

REASSESSMENT OF THE SMALL ‘ARCTOCYONID’ *PROLATIDENS WAUDRUAЕ* FROM THE EARLY PALEOCENE OF BELGIUM, AND ITS PHYLOGENETIC RELATIONSHIPS WITH UNGULATE-LIKE MAMMALS

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ABSTRACT—‘Arctocyonids’ are generally considered as including some of the most primitive ‘ungulates’ from the Paleocene. Although more than 15 genera are known from North America, European members of this order are less common and mainly belong to derived genera such as *Arctocydon*. However, one species of primitive arctocyonid, *Prolatidens waudruae*, was described from the early Paleocene of Hainin, Mons Basin, Belgium. Here we describe new dental positions of this small taxon, including for the first time upper molars and upper fourth premolar. Morphological comparisons confirm the position of *P. waudruae* among primitive ‘ungulates,’ with the closest North American arctocyonids being *Prothryptacodon furens* and *Oxyprimus galadriellae*. *Oxyprimus galadriellae* features slightly more primitive morphological traits than both other species. Apheliscids share several characters with *Prolatidens*, but the latter lacks the apomorphies defining the family. Among ‘arctocyonids,’ *Prolatidens* shares with only *Protungulatum* and *Oxyprimus* the incomplete lingual cingulum at the base of the protocone of M1. *Prolatidens waudruae* is unique among Procreodi in its combination of primitive and derived characters. The cladistic analysis places *P. waudruae* close to the base of the ingroup, indicating that this species is among the most primitive members of the Paleocene ‘ungulates.’ However, the lower nodes of the trees are not well supported and definitive conclusions should await more complete specimens and analysis. Apheliscids are situated relatively far from *Prolatidens*, suggesting that the resemblances between them are better considered as convergences. Based on the morphological comparisons, the arctocyonid from Hainin correlates best with North American Torrejonian taxa.

INTRODUCTION

Primitive ‘ungulates’ are a vast paraphyletic group that includes many different orders (Archibald, 1998). Among these, Procreodi account for one of the most primitive, despite the few relatively derived species it includes. The order Procreodi was originally established by Matthew (1915) in order to group the families Arctocyonidae and Oxyclaenidae. Some subsequent authors suggested that the genera included in Oxyclaenidae should instead form a subfamily of the Arctocyonidae (e.g., Simpson, 1945), whereas others continued to use the classification proposed by Matthew (e.g., McKenna and Bell, 1997). Most recent studies on the genus *Oxyclaenus* place it close to the mesonychids, which should prevent the use of the family name Oxyclaenidae for other Procreodi (Archibald, 1998; Williamson and Carr, 2007).

The family Arctocyonidae sensu lato was usually considered to be divided into three subfamilies (Cifelli, 1983). The subfamily Arctocyoninae group the most derived species that are characterized by very low crowned molars with crenulated enamel, upper molars protocone anteriorly placed, absence of protocone on P3, lower molars trigonids with three transverse crests, and paraconid fused to the metaconid (Cifelli, 1983). Shared characters of the Loxolophinae include the reduction to loss of P1 with concomitant development of diastemata, twinned lower molar entoconid and hypoconulid, and m3 paraconid in a median position (Cifelli, 1983). Finally, the Oxyclaeninae unite all the primitive arctocyonids that lack the apomorphies of the two other subfamilies; some are derived, but each in a different way. This classification mainly follows by Kondrashov and Lucas (2004), with

some changes in Oxyclaeninae. They also consider *Protungulatum* and *Oxyprimus* as Arctocyonidae incertae sedis. Gingerich et al. (1997) included a new subfamily Quettacyoninae in the Arctocyonidae, but later elevated it to the family rank given new material (Gingerich et al., 1998; Gingerich, 1999).

However, recent cladistic analyses do not support the monophyly of arctocyonid subfamilies such as described above (Archibald, 1998; Williamson and Carr, 2007). Apart from the genera *Baioconodon* and *Oxyclaenus* that are referred to basal Cete, Arctocyonidae are considered monophyletic by Archibald (1998), with the Arctocyoninae being the only monophyletic subfamily in that study. Williamson and Carr (2007) also place *Oxyclaenus* close to the mesonychids, and the arctocyonids are no longer considered monophyletic but polyphyletic. A part of the arctocyonids is still considered as monophyletic, allying the genera *Mimotricentes*, *Deuteronodon*, *Chriacus*, *Arctocydon*, and *Loxolophus*. These genera form a clade, but this clade does not include more basal genera that were formerly included within Arctocyonidae. The terms ‘arctocyonids,’ ‘Procreodi,’ ‘condylarths,’ and ‘ungulates’ refer to non-monophyletic groups and are used informally throughout this paper.

European arctocyonids are mainly known from the late Paleocene of Cernay-Berru (MP6) and Walbeck (MP75). Most genera and species present in these localities, namely, *Arctocydon primaevus*, *Arctocydon matthesi*, *Arctocyonides trouessarti*, *Arctocyonides weigelti*, *Arctocyonides arenae*, and *Mentoclaenodon walbeckensis*, are large and display derived characters including very low-crowned, square upper and lower molars and presence of a hypocone (Weigelt, 1960; Russell, 1964). Primitive species are few and relatively uncommon in the European late Paleocene and only represented by two species, *Landenodon lavocati* and *Landenodon phelizoni*. Conversely, in North America primitive Procreodi are more diversified and several genera display more

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primitive morphology, including *Protungulatum*, *Oxyprimus*, and *Prothryptacodon*, each represented by several species. This observation, however, is countered by a strong sampling bias due to the high number of early to middle Paleocene localities found in North America compared with Europe, where only Hainin and Fontllonga are known in that time span (Pelaez-Campomanes et al., 2000).

The early Paleocene locality of Hainin, Mons Basin, Belgium (see situation map in De Bast et al., 2012), has yielded the oldest Cenozoic continental vertebrate fauna of Europe (Folie et al., 2005; De Bast et al., 2012) and was chosen as the earliest reference level of the Mammalian biochronological scale for the European Paleogene (level MP1-5 of Schmidt-Kittler, 1987). The age of the Hainin deposits is generally considered by mammalogists to be early Paleocene (Russell, 1982; McKenna and Bell, 1997; Sigé and Marandat, 1997); based on the stratigraphic data of the area, the age of the deposits that could range between the end of the Danian and the beginning of the Thanetian (Godfriaux and Robaszynski, 1974), the age indicated by large-scale correlations is approximately early Selandian (Steurbaud, 1998). One of the two condylarth species described from Hainin is the very small and primitive arctocyonid *Prolatidens waudruae* Sudre and Russell, 1982, that was originally described based on three lower molars. Based on the relatively few derived characters the molars of *P. waudruae* presented, Sudre and Russell (1982) suggested affinities with Oxyclaeninae, and believed the genus *Oxyprimus* to be the closest relative to *P. waudruae*. In the same paper, Sudre and Russell (1982) described the oldest known lousinid *Monshyus praeivus*, based on upper molars only. In a recent paper, Hooker and Russell (2012) considered *Prolatidens* to be a junior synonym of *Monshyus*, based on the material published in 1982. Here we describe new dental positions, including the first upper teeth, of *P. waudruae*, therefore reestablishing *P. waudruae* as a valid species. We also analyze the phylogenetic relationships of this species among arctocyonids and other basal ungulates. The presence of primitive arctocyonids in Europe from the early Paleocene is important in understanding the evolution and migration patterns of the basal ungulates.

Institutional Abbreviations—**IRSNB**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **PU**, Princeton University, Princeton, New Jersey, U.S.A.; **USNM**, United States National Museum, Washington, D.C., U.S.A.

MATERIALS AND METHODS

The fossil specimens were collected in 1973–1974 from a well. The marlstone sediment has been screen washed using meshes of 0.43 mm after treatment with formic acid and a tricalcic phosphate buffer in order to dissolve the calcareous fraction. We used a scanning electron microscope (SEM) to acquire images of specimens.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Grandorder 'UNGULATA' Linnaeus, 1758

PROLATIDENS WAUDRUA Sudre and Russell, 1982
(Figs. 1, 2, Table 1)

Holotype—IRSNB M1972 (= R1-08), left m1.

Referred Material—IRSNB M2053 (= N2-15), left P4; IRSNB M2054 (= Q2-19), left M1 or M2; IRSNB M2055 (= Q1-16), right M1 or M2; IRSNB M2056 (= O1-05), left dp4; IRSNB M2115 (= MN1.2-03), left m1; IRSNB M2116 (= N2-01), right m1; IRSNB M1973 (= O1-01), left m2; IRSNB M2117 (= N1-05), right m1 or m2.

TABLE 1. Measurements in millimeters of cheek teeth of *Prolatidens waudruae* from the early Paleocene of Hainin, Belgium.

IRSNB no.	Field no.	Position	Length	Width
IRSNB M2053	N2-15	P4	2.56	3.03
IRSNB M2054	Q2-19	M1	2.37	2.9
IRSNB M2055	Q1-16	M1	—	2.96
IRSNB M2056	O1-05	dp4	3.29	1.81
IRSNB M2115	MN1.2-03	m1	2.97	1.59
IRSNB M2116	N2-01	m1	2.85	1.87
IRSNB M2117	N1-05	m1	3.02	1.85
IRSNB M1972	R1-08	m1	3.09	1.85
IRSNB M1973	O1-01	m2	3.40	2.08

The dash denotes dimension that could not be measured.

Emended Diagnosis—Differs from all arctocyonids by narrower lower molars, and smaller size than all arctocyonid species except *Oxyprimus galadriellae*. Lower molars further differ from *Prothryptacodon furens* by the slightly lower crown and more bulbous cuspids of m1 and the absence of a cingulid at the posterior base of the hypoconid. Lower molars differ from *Oxyprimus* by the lower crown and more bulbous cuspids. Lower molars differ from all apheliscids by the presence of a crest rather than a notch between the hypoconulid and entoconid, the proportionally higher trigonid, and the absence of a labial cingulum even in the hypoflexid. Upper molars differ from those of all arctocyonids except the genera *Oxyprimus* and *Protungulatum* by the absence of a lingual cingulum. Upper molars further differ from those of *Princetonina* cf. *P. yalensis* by the less transverse development, the less marked thickening of the hypocone region, and the wider ectocingulum. Upper molars differ from those of apheliscids by the less marked hypocone and more transversally developed stylar shelf. P4 differs from that of *Phenacodaptes sabulosus* by the smaller size (15% shorter), slightly larger metastylar shelf, the presence of faint precingulum and postcingulum, and proportionally less transverse development.

Description

P4—The P4 (Fig. 1A) is relatively massive. The parastyle is well developed and directed anteriorly. There is no preparacrista and no visible trace of metacone. The postparacrista is oriented posteriorly. A very thin cingulum is present at the labial base of the paracone and somewhat broadens on the posterolabial margin of the tooth. The protocone is relatively large for an arctocyonid, reaching about half the size and height of the paracone. There is almost no protofossa. No conules are visible but this could be the result of the wear or a small missing part of the tooth. There are hints of cingula at the anterior and posterior bases of the protocone. The postprotocrista shows heavy wear and seemed rather well developed.

M1—IRSNB M2055 (Fig. 1C) is likely an M1 based on the relatively small size and low transverse development. The specimen is incomplete, lacking half the paracone and the posterior margin of the tooth. The cusps are relatively sharp compared with other arctocyonids. The stylar shelf is more developed than in most arctocyonids. The paracone is higher than the metacone; the paracone and metacone are linked by a rectilinear centrocrista. The postmetacrista is not well marked and positioned posterolabially. The beginning of a paracingulum is visible but its length cannot be estimated due to the broken paracone. The paraconule is well developed but smaller than in many other arctocyonid genera, and displays no postparaconule crest; it is situated at a similar distance from the paracone than the protocone. The metaconule is broken but seems of similar size as the paraconule, and features a short crest that joins the base of the metacone; it is situated

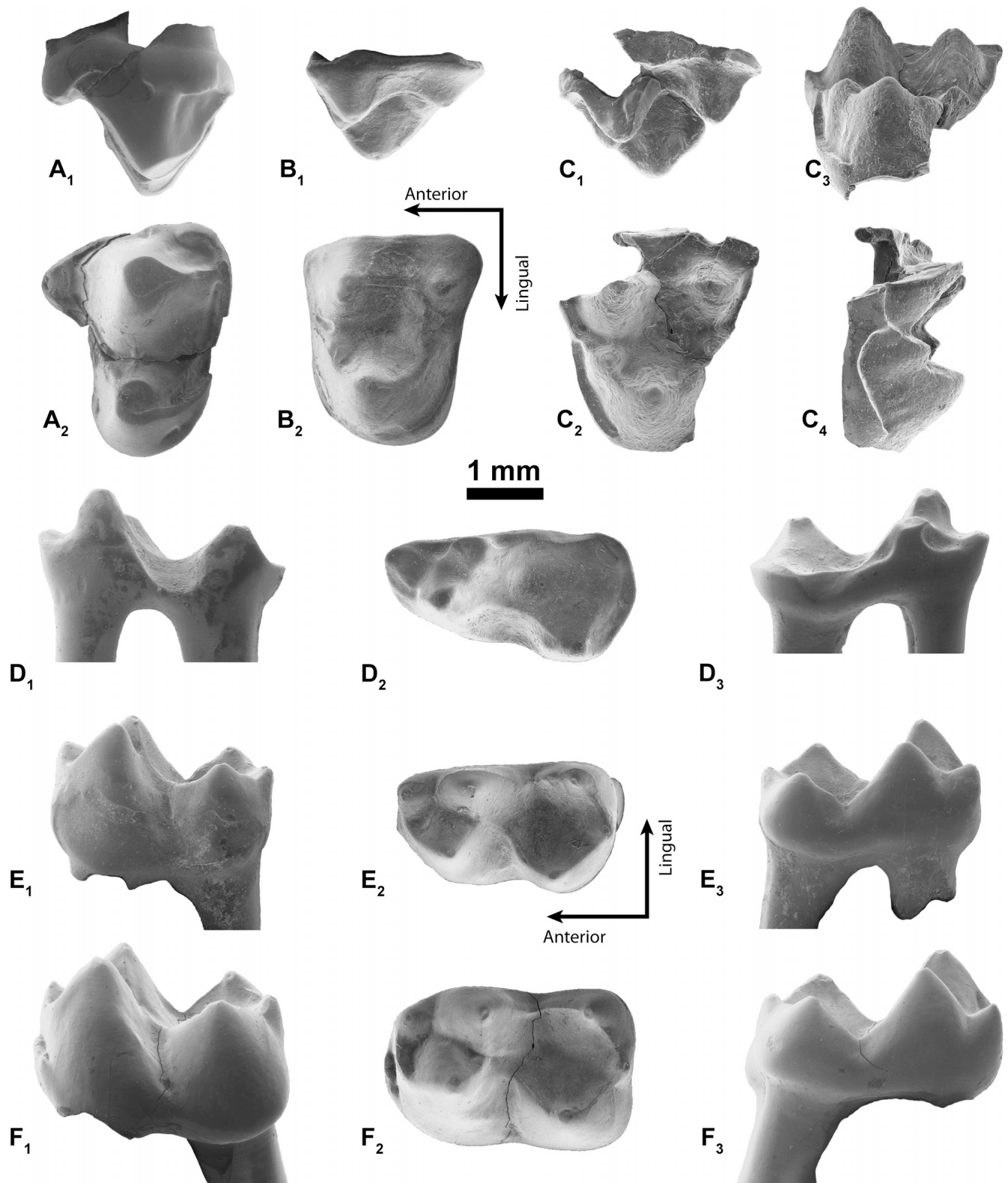


FIGURE 1. The small arctocyonid *Prolatidens waudruae* from the early Paleocene of Hainin, Belgium. **A**, IRSNB M2053 (= N2-15), left P4; **B**, IRSNB M2054 (= Q2-19), left M1 or M2; **C**, IRSNB M2055 (= Q1-16), right M1 or M2; **D**, IRSNB M2056 (= O1-05), left dp4; **E**, IRSNB M1972 (= R1-08), left m1; **F**, IRSNB M1973 (= O1-01), left m2. All in labial (1), occlusal (2), lingual (3), and anterior (4) views.

closer to the metacone than to the protocone, thus more labially than the paracone. The protocone is the largest cusp; it is only slightly displaced anteriorly. A narrow but long precingulum extends at its anterior base. The basal cingulum does not enclose the protocone lingually.

IRSNB M2054 (Fig. 1B) is worn but its size and morphology are compatible with IRSNB M2055 (paracone larger than metacone, long cingula around the protocone base, position of the conules). The outline of the tooth is closer to rectangular than triangular. The hypocone region is not well preserved but the lingual cingulum of the protocone is slightly thickened at the position of the hypocone. There was probably no cuspidate hypocone but rather a slightly enlarged posterolingual cingulum at the place the hypocone would occupy. The preparacrista is directed anteriorly and slightly labially.

dp4—The dp4 (Fig. 1D) has a triangular outline. The cusps are relatively slender, with the same relative height difference between trigonid and talonid as in the molars. The paraconid occupies a very anterior position on the labial margin of the tooth, and projects slightly anteriorly. The protoconid and metaconid are small, not inflated at their base and their tips are close to one another. The talonid is almost twice as wide as the trigonid and slightly longer. The hypoconid is markedly more developed than the hypoconulid and entoconid. The oblique cristid is marked, reaches the posterior wall of the trigonid at the base of the protoconid, and extends on this wall towards the tip of the protoconid. The talonid basin is relatively shallow compared with the molars. The relatively large size of the tooth and especially of the talonid suggests that the p4 was not reduced.

m1—The m1 (Figs. 1F, 2A–C) is relatively narrow and features low and strong cusps with a sharp apex. The crown height difference between the trigonid and the talonid is relatively low in absolute value but higher than in most arctocyonids. The trigonid and talonid have similar lengths. The paraconid is smaller than the protoconid and the metaconid but relatively large for an arctocyonid, and occupies a lingual position. The paracristid curves lingually. The protoconid and metaconid are about the same height. The metaconid is situated posteriorly to the protoconid. The three trigonid cusps are equidistant. There is only a hint of precingulid. The talonid is broader and slightly longer than the trigonid. The talonid basin is relatively deep, especially for an arctocyonid. The hypoconid and entoconid occupy about the same occlusal space, the hypoconid being much higher; the slightly smaller hypoconulid occupies a median position. The crests linking these cusps are straight. The oblique crest is marked, curved, and extends on the posterior wall of the trigonid, reaching the groove between the protoconid and the metaconid. The lingual side of the talonid is low and closed by a crest displaying a small notch.

m2—The m2 (Figs. 1G, 2D, E) is slightly longer and much broader than m1. The trigonid and talonid cusps, and especially the protoconid and hypoconid, have more massive and rounded bases, resulting in a broader outer outline than in m1 but with similar size of the trigonid and talonid basins. There is a small precingulid; the paraconid is less lingually oriented and is linked to the protoconid by a longer and more curved crest.

DISCUSSION

Association of Upper and Lower Teeth

The upper molars described above are referred to *Prolatidens waudruae* based on their relatively large size compared with most taxa from the fauna, their similar occlusal pattern (relatively low crown, lack of large hypocone consistent with the morphology of the trigonid), and their relative abundance. They correspond better in size and morphology to the lower molars of *P. waudruae*

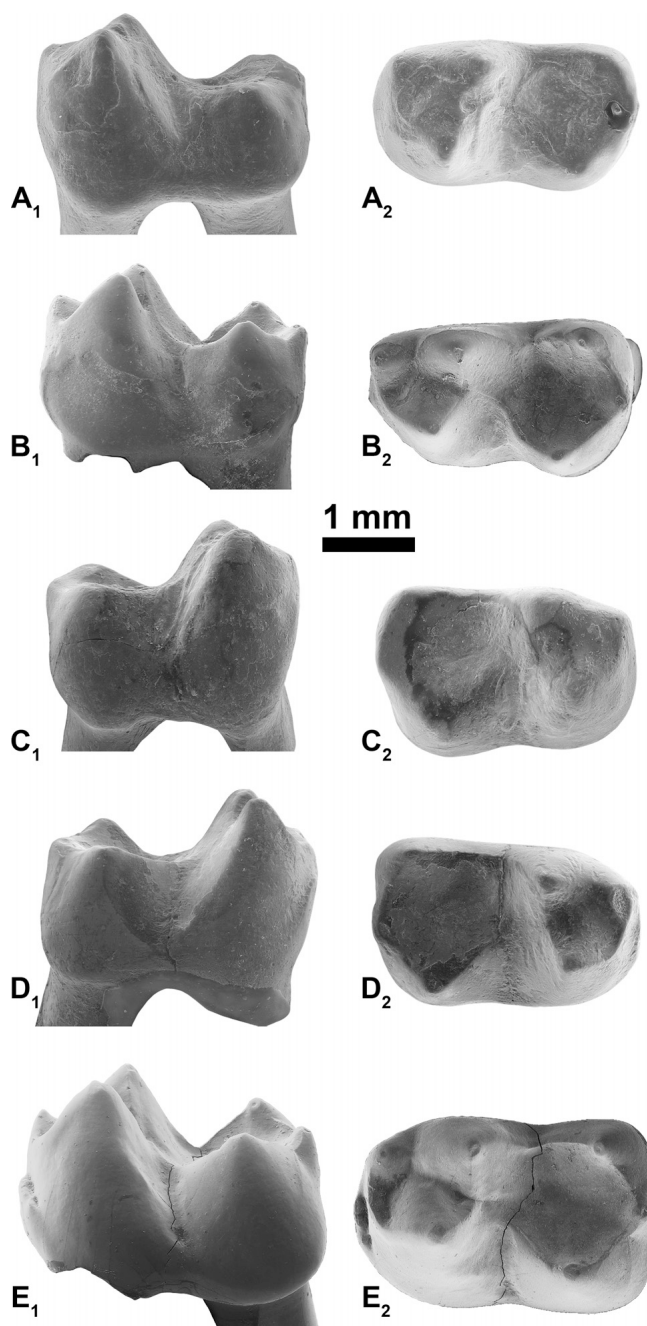


FIGURE 2. Morphological variation in the lower molars of *Prolatidens waudruae*. **A**, IRSNB M2115 (= MN1.2-03), left m1; **B**, IRSNB M1972 (= R1-08), left m1; **C**, IRSNB M2116 (= N2-01), right m1; **D**, IRSNB M2117 (= N1-05), right m1 or m2; **E**, IRSNB M1973 (= O1-01), left m2.

than the upper molars of *Monshyus praeivius* (see Hooker and Russell, 2012).

Morphological Comparisons

Primitive European condylarths are scarce, mainly due to the poor fossil record earlier than the late Paleocene. However, two genera with relatively bulbous lower molars have been described from the Late Cretaceous of Spain and France: *Lainodon* and *Labes* (Pol et al., 1992; Gheerbrant and Astibia, 1994, 1999). Only

lower teeth are known for these genera, the comparisons with *Prolatidens* are therefore restricted. *Prolatidens waudruae* shares with these genera the relatively low crown and bulbous cuspids exhibiting strong wear, the narrowness of the lower molars, and the unusually small size for the type of tooth compared with most North American species. *Prolatidens* differs from both genera by the lower trigonid, more massive cuspids at the base, the more oblique cristid, the more curved paracristid, and the precingulid crest not extending to the tip of the paraconid (more marked in *Lainodon*). The median hypoconulid of *P. waudruae* is shared with *Labes* but not with *Lainodon* that displays a close approximation of the hypoconulid and entoconid. The dp4 of *P. waudruae* presents a highly unusual morphology compared with the few figured dp4s of North American condylarths (e.g., Matthew, 1937; West, 1971), with an enlarged and elongated talonid rather than trigonid. The morphology of the dp4 is remarkably similar to the tooth interpreted as the dp4 of *Lainodon*, n. sp. (Gheerbrant and Astibia, 1999); the shared characters include the development in width and length of the talonid, the low and very anterior paraconid, and the metaconid positioned more posteriorly relative to the protoconid. The trigonid is narrower and the hypoconid higher in *P. waudruae* than in *Lainodon*.

Wible et al. (2007, 2009), followed by Archibald and Averianov (2012), proposed including *Lainodon* within the Cretaceous Zhelestidae. Cretaceous zhelestids differ from other contemporaneous groups by the lower cusps of upper molars, the longer lingual slope of the protocone, the development of anterior and posterior cingula at the base of the protocone, the reduction of the styral shelf, the equal size of paracone and metacone, the labiolingual expansion of the talonid, and the lesser height difference between the trigonid and talonid (Cifelli, 1983; Nessov et al., 1998). All these characters are visible in *Prolatidens waudruae*. Primitive ungulates of the Paleocene differ from these 'zhelestids' by the metacringulum formed by the postmetaconule crista continuing onto the metastylar lobe, the number of premolars reduced to four or less, the reduced parastylar region with only one cusp, and the lesser development of the postparaconule and premetaconule crista (Nessov et al., 1998). Only the first and fourth of these characters can be assessed with certainty in *P. waudruae*. The metacringulum is indeed formed by the postmetaconule crista continuing onto the metastylar lobe. The internal crests of the conules are weak but visible, not quite as developed as in *Aspanlestes aptap* (Coniacian, Byssesky Formation, Dzharakuduk, Uzbekistan) for instance, but similar to several arctocyonid genera, although many more-derived genera of arctocyonids or other families of condylarths do not feature any internal crests. The number of premolars in *P. waudruae* cannot be ascertained but is likely to be four, because no example of a placental with five premolars is known from the Paleocene. These characters indicate that *P. waudruae* should be classified among one of the many Paleocene 'ungulate'-like families and not among 'zhelestids.'

Luo (1991) suggested that the length of the lingual slope of the protocone is a derived character of arctocyonids when compared with other more primitive Paleocene and Cretaceous taxa. The base of the protocone of all arctocyonids is indeed developed lingually. *Prolatidens waudruae* displays a relatively long protocone lingual slope, not as long as in *Protungulatum donnae* (Puerican, Hell Creek-Tullock Formation, Garfield County, Montana, U.S.A.) or *Arctocyon primaevus* (Thanetian, MP6, Châlons-sur-Vesles Formation, Paris Basin, France), but longer than other arctocyonids such as *Chriacus pelvidens* (Torrejonian, Nacimiento Formation, San Juan Basin, New Mexico, U.S.A.) and *Thryptacodon antiquus* (Wasatchian, Willwood Formation, Clark's Fork Basin, Wyoming, U.S.A.). This character, although consistent within single species, seems highly variable at generic and familial levels among all primitive condylarths, with primitive genera displaying long (*P. donnae*) or short (*C. pelvidens*) lingual slopes, whereas derived taxa show the same pattern with genera

with long (*A. primaevus*) or short (*T. antiquus*) lingual slopes. It is therefore difficult to determine whether *Prolatidens waudruae* should be placed among arctocyonids based on this character. In the same paper, Luo (1991) states that the trigonid of primitive condylarths is of larger proportions than in contemporaneous taxa. *Prolatidens waudruae* trigonids are relatively well developed, but not as much as in *Protungulatum donnae*. Again, several more-derived taxa show significant enlargement of the talonid, thus rendering comparisons difficult with arctocyonids as a whole.

Prolatidens waudruae differs from all Mesonychidae and Trisodontidae in that the enamel is not crenulated, lower molars display no labial cingulum, the hypoconulid is not reduced, and the talonid basin is enclosed lingually. *P. waudruae* differs from Hyposodontidae by the premolariform P4 and presumably also p4, the lingual position and individualization of the molar paraconids, and the lack of hypocone. *P. waudruae* differs from all Peripitychidae by the lack of lingual extension of the protocone coupled with the labial shift of the protocone, and the lack of bulbous premolars. Mioclaenidae have lingually open talonid basins, slightly to extremely inflated premolars, and molars simplified by the loss of cusps (Archibald, 1998). M3/m3 are not known in *P. waudruae*, but molars display a very primitive morphology, with all cusps well formed, and P4 is not inflated to any extent. Phenacodontidae are characterized by inflated molar cusps, the presence of a well-developed hypocone, a metacone on P4, and a metaconid as large as the protoconid on p4 (Thewissen, 1990). None of these characters is observed in *P. waudruae*, and additional differences from phenacodontids include the large size of the paraconid, the talonid basin enclosed lingually, the significantly narrower lower molars, and the absence of labial cingulid on lower molars.

Prolatidens waudruae shares with Apheliscidae the relatively narrow, but bulbous, lower molars, m2 larger than m1, low position of the paraconid, and median hypoconulid, considered synapomorphies of the family by Zack et al. (2005). The simple morphology of P4 with a large protocone, no metacone, no preparacrista, no basin, the anteriorly projecting parastyle, the shape of the three crests running from the protocone, and the large size relative to M1 are similar in *P. waudruae* and Apheliscidae. The resemblance is particularly marked with *Phenacodaptes sabulosus* (Late Tiffanian, Fort Union Formation, Bighorn Basin, Wyoming, U.S.A.). However, *P. waudruae* differs from all apheliscids by the presence of a crest connecting the hypoconulid to the entoconid instead of a notch, and not well-developed hypocone, both synapomorphies of the family (Zack et al., 2005). Moreover, the styral shelf of the upper molars is more developed than in any species of apheliscid, the postparacrista is less marked, and the lower molars paraconids are situated close to the lingual margin of the teeth. *Phenacodaptes* further differs from *Prolatidens* by the anteroposterior orientation of the preparacrista and postmetacrista, the larger conules, and the interrupted centrocrista (this last character is considered a synapomorphy of the Apheliscinae by Zack et al., 2005).

Prolatidens waudruae lacks all the synapomorphies of Arctocyoninae or Loxolophinae proposed by Cifelli (1983). *P. waudruae* presents a completely different morphology than the Arctocyon-like European arctocyonids by its very small size and primitive morphology. *Landenodon woutersi* (earliest Ypresian, MP7, Tienen Formation, Dormaal, Belgium) is closer to *P. waudruae*, but still presents derived characters that are absent in *P. waudruae*. Only the most primitive genera of North American arctocyonids compare relatively well with *P. waudruae*. The primitive morphology of most 'Oxyclaeninae' (sensu Cifelli 1983) is generally closer to *P. waudruae*. Several genera display a lower molar morphology close to that of *P. waudruae*, including *Protungulatum*, *Oxyprimus*, *Princetonia*, *Prothryptacodon*, etc. There are minor differences between the different genera, and the closest

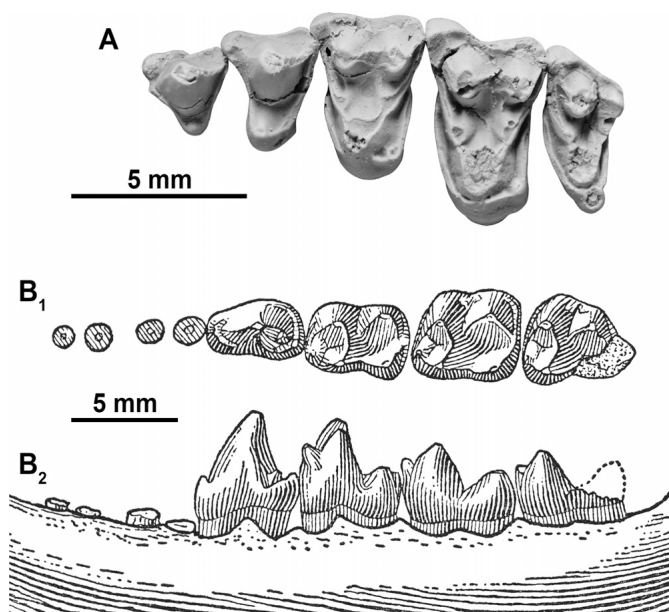


FIGURE 3. The arctocyonids *Oxyprimus galadriellae* from the Puercan of Mantua Quarry, Wyoming, U.S.A., and *Prothryptacodon furens* from the Torrejonian of Gidley Quarry, Montana, U.S.A. **A**, *O. galadriellae*, cast of PU16866 (type specimen): left maxillary with P3–M3, in occlusal view. **B**, *P. furens*, USNM 92604 (type specimen): right dentary with p4–m1, in occlusal (B₁) and lingual (B₂) views. **B** modified from Simpson (1937).

lower molar morphology is observed in *Prothryptacodon furens* (Torrejonian, Lebo Formation, Crazy Mountain Area, Montana, U.S.A.; Fig. 3B) and *Oxyprimus galadriellae* (Puercan, Fort Union Formation, Bighorn Basin, Wyoming, U.S.A.). The m1 of *Prolatidens waudruae* has lower and more bulbous cusps, and a more elongated trigonid than that of *Prothryptacodon* spp. and *Oxyprimus* spp. *Oxyprimus* has well-developed labial cingula that are less developed on *Prothryptacodon* and absent on *Prolatidens waudruae*. The most striking feature of *P. waudruae* that is not shared with any arctocyonid species is the combination of low bulbous cusps with a narrow shape of the lower molars. The broader m2 than m1 is a common feature in arctocyonids, and particularly in primitive species. Upper molars of *P. waudruae* compare best with those of *Princetonina* cf. *P. yalensis* (Tiffanian, Fort Union Formation, Bighorn Basin, Wyoming, U.S.A.) figured by Secord (2008) and of *O. galadriellae* (Fig. 3A). *Prolatidens waudruae* is less transversely developed than both species, has a more developed ectocingulum, and has less marked thickening of the hypocone region on the postcingulum. The lingual cingulum at the base of the protocone is not complete in *O. galadriellae* and *P. waudruae*, but well developed on *Princetonina* cf. *P. yalensis*. This last feature is observed consistently among arctocyonids only in the genera *Protungulatum* and *Oxyprimus*; some genera are polymorphic for this character, either between specimens (*Loxolophus*, *Baioconodon*) or between teeth of a single specimen (*Mimotricentes*, *Colpoclaenus*, *Loxolophus*). Absence of an enclosed lingual cingulum is considered primitive because it is not present in more basal groups such as zhelestids, kennalestids, etc. Upper molars of *Prothryptacodon furens* are unfortunately not described.

Prolatidens waudruae differs from most arctocyonids in several characters. The lower molars are relatively narrow. Some arctocyonids have narrow lower molars but in this case display high and pointed cusps, which can be considered as primitive mor-

phology. *P. waudruae*, contrary to other arctocyonids and most condylarths, combines narrow lower molars with low and bulbous cusps and relatively long trigonids. In parallel, the transverse development of upper molars is also unusually low when compared with other primitive arctocyonids. Upper molars lack a complete lingual cingulum around the base of the protocone. The complete lingual cingulum at the base of the protocone is observed among condylarths only in arctocyonids and the Acreodi *Mondegodon eutrigonus* (earliest Ypresian, MP7, Silveirinha, Portugal) (Tabuce et al., 2011) and was considered a synapomorphy of Arctocyonidae by Prothero et al. (1988). The only genera considered as arctocyonids that do not feature a complete lingual cingulum are *Protungulatum* and *Oxyprimus*, although both genera are extremely primitive and have been classified in other ungulate families or as Arctocyonidae incertae sedis (Archibald, 1998; Kondrashov and Lucas, 2004). Lower molars of *P. waudruae* do not feature any labial cingulum, which is typically the primitive condition for ungulates. Another unusual feature is the relative size of the paracone and metacone. In *P. waudruae*, the paracone is markedly higher and larger than the metacone, whereas the cusps remain well separated to their base. Similar development of the paracone and metacone are observed in most stem eutherians, including zhelestids, kennalestids, zalambdalestids, and leptictids, and can thus be considered primitive among basal eutherians. Some mesonychid genera display a larger paracone than metacone, but in that case the two cusps are partially merged.

Cladistic Analyses

We conducted a large-scale cladistic analysis in order to confirm the phylogenetic position of *Prolatidens waudruae* at the base of the ungulates. We therefore added *P. waudruae* to the matrix constructed by Wible et al. (2009) (see Appendix 1). The analysis was performed using the heuristic algorithm of TNT 1.1 (Goloboff et al., 2008), multistate characters were considered unordered. Twenty-five most parsimonious trees were retained with a length of 2302 steps, i.e., eight steps longer than the initial trees obtained by Wible et al. (2009). The topology of the strict consensus (Fig. 4A) is identical to that of the consensus obtained by Wible et al. (2009), with *P. waudruae* appearing as sister taxon to the clade (*Protungulatum* + *Oxyprimus*).

A second more detailed cladistic analysis was performed in order to place *Prolatidens waudruae* among the various arctocyonids and other Paleocene condylarths. The matrix initially constructed by Williamson and Carr (2007) was adapted for this analysis. The new matrix (see Appendix 1) includes arctocyonids, apheliscids, mesonychids, triisodontids, hyopsodontids, phenacodontids, mioclaenids, and peripitychids. A few characters used by Williamson and Carr were deleted because they were uninformative due to the absence of certain taxa, others have been changed, and several characters have been added to the matrix, partly from Ladevèze et al. (2010) and Wible et al. (2009). In total, 77 characters were coded for 34 taxa (see Appendix 2 for character definitions). Because of the primitive morphology of the taxon of interest and because the closest sister group to Paleocene condylarths is unclear, a relatively wide set of outgroups were chosen among Late Cretaceous taxa: *Aspanlestes aptap* Nessov, 1985; *Parazhelestes robustus* Nessov, 1993 (Coniacian, Byssekty Formation, Dzharakuduk, Uzbekistan); *Kennalestes gobiensis* Kielan-Jaworowska, 1968 (Campanian, Djadokhta Formation, Bayn Dzak, Mongolia); *Cimolestes incisus* Marsh, 1889 (Maastrichtian, Lance Formation, Wyoming, U.S.A.); *Gypsonictops hypoconus* Simpson, 1927 (Maastrichtian, Lance Formation, Wyoming, U.S.A.); and *Kulbeckia kulbecke* Archibald and Averianov, 2003 (Coniacian, Byssekty Formation, Dzharakuduk, Uzbekistan). All characters were considered unordered. Multistate characters were coded and treated as



FIGURE 4. **A**, the strict consensus of the 25 most parsimonious trees obtained from the cladistic analysis of the matrix from Wible et al. (2009) with addition of *Prolatidens waudruae*. **B**, the strict consensus of the 21 most parsimonious trees obtained from the cladistic analysis of the matrix in Appendix 1. The lower part of the ingroup is not resolved. **C**, the strict consensus of eight most parsimonious cladograms obtained from the cladistic analysis of the matrix in Appendix 1, after pruning the most unstable taxon *Prothryptacodon furens*. *Prolatidens waudruae* branches in the lower part of the ingroup, before the separation of the various 'condylarths' families included in the analysis. For each node, the list of the synapomorphies is given, each synapomorphy being represented by a point (black for unambiguous synapomorphy and white for homoplasies) accompanied by the character number above and character state below. Bremer decay indices above 2 are indicated at the right of their respective nodes.

polymorphisms. Morphology was assessed through a review of the literature (Matthew, 1897, 1901, 1915, 1918, 1937; Matthew and Granger, 1915; Jepsen, 1930; Simpson, 1935, 1937; Russell, 1964; Sloan and Van Valen, 1965; Gazin, 1968; Kielan-Jaworowska, 1968; Lillegraven, 1969; Van Valen, 1978; Godinot, 1980; Archibald, 1982; Nessov, 1987; Ting and Li, 1987; Gingerich, 1989; Thewissen, 1990; Luo, 1991; Lofgren, 1995; Nessov et al., 1998; Archibald and Averianov, 2003, 2005, 2012; Williamson and Carr, 2007; Secord, 2008), as well as through observation of fossils and casts. We checked the entire matrix from Williamson and Carr and made very few changes in the previously coded character states. Taxa with five premolars were coded with p5 equivalent to p4.

The analysis, conducted under the random addition sequence mode of TNT 1.1 (Goloboff et al., 2008) with 1000 repetitions, yielded 21 equally most parsimonious cladograms of 362 steps each. The strict consensus tree (Fig. 4B) had a consistency index (CI) = 0.289 and a retention index (RI) = 0.527. The tree is partly unresolved, especially at the base of the ingroup. We therefore calculated the taxon instability index using Mesquite (Maddison and Maddison, 2010), which revealed that *Prothryptacodon* was the most unstable taxon. This instability is likely due to the lack of described upper dentition for *Prothryptacodon*, resulting in a low number of informative characters. The analysis was therefore repeated after the pruning of *Prothryptacodon*, and yielded eight most parsimonious cladograms of 357 steps. The strict consensus tree (Fig. 4C) was much more resolved and had better values of CI = 0.307 and RI = 0.561.

Apheliscids, mesonychids, mioclaenids, phenacodontids, and peritrichids appear monophyletic on the tree, whereas triisodontids appear paraphyletic and Procreodi and hyposodontids are polyphyletic. *Prolatidens waudruae* diverges relatively close to the base of the ingroup, with only *Oxyprimus*, *Mimatuta*, *Maiorana*, and *Protungulatum* in a more basal position.

Arctocyonids are scattered along the tree, concentrated in three places. Some branch very close to the base of the ingroup (*Oxyprimus*, *Protungulatum*), roughly corresponding to the ‘Oxycloeninae’ (sensu Cifelli, 1983). Three more-derived species (*Landenodon*, *Arctocyon*, and *Thryptacodon*) are included in a clade situated as sister group of the clade mesonychids + triisodontids, and could correspond to Arctocyoninae (sensu Cifelli, 1983). Lastly, two clades (*Mimotricentes* + *Loxolophus* and *Chriacus* + *Princetonina*) are positioned at a tritomy with as sister group the clade *Diacodexis* + apheliscids + arctocyonines + triisodontids + mesonychids, and is similar to the concept of ‘Loxolophinae’ (sensu Cifelli, 1983). Arctocyonids have been used as a wastebasket for basal ‘condylarths,’ and the primitive members of the family can be interpreted as the stock of primitive ungulates from which more-derived groups evolved.

Apheliscids are grouped in a clade nested between the clade *Hyopsodus* + phenacodontids and the clade arctocyonines + triisodontids + mesonychids, relatively far from the node where *Prolatidens* branches. Following these results, the resemblance between *Prolatidens* and the apheliscids are best considered as convergences.

Individual observation of the most parsimonious trees obtained from the first analysis including *Prothryptacodon* indicates that this taxon occupies three different positions in the tree: as sister taxon of *Protungulatum*; as sister taxon of a clade *Diacodexis* + mioclaenids; or branching just terminally to *Prolatidens*. We attribute the unstable placement of *Prothryptacodon furens* to missing data owing to the lack of described upper molars for this taxon.

Bremer decay indices (Fig. 4C) reveal that few of the lower nodes of the tree offer support, save from the ingroup. Phenacodontids and mesonychids show very strong support (Bremer index over 5). The clades *Mimotricentes* + *Loxolophus*, *Hyopsodus* + phenacodontids, *Thryptacodon* + *Arctocyon*, and tri-

isodontids + mesonychids offer strong support (Bremer index over 3). With the notable exception of ‘Arctocyonidae’ and hyposodontids, the ‘condylarth’ families are therefore relatively well supported, but the phylogenetic relationships between those families are less clear.

In conclusion, the cladistic analysis delivers interesting results that should be interpreted carefully due to the instability of most low nodes of the tree. More studies on primitive ungulates and thorough investigation of the informative characters on the whole skeleton and not restricted to tooth morphology seem vital to understanding the early evolution and resolving the phylogeny of primitive ungulates.

CONCLUSION

From morphological comparisons with European and North American condylarths, *Prolatidens waudruae* is the oldest and most primitive ‘arctocyonid’ of Europe, and surely among the most primitive known. *Prolatidens waudruae* displays several typically primitive characters that suggest that its position among ungulates is close to the base. These plesiomorphies include the lack of labial cingulum on lower molars, the absence of complete lingual cingulum on upper molars, the small size or even absence of hypocone, the narrowness of lower molars, the presence of faint postparacone and premetacone cristae, the taller paracone than metacone, and the posterolabial orientation of the postmetacrista. Its morphology best compares with the North American genera *Prothryptacodon* from the Torrejonian and *Oxyprimus* from the Puercan. *Oxyprimus* seems morphologically more primitive than *Prothryptacodon* and *Prolatidens*; the absence of described upper molars of *Prothryptacodon* restricts the comparison with the two other taxa. The resemblance of *Prolatidens* with *Prothryptacodon* and the slightly more derived aspect than *Oxyprimus* suggests that the Hainin deposits may correlate best with the North American Torrejonian, corresponding to the end of early Paleocene and beginning of middle Paleocene. The cladistic analysis places *Prolatidens waudruae* close to the base of the tree, suggesting that it represents one of the most primitive ungulates. However, *P. waudruae* features a combination of primitive and some derived characters that sets it apart from all American species, indicating a split between the primitive ungulates of Europe and North America before the age of Hainin, around the Cretaceous–Paleogene boundary. The cladistic analysis also highlights the need for more material, and thorough comparisons and study of evolutionarily meaningful characters among primitive ungulates, in order to better resolve their phylogeny.

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APPENDIX 1. Character-taxon matrix used for the phylogenetic analysis. Symbols used for polymorphic states: **A**, (01); **B**, (02); **C**, (12); **D**, (23).

	10	20	30	40
<i>Aspanlestes aptap</i>	0110001010	0111000001	1011100220	-0-00220?0
<i>Parazhelestes</i> spp.	001000C000	0010000001	1011100220	-0-1022000
<i>Cimolestes</i> spp.	11110100A0	0100000000	0120000220	-0-0100001
<i>Kennalestes gobiensis</i>	1011010010	1111000001	0011000120	-0-1022000
<i>Kulbeckia kulbecke</i>	1001010010	1000000001	0012010110	-0-0000000
<i>Gypsonyctops</i> spp.	A?02112010	1111100001	0012000220	-100022000
<i>Protungulatum donnae</i>	1?01010001	1111000001	0002110110	01A0022001
<i>Hyopsodus paulus</i>	1102010000	1111001111	100111A220	1120023001
<i>Litomylos dissentaneus</i>	1?????????	?????01111	0002110120	111002200?
<i>Oxyprimus</i> spp.	1?01010001	1111000001	0002110110	01A002200?
<i>Hapalodectes hetangensis</i>	11????????	???????1112	212011000-	-1201B2011
<i>Dissacus navajovius</i>	1112112110	1000011112	212001000-	-0-0112011
<i>Eoconodon coryphaeus</i>	1111010001	0101011111	1100110111	0100123001
<i>Goniocodon levisanus</i>	1011010001	1101011111	1101110220	0100123011
<i>Triisodon quivirensis</i>	1?11010101	1101011111	1111110111	00-0123001
<i>Oxyclaenus cuspidatus</i>	1?11010111	111101A101	1101110110	0100123A1?
<i>Mimatuta minuial</i>	1?02010000	1111000001	0003010110	0100022001
<i>Maiorana noctiluca</i>	1102010000	1111000001	0003110110	010002200?
<i>Protoselene opisthacus</i>	1?01011000	1012001111	0002111120	111112300?
<i>Litaletes disjunctus</i>	1101011000	1111001111	0002110220	0101023001
<i>Tetraclaenodon puercensis</i>	1102212000	1112111101	100111A220	1121123001
<i>Ectocion osbornianus</i>	1002212000	1112111111	0011111220	0121123001
<i>Chriacus pelvidens</i>	11010101A0	1112001101	0001110220	0100023101
<i>Loxolophus hyattianus</i>	1101A10001	0111011101	1001110220	01A0023A01
<i>Mimotricentes subtrigonus</i>	2-01010001	1111011111	1000110220	01A0023A02
<i>Arctocyon primaevus</i>	C1A0010001	1112011111	1002110220	112012311C
<i>Landenodon woutersi</i>	1110010011	1112001111	1000110220	0100123101
<i>Princetonina yalensis</i>	1?0010100	1112001101	0001110220	010002310?
<i>Prolatidens waudruae</i>	?????00000	010200?01	?01211?120	010??230??
<i>Prothryptacodon furens</i>	1?????????	?????0?0??	???????????	???????????
<i>Thryptacodon antiquus</i>	1?10010001	1112001111	1001110220	11C0123111
<i>Diacodexis</i>	1111010000	1112011111	0002110110	00-0023011
<i>Apheliscus</i> spp.	1?10000100	0012001111	2001110220	010002301?
<i>Phenacodaptes sabulosus</i>	1?????0100	0102001111	1002110220	0110023001

	50	60	70	77
<i>Aspanlestes aptap</i>	0?00000111	1110000000	0110010120	0011020
<i>Parazhelestes spp.</i>	0000000001	110A000000	0210010221	0011020
<i>Cimolestes spp.</i>	0000000013	1111000010	00C0000011	0111001
<i>Kennalestes gobiensis</i>	0000000003	1110000010	0110001111	0111020
<i>Kulbeckia kulbecke</i>	0?????0001	0011000000	0210010121	1011020
<i>Gypsonyctops spp.</i>	00AC010000	00111001A0	0210010121	1311020
<i>Protungulatum donnae</i>	001000000C	1101000000	0110010110	0111021
<i>Hyopsodus paulus</i>	0000000000	1001001000	02C0020110	1300020
<i>Litomylus dissentaneus</i>	0010000001	1011000100	0210010210	12100B1
<i>Oxyprimus spp.</i>	0?10000001	0011000000	0010010111	1100121
<i>Hapalodectes hetangensis</i>	11?????1?13	1110210121	100110200-	-322011
<i>Dissacus navajovius</i>	0010101003	1101210021	100110200-	-322011
<i>Eoconodon coryphaeus</i>	0000001103	1011010101	1020010201	1111101
<i>Goniacodon levisanus</i>	00110?1113	101?000101	1020011111	1121001
<i>Triisodon quivirensis</i>	0100001113	1011010011	1020011111	1121101
<i>Oxyclaenus cuspidatus</i>	10?????0?13	1111000101	0020001200	1A21001
<i>Mimatuta minuial</i>	001A000001	0011000000	0010010000	0100121
<i>Maiorana noctiluca</i>	00??0?0001	0011000000	0020010110	011?101
<i>Protoselene opisthacus</i>	001000000D	1111A00000	0110020211	1300021
<i>Litalates disjunctus</i>	0010000000	0001000100	0210020211	1300021
<i>Tetraclaenodon puercensis</i>	0010010000	0011000000	01C0020111	13100BA
<i>Ectocion osbornianus</i>	0000010000	0011001000	0120020111	1310001
<i>Chriacus pelvidens</i>	00000A0001	10A1000100	0A20010C21	1200A01
<i>Loxolophus hyattianus</i>	1010000001	1001000000	0AC0020221	0001021
<i>Mimotricentes subtrigonus</i>	00000000AC	0011A0A000	0120020221	0100001
<i>Arctocyon primaevus</i>	11000001A3	1111101100	0111223211	1010001
<i>Landenodon woutersi</i>	A000000002	1101001100	0020010111	0021001
<i>Princetonina yalensis</i>	0000000002	1011000000	0120010221	1210001
<i>Prolatidens waudruae</i>	???????????	????000000	0010011210	02??020
<i>Prothryptacodon furens</i>	0??????0?13	1101000100	0110010210	0010021
<i>Thryptacodon antiquus</i>	1000000012	110?100100	0020010221	10100B1
<i>Diacodexis</i>	0010000003	1111000000	01C0020211	1000021
<i>Apheliscus spp.</i>	0000001213	0011100110	1110020211	1201021
<i>Phenacodaptes sabulosus</i>	0010001213	1011101100	1110020211	1211021

[illegible]

APPENDIX 2. List of characters and definition of character states used in the cladistic analysis. Asterisks indicate modified characters. All characters are treated unordered.

Upper Premolars

- (1) Premolar number: five, including retained dP3 (0); four (1); three (2) (Wible et al., 2009:character 29*).
- (2) P1 roots: two (0); one (1) [taxa without first upper premolar are scored inapplicable] (Wible et al., 2009:character 33*).
- (3) P3 width: length approximately equals width (0); length exceeds width (1) (Williamson and Carr, 2007:character 6*).
- (4) P3 protocone: absent (0); small lingual bulge (1); with an enlarged basin (2) (Wible et al., 2009:character 36).
- (5) P3 metacone: absent (0); crest-like (1); present as a distinct cusp (2).
- (6) P3 roots: two (0); three (1); one (2) (Wible et al., 2009:character 39).
- (7) P4 metacone: absent (0); crest-like (1); present as distinct cusp (2) (Williamson and Carr, 2007:character 9*).
- (8) P4 premolar pre- and postprotocone crests: extend labially beyond lingual base of paracone (0); extend labially only to base of metacone and terminate at a mesiodistally oriented groove (1) (Williamson and Carr, 2007:character 11).
- (9) P4 parastylar lobe: broadly rounded mesially (0); labiolingually constricted so that lingual and labial borders are subparallel (1) (Williamson and Carr, 2007:character 12).
- (10) P4 protocone size: equally large or larger than half the size of the paracone (0); smaller than half the size of the paracone (1).
- (11) Preparacrista on P4: absent (0); present (1).
- (12) Labial cingulum on P4: absent (0); present (1).
- (13) P4 precingulum: absent (0); present (1) (Wible et al., 2009:character 43).
- (14) P4 postcingulum: absent (0); present, not reaching the labial margin of the tooth (1); present, reaching the labial margin of the tooth (2) (Wible et al., 2009:character 44*).
- (15) P4 paraconule: absent (0); present (1).
- (16) Enamel texture: smooth (0); crenulated (1) (Williamson and Carr, 2007:character 13*).
- (17) M2 parastylar cusps: multiple (0); single cusp mesial to paracone (1) (Williamson and Carr, 2007:character 14).
- (18) M2 preparacrista: extends labially to labial stylocone (0); extends mesially to cone on precingulum (parastylocone) (1) (Williamson and Carr, 2007:character 15).
- (19) M2 postmetacrista: extends labially (0); extends distally (1).
- (20) Size (labiolingual width) of M2 labial stylar shelf at maximum: more than 25% (0); less than 25% (1); absent (2) (Wible et al., 2009:character 65*).
- (21) M1 shape: transverse with an M1 mesiodistal length/mesial labiolingual width less than 0.85 (0); approaching square (M1 mesiodistal length/mesial labiolingual width reduced relative to length is greater than 0.85 and less than 1.0) (1); square (M1 mesiodistal length/mesial labiolingual width is greater than 1.0) (2) (Williamson and Carr, 2007:character 19).
- (22) M1–3 paracone and metacone: separated but connected by centrocrista (0); close so that bases merge (1) (Williamson and Carr, 2007:character 20*).
- (23) M1–2 size of paracone relative to metacone: subequal (0); paracone somewhat larger (1); paracone twice as large (2) (Williamson and Carr, 2007:character 22).
- (24) Degree of labial shift of protocone (distance from protocone apex to lingual border vs. total tooth width, in%): no labial shift (10–20%) (0); moderate labial shift (21–30%) (1); substantial labial shift (30–45%) (2); very strong labial shift (>45%) (3) (Wible et al., 2009:character 95*).
- (25) Protocone anteroposterior expansion: none, subequal to paracone (0); expanded, larger than paracone (1) (Wible et al., 2009:character 93).
- (26) M1–3, postmetaconule crista: forms metacingulum (0); metacingulum formed by the postmetaconule crista continuing onto the metastylar lobe (1) (Nessov et al., 1998:table 3, character 4).
- (27) M1–3 mesostyle: absent (0); present (1) (Williamson and Carr, 2007:character 26).
- (28) M1–2 paraconules: weak or absent (0); prominent, closer to protocone (1); prominent, midway or closer to paracone (2) (Wible et al., 2009:character 88).
- (29) M1–2 metaconules: weak or absent (0); prominent, closer to protocone (1); prominent, midway or closer to metacone (2) (Wible et al., 2009:character 89).
- (30) M2 metaconular region: bears single metaconule (0); bears twin cusps positioned on postprotocrista (1) [taxa without metaconule are scored inapplicable] (Williamson and Carr, 2007:character 30*).
- (31) M1 metaconule: smaller than metacone (and hypocone) (0); similarly sized (1) [taxa without metaconule are scored inapplicable].
- (32) M1–2 hypocone: absent (0); present (1) (Williamson and Carr, 2007:character 31*).
- (33) M2 hypocone shape: elongated linguolabially thickening of the postcingula, sometimes with multiple swellings (0); forms a distinct circular cusp, lower than protocone (1); forms a distinct circular cusp, subequal to protocone (2) [taxa without hypocone are scored inapplicable] (Williamson and Carr, 2007:character 32*).
- (34) M1–2 relative size: M2 is larger than M1 (0); M1 is subequal or larger than M2 (1) (Williamson and Carr, 2007:character 33).
- (35) M1–3 relative size: M3 is not reduced but is subequal to M1 (0); M3 is moderately to greatly smaller M1 (1) (Williamson and Carr, 2007:character 34).
- (36) Precingulum: absent or weak (0); present, but not reaching labially past the paraconule or paraconule position (1); present, reaching labially past the paraconule or paraconules position (2) (Wible et al., 2009:character 97).
- (37) Postcingulum: absent or weak (0); present, lingual to metaconule or metaconule position (1); present, reaching labially past metaconule or metaconule position (2); present, extending to labial margin (3) (Wible et al., 2009:character 98).
- (38) M1 basal endocingulum: absent (0); present (1) (Williamson and Carr, 2007:character 35).
- (39) M3 parastylar lobe: projects mesiolabially to near the labial edge of M2 (0); broadly rounded and not projecting (1) (Williamson and Carr, 2007:character 36).

Upper Molars

- (16) Enamel texture: smooth (0); crenulated (1) (Williamson and Carr, 2007:character 13*).
- (17) M2 parastylar cusps: multiple (0); single cusp mesial to paracone (1) (Williamson and Carr, 2007:character 14).
- (18) M2 preparacrista: extends labially to labial stylocone (0); extends mesially to cone on precingulum (parastylocone) (1) (Williamson and Carr, 2007:character 15).
- (19) M2 postmetacrista: extends labially (0); extends distally (1).
- (20) Size (labiolingual width) of M2 labial stylar shelf at maximum: more than 25% (0); less than 25% (1); absent (2) (Wible et al., 2009:character 65*).
- (21) M1 shape: transverse with an M1 mesiodistal length/mesial labiolingual width less than 0.85 (0); approaching square (M1 mesiodistal length/mesial labiolingual width reduced relative to length is greater than 0.85 and less than 1.0) (1); square (M1 mesiodistal length/mesial labiolingual width is greater than 1.0) (2) (Williamson and Carr, 2007:character 19).
- (22) M1–3 paracone and metacone: separated but connected by centrocrista (0); close so that bases merge (1) (Williamson and Carr, 2007:character 20*).
- (23) M1–2 size of paracone relative to metacone: subequal (0); paracone somewhat larger (1); paracone twice as large (2) (Williamson and Carr, 2007:character 22).
- (24) Degree of labial shift of protocone (distance from protocone apex to lingual border vs. total tooth width, in%): no labial shift (10–20%) (0); moderate labial shift (21–30%) (1); substantial labial shift (30–45%) (2); very strong labial shift (>45%) (3) (Wible et al., 2009:character 95*).
- (25) Protocone anteroposterior expansion: none, subequal to paracone (0); expanded, larger than paracone (1) (Wible et al., 2009:character 93).
- (26) M1–3, postmetaconule crista: forms metacingulum (0); metacingulum formed by the postmetaconule crista continuing onto the metastylar lobe (1) (Nessov et al., 1998:table 3, character 4).
- (27) M1–3 mesostyle: absent (0); present (1) (Williamson and Carr, 2007:character 26).
- (28) M1–2 paraconules: weak or absent (0); prominent, closer to protocone (1); prominent, midway or closer to paracone (2) (Wible et al., 2009:character 88).
- (29) M1–2 metaconules: weak or absent (0); prominent, closer to protocone (1); prominent, midway or closer to metacone (2) (Wible et al., 2009:character 89).
- (30) M2 metaconular region: bears single metaconule (0); bears twin cusps positioned on postprotocrista (1) [taxa without metaconule are scored inapplicable] (Williamson and Carr, 2007:character 30*).
- (31) M1 metaconule: smaller than metacone (and hypocone) (0); similarly sized (1) [taxa without metaconule are scored inapplicable].
- (32) M1–2 hypocone: absent (0); present (1) (Williamson and Carr, 2007:character 31*).
- (33) M2 hypocone shape: elongated linguolabially thickening of the postcingula, sometimes with multiple swellings (0); forms a distinct circular cusp, lower than protocone (1); forms a distinct circular cusp, subequal to protocone (2) [taxa without hypocone are scored inapplicable] (Williamson and Carr, 2007:character 32*).
- (34) M1–2 relative size: M2 is larger than M1 (0); M1 is subequal or larger than M2 (1) (Williamson and Carr, 2007:character 33).
- (35) M1–3 relative size: M3 is not reduced but is subequal to M1 (0); M3 is moderately to greatly smaller M1 (1) (Williamson and Carr, 2007:character 34).
- (36) Precingulum: absent or weak (0); present, but not reaching labially past the paraconule or paraconule position (1); present, reaching labially past the paraconule or paraconules position (2) (Wible et al., 2009:character 97).
- (37) Postcingulum: absent or weak (0); present, lingual to metaconule or metaconule position (1); present, reaching labially past metaconule or metaconule position (2); present, extending to labial margin (3) (Wible et al., 2009:character 98).
- (38) M1 basal endocingulum: absent (0); present (1) (Williamson and Carr, 2007:character 35).
- (39) M3 parastylar lobe: projects mesiolabially to near the labial edge of M2 (0); broadly rounded and not projecting (1) (Williamson and Carr, 2007:character 36).

Lower Premolars

- (40) p1 roots: two (0); one (1); first lower premolar is absent (2) (Wible et al., 2009:character 48*).
- (41) Diastema between mesial premolars: mesial premolars closely spaced with relatively small diastema between p2 and p4 (0); mesial premolars p2 and p4 separated by significant diastema (1) (Williamson and Carr, 2007:character 37).
- (42) p2 talonid: bears distinct 'heel' (0); lacks distinct heel (1) (Williamson and Carr, 2007:character 38).
- (43) p3 paraconid: absent or indistinctive (0); present and distinctive (1) (Wible et al., 2009:character 52).

- (44) p3 premolar talonid cusps: one (0); two (1); three (2) (Wible et al., 2009:character 54).
- (45) p3 protoconid cusp orientation: vertical (0); apex canted distally (the angle formed by the distal carinae and the base of tooth form an acute angle distally) (1) (Williamson and Carr, 2007:character 39).
- (46) p3 metaconid: absent (0); present as lingual ridge (1).
- (47) p4 protoconid cusp orientation: vertical (0); apex canted distally (the angle formed by the distal carinae and the base of tooth form an acute angle distally) (1) (Williamson and Carr, 2007:character 40).
- (48) p4 length/p3 length: subequal, greater than 0.9 and less than 1.25 (0); greater than 1.25 and less than 1.5 (1); greater than 1.5 (2) (Williamson and Carr, 2007:character 41*).
- (49) p4 paraconid: present (0); greatly reduced or absent (1) (Williamson and Carr, 2007:character 42).
- (50) p4 metaconid: well individualized and as large as the protoconid (0); well individualized but smaller than the protoconid (1); reduced to lingual ridge (2); absent (3) (Williamson and Carr, 2007:character 43*).
- (51) p4 protoconid: distal face is smooth (0); bears distinct distally directed postprotoconid cristid (1) (Williamson and Carr, 2007:character 45).
- (52) p4 talonid: two or more cuspids and/or with talonid basin (0); simplified with just one central blade and no talonid basin (1) (Williamson and Carr, 2007:character 44).
- (53) p4 small relative to m1 (ultimate lower premolar length/m1 length is less than 0.95) (0); large relative to m1, (ultimate lower premolar length/m1 length is greater than or equal to 0.95) (1) (Williamson and Carr, 2007:character 46).
- (54) p4 anterolabial cingulid: absent (0); present (1) (Wible et al., 2009:character 60*).
- inct cingular shelf continuing along labial border to the hypoflexid (2); absent (3) (Wible et al., 2009:character 114*).
- (64) m1–3 postprotocristid: absent (0); distally directed crest extends distally from protoconid (1) (Williamson and Carr, 2007:character 55).
- (65) m1–3 crista obliqua: oriented mesiolingually (0); oriented mesiodistally to form cutting edge with ‘notch’ between postprotoconid and crista obliqua (1); two crests reaching the hypoconid, one oriented mesiolingually and the other mesiodistally (2) (Williamson and Carr, 2007:character 56*).
- (66) m2 metaconid and protoconid height relative to hypoconid: much higher, with protoconid more than twice the height of hypoconid (0); relatively low, with of protoconid less than twice the height of hypoconid above the tooth base (1); subequal, with no difference height between trigonid and talonid (2) (Williamson and Carr, 2007:character 57*).
- (67) Molar shape: ‘average,’ m2 distal width/m2 length is greater or equal to 0.7 and less than 0.85 (0); somewhat narrow, m2 distal width/m2 length is less than 0.7 and greater than or equal to 0.5 (1); narrow (trenchant), m2 distal width/m2 length is less than 0.5 (2); wide, m2 distal width/m2 length is greater than 0.85 (3) (Williamson and Carr, 2007:character 58).
- (68) Talonid width relative to trigonid: talonid narrower than trigonid (0); talonid subequal to talonid (1); talonid wider than trigonid (2) (Rougier et al., 1998:character 50*; Wible et al., 2009:character 119*).
- (69) Anteroposterior shortening at base of trigonid relative to talonid: some shortening (75–55% of tooth length) (0); anteroposterior compression of trigonid (45–55% of tooth length) (1); strong anteroposterior compression of trigonid (less than 45% of tooth length) (2) (Luo and Wible, 2005:character 78*).
- (70) m2 hypoconid and entoconid, relative size: hypoconid and entoconid are subequal in size (0); hypoconid is larger than entoconid (1) [taxa lacking an entoconid are scored inapplicable].
- (71) m1–2 hypoconulid and entoconid, relative size: hypoconulid and entoconid are subequal in size (0); entoconid is larger than hypoconulid (1) [taxa lacking a hypoconulid are scored inapplicable] (Williamson and Carr, 2007:character 61*).
- (72) m1–3 entocristid: extends mesiodorsally on the base of the distal wall of the metaconid (talonid basin enclosed lingually) (0); extends mesioventrolingually on distolingual base of metaconid to lingual cingulid (if present) (1); extends mesiodorsally to the base of the distal wall of the metaconid, but not climbing the metaconid, thus creating a ‘notch’ (2); entocristid absent or extremely faint, talonid basin widely open lingually (3) (Williamson and Carr, 2007:character 62*).
- (73) m3: longer than m2; m3 mesiodistal length/m2 length ≥ 1.1 (0); length subequal to m2; m3 length/m2 length < 1.1 and ≥ 0.9 (1); much shorter than m2; m2 length/m3 length < 0.9 (2) (Williamson and Carr, 2007:character 64).
- (74) m3 hypoconulid: long, protrudes as separate distal lobe (0); short, does not protrude substantially beyond rest of talonid (1); absent (2) (Ladevèze et al., 2010:character 43).
- (75) Lingual cingulid on one or more molars, especially lingual face of metaconid: absent (0); present (1) (Archibald et al., 1983:character 2).
- (76) Molar labial cingulid at base of hypoconid: present and sharp (0); present and subdued forming a ‘shoulder’ (1); absent (2) (Williamson and Carr, 2007:character 66*).
- (77) Molar labial cingulid at base of hypoflexid: absent (0); present (1).

Lower Molars

- (55) m1–2 paraconid position: lingual (0); mesial to position between metaconid and protoconid (1); mesial to protoconid (2) (Williamson and Carr, 2007:character 48).
- (56) Paraconid orientation: erect (0); projects mesially (1) (Williamson and Carr, 2007:character 49).
- (57) m2–3 paraconid: present as a well-individualized cuspid (0); reduced so that it is not discernible from the paracristid (1).
- (58) m2 metaconid position: distolingual to protoconid (0); lingual to protoconid (1) (Williamson and Carr, 2007:character 50*).
- (59) Molar metaconid height: subequal to protoconid (0); somewhat smaller than protoconid (1); significantly smaller than protoconid (2) (Williamson and Carr, 2007:character 52*).
- (60) Metaconid and protoconid shape: distinct (0); inflated and confluent at base above trigonid basin or ‘twinned’ (1) (Williamson and Carr, 2007:character 53).
- (61) m1–3 paracristid: curves mesiolingually (0); forms distinct, mesially directed crest that rises mesiodorsal to protoconid (1) (Williamson and Carr, 2007:character 54).
- (62) m1 trigonid configuration: open, with paraconid anteromedial, paracristid-protocristid angle more than 50° (0); more acute, with paraconid more posteriorly placed, paracristid-protocristid angle between 36° and 49° (1); anteroposteriorly compressed, paracristid-protocristid angle 35° or less (2) [taxa lacking a paraconid are scored inapplicable] (Wible et al., 2009:character 111*).
- (63) Anterior and labial (mesiobuccal) cingular cuspule (f): present, without a distinct cingular shelf posteroventrally directed from it (0); present, with a distinct cingular shelf posteroventrally directed from it (1); present, with a distinct

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