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An African radiation of ‘Dryolestoidea’ (Donodontidae, Cladotheria) and its significance for mammalian evolution

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Abstract

The Ksar Metlili Formation, from the Jurassic – Cretaceous transition (Tithonian – Berriasian) of eastern High Atlas Mountains, Morocco, yielded one of the richest microvertebrate assemblages from the Mesozoic of Gondwana. With at least 19 species, mammaliaforms are particularly diverse. ‘Dryolestoidea’ are the most abundant and the most diverse; nevertheless, only one species, *Donodon perscriptoris* Sigogneau-Russell, 1991, of the monotypic Donodontidae, had been described so far. Here, we describe four new species and three new genera of ‘dryolestoids’ from the Ksar Metlili deposits: *Donodon minor* sp. nov., *Stylodens amerrukensis* gen. et sp. nov., *Anoualestes incidens* gen. et sp. nov., and *Amazighodon orbis* gen. et sp. nov, which are all included into the Donodontidae based on their dental morphology. We present the first phylogenetic analysis that incorporates the five donodontid species from the Ksar Metlili site into the cladotherian phylogeny. Our new analysis provides evidence for the paraphyly of the ‘Dryolestoidea’: Dryolestidae, ‘Paurodontidae’, Donodontidae and Zatheria form a clade, to the exclusion of the South American Meridiolestida. Donodontids are found to be closer to prototribosphenidans and zatherians than to any other ‘dryolestoid’ family and are more derived than meridiolestidans. This topology refutes previous hypothesis that meridiolestidans are phylogenetically rooted among donodontids. Our phylogenetic analysis also supports Donodontidae as an endemic African monophyletic group. The close relationships of the donodontids and zatherians suggest for the zatherians a geographical origin possibly from Africa or Gondwana, instead of Laurasia.

Keywords: Dryolestoidea • Mammalia • Morocco • Africa • Jurassic-Cretaceous transition • Gondwana

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Introduction

Since the time of its discovery in 1983 and the field expeditions that followed in 1986 and 1988, the microvertebrate assemblage from the Upper Jurassic – lowest Cretaceous of the Ksar Metlili site (KM), Anoual Syncline, eastern Morocco (**Fig. 1**), has emerged as one of the richest and taxonomically most diverse vertebrate assemblages from the Mesozoic of Africa and Gondwana (Sigogneau-Russell et al. 1990, 1998; Lasseron 2020; Lasseron et al. 2020). Thirty-nine species of various groups – chondrichthyans, actinopterygians, non-tetrapod sarcopterygians, lissamphibians, turtles, lepidosaurs, choristoderans, crocodyliforms, pterosaurs, dinosaurs and mammals – have been identified (Sigogneau-Russell et al. 1988, 1990, 1998; Sigogneau-Russell 1989, 1991a, 1991b, 1991c, 1992, 1995a, 1995b, 1999, 2003a; Duffin and Sigogneau-Russell 1993; Richter 1994; Sigogneau-Russell and Ensom 1994, 1998; Gmira 1995; Broschinski and Sigogneau-Russell 1996; Evans and Sigogneau-Russell 1997, 2001; Knoll 2000; Gardner et al. 2003; Hahn and Hahn 2003; Jones et al. 2003; Knoll and Ruiz-Omeñaca 2009). The discovery of this taxonomically exceptionally diverse fauna has led to three additional field expeditions, in 2010, 2015 and 2018, which sampled six new fossil-bearing loci (KM-A1, KM-A2, KM-B', KM-C, KM-D1, KM-D2) around the historical site discovered in 1983; together, these seven loci constitute the current meaning of the KM site (**Fig. 2**). Following the new field campaigns, the complete KM vertebrate assemblage has been revised, leading to an update of its faunal list, now including at least 53 distinct species (Lasseron 2019, 2020; Lasseron et al. 2020).

<<Fig. 1 here>>

<<Fig. 2 here>>

The best known and most intensively studied component of the fossil assemblage from the KM site are the mammaliaforms, especially the mammals. At least 19 species have been identified (Lasseron 2020), belonging to haramiyidans, eutriconodontans, non-cladotherian trechnotherians, ‘dryolestoids’, stem-zatherians (‘peramurans’) and tribosphenidans (**Table 1**). It is the richest mammalian fauna known in Africa, comparable to the richest contemporary mammalian faunas from Laurasia. Among them, ‘dryolestoids’ are of peculiar interest. This diverse grouping of mostly Jurassic and Cretaceous stem cladotherians includes dryolestids, meridiolestidans, ‘paurodontids’ and donodontids. Like in other cladotherians, the dentition of ‘dryolestoids’ consists of a series of reversed triangles, with the upper molars wider than the lowers (Martin 1999; Luo et al. 2002; Kielan-Jaworowska et al. 2004), and they constitute a radiation of pre-tribosphenic mammals (Martinelli et al. 2021). Their lower jaw shows a distinct angular process and sophisticated musculature, allowing a complex mastication with a major transverse component in the chewing cycle (Crompton 1971; Prothero 1981; Davis 2011; Schultz and Martin 2014). Jurassic ‘dryolestoids’ retain a well-defined Meckelian groove, as well as the splenial and coronoid bones, while geologically younger taxa have a shallower Meckelian groove and likely lost the splenial and coronoid bones (Krebs 1971; Martin 1999; Kielan-Jaworowska et al. 2004; Rougier et al. 2021; Martin et al. 2022). The ‘prototribosphenic’ molar of ‘dryolestoids’ marked a critical step in the evolution of the tribosphenic molar, with the appearance of talonid shelf in stem-cladotherians such as ‘dryolestoids’, which acted as an extending shearing surface and likely assisted in medial movement during occlusion (Grossnickle 2017; Martin et al. 2020). Previous studies have demonstrated considerable phylogenetic uncertainty for ‘dryolestoids’, which are recovered either paraphyletic (Rougier et al. 2012; Averianov et al. 2013, 2014; O’Meara and Thompson 2014; Wible and Rougier 2017) or monophyletic (Rougier et al. 2011; Chimento et al. 2012; Martinelli et al. 2021). ‘Dryolestoids’ are the most abundant mammals from the KM

site, representing more than 34% of the discovered mammaliaform specimens (**Fig. 3**). Paradoxically, ‘dryolestoids’ represent the least studied mammal group from the KM fauna, with only one identified species, *Donodon perscriptoris*, belonging to the monotypic Donodontidae and which was described on the basis of three teeth (Sigogneau-Russell 1991a).

<<Table 1 here>>

<<Fig. 3 here>>

‘Dryolestoids’ are known both in Laurasia and Gondwana from the Middle Jurassic (Bathonian; Freeman 1976, 1979; Kielan-Jaworowska et al. 2004; Averianov et al. 2014; Haddoumi et al. 2016; Lasseron et al. 2020) to the Paleocene (Gelfo and Pascual 2001; Kielan-Jaworowska et al. 2004); *Necrolestes* Ameghino, 1891 even survived into the Neogene (Miocene) of Argentina (Chimento et al. 2012; Rougier et al. 2012; Averianov et al. 2013; O’Meara and Thompson 2014). ‘Dryolestoid’ fossils are often dominant in the respective mammalian faunas (Forasiepi et al. 2012). Accordingly, ‘dryolestoids’ are also the most abundant mammals at the KM site (34% of all mammaliaform specimens). The same applies, for example, for the Upper Jurassic of the Guimarota coal mine, Portugal (49% of all mammaliaform specimens; Martin 1999, 2001, 2018), and the Upper Cretaceous of the La Colonia Formation, Argentina (Rougier et al. 2009b). In the basal Cretaceous of Cherves-de-Cognac, France, they are the second most abundant mammal group (23% of all mammalian specimens), after the multituberculates (50%; Pouech 2008). ‘Dryolestoids’ are also often among the taxonomically most diverse mammaliaforms at these sites: they are the most diverse at KM (five species, including the four new ones we describe in the present article) and the second most diverse (five species; Martin 1999) after the multituberculates (19 species, but this is probably an overestimate; Hahn and Hahn 2000; Hahn 2001; Martin 2018) at the Guimarota coal mine.

A re-study of the mammalian specimens from the KM site (Lasseron 2020) led to the discovery of 46 additional isolated teeth and mandibular fragments of ‘dryolestoids’, some of them belonging to the previously known *Donodon perscriptoris*, others representing four new species. We also present the first phylogenetic analysis of ‘Dryolestoidea’ that incorporates the Moroccan species into cladotherian phylogeny, in order to determine their relationships and to test the monophyly of ‘Dryolestoidea’.

Geological context

The KM site is located on the northern margin of eastern High Atlas Mountains, in the northeast of Morocco, approximately 12 km west-northwest of Anoual City, near the Ksar Metlili fort. It is situated in the ‘Couches Rouges’, or ‘Red Beds’ (or ‘Continental Intercalaire’; Kilian 1931), which constitute a series of mainly continental detritic deposits, widely spread in the Moroccan Atlasic domain and in North Africa (Haddoumi et al. 1998, 2008, 2016; Allain and Aquesbi 2008; Charrière and Haddoumi 2016). These ‘Red Beds’ are classically interpreted as marking the filling of the Atlas furrows (Dresnay 1979) and are found in many basins, with thicknesses ranging from a few hundred to about 2000 meters (Haddoumi et al. 2008). In the Anoual Syncline, where KM is located, these layers are moderately affected by tectonics and are about 500 m thick (Haddoumi et al. 2008, 2016).

The age of these ‘Red Beds’, which are rarely fossiliferous, has long been debated, due to the lack of reliable chronostratigraphic markers (Monbaron 1988; Sigogneau-Russell et al. 1990; Haddoumi et al. 1998, 2008; Charrière and Haddoumi 2016). An age between the Middle Jurassic and the Lower Cretaceous, or even the beginning of the Upper Cretaceous, has been attributed to them, but opinions on the stratigraphic interpretation of this sequence diverge (see Lasseron 2020 and Lasseron et al. 2020, and references therein). For the Anoual

Syncline, the latest works (Haddoumi et al. 1998, 2008; Charrière and Haddoumi 2016) distinguished three stratigraphic units within the ‘Red Beds’ (from base to top): the Anoual Formation, the Ksar Metlili Formation, and the Dekkar Group (**Fig. 4**). The Ksar Metlili Formation, where the KM site is located, consists of a continental lenticular calcareous deposit of 0-80 m thickness (Haddoumi et al. 2008). Its lithology corresponds to a fluvially dominated deltaic floodplain. A ?Berriasian age has been proposed based on calcareous nanofossils found below the KM microvertebrate lens (Sigogneau-Russell et al. 1990, 1998), and Porocharaceae gyrogonites found above the microvertebrate lens suggest an uppermost Tithonian – Lower Berriasian age (Haddoumi et al. 2008; Mojon et al. 2009). New data on the microvertebrate association of the KM site and large-scale comparisons with subcontemporaneous faunas of the Jurassic – Cretaceous transition around the world suggest that this site has a similar facies as the Purbeck. Based on this we propose a Tithonian – Berriasian age estimate for this site (Lasseron 2020; Lasseron et al. 2020).

<<**Fig. 4 here**>>

Material and methods

Institutional abbreviations CR2P: Centre de Recherche en Paléontologie – Paris (UMR 7207, Muséum national d’Histoire naturelle-Sorbonne Université-Centre national de la recherche scientifique), Paris, France; ISEM: Institut des Sciences de l’Évolution – Montpellier, Montpellier, France; MNHN: Muséum national d’Histoire naturelle, Paris, France.

Other abbreviations KM: Ksar Metlili site, Ksar Metlili Formation, eastern High Atlas, Figuig Province, Oriental Region, Morocco; MCM: Maroc Mésozoïque, collections of Moroccan fossils from the Anoual Syncline, MNHN, Paris, France; SA: Anoual Syncline.

Material The ‘dryolestoid’ material from the KM site includes 49 isolated molars and premolars, the latter permanent or deciduous (isolated incisors and canines of mammals are present in the KM material, but their identification is uncertain; they are not considered here). In this material, 38 specimens belong to the collections sampled in the 1983, 1986 and 1988 field campaigns, and 11 specimens are from the collections sampled in 2010, 2015 and 2018. The specimens collected in the 1980s have catalogue numbers with the MCM prefix and are deposited at the MNHN, Paris, France. The specimens collected in the 2010s have catalogue numbers with the prefix KM-A1, KM-A2, KM-B’, KM-C, KM-D1 or KM-D2, depending on their locus of discovery; they are currently deposited at the MNHN, and will be permanently stored after study at the Aïn Chock Faculty of Science, Hassan II University, Casablanca, Morocco, with the FSAC acronym.

The following specimens were studied (the SA numbers given in brackets correspond to the old catalogue numbers of Sigogneau-Russell 1991a): MCM 557 (= SA 31), MCM 578, MCM 579, MCM 595, MCM 596, MCM 599, MCM 600 (maxillary fragment with three teeth), MCM 605, KM-B’-11, KM-B’-95, right upper molars; MCM 559 (= SA 1), MCM 598, MCM 601, MCM 603, MCM 604, MCM 615, KM-A1-2, KM-D2-5 (deciduous), left upper molars; MCM 622, MCM 623, KM-B’-1, KM-B’-2, KM-B’-37, KM-B’-96, right lower molars; MCM 558 (= SA 44, mandible fragment with two teeth), MCM 581, MCM 588, MCM 592, MCM 617, MCM 618, MCM 620, MCM 621, KM-A1-1, KM-B’-97, KM-D2-4, left lower molars; MCM 594 (deciduous), right upper premolar; MCM 501 (deciduous), MCM 587 (deciduous), MCM 591 (deciduous), right lower premolars; MCM 586

(deciduous), MCM 589 (deciduous), left lower premolars; MCM 607, two edentulous right mandibles and one edentulous left mandible fragments; MCM 614, right upper molariform fragment; MCM 616, molar fragment.

Specimen preparation Calcareous sandstone rocks containing the microremains were processed by acid digestion, using 7% diluted formic acid saturated with tricalcium phosphate. The remaining lithoclasts and bioclasts were subsequently treated with hydrogen peroxide. If necessary, a solution of dithionite was used to dissolve gypsum content. The residue was separated in different fractions using sieves of 5-, 2-, 1- and 0.5-mm mesh size and then sorted under a stereomicroscope.

Phylogenetic analyses Phylogenetic analyses were performed using TNT (v. 1.5; Goloboff and Catalano 2016). The taxon/character matrix was created with Mesquite (v. 3.61, build 927; Maddison and Maddison 2019). Synapomorphies were visualised in Winclada (v. 1.61; Nixon 2002).

Outgroup *Phascolotherium bucklandi* Broderip, 1828, from the Middle Jurassic of Britain (Butler and Sigogneau-Russell 2016), was chosen as outgroup, following the works of Averianov et al. (2013, 2014). The triconodont dentition of this amphilestid with three mesiodistally aligned cusps, is probably the plesiomorphic condition for the clade including ‘Dryolestoidea’ and Theria (Mills 1971; Kielan-Jaworowska and Dashzeveg 1998; Rougier et al. 2007; Averianov and Lopatin 2011). It was preferred to *Probainognathus* Romer, 1970, which was used as outgroup in the analyses of Rougier et al. (2011, 2012), Chimento et al. (2012), O’Meara and Thompson (2014), Wible and Rougier (2017) and Martinelli et al. (2021), because we consider *Probainognathus* to be too distant from the group of interest, which might cause problems of homology and of character applicability.

Matrix construction and choice of characters The character matrix used in the phylogenetic analyses is mainly based on a compilation of the dental and mandibular characters extracted from the matrices of Rougier et al. (2011) and Averianov et al. (2013), with subsequent modifications by Rougier et al. (2012), Averianov et al. (2014) and Wible and Rougier (2017), to which we added eight new characters. These matrices were also used in other recent works (Chimento et al. 2012; O’Meara and Thompson 2014; Harper et al. 2019; Martinelli et al. 2021). Moreover, they include a large number of ‘Dryolestoidea’, and especially of Meridiolestida, which are thought to be related to the KM donodontids. We have chosen to focus the analysis on the dental and mandibular characters, without considering the cranial and postcranial characters that are coded in those matrices: this aims to optimize the final matrix resolution by limiting the amount of missing data (and thus of character optimizations) for the KM species, which are only represented by teeth and a few mandible fragments, as are most of the taxa of our dataset, with a few exceptions (e.g., *Henkelotherium* Krebs, 1991). Furthermore, the additional analyses including the cranial and postcranial characters from the works of Averianov et al. (2013, 2014) that we conducted showed only marginal and minor differences from the topologies recovered without these characters and discussed in this article: the inclusion of cranial and postcranial characters does not modify or add anything to the relationships of the KM donodontids with the other cladotherians. Some taxa (*Groebertherium* Bonaparte, 1986; *Maotherium asiaticum* Ji et al., 2009; *Achyrodon* Owen, 1871; *Phascolestes* Owen, 1871; *Mozomus* Li et al., 2005) have been removed due to a lack of reliable information on their teeth and mandibles. Thus, we obtained a final matrix comprising 48 taxa and 190 characters. Of these 190 characters, 152 are from the dentition and 38 are from the mandible. Twenty-nine characters illustrate morphoclines and are thus ordered (2, 13, 15, 20, 28, 30, 35, 38, 51, 53, 58, 65, 70, 73, 79, 91, 103, 105, 131, 139, 142, 144, 155, 156, 165, 166, 167, 173, 178), the 161 others are not. Sixteen of the 190 characters

are constant and 14 others are parsimony-uninformative, presumably due to the exclusion of the above-mentioned taxa. 97 characters (51.05%) are taken (four of them are modified) from Rougier et al. (2011), six (3.16%) are taken (one modified) from Rougier et al. (2012), 79 (41.58%) are taken (ten of them are modified) from Averianov et al. (2013), and eight (4.21%) are new. The details of these characters and of their coding are provided in **Online Resource 1**, and the taxon/character matrix is available in TNT format in **Online Resource 2**. The proportions of dental and mandibular characters that could be scored for each species are presented in **Table 2**.

<<**Table 2 here**>>

Terminology The dental nomenclature of ‘dryolestoid’ teeth used in the descriptions and comparisons below is detailed in **Fig. 5**. The identification of wear facets, when possible, follows the nomenclature established by Crompton (1971). For the lower molars, we follow Crompton (1971), Luo et al. (2002) and Schultz and Martin (2011) in calling “hypoconulid” the elevated version of the cusp d (on the talonid) of *Kuehneotherium* Kermack et al., 1968 and spalacotheriids that occurs in ‘dryolestoids’. Consequently, the crest that runs at the bottom of the talonid would be homologous to the hypocristid of tribosphenic molars: this name is therefore used for this crest in the following descriptions.

<<**Fig. 5 here**>>

Illustration SEM photographs were taken at the CR2P with a JEOL JCM 600 and a Hitachi FlexSEM 1000 II. Computed microtomography scanning was performed at the MRI (Montpellier Ressources Imagerie, ISEM) platform, with a EasyTom 150 computed

microtomography scanner, with beam energy of 90 kV and a flux of 53 μ A at a resolution of 5 μ m per voxel. 3D reconstructions were made with Materialise Mimics Innovation Suite softwares (Mimics Research v. 21.0 and 3-matic Research v. 3.0) at the 3D imaging platform of the CR2P.

Systematic paleontology

‘Dryolestoids’ belong to the Cladotheria clade (McKenna 1975; Prothero 1981). While their position among cladotherians (here defined as a stem-based taxon comprising all taxa closer to *Mus musculus* Linnaeus, 1758 than to *Spalacotherium tricuspides* Owen, 1854; Averianov et al. 2013) is generally accepted, the taxonomic composition of ‘Dryolestoidea’ greatly varies among authors, as does their monophyly and content. There is considerable uncertainty about their phylogeny, and different topologies have been proposed. According to Kielan-Jaworowska et al. (2004), they form a monophyletic group and include two major taxa: (1) the Dryolestida, including Dryolestidae, ‘Paurodontidae’, Donodontidae, Mesungulatidae and Brandoniidae, and (2) the Amphitheriida, including the Amphitheriidae. Kielan-Jaworowska et al. (2004) have added the genus *Chunnelodon* Ensom & Sigogneau-Russel, 1998, of uncertain affinities. Rougier et al. (2011) consider the ‘Dryolestoidea’ to be monophyletic, but they exclude Amphitheriida and *Chunnelodon* from that group. Within ‘Dryolestoidea’, they place some of the Dryolestida of Kielan-Jaworowska et al. (2004) in a new clade, Meridiolestida, as sister-group of ‘Paurodontidae’ and including all the ‘dryolestoids’ closer to *Peligrotherium* Bonaparte et al., 1993 than to *Dryolestes* Marsh, 1878 or *Paurodon* Marsh, 1887. All the meridiolestidans known to date are South American. A molar fragment discovered in Antarctica, lost before its formal description, was tentatively attributed to Meridiolestida (Martinelli et al. 2014; Gelfo et al. 2019), but is of dubious identification. The

Meridiolestida clade, including Mesungulatidae, Brandoniidae, Peligrotheriidae, Reigitheriidae and Austrotriconodontidae (previously attributed to Triconodonta), has been recognized in all following studies, with the addition of the genus *Necrolestes* (Rougier et al. 2012; Chimento et al. 2012; Averianov et al. 2013, 2014; O’Meara and Thompson 2014; Wible and Rougier 2017). In these studies, Amphitheriida are no longer included in the ‘Dryolestoidea’, and, except of Chimento et al. (2012), ‘dryolestoids’ are not considered as monophyletic, but have been found to be diphyletic. Even if ‘dryolestoids’ are considered non-monophyletic, Meridiolestida are still sister-group of ‘Paurodontidae’, but closer to Tribosphenida than to Dryolestidae (Rougier et al. 2012; O’Meara and Thompson 2014; Wible and Rougier 2017); alternatively, they are regarded as sister-group of Spalacotheriidae, outside Cladotheria (Averianov et al. 2013, 2014). Following these studies, ‘Dryolestoidea’ would represent a morphological grade and not a clade. However, a recent study (Martinelli et al. 2021) has again found ‘dryolestoids’ to be monophyletic. Here we use the terms ‘Dryolestoidea’ and ‘dryolestoids’ as defined by Rougier et al. (2011), comprising Dryolestidae, ‘Paurodontidae’ and Meridiolestida, and add the Donodontidae, being aware of the phylogenetic uncertainties stated above.

Mammalia Linnaeus, 1758

Theriiformes Rowe, 1988

Trechnotheria McKenna, 1975

Cladotheria McKenna, 1975

Family **Donodontidae** Sigogneau-Russell, 1991

Type genus *Donodon* Sigogneau-Russell, 1991.

Included genera *Donodon* Sigogneau-Russell, 1991; *Stylodens* gen. nov.; *Anoualestes* gen. nov.; *Amazighodon* gen. nov.

Emended diagnosis Uppers molars of Donodontidae are characterized by the following combination of features: (1) absence of mesio-distal compression; tooth crown almost as long as wide, or longer than wide (*Donodon minor*, *Anoualestes incidens*), which is unique within ‘Dryolestoidae’; (2) parastylar groove well developed; (3) paracrista well developed and sharp; (4) metacrista bearing a metacone near the middle of its length; (5) distal root much larger than the mesial one. Lower molars of Donodontidae are characterized by the following combination of features: (1) trigonid with a high and acute protoconid and lower metaconid and paraconid; (2) metaconid at least 40% as high as the paraconid; (3) paraconid longitudinally aligned with the metaconid on the lingual side of the tooth, or slightly more lingual, as in Dryolestidae ; (4) talonid crescent-shaped, transversally wide behind the metaconid, and mesiodistally shortened when compared to Zatheria; (5) protoconid relatively lower and paraconid higher than in ‘Paurodontidae’; (6) transverse mesial cingulid present as a small shelf below the trigonid, without occlusal contact with the upper molars; (7) in their lingual area, paracristid and protocristid transverse relatively to the longitudinal axis of the lower molars; (8) presence of a cingulid cuspule e; (9) mesio-lingual surface of the paraconid forming a keel; (10) notched lingual margin of lower molars.

Genus *Donodon* Sigogneau-Russell, 1991

Type species *Donodon perscriptoris* Sigogneau-Russell, 1991.

Included species *Donodon perscriptoris* Sigogneau-Russell, 1991; *Donodon minor* sp. nov.

Emended diagnosis ‘Dryolestoid’ with robust teeth, characterized as follows:

Upper molars ‘Dryolestoid’ genus differing from other the donodontids by presence of a high labial cingulum bearing two cusps, the median stylar cusp and the stylocone. Paracone connected to median stylar cusp by a low and large median ridge (not present in the other donodontids). Median ridge dividing the trigon in two shallow basins; enlarged parastylar region, forming a protruding wing. Paracone crests forming a wide angle and asymmetrical, paracrista steeper than metacrista. Metacrista always longer and more inclined than paracrista.

Lower molars Paraconid pyramidal in shape in occlusal and mesial views (**Fig. 6**). Talonid narrow, in contrast to *Anoualestes* and to *Zatheria*. Talonid with a hypocristid, which extends onto the trigonid and labio-lingually divides the talonid in two parts. Roots of subequal size.

<<**Fig. 6 here**>>

Remarks The high labial cingulum with a stylocone and a median stylar cusp of the upper molars distinguishes *Donodon* from the other donodontids, and also from Dryolestidae and ‘Paurodontidae’. Within ‘dryolestoids’, a large median ridge as seen in *Donodon*, connecting paracone and median stylar cusp, is known only in *Laolestes* Simpson, 1927 (Dryolestidae) and *Leonardus* Bonaparte, 1990 and *Mesungulatum* Bonaparte & Soria, 1985 (Meridiolestida). A paracrista that is steeper than the metacrista is a common feature with

Zatheria and some Dryolestidae (e.g., *Crusafontia* Henkel & Krebs, 1969, *Krebsotherium* Martin, 1999), and differs from Meridiolestida.

‘Dryolestoid’ species are considered to be generalist insectivores, with the exception of meridiolestidans, which are thought to be omnivorous or herbivorous (Rougier et al. 2011; Harper et al. 2019), due to the thick enamel of their teeth and to their complex tooth-to-tooth occlusion. The robustness of the molars of the two *Donodon* species, associated with their thick enamel (about 150 µm thick), suggests that they have fed on quite hard food, compared to other ‘dryolestoids’: they may have fed on insects with hard exoskeletons (e.g., beetles), on tough plant elements, or both. This kind of dental adaptation and diet was not reported for any ‘dyolestoid’ mammal so far.

Donodon perscriptoris Sigogneau-Russell, 1991

(Figs. 7, 8)

Holotype MCM 557 (= SA 31, Sigogneau-Russell 1991a), right upper molar with completely preserved crown but lacking most of the distal root and a large part of the mesial one.

Referred material Eight upper molars, nine lower molars and three lower premolars – MCM 501, right lower deciduous premolar; MCM 558 (= SA 44, Sigogneau-Russell 1991a), left mandible fragment with two molars ; MCM 559 (= SA 1, Sigogneau-Russell 1991a), left upper molar; MCM 581, left lower molar; MCM 587, right lower deciduous premolar; MCM 589, left lower deciduous premolar; MCM 603, left upper molar; MCM 604, left upper molar; MCM 605, right upper molar; MCM 615, left upper molar; MCM 617, left lower molar; MCM 621, left lower molar; MCM 622, right lower molar; KM-A1-2, left upper molar; KM-

B'-11, right upper molar; KM-B'-37, right lower molar; KM-B'-95, right upper molar; KM-B'-96, right lower molar; KM-D2-4, left lower molar.

Type locality Ksar Metlili site, on the northern margin of eastern High Atlas Mountains, Figuig Province, Oriental Region, Morocco, Ksar Metlili Formation, 'Red Beds' of the Anoual Syncline. Faunal association and comparisons indicate a Purbeckian facies of Tithonian – Berriasian age (Lasseron 2020; Lasseron et al. 2020).

Emended diagnosis Donodontid species characterized by the following characters:

Upper molars Occlusal outline symmetrical. Paracone slightly inclined posteriorly and labially, aligned with the median styler cusp on the labio-lingual axis of the tooth, differing from the upper molars of *Donodon minor*. Upper molars of *D. perscriptoris* further differ from those of *D. minor* by their median ridge which reaches the labial edge and is in the direct extension of the median styler cusp in labial view (while it is shifted between the median styler cusp and the stylocone in *D. minor*, due to the mesial shift of the paracone). Ectoflexus missing or only slightly expressed. Almost flat paracone lingual profile in mesial and distal views.

Lower molars Trigonid compact, occlusal outline roughly circular. In posterior view, talonid horizontal or very slightly inclined lingually. Posterior crest of the talonid bearing a hypoconulid and two small and weak cuspules lingual of hypoconulid. Hypocristid originates from the basis of the hypoconulid labial face, divides talonid in two parts, and extends onto trigonid, reaching protocristid notch between paraconid and metaconid. Paraconid not detached towards the anterior part of the tooth.

Description 21 cheek teeth are known for this species, of which nine are upper molars, nine are lower ones and three are deciduous premolars.

Upper molars The three main cusps (paracone, stylocone and metastyle) of the upper molars of *Donodon perscriptoris* mark the corners of an almost isosceles triangular basin in occlusal view (**Fig. 7a, b, c, d, e, f, left**). In some specimens (e.g., MCM 603; **Fig. 7c, left**), the distal part of the trigon basin, behind the median ridge, is significantly shallower than in the holotype (MCM 557; **Fig. 7a, left**), which possibly indicates a more anterior position in the tooth row. Sometimes, the metacone is strongly reduced and represented only by a small bulging on the metacrista (e.g., MCM 605, KM-B'-95; **Fig. 7f, left, middle**). The median styler cusp, which is usually larger than the stylocone, can be of similar size in some specimens (e.g., KM-B'-11; **Fig. 7e**). Some specimens are worn: the metastyle is strongly abraded in MCM 605 and KM-B'-95, which is smaller than the other teeth, has proportionally lower cusps than the holotype at equal size, which is due to age-related wear (**Fig. 7f**). KM-A1-2 is almost identical to the holotype, but shows a supplementary minute cuspule in the parastylar area, the preparastyle, in addition to the parastyle (**Fig. 7 left, middle left**). Below the metacone, an incipient cingulum is present in some specimens (e.g., MCM 557, MCM 603, KM-B'-11; **Fig. 7a, c, middle**).

Lower molars As the upper ones, the lower molars of *Donodon perscriptoris* have a triangular shape in occlusal view. Some specimens (e.g., MCM 622) have a small concavity at the base of the labial aspect of the protoconid, which is noticeable in mesial or distal views. Cusp e, which is present in all specimens with well-preserved mesiolingual part (**Fig. 8**), is sometimes strongly reduced and hardly visible (KM-B'-96), forming a minute bulging rather than a real cusp.

Deciduous teeth Within the 'dryolestoid' material from KM, some lower cheek teeth (MCM 501, MCM 587, MCM 589) are morphologically similar to lower molars of

Donodon perscriptoris but have diverging roots. Paraconid and metaconid are widely spaced and separated by a bench, and the talonid is strongly inclined labially in distal view. These characters, especially the diverging roots, combined with somewhat smaller size than the other *D. perscriptoris* specimens, suggest that these specimens are deciduous premolars (probably dp3 or dp4). MCM 587 is strongly worn with large wear facets and missing enamel, possibly representing a digested tooth.

Discussion If the upper molars of *D. perscriptoris* belong with no doubt to ‘Dryolestoida’, it should be noted that Averianov (2002) thought that this is not the case for the mandible fragment MCM 558, referred to *D. perscriptoris* by Sigogneau-Russell (1991a). According to Averianov (2002), the acute angle of the trigonid basin (approximately 65° and 72° for the two teeth), the small, roughly equal metaconid and paraconid, the small talonid and the unreduced posterior root are reminiscent of ‘Symmetrodonta’. The orientation of the para- and protocristids in their lingual region, where they bend toward the paraconid and the metaconid respectively, shows that the transverse shearing surface that is typical for Cladotheria was not present on these two teeth. Finally, he noted that the lingual cingulid reduction and the presence of a cuspule f are similar to what can be seen in the ‘symmetrodont’ *Gobiotheriodon* Trofimov, 1980. However, the proportions and the morphology of these lower teeth are compatible with those of the upper molars of *D. perscriptoris*, and their attribution has not been questioned in any other study. Moreover, we did not observe the cuspule f noticed by Averianov (2002). Thus, we follow here the original interpretation by Sigogneau-Russell (1991a) and retain the upper and lower molars in the same taxon.

Measurements See Table 3.

<<Fig. 7 here>>

<<Fig. 8 here>>

Donodon minor sp. nov.

(Figs. 9, 10)

LSID urn:lsid:zoobank.org:act:2A0630DE-CDC0-414B-BD3F-10AEC25CDEAA

Holotype MCM 595, right upper molar, lacking the tips of the roots and the lingual side of the distal root.

Referred material Two upper molars, two lower molars, two upper premolars and two lower premolars – MCM 586, left lower deciduous premolar; MCM 588, left lower molar; MCM 591, right lower deciduous premolar; MCM 592, left lower molar; MCM 594, right upper deciduous premolar; MCM 596, right upper molar; MCM 598, left upper molar; KM-D2-5, left upper deciduous premolar.

Type locality Ksar Metlili site, on the northern margin of eastern High Atlas Mountains, Figuig Province, Oriental Region, Morocco, Ksar Metlili Formation, ‘Red Beds’ of the Anoual Syncline. Faunal association and comparisons indicate a Purbeckian facies of Tithonian – Berriasian age (Lasseron 2020; Lasseron et al. 2020).

Etymology From the Latin word “minor”, meaning “smaller”, in reference to the minute size of the teeth in comparison to those of *Donodon perscriptoris*.

Diagnosis Species of *Donodon* with molars very similar to those of *D. perscriptoris*, but much smaller.

Upper molars Paracone slightly shifted mesially towards the parastylar region: in labial view, it is not in the same axis as the median stylar cusp, as in *D. perscriptoris*, but it faces the crest connecting the median stylar cusp and the stylocone (might reflect positional variation). Tooth longer than wide in occlusal view. Metastyle shifted posteriorly and labially compared to the cusp's location in other 'dryolestoids'. Trigon basin less symmetrical than in *D. perscriptoris*, with a wider opening angle in occlusal view. Metastyle significantly larger than in *D. perscriptoris*.

Lower molars Lower molars less robust than those of *D. perscriptoris*. Talonid more labially inclined in distal view. Paraconid shifted forward and towards the lingual face; it is more individualized and more distant from the protoconid and the metaconid than in *D. perscriptoris*. Trigonid more elongated mesio-distally. Hypocristid originates from the basis of the hypoconulid, as in *D. perscriptoris*, but it reaches the protocristid at a much higher point on the metaconid, almost at its apex.

Description Nine cheek teeth are known for this species, of which three are upper molars, two are lower molars, two are upper deciduous premolars and two are lower deciduous premolars.

General characteristics On the upper cheek teeth, the stylocone and the median stylar cusps are larger relative to the paracone than in *D. perscriptoris* (**Fig. 9a, b, c, middle left, middle right**). The metastyle is transversely shorter and the ectoflexus is longer (**Fig. 9a, b, c, left**). In mesial and distal views (**Fig. 9a, b, c, middle left, middle**), the paracone is more convex than in *D. perscriptoris*. The upper molar MCM 596 is heavily damaged, but its

general morphology is reminiscent of the genus *Donodon*, and its small size makes it more similar to *D. minor* than to *D. perscriptoris*. MCM 598 shows a larger crest opening angle in occlusal view, along with a less convex paracone aspect in mesial and distal views. This suggests an attribution to *D. perscriptoris*, but it is half the size of this species and apparently is not a deciduous tooth. Although the teeth of ‘Dryolestoidea’ can vary in size (e.g., depending on their position in the tooth row), such a difference between permanent and deciduous teeth (50%) has never been documented and appears highly improbable. MCM 598 is in the same size range as the upper molars of *D. minor*, and therefore an attribution to this species appears justified.

On the lower cheek teeth, the protoconid is vertical (**Fig. 10a, b middle left, middle**). The lingual groove between the paraconid and the metaconid is larger and more rounded than in *D. perscriptoris* (**Fig. 10a, b, left**). The posterior talonid crest only bears two small, weakly developed cusps, without pointed tips (**Fig. 10a, b, middle**).

Deciduous premolars In the ‘dryolestoid’ material from KM, some upper cheek teeth (MCM 594, KM-D2-5; **Fig. 9b, c**) are generally similar to the upper molars of *D. minor*, but are somewhat smaller. They are less robust; the median stylar cusp and the stylocone are of equivalent size (**Fig. 9b, c, middle right**); the paracone is larger relatively to the labial cusps (**Fig. 9b, c, middle left, middle, middle right**); the ectoflexus, even if it is still wide, is less marked than in the teeth described above (**Fig. 9b, c, left**), and almost flat in labial view (**Fig. 9b, c, middle right**); and the parastylar lobe is more inclined lingually in mesial view (**Fig. 9b, c, middle right**), whereas it is almost horizontal in the other specimens. These morphological differences, associated with a weak mineralization, suggest that these teeth are upper deciduous premolars of *D. minor*. A few lower deciduous premolars of this species have also been identified (MCM 586, MCM 591; **Fig. 10b**). Here again, their general morphology is almost identical to that of the permanent lower molars, but the mineralization

is weaker, the teeth are less robust, the talonid is strongly inclined labially in distal view, and the lingual side of the protoconid is less bulging (**Fig. 10b, left, middle left**). MCM 588 (**Fig. 10a**) shows features of permanent teeth (marked lingual notch, strongly bulging lingual side of the protoconid), but exhibits also some similarities with lower deciduous premolars (talonid strongly inclined labially in distal view). Therefore, we cannot completely rule out the possibility that it is a lower deciduous molar.

Individual variations Above mentioned MCM 598, with reduced crest opening angle, possibly represents a posterior (ultimate or penultimate) upper molar of *D. minor*. In MCM 586 (**Fig. 10b**), the paraconid and metaconid are even more widely spaced than in permanent teeth, with a small plane area between the two cusps (**Fig. 10b, left, middle right**), which is not the case in MCM 591, which is also a deciduous tooth; the latter possibly derives from a more posterior locus in the tooth row.

On the upper molars, wear facet 1 is noticeable on the mesial side of the paracone. We also observed a wear groove on the parastylar wing. Wear facet 2, on the distal side of the paracone, is less clear. On the lower molars, wear facet 1 is discernible on the disto-lingual side of the protoconid, as well as wear facet 2 on its mesio-lingual side, and wear facet 3 in the incipient talonid.

Discussion The attribution of these lower molars and lower deciduous premolars to *D. minor* is based on the following observations. Due to their smaller size, an attribution to *D. perscriptoris* can be excluded. The teeth of *D. perscriptoris* are 1.3 to 1.8 times higher, 1.2 to 1.6 times longer and 1.2 to 2.2 times wider, and are more robust than those of *D. minor*. Moreover, these lower molars and lower deciduous premolars perfectly the size of the uppers identified as belonging to *D. minor* (see **Table 3**), but not those of *D. perscriptoris* (which are up to 1.5 times higher, up to 1.9 times longer and up to 2.5 times wider) nor those of *S.*

amerrukensis (which are 1.2 to 1.8 times smaller, up to 1.5 times shorter and up to 1.2 times narrower; see below and **Table 3**). Finally, the general morphology and the wear facets of upper and lower molars and lower deciduous premolars attributed to *D. minor* are consistent and allow an occlusal fit.

Measurements See **Table 3**.

<<**Fig. 9 here**>>

<<**Fig. 10 here**>>

Genus *Stylodens* gen. nov.

LSID urn:lsid:zoobank.org:act:F89C551A-1B16-43E2-85AA-1F68554CE0C4

Type species *Stylodens amerrukensis* gen. et sp. nov.

Etymology A combination of the Latin words “stylus”, meaning “pointed”, “punch”, and “dens”, meaning “tooth”, in reference to the well-developed stylocone on the upper molars: “the pointed tooth”.

Diagnosis As for the type and only species.

Stylodens amerrukensis sp. nov.

(**Fig. 11**)

LSID urn:lsid:zoobank.org:act:52B400F2-B15F-41DC-B40C-8D6ACE7E49A3

Holotype MCM 578, right upper molar, preserving only the crown and lacking the tip of the paracone.

Referred material MCM 579, right upper molar.

Type locality Ksar Metlili site, on the northern margin of eastern High Atlas Mountains, Figuig Province, Oriental Region, Morocco, Ksar Metlili Formation, ‘Red Beds’ of the Anoual Syncline. Faunal association and comparisons indicate a Purbeckian facies of Tithonian – Berriasian age (Lasseron 2020; Lasseron et al. 2020).

Etymology Latinization of the Berber name of Morocco, “Amerruk”: “the pointed tooth from Morocco”.

Diagnosis Donodontid with upper molars differing from that of all other ‘dryolestoids’, including *Donodon*, by a high and large stylocone that reaches about two-thirds of the paracone height. Metastyle very low, strongly shifted towards the labial face and almost horizontal, forming a flat surface in labial view. Differs from *Donodon* by a narrow and strongly inclined parastylar region, which does not form a protruding wing. Differs from *Donodon* by the lack of median stylar cusp, missing median ridge and a flat and undivided primary trigon basin. Parastyle well-marked and placed low relatively to the crown height.

Description Only two molars, both right uppers, are known for this species (**Fig. 11**).

General characteristics In both molars, the roots are lacking. In labial view, the paracone appears to be transversely short, and it does not show any mesial nor distal enlargement (**Fig. 11a, b, middle right**). The metacone is broken in both specimens, but its base is still visible in the middle of the metacrista (**Fig. 11a, b, left**); the size of this base suggests that the metacone was large and significantly larger than in *D. perscriptoris*. A small bump is present on the crest joining the paracone and the stylocone (**Fig. 11a, b, left**).

Individual variations Specimen MCM 578 is relatively well preserved, with the exception of the metacone and the paracone, of which a part is missing. The metacrista and paracrista are present but not as sharp as in *D. perscriptoris* (**Fig. 11a, b, middle right**). MCM 579 is of nearly identical morphology, except that the parastylar lobe is more developed (**Fig. 11b, middle left**). However, it remains much smaller than what is seen in *Donodon*.

The upper molars show a large wear facet 1 on the mesial side of the paracone. Other wear facets are not discernible.

Discussion At first glance, the upper molars here attributed to *Stylodens amerrukensis* resemble to that of some stem-therians, such as *Palaeoxonodon ooliticus* Freeman, 1976: both taxa have a prominent metacone and a high stylocone, almost as high as the paracone (Freeman 1976; Sigogneau-Russell 2003b). However, there are clear differences: (1) in upper molars referred to *Palaeoxonodon*, the metacone shares a common base with the paracone (Freeman 1976), which is not the case in *Stylodens*; (2) in *Palaeoxonodon*, the metacrista bears three small labial cusps, including a distinct cusp C (Freeman 1976), whereas in *Stylodens* no cusp C is present; metastyle and a metacone are small; (3) most of the upper molars referred to *Palaeoxonodon* are labio-lingually elongated and often have a stronger extoflexus (Freeman 1976; Sigogneau-Russell 2003b) than in the two molars attributed to

Stylodens, which are almost as wide as long; and (4), the parastylar region is more protruding in *Palaeoxonodon* (Sigogneau-Russell 2003b) than in *Stylodens*, where it is narrower. Apart from morphology, the attribution of *Stylodens* to the Donodontidae is supported by the phylogenetic analysis (see below): all five new species, including *Stylodens*, appear close to each other in the cladogram. According to the phylogenetic analysis, donodontids (including *Stylodens*) are on the stem lineage of Zatheria, as is *Palaeoxonodon* (see below).

Measurements See **Table 3**.

<<**Fig. 11 here**>>

Genus *Anoualestes* gen. nov.

LSID urn:lsid:zoobank.org:act:98FA9289-0FE9-458D-AC1B-9551298D5AAF

Type species *Anoualestes incidens* gen. et sp. nov.

Etymology A combination of Anoual, the nearest city to the fossiliferous site of Ksar Metlili, and of the Greek word “ληστής” (“lestes”), meaning “robber”, “predator”: “the robber from Anoual”.

Diagnosis As for the type and only species.

Anoualestes incidens sp. nov.

(**Fig. 12**)

LSID urn:lsid:zoobank.org:act:2E143340-6390-4BE8-80DE-5BAF7287CAB8

Holotype KM-B'-97, almost complete left lower molar, lacking the tips of the roots.

Referred material Four lower molars – MCM 620, left lower molar; MCM 623, right lower molar; KM-B'-1, right lower molar; KM-A1-1, left lower molar.

Type locality Ksar Metlili site, on the northern margin of eastern High Atlas Mountains, Figuig Province, Oriental Region, Morocco, Ksar Metlili Formation, 'Red Beds' of the Anoual Syncline. Faunal association and comparisons indicate a Purbeckian facies of Tithonian – Berriasian age (Lasseron 2020; Lasseron et al. 2020).

Etymology From Latin "incidens", meaning "cutting", "making an incision", in reference to the carnassial-like notch observed on the lower molars of this species: "the robber from Anoual with a cutting tooth".

Diagnosis Donodontid with mesio-distally elongated lower molars that are longer than wide. Strong roots, parallel and of subequal size. Differs from *Donodon perscriptoris* and *Amazighodon orbis* by lingually widely open trigonid with diverging and widely spaced paraconid and metaconid, separated from each other by a flat surface; in *Donodon minor*, paraconid and metaconid are also spaced, but to a lesser extent. Both cusps nevertheless close to the protoconid, with well-marked valleys. Paracristid and protocristid notches with a vertical incision, which possibly corresponds to a carnassial-like notch, a rare feature within 'Dryolestoidea'. In lingual view, paraconid oriented mesially at its base and then bending

upward, which differs from other Donodontidae. Talonid large for a pretribosphenic taxon, resembling zatherian teeth and differing from other donodontids which have narrow talonids. Posterior crest of the talonid with well-distinct hypoconulid, labio-lingually surrounded by two smaller accessory cuspules (hypoconid and entoconid?), of which the lingual one is much smaller and reduced to a small bulge. The hypocristid originates from the apex of the hypoconulid, dividing the talonid labio-lingually in two parts; it reaches the protocristid in the middle of the metaconid height.

Description This species is only known by five lower molars from KM.

General characteristics The paraconid is pyramidal in occlusal and mesial views, and it is slight shifted anteriorly (**Fig. 12a, b, left, middle left**). It is smaller than the metaconid and located more lingually than the latter (**Fig. 12a, b, left, middle left**). The lingual side of the protoconid is convex (**Fig. 12a, b, left, middle left, middle**). The protoconid is vertically oriented and slightly recurved toward the distal end of the tooth (**Fig. 12a, b, middle right, right**). The anterior crest of the protoconid is longer and less steep than the posterior one, so the protoconid appears larger mesially than distally in lingual view (**Fig. 12a, b, right**). A well-developed cusp e is present below the paraconid; it is connected by a short vertical ridge to the apex of the paraconid (**Fig. 12a, b, left, middle left, middle right**).

Individual variations The holotype, KM-B'-97, and KM-B'-1 show a small well-distinct bulge on both the mesial and distal crests of the protoconid (**Fig. 12a, b, middle left, middle**). Each bulge is located at the lowest point of the crest, at the trigonid basin level, where the crest bends before rising towards the lingual cusps, thus forming the carnassial-like notch. However, these bulges are not present in all specimens: e.g., the distal bulge is absent MCM 623, and in MCM 620 and KM-A1-1, both bulges are absent. The median ridge present in the holotype can be larger (MCM 620, MCM 623, KM-B'-1; **Fig. 12b, right**), less distinct

(MCM 623) or even absent (KM-A1-1). MCM 620 is more compact and mesio-distally shorter than the holotype, almost as wide as long; its protoconid is larger and has three times the height of the metaconid; in the holotype it has the double height of the metaconid. This suggests a more posterior position in the tooth. In KM-B'-1, the metaconid attains also only one third of the protoconid height (**Fig. 12b, right**), but here the metaconid seems to be less developed, since it has approximately the same size as the paraconid (while larger than the paraconid in the holotype) and since the protoconid has similar proportions as in the holotype. In MCM 623, the metaconid is broken, but the size of its base suggests that it was larger than the paraconid, as in the holotype. The paraconid which is slightly anteriorly inclined in most specimens, can sometimes be almost vertical (e.g., KM-B'-1; **Fig. 12b, right**). The talonid is not preserved in some specimens (e.g., MCM 620, KM-B'-1; **Fig. 12b, left, middle, middle right, right**); it is present but damaged in MCM 623, where the three cusps of its posterior wall are difficult to identify (they are smaller than in the holotype). In specimens with a total or partial loss of the talonid, the distal part of the hypocristid usually is not preserved, but its anterior part, extending onto the trigonid wall, is always visible (MCM 623, KM-B'-1; **Fig. 12b**). KM-A1-1 (**Fig. 12c**) differs from the other specimens attributed to *An. incidens*: it is strongly worn and the cristids are largely removed. Its roots are parallel, but the posterior root is significantly larger than the anterior (**Fig. 12c, middle right, right**). The protoconid is very low, and the lingual cusps are poorly developed, the metaconid being reduced to a small bump at the end of the protocristid, and not larger than the paraconid (which is the case in other specimens; e.g., **Fig. 12c, left, middle left, middle**). The lingual cusps are very close to the protoconid, almost aligned with it in mesio-distal direction (**Fig. 12c, left**). The cristids are poorly developed, without valleys in between (**Fig. 12c, left**). Cusp e is present, but without connecting cristid to the paraconid, which is worn and hardly larger than cusp e. The talonid is wide, and its posterior wall is not preserved (**Fig. 12c, left**). At first glance, KM-A1-1

resembles an upper molar of a gobiconodontid eutriconodontan such as *Gobiconodon palaios* Sigogneau-Russell, 2003, also recovered at KM (Sigogneau-Russell 2003a). However, in contrast to *G. palaios* and other gobiconodontids, KM-A1-1 has no complete labial cingulum, which is typical for eutriconodontan upper molars, and the labial indentation is stronger in KM-A1-1 (see Sigogneau-Russell 2003a, text p. 30 and figure 1; Cuenca-Bescós and Canudo 2003; Averianov et al. 2005; Butler and Sigogneau-Russell 2016). A similarly wide talonid as present in KM-A1-1 occurs among the KM ‘dryolestoids’ only in *An. incidens*. Thus, we refer this specimen to *An. incidens* and we consider it as a lower premolar of this taxon.

Discussion The lower molars of *An. incidens* are well distinct from those of the two *Donodon* species. Although they show a superficial resemblance to MCM 586, identified above as a deciduous premolar of *D. minor*, they differ in several aspects. The most significant is the development of the talonid: when preserved, the talonid of *An. incidens* teeth is 0.24-0.28 mm long in its mesiodistal length, and 0.56-0.58 mm long in its labiolingual length, versus 0.20 mm and 0.37 mm respectively for MCM 586. Such a difference (~20% in mesiodistal length, ~54% in labiolingual length) is too important for these teeth to belong to one and the same taxon. Other notable differences are: the orientation of the posterior crest of the talonid relatively to the mesiodistal axis of the tooth (oblique in MCM 586, subperpendicular in *An. incidens*); the presence of a carnassial-like notch in some of the teeth referred to *An. incidens*, but not in MCM 586; the presence of three cuspules on the posterior crest of the talonid in *An. incidens*, while MCM 586 has only two; and the development of cuspule e, significantly larger in *An. incidens* teeth than in MCM 586 (except in KM-A1-1, which can be explained by its deciduous nature). Thus, despite their superficial similarities, the lower teeth described here do not belong to the same taxon as that represented by MCM 586: they belong to a species distinct from *D. minor*. They cannot be deciduous teeth of *D.*

perscriptoris either, because their roots are not diverging (contrary to those of *D. perscriptoris* milk teeth), they appear more mineralized, and they are much smaller than milk teeth known in *D. perscriptoris*. Thus, the five lower molars described here belong to a species distinct from those of the genus *Donodon*. However, as this species is known only by lower molars, and as *S. amerrukensis* is only represented by upper molars, the question of a possible synonymy of the two species must be addressed. The teeth referred to *S. amerrukensis* are much smaller than those attributed to *An. incidens*, and all are permanent teeth: thus, the size difference cannot be explained by ontogeny. The observed size difference between upper and lower teeth is highly unlikely to occur within the same species. Moreover, the proportions of the teeth do not fit, as the upper molars of *S. amerrukensis* are labio-lingually expanded, while the lower molars described here are mesio-distally elongated (longer than wide). Therefore, it can be excluded that these lower molars belong to *S. amerrukensis*, and we refer then to a separate new genus and species.

The presence of carnassial-like notches in *Anoualestes* is quite remarkable for a ‘dryolestoid’ mammal, as it is otherwise known only in *Brandonia* Bonaparte, 1990 (Rougier et al. 2009a) and in *Anthracolestes* Averianov et al., 2014. It possibly suggests a carnivorous diet for *Anoualestes*, which is supported by the relatively large size of its teeth (as carnivores are usually bigger than insectivores; see Pineda-Munoz et al. 2016, fig. 1) and by its long, linguo-buccally compressed molars, similar to those of modern carnivorans (e.g., *Vulpes vulpes*; Gingerich and Winkler 1979; Evans et al. 2007).

Measurements See **Table 3**.

<<**Fig. 12 here**>>

Genus *Amazighodon* gen. nov.

LSID urn:lsid:zoobank.org:act:51C07D79-C5DF-485E-8F71-D6675DC89C88

Type species *Amazighodon orbis* gen. et sp. nov.

Etymology From “Amazigh”, the other name of the Berbers, an indigenous ethnic group from North Africa, thus referring to the place of discovery, and the Greek work “ὀδοῦς” (“odoús”), meaning “tooth”: “the Amazigh tooth”.

Diagnosis As for the type and only species.

Amazighodon orbis sp. nov.

(Fig. 13)

LSID urn:lsid:zoobank.org:act:FE90C73E-5390-41B7-8AFB-5495EB3B63AF

Holotype MCM 618, left lower molar, lacking the mesial root and the tip of the distal one.

Referred material KM-B'-2, right lower molar.

Type locality Ksar Metlili site, on the northern margin of eastern High Atlas Mountains, Figuig Province, Oriental Region, Morocco, Ksar Metlili Formation, ‘Red Beds’ of the Anoual Syncline. Faunal association and comparisons indicate a Purbeckian facies of Tithonian – Berriasian age (Lasseron 2020; Lasseron et al. 2020).

Etymology From the Latin word “orbis”, meaning “round”, “circle”, in reference to the circular outline of the tooth of this species in occlusal view: ‘the round Amazigh tooth’.

Diagnosis Donodontid with tiny lower molars, even smaller than those of *Donodon minor*. Lower molars stocky and bulging and of circular outline in occlusal view. Protoconid low, about twice as high as paraconid. In occlusal view, protoconid crests recurved and bent towards each other in their lingual part, which differs from all other ‘Dryolestoidea’. In mesial and distal views, protoconid narrow and labially slightly convex. Talonid small and mesiodistally constricted, as in *Donodon*. Posterior crest of talonid with two weak cuspules: hypoconulid and another, more labial cuspule. In occlusal view, distal part of hypocristid skews towards the labial face, which differs from the genus *Donodon* and from *Anoualestes incidens*, which have a straight or only slightly oblique hypocristid. Hypocristid reaching the protocristid slightly more labially than its notch. Mesial root larger than the distal one, which differs from the other donodontids which have subequal roots in the lower molars.

Description This species is known by two lower molars (**Fig. 13**).

General characteristics The lower molars are of peculiar morphology. Their paraconid is very long in lingual view (**Fig. 13a, b, right**) and bears a small but distinct cusp e (**Fig. 13a, b, left, middle left, middle right, right**) which is slightly higher than the metaconid. The lingual cusps are well spaced and diverge (**Fig. 13a, b, left, right**). The paracristid is longer and less steep than the protocristid (**Fig. 13a, b, right**). The two roots are fused in their preserved part, but a small groove on the lingual side marks the border between them (**Fig. 13b, middle left, middle, middle right, right**).

Individual variations The talonid of specimen KM-B'-2 is wider and lower placed relatively to the trigonid than in MCM 618 (**Fig. 13, left, middle, middle right, right**). The hypocristid is shorter in MCM 618 than in KM-B'-2 which has a stronger bulging lingual cingulum (**Fig. 13b, right**). In distal view, the angle formed by the labial and lingual segments of the protocristid is more open in MCM 618 than in KM-B'-2 (**Fig. 13a, middle**). Finally, in mesial and distal views, the lingual profiles of the paraconid and of the metaconid are almost vertical in KM-B'-2 (**Fig. 13b, middle left, middle**), while they are lingually inclined in MCM 618 (**Fig. 13a, middle left, middle**).

The paraconid bears a wear facet on its mesial side. Wear facet 1 is present on the distal side of the protoconid, as well as wear facet 3 within the incipient talonid, and wear facet 2, less distinct, on the mesial side of the protoconid.

Discussion At first glance, the minute size of these lower teeth could remind *D. minor*; however, they are even smaller than the smallest lower teeth referred to *D. minor*, and their measurements do not seem to match those of the upper molars of *D. minor* either, especially as the measurements of the lower and upper teeth of *D. minor* are relatively homogeneous. Moreover, these two lower teeth are quite globular and stocky, and thus quite different and incompatible with the upper molars reported for *D. minor*. More importantly, they have unique morphological features that differ from *Donodon*: protoconid crests converging in their lingual part, skewing of the distal part of the hypocristid toward the labial face and, above all, a mesial root significantly larger than the distal one, while *Donodon* is characterized by roots of subequal size on lower molars. All these elements lead us to consider that these two lower molars belong to a species distinct from *Donodon*. Because this species is represented by lower molars only, the possibility of being conspecific with *S. amerrukensis*, known by upper molars only, needs to be discussed. However, there is a

significant difference in size, as these lower molars are 1.5 times larger than the upper molars of *S. amerrukensis*. Because they are permanent teeth, the size difference cannot be explained by ontogeny. Thus, we refer these teeth material to a separate new genus and species.

Measurements See **Table 3**.

<<**Fig. 13 here**>>

<<**Table 3 here**>>

The distribution of the tooth dimensions for each species can be visualised and compared using a box and whisker plot (**Fig. 14**). For all the considered dimensions (maximum crown height, maximum crown length in occlusal view and maximum crown width in occlusal view), the five donodontid species can be clearly distinguished, even though the maximum crown width is not discriminative between *D. minor*, *S. amerrukensis*, *An. incidens* and *Am. orbis*, contrary to their maximum crown length which differs significantly.

<< **Fig. 14 here**>>

?‘Dryolestoidea’ indet.

Referred material MCM 559, right upper molar fragment; MCM 600, right maxillary fragment with three molars; MCM 601, left upper molar; MCM 607, two toothless fragments of right mandible and one toothless fragment of left mandible; MCM 614, right upper molariform fragment; MCM 616, molar fragment.

Description Among the ‘dryolestoid’ material from KM, some specimens are too incomplete or too strongly worn to be identified at a low taxonomic level. However, their general morphology suggests an attribution to ‘dryolestoids’.

In specimen MCM 599, only the mesial part is preserved, with a strongly worn parastyle, the stylocone, part of the median styler cusp and part of the mesial side of the paracone. Its size excludes an attribution to *D. perscriptoris* and to *An. incidens*, but corresponds *D. minor*, *S. amerrukensis* and *Am. orbis*.

The right maxillary fragment MCM 600 bears three molars that are almost completely abraded, preserving only their bases. The original position of the cusps is thus impossible to determine, as is their identification beyond ‘dryolestoids’. The teeth seem to have been approximately of the same size.

In MCM 601 the paracone is missing, and all the remaining cusps are strongly abraded. The stylocone is hard to identify, and the parastylar area is not clearly defined. When it was complete, the tooth may have been similar in size to those of *D. perscriptoris* and *An. incidens*.

The specimens grouped under the collection number MCM 607 are three toothless (posterior?) mandible fragments. The alveoli suggest teeth of subequal size and roots with a diameter similar to those of *D. perscriptoris* molars. These fragments do not carry any diagnostic information, and without any dental characters, a more precise taxonomic identification is not possible.

Specimen MCM 614 bears a high cusp, identified as the paracone, as well as a small parastylar area. The large size of this fragment excludes an attribution to any KM donodontid, *D. perscriptoris* excepted.

Specimen MCM 616 only preserves the apical part of a high cusp, which might be a paracone or a protoconid. When it was complete, this cusp may have been of the size of the large cusps of *D. perscriptoris* and *An. incidens* molars.

Because of the lack of characters allowing a more precise taxonomic identification, all these specimens are here identified as ?‘Dryolestoidea’ indet.

Phylogenetic analyses

As previously stated, the taxonomic composition of ‘Dryolestoidea’ varies depending on the studies, and there is considerable uncertainty regarding their phylogeny. They are most often recovered as paraphyletic (Rougier et al. 2012; Averianov et al. 2013, 2014; O’Meara and Thompson 2014; Wible and Rougier 2017), but they are still found as monophyletic by some authors (Chimento et al. 2012; Martinelli et al. 2021). Moreover, even if the genus *Donodon* is referred to ‘dryolestoids’ since its discovery in 1991, it has never been included in a phylogenetic analysis. Some authors (Sigogneau-Russell 1991a; Bonaparte 1992, 1994, 2002) suggested a close relationship between the KM ‘dryolestoids’ and the South American ones, such as *Mesungulatum*, but they did not provide a detailed comparison. Bonaparte (1994) proposed that the KM ‘dryolestoids’ are derived from an African taxonomic radiation, which then would have been at the origin of the meridiolestidan taxonomic radiation in South America. He wrote that “the presence of this species [*Donodon perscriptoris*] in the Early Cretaceous of Morocco [...] suggests that the Dryolestida of North Africa were related to those from the Late Cretaceous Los Alamos Formation” (Bonaparte 1994). He also suggested (Bonaparte 2002) that the differences between *Mesungulatum* and *Donodon* (i.e., the lack of cingula and the presence of a parastylar wing in *Donodon*) were plesiomorphic characters in the latter.

In order to test the monophyly of ‘Dryolestoidae’ and the hypothesis of a close relationship between their North African representatives and the South American meridiolestidans, we present here the first phylogenetic analysis that includes the KM Donodontidae. This analysis will also help to clarify the relationships between the five species of donodontids and the monophyly of the family.

First analysis We first conducted a traditional search analysis with TNT (heuristic search, random stepwise addition with replicates = 1000, random seed = 10, trees to save per replication = 10, TBR method). Analysis 1a uses the collapsing rule 1 (collapsing branches if supported ambiguously, i.e., if some optimisation lacks support; min. length = 0). 47 most parsimonious trees (MPTs) of 630 steps were obtained. Their strict consensus tree (**Fig. 15**) shows some differences to the topologies recovered in the previous studies. *Vincelestes* Bonaparte, 1986 is placed as a stem-Zatheria in our phylogeny, a moderately supported position (Bremer index $b = 2$) that is more consistent with the current consensus of a sister-group relationship to marsupials and placentals, than in the view of Averianov et al. (2013, 2014), who considered it as a member of Dryolestida (a stem-based taxon comprising all taxa that are closer to *Dryolestes priscus* Marsh, 1878 than to *Peramus tenuirostris* Owen, 1871; Averianov et al. 2013). ‘Dryolestoidae’ turn out to be paraphyletic, as in the majority of previous studies but contrary to Martinelli et al. (2021). The ‘Paurodontidae’ appear to be paraphyletic, as *Drescheratherium* Krebs, 1998, which is usually identified as a ‘paurodontid’, is placed as an early-branching Dryolestidae in a polytomy with *Henkelotherium*, the latter being considered as a dryolestid or an early ‘dryolestoid’ by some studies (e.g., Rougier et al. 2012; Martinelli et al. 2021). However, this may be due to the large number of missing data for *Drescheratherium* (130 characters out of 190 are coded as missing data or inapplicable, i.e., 68% of the characters, and even 81% if we consider only the

160 informative characters). Our analysis confirms that ‘paurodontids’ are stem dryolestids (Averianov et al. 2013). *Anthracoolestes* appears as a member of the ‘paurodontid’ stem dryolestids, grouped with *Tathiodon* Simpson, 1927, *Paurodon* and *Euthlastus* Simpson, 1927, and thus in a more stemward position than what was found by Averianov et al. (2014), who considered it as sister taxon of all other dryolestids. However, this grouping is weakly supported ($b = 1$). *Thereuodon* Sigogneau-Russell, 1989 is placed within Dryolestidae, close to *Krebsotherium*, *Guimarotodus* Martin, 1999 and *Crusafontia*. This is different from the opinions of Martin (1999, 2002), Bonaparte (2002) and Chornogubsky (2011), who had suggested that the teeth of *Thereuodon* were zatherian deciduous premolars. However, here we coded its teeth as molars, following the interpretation of Sigogneau-Russell and Ensom (1998). According to our analysis, spalacotheriids are sister-group of cladotherians, and not of Meridolestida as suggested by Averianov et al. (2013, 2014), and the latter are recovered as cladotherians. *Laolestes* replaces *Krebsotherium* as the sister-group of *Dryolestes*, with a moderate support ($b = 2$). The two newly described “dryolestoids”, *Orretherium tzen* Martinelli et al., 2021, and *Hercynodon germanicus* Martin et al., 2021, appear within the same clades as in the corresponding studies: *Orretherium tzen* as a mesungulatoid meridolestidan (Martinelli et al. 2021), and *Hercynodon germanicus* as a derived dryolestid, sister-group of *Crusafontia* (Martin et al. 2021).

In our phylogenetic analysis, the most important results concern the position of the Meridolestida and of the Donodontidae. The Meridolestida are separated from the other ‘dryolestoids’: dryolestids, ‘paurodontids’ and donodontids are more closely related to zatherians than they are to meridolestidans. This separation is moderately supported ($b = 2$) and provides evidence for a paraphyletic nature of ‘Dryolestoidea’. The KM donodontids are found in a polytomy close to Prototribosphenida (a node-based clade including the common ancestor of *Vincelestes* and of living therians (Wible et al. 1995; Rougier et al. 1996; Luo et

al. 2002)), and thus close to Zatheria (defined as the node-based taxon including *Mus musculus*, *Peramus tenuirostris*, their most recent common ancestor, and all of their descendants), but this proximity is weakly supported ($b = 1$). This possible close relationship is discussed further below.

The 50% majority rule consensus tree (**Fig. 16**) has more or less the same topology as the strict consensus, except that *Thereuodon* forms a clade with *Krebsotherium*. *Peramus* Owen, 1871 and *Arguimus* Dashzeveg, 1979 are grouped in a clade, sister-group of Tribosphenida. *Palaeoxonodon* is sister-group of the clade unifying these two groups and corresponding to Zatheria, and the clade *Nanolestes* Martin, 2002 + *Amphibetulimus*, Lopatin & Averianov, 2007 is sister-group of the clade (*Palaeoxonodon*, Zatheria) within Prototribosphenida. Zatherians are recovered as monophyletic. However, the most significant change is the following: the Donodontidae, even though their five species are still forming a polytomy, are recovered as a distinct clade, sister-group of Prototribosphenida.

<<**Fig. 15 here**>>

<<**Fig. 16 here**>>

In order to test the impact of the collapsing rules on our topologies, we conducted a second analysis, analysis 1b, with the same parameters but using collapsing rule 3 (collapsing branches with no possible support, i.e., keep branches if some optimisation implies support; max. length = 0). This analysis 1b recovered 241 MPTs of 630 steps. The strict consensus tree is identical to that recovered in analysis 1a (**Online Resource 3, Fig. S1**). The 50 % majority rule consensus (**Online Resource 3, Fig. S2**) is nearly identical to that obtained in analysis 1a, but with a major difference. The Donodontidae are still forming a clade which is sister-group of Prototribosphenida, close to Zatheria, but they are now divided in two branches:

Stylodens on the one hand, and a clade grouping all the other donodontid species in a polytomy on the other hand.

Second analysis Within the Donodontidae, our morphological study supports the distinction of the new species *Donodon minor* from the type species *D. perscriptoris* (see Systematic Paleontology above). With exception of their minute size, these teeth of *Donodon minor* are morphologically very close to those of *D. perscriptoris*: the observed minor differences are not sufficient to erect a new genus, but rather a new species of *Donodon*. However, the two species do not form a clade in our phylogenetic analysis. This suggests that the generic characters of *Donodon* are not recognised in the analysis or are highly homoplastic. So, we conducted a second set of analyses with a constrained clade *Donodon*. With the exception of this constraint, the parameters were the same as in the first analysis. Our analysis 2a uses collapsing rule 1. 30 MPTs of 630 steps were found. Their strict consensus is identical to those found in analyses 1a and 1b (**Online Resource 3, Fig. S3**): surprisingly, the constrained clade *Donodon* does not appear on this consensus. The 50% majority rule consensus topology (**Fig. 17**) shows a clade ((*Nanolestes*, *Amphibetulimus*), (*Palaeoxonodon*, ((*Peramus*, *Arguimus*), (*Prokennalestes*, *Kielantherium*))))), and *Thereuodon* and *Krebsotherium* do not form a clade but are recovered in a polytomy at the same node as the clade (*Guimarotodus*, (*Crusafontia*, *Hercynodon*)). The donodontids form a clade which is sister-group of Prototribosphenida, with a 3-branches polytomy: a first branch with *Stylodens*, a second one with the clade (*Amazighodon*, *Anoualestes*), and a third one with the constrained clade (*Donodon perscriptoris*, *Donodon minor*).

<<**Fig. 17 here**>>

In order to test the impact of collapsing rules on the recovered topologies, we conducted an analysis 2b using the same parameters as in 2a but with collapsing rule 3. This analysis 2b recovered 83 MPTs of 630 steps. The strict consensus is nearly identical to those obtained in previous analyses, but this time the constrained generic clade *Donodon* is present within the polytomy that includes other donodontids and Prototribosphenida (**Online Resource 3, Fig. S4**). The 50% majority rule consensus (**Online Resource 3, Fig. S5**) differs from that found in analysis 2a by the presence of a clade (*Thereuodon*, *Krebsotherium*) as the sister-group of (*Guimarotodus*, (*Crusafontia*, *Hercynodon*)) only.

Putting a constraint on the clade (*Donodon perscriptoris*, *Donodon minor*) did not modify the length of the trees we found. Moreover, this constraint does not significantly modify the topology of the trees, which remain roughly similar to what we found in analysis 1, without constraint. Apparently the absence of this generic clade without constraint is only due to a lack of resolution in the matrix and the two species can be grouped in the same genus, as strongly suggested by their morphology.

Discussion

Although our phylogenetic analyses are based on relatively limited morphological data, i.e. mainly isolated molars, they provide important results about the ‘Dryolestoidea’ in general and the Donodontidae in particular. Following our phylogenetic analyses, the ‘Dryolestoidea’ are paraphyletic, in accordance with most recent works since 2012 (Rougier et al. 2012; Averianov et al. 2013, 2014; O’Meara and Thompson 2014; Wible and Rougier 2017), but in disagreement with those of Chimento et al. (2012) and Martinelli et al. (2021), in which they are monophyletic. ‘Paurodontidae’ are also found paraphyletic and recovered as

early diverging Dryolestida. *Thereuodon* is always recovered as a dryolestid, which differs from the interpretation of Martin (1999, 2002), Bonaparte (2002) and Chornogubsky (2011), who considered its teeth to belong to a stem-zatherian. But the most important result of our phylogenetic analyses concerns the position of the Donodontidae. In all our topologies, they are more derived than Meridiolestida; our analyses refute Bonaparte's hypothesis (Bonaparte 1992, 1994, 2002) that a taxonomic radiation of 'dryolestoids' in North Africa was at the origin of the meridiolestidan radiation in South America. In all our analyses, donodontids are closer to prototribosphenidans and zatherians than to any other 'dryolestoid' group, either in polytomy or forming a clade. Bremer indices (b) have been calculated in order to assess the degree of support of the clade grouping donodontids with zatherians and prototribosphenidans, by the mean of a search for suboptimal trees (with scores up to ten worse than best) with TNT. The results are identical for all four analyses: the node grouping donodontids with zatherians and stem-zatherians is weakly supported, with $b = 1$, but it is as well-supported as other widely accepted clades such as Tribosphenida, Dryolestida, Dryolestidae and Mesungulatidae. Moreover, only five of all 37 nodes have a $b > 2$. This result, combined with the fact that the clade (Donodontidae + Prototribosphenida) has been recovered by all of our analyses, strongly supports the hypothesis of a close relationship between Donodontidae and Prototribosphenida – and beyond them with Zatheria. Moreover, this proximity is consistent with the African fossil record, as stem-zatherians and zatherians are known in the Mesozoic of Africa. For instance, the Amphitheriidae, which were thought to be restricted to the Middle and Late Jurassic of Laurasia for a long time (Blainville 1838a, 1838b; Freeman 1979; Martin 2002; Lopatin and Averianov 2007; Martin and Averianov 2010; Martin et al. 2010), are now also known from the Bathonian of Guelb el Ahmar, Morocco (Haddoumi et al. 2016; Lasseron 2020). Stem-zatherians are also known in the Upper Jurassic of Tanzania with *Brancaatherulum* Dietrich, 1927 (Branca 1916; Dietrich 1927;

Heinrich 1991). Possible stem-tribosphenidans ('peramurids') have also been reported from the Upper Jurassic of Tanzania and Ethiopia, with *Tendagurutherium* Heinrich, 1998 (Heinrich 1998) and a fragmentary lower molar (Clemens et al. 2007). The Jurassic-Cretaceous of KM also yielded stem-tribosphenidans (with an unknown species of *Peramus*; Sigogneau-Russell 1999) and two of the oldest known tribosphenidans (*Hypomylos* and *Tribotherium*; Sigogneau-Russell 1991c, 1992, 1995a). Finally, zatherians are also present in the Lower Cretaceous of Cameroon with the genus *Abelodon* (Brunet et al. 1990). The KM site adds to the 'dryolestoid' African fossil record and our phylogenetic analyses suggest that the Donodontidae are on the stem lineage of Zatheria.

Zatherians are currently thought to be of Laurasian origin (Luo et al. 2001). However, the close relationship of the KM donodontids with zatherians found here challenges this view. It favours instead a Pangean distribution of zatherians during the Middle Jurassic or even an African origin of this group.

To further evaluate the relationship between donodontids and prototribosphenidans, and thus between donodontids and zatherians, it is necessary to discuss the synapomorphies supporting this clade in our resulting trees, and to verify if they are consistent with our morphological study. Our morphological observations suggest that all the 'dryolestoid' species from KM should be grouped in one clade, the Donodontidae. Although this clade does not appear in our strict consensus topologies, it is present in a lot of the MPTs (as illustrated by its presence in the 50% majority rule consensus obtained in analysis 2): it appears in 35 out of the 47 MPTs (74.5 %) in analysis 1a, in 121 out of 243 MPTs (49.8%) in analysis 1b, in 24 out of 30 MPTs (80%) in analysis 2a, and in 61 out of 83 MPTs (73.5%) in analysis 2b. The following synapomorphies (visualised in Winclada (Nixon 2002) in the trees) support the monophyly of Donodontidae.

Based on our phylogenetic analyses, 11 synapomorphies were recovered for the node (Donodontidae + Prototribosphenida), while the clade Donodontidae is supported by nine synapomorphies (for the MPTs in which it occurs). Six of these nine synapomorphies are common with those recovered for the grouping (Donodontidae + Prototribosphenida), including 65 (2), 80 (0), 147 (1), 162 (0), 169 (1) and 177 (0). Due to the data missing from our dataset, these six synapomorphies might be homoplastic, but nonetheless they could support either of the two groupings of interest here. To determine which grouping is supported by each of these traits, it is necessary to follow the evolution of their state changes throughout the tree, and if they are consistent with our morphological observations.

Transverse protocristid – character state 65 (2) – is present in Donodontidae but not in Prototribosphenida: it is therefore more likely a synapomorphy of donodontids rather than of prototribosphenidans. The same applies to the keel shape of the mesiolingual surface of the paraconid – character state 147 (1) – and to the notched lingual margin of lower molars – character state 162 (0) –, which are present in donodontids but not in prototribosphenidans. Character state optimisation reveals that the replacement of at least some functional molariforms – character state 177 (0) – is present within Donodontidae but not within Prototribosphenida. However, a replacement of molar-shaped teeth is also present in other cladotherians such as dryolestids, where molariform DP3/dp3 and DP4/dp4 are replaced by premolariform P3/p3 and P4/p4 (Martin 1997): then, this character is not a synapomorphy of Donodontidae. Both donodontids and most derived prototribosphenidans (i.e., *Palaeoxonodon*, *Arguimus*, *Peramus* and *Kielantherium*, but not *Prokennalestes*) have a cingulid cuspule e – character state 80 (0) –, and this feature is more likely to be a synapomorphy of (Prototribosphenida + Donodontidae) rather of Donodontidae alone. Finally, both donodontids, tribosphenidans, *Arguimus* and dryolestids have a wear pattern on the talonid – character state 169 (1). However, in donodontids, and as in dryolestids (Martin et

al. 2020), this wear pattern occurs within the hypoflexid groove, on the labial side of the single talonid cusp, while the wear pattern of derived zatherians takes place within the talonid basin (Martin et al. 2020): thus, this character cannot be regarded as a synapomorphy of either donodontids or prototribosphenidans.

The node (Donodontidae + Prototribosphenida) thus appears relatively well supported by six unambiguous synapomorphies. Among them, two are non-homoplastic (RI = 1): a talonid/protoconid height ratio > 20% (76 (1)), and a hypoconulid elevated above the cingulid level (85 (1)). Another one has a $RI \geq 0.750$ and thus can be considered weakly homoplastic: upper molars are as long as wide, or longer (length/width>0.99) (30 (0); RI = 0.769), a character that we identified as distinctive for donodontids relatively to other ‘dryolestoids’ based on our morphological study. The remaining three characters are strongly homoplastic (RI < 0.750): presence of a cingulid cuspule e on lower molars (80 (0); RI = 0.625); on the dentary, labial and lingual alveolar borders are subequal (height ratio of at least 80%) (94 (0); RI = 0.643); and the paracone is erect, not recumbent nor procumbent (174 (0); RI = 0.417). Other characters, which appeared to be distinctive for Donodontidae relatively to other ‘Dryolestoidea’ and which are close to what is seen in Zatheria, such as the relatively well-developed talonid (74; RI = 0.952), are not present on this list of synapomorphies. Two additional ambiguous synapomorphies were recovered under DELTRAN optimisation, for all four analyses: a metaconid that has more than 40% of the protoconid height (62 (1); RI = 0.737), and a protocristid that is transversely oriented relatively to the longitudinal axis of the molars (145 (2); RI = 0.545). Under ACCTRAN optimisation, seven ambiguous synapomorphies are added to the original set of unambiguous synapomorphies for analyses 1a, 1b and 2a: there are three or fewer upper molars (28 (0)); the absence of a mandibular foramen dorsally to a prominent longitudinal ridge (101 (1)); a downturned angular process (113 (4)); the absence of a functional protocone on the last upper premolar (134 (0)); an

elongated postprotocrista that extends labially beyond the metacone (136 (1)); an oblong m1 outline with strong labial bulge (161 (3)); and a labial orientation of the trigon major axis (178 (0)). For analysis 2b, ACCTRAN optimisation found the same seven additional ambiguous synapomorphies plus another one, the presence of a hypoconid (148 (1)).

The clade Donodontidae, for its part, is supported by six synapomorphies: a metaconid of at least 40% of the protoconid height (62; RI = 0.737); a transversely oriented protocristid on lower molars (65; RI = 0.765); the presence of a mesial transverse cingulid, forming a continuous shelf below the trigonid but without any occlusal function (79; RI = 0.762); a paracristid transversely oriented relatively to the longitudinal axis of lower molars (145; RI = 0.545); a mesiolingual surface of the paraconid forming a keel (147; RI = 0.400); and a notched lingual margin in lower molars (162; RI = 0.375).

The combination of the Bremer indices, the synapomorphies found here and the previously known African fossil record show that the hypothesis of a close relationship between Donodontidae and Prototribosphenida, and thus between Donodontidae and Zatheria, is well supported. The existence of the clade Donodontidae, suggested by their morphology, is supported by the phylogenetic analyses, even though most of its synapomorphies are homoplastic. As all these recovered synapomorphies are consistent with our morphological observations, we included them in the emended diagnosis we propose for this family.

Conclusions

Both our morphological and phylogenetic studies support the hypothesis that the five ‘dryolestoid’ species of Ksar Metlili form a clade and can all be grouped within Donodontidae (even though the phylogenetic evidence for a monophyletic Donodontidae needs to be

regarded with caution, as it appears in only a few of our consensus trees). This clade is well-supported by six synapomorphies which are consistent with our morphological observations and form a unique combination within ‘dryolestoids’. Accordingly, we provide an emended diagnosis of the Donodontidae (see Systematic Paleontology). Contrary to what had been proposed earlier based on the dental morphology of *Donodon perscriptoris* (Sigogneau-Russell 1991a; Bonaparte 1992, 1994, 2002), according to our analyses the donodontids are not at the origin of the meridiolestidan taxonomic radiation in South Africa during the Late Cretaceous, but are more derived than meridiolestidans. Africa appears to have been the centre of a major taxonomic radiation of endemic ‘dryolestoids’, which differ from Laurasian and South American ‘dryolestoids’ not only by their unique dental morphology, but also by their association with tribosphenidan mammals, a pattern unknown elsewhere in the world. Our work also strongly suggests that this clade is closer to stem-zatherians and zatherians (= Prototribosphenida) than to any other ‘dryolestoid’ group: donodontids appear to be on the stem-lineage of zatherians. This close relationship, supported by six synapomorphies, renews the question of the origin of the Zatheria, which were considered to be of Laurasian origin until now. Their proximity with donodontids opens up the possibility of an African or Gondwanan origin of zatherians during the Middle Jurassic, or that they reached a Pangean distribution at that time and then specialised and diversified in Africa, which has an important bearing for the understanding of the phylogenetic, evolutionary and paleobiogeographical history of therian mammals. This evokes the “Garden of Eden” hypothesis (Foote et al. 1999), which postulates an early eutherian origin and basal taxonomic diversification in areas with a poor fossil record, such as Gondwana, followed by dispersal to other (northern) continents that became taxonomic diversification centres (Foote et al. 1999; Murphy et al. 2001; Rich 2008). Our study fits with such a “Garden of Eden” model for the Zatheria, with a centre of origin in poorly sampled areas such as Gondwana and Africa rather than in Laurasia that has

the richest fossil record. It stresses again the importance of Africa for our understanding of the evolution of major vertebrate lineages, including therian mammals. More work is needed to identify more discriminant characters for donodontids, in order to further test their monophyly suggested by the morphology, as well as their interrelationships.

Declarations

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Material availability All specimens are currently deposited at the MNHN, Paris, France. The 2010s specimens will be stored after study at the Aïn Chock Faculty of Science from the Hassan II University, Casablanca, Morocco.

Data availability The matrix and detail of morphological characters used in our phylogenetic analyse are available in **Online Resources 1, 2**.

Code availability Not applicable.

Competing interests The authors declare they have no competing interests related to this research.

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Figure captions

Fig. 1 Geographical and geological context of the Anoual Syncline (Oriental Region, Morocco). **a.** Geographical situation in northwestern Africa; **b.** Simplified geological map, showing the location of the microvertebrate site of Ksar Metlili (KM). Abbreviations: *Fm* Formation, *L* Lower, *U* Upper. Reprinted (with modifications) from Haddoumi et al. (2016), by permission from Elsevier

Fig. 2 Location of the different fossiliferous loci from the Ksar Metlili site (Oriental Region, Morocco), Tithonian – Berriasian. **Top.** Geologic section of the Ksar Metlili Formation (Fm); **Bottom.** Location of the sampled fossiliferous loci from the Ksar Metlili site (2010 field campaign, photo © R. Allain): KM-ASH, KM-A1, KM-A2, KM-B', KM-C, KM-D1 and KM-D2. These loci are only a few meters apart from each other (up to 10-20 m). Reprinted (with modifications) from Lasseron et al. (2020), by permission from Cambridge University Press

Fig. 3 Relative abundances of the different groups of mammaliaforms from the Ksar Metlili site (Oriental Region, Morocco), Tithonian – Berriasian, based on the number of identified elements (N). The minimal number of individuals (MNI) is indicated within the silhouettes. Silhouettes by J. Lacerda ('Dryolestoidea'), P. Riha (Eutriconodonta), A. Neander (Tribosphenida), E. Gröning (Zatheria), M. A. Kingler (non-cladotherian Trechnotheria) and Z. Chuang (Haramiyida)

Fig. 4 Stratigraphic log and sequential evolution of the 'Red Beds' exposed in the Anoual Syncline (Oriental Region, Morocco), with indications of the stratigraphic position of the

Ksar Metlili site (KM, Tithonian – Berriasian). Abbreviations: *Barr* Barremian, *Cr* Cretaceous, *Fm* Formation, *Jur* Jurassic, *limest* limestones, *Turon* Turonian. Modified from Haddoumi et al. 2008

Fig. 5 Dental anatomy and nomenclature of ‘Dryolestoidea’ teeth, illustrated by molars of *Donodon perscriptoris* Sigogneau-Russell, 1991. **a.** Dental anatomy of ‘dryolestoid’ upper molars (illustrated specimen: MCM 557, right upper molar); **b.** Dental anatomy of ‘dryolestoid’ lower molars (illustrated specimen: MCM 558, left lower molar). Scale bar equals 1 mm. 3D models based on CT-scan data

Fig. 6 Lower molars of *Donodon* in occlusal (top) and mesial (bottom) views, showing the pyramidal shape of the paraconid, outlined with dashed line. **a.** MCM 558, left lower molar of *Donodon perscriptoris*; **b.** MCM 588, left lower molar of *Donodon minor* sp. nov. Scale bar equals 1 mm. 3D models based on CT-scan data

Fig. 7 *Donodon perscriptoris* Sigogneau-Russell, 1991, Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Upper molars. **a.** MCM 557 (holotype), right upper molar; **b.** MCM 559, left upper molar; **c.** MCM 603, left upper molar; **d.** KM-A1-2, left upper molar; **e.** KM-B’-11, right upper molar; **f.** KM-B’-95, right upper molar. Occlusal (left), mesial (middle left), distal (center), labial (middle right) and lingual (right) views. Scale bars equals 1 mm. a-d, f: 3D models based on CT-scan data. e: SEM photographs

Fig. 8 *Donodon perscriptoris* Sigogneau-Russell, 1991, Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Lower molars. **a.** MCM 558, left mandible fragment with the last two molars; **b.** MCM 581, left lower molar. Occlusal (left), mesial (middle left), distal

(middle), labial (middle right) and lingual (right) views. Scale bar equals 1 mm. 3D models based on CT-scan data

Fig. 9 *Donodon minor* sp. nov., Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Upper molars. **a.** MCM 595 (holotype), right upper molar; **b.** MCM 594, right upper deciduous premolar; **c.** KM-D2-5, left upper deciduous premolar. Occlusal (left), mesial (middle left), distal (middle), labial (middle right) and lingual (right) views. Scale bar equals 1 mm. 3D models based on CT-scan data

Fig. 10 *Donodon minor* sp. nov., Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Lower molars. **a.** MCM 588, left lower molar; **b.** MCM 586, left lower deciduous premolar. Occlusal (left), mesial (middle left), distal (middle), labial (middle right) and lingual (right) views. Scale bar equals 1 mm. 3D models based on CT-scan data

Fig. 11 *Stylodens amerrukensis* gen. et sp. nov., Ksar Metlili (oriental Region, Morocco), Tithonian – Berriasian. Upper molars. **a.** MCM 578 (holotype), right upper molar; **b.** MCM 579, right upper molar. Occlusal (left), mesial (middle left), distal (middle), labial (middle right) and lingual (right) views. Scale bar equals 500 μ m. 3D models based on CT-scan data

Fig. 12 *Anoualestes incidens* gen. et sp. nov., Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Lower teeth. **a.** KM-B'-97 (holotype), left lower molar; **b.** KM-B'-1, right lower molar; **c.** KM-A1-1, left lower ?premolar. Occlusal (left), mesial (middle left), distal (middle), labial (middle right) and lingual (right) views. Scale bar equals 1 mm. a, b: 3D models based on CT-scan data; c: SEM photographs

Fig. 13 *Amazighodon orbis* gen. et sp. nov., Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Lower molars. **a.** MCM 618 (holotype), left lower molar; **b.** KM-B'-2, right lower molar. Occlusal (left), mesial (middle left), distal (middle), labial (middle right) and lingual (right) views. Scale bar equals 500 μ m. 3D models based on CT-scan data

Fig. 14 Box and whisker plot of the cheek teeth dimensions (mm) of the five donodontid species from Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. **a.** Maximum crown height; **b.** Maximum crown length in occlusal view. (c) Maximum crown width in occlusal view

Fig. 15 Strict consensus of 47 most parsimonious trees of 630 steps, obtained with TNT, resulting from analysis 1a (collapsing rule 1). L = 657; CI = 0.361; RI = 0.676. Values above the nodes correspond to Bremer indices. Abbreviations: *A* Alethinotheria, *C* Cladotheria, *D* Dryolestida, *d* Dryolestidae, *M* Meridiolestida, *m* Mesungulatoidea, *P* Prototribosphenida, *S* Spalacotheriidae, *T* Trechnotheria, *t* Tribosphenida. The same topology is recovered for strict consensus of analyses 1b and 2a (see text and **Online Resource 3, Figs. S1, S2**).

Fig. 16 50% majority rule consensus of 47 most parsimonious trees of 630 steps, obtained with TNT, resulting from analysis 1a (collapsing rule 1). L = 645; CI = 0.367; RI = 0.686. Abbreviations: *Z* Zatheria; see Fig. 15 caption for other abbreviation meaning

Fig. 17 50% majority rule consensus of 30 most parsimonious trees of 630 steps, obtained with TNT, resulting from analysis 2a (collapsing rule 1, constraint on generic clade *Donodon*). L = 631; CI = 0.376; RI = 0.696. Abbreviations: *do* = Donodontidae; Abbreviations: *Z* Zatheria; see Fig. 15 caption for other abbreviation meaning

Table captions

Table 1 Mammaliaform species from the Ksar Metlili site (Oriental Region, Morocco), Tithonian – Berriasian, described prior to this work, and first published reference

Table 2 Proportions (%) of dental and mandibular characters that have been be scored in our taxon/character matrix (i.e., missing and non-applicable data excluded), and total proportion of scored characters. Taxa are ordered by decreasing total proportion of scored characters, except for the outgroup. Donodontidae are shown in bold

Table 3 Measurements (mm) of the Donodontidae cheek teeth from Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Values correspond to minimum and maximum dimensions observed for each species. Upper case letters are for upper molars, lower case letters are for lower molars. Abbreviations: *H*, *h* maximum crown height, *L*, *l* maximum crown mesiodistal length in occlusal view, *W*, *w* maximum crown labiolingual width in occlusal view

Online Resources

Online Resource 1 List of the 190 morphological characters used in our phylogenetic analyses, and detail of their characters states and coding.

Online Resource 2 Character matrix used in our cladistic analyses, in TNT format.

Online Resource 3 Supplementary topologies issued from our phylogenetic analyses. It includes the strict consensus tree (Fig. S1), and the 50% majority rule consensus tree of analysis 1b (Fig. S2), the strict consensus tree of analysis 2a (Fig. S3), and the strict consensus tree (Fig. S4) and the 50% majority rule consensus tree of analysis 2b (Fig. S5).

Table 1 Mammaliaform species from the Ksar Metlili site (Oriental Region, Morocco), Tithonian – Berriasian, described prior to this work, and first published reference

| Taxon | First reference |
|-------------------------------------|---------------------------|
| Mammaliaformes | |
| Haramiyida | |
| <i>Hahnodon taqueti</i> | Sigogneau-Russell (1991b) |
| <i>Denisodon moroccensis</i> | Hahn and Hahn (2003) |
| Mammalia | |
| Eutriconodonta | |
| <i>Dyskritodon amazighi</i> | Sigogneau-Russell (1995b) |
| <i>Ichthyoconodon jaworowskorum</i> | Sigogneau-Russell (1995b) |
| <i>Gobiconodon palaios</i> | Sigogneau-Russell (2003) |
| <i>Kryptotherium polysphenos</i> | Sigogneau-Russell (2003) |
| Trechnotheria | |
| <i>Atlasodon monbaroni</i> | Sigogneau-Russell (1991a) |
| <i>Microderson laaroussii</i> | Sigogneau-Russell (1991a) |
| <i>Thereuodon dahmanii</i> | Sigogneau-Russell (1989) |
| <i>Minimus richardfoxi</i> | Sigogneau-Russell (1999) |
| <i>Afriquiamus nessovi</i> | Sigogneau-Russell (1999) |
| ‘Dryolestoidea’ | |
| <i>Donodon perscriptoris</i> | Sigogneau-Russell (1991a) |
| Zatheria | |
| <i>Peramus</i> sp. | Sigogneau-Russell (1999) |
| Stem Tribosphenida | |
| <i>Hypomylos phelizoni</i> | Sigogneau-Russell (1992) |
| <i>Hypomylos micros</i> | Sigogneau-Russell (1995a) |
| <i>Tribotherium africanum</i> | Sigogneau-Russell (1991c) |

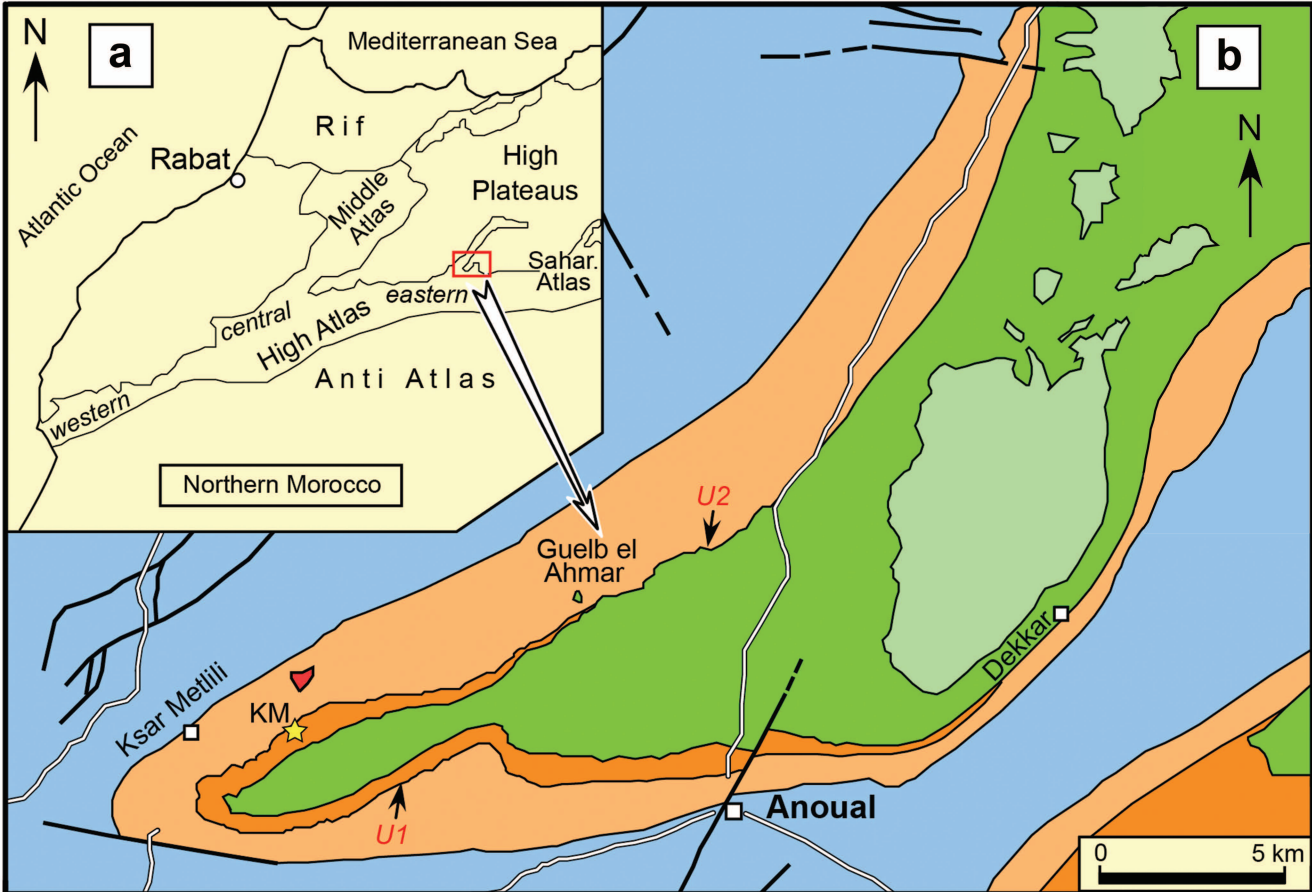
Table 2 Proportions (%) of dental and mandibular characters that have been scored in our taxon/character matrix (i.e., missing and non-applicable data excluded), and total proportion of scored characters. Taxa are ordered by decreasing total proportion of scored characters, except for the outgroup. Donodontidae are shown in bold

| | Dental characters | Mandibular characters | Total |
|---|------------------------------|----------------------------------|--------------|
| <i>Phascolotherium bucklandi</i> (outgroup) | 51.97 | 89.47 | 59.47 |
| <i>Prokennalestes</i> spp. | 99.34 | 78.95 | 95.26 |
| <i>Dryolestes leiriensis</i> | 92.76 | 100 | 94.21 |
| <i>Vincelestes neuquenianus</i> | 92.11 | 94.74 | 92.63 |
| <i>Laolestes eminens</i> | 89.47 | 100 | 91.58 |
| <i>Peramus tenuirostris</i> | 88.82 | 100 | 91.05 |
| <i>Amblotherium gracile</i> | 83.55 | 100 | 86.84 |
| <i>Amblotherium pusillum</i> | 82.89 | 100 | 86.32 |
| <i>Dryolestes priscus</i> | 84.21 | 92.11 | 85.79 |
| <i>Kiyatherium cardiodens</i> | 85.53 | 84.21 | 85.26 |
| <i>Zhangheotherium quiquecuspidens</i> | 76.97 | 84.21 | 85.26 |
| <i>Peligrotherium tropicalis</i> | 83.55 | 84.21 | 83.68 |
| <i>Spalacotherium tricuspidens</i> | 83.55 | 81.58 | 83.16 |
| <i>Coloniatherium cilinskii</i> | 85.53 | 65.79 | 81.58 |
| <i>Crusafontia cuencana</i> | 76.97 | 100 | 81.58 |
| <i>Henkelotherium guimarotae</i> | 80.26 | 86.84 | 81.58 |
| <i>Cronopio dentiactus</i> | 76.63 | 86.84 | 79.47 |
| <i>Necrolestes patagonensis</i> | 75.66 | 94.74 | 79.47 |
| <i>Maotherium sinense</i> | 82.89 | 57.89 | 77.89 |
| <i>Tinodon bellus</i> | 76.32 | 84.21 | 77.89 |
| <i>Amphitherium prevostii</i> | 67.76 | 100 | 74.21 |
| <i>Paurodon valens</i> | 75 | 65.79 | 73.16 |
| <i>Kielantherium gobiense</i> | 71.05 | 68.42 | 70.53 |


| | | | |
|--------------------------------------|--------------|-------------|--------------|
| <i>Yermakia domitor</i> | 65.79 | 84.21 | 69.47 |
| <i>Nanolestes drescherae</i> | 71.71 | 55.26 | 68.42 |
| <i>Spalacolestes cretulablatta</i> | 67.11 | 52.63 | 64.21 |
| <i>Amphilestes broderipi</i> | 57.89 | 84.21 | 63.16 |
| <i>Krebsotherium lusitanicum</i> | 51.97 | 92.11 | 60 |
| <i>Gobiotheriodon infinitus</i> | 55.92 | 68.42 | 58.42 |
| <i>Leonardus cuspidatus</i> | 71.71 | 5.26 | 58.42 |
| <i>Reigitherium bunodontum</i> | 63.16 | 39.47 | 58.42 |
| <i>Mesungulatum houssayi</i> | 69.08 | 13.16 | 57.89 |
| <i>Guimarotodus inflatus</i> | 59.92 | 42.11 | 53.16 |
| <i>Donodon perscriptoris</i> | 61.84 | 7.89 | 51.05 |
| <i>Orretherium tzen</i> | 57.23 | 26.32 | 51.05 |
| <i>Tathiodon agilis</i> | 61.84 | 5.26 | 50.53 |
| <i>Palaeoxonodon ooliticus</i> | 61.18 | 2.63 | 49.47 |
| <i>Arguimus khosbajari</i> | 53.29 | 31.59 | 48.95 |
| <i>Donodon minor</i> | 61.18 | 0 | 48.95 |
| <i>Amphibetulimus krasnolutskii</i> | 26.32 | 31.59 | 41.05 |
| <i>Anthracolestes sergei</i> | 36.18 | 50 | 38.95 |
| <i>Anoualestes incidens</i> | 43.42 | 0 | 34.74 |
| <i>Hercynodon germanicus</i> | 43.42 | 0 | 34.74 |
| <i>Drescheratherium acutum</i> | 38.16 | 0 | 30.53 |
| <i>Amazighodon orbis</i> | 36.18 | 0 | 28.95 |
| <i>Euthlastus cordiformis</i> | 25.66 | 2.63 | 21.05 |
| <i>Stylodens amerrukensis</i> | 25 | 0 | 20 |
| <i>Thereuodon dahmanii</i> | 21.71 | 0 | 17.37 |

Table 3 Measurements (mm) of the Donodontidae cheek teeth from Ksar Metlili (Oriental Region, Morocco), Tithonian – Berriasian. Values correspond to minimal and maximal dimensions observed for each species. Upper case letters are for upper molars, lower case letters are for lower molars. Abbreviations: *H*, *h* maximum crown height, *L*, *l* maximum crown mesiodistal length in occlusal view, *W*, *w* maximum crown labiolingual width in occlusal view


| | Upper molars | | | Lower molars | | |
|---|--------------|-----------|-----------|--------------|-----------|-----------|
| | H | L | W | h | l | w |
| <i>Donodon perscriptoris</i> | 0.99-1.21 | 0.92-1.75 | 0.91-1.35 | 1.27-1.40 | 1.47-1.62 | 0.93-1.13 |
| <i>Donodon minor</i> sp. nov. | 0.65-0.83 | 1.01-1.12 | 0.56-0.68 | 0.84-0.97 | 0.95-1.18 | 0.53-0.72 |
| <i>Stylodens amerrukensis</i> gen. et sp. nov. | 0.55-0.61 | 0.78-0.80 | 0.63-0.64 | ? | ? | ? |
| <i>Anoualestes incidens</i> gen. et sp. nov. | ? | ? | ? | 0.66-1.06 | 1.28-1.46 | 0.64-0.78 |
| <i>Amazighodon orbis</i> gen. et sp. nov. | ? | ? | ? | 0.57-0.84 | 0.72-0.95 | 0.68-0.77 |




 *U2: Cartographic unconformity*


 Ksar Metlili Fm. (U. Tithonian - L. Berriasian)


 *U1: Erosional disconformity*

 Anoual Fm. (Early Bathonian)

 Marine Jurassic

 Intrusive gabbro and dolerite

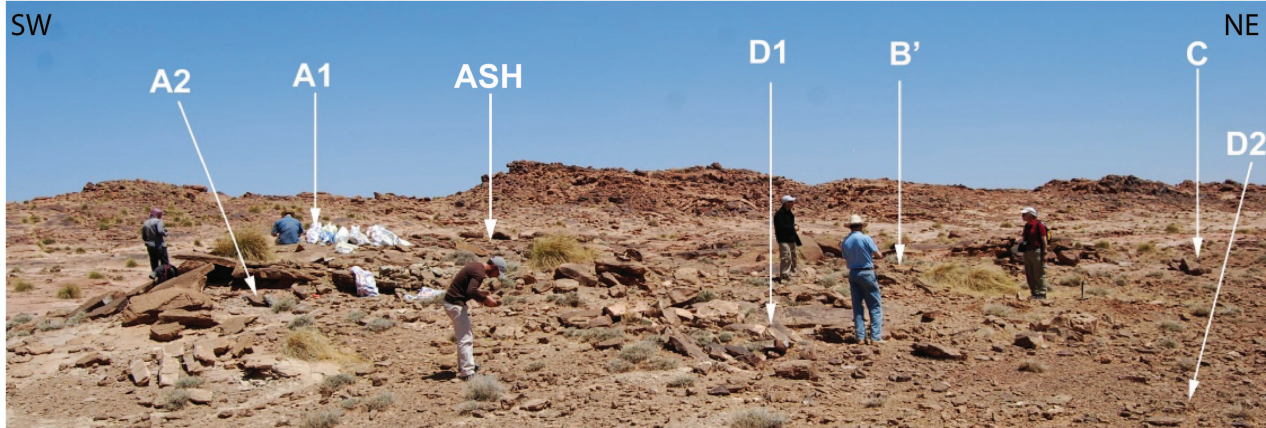
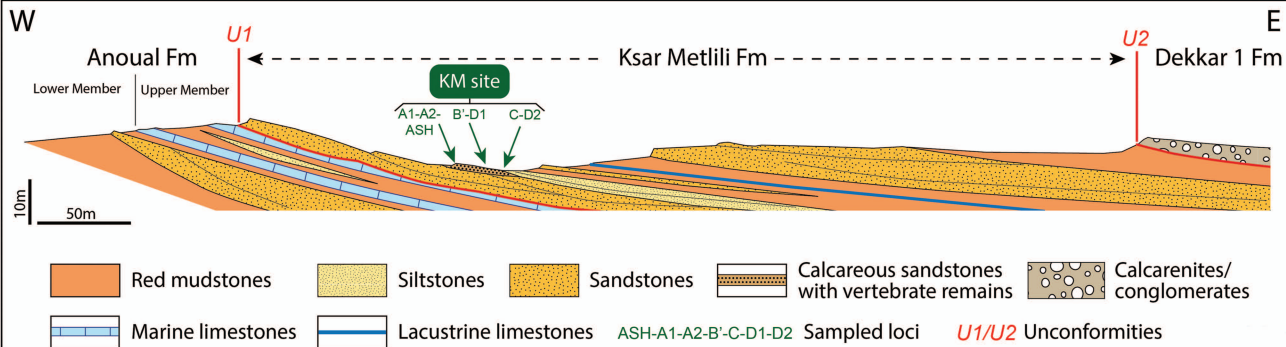
 Cenomanian-Turonian-Senonian

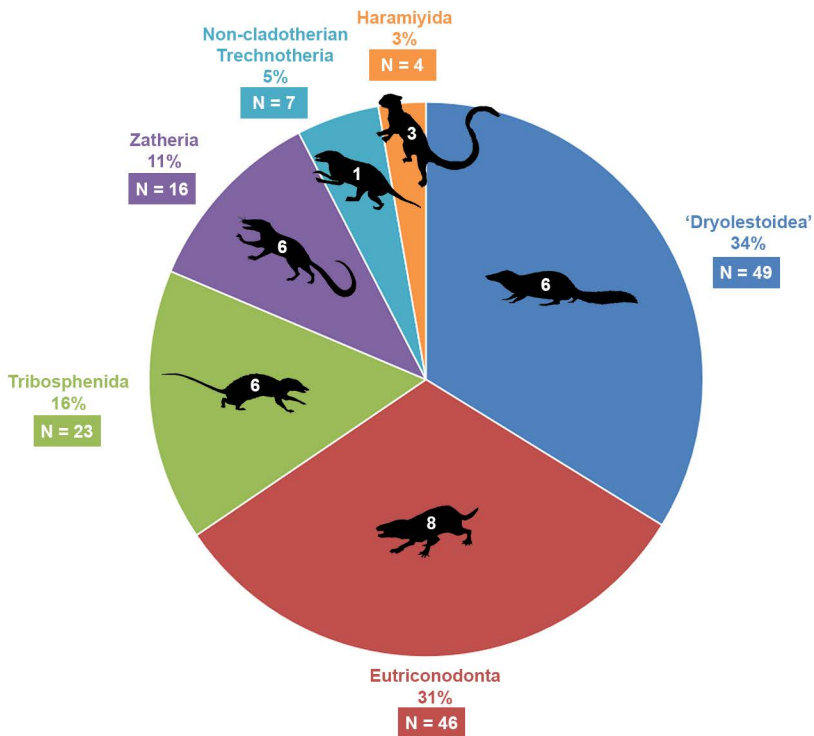
 Dekkar Group (Aptian-Cenomanian)

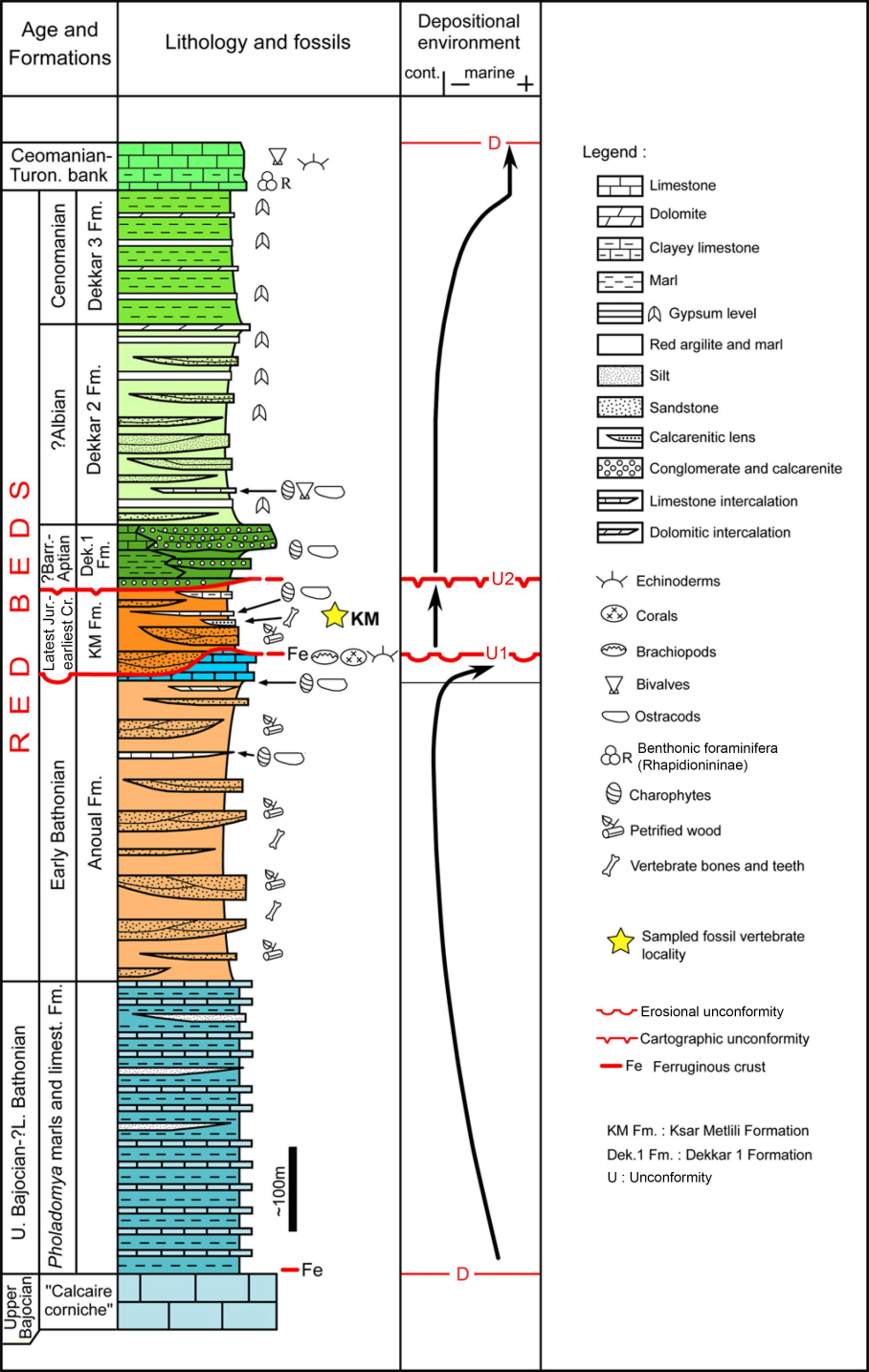
 Fault

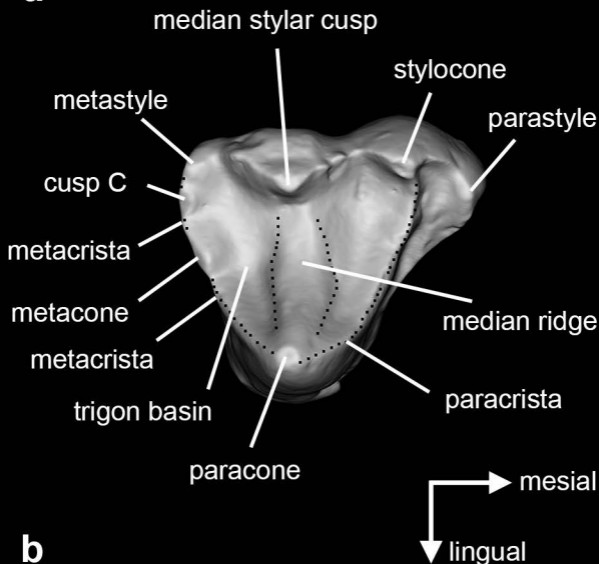
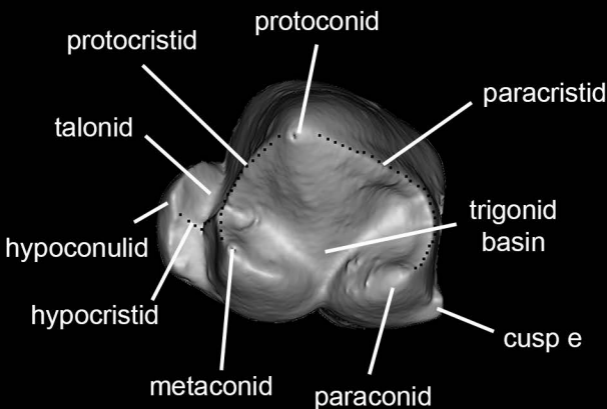
 Road and track

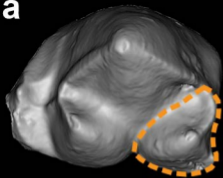
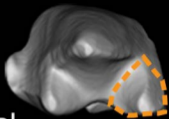
 Vertebrate site







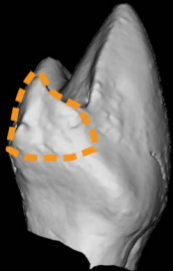
a**b**

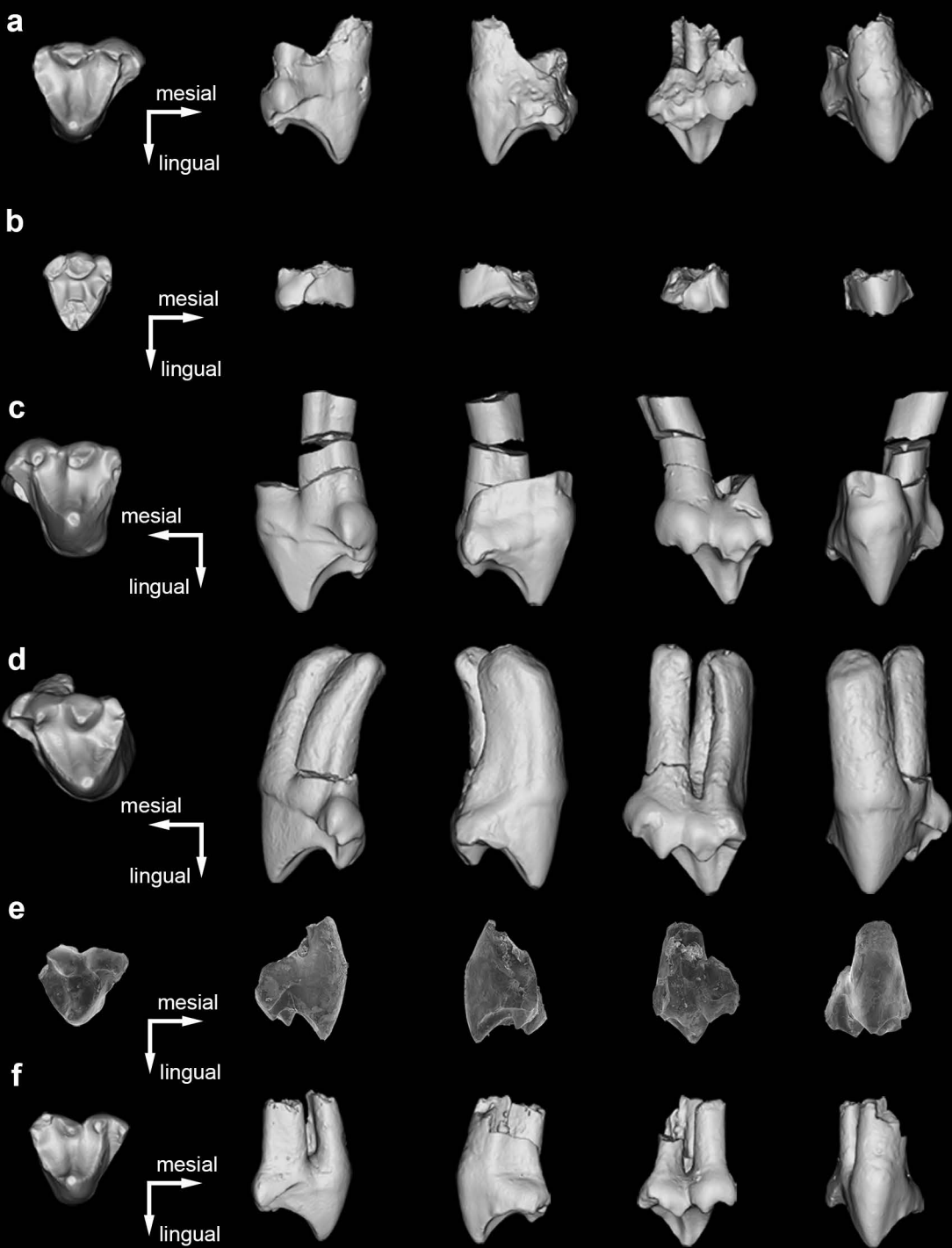
a**b**

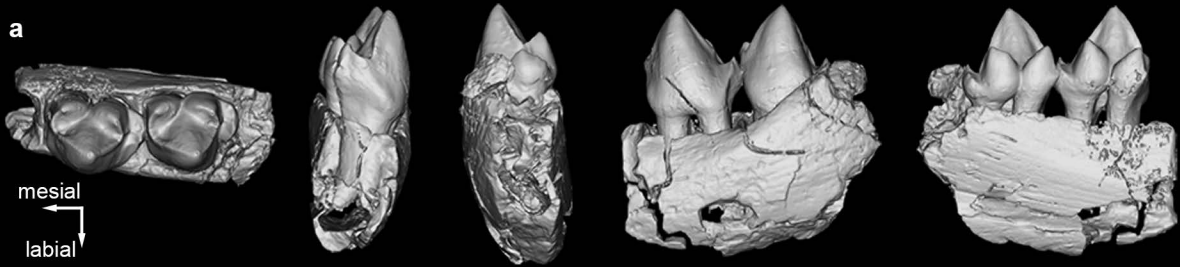
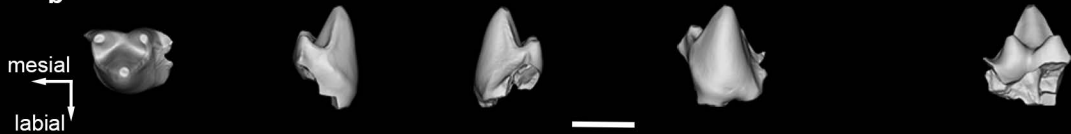
labial

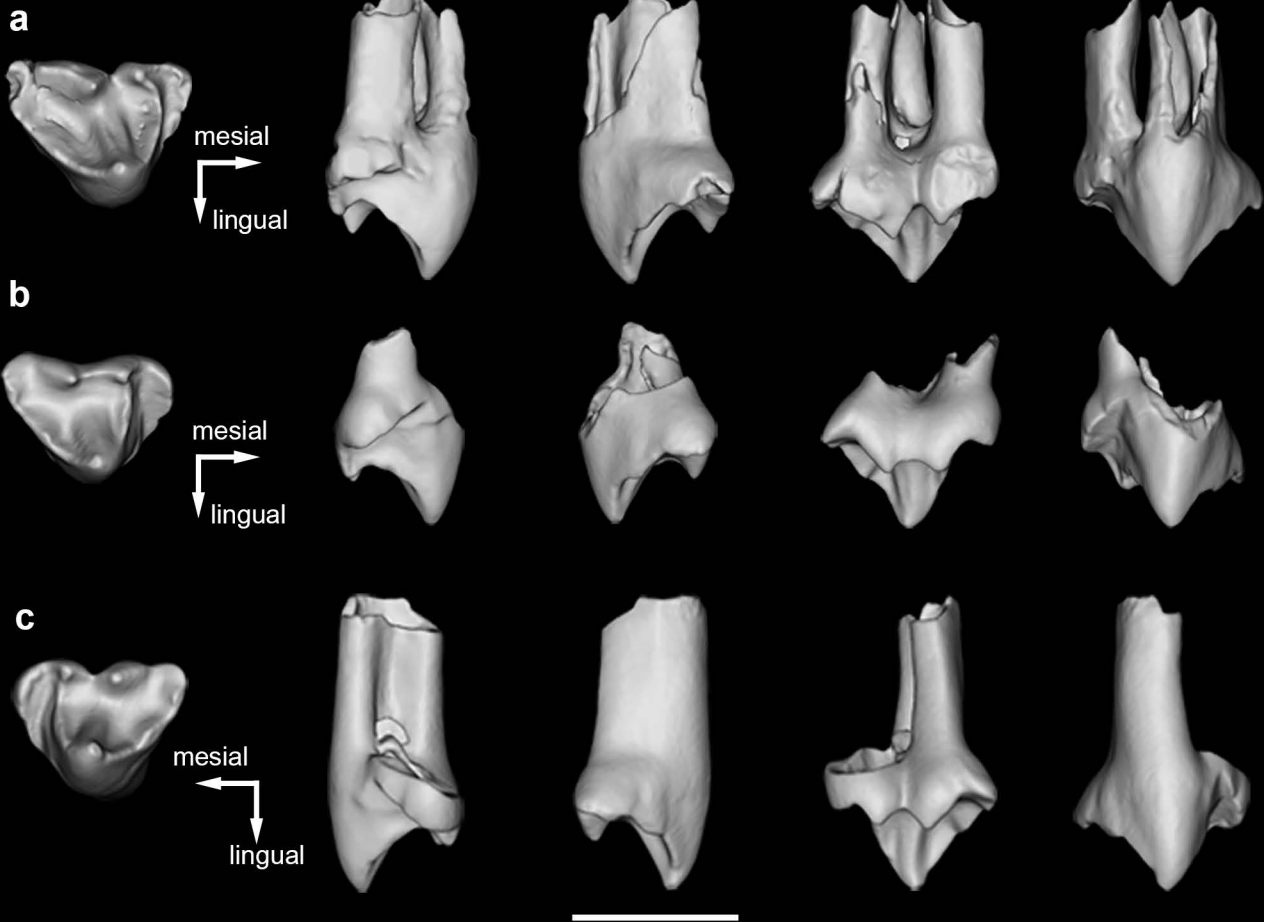


mesial





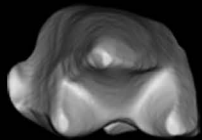
a**b**



a

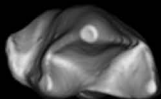
labial

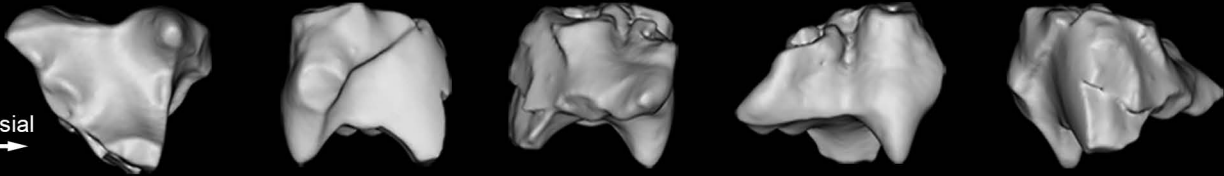
mesial

**b**

labial

mesial

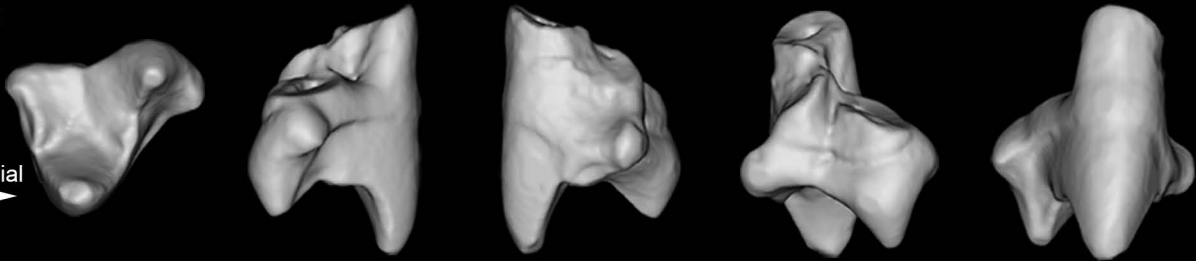


a

mesial



lingual

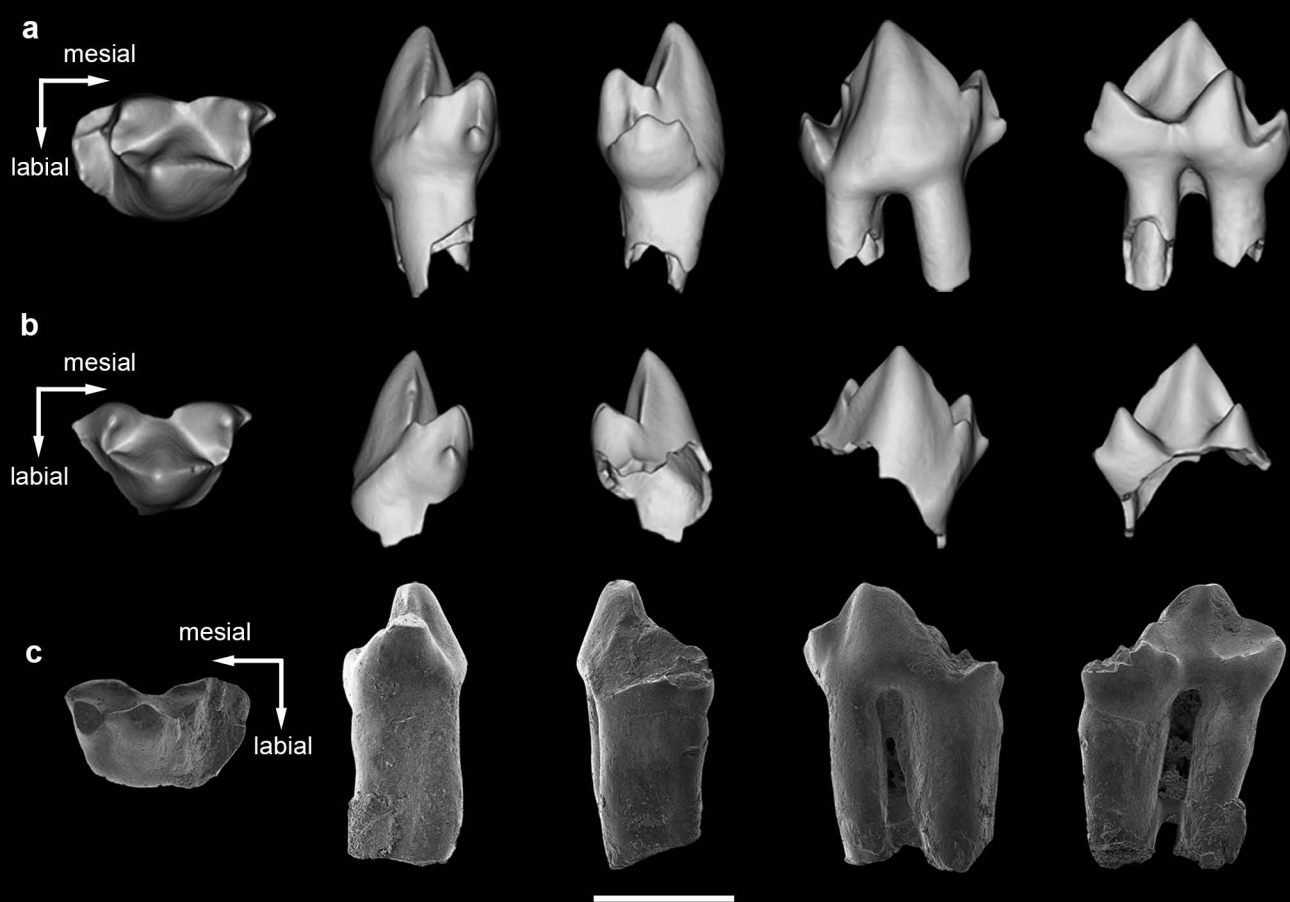
**b**

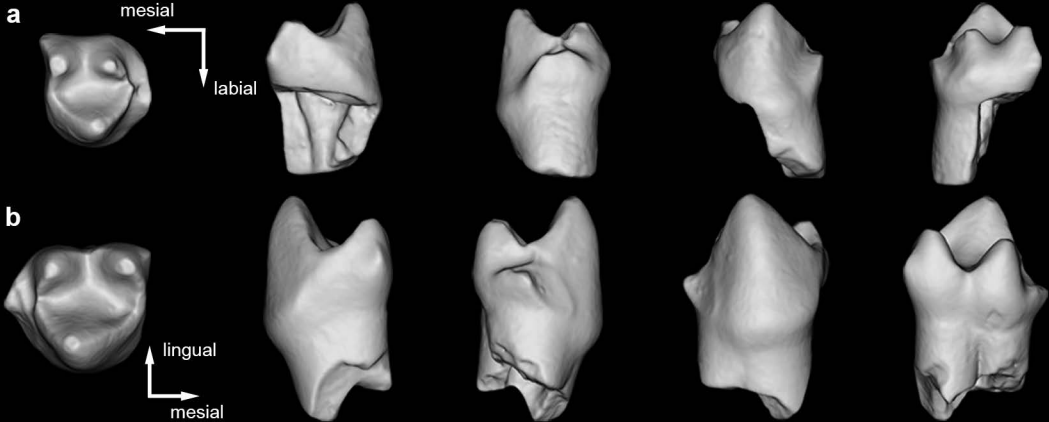
mesial

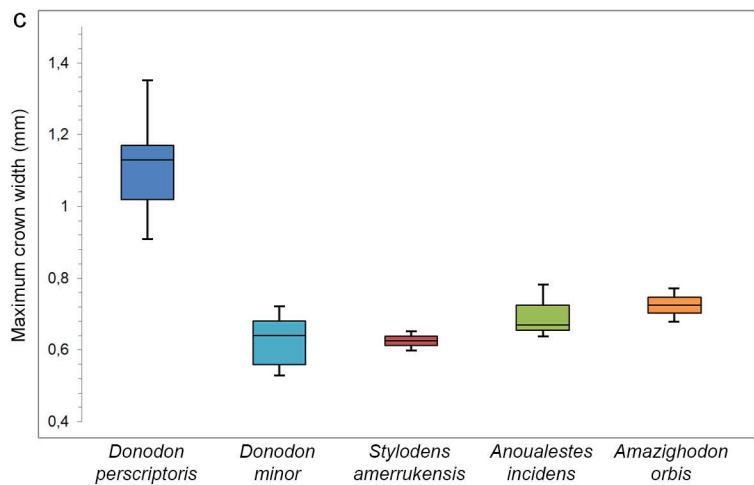
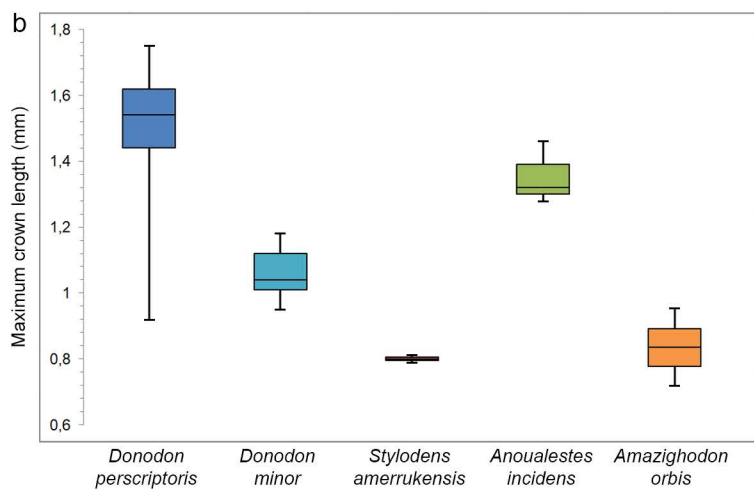
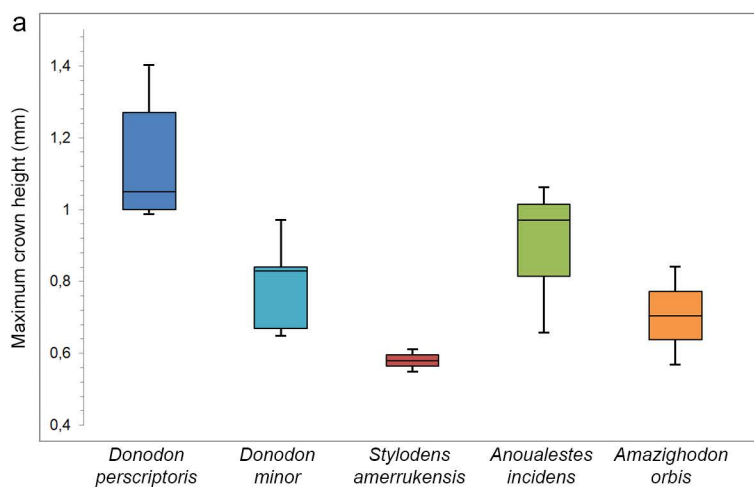


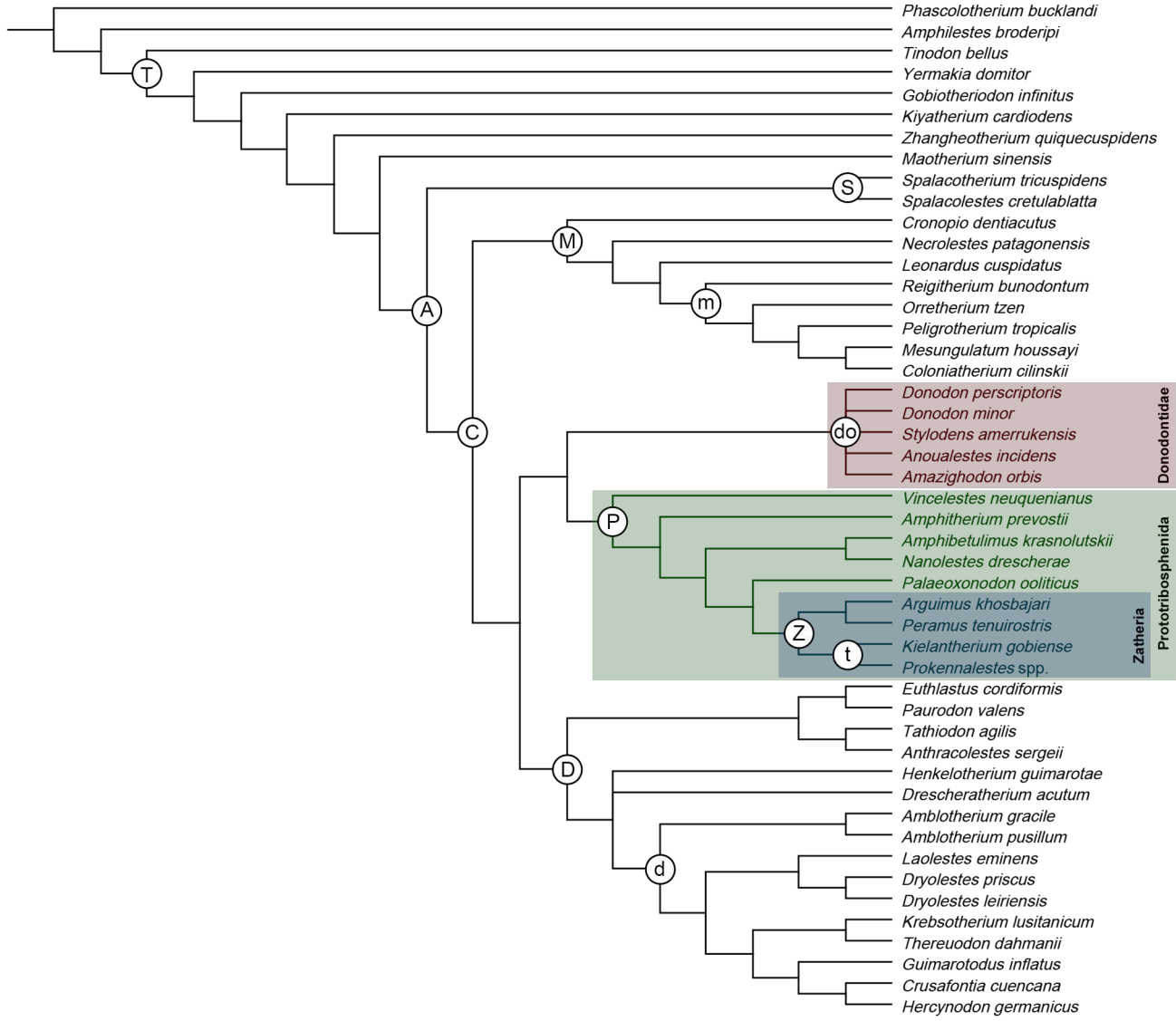
lingual

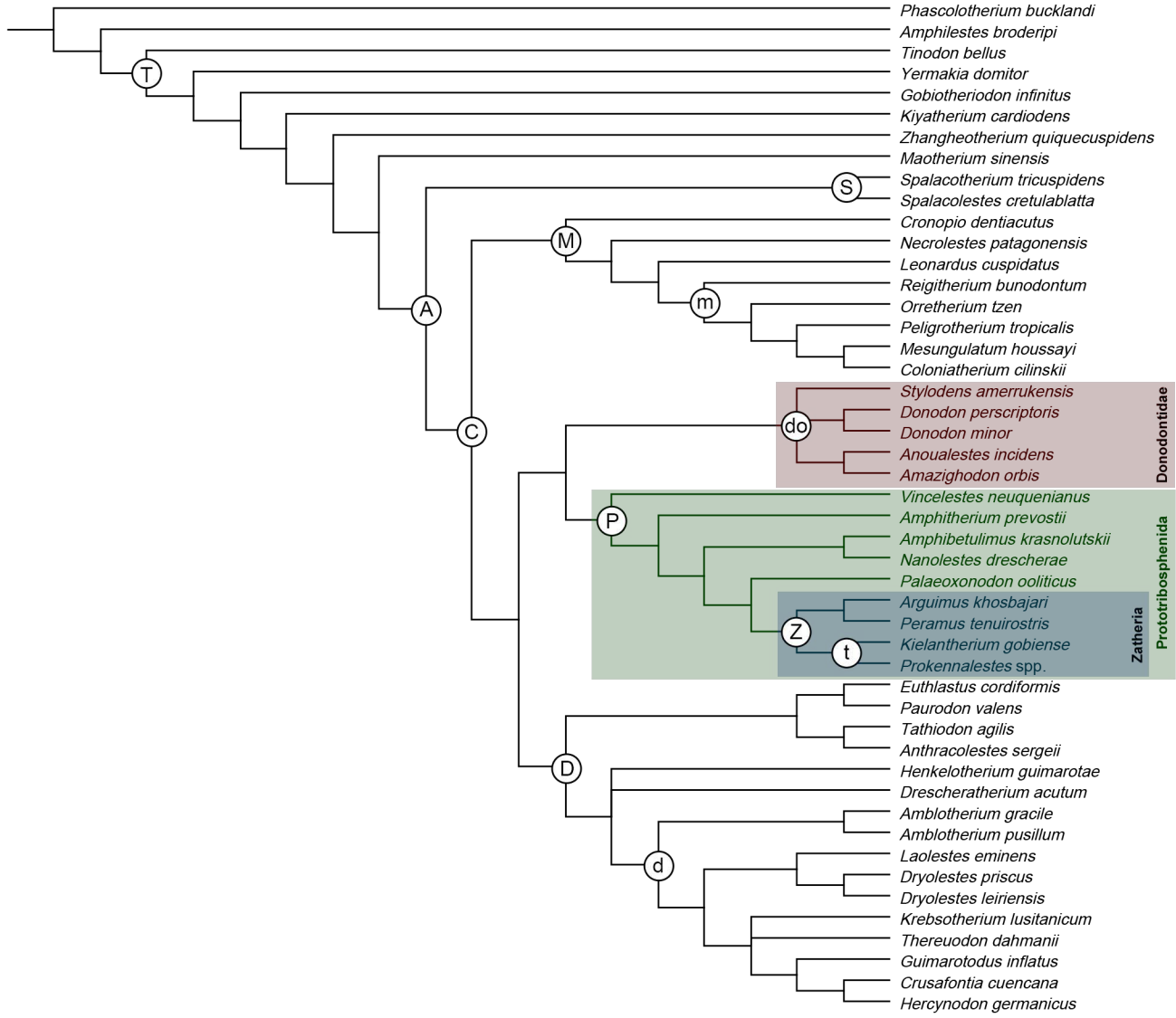












An African radiation of ‘Dryolestoidea’ (Donodontidae, Cladotheria) and its significance for mammalian evolution

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Online Resource 1 – Phylogenetic analyses of ‘Dryolestoidea’: list and detail of characters

This Online Resource presents the list of the 190 morphological characters we used in our two phylogenetic analyses of ‘Dryolestoidea’. It also gives the detail of their character states and how they have been coded in our matrix.

Among these 190 characters, 152 are dental characters and 38 are mandibular ones. 29 illustrate morphoclines and are thus ordered, which is indicated between brackets. 97 characters (51.05%) are taken (and modified for four of them) from Rougier et al. (2011), six (3.16%) are taken (and modified for one of them) from Rougier et al. (2012), 79 (41.58%) are taken (and modified for ten of them) from Averianov et al. (2013), and eight (4.21%) are new.

1. Maxillary incisor

- 0. Absent
- 1. Present

From Rougier et al. 2011 (31)

2. Lower incisors, number (ordered)

- 0. Four or more
- 1. Three
- 2. Fewer than three

From Rougier et al. 2011 (30), modified by Averianov et al. 2013 (2)

3. Lower anteriormost incisor (i1) enlargement and procumbency

- 0. Absent
- 1. Present, both procumbent and enlarged more than 50% the second incisor (i2)

From Rougier et al. 2011 (135)

4. Upper canine, height

- 0. Long, at least twice the height of tallest postcanine
- 1. Short, less than twice the height of the tallest postcanine

From Rougier et al. 2011 (35)

5. Upper canine, number of roots

- 0. Two
- 1. One

From Averianov et al. 2013 (5)

6. Lower canine, shape

- 0. Caniniform (unlike premolars)
- 1. Premolariform (similar in shape and size with last premolar, possibly with posterior cingulid or cingulid cusp)

From Averianov et al. 2013 (6)

7. Lower canine, number of roots

- 0. One
- 1. Two

From Averianov et al. 2013 (7)

8. Upper postcanine tooth-row

- 0. Straight
- 1. Arcuate

From Averianov et al. 2013 (8)

9. Diastema separating P1 from P2 (distance equal or larger than half of the P1). Taxa missing P1 or/and P2 coded inapplicable.

- 0. Present
- 1. Absent

From Rougier et al. 2011 (39), modified by Averianov et al. 2013 (9)

10. Ultimate upper premolar

- 0. Similar in length or shorter and narrower than M1
- 1. Robust, about twice longer and similar in width with M1

From Averianov et al. 2013 (10)

11. Ultimate upper premolar, anterior accessory cusp

- 0. Distinct crown cusp
- 1. Cingular cusp or absent

From Averianov et al. 2013 (11)

12. Ultimate upper premolar, posterior accessory cusp

- 0. Distinct crown cusp
- 1. Cingular cusp or absent

From Averianov et al. 2013 (12)

13. Ultimate upper premolar, cingulum (*ordered*)

0. Complete around the crown
1. Only labial cingulum
2. No cingulum
3. Labial and distal cingulum

From Averianov et al. 2013 (13)

14. Ultimate upper premolar, supernumerary roots

0. Absent
1. Present

From Rougier et al. 2011 (143), modified by Averianov et al. 2013 (14)

15. Lower premolars, number (ordered)

0. Three or less
1. Four
2. Five or more

From Rougier et al. 2011 (38), modified by Averianov et al. 2013 (15)

16. Lower premolars, relative size

0. Gradual increase in size posteriorly
1. p2 smaller than p1 and p3
2. p1-2 similar in size and distinctly smaller than p3-4
3. Only p3-4 present
4. Gradual increase in size but ultimate premolar smaller than penultimate

From Averianov et al. 2013 (16)

17. Lower premolars, anterior accessory cusp

0. Distinct cusp on all premolars
1. Distinct cusp on ultimate premolar, precingulid or absent on more anterior premolars
2. Precingulid or absent on all premolars

From Rougier et al. 2011 (43), modified by Averianov et al. 2013 (17)

18. Lower premolars, lingual cingulid

0. Continuous
1. Incomplete or absent

From Rougier et al. 2011 (49), modified by Averianov et al. 2013 (18)

19. Ultimate lower premolar, size relative to first molar

0. Lower or subequal
1. Taller

From Rougier et al. 2011 (47), modified by Averianov et al. 2013 (19)

20. Ultimate lower premolar, W/L ratio (ordered)

- 0. 0.50 or less
- 1. Between 0.51 and 0.70
- 2. 0.71 or greater

From Rougier et al. 2011 (46), modified by Averianov et al. 2013 (20)

21. Ultimate lower premolar, molarization (arrangement of principal cusps a, b (if present) and c)

- 0. Premolariform (cusps a, b [if present] and c aligned straight or a slight angle)
- 1. Molariform, with three trigonid cusps forming a triangle (distinctive triangulation)

From Rougier et al. 2011 (44), modified by Averianov et al. 2013 (21)

22. Ultimate lower premolar, symmetry of the main cusp a (protoconid)

- 0. Symmetrical, anterior and posterior cutting edges are straight and equal or subequal in length
- 1. Asymmetrical, anterior edge is convex in outline than the posterior edge
- 2. Asymmetrical, posterior edge is concave in outline and longer than the anterior edge
- 3. Asymmetrical, anterior edge is concave and longer than the posterior edge

From Rougier et al. 2011 (42), modified by Averianov et al. 2013 (22)

23. Ultimate lower premolar, distinct distal cingulid cusp d

- 0. Absent, labial and lingual cingulids if present converging to the pointed posterior end of the crown
- 1. Present as cingulid cusp
- 2. Posterior part of the crown rectangular, with a prominent transverse distal cingulid

From Rougier et al. 2011 (45), modified by Averianov et al. 2013 (23)

24. Ultimate lower premolar, supernumerary roots

- 0. Absent
- 1. Present

From Rougier et al. 2011 (144), modified by Averianov et al. 2013 (24)

25. Ultimate lower premolar cusp c (between main cusp a and cingulid cusp d)

- 0. Present
- 1. Absent

From Rougier et al. 2011 (50), modified by Averianov et al. 2013 (25)

26. Ultimate lower premolar, distal root (taxa with single root coded inapplicable)

- 0. Subequal to mesial root
- 1. Large, elongated root, more than 50% of crown length

From Rougier et al. 2011 (147), modified by Averianov et al. 2013 (26)

27. Replacement in first molariform locus

- 0. Present

1. Absent

From Rougier et al. 2011 (134), modified by Averianov et al. 2013 (27)

28. Upper molars, number (*ordered*)

0. Three or less
1. Four
2. Five
3. Six
4. Seven or eight

From Rougier et al. 2011 (127), modified by Averianov et al. 2013 (28)

29. Upper molars, contact

0. Upper molars extensively contact each other
1. Upper molars do not contact each other, or barely do so

From Rougier et al. 2011 (149)

30. Upper molar shape (calculated on widest molar in series when possible) (*ordered*)

0. As long as wide, or longer ($L/W > 0.99$)
1. Wider than long ($0.75 < L/W < 0.99$)
2. Much wider than long ($L/W < 0.75$)

From Averianov et al. 2013 (30)

31. Upper molars, labial cingulum

0. Long, extending between marginally placed small stylocone (or parastyle) and metastyle
1. Reduced to a short ridge between metastyle and enlarged stylocone and displaced somewhat lingually
2. Reduced to few marginal cusplets or absent

From Averianov et al. 2013 (31)

32. Upper molars, precingulum

0. Narrow and closely attached to crown, to absent
1. Developed forming a lingual cusp

From Rougier et al. 2011 (137)

33. Upper molars, postcingulum

0. Narrow and closely oppressed to crown, to absent
1. Developed forming a lingual cusp

From Rougier et al. 2011 (138)

34. Upper molars, pre- and postcingulum elevation

0. Pre- and postcingulum absent, or little differentiated, or close to crown base
1. Elevated reaching occlusal surface

From Rougier et al. 2011 (144), modified by Averianov et al. 2013 (34)

35. Upper molars, number of roots (*ordered*)

0. One
1. Two
2. Three
3. More than three

From Rougier et al. 2011 (141)

36. Upper molars, position of lingual root (taxa with single root coded inapplicable) (*ordered*)

0. Absent
1. Under paracone
2. Under protocone or trigon

Modified from Averianov et al. 2013 (36)

37. First upper molar, supernumerary roots (*ordered*)

0. Absent
1. Present

From Rougier et al. 2011 (146), modified by Averianov et al. 2013 (37)

38. Upper molars, stylocone (=cusp B) (*ordered*)

0. Absent
1. Present, small stylar cusp
2. Present, prominent cusp subequal or larger than paracone

Modified from Rougier et al. 2011 (127)

39. Upper molars, metacone (=cusp C)

0. Present
1. Absent

From Rougier et al. 2011 (126)

40. Upper molars, metacone (=cusp C), position relative to paracone (taxa with metacone absent coded inapplicable)

0. Metacone labial to paracone
1. Metacone approximately aligned mesiodistally with paracone

From Rougier et al. 2012 (131)

41. Upper molars, metacone (=cusp C), shape and size (taxa with metacone absent coded inapplicable)

0. Metacone higher and larger than paracone
1. Cusp-like, smaller but compatible in size with paracone
2. Crest-like, distinctly smaller than paracone

Modified from Averianov et al. 2013 (41)

42. Upper molars, (pre)paracrista

- 0. Extended labially or mesiolabially towards parastyle or small stylocone
- 1. Recurved distally towards enlarged and central stylocone

From Rougier et al. 2011 (122), modified by Averianov et al. 2013 (42)

43. Upper posterior molars, stylocone position

- 0. Along buccal edge
- 1. Separated

From Rougier et al. 2011 (121)

44. Upper molars, median crest

- 0. Absent
- 1. Present, between stylocone and paracone
- 2. Present, between median styler cusp and paracone

Modified from Averianov et al. 2013 (45)

45. Upper molars, crest between stylocone and metacone (taxa with metacone absent coded inaplicable)

- 0. Absent
- 1. Present

From Averianov et al. 2013 (46)

46. Upper molars, ectoflexus

- 0. Present
- 1. Absent

From Rougier et al. 2011 (129), modified by Averianov et al. 2013 (47)

47. Upper molars, parastylar lobe

- 0. Absent or poorly developed
- 1. Present

Modified from Averianov et al. 2013 (48)

48. Upper molars, lingual cingulum (taxa with protocone coded as present)

- 0. Present
- 1. Absent

From Rougier et al. 2012 (141), modified by Averianov et al. 2013 (50)

49. Upper molars, with a functional lingual protocone that grinds against a basin on the lowers (for taxa with unknown upper molars inferred from lowers)

- 0. Absent

1. Present

From Rougier et al. 2011 (94)

50. Penultimate and ultimate upper molars, both have "last molar" appearance with reduced metastylar region

0. Absent
1. Present

From Averianov et al. 2013 (52)

51. First lower molar, trigonid angle (*ordered*)

0. Main cusps forming a simple longitudinal row
1. Acute angle
2. Obtuse angle

Modified from Rougier et al. 2011 (54)

52. First lower molar, supernumerary roots

0. Absent
1. Present

From Rougier et al. 2011 (145), modified by Averianov et al. 2013 (54)

53. Lower molars, number (*ordered*)

0. Three or less
1. Four
2. Five
3. Six or seven
4. Eight or more

Modified from Averianov et al. 2013 (55)

54. Lower molars, unilateral hypsodonty (buccal side much taller than the lingual side or not)

0. Absent
1. Present

From Rougier et al. 2011 (107), modified by Averianov et al. 2013 (56)

55. Lower molars, length to width ratio (L/W)

0. More than 1.1
1. 1.1 or less

From Rougier et al. 2011 (104), modified by Averianov et al. 2013 (57)

56. Lower molars, minimum trigonid angle

0. Main cusps forming a simple longitudinal row
1. Obtuse angle (>95)
2. Acute angle (<90)

Modified from Rougier et al. 2012 (56)

57. Lower molars, contact

0. Lower molars contact each other somewhere along the mesial and distal edges of the crown

1. Lower molars do not contact each other, being separated by interdental spaces

From Rougier et al. 2011 (148)

58. Lower molars, roots (ordered)

0. Subequal

1. Posterior root much smaller

2. Single root (posterior root absent)

3. Anterior root smaller

From Rougier et al. 2012 (136)

59. Lower molars, roots section

0. Oval or circular

1. Mesiodistally compressed

From Rougier et al. 2011 (133)

60. Lower molars, roots separation

0. Roots divided

1. Incipient or incomplete separation

From Rougier et al. 2011 (130), modified by Averianov et al. 2013 (62)

61. Lower molars, main cusps labiolingual compression (at the level of the cusp base but above the cingulid)

0. Present

1. Absent

From Rougier et al. 2011 (66), modified by Averianov et al. 2013 (63)

62. Lower molars, relative height of the primary cusp a (protoconid) to cusp c (metaconid) (measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusp, on m1)

0. Posterior cusp c is less than 40% of the primary cusp a (protoconid)

1. Posterior cusp c is more than 40% of cusp a

From Rougier et al. 2011 (58)

63. Lower molars, paracristid-protocristid in occlusal view

0. In one line

1. Uppercase lambda shaped

2. D-shaped

From Averianov et al. 2013

64. Lower molars, paracristid and protocristid, lowest point

0. Approximately at the same level
1. Distinctly higher on protocristid
2. Higher on paracristid

From Averianov et al. 2013

65. Lower molars, protocristid orientation (*ordered*)

0. Longitudinal
1. Oblique
2. Transverse

From Rougier et al. 2011 (116)

66. Lower molars, labial curvature of protoconid (cusp a) at the base level relative to the curvature of paraconid (cusps b) and metaconid (cusp c)

0. Cusps a, b, and c have the same degree of bulging
1. Cusp a is far more bulging than cusps b, c

From Rougier et al. 2011 (64)

67. Lower molars, paraconid direction (procumbency of the paraconid)

0. Almost vertical, parallel to protoconid (no procumbency)
1. Mesiodorsally directed, deviated from protoconid (paraconid projected as a conical cusp beyond the crown base)

From Rougier et al. 2011 (78), modified by Averianov et al. 2013 (69)

68. Lower molars, paraconid, size relative to metaconid

0. Subequal
1. Paraconid smaller than metaconid
2. Paraconid higher than metaconid

Modified from Rougier et al. 2011 (59)

69. Lower molars, metaconid

0. Pointed
1. Blunt, or chisel-like, or bifid

From Rougier et al. 2011 (117), modified by Averianov et al. 2013 (71)

70. Lower molars, paraconid and metaconid proximity (*ordered*)

0. Bases widely separated
1. Bases approaching each other becoming confluent
2. Single cusp (amphyconid)

From Rougier et al. 2011

71. Lower molars, distal metacristid

- 0. Absent
- 1. Incomplete
- 2. Complete

From Rougier et al. 2011 (119), modified by Averianov et al. 2013 (73)

72. Lower molars, cristid obliqua

- 0. Absent
- 1. Present

From Rougier et al. 2011 (61)

73. Lower molars, hypoflexid (*ordered*)

- 0. Absent or shallow
- 1. Deep (but less than 50% of the talonid width)
- 2. Very deep (>50% of the talonid width)

Modified from Rougier et al. 2011 (81)

74. Lower molars, talonid

- 0. Absent or cingulid cusp d
- 1. Present, single-cusped, heel-like (talonid cusp somewhat lingual to paraconid-metaconid line)
- 2. Present, single-cusped, shelf-like (talonid cusp on paraconid-metaconid line)
- 3. Present, two or three cusped

From Rougier et al. 2011 (83), modified by Averianov et al. 2013 (76)

75. Lower molars, talonid to trigonid ratio

- 0. Narrow (talonid <40% of trigonid)
- 1. Wide (talonid is >40% of trigonid)

From Rougier et al. 2011 (80), modified by Averianov et al. 2013 (77)

76. Lower molars, talonid elevation

- 0. Talonid/protoconid height ratio < 20%
- 1. Talonid/protoconid height ratio > 20%

From Rougier et al. 2011 (91), modified by Averianov et al. 2013 (78)

77. Lower molars, talonid basin

- 0. Absent
- 1. Incipient
- 2. Present

From Rougier et al. 2011 (82), modified by Averianov et al. 2013 (79)

78. Lower molars, cingulid cuspule f

- 0. Absent

1. Present

From Rougier et al. 2011 (69)

79. Lower molars, mesial transverse cingulid (ordered)

0. Absent
1. Present as a continuous shelf below the trigonid without occlusal function
2. Present, having occlusal contact with the upper molar

From Rougier et al. 2011 (70)

80. Lower molars, cingulid cuspule e

0. Present
1. Absent

From Rougier et al. 2011 (68)

81. Lower molars, lingual cingulid on trigonid

0. Complete
1. Incomplete or absent

From Averianov et al. 2013 (83)

82. Lower molars, posterior lingual cingulid

0. Distinctive
1. Weak or absent

From Rougier et al. 2011 (67), modified by Averianov et al. 2013 (84)

83. Lower molars, labial cingulid

0. Absent or incomplete
1. Complete

From Averianov et al. 2013 (85)

84. Lower molars, posterolabial cingulid (postcingulid)

0. Absent or short
1. Present, connected to hypoconulid, extending between talonid and the base of protoconid
2. Present, horizontal above the gum level

Modified from Averianov et al. 2013 (86)

85. Lower molars, hypoconulid (cusp d)

0. At the cingulid level
1. Elevated above the cingulid level

From Rougier et al. 2011 (85), modified by Averianov et al. 2013 (87)

86. Lower molars, accessory cusps on labial side

- 0. Absent
- 1. Present

From Rougier et al. 2011 (128)

87. Lower molars, extensive wear in hypoflexid (facet 3)

- 0. Absent
- 1. Present

From Rougier et al. 2011 (112), modified by Averianov et al. 2013 (89)

88. Wear facets

- 0. Absent for lifetime
- 1. Absent at eruption but later development by extensive wear of the cusps, which changes the shape of the crown
- 2. Development of wear facets on a morphology approximatively present upon eruption (basic crown shape present upon eruption of the teeth, with only limited remodeling by wear facets)

Modified from Rougier et al. 2011 (108) and Averianov et al. 2013 (90)

89. Anterior end of dentary upturned dorsally so the incisors placed above the level of molars

- 0. Absent
- 1. Present

From Averianov et al. 2013 (91)

90. Mandibular symphysis, posterior end

- 0. At canine or p1
- 1. Anterior to canine
- 2. At p2-3 or more posterior

From Averianov et al. 2013 (92)

91. Posterior mental foramen, position (*ordered*)

- 0. In canine and anterior premolar region
- 1. At penultimate premolar
- 2. At ultimate premolar
- 3. At first molar or more posterior

From Rougier et al. 2011 (2), modified by Averianov et al. 2013 (93)

92. Ratio of dentary height to crown height under tallest molar (measured on lingual side)

- 0. Less than twice
- 1. Twice or more

From Averianov et al. 2013 (94)

93. Height of mandibular ramus between canine and last molariform

- 0. Sub-uniform
- 1. Becomes higher posteriorly

From Averianov et al. 2013 (95)

94. Dentary, height of labial alveolar border relative to the lingual border

- 0. Subequal (at least 80%)
- 1. Labial border much lower than the lingual one (less than 80 %)

Modified from Rougier et al. 2011 (4) and Averianov et al. 2013 (96)

95. Masseteric fossa, ventral border

- 0. Absent
- 1. Present as a broad and low crest
- 2. Present as a well-defined and thin crest

From Rougier et al. 2011 (17)

96. Dentary, masseteric process

- 0. Absent
- 1. Present

From Averianov et al. 2013 (98)

97. Meckelian groove in adults

- 0. Present
- 1. Vestigial or absent

From Rougier et al. 2011 (5), modified by Averianov et al. 2013 (99)

98. Meckelian groove, extension (taxa without Meckelian groove coded inapplicable)

- 0. Does not reach mandibular symphysis anteriorly
- 1. Extended between mandibular symphysis and mandibular foramen

From Averianov et al. 2013 (100)

99. Meckelian groove, orientation (taxa without Meckelian groove coded inapplicable)

- 0. Convergent on ventral border
- 1. Parallel to ventral border

From Averianov et al. 2013 (101)

100. Mandibular foramen, position to coronoid process

- 0. Below or near the level of the anterior border of the coronoid process
- 1. Posterior to the anterior edge of the coronoid process (the distance between the mandibular foramen and the level of beginning of the anterior edge of the coronoid process is greater than length of two middle molars)

Modified from Rougier et al. 2011 (18) and Averianov et al. 2013 (102)

101. Mandibular foramen dorsal to prominent longitudinal ridge

- 0. Absent
- 1. Present

From Averianov et al. 2013 (103)

102. Shape of the coronoid process

- 0. Anteroposteriorly broad
- 1. Narrow, separated from condylar process by deep mandibular notch

From Averianov et al. 2013 (104)

103. Tilting of the coronoid process of dentary (measured as the angle between the alveolar line and anterior border of coronoid process) (ordered)

- 0. Coronoid process is strongly reclined and the coronoid angle is obtuse ($>135^\circ$)
- 1. Coronoid process less reclined ($135-115^\circ$)
- 2. Coronoid process is near vertical and the coronoid angle small ($95-115^\circ$)

From Rougier et al. 2011 (26), modified by Averianov et al. 2013 (105)

104. Pterygoid fossa

- 0. Absent
- 1. Restricted to a small area posterior to mandibular foramen
- 2. Expanded on coronoid process

Modified from Rougier et al. 2011 (14) and Averianov et al. 2013 (106)

105. Pterygoid crest (ordered)

- 0. Present, reaching dentary condyle
- 1. Present, extending to base of angular process
- 2. Absent

From Rougier et al. 2011 (15), modified by Averianov et al. 2013 (107)

106. Angular process

- 0. Absent
- 1. Present, as extension of medial pterygoid shelf
- 2. Present, divergent from medial pterygoid shelf

From Rougier et al. 2011 (8), modified by Averianov et al. 2013 (108)

107. Coronoid, or its attachment scar, in adults

- 0. Present
- 1. Absent

From Rougier et al. 2011 (12)

108. Retromolar space, at least half the length of the last molar

- 0. Present

1. Absent

From Rougier et al. 2011 (27), modified by Averianov et al. 2013 (110)

109. Dentary peduncle, orientation

0. Dentary condyle is continuous with the semicircular posterior margin of the dentary
1. Dentary peduncle forms an angle less than 40 degrees to the alveolar margin
2. Dentary peduncle forms an angle of 40 degrees or greater to the alveolar margin

From Rougier et al. 2011 (22), modified by Averianov et al. 2013 (111)

110. Symphysis height

0. Robust, verticalized
1. Slender, oblique, or approaching horizontal

From Rougier et al. 2011 (1)

111. Postdentary trough

0. Present
1. Absent

From Rougier et al. 2011 (3)

112. Groove for replacement of dental lamina

0. Present
1. Absent

From Rougier et al. 2011 (7)

113. Angular process direction

0. Small knobby process, not projected
1. Straight process, posteriorly directed
2. Transversely flaring
3. Inflected
4. Downturned

From Rougier et al. 2012 (9)

114. Antero-posterior position of the angular process relatively to the dentary condyle

0. Anterior position, the angular process is below the main body of the coronoid process
1. Posterior position, the angular process is placed at the level of the posterior end of the coronoid process

From Rougier et al. 2011 (10)

115. Vertical position of the angular process

0. Low, at or near the level of the ventral border of the mandibular horizontal ramus
1. High, at or near the level of the molar alveolar line

From Rougier et al. 2011 (11)

116. Medial fossa on the angular process of the dentary

- 0. Present
- 1. Absent

From Rougier et al. 2011 (13)

117. Pterygoid shelf

- 0. Absent
- 1. Present

From Rougier et al. 2011 (16)

118. Masseteric foramen

- 0. Absent
- 1. Present

From Rougier et al. 2011 (19)

119. Crest of the masseteric fossa along the anterior border of the coronoid process

- 0. Absent or weakly developed
- 1. Present as a distinctive anterior border

From Rougier et al. 2011 (20)

120. Mylohyoid process at the level of the anterior border of the coronoid process

- 0. Absent
- 1. Present

From Rougier et al. 2011 (21)

121. Lower mandibular margin/condylar peduncle

- 0. Not continuous, interrupted by an angular process or a sharp angle
- 1. Continuous as a single line in lateral view

From Rougier et al. 2012 (23)

122. Shape and relative size of the dentary articulation

- 0. Small and dorsoventrally compressed
- 1. Condyle is massive and bulbous, transversely broad in its dorsal aspect
- 2. Condyle mediolaterally narrow and vertically deep, forming a broad arc in lateral outline, either ovoid or triangular in posterior view

From Rougier et al. 2011 (23)

123. Ventral border of the dentary peduncle

- 0. Posteriorly tapering without a condyle
- 1. Columnar or ridge-like
- 2. Ventrally flaring

3. Robust and short

From Rougier et al. 2011 (24)

124. Position of the dentary condyle relatively to the vertical level of the postcanine alveoli

- 0. Below or about the same level as the postcanine alveoli
- 1. Above the level of the postcanine alveoli

From Rougier et al. 2011 (25)

125. Alignment of the ultimate molar to the anterior margin of the coronoid process of the dentary

- 0. Ultimate functional molar is medial to the coronoid process
- 1. Ultimate functional molar is in alignment with the anterior margin of the coronoid process

From Rougier et al. 2011 (28)

126. Shape of the ventral edge of the jaw in the area of the angular process

- 0. Straight
- 1. Convex
- 2. Concave

From Rougier et al. 2012 (30)

127. Incisor replacement

- 0. Alternating and multiple replacement
- 1. Diphyodont replacement or none

From Rougier et al. 2011 (29)

128. Staggered incisor

- 0. Absent
- 1. Present

From Rougier et al. 2011 (32)

129. Canine replacement

- 0. Multiple replacements
- 1. Diphyodont

From Rougier et al. 2011 (33)

130. Replacement of premolariforms

- 0. Multiple replacements
- 1. One replacement or none

From Rougier et al. 2011 (37)

131. Penultimate lower premolar size (ordered)

0. Small and subequal to other premolars
1. Larger than any of the other premolars, longer and/or taller
2. Hypertrophied, dominant tooth in the series

From Rougier et al. 2011 (40)

132. Penultimate lower premolar - paraconid (cusp b)

0. Much smaller than metaconid (cusp c) of the same tooth, or absent
1. Well-developed as an important cusp of the trigonid

From Rougier et al. 2011 (41)

133. Last lower premolar - anterior cusp b (paraconid)

0. Present, at least subequal to cusp c, or posterior cingular cusp of the same tooth
1. Small, much smaller than cusp c or posterior cingular of the same tooth, or vestigial to absent

From Rougier et al. 2011 (43)

134. Last upper premolar - functional protocone

0. Absent
1. Present

From Rougier et al. 2011 (51)

135. Last upper premolar - parastylar hook

0. Present
1. Absent or very small

From Rougier et al. 2011 (52)

136. Development of postprotocrista on upper molars for double rank postvallum shear (for molars with reversed triangulation of molar cusps only)

0. Postprotocrista is short and does not extend labially beyond metacone
1. Postprotocrista is long and extends labially beyond metacone

From Rougier et al. 2011 (55)

137. Precise opposition of upper and lower molars (either one-to-one, or occluding at the opposite embrasure or talonid)

0. Absence of precise opposition of upper and lower molars
1. Present (either one-to-one, or occluding at the opposite embrasure or talonid)

From Rougier et al. 2011 (56)

138. Relative elevation of the bases of the paraconid (cusp b) and the metaconid (cusp c)

0. Almost or at the same level
1. Base of the paraconid higher than the base of the metaconid
2. Base of the metaconid higher than the base of the paraconid

From Rougier et al. 2011 (60)

139. Cristid obliqua orientation (ordered)

0. Oriented to or lingual to the metaconid-protoconid notch
1. Hypertrophied and directed to the posterior part of the metaconid
2. Short and pointed anteriorly between the metaconid-protoconid notch and the protoconid

From Rougier et al. 2011 (62)

140. Lower molar - pre-entocristid on the talonid heel

0. Talonid lacks medial and longitudinal crest
1. Pre-entoconid cristid of talonid is in alignment with the metaconid or with the postmetacristid if the latter is present
2. Pre-entocristid crest is offset from the metaconid and it is lingual to the base of the metaconid

From Rougier et al. 2011 (63)

141. Labial curvature of the main cusps a, b and c at the level of cusp valley of the penultimate and ultimate upper molars

0. Cusps a, b and c have about the same degree of bulging
1. Cusp a is slightly concave (or far less convex than either cusp b or c)

From Rougier et al. 2011 (64)

142. Cingulid shelf wrapping around anterointernal corner of lower molar to extend to the lingual side of the trigonid below the paraconid (ordered)

0. Absent
1. Present, weakly developed and restricted to the mesial aspect of the paraconid base
2. Present, strongly developed, running along most of the lingual base of the paraconid

From Rougier et al. 2011 (71)

143. Interlocking mechanism between two adjacent lower molars

0. Absent
1. Present, posterior cingular cuspule d of the preceding molar fits in between cingular cupsules e and f of the succeeding molar or flat surfaces of mesial cingula or cusp b
2. Present, posterior cingular cuspule d fits in between cingular cuspule e and cusp b of the succeeding molar
3. Present, posterior cingular cuspule d of the preceding molar fits into and embayment or vertical groove of the anterior aspect of cusp b of the succeeding molar

From Rougier et al. 2011 (73)

144. Size ratio of posterior molars (lower molars preferred when available) (ordered)

0. Last three postcanines forming a series of posteriorly decreasing size
1. Penultimate molar is the largest of the molars
2. Ultimate molar is the largest of the molars

From Rougier et al. 2011 (74)

145. Orientation of the paracristid relatively to the longitudinal axis of molars

- 0. Longitudinal
- 1. Oblique
- 2. Transverse

From Rougier et al. 2011 (75)

146. Paraconid presence on lower molars

- 0. Present
- 1. Absent

From Rougier et al. 2011 (76)

147. Mesiolingual surface of paraconid on lower molars

- 0. Rounded
- 1. Forming a keel

From Rougier et al. 2011 (147)

148. Hypoconid

- 0. Absent
- 1. Present

From Rougier et al. 2011 (85)

149. Hypoconulid orientation

- 0. Cusp tip erect or procumbent
- 1. Cusp tip recumbent (reclined posteriorly)

From Rougier et al. 2011 (86)

150. Entoconid

- 0. Absent
- 1. Present but far from hypoconulid, at least equal to one cusp length
- 2. Present and twinned with hypoconulid

From Rougier et al. 2011 (87)

151. Height of the entoconid compared with other talonid cusps

- 0. Lower than the hypoconulid (or even vestigial)
- 1. Subequal height to the hypoconulid

From Rougier et al. 2011 (88)

152. Alignment of the paraconid, the metaconid and the entoconid

- 0. Cusps not aligned
- 1. Cusps aligned

From Rougier et al. 2011 (89)

153. Trigon basin (protocone must be present)

- 0. Absent
- 1. Present, the labial slope of the protocone determines a basin against the lingual slope of the paracone/metacone

From Rougier et al. 2012 (98)

154. Transverse width of protocone on upper molars

- 0. Narrow (distance from the protocone apex to the paracone apex is <0.60 of the total tooth width)
- 1. Strongly transverse (distance from the protocone apex to the paracone apex is >0.60 of the total tooth width)

From Rougier et al. 2011 (95)

155. Anteroposterior development of the lingual region on upper molars (protocone must be present) (*ordered*)

- 0. Narrow (anteroposterior distance medial to the paracone and metacone is <0.30 of the total length)
- 1. Moderate development (distance between position of conules = $0.31-0.50$ of the total tooth length)
- 2. Long (distance between conules >0.51 of the total tooth length)

From Rougier et al. 2011 (96)

156. Conules on upper molars (*ordered*)

- 0. Absent
- 1. Present but weak and without cristae
- 2. Conules distinctive, with cristae

From Rougier et al. 2011 (97)

157. Centrocrista between paracone and metacone of upper molars (only for tribosphenic forms)

- 0. Straight
- 1. V-shaped, with labially directed postparacrista and premetacrista

From Rougier et al. 2011 (99)

158. Upper molars cuspule E

- 0. Present
- 1. Absent

From Rougier et al. 2011 (100)

159. Upper molars interlock

- 0. Absent

1. Tongue-in-groove interlock

From Rougier et al. 2011 (101)

160. Central crest (medianergrat) in triangular upper molariforms

0. Absent
1. Present

From Rougier et al. 2011 (102)

161. Outline of m1

0. Oval-shaped
1. Laterally compressed
2. Oblong with slight labial bulge
3. Oblong with strong labial bulge
4. Triangular or tear-drop shaped
5. Rectangular or slightly rhomboidal

From Rougier et al. 2011 (103)

162. Shape of the lingual margin in lower molars

0. Notched
1. Flat

From Rougier et al. 2011 (105)

163. Aspect ratio of M1

0. Laterally compressed
1. Oval-shaped or spindle-shaped
2. Triangular outline dumbbell-shaped
3. Rectangular or nearly so

From Rougier et al. 2011 (106)

164. Topographic relationships of wear facets to main cusps

0. Lower cusps a and c support two different wear facets (1 and 4) that contact the upper main cusp A
1. Lower cusps a and c support a single wear facet (4) that contacts the upper primary cusp B

From Rougier et al. 2011 (109)

165. Development and orientation of prevallum/postvallid shearing (*ordered*)

0. Absent
1. Present, and obtuse
2. Present, hypertrophied, and transverse

From Rougier et al. 2011 (110)

166. Upper molar - development of facet 1 and preprotocrista (or paracrista) (*ordered*)

- 0. Facet 1 (prevallum crest) is short, and does not extend to the stylocone area
- 1. Wear facet 1 extends beyond into the hook-like area near the stylocône
- 2. Long preprotocrista (below the paracone-stylocone crest) is added to the prevallum shear and extends labially beyond the paracone

From Rougier et al. 2011 (111)

167. Differentiation of wear facet 3 and wear facet 4 (ordered)

- 0. Absent
- 1. Present
- 2. Facet hypertrophied on the flanks of the V-shaped talonid

From Rougier et al. 2011 (112)

168. Orientation of wear facet 4

- 0. Present and oblique to the long axis of the tooth
- 1. Present and forming a more transverse angle to the long axis of the tooth

From Rougier et al. 2011 (113)

169. Wear pattern on the talonid

- 0. Absent
- 1. Present

From Rougier et al. 2011 (114)

170. Direction of jaw movement during occlusion

- 0. Dorsomedial movement
- 1. Dorsomedial movement with a significant medial component
- 2. Dorsoposterior movement

From Rougier et al. 2011 (115)

171. Upper molars, bifid metastyle

- 0. Absent
- 1. Present

From Rougier et al. 2011 (118)

172. Superficial features on occluding surfaces of wear facets 5 and 6 in talonid for basined talonid

- 0. Smooth surface on the talonid (or on cusp d)
- 1. Multiple ridges within the talonid

From Rougier et al. 2011 (120)

173. Stylocone relationships in triangular upper teeth (ordered)

- 0. Stylocone connected to paracrista or mesial to its end
- 1. Stylocone distal to labial ending of the paracrista

2. Stylocone detached of the paracrista occupying a central position on the crown

From Rougier et al. 2011 (122)

174. Upper molars, paracone orientation

0. Erect
1. Recumbent
2. Procumbent

From Rougier et al. 2011 (125)

175. Upper molars, accessory cusps on buccal side

0. Absent
1. Present

From Rougier et al. 2011 (128)

176. Lower molariforms, number of roots

0. One
1. Two
2. Three or more

From Rougier et al. 2011 (131)

177. Replacement of at least some functional molariforms

0. Present
1. Absent

From Rougier et al. 2011 (134)

178. Trigon major axis orientation, as indicated by the distal wall of the trigonid (ordered)

0. Labially
1. Mesially
2. Sharply distal

From Rougier et al. 2011 (136)

179. Prehypoconulid crest (a crest connecting the metaconid with the hypoconulid along the lingual edge of the tooth)

0. Absent
1. Present

From Rougier et al. 2011 (140)

180. Penultimate upper premolar, supernumerary roots

0. Absent
1. Present

From Rougier et al. 2011 (143)

181. Penultimate lower premolar, supernumerary roots

- 0. Absent
- 1. Present

From Rougier et al. 2011 (144)

182. Penultimate lower premolar, distal root

- 0. Subequal to mesial root
- 1. Large, elongated root, more than 50% of the crown length

From Rougier et al. 2011 (147)

183. Upper molars, median stylar cusp (*new*)

- 0. Absent
- 1. Present

184. Extension of the median ridge in triangular upper molariform (central crest/medianergrat) (*new*)

- 0. Reaching the labial edge of the tooth crown
- 1. Interrupting in the middle of the primary trigon basin and not reaching the labial edge of the tooth crown

185. Asymmetry of the paracone crests (*new*)

- 0. Absent, paracrista and metacrista of subequal slope
- 1. Present, paracrista steeper than metacrista

186. Relative position of the paracone to the median stylar cusp (taxa without median stylar cusp coded inaplicable) (*new*)

- 0. Paracone and median stylar cusp labio-lingually aligned, facing each other
- 1. Paracone slightly deported toward parastylar hook, thus not labiolingually aligned with median stylar cusp and not facing it

187. Posteriorly (and labially) deported metastyle (*new*)

- 0. Absent
- 1. Present

188. Paraconid axis with two different orientations in lingual view (forward then upward) (*new*)

- 0. Absent
- 1. Present

189. Orientation of the para- and protocristid in their lingual area (for lower molariforms with triangular occlusal outline) (*new*)

- 0. Divergent
- 1. Parallel
- 2. Convergent

190. Asymmetry of the protoconid crests of posterior lower molars in labial view (for triangular and tribosphenic lower molars) (*new*)

0. Absent, paracristid and protocristid of subequal slope
1. Present, paracristid less steep than protocristid

References

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An African radiation of ‘Dryolestoidea’ (Donodontidae, Cladotheria) and its significance for mammalian evolution

Journal of Mammalian Evolution

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Online Resource 2 – Phylogenetic analyses of ‘Dryolestoidea’: character matrix

The character matrix we used in our cladistics analyses is mainly based on characters extracted from the matrices of Rougier et al. (2011) and Averinaov et al. (2013), with modifications by Rougier et al. (2012), Averianov et al. (2014) and Wible and Rougier (2017), in order to which we added eight new characters. We have chosen to focus the analysis on the dental and mandibular characters, without considering the cranial and postcranial characters that are coded in those matrices: this aims to optimize the final matrix resolution by limiting the amount of missing data (and thus of character optimizations) for the KM species, which are only represented by teeth and a few mandible fragments, as are most of the taxa of our dataset, with a few exceptions (e.g., *Henkelotherium* Krebs, 1991). Furthermore, the additional analyses including the cranial and postcranial characters from the works of Averianov et al. (2013, 2014) that we conducted showed only marginal and minor differences from the topologies recovered without these characters and discussed in this article: the inclusion of cranial and postcranial characters does not modify or add anything to the relationships of the KM donodontids with the other cladotherians. Some taxa (*Groebertherium* Bonaparte, 1986, *Maothierium asiaticum* Ji et al., 2009, *Achyrodon* Owen, 1871, *Phascolestes* Owen, 1871 and *Mozomus* Li et al., 2005) have been removed due to a lack of reliable information on their teeth and mandibles. The final matrix includes 48 taxa and 190 characters. 16 characters are constant (114, 115, 120, 122, 127, 130, 137, 138, 152, 153, 157, 159, 164, 168, 172, 179) and 14 are parsimony-uninformative (34, 110, 111, 112, 123, 125, 136, 139, 146, 150, 151, 154, 155, 156).

The matrix is given here in its TNT script.

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190 48
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Amphilestes_broderipi
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Tinodon_bellus
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Yermakia_domitor

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Gobiotheriodon_infinitus

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Kiyatherium_cardiodens

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Zhangheotherium_quiquecuspidens

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Maotherium_sinensis

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Spalacolestes_cretulablatta

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Dryolestes_priscus

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Dryolestes_leiriensis

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Krebsotherium_lusitanicum

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Guimarotodus_inflatus

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Amblotherium_gracile

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Amblotherium_pusillum

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Crusafontia_cuencana

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Euthlastus_cordiformis

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1?0?21?1????0?010??????0-1-00??

Tathiodon_agilis

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100?121?10-010?0101??0??0-1-0010

Paurodon_valens

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Henkelotherium_guimarotae

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Drescheratherium_acutum

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1???1?010?????????001??2111????1?1001?1?0?0?0-0???

Amphitherium_prevostii

?00???1??????20210101[01]0101?????????????????????0?10300200001011111000211111
01011100101202000010010000112211111141010010011112?0??0010??10001010100110??
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Palaeoxonodon_ooliticus

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Amphibetulimus_krasnolutskii

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Nanolestes_drescherae

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Arguimus_khosbajari

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Peramus_tenuirostris

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Kielantherium_gobiense

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0011001012?00000100011?????00?111410?01100??11?????00100-
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Prokennalestes_spp.

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1101111000?31212210111000011000000-0-0011

Vincelestes_neuquenianus

021000001111100321110110101000000021011??00?1000020000110001011110000000101
000111001002100100201??1101211012111[1 4]101001001111[0 2]?01?00110-
100010001000000?1000?0003111111001000001?000000-0-0011

Cronopio_dentiacutus

0??0100100102000?11??220?1?1122000[01]0011??000?111002011121?11101?11???1?0000
00?0?110?0002020111111??1?11??010011131010010111111??1?10120-10?01000200000--
?--0?0004121110?011?01001100010-1-0010

Leonardus_cuspidatus

???????1?????????101132?01??12200010011??012?1010111?1121010101011000100000000
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Reigitherium_bunodontum

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111020102??21?1??1?????2??0?111????0?10????12????10100-
1??0000011?000?????0?00[0 1]5121010?01??2011100?0010000010

Mesungulatum_houssayi

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Coloniatherium_cilinskii

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Peligrotherium_tropicalis

02000011?0113103?1????21??0102211121111??010?10101111112001011102100?1000000
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Necrolestes_patagonensis

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0?1004[0 1]21110?-1??0000?1000?0-0-0010

Anthracolestes_sergeii

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Electronic Supplementary Material to

An African radiation of ‘Dryolestoidea’ (Donodontidae, Cladotheria) and its significance for mammalian evolution

Journal of Mammalian Evolution

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Online Resource 3 – Phylogenetic analyses: supplementary figures

This Online Resource presents supplementary topologies issued from our phylogenetic analyses of ‘Dryolestoidea’. They consist in the strict consensus tree (**Fig. S1**) and the 50% majority rule consensus tree of analysis 1b (**Fig. S2**), the strict consensus tree of analysis 2a (**Fig. S3**), and the strict consensus tree (**Fig. S4**) and the 50% majority rule consensus tree of analysis 2b (**Fig. S5**).

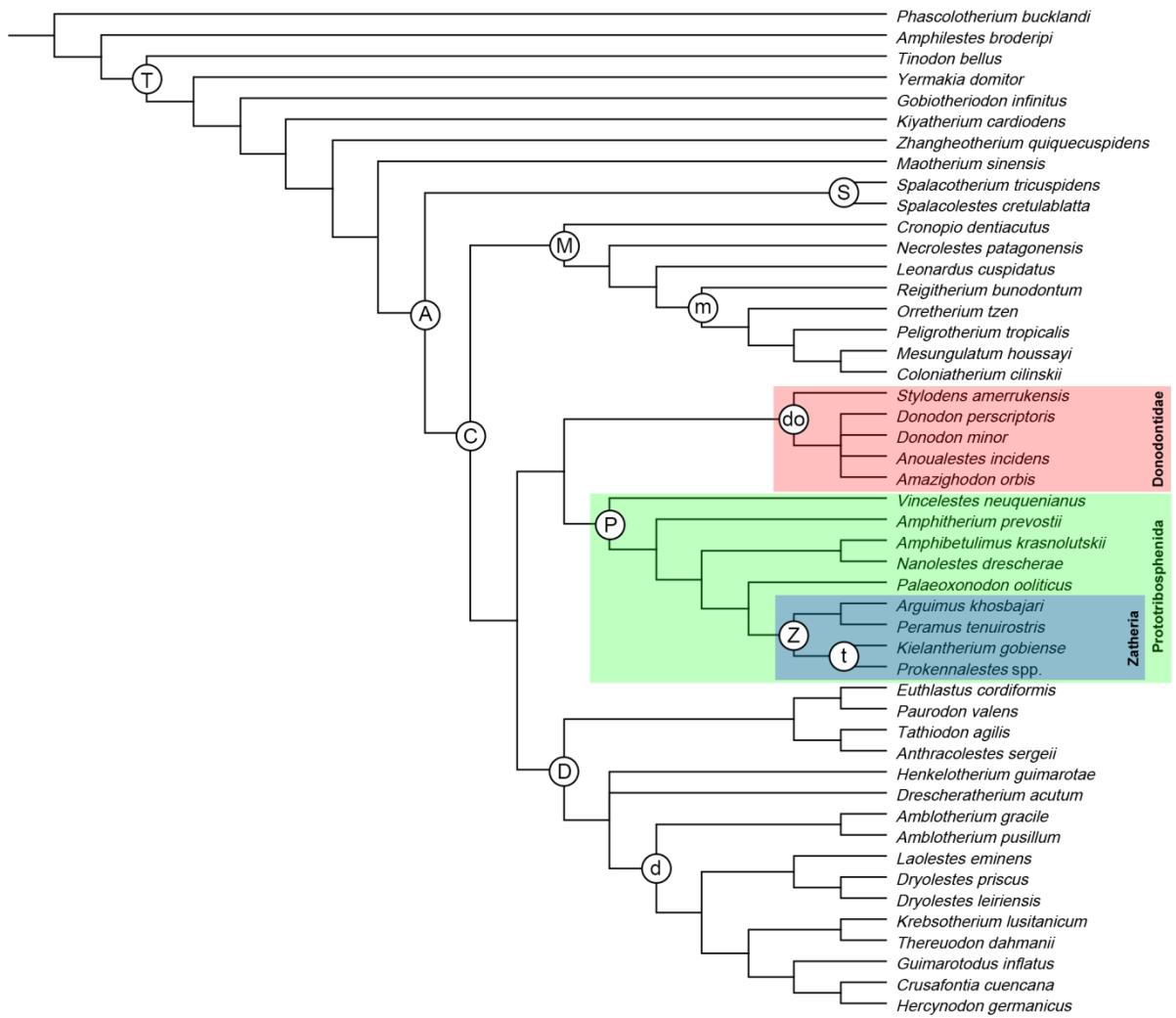


Fig. S2 50% majority rule consensus of 241 most parsimonious trees of 630 steps, obtained with TNT, resulting from analysis 1b (collapsing rule 3). L = 631; CI = 0.376; RI = 0.696. Abbreviations: *do* Donodontidae, *Z* Zatheria; see Fig. 15 caption for other abbreviation meaning

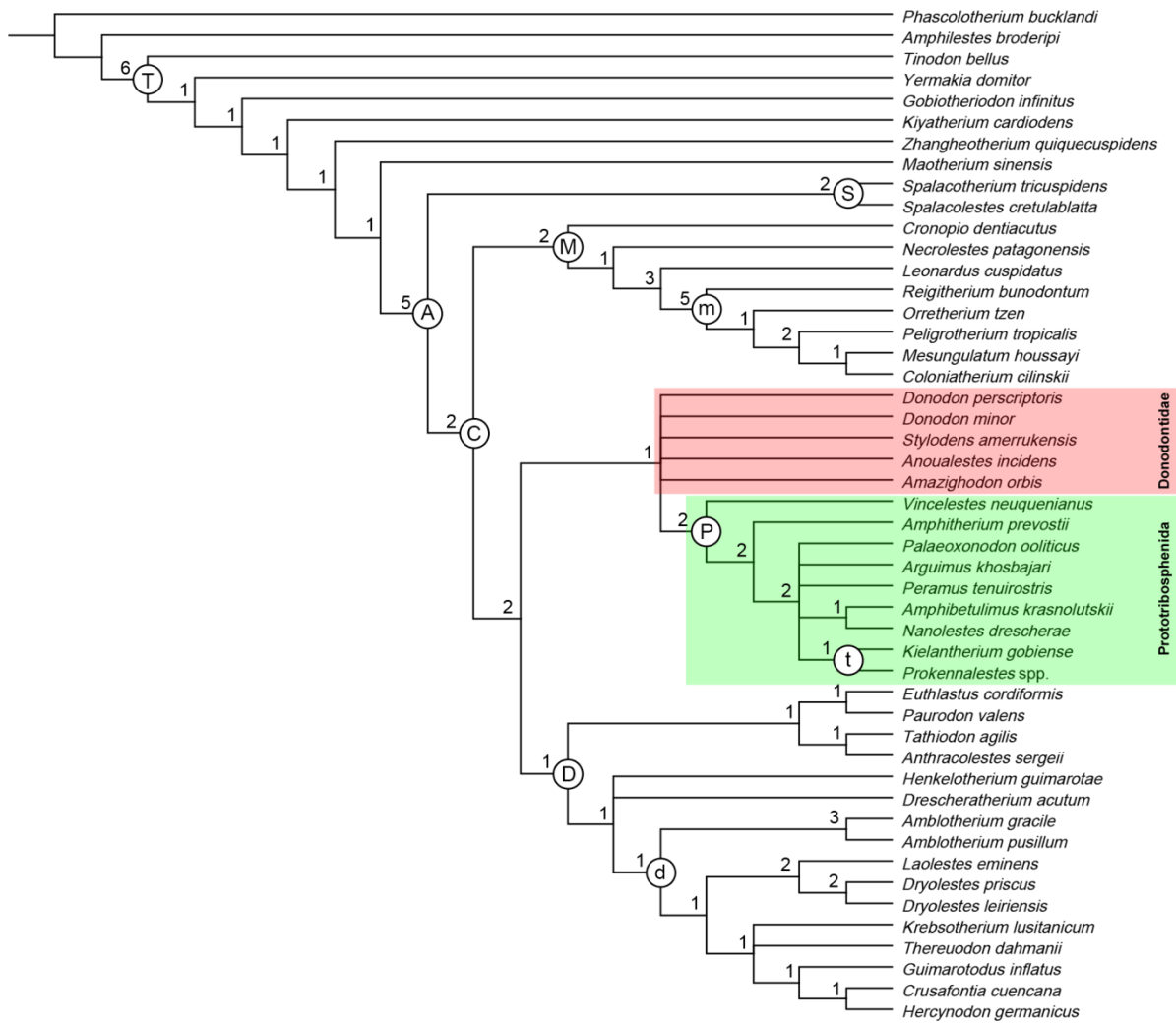


Fig. S3 Strict consensus of 30 most parsimonious trees of 630 steps, obtained with TNT, resulting from analysis 2a (collapsing rule 1, constraint on generic clade Donodon). L = 657; CI = 0.361; RI = 0.676. Values above the nodes correspond to Bremer indices. Abbreviations: see Fig. 15 caption

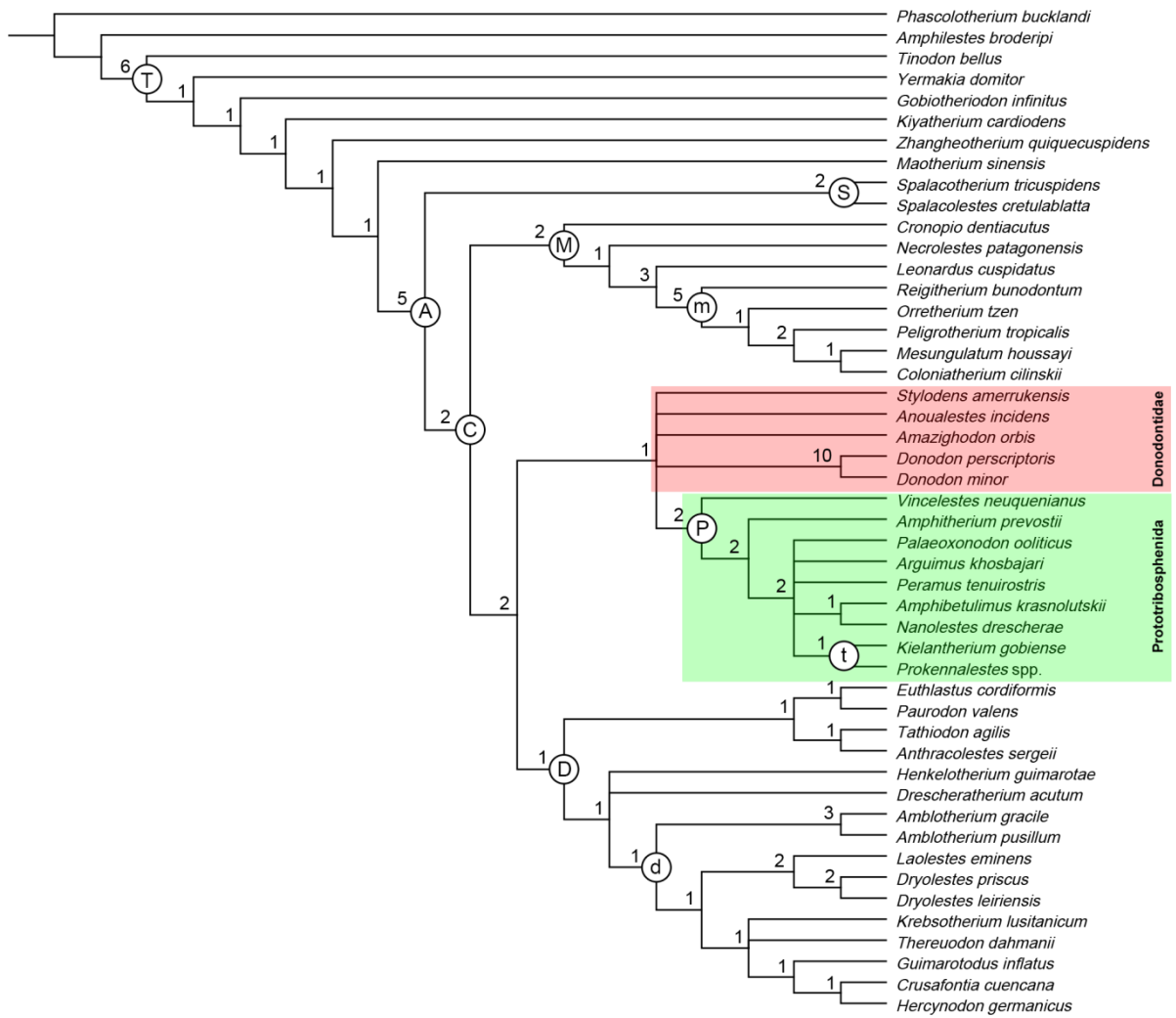


Fig. S4 Strict consensus of 83 most parsimonious trees of 630 steps, obtained with TNT, resulting from analysis 2b (collapsing rule 3, constraint on generic clade Donodon). L = 653; CI = 0.363; RI = 0.680. Values above the nodes correspond to Bremer indices. Abbreviations: see Fig. 15 caption

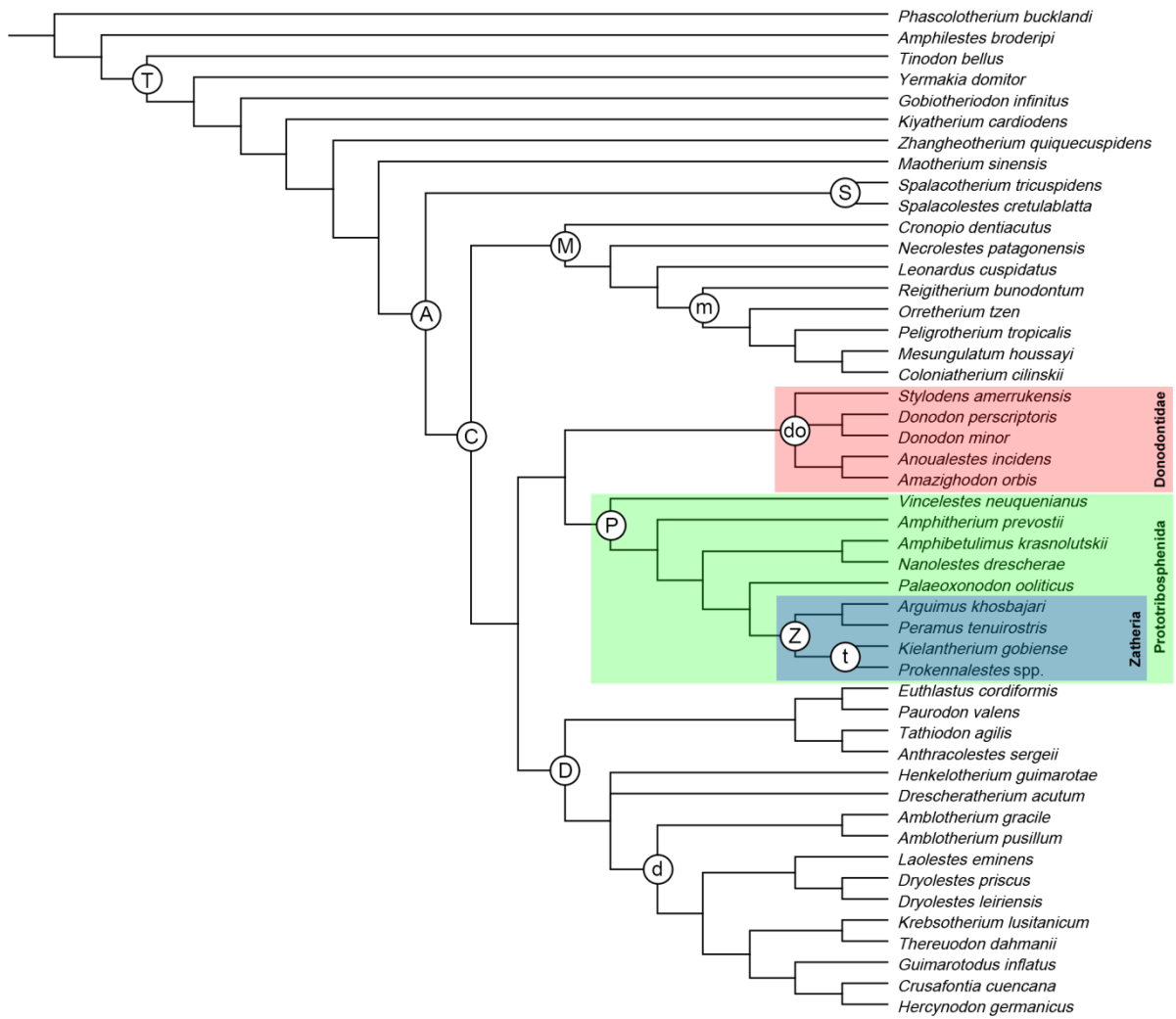


Fig. S5 50% majority rule consensus of 83 most parsimonious trees of 630 steps, obtained with TNT, resulting from analysis 2b (collapsing rule 3, constraint on generic clade Donodon). L = 630; CI = 0.376; RI = 0.697. Abbreviations: *do* Donodontidae, *Z* Zatheria; see Fig. 15 caption for other abbreviation meaning