.** The justification for the erection of the new family Robiacinidae is provided in the  
38  
39 16 following section and ensues the results of phylogenetic analysis.  
40  
41  
42  
43  
44

## 45 18 **Results and Discussion**

### 46 47 48 49 20 **Dental nomenclature**

50  
51  
52 21 Premolar and molar cusp/id patterns of Cainotheriidae differ from other Artiodactyla,  
53  
54 22 which resulted in different dental nomenclatures for premolars and lower molars (Fig. 1A-E,  
55  
56 23 I). According to Berthet (2003), the disto-lingual cusp of upper premolars corresponds to an  
57  
58 24 hypocone while, according to Hürzeler (1936), Gentry & Hooker (1988), and Boissarie *et al.*  
59  
60

1 (2010), this cusp would correspond to the protocone instead. For lower premolars, these authors  
2 identify the mesial cuspid as the paraconid and the medio-lingual cuspid of P/4 as a metaconid.  
3 Berthet (2003) considers the mesial cuspid of lower premolars as a protoconulid, and the medio-  
4 lingual cuspid of P/4 an entoconid. Problems of identification of the cusps/ids also occur for  
5 the lower molars. According to Hürzeler (1936), the three lingual cusps of lower molars  
6 correspond to: a mesial cuspid identified as a metaconid, and two distal ones, that would  
7 correspond to the entoconid and to the hypoconulid that would lie in a lingual position.  
8 According to Sudre (1977), the medio-lingual cuspid would not be an entoconid but a  
9 neoformation called the mesoconid. This mesoconid would originate from a duplication of the  
10 metaconid (Sudre 1977). Gentry & Hooker (1988) and Hooker & Weidmann (2000) identify  
11 the medio-lingual cuspid as a metastylid, originating from the cingulid. In this framework, the  
12 entoconid would also be placed distally.

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

19  
20 Concerning the premolars, the disto-lingual cusp of the upper premolars of *Oxacron* and  
21 *Robiacina* does not derive from the cingulum, and therefore is identified here as the protocone.  
22 For lower premolars, we consider that the medio-lingual cuspid of P/4 represent the metaconid  
23 and that the distal cuspid is the entoconid, by homology of position with lower molars. This  
24 corresponds to the nomenclature proposed by Gentry & Hooker (1988) and Boisserie *et al.*  
25 (2010).

1  
2  
3 1 For the lower molars, we identify the medio-lingual cuspid as a neoformed structure, in  
4  
5 2 agreement with Sudre (1977), based on the presence of a small neoformed accessory cuspid at  
6  
7 3 the base of the metaconid, in the lower molars of *Robiacina* (Fig. 1F, 1H). Indeed, the  
8  
9 4 hypothesis of a duplication of the metaconid proposed by Sudre (1977) seem to be more  
10  
11 5 parsimonious than a medio-lingual position of the entoconid and a concurrent lingual  
12  
13 6 displacement of the hypoconulid as hypothesised by Hürzeler (1936). The latter hypothesis  
14  
15 7 would imply a fusion/disappearance of the anterior and/or posterior crests of the talonid  
16  
17 8 crescent, with a mesial migration of the entoconid and a lingual displacement of the  
18  
19 9 hypoconulid. Moreover, according to this hypothesis, the entoconid would be located in front  
20  
21 10 of the protocone during the occlusion with upper molars, contrary to most other artiodactyls  
22  
23 11 (Sudre 1977). Finally, if Hürzeler's (1936) hypothesis is considered, with the hypoconulid in  
24  
25 12 disto-lingual position on M/1 and M/2, what would then be the distalmost cuspid on the M/3?  
26  
27 13 As concluded by Sudre (1977), the distalmost cuspid on M/3 is necessarily the hypoconulid. A  
28  
29 14 hypoconulid is clearly visible on the M/1 and M/2 of *Robiacina*, positioned just distal to the  
30  
31 15 entoconid (Fig. 1F). This disposition of the hypoconulid relative to the entoconid is also found  
32  
33 16 on M/3 of *Cainotheriidae*, which lack a hypoconulid on M/1 and M/2. Finally, the hypothesis  
34  
35 17 of a metastylid as medio-lingual cuspid, proposed by Gentry & Hooker (1988) and Hooker &  
36  
37 18 Weidmann (2000), is here rejected as it does not originate from the cingulid, neither in  
38  
39 19 *Robiacina*, nor in *Oxacron*. Contrary to Sudre (1977), we use the term 'metaconulid' instead of  
40  
41 20 'mesoconid', in order to homogenized with the nomenclatural system of Boisserie *et al.* (2010),  
42  
43 21 and because mesoconid is used for another structure in other mammalian group (Klingener  
44  
45 22 1964; Skwara 1986; Hooker & Russell 2012).

53  
54 23 Thus, according to the hypotheses of Sudre (1977; molars) and of Gentry & Hooker  
55  
56 24 (1988) and Boisserie *et al.* (2010; premolars), the three lingual cuspids of lower molars would  
57  
58 25 correspond to the metaconid (mesial), the metaconulid (medial, originates from metaconid  
59  
60

1 duplication), and the entoconid (distal). The disto-lingual cusp of upper premolars is here  
2 identified as the protocone, and the mesial cuspid of lower premolars as the paraconid. The P/4  
3 bears a metaconid (medio-lingual) and an entoconid (one distal).

## 5 **Phylogenetic analysis**

6 The heuristic search of the parsimony analysis retained a single parsimonious tree (L =  
7 170, CI = 0.48, RI = 0.73; CI with only parsimony-informative characters = 0.46) (Fig. 13),  
8 reflecting a well-structured signal and relatively weakly homoplastic characters. Cainotheriidae  
9 are monophyletic and split into two subgroups, interpreted as subfamilies: Oxacroninae, with  
10 *Oxacron* and *Paroxacron*; and Cainotheriinae, with *Plesiomeryx*, *Caenomeryx*, and  
11 *Cainotherium*. Cainotheriidae, together with Mixtotheriidae, Anoplotheriidae and  
12 representatives of *Robiacina* form a clade, sister group to ruminants. Tylopoda split earlier in  
13 the tree, together with *Amphimeryx* and *Xiphodon*.

14 The monophyly of Cainotheriidae is supported by 13 non-ambiguous synapomorphies  
15 and a high Bremer index (IB = 7). They are characterised by the presence on their upper molars  
16 of a large parastyle similar to other styles (8<sup>1</sup>; IR = 0.67), a disto-lingual protocone (11<sup>2</sup>; IR =  
17 0.94), a very strong dilambdodonty (20<sup>1</sup>; IR = 0.88), a long (26<sup>1</sup>; IR = 0.40) and distally  
18 orientated (27<sup>1</sup>; IR = 1.00) postprotocrista, a postparacristula (29<sup>1</sup>; IR = 0.86) and the lack of  
19 preprotocrista and paraconule junction (15<sup>1</sup>; IR = 0.67); on their lower molars, they present a  
20 large (34<sup>2</sup>; IR = 1.00) and individualised (35<sup>0</sup>; IR = 1.00) metaconulid, a very distal entoconid  
21 and close to the hypoconulid (40<sup>2</sup>; IR = 1.00), a neotrigonid (47<sup>1</sup>; IR = 1.00), the absence of  
22 posthypocristulid (50<sup>0</sup>; IR = 0.67) and hypoconulids on M/1 and M/2 (38<sup>0</sup>; IR = 0.75).  
23 Cainotheriidae are composed of two clades: the Oxacroninae, characterised by the presence of  
24 styles without crests on upper molars (7<sup>0</sup>; IR = 0.44), a protocone more mesial than the paracone  
25 on P4/ (56<sup>1</sup>; IR = 0.50), as well as a biradicate P/1 (70<sup>1</sup>; IR = 1.00); Cainotheriinae, supported



1  
2  
3 1 by the presence of a postparacristula buccally long joining the preprotocrista on upper molars  
4  
5 2 (30<sup>1</sup>; IR = 1.00)<sup>30</sup> and of a large postprotoconulid on lower premolars (69<sup>1</sup>; IR = 1.00). They  
6  
7 3 further differ from Oxacroninae by the presence of a uniradicate P/1 (70<sup>0</sup>; IR= 1.00) and large  
8  
9 4 premolars (73<sup>1</sup>; IR = 0.67), which represent plesiomorphic states of characters.

10  
11  
12 5 Within Oxacroninae, *Paroxacron* is paraphyletic. *Paroxacron bergeri* is excluded from  
13  
14 6 the (*Paroxacron valdense*, *Oxacron courtoisii*) clade by the presence of quadrangular molars  
15  
16 7 (31<sup>2</sup>; IR = 0.60) with a pinched mesostyle (10<sup>1</sup>; IR = 1.00) and the absence of diastemata  
17  
18 8 between P1/-P2/ (5<sup>0</sup>; IR = 0.50) and P/2-P/3 (6<sup>0</sup>; IR = 0.33).

19  
20  
21 9 Within Cainotheriinae, *Cainotherium* is sister taxon to the clade (*Caenomeryx*,  
22  
23 10 *Plesiomeryx*). *Cainotherium laticurvatum* is characterised by numerous autapomorphies, such  
24  
25 11 as the absence of a valley between the entoconid and the metaconulid on lower molars (41<sup>0</sup>; IR  
26  
27 12 =0.78), the presence of a protocone at the same level (bucco-lingual axis) as the paraconule on  
28  
29 13 the M3/ (17<sup>0</sup>; IR= 0.50), the absence of a triangular P3/ (quadrangular shape) (61<sup>0</sup>; IR = 0.50)  
30  
31 14 and a wide cingulum/id on the premolars (72<sup>1</sup>; IR = 0.50)<sup>72</sup>. The clade (*Caenomeryx*,  
32  
33 15 *Plesiomeryx*) is supported by the presence of a protocone on P2/ (64<sup>1</sup>; IR = 0.57) and diastemata  
34  
35 16 between C-P1/ (3<sup>1</sup>; IR=0.75) and P/1-P/2 (5<sup>1</sup>; IR = 0.86).

36  
37  
38 17 *Robiacina* is sister taxon to the Cainotheriidae clade. This position is supported by the  
39  
40 18 presence of a more distal (11 ;IR = 0.94) and lingual protocone (17<sup>1</sup>; IR = 0.50) on upper molars  
41  
42 19 and M3/, respectively, but also by sub-equal paracone and metacone on P3/ (60<sup>1</sup>; IR = 1.00),  
43  
44 20 the absence of protocone on P2/ (64<sup>0</sup>; IR = 0.57), the presence of a small hypoconid on P/2-P/3  
45  
46 21 (67<sup>0</sup>; IR = 0.75) and of a postprotoconulid on premolars (68<sup>1</sup>; IR = 1.00). This result does not  
47  
48 22 support the hypothesis of Sudre (1977) who placed *Robiacina* within Anoplotheriidae, close to  
49  
50 23 Anoplotheriinae. Our results also slightly contrast with the hypothesis of Gentry & Hooker  
51  
52 24 (1988) who placed *Robiacina* within Cainotheriidae. The clade composed of representatives of  
53  
54 25 *Robiacina* is excluded from the Cainotheriidae clade by 13 unambiguous characters (see  
55  
56  
57  
58  
59  
60

1 support of Cainotheriidae clade above) and it further differs from it by sharing three  
2 synapomorphies: sub-triangular upper molars (31<sup>1</sup>; IR = 0.60), a small paraconule (14<sup>0</sup>; IR =  
3 0,43), and a short preparacrista (25<sup>1</sup>; IR = 1,00). This marked morphological divergence  
4 between Cainotheriidae and the *Robiacina* clade leads us to recognise this clade as a new  
5 family, here named Robiacinidae. It would therefore constitute the closest family to  
6 Cainotheriidae, and forms with it the superfamily Cainotherioidea Camp & VanDerHoof, 1940.

7 Anoplotheriidae and Cainotherioidea form a clade (B) supported by the presence of a  
8 metaconulid (33<sup>1</sup>; IR = 1.00), an entoconid positioned at the back of the hypoconid (40<sup>1</sup>; IR =  
9 1.00) and a valley between entoconid and metaconulid on the lower molars (41<sup>1</sup>; IR = 0.78), as  
10 well as a connected paracone and metacone on P4/ (55<sup>0</sup>; IR = 0.50). The Mixtotheriidae,  
11 Anoplotheriidae, and Cainotherioidea together form a clade (A) supported by the presence of a  
12 very large parastyle (8<sup>0</sup>; IR = 0.67) and an absent to reduct postprotocrista (26<sup>0</sup>; IR=0.40) on  
13 the upper molars, a 'loop-like' entoconid (39<sup>1</sup>; IR = 1.00) on the lower molars, and the absence  
14 of a diastema between P/1-P/2 (5<sup>0</sup>; IR = 0.86).

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

## 21 **Impact on artiodactyl systematics**

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

1  
2  
3 1 We therefore chose to maintain the genus *Oxacron*. *Paroxacron valdense* is the type species of  
4  
5 2 *Paroxacron*. Our results raise the question of the erection of a new genus for the species *P.*  
6  
7 3 *bergeri*. However, the latter has no dental autapomorphies based on our results. For the time  
8  
9 4 being, based on dental data only, we therefore choose to keep *Paroxacron* as a paraphyletic  
10  
11 5 assemblage.  
12  
13

14  
15 6 **Robiacinidae, fam. nov.** Our results retrieve a monophyletic assemblage of *Robiacina* species.  
16  
17 7 This clade appears as sister taxon to Cainotheriidae. This contrasts with the hypothesis of  
18  
19 8 Hooker & Weidmann (2000), according to which *Robiacina lavergnensis* should be referred to  
20  
21 9 *Mixtotherium*. Following these authors, *R. lavergnensis* shares many characters with the species  
22  
23 10 of *Mixtotherium*: a short premetacristula, a pre-cingulum and crested styles on the upper molars;  
24  
25 11 a prehypocristid fused with the postprotocristid, a basined hypoconulid in basin and a high  
26  
27 12 crown on the lower molars, and a caniniform lower canine. However, we disagree on the coding  
28  
29 13 of some of these characters for *Mixtotherium* by Hooker & Weidmann (2000). According to  
30  
31 14 our observations, there is no basin on the hypoconulid, the premetacristula is long and the  
32  
33 15 prehypocristid is unfused. Besides, the results of our phylogenetic analyses place *Robiacina* as  
34  
35 16 sister taxon to Cainotheriidae, and far apart from *Mixtotherium*. The presence of crested styles  
36  
37 17 in *Mixtotherium* and *R. lavergnensis* as mentioned by Hooker & Weidmann (2000) is here a  
38  
39 18 symplesiomorphy. Contrary to Hooker & Weidmann (2000), we retain the binomen *Robiacina*  
40  
41 19 *lavergnensis* instead of *Mixtotherium lavergnense*.  
42  
43  
44  
45  
46  
47

48 20 **Cainotherioidea.** We propose here to recognize the clade (Robiacinidae + Cainotheriidae) as  
49  
50 21 defining the Cainotherioidea. The concept of this compound was defined by Simpson (1945) as  
51  
52 22 single-family, then Hooker & Weidmann (2000) extended it by including the genera *Robiacina*  
53  
54 23 and *Mixtotherium*. However, and according to our results, we propose here to exclude  
55  
56 24 *Mixtotherium* from the Cainotherioidea.  
57  
58  
59  
60

## 1 Relationships of Cainotheriidae within Artiodactyla

2 The phylogenetic position of Cainotheriidae within Artiodactyla remains controversial.  
3 Gentry & Hooker (1988, fig. 9.8) supported the placement of cainotheriids within Tylopoda in  
4 their (informal) “preferred analysis”, but retrieved them in a much more basal position, in their  
5 formal analysis (Gentry & Hooker 1988, fig. 9.7), i.e. outside of the “Selenodontia” clade (i.e.,  
6 Tylopoda + Ruminantia). More recent phylogenetic analyses placed them either close to  
7 Tylopoda (e.g., Geisler & Uhen 2003, Geisler *et al.* 2007, Thewissen *et al.* 2007), or as an early  
8 offshoot of a wide clade including Ruminantia (e.g., Geisler & Uhen 2005; O’Leary & Gatesy  
9 2007, Lihoreau *et al.* 2015). Our results are congruent with the previous studies that excluded  
10 Cainotheriidae from Tylopoda (Webb & Taylor 1980), and placed Cainotheriidae closer to  
11 Ruminantia (Geisler & Uhen 2005; O’Leary & Gatesy 2007; Lihoreau *et al.* 2015). Indeed,  
12 according to our sample, Cainotherioidea, Anoplotheriidae and Mixtotheriidae are sister group  
13 to Ruminantia. As far as direct relationships of Cainotherioidea are concerned, according to our  
14 results, Anoplotheriidae are their closest relatives.

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

23 These relationships rely on dental characters only and it is necessary to extend the data  
24 matrix with mandibular, cranial and post-cranial characters, in order to test further the

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2  
3 1 phylogenetic relationship of Cainotheriidae. These characters could bring additional support to  
4  
5 2 clades with relatively low Bremer index.  
6  
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8 3

#### 4 **Evolutionary history of Cainotheriidae around the Grande Coupure**

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

24 The Eocene-Oligocene transition further documents a body size increase in  
25 Cainotheriidae, as shown in *Plesiomeryx huerzeleri*, *Paroxacron bergeri* but also

1  
2  
3 1 representatives of *Caenomeryx* and *Cainotherium* (see Tab. S1-S12). However, small species  
4  
5 2 are still present after the Grande Coupure with *Paroxacron* sp. and *Plesiomeryx cadurcensis*.  
6  
7 3 This reflects an increase in the size range of Cainotheriidae after the Grande Coupure, and thus  
8  
9 4 likely an expansion in the occupation of different ecological niches. It is probable that the  
10  
11 5 Cainotheriidae were quite generalist in terms of diet, and that they took the ecological niches  
12  
13 6 released by endemic families of Europe which had become extinct at this transition, such as  
14  
15 7 Xiphodontidae, Dacrytheriinae, or Mixtotheriidae (Blondel 2001).  
16  
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18

19 8 The Grande Coupure coincides with a major mammalian faunal turnover concurrent to  
20  
21 9 climatic, geographic, and oceanic circulation changes (Legendre 1987; Berggren & Prothero  
22  
23 10 1992; Akhmetiev & Beniamovski 2009). The increase of the chewing surface, with the  
24  
25 11 appearance of more quadrangular molars, and the reduction of diastemata as observed in some  
26  
27 12 species of Oligocene Cainotheriidae (notably in Dams) could be linked to changes in their diet  
28  
29 13 (Fig. 14; Blondel 2001). Environmental changes were drastic during the concerned interval,  
30  
31 14 with a shift from a rainforest under tropical/sub-tropical conditions to open environments under  
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33 15 a much drier climate (Collinson 1992; Cavagnetto & Anadón 1996; Akhmetiev & Beniamovski  
34  
35 16 2009).  
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## 42 18 **Conclusion**

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47 20 Dams is an exceptional fossil site that yields distinct deposits broadly bracketing the  
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49 21 Grande Coupure. Cainotheriid remains are documented by thousands specimens and as such,  
50  
51 22 they allow for in-depth insights into the history and systematics of this family. In the DAM1  
52  
53 23 deposits (MP19, late Eocene), a single species occurs: *Paroxacron valdense*. The DAM3  
54  
55 24 channel (MP22, early Oligocene) yields a higher taxonomic diversity with at least five species:  
56  
57 25 *Paroxacron* sp., *Paroxacron bergeri*, *Plesiomeryx huerzeleri*, *Plesiomeryx cadurcensis*, and  
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3 1 *Caenomeryx* cf. *procommunis*. Dams localities highlight a phase of local diversification of  
4  
5 2 cainotheriids by early Oligocene times, thus confirming the hypothesis of Blondel (2005).  
6  
7 3 Among Cainotheriidae, this diversity increase mainly concerns Cainotheriinae. Yet, both  
8  
9 4 Cainotheriinae and Oxacroninae survive to major environmental changes related to the Grande  
10  
11 5 Coupure, contrary to many other European endemic artiodactyls.  
12  
13

14 6 Our phylogenetic analysis, including Dams taxa described in this work, constitutes the  
15  
16 7 first formal phylogeny of Cainotheriidae. Our results, based on dental characters, allow for (i)  
17  
18 8 clarifying relationships within Cainotheriidae, with Oxacroninae as sister group to  
19  
20 9 Cainotheriinae, (ii) defining *Robiacina* (and the new family Robiacinidae) as being the sister  
21  
22 10 taxon to Cainotheriidae among Cainotherioidea and, more broadly, (iii) discussing the  
23  
24 11 controversial position of Cainotheriidae within Artiodactyla, as being more closely related to  
25  
26 12 Ruminantia than to Tylopoda.  
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36  
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54  
55 25 Orliac.  
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## Figure captions

- 24 **Figure 1.** Dental diagrams in occlusal view. P/4 of Cainotheriidae: **A**, Nomenclature of Berthet (2003);  
25 **B**, Nomenclature of Boissérie *et al.* (2010). M/1-M/2 of Cainotheriidae: **C**, Nomenclature of Hürzeler  
26 (1936); **D**, Nomenclature of Sudre (1977); **E**, Nomenclature of Gentry & Hooker (1988). M/1-M/2: **F**,  
27 *Robiacina*; **G**, *Dacrytherium*. M/3: **H**, *Robiacina*; **I**, Cainotheriidae. **Proto<sup>ulid</sup>**, protoconulid. For the rest  
28 of the legend, see Fig. 2.  
29

1 **Figure 2.** Dental diagrams of the *Paroxacron valdense* dentition according to dental nomenclature of  
 2 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  
 3 view: **E, F**. Abbreviations: dist., distostyle; med., mediostyle; mes., mesostyle; met., metastyle; par.,  
 4 parastyle; **Meta.**, metacone; **Meta<sup>ul</sup>.**, metaconule; **Para.**, paracone; **Para<sup>ul</sup>.**, paraconule; **Proto.**,  
 5 protocone; post<sup>ylid</sup>., poststylid; pre<sup>ylid</sup>., prestylid; **Centro<sup>ulid</sup>.**, centroconulid; **Ento<sup>d</sup>.**, entoconid; **Hypo<sup>d</sup>.**,  
 6 hypoconid; **Hypo<sup>ulid</sup>.**, hypoconulid; **Meta<sup>d</sup>.**, metaconid; **Meta<sup>ulid</sup>.**, metaconulid; **Para<sup>d</sup>.**, paraconid;  
 7 **Post<sup>ulid</sup>.**, postconulid; **Pre<sup>ulid</sup>.**, preconulid; **Proto<sup>d</sup>.**, protoconid; -c., -crista; -c<sup>ula</sup>., -cristula; -c<sup>yla</sup>., -  
 8 cristyla; -c<sup>id</sup>., -cristid; -c<sup>ulid</sup>., -cristulid; -c<sup>ylid</sup>., -cristylid; -f., fossa; -f<sup>d</sup>., fossid. Full circles:  
 9 cusp/style/conule/conulid; full lines: crest; dashed lines: valley/fosse; dotted lines: cingulum/cingulid;  
 10 bold dashed lines: lobe contour; bold full lines: crown contour.

11  
 12 **Figure 3.** Dental diagrams of the permanent lower dentition of *Paroxacron valdense*. **A, B**, P/1-2; **C, D**,  
 13 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  
 14 lingual view: **B, D, F, K, L**. In buccal view: **H, J**. Scale 1mm. Abbreviations: **Postproto<sup>ulid</sup>.**,  
 15 postprotoconulid; disto<sup>ylid</sup>., distostylid; co<sup>ulid</sup> x., conulid x.

16  
 17 **Figure 4.** Dental diagrams of the permanent upper dentition of *Paroxacron valdense*. **A, B**, P1/; **C, D**,  
 18 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  
 19 lingual view: **B, D, F, H, I, J, K, L**. Scale 1mm. Abbreviations: co<sup>ul</sup> x., conule x.

20  
 21 **Figure 5.** Dental diagrams of the deciduous dentition of *Paroxacron valdense*. **A, B**, DP/1; **C, D**, DP/2-  
 22 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:  
 23 **B, D, H, J, L**. In buccal view: **F**. Scale 1 mm. Abbreviations: **Primo<sup>d</sup>.**, primoconid.

24  
 25 **Figure 6.** Material of the lower dentition of *Paroxacron valdense*. **A**, right I/1 (DAM1 174); **B**, left I/2-3  
 26 (DAM1 194; mirror view); **C**, right lower canine (DAM1 199); **D, E**, right P/1 (DAM1 40); **F, G**, right  
 27 DP/1 (DAM1 126); **H, ; I**, left DP/2-3 (DAM1 117); **J, ; K**, left DP/4 (DAM1 103); **L**, left mandibular  
 28 fragment with P/1-M/3 (DAM1 22); **M**, left P/3 (DAM1 269); **N**, right mandibular fragment with P/2-

1 M/3 (DAM1 21); **O**, left mandibular fragment with P/1-M/3 (DAM1 22); **P**, **Q**, right mandibular  
 2 fragment with M/3 (DAM1 268); **R**, right mandibular fragment with P/2-M/3 (DAM1 21). In lingual  
 3 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  
 4 mm.

5  
 6 **Figure 7.** Material of the upper dentition of *Paroxacron valdense*. **A**, right I3/ (DAM1 252); **B**, right  
 7 I2/ (DAM1 228); **C**, right I1/ (DAM1 213); **D**, left upper canine (DAM1 261); **E**, **F**, right DP1-2/  
 8 (DAM1 164); **G**, **H**, right DP3/ (DAM1 160); **I**, **J**, left P1/ (DAM1 66); **K**, **L**, right DP4/ (DAM1 144);  
 9 **M**, right maxillary fragment with P1/-M3/ (DAM1 08). In lingual view: **A**, **B**, **C**, **D**, **F**, **H**, **I**, **L**. In  
 10 occlusal view: **E**, **G**, **J**, **K**, **M**. Scale 1 mm.

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

18  
 19 **Figure 9.** Material of the *Paroxacron bergeri* dentition. **A**, **B**, left P4/ (DAM3 30); **C**, **D**, left M1/  
 20 (DAM3 29); **E**, **F**, right M2/ (DAM3 26; mirror view); **G**, **H**, right M3/ (DAM3 24; mirror view); **I**, **J**,  
 21 left P1/ (DAM3 33); **K**, **L**, left P2/ (DAM3 32); **M**, **N**, right P3/ (DAM3 31; mirror view). In occlusal  
 22 view: **A**, **C**, **E**, **G**, **I**, **K**, **M**. In lingual view: **B**, **D**, **F**, **H**, **J**, **L**, **N**.

23  
 24 **Figure 10.** Material of the *Plesiomeryx cadurcensis* dentition. **A**, **B**, right P3/ (DAM3 48; mirror view);  
 25 **C**, **D**, right P4/ (DAM3 47; mirror view); **E**, **F**, right M1/ (DAM3 44; mirror view); **G**, **H**, left M2/  
 26 (DAM3 37); **I**, **J**, left M3/ (DAM3 34); **K**, **L**, left M/3 (DAM3 52; mirror view); **M**, **N**, right P1/ (DAM3  
 27 50; mirror view); **O**, **P**, right P2/ (DAM3 51; mirror view); **Q**, **R**, right DP4/ (DAM3 45; mirror view);  
 28 **S**, **T**, right P/2 (DAM3 77); **U**, **V**, right mandibular fragment with P/3-P/4 (DAM3 79); **W**, **X**, right M/1

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*).

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- 3 1 Dotted-line: long diastemata, sub-triangular molars; simple line: diastemata reduction trend,
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- 5 2 quadrangular molars.
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For Review Only



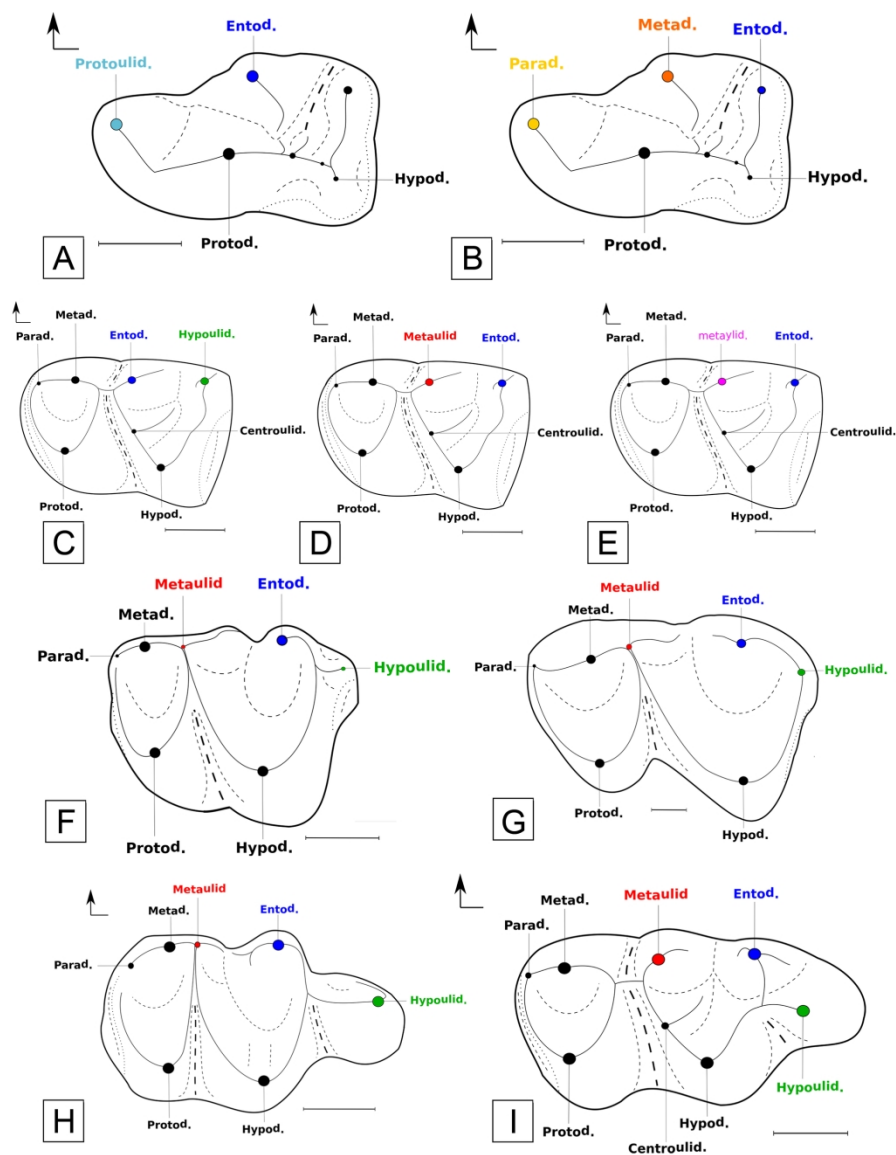


Figure 1. Dental diagrams in occlusal view. P/4 of Cainotheriidae: A, Nomenclature of Berthet (2003); B, Nomenclature of Boisserie et al. (2010). M/1-M/2 of Cainotheriidae: C, Nomenclature of Hürzeler (1936); D, Nomenclature of Sudre (1977); E, Nomenclature of Gentry & Hooker (1988). M/1-M/2: F, Robiacina;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

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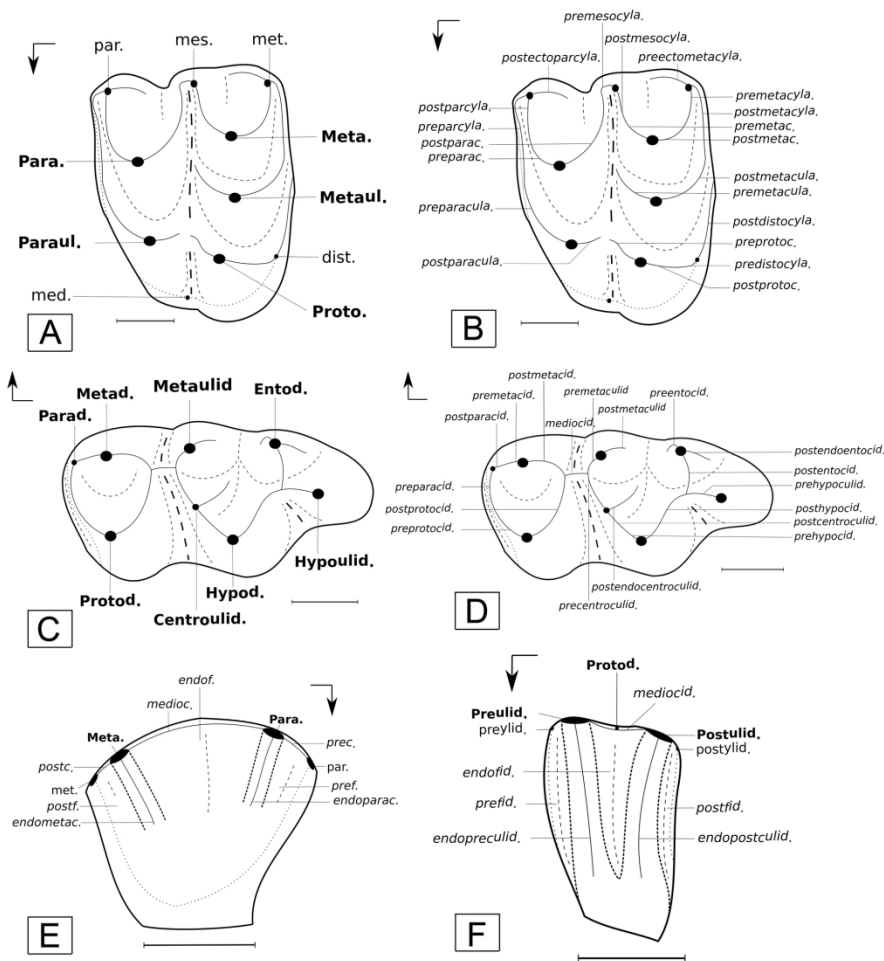


Figure 2. Dental diagrams of the Paroxacron valdense dentition according to dental nomenclature of Boisserie et al. (2010). A, B, M1/-M2/; C, D, M/3; E, I1/; F, I/1. In occlusal view: A, B, C, D. In lingual view: E, F. Abbreviations: dist., distostyle; med., mediostyle; mes., mesostyle; met., metastyle; par., parastyle; Meta., metacone; Metaul., metaconule; Para., paracone; Paraul., paraconule; Proto., protocone; postylid., poststyle; preylid., prestyle; 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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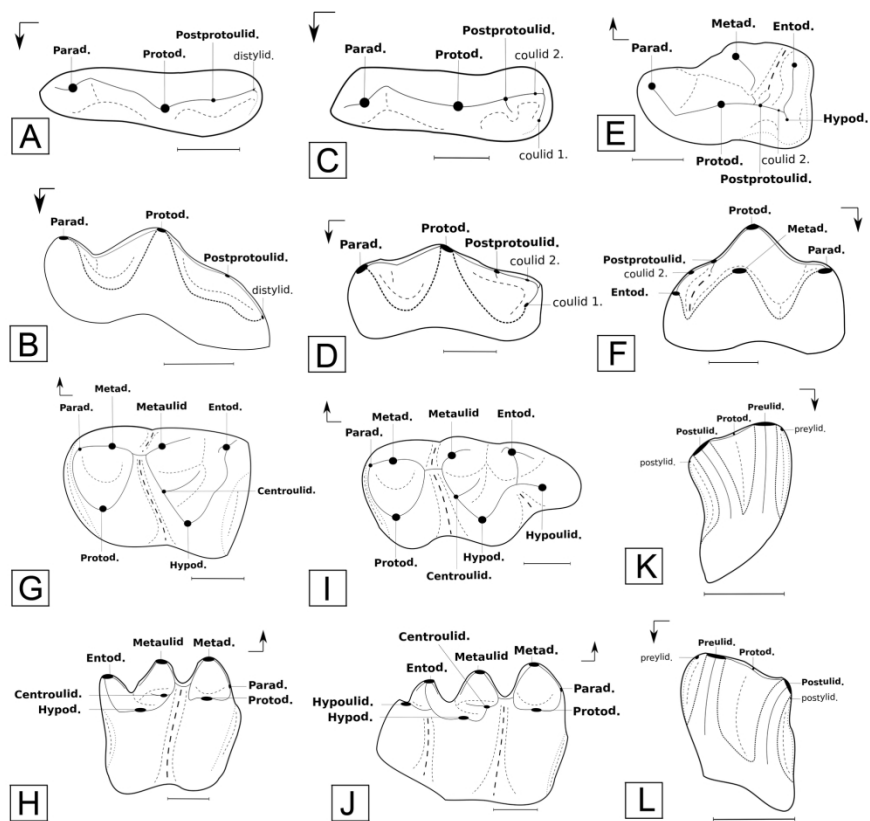


Figure 3. Dental diagrams of the permanent lower dentition of *Paroxacron valdense*. A, B, P/1-2; C, D, P/3; E, F, P/4; G, H, M/1-2; I, J, M/3; K, I/2-3; L, lower canine. In occlusal view: A, C, E, G, I. In lingual view: B, D, F, K, L. In buccal view: H, J. Scale 1mm. Abbreviations: Postprotoulid., postprotoconulid;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

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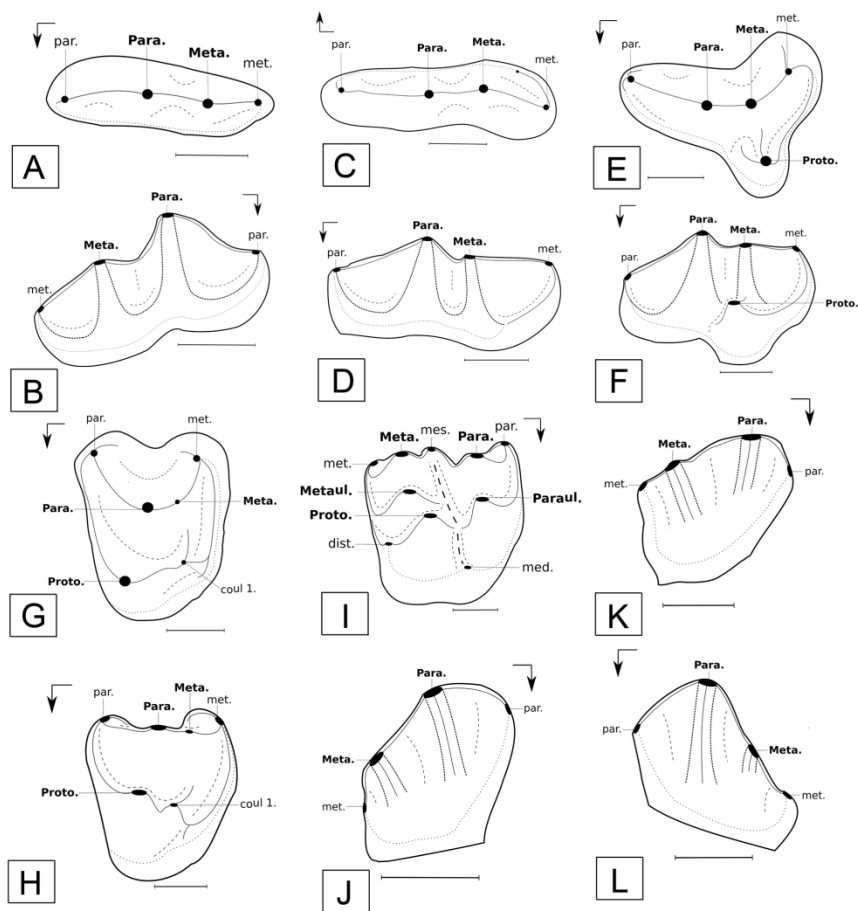


Figure 4. Dental diagrams of the permanent upper dentition of *Paroxacron valdense*. A, B, P1/; C, D, P2/; E, F, P3/; G, H, P4/; I, M1-2/; J, I3/; K, I2/; L, upper canine. In occlusal view: A, C, E, G. In lingual view: B, D, F, H, I, J, K, L. Scale 1mm. Abbreviations: coul x., conule x.

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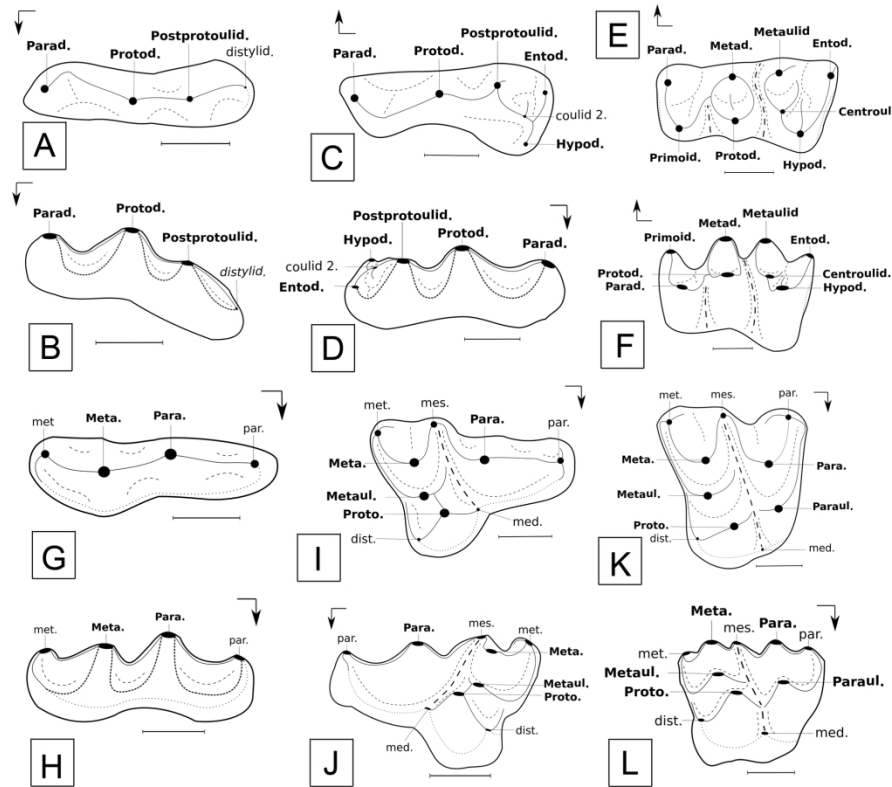


Figure 5. Dental diagrams of the deciduous dentition of *Paroxacron valdense*. A, B, DP/1; C, D, DP/2-3; E, F, DP/4; G, H, DP1-2/; I, J, DP3/; K, L, DP4/. In occlusal view: A, C, E, G, I, K. In lingual view: B, D, H, J, L. In buccal view: F. Scale 1 mm. Abbreviations: Primoid., primoconid.

173x232mm (300 x 300 DPI)

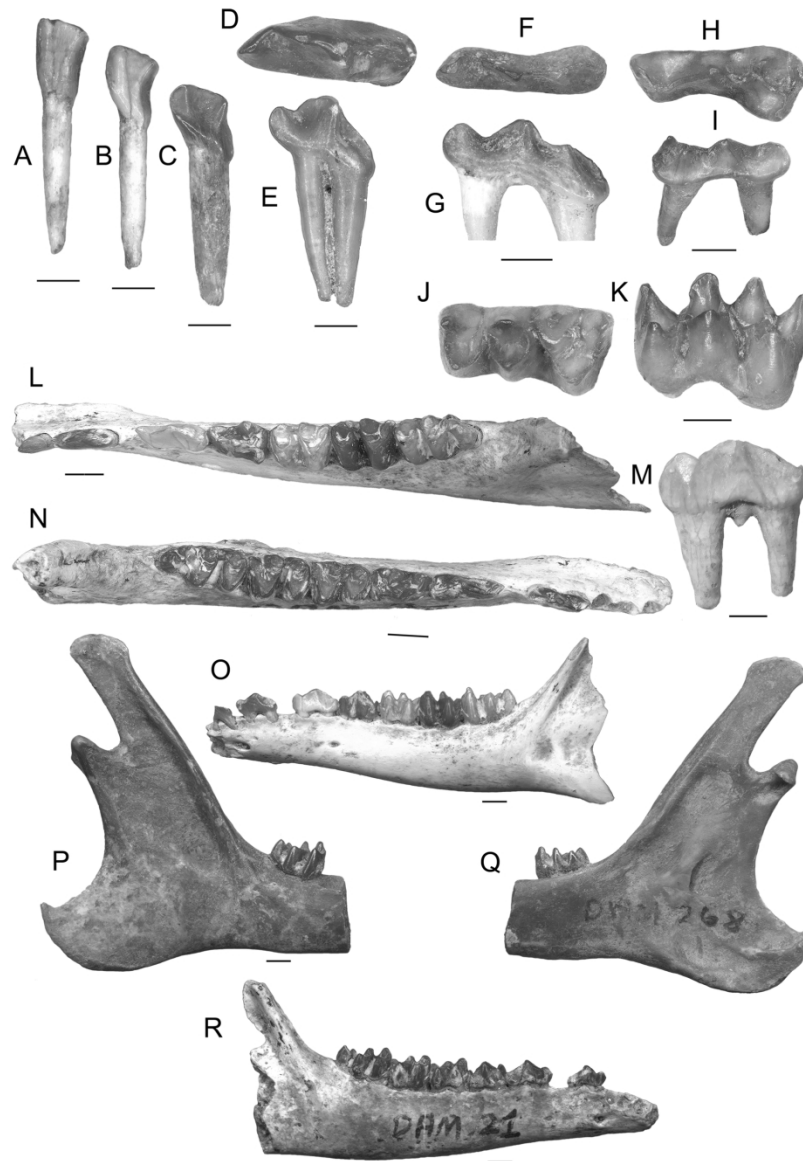


Figure 6. Material of the lower dentition of *Paroxacron valdense*. A, right I/1 (DAM1 174); B, left I/2-3 (DAM1 194; mirror view); C, right lower canine (DAM1 199); D, E, right P/1 (DAM1 40); F, G, right DP/1 (DAM1 126); H, ; I, left DP/2-3 (DAM1 117); J, ; K, left DP/4 (DAM1 103); L, left mandibular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

160x231mm (300 x 300 DPI)

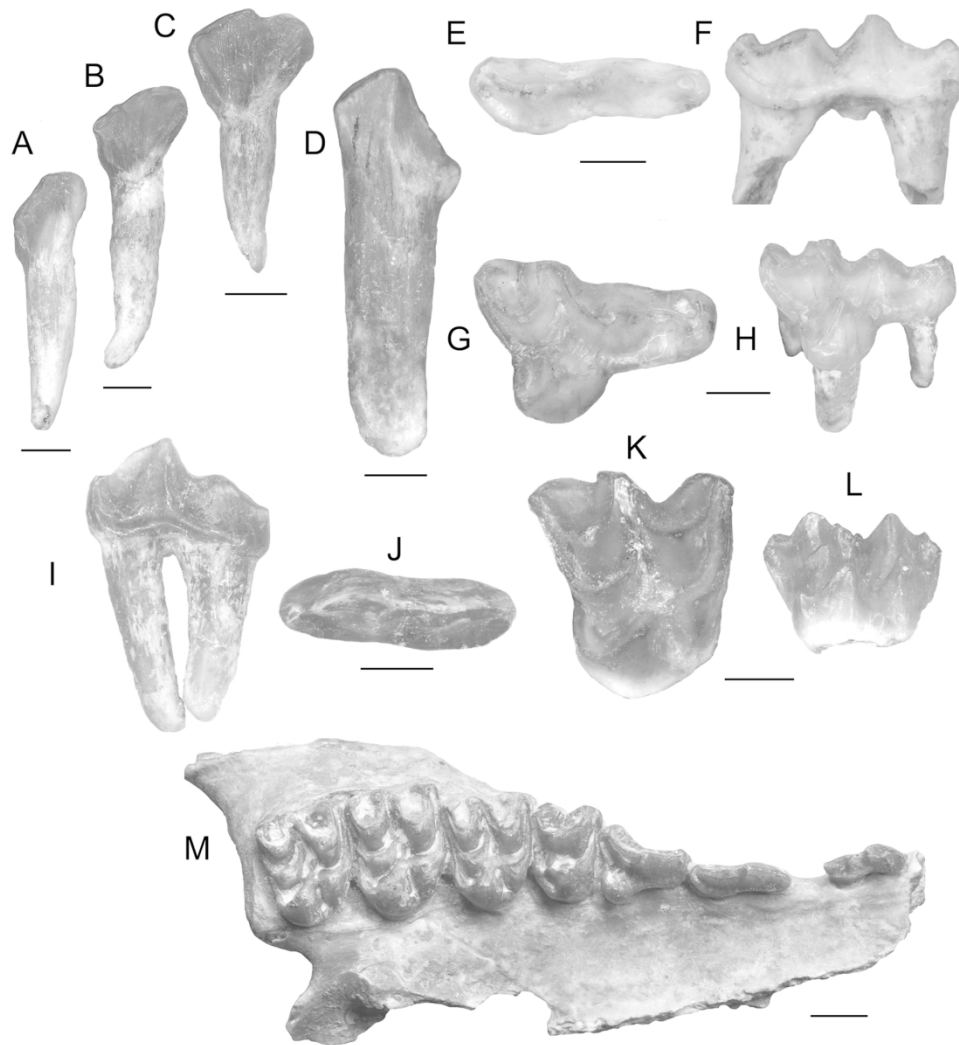


Figure 7. Material of the upper dentition of *Paroxacron valdense*. A, right I3/ (DAM1 252) ; B, right I2/ (DAM1 228); C, right I1/ (DAM1 213); D, left upper canine (DAM1 261); E, F, right DP1-2/ (DAM1 164); G, H, right DP3/ (DAM1 160); I, J, left P1/ (DAM1 66); K, L, right DP4/ (DAM1 144); M, right 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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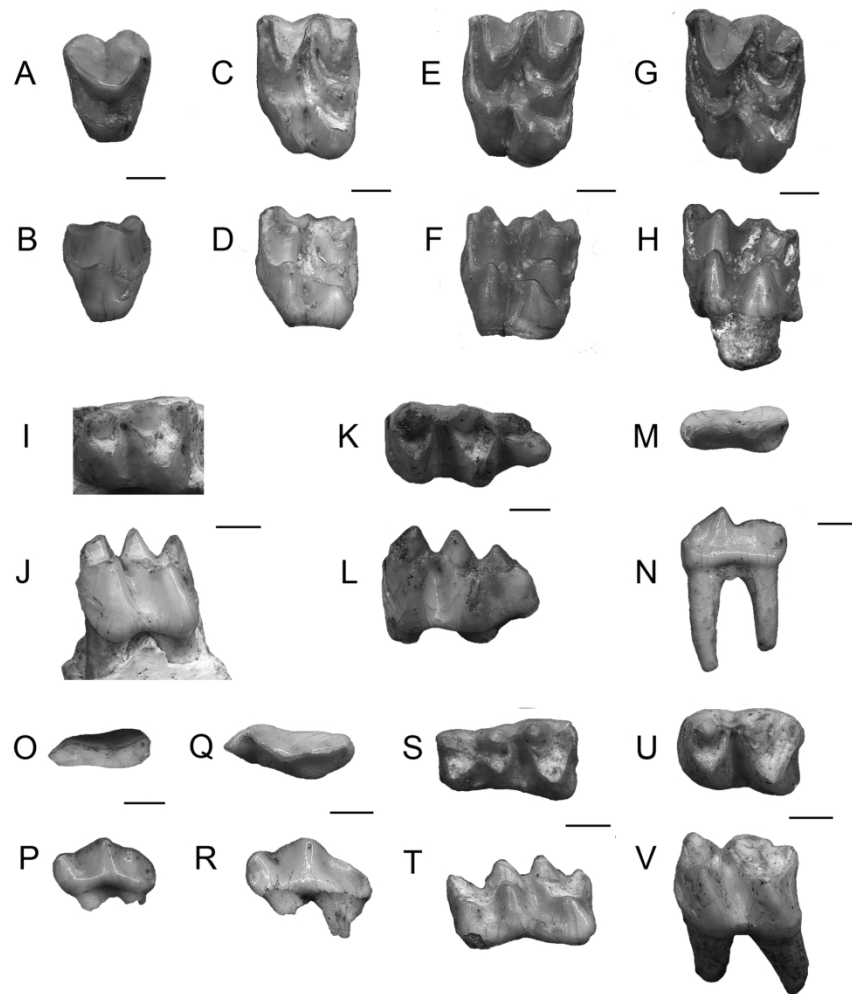


Figure 8. Material of the *Paroxacron* sp. dentition. A, B, right P4/ (DAM3 09; mirror view); C, D, right M1/ (DAM1 06; mirror view); E, F, left M2/ (DAM3 04); G, H, left M3/ (DAM3 03); I, J, left M/2 (DAM3 21; mirror view); K, L, right M/3 (DAM3 11); M, N, right P1/ (DAM3 10; mirror view); O, P, right 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.

170x231mm (300 x 300 DPI)



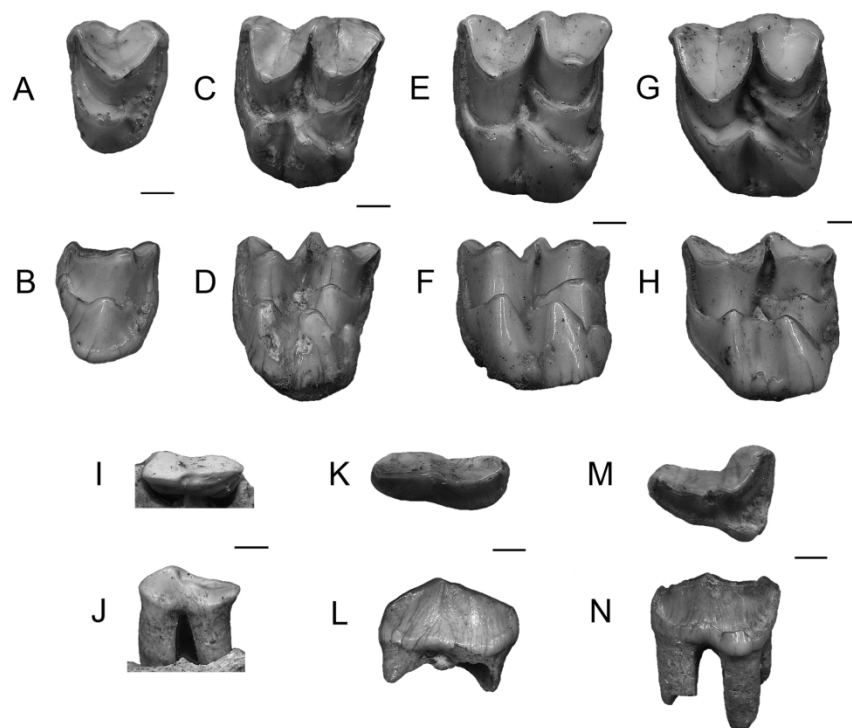


Figure 9. Material of the *Paroxacron bergeri* dentition. A, B, left P4/ (DAM3 30); C, D, left M1/ (DAM3 29); E, F, right M2/ (DAM3 26; mirror view); G, H, right M3/ (DAM3 24; mirror view); I, J, left P1/ (DAM3 33); K, L, left P2/ (DAM3 32); M, N, right P3/ (DAM3 31; mirror view). In occlusal view: A,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

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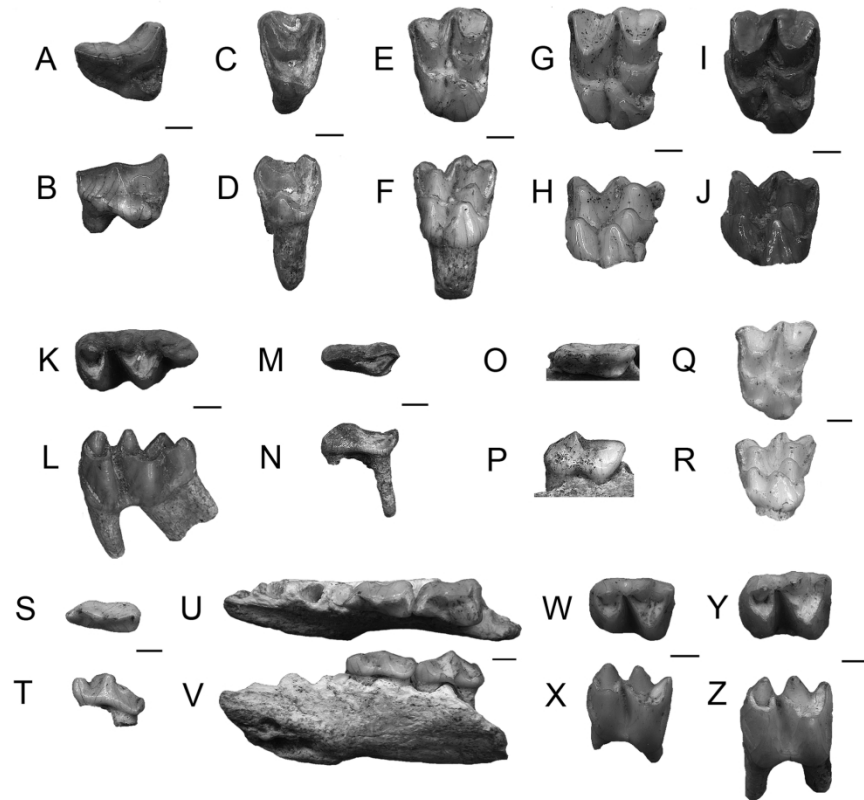


Figure 10. Material of the *Plesiomyx cadurcensis* dentition. A, B, right P3/ (DAM3 48; mirror view); C, D, right P4/ (DAM3 47; mirror view); E, F, right M1/ (DAM3 44; mirror view); G, H, left M2/ (DAM3 37); I, J, left M3/ (DAM3 34); K, L, left M/3 (DAM3 52; mirror view); M, N, right P1/ (DAM3 50; mirror 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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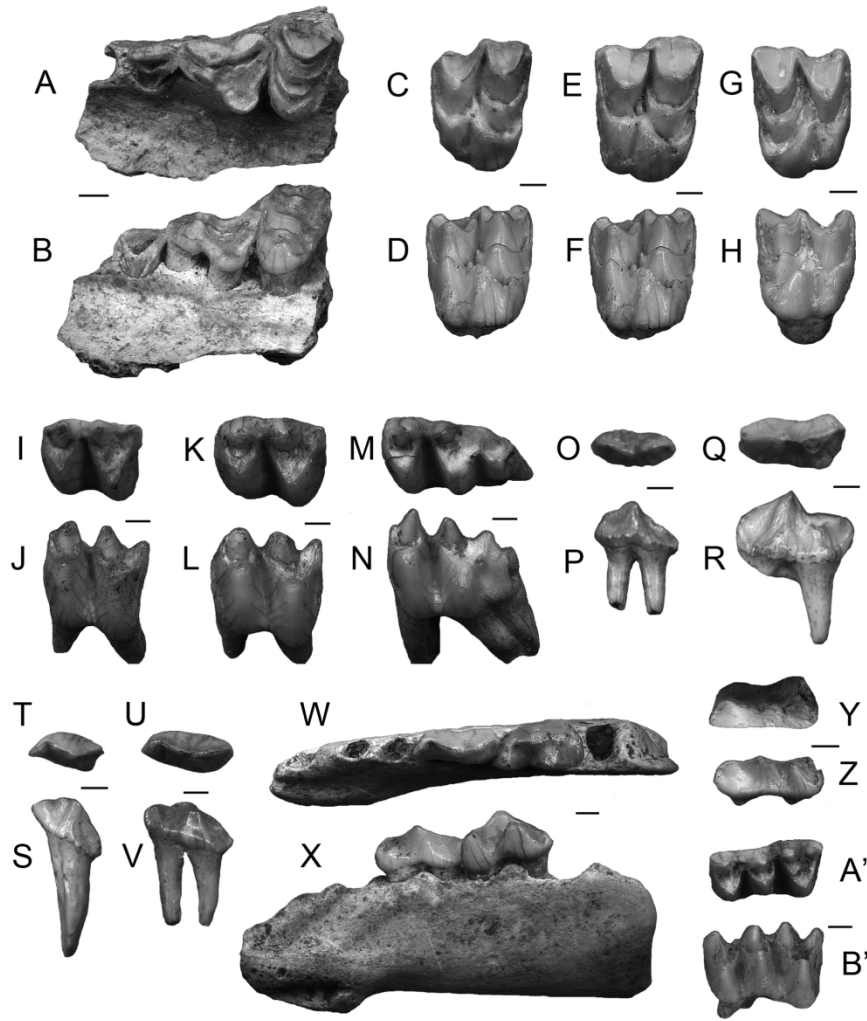


Figure 11. Material of the *Plesiomeryx huerzeleri* dentition. A, B, left maxillary fragment with P3/-P4/ (DAM3 101); C, D, right M1/ (DAM3 88; mirror view); E, F, right M2/ (DAM3 83; mirror view); G, H, right M3/ (DAM3 81; mirror view); I, J, right M/1 (DAM3 111); K, L, right M/2 (DAM3 107); M, N, right 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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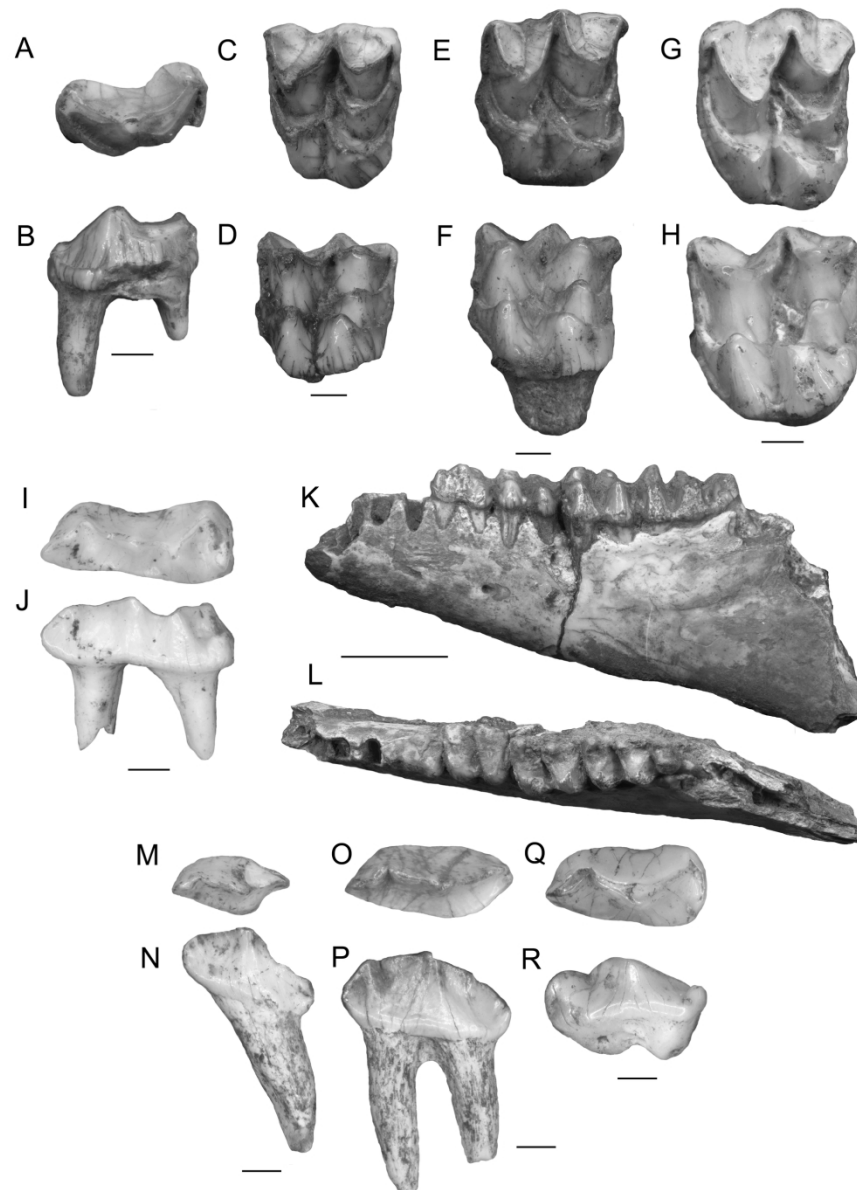


Figure 12. Material of the *Caenomeryx procommunis* dentition. A, B, right P3/ (DAM3 135; mirror view); C, D, left M1/ (DAM3 133); E, F, right M2/ (DAM3 132; mirror view); G, H, right M3/ (DAM3 129; mirror view); I, J, right DP/2-3 (DAM3 145); K, L, right mandibular fragment with P/4-M/3 (DAM3 152); 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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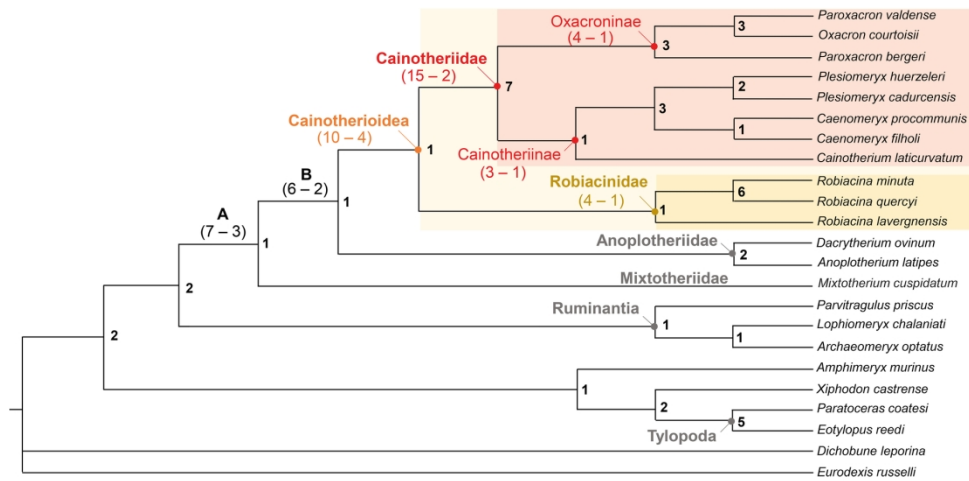


Figure 13. Phylogeny of Cainotheriidae and their position within artiodactyls. Most parsimonious tree at 170 steps, with IC=0.48 and IR=0.73. The Bremer Index (IB) is indicated in bold at each node. X a - b: X, node number; a, number of synapomorphies; b, number of ambiguous characters (Acctran optimization).

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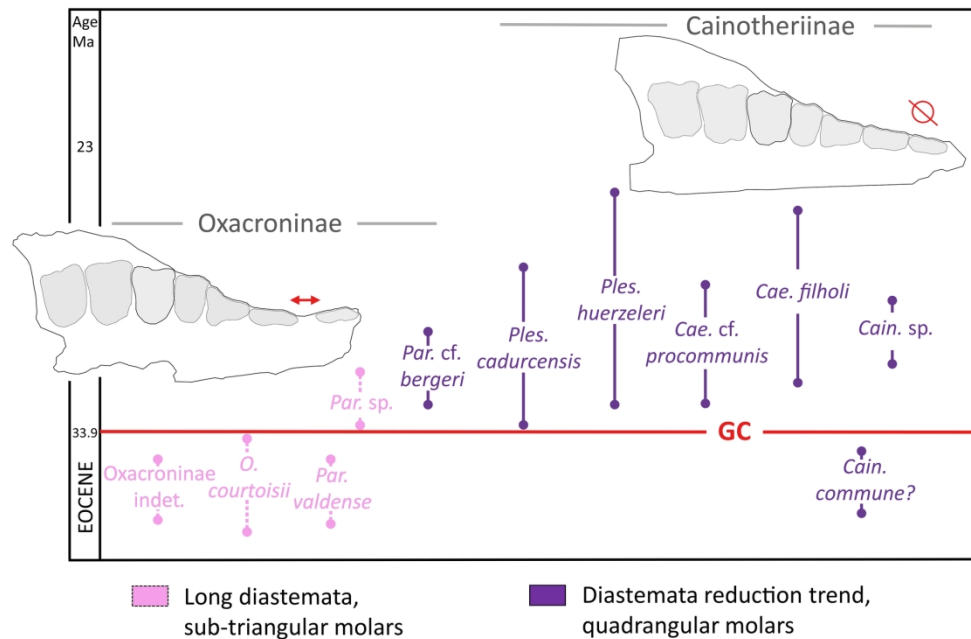


Figure 14. Trends and stratigraphical extensions of cainotheriid species from Quercy, around the Grande Coupure (modified from Blondel (2005; fig. 5) on the stratigraphical position of *Paroxacron valdense* and *Paroxacron sp.*, with the attribution of Escamps specimens to *Paroxacron valdense*). Dotted-line: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

172x113mm (300 x 300 DPI)

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3 **Supplementary data: Cainotheriidae (Mammalia, Artiodactyla) from Dams (Quercy,**  
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6 **SW France); phylogenetic relationships and evolution around the Eocene-**  
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8 **Oligocene transition (MP19-MP21).**  
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13 **Dataset S1. Characters list**

- 14  
15 **1. Lower incisors.**  
16 0. one endocristulid  
17 1. two endocristulids  
18  
19 **2. Lower canine.** Hooker & Weidmann (2000)  
20 0. caniniform  
21 1. incisiform  
22  
23 **3. Diastema between C-P1/.**  
24 0. absence  
25 1. presence  
26  
27 **4. Diastema between P1/-P2/.**  
28 0. absence  
29 1. presence  
30  
31 **5. Diastema between P/1-P/2.**  
32 0. absent to reduced  
33 1. short to long  
34  
35 **6. Diastema between P/2-P/3.**  
36 0. absent to reduced  
37 1. short to long  
38  
39 **7. Upper M: styles, crests.** Hooker & Weidmann (2000)  
40 0. absence  
41 1. presence  
42  
43 **8. Upper M: parastyle, size.** Modified from Gentry & Hooker (1988)  
44 0. very large, superior to other styles  
45 1. large, like other styles  
46  
47 **9. Upper M: mesostyle.**  
48 0. absence  
49 1. presence  
50  
51 **10. Upper M: mesostyle, shape.** Gentry & Hooker (1988)  
52 0. looped  
53 1. pinched  
54  
55 **11. Upper M: position of the protocone (A).**  
56 0. mesial  
57 1. subcentral  
58 2. distal  
59  
60 **12. M1/-M2/: hypocone.**  
0. absence  
1. presence  
  
**13. Upper M: paraconule.** Modified from Gentry & Hooker (1988)  
0. absence  
1. presence

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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 significantly 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



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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

- 1  
2  
3 3. postprotocristid then preentocristid  
4  
5 **45. Lower M: prehypocristid.**  
6 0. straight to convex buccally  
7 1. concave buccally  
8  
9 **46. Lower M: postprotocristid and postmetacristid, fused.**  
10 0. absence  
11 1. presence  
12  
13 **47. Lower M: neotrigonid (Centroconulid + Postendocentrocristulid). Sudre (1977)**  
14 0. absence  
15 1. presence  
16  
17 **48. M/3: prehypocristulid, fused (cusp or crest).**  
18 0. absence  
19 1. presence  
20  
21 **49. M/3: prehypocristulid, junction with.**  
22 0. posthypocristid  
23 1. posthypocristid and postentocristid  
24  
25 **50. M/3: posthypocristulid.**  
26 0. absence  
27 1. presence  
28  
29 **51. M/3: posthypocristulid, inclined.**  
30 0. mesio-buccally  
31 1. mesio-distally  
32  
33 **52. Lower M: hypolophid. Gentry & Hooker (1988)**  
34 0. absence  
35 1. presence  
36  
37 **53. Lower M: straight buccal wall.**  
38 *Straight buccal wall: buccal crests are aligned mesio-distally*  
39 0. absence  
40 1. presence  
41  
42 **54. P4/: metacone. Modified from Hooker & Weidmann (2000)**  
43 0. absence  
44 1. presence  
45  
46 **55. P4/: paracone et metacone, individualized. Modified from Hooker & Weidmann (2000)**  
47 0. absence  
48 1. presence  
49  
50 **56. P4/: paracone and protocone, level.**  
51 0. at the same level  
52 1. protocone more mesial  
53 2. paracone more mesial  
54  
55 **57. P4/: postprotocrista. Modified from Gentry & Hooker (1988)**  
56 0. absent to reduced  
57 1. long  
58  
59 **58. P3/-P4/: styles, crests. Hooker & Weidmann (2000)**  
60 0. absence  
1. presence  
61  
62 **59. P3/: metacone.**  
63 0. absence  
64 1. presence  
65  
66 **60. P3/: metacone and paracone, relative size. Hooker & Weidmann (2000)**  
67 0. metacone smaller than paracone  
68 1. metacone and paracone sub-equal  
69  
70

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4 **61. P3/: triangular.**  
5 0. absence  
6 1. presence
- 7 **62. P3/: mesial lobe, very elongated.**  
8 0. absence  
9 1. presence
- 10  
11 **63. P3/: protocone, mesio-distal width.** Modified from Hooker & Weidmann (2000)  
12 0. small  
13 1. large
- 14 **64. P2/: protocone.**  
15 0. absence  
16 1. presence
- 17  
18 **65. P3/: metaconid (visible groove):** Modified from Gentry & Hooker (1988)  
19 0. absence  
20 1. presence
- 21 **66. P3/: entoconid.**  
22 0. absence  
23 1. presence
- 24  
25 **67. P2-P3/: hypoconid.**  
26 0. absent to small  
27 1. large
- 28 **68. Lower P : postprotoconulid.**  
29 0. absence  
30 1. presence
- 31  
32 **69. Lower P : postprotoconulid, size.**  
33 0. very small  
34 1. small to large
- 35 **70. P/1: roots.**  
36 0. uniradicate  
37 1. biradicate
- 38  
39 **71. P/1: shape.** Modified from Gentry & Hooker (1988)  
40 0. caniniform  
41 1. premolariform
- 42 **72. P: cingulum/id pronounced.**  
43 0. absence  
44 1. presence
- 45 **73. Lower P: large premolars with strong main cusp.**  
46 0. absence  
47 1. presence
- 48  
49

50 **(A) Ordered characters; (NA) Unordered characters**  
51  
52  
53  
54

55 **Dataset S2.** Taxa/characters matrix from dental material (provided as .nex format)  
56

57 #NEXUS  
58

59 [ File saved by NDE version 0.5.0, Sun Jan 13 10:07:54 2019 ]  
60

```

1
2
3 BEGIN TAXA;
4     DIMENSIONS NTAX=23;
5     TAXLABELS
6         'Paroxacron valdense'
7         'Paroxacron bergeri'
8         'Oxacron courtoisii'
9         'Plesiomeryx huerzeleri'
10        'Plesiomeryx cadurcensis'
11        'Caenomeryx procommunis'
12        'Caenomeryx filholi'
13        'Cainotherium laticurvatum'
14        'Robiacina minuta'
15        'Robiacina quercyi'
16        'Robiacina lavergnensis'
17        'Dacrytherium ovinum'
18        'Anoplotherium latipes'
19        'Mixtotherium cuspidatum'
20        'Parvitrugulus priscus'
21        'Lophiomeryx chalaniati'
22        'Archaeomeryx optatus'
23        'Amphimeryx murinus'
24        'Xiphodon castrense'
25        'Paratoceras coatesi'
26        'Eotylopus reedi'
27        'Dichobune leporina'
28        'Eurodexis russelli'
29        ;
30 ENDBLOCK;
31
32 BEGIN CHARACTERS;
33     DIMENSIONS NCHAR=73;
34     FORMAT DATATYPE=STANDARD MISSING=? GAP=- SYMBOLS="0123";
35     CHARLABELS
36         [1] 'Lower incisors'
37         [2] 'Lower canine'
38         [3] 'Diastema between C-P1/'
39         [4] 'Diastema between P1-P2/'
40         [5] 'Diastema between P1-P2/'
41         [6] 'Diastema between P2-P3/'
42         [7] 'Upper M: styles, crests'
43         [8] 'Upper M: parastyle, size'
44         [9] 'Upper M: mesostyle'
45         [10] 'Upper M: mesostyle, shape'
46         [11] 'Upper M: position of the protocone (A)'
47         [12] 'M1-M2: hypocone'
48         [13] 'Upper M: paraconule'
49         [14] 'Upper M: paraconule, size'
50         [15] 'Upper M: preprotocrista and paraconule, junction'
51         [16] 'Upper M: metaconule, size'
52         [17] 'M3: position of protocone relative to mesial or distal lingual cusp (bucco-lingual axis)'
53         [18] 'Upper M: cingulum surrounding the protocone (A)'
54         [19] 'Upper M: dilambdodonty'
55         [20] 'Upper M: dilambdodonty, type'
56         [21] 'Upper M: premetacristula'
57         [22] 'Upper M: premetacristula, length'
58         [23] 'Upper M: premetacristula, shape'
59         [24] 'Upper M: postmetacristula and metastyle, junction'
60         [25] 'Upper M: preparacrista, length'
61         [26] 'Upper M: postprotocrista'
62         [27] 'Upper M: postprotocrista, direction'
63         [28] 'Upper M: postprotocrista, bifurcation'
64         [29] 'Upper M: postparacristula'
65         [30] 'Upper M: postparacristula long and joins preprotocrista in the center of the tooth'
66         [31] 'Upper M: shape (A)'
67         [32] 'Upper M: elongated bucco-lingually'
68         [33] 'Lower M: metaconulid'
69         [34] 'Lower M: metaconulid, size (A)'

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3 [35] 'Lower M: metaconulid and metaconid, linked'  
4 [36] 'Lower M: metastylid'  
5 [37] 'M/3: hypoconulid in basin-shape'  
6 [38] 'M/1-M/2: hypoconulid'  
7 [39] 'Lower M: entoconid in 'loop-like''  
8 [40] 'Lower M: entoconid and hypoconid, relative position (mesio-distal axis) (A)'  
9 [41] 'Lower M: valley between entoconid and metaconid or metaconulid'  
10 [42] 'Lower M: paraconid'  
11 [43] 'Lower M: prehypocristid, fused (cusp or crest)'  
12 [44] 'Lower M: prehypocristid (oblique cristid), junction with (NA)'  
13 [45] 'Lower M: prehypocristid'  
14 [46] 'Lower M: postprotocristid and postmetacristid, fused'  
15 [47] 'Lower M: neotrigonid (Centroconulid + Postendocentrocristulid)'  
16 [48] 'M/3: prehypocristulid, fused (cusp or crest)'  
17 [49] 'M/3: prehypocristulid, junction with'  
18 [50] 'M/3: posthypocristulid'  
19 [51] 'M/3: posthypocristulid, inclined'  
20 [52] 'Lower M: hypolophid'  
21 [53] 'Lower M: straight buccal wall'  
22 [54] 'P4/: metacone'  
23 [55] 'P4/: paracone et metacone, individualized'  
24 [56] 'P4/: paracone and protocone, level'  
25 [57] 'P4/: postprotocrista'  
26 [58] 'P3/-P4/: styles, crests'  
27 [59] 'P3/: metacone'  
28 [60] 'P3/: metacone and paracone, relative size'  
29 [61] 'P3/: triangular'  
30 [62] 'P3/: mesial lobe, very elongated'  
31 [63] 'P3/: protocone, mesio-distal width'  
32 [64] 'P2/: protocone'  
33 [65] 'P3/: metaconid (visible groove)'  
34 [66] 'P3/: entoconid'  
35 [67] 'P/2-P/3: hypoconid'  
36 [68] 'Lower P : postprotoconulid'  
37 [69] 'Lower P : postprotoconulid, size'  
38 [70] 'P/1: roots'  
39 [71] 'P/1: shape'  
40 [72] 'P: cingulum/id pronounced'  
41 [73] 'Lower P: large premolars with strong main cusp'

## STATELABELS

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9
- 'one endocristulid'  
'two endocristulids',
- caniniform  
incisiform,
- absence  
presence,
- absence  
presence,
- 'absent to reduced'  
'short to long',
- 'absent to reduced'  
'short to long',
- absence  
presence,
- 'very large, superior to other styles'  
'large, like other styles',
- absence

1		
2		
3		presence,
4	10	
5		looped
6		pinched,
7	11	
8		mesial
9		subcentral
10	12	distal,
11		absence
12	13	presence,
13		absence
14		presence,
15	14	
16		small
17		large,
18	15	
19		absence
20	16	presence,
21		small
22		large,
23	17	
24		'at the same level'
25	18	'protocone more lingual',
26		'absent to very weak'
27		'weak'
28		wide
29		'very wide',
30	19	
31		absence
32	20	presence,
33		'strong, with crests weakly oblique and pronounced'
34		'very strong, with crests very oblique and pronounced',
35	21	
36		absence
37	22	presence,
38		short
39		'long, extend into the central valley',
40	23	
41		continuous
42	24	discontinuous,
43		absence
44		presence,
45	25	
46		'as long as the postparacrista'
47		'shorter than postparacrista',
48	26	
49		'absent to reduced'
50		long,
51	27	
52		'disto-buccally directed'
53	28	'distally directed',
54		absence
55	29	presence,
56		absence
57		presence,
58	30	
59		absence
60		presence,

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3	31	
4		triangular
5		subtriangular
6		quadrangular,
7	32	
8		absence
9		presence,
10	33	
11		absence
12		presence,
13	34	
14		small
15		medium
16		'large (like other cuspids)',
17	35	
18		absence
19		presence,
20	36	
21		absence
22		presence,
23	37	
24		absence
25		presence,
26	38	
27		absence
28		presence,
29	39	
30		absence
31		presence,
32	40	
33		'opposed, to entoconid more mesial'
34		'entoconid slightly more distal'
35		'entoconid very distal',
36	41	
37		absence
38		presence,
39	42	
40		'absent to small'
41		large,
42	43	
43		absence
44		presence,
45	44	
46		postprotocristid
47		'metaconulid or metastylid'
48		preentocristid
49		'postprotocristid then preentocristid',
50	45	
51		'straight to convex buccally'
52		'concave buccally',
53	46	
54		absence
55		presence,
56	47	
57		absence
58		presence,
59	48	
60		absence
		presence,
	49	
		'posthypocristid '
		'posthypocristid and postentocristid',
	50	
		absence
		presence,
	51	
		'mesio-buccally'

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2		
3		'mesio-distally',
4	52	
5		absence
6		presence,
7	53	
8		absence
9		presence,
10	54	
11		absence
12		presence,
13	55	
14		absence
15		presence,
16	56	
17		'at the same level'
18		'protocone more mesial'
19		'paracone more mesial',
20	57	
21		'absent to reduced'
22		long,
23	58	
24		absence
25		presence,
26	59	
27		absence
28		presence,
29	60	
30		'metacone smaller than paracone'
31		'metacone and paracone sub-equal',
32	61	
33		absence
34		presence,
35	62	
36		absence
37		presence,
38	63	
39		small
40		large,
41	64	
42		absence
43		presence,
44	65	
45		absence
46		presence,
47	66	
48		absence
49		presence,
50	67	
51		'absent to small'
52		'large',
53	68	
54		absence
55		presence,
56	69	
57		'very small'
58		'small to large',
59	70	
60		uniradicated
		biradicated,
	71	
		caniniform
		premolariform,
	72	
		absence
		presence,
	73	
		absence



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1
2
3           presence,
4           ;
5           MATRIX
6 'Paroxacron valdense'      1101010110 2011011111 1001011010 1012000012 1011011110 -001011111
7 1100000101 100
8 'Paroxacron bergeri'      ?100000111 2011011111 1001011010 201200????2 ?0????????? ?01011111
9 1100??0??1 100
10 'Oxacron courtoisii'     1101010110 2010011111 1001011010 1012000012 1011011110 -001011111
11 1000000101 000
12 'Plesiomeryx huerzeleri' 1110100111 2010011111 1001011011 2012000012 1011011110 -001001111
13 1011000110 101
14 'Plesiomeryx cadurcensis' ?110100111 2010011111 1001011011 2012000012 1011011110 -001001111
15 1011000110 101
16 'Caenomeryx procommunis' 1110101111 2011011111 1001011011 2112000012 1011011110 -001001111
17 1011000110 101
18 'Caenomeryx filholi'    ??10101111 2011011111 1001011011 2112000012 1011011110 -001001111
19 1011000110 101
20 'Cainotherium laticurvatum' 1100001111 2011010111 1001011011 2012000012 0011011110 -001001111
21 0000000110 111
22 'Robiacina minuta'      ?1??010011 1010111010 111111000- 1010101111 1011010111 0001000011
23 100?100100 100
24 'Robiacina quercyi'     ?100??1011 1010111010 111110-00- 1010101111 1011010111 0001000011
25 1000??0?? ?00
26 'Robiacina lavergnensis' ?0????1011 1010111210 100110-00- 1011101111 1010010111 0001011111
27 101?100??0 ?00
28 'Dacrytherium ovinum'   0100001011 00111110210 100100-00- 2011101111 1011010111 0001001110
29 00111010-? 111
30 'Anoplotherium latipes' ??00001011 001111?210 100100-00- 201110??11 11110101?? ?001001110
31 00111010-? ?11
32 'Mixtotherium cuspidatum' ?000001011 00101110210 110100-00- 200--10110 000-110111 0001100110
33 10110010-? 101
34 'Parvitrugulus priscus' ????10110- 000--1000- 11010100-- 200--00000 0013010101 1011101110 101110?0-0
35 000
36 'Lophiomeryx chalaniati' ????101111 000--10310 11010100-- 200--00100 0012010100 -000-01010 01111010-0
37 010
38 'Archaeomeryx optatus' ?1--101111 000--10310 11010100-- 200--00?00 0012010101 0000-11110 1110?010-0
39 000
40 'Amphimeryx murinus'   ??????0111 0011011211 1001010010 200--00100 000-110110 -00100101?
41 110????0-? ???
42 'Xiphodon castrense'   ?????01011 0011010210 1001010010 200--00000 00120100-1 001100101? 000?0100-
43 ? ?10
44 'Paratoceras coatesi ' ?????101111 000--1120- 10000100-- 200--00000 000-0000-1 0000-01010 00000100-0
45 011
46 'Eotylopus reedi'      0111100111 000--1110- 10000101-- 200--00000 000-0000-1 0000-01010 00100100-0
47 111
48 'Dichobune leporina'   ?????11010- 011101130- 0--100-00- 200--0?100 1?0-010100 -101121??? ?????000-0
49 ??0
50 'Eurodexis russelli'   ??????010- 101010130- 0--101000- 000--00100 010-010101 0000-0000- 100?????-?
51 ???
52           ;
53 ENDBLOCK;
54 BEGIN ASSUMPTIONS;
55     OPTIONS DEFTYPE=UNORD POLYTCOUNT=MINSTEPS;
56     TYPESET * default = ORD: 11 18 31 34 40;
57 ENDBLOCK;

```

### Dataset S3. Apomorphy lists

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

1			
2			
3	node_36 --> node_37	7 (Upper M: styles, crests)	1 0.167 0 --> 1
4		9 (Upper M: mesostyle)	1 0.500 0 ==> 1
5		18 (Upper M: cingulum surrounding the protoco)	1 0.375 3 ==> 2
6		19 (Upper M: dilambdodonty)	1 0.333 0 ==> 1
7		21 (Upper M: premetacristula)	1 1.000 0 ==> 1
8		49 (M/3: prehypocristulid, junction with)	1 0.500 0 --> 1
9		59 (P3/: metacone)	1 1.000 0 --> 1
10			
11	node_37 --> node_38	15 (Upper M: preprotocrista and paraconule, j)	1 0.333 0 --> 1
12		17 (M3/: position of protocone relative to me)	1 0.250 1 ==> 0
13		22 (Upper M: premetacristula, length)	1 0.333 0 --> 1
14		43 (Lower M: prehypocristid, fused (cusp or c)	1 0.333 0 --> 1
15		58 (P3/-P4/: styles, crests)	1 0.333 0 ==> 1
16		63 (P3/: protocone, mesio-distal width)	1 0.200 0 ==> 1
17		64 (P2/: protocone)	1 0.250 0 --> 1
18		65 (P3/: metaconid (visible groove))	1 0.333 0 --> 1
19		67 (P/2-P/3: hypoconid)	1 0.500 0 ==> 1
20	node_38 --> node_39	5 (Diastema between P/1-P/2)	1 0.500 1 ==> 0
21		8 (Upper M: parastyle, size)	1 0.333 1 ==> 0
22		26 (Upper M: postprotocrista)	1 0.250 1 ==> 0
23		39 (Lower M: entoconid in ?loop-like?)	1 1.000 0 ==> 1
24		44 (Lower M: prehypocristid (oblique cristid))	1 1.000 2 --> 1
25		71 (P/1: shape)	1 0.333 0 --> 1
26		73 (Lower P: large premolars with strong mai)	1 0.250 0 --> 1
27	node_39 --> node_40	22 (Upper M: premetacristula, length)	1 0.333 1 --> 0
28		33 (Lower M: metaconulid)	1 1.000 0 ==>
29	1		
30		37 (M/3: hypoconulid in basin-shape)	1 0.500 0 --> 1
31		40 (Lower M: entoconid and hypoconid, relativ)	1 1.000 0 ==> 1
32		41 (Lower M: valley between entoconid and met)	1 0.333 0 ==> 1
33		55 (P4/: paracone et metacone, individualized)	1 0.500 1 ==> 0
34	node_40 --> node_41	1 (Lower incisors)	1 1.000 0 --> 1
35		11 (Upper M: position of the protocone (A))	1 0.667 0 ==> 1
36		17 (M3/: position of protocone relative to me)	1 0.250 0 ==> 1
37		18 (Upper M: cingulum surrounding the protoco)	1 0.375 2 --> 1
38		60 (P3/: metacone and paracone, relative size)	1 1.000 0 ==> 1
39		63 (P3/: protocone, mesio-distal width)	1 0.200 1 --> 0
40		64 (P2/: protocone)	1 0.250 1 ==> 0
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3		67 (P/2-P/3: hypoconid)	1 0.500 1 ==> 0
4		68 (Lower P : postprotoconulid)	1 1.000 0 ==> 1
5		73 (Lower P: large premolars with strong mai)	1 0.250 1 - -> 0
6			
7			
8	node_41 --> node_42	8 (Upper M: parastyle, size)	1 0.333 0 ==> 1
9			
10		11 (Upper M: position of the protocone (A))	1 0.667 1 ==> 2
11		15 (Upper M: preprotocrista and paraconule, j)	1 0.333 1 ==> 0
12			
13		20 (Upper M: dilambdodonty, type)	1 0.500 0 ==> 1
14		26 (Upper M: postprotocrista)	1 0.250 0 ==> 1
15			
16		27 (Upper M: postprotocrista, direction)	1 1.000 0 ==> 1
17			
18		29 (Upper M: postparacristula)	1 0.500 0 ==> 1
19		34 (Lower M: metaconulid, size (A))	1 1.000 1 ==> 2
20			
21		35 (Lower M: metaconulid and metaconid, linked)	1 1.000 1 ==> 0
22			
23		37 (M/3: hypoconulid in basin-shape)	1 0.500 1 - -> 0
24		38 (M/1-M/2: hypoconulid)	1 0.333 1 ==> 0
25			
26		40 (Lower M: entoconid and hypoconid, relativ)	1 1.000 1 ==> 2
27		47 (Lower M: neotrigonid (Centroconulid + Pos)	1 1.000 0 ==> 1
28			
29		50 (M/3: posthypocristulid)	1 0.250 1 ==> 0
30			
31		65 (P/3: metaconid (visible groove))	1 0.333 1 - -> 0
32	node_42 --> node_43	7 (Upper M: styles, crests)	1 0.167 1 ==> 0
33			
34		56 (P4/: paracone and protocone, level)	1 0.500 0 ==> 1
35		62 (P3/: mesial lobe, very elongated)	1 0.250 0 - -> 1
36			
37		70 (P/1: roots)	1 1.000 0 ==> 1
38	node_43 --> node_44	4 (Diastema between P1/-P2/)	1 0.500 0 ==> 1
39			
40		6 (Diastema between P/2-P/3)	1 0.333 0 ==> 1
41			
42		10 (Upper M: mesostyle, shape)	1 1.000 1 ==> 0
43		31 (Upper M: shape (A))	1 0.500 2 ==> 1
44	node_44 --> O. courtoisii	14 (Upper M: paraconule, size)	1 0.200 1 ==> 0
45			
46		62 (P3/: mesial lobe, very elongated)	1 0.250 1 - -> 0
47			
48		71 (P/1: shape)	1 0.333 1 ==> 0
49	node_42 --> node_27	30 (Upper M: postparacristula long and joins )	1 1.000 0 ==> 1
50			
51		69 (Lower P : postprotoconulid, size)	1 1.000 0 ==> 1
52			
53		73 (Lower P: large premolars with strong mai)	1 0.250 0 - -> 1
54	node_27 --> node_26	3 (Diastema between C-P1/)	1 0.500 0 ==> 1
55			
56		5 (Diastema between P/1-P/2)	1 0.500 0 ==> 1
57			
58		63 (P3/: protocone, mesio-distal width)	1 0.200 0 - -> 1
59		64 (P2/: protocone)	1 0.250 0 ==> 1
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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 --> <i>Cai. laticurvatum</i>	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: preparamacrista, 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 protocone)	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 --> <i>R. minuta</i>	7 (Upper M: styles, crests)	1 0.167 1 ==> 0
	26 (Upper M: postprotocrista)	1 0.250 0 ==> 1
node_29 --> <i>R. lavergnensis</i>	2 (Lower canine)	1 0.500 1 ==> 0
	18 (Upper M: cingulum surrounding the protocone)	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 --> <i>A. latipes</i>	42 (Lower M: paraconid)	1 0.500 0 ==> 1
node_39 --> <i>M. cuspidatum</i>	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 (P3/: 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

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3	node_32 --> P. priscus	9 (Upper M: mesostyle)	1 0.500 1 ==> 0
4		18 (Upper M: cingulum surrounding the protocone)	2 0.375 2 ==> 0
5		19 (Upper M: dilambdodonty)	1 0.333 1 ==> 0
6		38 (M/1-M/2: hypoconulid)	1 0.333 1 ==> 0
7		44 (Lower M: prehypocristid (oblique cristid))	1 1.000 2 ==> 3
8		51 (M/3: posthypocristulid, inclined)	1 1.000 0 ==> 1
9		53 (Lower M: straight buccal wall)	1 0.500 0 ==> 1
10			
11	node_32 --> node_31	18 (Upper M: cingulum surrounding the protocone)	1 0.375 2 ==> 3
12		54 (P4/: metacone)	1 0.333 1 ==> 0
13		62 (P3/: mesial lobe, very elongated)	1 0.250 0 ==> 1
14			
15	node_31 --> L. chalaniati	50 (M/3: posthypocristulid)	1 0.250 1 ==> 0
16		58 (P3/-P4/: styles, crests)	1 0.333 1 ==> 0
17		61 (P3/: triangular)	1 0.250 1 ==> 0
18		72 (P: cingulum/id pronounced)	1 0.250 0 ==> 1
19			
20	node_31 --> Arc. optatus	56 (P4/: paracone and protocone, level)	1 0.500 0 ==> 1
21		64 (P2/: protocone)	1 0.250 1 ==> 0
22			
23	node_37 --> node_35	3 (Diastema between C-P1/)	1 0.500 0 --> 1
24		4 (Diastema between P1/-P2/)	1 0.500 0 --> 1
25		29 (Upper M: postparacristula)	1 0.500 0 ==> 1
26		55 (P4/: paracone et metacone, individualized)	1 0.500 1 ==> 0
27		66 (P3/: entoconid)	1 1.000 0 --> 1
28		72 (P: cingulum/id pronounced)	1 0.250 0 --> 1
29			
30	node_35 --> Amp. murinus	7 (Upper M: styles, crests)	1 0.167 1 --> 0
31		20 (Upper M: dilambdodonty, type)	1 0.500 0 ==> 1
32		45 (Lower M: prehypocristid)	1 0.500 0 ==> 1
33		50 (M/3: posthypocristulid)	1 0.250 1 ==> 0
34		62 (P3/: mesial lobe, very elongated)	1 0.250 0 ==> 1
35			
36	node_35 --> node_34	38 (M/1-M/2: hypoconulid)	1 0.333 1 ==> 0
37		48 (M/3: prehypocristulid, fused (cusp or cre))	1 1.000 1 ==> 0
38		61 (P3/: triangular)	1 0.250 1 ==> 0
39			
40	node_34 --> X. castrense	8 (Upper M: parastyle, size)	1 0.333 1 ==> 0
41		17 (M3/: position of protocone relative to me)	1 0.250 1 ==> 0
42		43 (Lower M: prehypocristid, fused (cusp or c))	1 0.333 0 ==> 1
43		53 (Lower M: straight buccal wall)	1 0.500 0 ==> 1
44			
45	node_34 --> node_33	13 (Upper M: paraconule)	1 0.500 1 ==> 0
46		19 (Upper M: dilambdodonty)	1 0.333 1 ==> 0
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		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 (P1/: shape)	1	0.333	0 --> 1
node_36 --> D. leporina		6 (Diastema between P2-P3)	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 (M3/: 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

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3			h	1.73-2.00	1.84 ± 0.02	0.08	4.17
4	Lower	15	L	1.26-1.98	1.46 ± 0.04	0.16	11.1
5	canine		lp	0.79-0.97	0.87 ± 0.01	0.04	5.08
6			h	1.76-2.13	1.91 ± 0.03	0.11	5.96
7	P/1	15	L	2.35-3.17	2.83 ± 0.07	0.26	9.34
8		16	lp	0.86-1.10	0.97 ± 0.02	0.08	7.90
9			la	0.76-0.96	0.87 ± 0.02	0.06	7.01
10			h	1.43-1.83	1.63 ± 0.03	0.12	7.09
11	P/2	10	L	3.10-3.58	3.32 ± 0.05	0.17	5.16
12			lp	1.02-1.18	1.08 ± 0.01	0.04	4.00
13			la	0.86-0.95	0.91 ± 0.01	0.04	4.23
14			h	1.45-1.97	1.69 ± 0.05	0.16	9.29
15	P/3	17	L	3.48-4.05	3.76 ± 0.04	0.16	4.24
16			lp	1.38-1.71	1.56 ± 0.02	0.10	6.50
17			la	1.05-1.29	1.16 ± 0.02	0.07	5.69
18			h	1.41-2.06	1.82 ± 0.04	0.18	9.80
19	P/4	18	L	2.92-3.42	3.14 ± 0.03	0.14	4.51
20			lp	1.83-2.50	2.12 ± 0.04	0.18	8.42
21			la	1.44-1.79	1.62 ± 0.03	0.11	6.64
22			h	1.34-2.35	1.79 ± 0.07	0.29	16.20
23	M/1	17	L	2.96-3.40	3.15 ± 0.03	0.12	3.92
24			lp	2.33-2.81	2.58 ± 0.03	0.14	5.53
25			la	2.12-2.73	2.37 ± 0.04	0.15	6.50
26			h	1.33-2.15	1.73 ± 0.05	0.22	12.49
27	M/2	15	L	3.19-3.51	3.34 ± 0.02	0.09	2.82
28			lp	2.54-3.01	2.72 ± 0.04	0.14	5.18
29			la	2.39-3.01	2.60 ± 0.04	0.17	6.68
30			h	1.48-2.38	1.99 ± 0.07	0.26	13.01
31	M/3	15	L	4.35-4.77	4.51 ± 0.03	0.12	2.69
32			lp	2.25-2.63	2.42 ± 0.03	0.12	5.06
33			la	2.17-2.67	2.39 ± 0.04	0.16	6.56
34			h	1.73-2.50	2.18 ± 0.06	0.24	11.16
35			L3	1.02-1.43	1.22 ± 0.03	0.12	9.45
36			l3	1.05-1.52	1.23 ± 0.03	0.12	9.87
37	M/1-M/3	14	L	10.62-11.39	10.97 ± 0.07	0.26	2.36
38	P/3-P/4	19	L	6.26-7.29	6.82 ± 0.06	0.26	3.80
39	P/2-P/4	10	L	10.32-11.61	11.06 ± 0.13	0.40	3.59
40	P/1-P/4	2	L	13.39-13.44	13.41		
41	Dia P/2-P/3	16	L	0.45-1.58	1.11 ± 0.08	0.33	30.00
42	Dia P/1-P/2	8	L	0.05-0.85	0.49 ± 0.06	0.21	42.81
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**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
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3	I1/	10	L	1.73-2.03	1.92 ± 0.03	0.11	5.56
4			lp	0.80-0.93	0.87 ± 0.01	0.04	4.97
5			h	1.55-1.93	1.72 ± 0.05	0.15	8.53
6	I2/	15	L	1.53-1.90	1.74 ± 0.03	0.1	5.73
7			lp	0.70-0.95	0.81 ± 0.02	0.07	8.71
8			h	1.63-2.14	1.88 ± 0.03	0.13	6.86
9	I3/	15	L	1.45-1.75	1.56 ± 0.02	0.09	5.83
10			lp	0.65-0.94	0.78 ± 0.02	0.07	8.65
11			h	1.49-1.94	1.77 ± 0.04	0.14	8.21
12	Upper	15	L	1.56-2.00	1.75 ± 0.03	0.13	7.31
13	canine		lp	0.90-1.12	1.02 ± 0.02	0.06	6.23
14			h	1.99-2.23	2.08 ± 0.02	0.07	3.56
15	P1/	16	L	2.67-3.54	3.08 ± 0.06	0.23	7.59
16			lp	0.82-1.05	0.94 ± 0.01	0.07	5.98
17			la	0.87-1.05	0.96 ± 0.01	0.05	5.26
18			h	1.49-1.96	1.76 ± 0.03	0.13	7.56
19	P2/	11	L	3.46-4.15	3.75 ± 0.06	0.21	5.67
20			lp	1.15-1.73	1.34 ± 0.05	0.18	13.2
21			la	1.04-1.20	1.11 ± 0.02	0.06	5.49
22			h	1.49-1.87	1.72 ± 0.04	0.14	8.03
23	P3/	12	L	3.21-3.86	3.53 ± 0.06	0.22	6.31
24			lp	2.55-3.18	2.83 ± 0.05	0.17	6.17
25			la	1.39-1.86	1.68 ± 0.04	0.14	8.09
26			h	1.39-2.18	1.85 ± 0.07	0.23	12.2
27	P4/	17	L	2.39-2.78	2.55 ± 0.03	0.12	4.64
28			lp	3.07-3.66	3.42 ± 0.04	0.15	4.46
29			h	1.65-2.58	2.03 ± 0.06	0.24	11.92
30	M1/	15	L	2.94-3.46	3.24 ± 0.04	0.15	4.54
31			lp	3.71-4.33	3.99 ± 0.05	0.20	4.92
32			la	3.26-3.75	3.52 ± 0.04	0.14	4.11
33			h	1.40-1.90	1.58 ± 0.03	0.13	8.53
34	M2/	15	L	3.34-3.74	3.55 ± 0.03	0.12	3.35
35			lp	4.13-4.71	4.37 ± 0.04	0.16	3.60
36			la	3.81-4.36	4.07 ± 0.05	0.18	4.40
37			h	1.62-2.09	1.81 ± 0.04	0.16	8.78
38	M3/	13	L	3.13-3.65	3.37 ± 0.04	0.15	4.55
39			lp	3.92-4.53	4.13 ± 0.04	0.16	3.76
40			la	3.79-4.16	3.97 ± 0.03	0.12	3.05
41			h	1.59-1.97	1.79 ± 0.04	0.13	7.14
42	M1/-M3/	13	L	9.08-10.57	9.89 ± 0.1	0.36	3.64
43	P3/-P4/	13	L	5.38-6.51	5.95 ± 0.09	0.33	5.48
44	P2/-P4/	10	L	8.95-10.44	9.62 ± 0.16	0.51	5.33
45	P1/-P4/	1	L		13.229		
46	Dia P1/-P2/	10	L	0-1.46	0.94 ± 0.13	0.41	43.17
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**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;  $\sigma$ , standard deviation; V, coefficient of variation.

	N	L/Lp/la/h	LV	M ± SE	$\sigma$	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;  $\sigma$ , 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	$3.04 \pm 0.03$	0.04	1.37
			lp	3.62-3.91	$3.77 \pm 0.15$	0.21	5.51
			la	3.08-3.58	$3.33 \pm 0.25$	0.35	10.64
			h	1.20-1.24	$1.22 \pm 0.02$	0.03	2.66
	M1/	3	L	3.08-3.34	$3.22 \pm 0.08$	0.13	4.07
			lp	4.15-4.28	$4.22 \pm 0.04$	0.06	1.50
			la	3.57-3.90	$3.76 \pm 0.10$	0.17	4.62
			h	1.40-1.90	$1.72 \pm 0.10$	0.17	9.89
	M2/	5	L	3.51-3.78	$3.61 \pm 0.05$	0.10	2.84
			lp	4.50-4.85	$4.65 \pm 0.06$	0.14	3.04
			la	3.83-4.32	$4.07 \pm 0.10$	0.22	5.52
			h	1.75-2.01	$1.86 \pm 0.05$	0.10	5.49
	M3/	3	L	3.14-3.69	$3.45 \pm 0.17$	0.31	8.78
			lp	4.17-4.60	$4.45 \pm 0.14$	0.25	5.57
			la	3.86-4.12	$4.01 \pm 0.08$	0.14	3.50
			h	1.74-2.00	$1.84 \pm 0.08$	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;  $M \pm SE$ , Mean  $\pm$  Standard Error;  $\sigma$ , standard deviation; V, coefficient of variation.

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

	N	L/lp/la/h	LV	M ± SE	$\sigma$	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;  $\sigma$ , 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

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