

New paroxyclaenid mammals from the early Eocene of the Paris Basin (France) shed light on the origin and evolution of these endemic European cimolestans

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We present new species of an enigmatic family of mammals, which is endemic to Europe, the Paroxyclaenidae: *Merialus bruneti* sp. nov., *Fratrodon tresvauxi* gen. et sp. nov., *Paraspaniella gunnelli* gen. et sp. nov., and *Sororodon tresvauxae* gen. et sp. nov. The fossils described come from six localities of the Ypresian of the Paris Basin (France): Pourcy (MP7), Mutigny, Avenay, Condé-en-Brie (MP8+9), Grauves and Prémontré (MP10). They allow the description of three new genera and four new species belonging to the subfamilies Merialinae and Paroxyclaeninae. Two of these new species represent the earliest occurrence of each subfamily. Fossils from Mutigny, Avenay and Condé-en-Brie indicate that merialines were more abundant than paroxyclaenines during the Ypresian. Surprisingly, merialines disappeared from the fossil record at the end of the Ypresian – the youngest records are close to MP10 – while the paroxyclaenines were present in Europe until the end of the middle Eocene. Based on comparison with the data presently available for European mammals during the Ypresian, we suggest the existence of two periods of faunal turnover that must be more extensively studied in the future in order to be fully characterized: the 'Intra-Ypresian Mammal Turnover' and the 'Ypresian-Lutetian Mammal Turnover'. Finally, because the oldest paroxyclaenids appear morphologically closer to cimolestids such as *Procerberus* than to pantolestans, it is suggested that similarities between paroxyclaenids and pantolestans could be due to convergence.

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Introduction

Paroxyclaenidae is an enigmatic family of archaic moderately small placental mammals, which are known only from Europe (Van Valen 1965; Russell & Godinot 1988). They ranged from the Ypresian (early Eocene) to the Priabonian (late Eocene) (Fig. 1). They have been placed variously by different authors in Carnivora, 'Creodonta', 'Condylarthra' and 'Insectivora', but have been considered members of Pantolesta since the 1970s (McKenna 1975; Russell & Godinot 1988; McKenna & Bell 1997; Rose 2006; Koenigswald *et al.* 2018).

The last extensive and comprehensive review of the paroxyclaenids is that of Russell & Godinot (1988), in which they described the oldest paroxyclaenid ever found – *Merialus martinae* from Palette (early Ypresian; France) – and reviewed several paroxyclaenid fossils. In order to describe the evolution of the Paroxyclaenidae, they divided these mammals into two subfamilies: Paroxyclaeninae and Merialinae (Fig. 1).

The dentition of paroxyclaenids consists of four premolars and three molars, resembling in other aspects those of primitive 'condylarths' such as *Phenacodus* and *Hyopsodus*, with, for example, enlarged canines and bunodont molars (Lavocat 1958). The dentition is highly specialized, with relatively enlarged posterior premolars and spaced cheek teeth, yet it is primitive in the absence of upper molar hypocones. The molars decrease in size from M1/m1 to M3/m3. The M3 and m3 are even more reduced in the youngest taxa. A particularity of the dentition of some paroxyclaenids is the tendency for enlargement and molarization of the third and fourth upper and lower premolars, generally exceeding the succeeding molars in size.

As stated by Russell & Godinot (1988), Paroxyclaeninae is characterized by a particular molarization of the p4: this tooth is notably characterized by the presence of a well-developed metaconid. The second distinctive dental feature of paroxyclaenines is the relatively wide separation of the paraconid and metaconid on the

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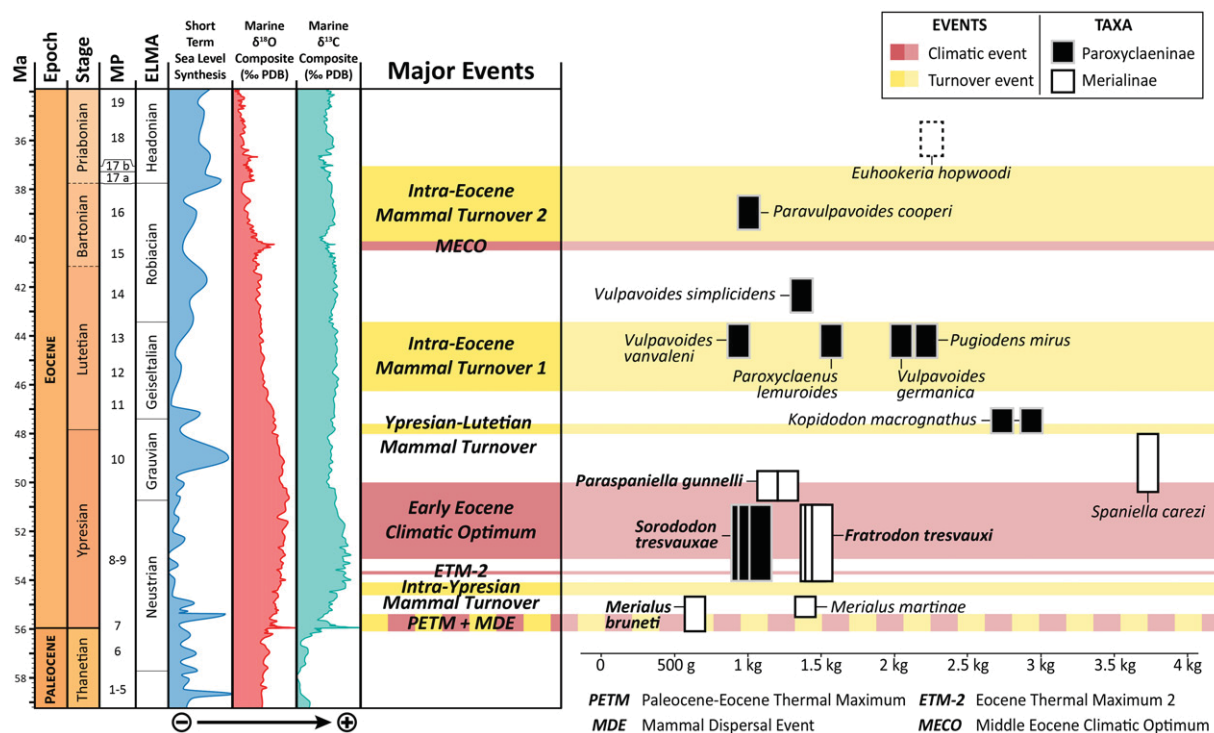


Figure 1. Temporal distribution and the evolution of body mass in paroxyclaenids. The values plotted are the averages of the body masses estimated using the method designed by Legendre (1986). The values are available in the Supplementary material, Files 1 and 2. The four new paroxyclaenids described in the present paper – *Merialus bruneti* sp. nov., *Fratrodon tresvauxi* gen. et sp. nov., *Paraspaniella gunnelli* gen. et sp. nov. and *Sorododon tresvauxae* gen. et sp. nov. – are in bold. The paroxyclaenid status of *Euhookeria hopwoodi* is uncertain (see text).

molars (compared to Merialinae). Paroxyclaeninae is the most diverse subfamily in Paroxyclaenidae, with seven species representing five genera: *Paroxyclaenus* Teilhard de Chardin, 1922; *Kopidodon* Weitzel, 1933; *Vulpavoides* Matthes, 1952; *Pugioidens* Matthes, 1952; and *Paravulpavoides* Harrison, 2009. Paroxyclaenines first appear in the Lutetian – with *Kopidodon* from Messel (Germany, reference locality of the reference level MP11 (MP = Mammal Paleogene reference-levels) of the mammalian biochronological scale for the European Palaeogene, BiochroM’97 1997; between 47–48 Myr, Lenz *et al.* 2015) (Wittich 1902; Weitzel 1933; Koenigswald 1983; Clemens & Koenigswald 1993; Koenigswald *et al.* 2018) – and last occur in the Bartonian – represented by *Paravulpavoides* from Creechbarrow (England, MP16) (Harrison 2009) (Fig. 1). It is worth mentioning that the paroxyclaenine *Paroxyclaenus lemuroides*, which was considered to be from late Eocene (e.g. Russell & Godinot 1988), has been identified in Cuzal, a locality that is close to the MP13–MP14 reference levels; consequently, Marandat *et al.* (1993) considered *Paroxyclaenus lemuroides* to be Lutetian in age rather than Priabonian.

On the other hand, Merialinae are characterized by the absence of the metaconid on p4, and by close

metaconids and paraconids on molars. Their biostratigraphical range is longer than that of the paroxyclaenines: they are known from the Ypresian to the Priabonian (Fig. 1). However, their evolutionary history is less well known than that of the paroxyclaenine family, as only three monospecific genera have been discovered so far: two in the Ypresian — *Merialus martiniae* from Palette (France; MP7) (Russell & Godinot 1988) and *Spaniella carezi* from Barranc de Forals (Spain; MP10) (Crusafont-Pairo & Russell 1967) – and one in the Priabonian – *Euhookeria hopwoodi* from the Headon beds (England; MP18) (Cray 1973). Remarkably, merialines are unknown in the Lutetian and Bartonian (Fig. 1).

Finally, it is worth mentioning that *Kiinkerishella*, which was referred to Paroxyclaeninae by Russell & Godinot (1988), is now considered a dyspternine pantolestean (Dashzeveg & Russell 1992; Lucas & Emry 2004).

As noted by Crusafont-Pairo & Russell (1967), paroxyclaenids are rare in mammal faunas: each species is represented by one or two individuals. This explains why paroxyclaenids are poorly known. Therefore, the fossils described in the present paper are crucial for understanding the evolution of the paroxyclaenids, and provide new information on their early radiation.

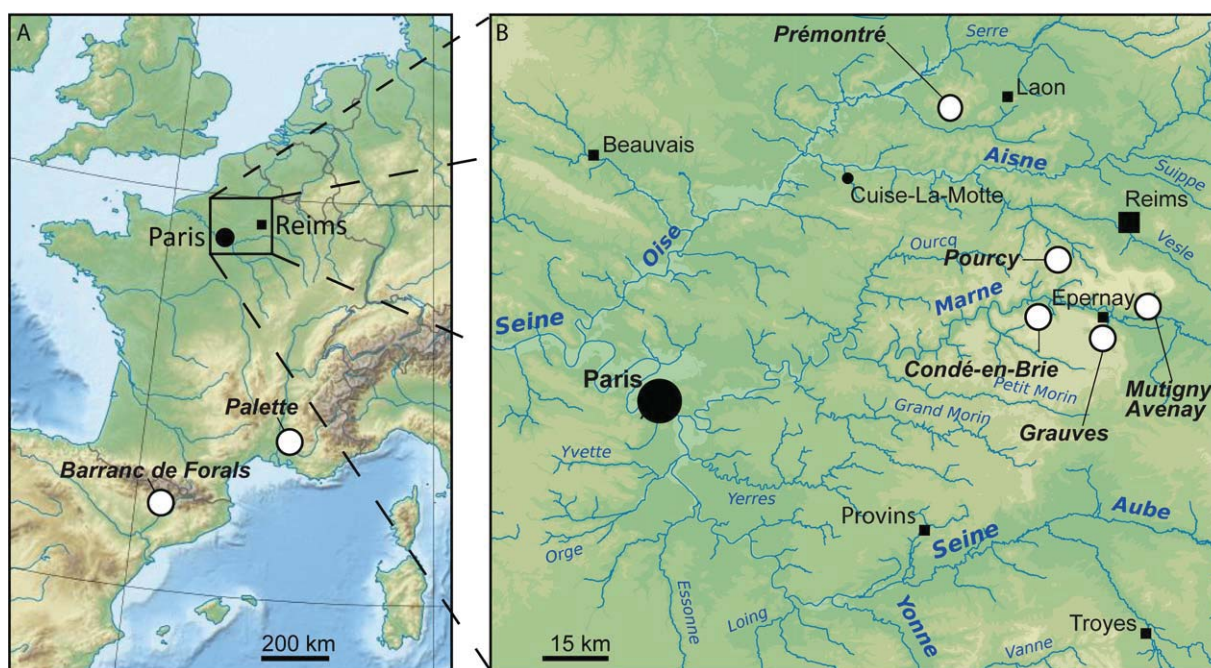


Figure 2. Geographical distribution of paroxylaenids in Europe during the Ypresian (A) with a close-up on the Paris Basin (B). *Merialus martinae*: Palette (MP7); *Merialus bruneti* sp. nov.: Pourcy (MP7); *Fratrodon tresvauxi* gen. et sp. nov.: Mutigny, Avenay, Condé-en-Brie (MP8 + 9); *Paraspaniella gunnelli* gen. et sp. nov.: Prémontré, Grauves (MP10); *Sorodon tresvauxae* gen. et sp. nov.: Mutigny, Avenay, Condé-en-Brie (MP8 + 9); *Spaniella carezi*: Barranc de Forals (MP10).

Table 1. Age, MP level and PE biozones of the principal localities discussed herein. See text for information concerning ages. MP levels are from BiochroM'97 (1997) and PE biozones from Hooker (1996, 1998).

Locality	Age (Myr)	MP level	PE biozones
Palette	~55	MP7	–
Pourcy	56–55	MP7	PE III
Mutigny	54–52	MP8 + 9	PE IV
Avenay	51–53	MP8 + 9	PE V
Condé-en-Brie	~51–53	MP8 + 9	PE V
Grauves	50–51	MP10	–
Prémontré	~50.4	MP10	–

Material and methods

Origin of the studied specimens

The only Ypresian paroxylaenids well described before the present work were *Merialus martinae* from Palette (France) and *Spaniella carezi* from Baranc de Forals (Spain) (Fig. 2). The fossils described in the present paper come from the Ypresian of the Paris Basin (Pourcy, Avenay, Mutigny, Condé-en-Brie, Prémontré and Grauves; Fig. 2). Some of the fossils discovered at Pourcy, Avenay and Mutigny have been described and illustrated previously by Rich (1971).

The locality of Pourcy is considered to be potentially close in age to Abbey Wood (Hooker 1996, 1998); the English locality dates from the early Eocene (≈ 55.12

Myr; MP8 + 9) (Hooker 2010). However, the presence at Pourcy of species otherwise known only from beds as old as Dormaal (reference locality of MP7), such as *Teilhardimys musculus*, together with others shared with younger localities (e.g. Mutigny, Avenay), such as *Platychoerops daubrei*, suggests that the Pourcy fauna contains taxa of mixed ages, and that the presence of older fossils is an indication of reworked sediments (Cavelier 1987). This leaves its status uncertain (Hooker 2010; see also Aubry *et al.* 2005 for a discussion concerning the age of deposits from Pourcy). Regardless, the age of the mammal fauna(s) of Pourcy is probably between 56 and 55 Myr (Hooker 1996, 1998). Despite this uncertainty, the locality of Pourcy is considered to be close to the MP7 reference locality (i.e. Dormaal) (BiochroM'97 1997) (Table 1).

Mutigny is younger than Pourcy: it is considered to be close to MP8 + 9 level (Avenay being the reference locality of the level MP8 + 9; BiochroM'97 1997); Mutigny is referred by Hooker (1996, 1998) to the PE IV biozone (PE biozone = Paleocene-Eocene biozone) (Table 1). The age of Mutigny is still uncertain: it varies between 54 and 52 Myr (Neal 1996; Duprat 1997; Escarguel 1999).

As Mutigny, Avenay and Condé-en-Brie are considered to be close in age to the MP8 + 9 reference level, but the two other localities are regarded as younger than Mutigny (Escarguel 1999), Hooker (1996) referred these

two localities to the PE V biozone (Table 1). Avenay could have an age close to 52–53 Myr (Neal 1996; Escarguel 1999), and a correlation between the mammal faunas of Avenay and the recently described one of Egem (Belgium) suggests an approximate age of 51–52 Myr for Avenay (T. Smith & Smith 2013, pp. 308–309: “The Egem mammal fauna thus best correlates with the international reference level MP8 + 9 of the mammalian biochronological scale for the European Paleogene [...] the base of the Egemkapel Clay Member in the middle part of the Tielt Formation that has been dated as middle NP12 (VI) subzone, indicating the early late Ypresian about 51–52 Ma”).

The presence at Condé-en-Brie of a species of *Lophiaspis*, which is unknown in Avenay but well known in the end of the Ypresian, allows placing Condé-en-Brie stratigraphically between Avenay and MP10 localities such as Grauves and Cuis (Louis 1996). However, Escarguel (1999) estimated that Condé-en-Brie is 200,000 years older than Avenay (Table 1).

Together, Mutigny, Avenay and Condé-en-Brie cover a period that approximatively corresponds to 54–51 Myr.

Grauves, which is the reference locality of the reference level MP10, belongs to the ‘Sables à Unios et Térédines’ *sensu stricto* together with the localities of Cuis, Mancy, Chavot and Monchenot (Laurain *et al.* 1983; Louis 1996; BiochroM’97 1997) – all of these localities are closely located. The mammalian faunas from these localities are considered to be from the end of the Ypresian (but see Duprat 1997 for a Lutetian age for some of these faunas). Prémontré is considered to be close in age to the localities from the ‘Sables à Unios et Térédines’ *sensu stricto* such as Grauves (BiochroM’97 1997; Escarguel 1999). According to Escarguel (1999), Prémontré and Grauves were deposited around 50–51 Myr. Recent study of the microfossil assemblages from the Prémontré Sands allowed an estimate that the deposition of the Prémontré mammal fauna postdated the onset of both NP13 and chron C22r, which are nearly coincident, by about 200–300 kyr, so around 50.4 Myr (Steurbaut *et al.* 2016) (Table 1).

Finally, it is worth mentioning the case of Palette (south of France) because its fauna provided one of the oldest paroxycloenids ever discovered. Palette is considered, as is Le Clot, at least 1 million years younger than the MP7 reference locality of Dormaal (Belgium; \approx 56 Myr) (Yans *et al.* 2014), hence close to 55 Myr and to Pourcy (Table 1).

The MNHN houses specimens from Mutigny, Avenay, Pourcy, Condé-en-Brie and Prémontré. The University of Montpellier houses one specimen from Pourcy. Several fossils from Avenay and Condé-en-

Brie, which are described in the present paper, have been found and prepared by one of us (A. Phélizon) and belong to his private collection, but they are accessible for study – to do so, please contact A. Phélizon by email (alain.phelizon@orange.fr). Moreover, casts of these specimens are housed at the Royal Belgium Institute of Natural Sciences (RBINS, Brussels, Belgium: collection RBINS Cast-Vert).

Principal component analysis

We performed a principal component analysis (PCA) in order to study the morphology of the lower molars of the four new paroxycloenid species described herein and to identify criteria that allow the species to be discriminated from each other. To do so, we performed five measurements on every complete specimen ($n = 46$): trigonid length, trigonid height, talonid length, talonid height and maximum tooth width. The measurements are available in the Supplementary material, File 1.

The PCA provides an overall analysis of the dataset by quantifying and analysing the gross variability. This is done using conformation ratios (Mosimann & James 1979; Fabre *et al.* 2014). For each individual, size was computed as the geometric mean of all measurements, and each measurement was divided by size to obtain the shape ratios. Then the log of this quantity was considered as raw data for subsequent analyses (Claude 2013). These ratios allow calculation of the isometric size by averaging the logarithms. By removing the isometric size from our logarithmic data, only the conformation ratios remain (Fabre *et al.* 2014). The advantage of this method is that it allows decomposing the shape in size and proportion, as in geometric morphometrics.

All analyses were carried out in reduction of dimensionality, meaning that analyses were carried out on the PCA axes. This allowed the possibility of choosing only a few variables by keeping the multivariate information and eliminating noise (Baylac & Friess 2005).

Body mass analysis

In order to analyse the evolution of paroxycloenid body mass through time, we estimated it for all the species presently known. We used the method developed by Legendre (1986) to estimate the body mass of extinct species; we used the parameters established (1) for all mammals, (2) for large mammals (> 500 g) and (3) for herbivores.

Dental terminology and measurements

We followed the dental terminology of Szalay (1969). The statistical parameters are the observed range (OR),

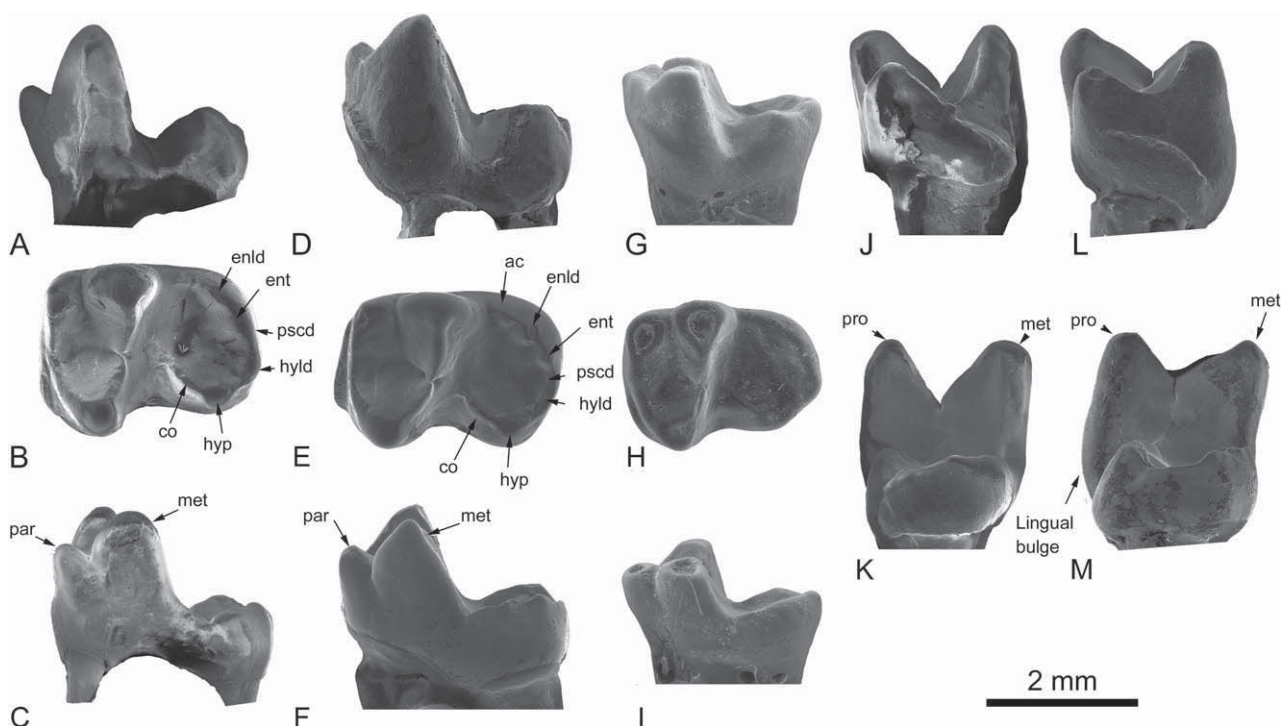


Figure 3. *Merialus bruneti* sp. nov. **A–C**, MNHN.F.Louis23.Py, left m2: **A**, labial view; **B**, occlusal view; **C**, lingual view. **D–F**, MNHN.F.Louis49.Py (holotype), right m2; **D**, labial view; **E**, occlusal view; **F**, lingual view; **G–I**, UM/POY12, left m3: **G**, labial view; **H**, occlusal view; **I**, lingual view. **J, K**, MNHN.F.Louis23.Py, left m2: **J**, mesial view; **K**, distal view. **L, M**, MNHN.F.Louis49.Py (holotype): **L**, mesial view; **M**, distal view. Reversed views: **C, D, E, I, L, M**. **Abbreviations:** **ac**, accessory cusp; **co**, cristid obliqua; **enld**, entoconulid; **ent**, entoconid; **hyld**, hypoconulid; **hyp**, hypoconid; **met**, metaconid; **par**, paraconid; **pro**, protoconid; **pscd**, postcristid.

mean (M) and standard deviation (SD) – the latter is only estimated when the number of available specimens is equal to or greater than 5.0.

Institutional and collection abbreviations

Av-Ph: Avenay, Private Collection Phélizon; **CB-Ph:** Condé-en-Brie, Private Collection Phélizon (France); **NHMUK:** Natural History Museum (London, United Kingdom); **HZM:** Harrison Institute collection (Sevenoaks, United Kingdom); **MNHN.F.:** Muséum National d'Histoire Naturelle (Paris, France), fossil collection; **MNHN.F.Av:** Avenay (Avenay); **MNHN.F.CEB:** Condé-en-Brie (MNHN); **MNHN.F.Condé Levé:** Condé-en-Brie, Collection Levé (MNHN); **MNHN.F.Louis.Py,** Pourcy, Collection Louis (MNHN); **MNHN.F.L-X-Av,** Avenay; Collection Louis (MNHN); **MNHN.F.L-X-Mut,** Mutigny, Collection Louis (MNHN); **MNHN.F.MCB:** Condé-en-Brie (MNHN); **MNHN.F.Mut:** Mutigny (MNHN); **RBINS:** Royal Belgian Institute of Natural Sciences (Brussels, Belgium); **RBINS Cast-Vert:** Royal Belgian Institute of Natural Sciences (Brussels, Belgium), collection of casts

of fossil vertebrates; **UM/POY:** Université Montpellier (Montpellier, France), from Pourcy (France).

Other abbreviations

L, length; **n,** number of specimens; **W,** width; **Lm2/Lm3,** length of the m2 divided by length of the m3; **L/W,** length divided by width: **LTalo/LTrigo,** length of the talonid divided by the length of the trigonid.

Systematic palaeontology

Order **Pantolestia** McKenna, 1975
 Family **Paroxyclaenidae** Weitzel, 1933
 Subfamily **Merialinae** Russell & Godinot, 1988

Emended diagnosis (after Russell & Godinot 1988). Paroxyclaenidae characterized by premolariform premolars (p4 without metaconid) with lingually located paraconid, lower molars with closely situated paraconid and metaconid, and precingulid very weak to absent, subrectangular upper molars in occlusal view.

Included genera. *Spaniella* Crusafont-Pairo & Russell, 1967; *Merialus* Russell & Godinot, 1988; *Fratrodon* gen. nov.; *Paraspaniella* gen. nov.

Genus *Merialus* Russell & Godinot, 1988

Type species. *Merialus martinae* Russell & Godinot, 1988.

Other species. *Merialus bruneti* sp. nov.

Emended diagnosis (after Russell & Godinot 1988). Merialine that differs from *Spaniella* by less inflated p2–p3, more ‘V’-shaped (in occlusal view) trigonids of m2 and m3, shorter m2 talonid, and the stronger and more lingually placed paraconid of m3. Differs from *Fratrodon* and *Paraspaniella* by lower talonid cusps, more developed paraconid, slightly more mesially located paraconid, and longer talonid on m3. Differs from *Paraspaniella* by widely separated paraconid and metaconid apexes.

Merialus bruneti sp. nov.
(Fig. 3)

1971 cf. Paroxyclaenidae; Rich: 61–64, fig. 17 j–l (*partim*).

Diagnosis. Differs from *Merialus martinae* by having smaller teeth (~10%). It also differs by widely separated paraconid and metaconid apexes, narrower and lower talonid, and a more pronounced difference in height between the trigonid and talonid on molars.

Derivation of name. Dedicated to Mr Julien Brunet (1983–) for his help and support to the first author (FS) over many years.

Holotype. MNHN.F.Louis49.Py, right m2.

Referred specimens. MNHN.F.Louis23.Py, left m2; UM/POY12, left m3.

Locality. Pourcy (France), Ypresian (MP7).

Measurements. UM/POY12: L = 2.63 mm, W = 2.02 mm. From Rich (1971, table 31): MNHN.F. Louis23.Py: L = 3 mm, W = 2.1 mm; MNHN.F.L-49-PY: L = 3.1 mm, W = 2.2 mm.

Description. MNHN.F.Louis49.Py and MNHN.F.Louis23.Py can be considered a possible m2 based on the closely situated paraconid and metaconid, the size of the m3 (UM/POY12), and comparison with the proportionally much longer m1 of *Merialus martinae*.

On the two m2s, the paraconid is mesiodistally appressed to the metaconid (the trigonid is therefore

mesiodistally compressed). These two cusps are poorly separated, but a distinct groove between them is visible in occlusal and lingual views (Fig. 3B, C, E, F). The paraconid, which is lingually located, is lower than the metaconid. The latter cusp is only slightly lower than the protoconid. The protocristid and paracristid are sharp. The paracristid is rather straight, less curved than in *Merialus martinae*, giving the trigonid an even more distinct ‘V’-shape. A notch is present on the protocristid (Fig. 3K, M), but no notch is distinguishable on the paracristid. The talonid is narrower and lower than the trigonid. The hypoconid is the largest talonid cusp. The hypoconulid and entoconid are very small but well distinguished on MNHN.F.Louis23.Py; they are less individualized on MNHN.F.Louis49.Py. The separation between the hypoconid and hypoconulid is visible on the two specimens. The cristid obliqua is oblique and runs along the posterior wall of the trigonid. The entocristid is high and bears an entoconulid; on MNHN.F.Louis49.Py, one can note the presence of an accessory cusp in front of the entoconulid (Fig. 3E). A notch is present between the entocristid and metaconid. A precingulid is present along the mesial part of the teeth (on both the paraconid and protoconid).

The trigonid on m3 is mesiodistally compressed. The trigonid basin is closed by an important contact between the base of paraconid and metaconid; the apices of the cusps are separated by a very small groove, however. The paraconid is poorly projected mesially and is the lowest trigonid cusp. The metaconid and protoconid are similar in height. The trigonid is higher than the talonid. The talonid is narrower than the trigonid. The cristid obliqua is only slightly oblique (distally shifted labially). The entoconid and hypoconid are distinctly higher and larger than the hypoconulid. The hypoconulid is clearly much more distally located than the hypoconid and entoconid (a feature that generally characterized the m3 of earliest eutherians). The precingulid is less developed than on m2s. The two roots of UM/POY12 are very close to each other (they are more separated on the two m2s).

Variability. The two m2 are very similar in size, but they display several differences. The angle between the protoconid and metaconid is more obtuse in MNHN.F. Louis49.Py (Fig. 3M) than in MNHN.F.Louis23.Py (Fig. 3K). The base of the protoconid of MNHN.F.Louis49.Py shows a bulge at its labial part (Fig. 3M), while the labial part of the protoconid is straighter on MNHN.F.Louis23.Py (Fig. 3K). The paraconid is more reduced on MNHN.F.Louis23.Py and the separation between the paraconid and the metaconid is less visible than on MNHN.F.Louis49.Py.

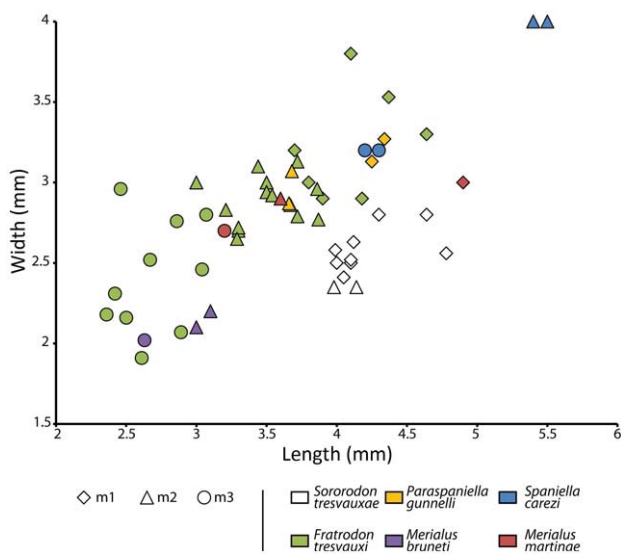


Figure 4. Comparison of the sizes (length × width) of the lower molars (m1–m3) of *Merialus bruneti*, *M. martinae*, *Fratrodon tresvauxi*, *Paraspaniella gunnelli*, *Sororodon tresvauxae* and *Spaniella carezi*.

The postcristid is rounder on MNHN.F.Louis49.Py (resulting in a wider talonid basin), while it is more oblique on MNHN.F.Louis23.Py. The labial facet of the hypoconid is more inclined (towards the metaconid) on MNHN.F.Louis49.Py than on MNHN.F.Louis23.Py (Fig. 3K, M). The cristid obliqua is more oblique on MNHN.F.Louis23.Py (it runs along the distal facet of the metaconid) than in MNHN.F.Louis49.Py (where it runs towards the notch of the metacristid).

By comparison with younger merialines, (1) this variability is similar (see below) and (2) the combination of the features varies depending on the specimens. Moreover, as for MNHN.F.Louis23.Py and MNHN.F.Louis49.Py, the sizes of the specimens are always very close. Therefore, we believe that these differences represent intra-specific variability only.

Comparison. The three molars referred to the present taxon are from the Ypresian locality of Pourcy. The molars MNHN.F.Louis23.Py and MNHN.F.Louis49.Py were previously described (among others from Avenay and Mutigny) by Rich (1971) and referred to as cf. Paroxyclaenidae. The specimen UM/POY12 is close in size and morphology to the previously described specimens; it is, however, narrower and shorter than the two other molars. Because of the narrow talonid and the distally located hypoconulid, and because UM/POY12 is distinctly smaller than MNHN.F.Louis49.Py and MNHN.F.Louis23.Py, we think that the former tooth is surely an m3. The two other teeth from Pourcy were considered possible m3s by Rich (1971, table 31), but we believe that they correspond to m2.

The morphology of the teeth is characterized by a closely appressed paraconid and metaconid and an enlarged talonid. This morphology agrees with that of the molars known for merialines, notably *Merialus martinae*. The teeth can be distinguished from those of the merialines *Spaniella carezi*, *Fratrodon tresvauxi*, and *Paraspaniella gunnelli* (see below for the description of the latter two species) by their smaller size and the presence of primitive features (compared to younger merialines): presence of a narrow talonid, more pronounced difference in height between the trigonid and talonid, hypoconulid less minute, and entoconid less crestiform. The presence of a deep groove between the paraconid and metaconid clearly resembles *Merialus martinae* rather than *Spaniella* and *Paraspaniella*. Generally, the morphology of the molars is less derived (i.e. with no separation between the paraconid and metaconid) than in the youngest merialines. The fossils from Pourcy differ from the holotype (and sole specimen) of *M. martinae* in that the talonid that is narrower than the trigonid on m2 and m3, the paraconid and metaconid apices are less closely appressed, and the more pronounced difference in height between the trigonid and talonid on molars. They are also about 10% smaller (Fig. 4).

As a result, the three isolated molars from Pourcy represent one of the most primitive members of Merialinae ever found. Based on the primitive morphology of the teeth recorded in Pourcy, their similarities with *Merialus martinae*, as well as their small size, we decided to refer them to a new species: *Merialus bruneti* sp. nov. This new species provides information on the morphology of the oldest paroxyclaenids, and therefore helps to polarize the evolution of their dental features.

Genus *Fratrodon* gen. nov.

Type species. *Fratrodon tresvauxi* sp. nov.

Diagnosis. As for the type species.

Derivation of name. ‘Frater’ = Brother (Latin) and ‘odon’ = tooth (Greek); in reference to the fact that Mr Frédéric Tresvaux du Fraval and Mrs Marie Tresvaux du Fraval are brother and sister.

Fratrodon tresvauxi sp. nov.
(Fig. 5)

1971 cf. Paroxyclaenidae; Rich: 61–64, fig. 17a–i, m–o (*partim*).

1971 cf. *Paroxyclaenus*; Rich: 58–60, fig. 16a (*partim*).

Diagnosis. Merialine that differs from *Merialus* by relatively smaller and more square-shaped lower molars, less difference in height between the trigonid and

talonid, paraconid close in height to the metaconid, distinctly less 'V'-shaped trigonids (in occlusal view), presence of a metastylid, common presence of cusplation on the posteristid and entoconid, and shorter talonid on m3. Differs from *Spaniella* by a less reduced paraconid on m2 and m3, more important difference in height between the trigonid and talonid, less reduced m3, more transversely elongated M2, more developed stylar shelf, parastylar and metastylar areas on M2, more developed paraconule and metaconule on M2, and a metacrista oriented more distally than labially on M2. Differs from *Paraspaniella* by having less reduced paraconid, lower entocristid, lower entoconid, deep trigonid and talonid basins, thin precingulid on molars, developed parastylar and metastylar projection, and more individualized metaconule on molars. Differs from all the paroxylaenids except *Paraspaniella* by the presence of a preparaconule crista that reaches the parastylar area and ectocingulum.

Derivation of name. Dedicated to Mr Frédéric Tresvaux du Fraval (1983–) for his help and support to the first author (FS) over many years.

Type locality. Mutigny (Marne, France), Ypresian (MP8 + 9).

Other localities. Avenay (Marne, France), Ypresian (MP8 + 9); Condé-en-Brie (Aisne, France), Ypresian (MP8 + 9).

Holotype. MNHN.F.L-189-Mu, right m1.

Referred specimens from Mutigny (Rich 1971). MNHN.F.Mu5942; right m1; MNHN.F.Mu6272, left m1; MNHN.F.L-190-Mu, right m2; MNHN.F.Mu6168, left m2; MNHN.F.Mu6304, left m2.

Referred specimens from Avenay (Rich 1971). MNHN.F.Av5898, left m1; MNHN.F.Av6759, right m1; MNHN.F.Louis-124-Av, left m1; MNHN.F.Av5002, left m1; MNHN.F.Av5731, right m2; MNHN.F.Av5656, right m2; MNHN.F.Av5714, left M2.

Newly referred specimens from Avenay. RBINS Cast-Vert-32468-2235 (Av-1920-Ph), left m1; RBINS Cast-Vert-32468-2236 (Av-1813-Ph), right m2; RBINS Cast-Vert-32468-2237 (Av-806-Ph), right m2; RBINS Cast-Vert-32468-2238 (Av-223-Ph), right m3; RBINS Cast-Vert-32468-2239 (Av-41-Ph), left m3; MNHN.F.Av5816, right m3; MNHN.F.Av628BN, left m3; RBINS Cast-Vert-32468-2240 (Av-1002-Ph), left M1; RBINS Cast-Vert-32468-2241 (Av-2075-Ph), right M1; RBINS Cast-Vert-32468-2242 (Av-1603-Ph), right M2; RBINS Cast-Vert-32468-2243 (Av-2076-Ph), left M2.

Table 2. Length (L) and width (W) data (in mm) for the teeth of *Fratrodon tresvauxi* gen. et sp. nov. from Mutigny (France; MP8 + 9, Ypresian), Avenay (France; MP8 + 9, Ypresian) and Condé-en-Brie (France; MP8 + 9, Ypresian). Partially based on Rich (1971, table 31). **Abbreviations:** M, mean; n, number of teeth; SD, standard deviation.

Locus		n	Observed range	M	SD
Mutigny					
m1	L	3	3.7–4.18	3.96	–
	W	3	2.7–3	2.93	–
m2	L	3	3.3–3.7	3.5	–
	W	2	2.7–3.2	2.95	–
Avenay					
M1	L	3	3.4–4.06	3.81	–
	W	3	4.9–5.44	4.85	–
M2	L	4	2.63–3.39	3.07	–
	W	4	4.26–4.97	4.6	–
m1	L	3	4.1–4.64	4.37	–
	W	5	3.1–3.8	3.43	0.26
m2	L	4	3–3.5	3.29	–
	W	4	2.83–3.1	2.98	–
m3	L	4	2.36–2.89	2.68	–
	W	4	1.91–2.76	2.23	–
Condé-en-Brie					
M1	L	1	3.99	–	–
	W	1	5.31	–	–
M2	L	2	3.37–3.56	3.47	–
	W	2	4.35–5.09	4.72	–
m2	L	9	3.29–3.87	3.61	0.22
	W	9	2.65–3.13	2.86	0.15
m3	L	6	2.42–3.07	2.69	0.29
	W	6	2.16–2.96	2.54	0.3

Referred specimens from Condé-en-Brie. RBINS Cast-Vert-32468-2244 (CB-633-Ph), left m2?; MNHN.F.Condé.Levé.862, right m2; MNHN.F.CB186, right m2?; MNHN.F.MCB277, right m2; MNHN.F.MCB0151, left m2; MNHN.F.CB1147, right m2; MNHN.F.Condé.Levé.1014, right m2; MNHN.F.CB784, left m2?; MNHN.F.CB974, left m2; MNHN.F.CB189, left m3; MNHN.F.CB15875, right m3; MNHN.F.CEB550, right m3; MNHN.F.CB190, right m3; RBINS Cast-Vert-32468-2245 (CB-94-Ph), right m3; RBINS Cast-Vert-32468-2246 (CB-396-Ph), right m3; MNHN.F.MCB0148, right M1; MNHN.F.CB681, left M2; MNHN.F.CB17, left M2.

Measurements. See Table 2.

Description. Because the M2 and M3 of the species *Spaniella carezi* are the only upper molars known for merialines, the morphology of the upper molars of Merialinae is poorly known. Therefore, we consider that the upper molars found in Avenay and Condé-en-Brie might correspond to *F. tresvauxi* rather than to *S. tresvauxae*, based on the relative abundance of the lower molars of the merialine *Fratrodon tresvauxi* compared to those of the paroxylaenine *Sororodon tresvauxae*,

present in the same sites, and based on global morphology and occlusion.

The M1s are triangular in occlusal view: the parastyle and parastylar area are mesially projected, while the metastylar area is shifted distally. The teeth therefore appear symmetrical in this view. The paracone and metacone are widely separated, and the paracone is slightly higher and larger than the metacone. The centrocrista is thin. The stylar shelf is long and the ectoflexus is present. The ectocingulum is defined but not high. The paraconule and metaconule are bulbous. The metaconule is distinctly separated from the protocone; the postprotocrista is thus short. The preprotocrista is long and bears a paraconule. The preparaconule crista joins the parastylar area and ectocingulum. The protocone is large. Its apex is shifted mesially. It is as high as the metacone and the paracone. No lingual cingulum is present.

The M2s are smaller than the M1s, but they are morphologically similar to the latter (e.g. separated paracone and metacone; paracone larger and higher than the metacone; no lingual cingulum; large paraconule and metaconule). The M2 differs from the M1 by the more reduced metastylar area. The reduction of the metastylar area results in an asymmetry of the M2 labial border (in occlusal view). The ectoflexus is shallower than on the M1s but it is still visible.

Nine m1s are known. The m1 is clearly the largest molar of the taxon (Table 2). The trigonid is higher than the talonid and is mesiodistally compressed. The protoconid is the highest trigonid cusp. The metaconid is higher than the paraconid in the oldest specimens (i.e. Mutigny), but they are almost equal in height in the youngest specimens (i.e. Avenay). These two cusps are only slightly lower than the protoconid. The base of the paraconid and metaconid are partially fused; a very shallow groove is distinguishable between the apices of the two cusps in lingual view. The paraconid is located lingually. The paracristid and protocristid are somewhat acute. The notches on these cristids are barely visible on the specimens from Mutigny, but undistinguishable on the fossils from Avenay. In the fossil samples from Avenay, only MNHN.F.L-124-Av shows a distinct notch on these cristids. Several m1s display an additional cusp on the paracristid (Fig. 5B). The talonid is short, as is the trigonid; it is as wide as the trigonid. The hypoconid is the largest and highest talonid cusp, but the entoconid and entocristid are only slightly lower than the hypoconid. The separation between the hypoconid and hypoconulid is clear. The hypoconulid and entoconid are not easily distinguishable: several tiny cusps (i.e. cuspulation) are present on the postcristid and entocristid. The hypoconulid when present is lower than the entoconid

and hypoconid. Together the entocristid and postcristid form a posterolingually convex ridge. The talonid basin is lingually closed by the high entocristid and a metastylid. The cristid obliqua is oblique (shifted labially distally). The hypoflexid is deep and distinctly separates the protoconid from the hypoconid. Only a very thin and short precingulid is visible at the base of the paraconid and protoconid (mesiolingual part); it is thinner in the youngest specimens.

The m2s are morphologically close to the m1s: presence of a metastylid; mesiodistal compression of the trigonid; very closely located paraconid and metaconid; short but wide talonid; cuspulation on the entocristid and postcristid; and a deep hypoflexid. They are, however, smaller and the crown is lower. The paraconid, paracristid and precingulid are more reduced than on m1. Some doubts persist on the determination of three molars from Condé-en-Brie (MNHN.F.CB784, RBINS Cast-Vert-32468-2244 (CB-633-Ph), MNHN.F.CB186) because these specimens are worn out and partially recall the m1s; however, their sizes agree with those of the m2s.

The m3s are morphologically similar to the m1s and m2s, but the structure of the teeth is more distorted; one can note the lesser development of the apices of the trigonid cusps, notably the paraconid. The difference in height between the trigonid and talonid is less pronounced than on m1s and m2s. The talonid is narrower and one can note the distal position of the hypoconulid area regarding the hypoconid and entoconid. The m3s also differ by their smaller size (Table 2). The m3s are single-rooted.

Variability. Because we have only very few upper molars, it is difficult to determine the variability of these teeth and to determine the morphological evolution of these teeth. The ectoflexus is absent on RBINS Cast-Vert-32468-2243 (Av-2076-Ph, M2), while it is deep on MNHN.F.CB681 (M2). The intra-specific variability of the ectoflexus is also seen in *Kopidodon* (T. Lehmann, pers. comm.).

The surface areas of the paraconid and metaconid tend to decrease during their evolution, and so does their separation. The angle of the two parts of the protocristid (i.e. between the protoconid and metaconid) increases through time (i.e. from Mutigny to Condé-en-Brie), while the differences in height between the trigonid cusps and between the talonid and trigonid tend to decrease. The paracristid and protocristid are less acute through time. MNHN.F.L-124-Av (m1) differs in having a large paraconid, a distinct notch on the para- and postcristid, and a small angle between the protoconid and metaconid; these probably represent the reappearance of primitive features. As indicated in the Description

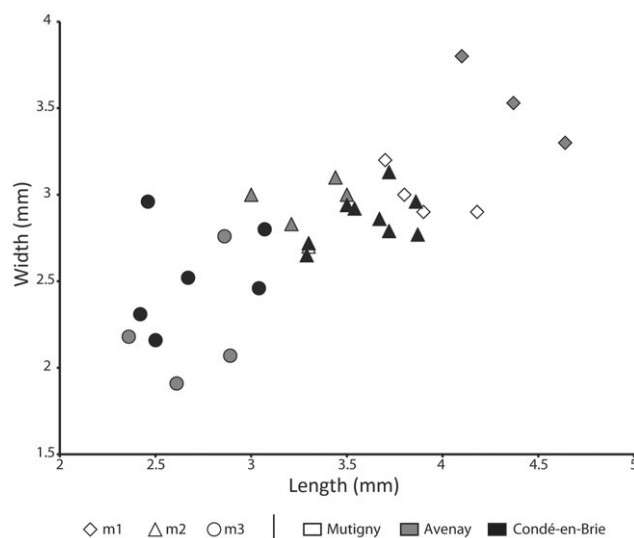


Figure 6. Comparison of the sizes (length \times width) of the lower molars (m1–m3) of *Fratrodon tresvauxi* from Mutigny, Avenay and Condé-en-Brie.

subfamily (Russell & Godinot 1988). These features clearly distinguish these fossils from Paroxyclaeninae.

Presently, it is hard to distinguish between the upper molars of paroxyclaenines and merialines; actually, the sole molars identified as belonging to merialines are the M2 and M3 of *Spaniella carezi*, but their morphology is different from those of paroxyclaenines such as *Vulpavoides*, *Paroxyclaenus* and *Kopidodon* (Crusafont-Pairo & Russell 1967). The sole upper molar (MNHN.F.Av5714) from the Paris Basin studied by Rich (1971) was considered an M1 and referred to cf. *Paroxyclaenus*. Based on the new sample, this tooth is considered an M2 rather than an M1 – the metastylar area is reduced. Rich (1971) considered that MNHN.F.Av5714 could belong to Paroxyclaeninae because he noted the upper molars of this subfamily – as well as MNHN.F.Av5714 – differ from those of the merialine *Spaniella* in having a larger paraconule and broader stylar shelf. Contrary to this conclusion, this tooth is here considered to be an M2 of a merialine species. This is partially based on the higher abundance of merialine lower teeth compared to those of the oldest paroxyclaenine in the MP8 + 9 localities (i.e. *Sororodon tresvauxae*; see below). Furthermore, the M1s referred to *Fratrodon tresvauxi* differ from the M1 of paroxyclaenines (notably *Kopidodon*, the oldest taxon represented by upper molars) by the reduction of the ectoflexus, meta- and parastylar areas and stylar shelf, meta- and parastylar areas more labially oriented, and centrally located protocone.

Moreover, the morphology of the M1s and M2s of the presently described taxon recalls the M2 of the merialine *Spaniella* and the M1s and M2s of the new

merialine from Prémontré (*Paraspaniella gunnelli*; see below). Based on the L/W ratio of the M1 and M2 (Table 3), one can notice that the M1 and M2 of merialines are less transversally elongated than most of the paroxyclaenines; only *Kopidodon* and *Vulpavoides simplicidens* have values close to those of *Fratrodon*, *Paraspaniella* and *Spaniella*. Therefore, the upper molars of merialines are generally more robust than in paroxyclaenines. The upper molars of merialines also generally differ by the features discussed above (i.e. less development and projection of the meta- and parastylar areas, and narrower ectoflexus), but one can argue that the M2 of *Fratrodon* has only a slightly larger stylar shelf than in *Kopidodon*. All of these differences confer a more triangular shape to the upper molars of paroxyclaenines compared to those of merialines. However, one can note that the upper molars of the merialines and paroxyclaenines share the important separation between the metacone and paracone, the large paraconule and metaconule, and the wide and long protocone.

The upper molars of *Fratrodon tresvauxi* differ from those of *Spaniella* by a more developed paraconule and metaconule on M2, more developed metastylar area, and a metacrista oriented more distally than labially on M2. More importantly, the upper molars of *Fratrodon* differ from all those of the other paroxyclaenids (except *Paraspaniella*, see below) by the presence of a preparaconule crista that reaches the parastylar area and ectocingulum.

The fossils referred here to *Fratrodon tresvauxi* differ from those referred to *Merialus* by a relatively smaller m3: the ratio Lm2/Lm3 is 1.13 in *Merialus martinae* and 1.16 in *M. bruneti*, while for *Fratrodon* it is 1.22 in

Table 3. Ratio of length (L)/width (W) of the DP4, M1, and M2 for several paroxyclaenid species. The minimum, maximum and mean ratios are provided, with the number of specimens following in parentheses.

	DP4	M1	M2
	Avenay	Avenay	Avenay
	-	0.73–0.78/0.76 (2)	0.65–0.72/0.68 (3)
<i>Fratrodon tresvauxi</i>	Condé-en-Brie -	Condé-en-Brie 0.75	Condé-en-Brie 0.70–0.78/0.74 (2)
<i>Paraspaniella gunnelli</i>	0.92	0.67–0.72/0.7 (2)	-
<i>Spaniella carezi</i>	-	-	0.73
<i>Kopidodon macrognathus</i>	0.98	0.76–0.77/0.77 (3)	0.66–0.71/0.67 (3)
<i>Paroxyclaenus lemuroides</i>	-	0.68	0.68
<i>Vulpavoides vanvaleni</i>	-	0.63	-
<i>Vulpavoides germanica</i>	-	0.63	0.58
<i>Vulpavoides simplicidens</i>	-	0.75	0.7
<i>Paravulpavoides cooperi</i>	-	0.61	-

Table 4. Ratio of length (L)/width (W) for the m1, m2 and m3 for several paroxyclaenid species. The minimum, maximum and mean ratios are provided, with the number of specimens following in parentheses.

	m1	m2	m3
<i>Merialus martinae</i>	1.63	1.24	1.19
<i>Merialus bruneti</i>	-	1.41–1.43/1.42 (2)	1.3
<i>Fratrodon tresvauxi</i>	Mutigny 1.27–1.35/1.35 (3)	Mutigny 1.16–1.22/1.19 (2)	Mutigny -
	Avenay 1.08–1.41/1.24 (3)	Avenay 1–1.17/1.10 (4)	Avenay 1.04–1.40/1.22 (4)
	Condé-en-Brie -	Condé-en-Brie 1.19–1.40/ 1.34 (9)	Condé-en-Brie 0.83–1.24/ 1.07 (6)
<i>Paraspaniella gunnelli</i>	1.33–1.36/1.35 (2)	1.2–1.28/1.24 (2)	-
<i>Spaniella carezi</i>	-	1.35–1.38/1.37 (2)	1.31–1.34/1.33 (2)
<i>Sorodon tresvauxae</i>	Mutigny 1.6–1.64/1.62 (2)	Mutigny -	Mutigny -
	Avenay 1.54–1.87/1.69 (3)	Avenay 1.76	Avenay -
	Condé-en-Brie 1.55–1.68 /1.61 (4)	Condé-en-Brie 1.69	Condé-en-Brie -
<i>Kopidodon macrognathus</i>	1.54–1.55/1.55 (2)	1.28–1.34/1.3 (2)	1.27–1.31/1.29 (2)
<i>Pugiodens mirus</i>	1.28	1.05	-
<i>Paroxyclaenus lemuroides</i>	1.45	1.34	1.29
<i>Paravulpavoides cooperi</i>	1.41	1.38	-

Avenay and 1.34 in Condé-en-Brie (based on m2 and m3 means) for the new taxon. It is worth remembering that the values of *M. bruneti* and *Fratrodon* are based on isolated teeth, while *M. martinae* is represented by a complete dentary bearing three molars. In *Spaniella carezi*, the ratio Lm2/Lm3 equals 1.29. It is worth noting that this ratio equals 1.22 in the paroxyclaenine *Kopidodon* (based on m2 and m3 means – this value is similar when independently calculating this ratio for each specimen). As a conclusion, the m3 is importantly reduced in *Fratrodon*, notably in the sample collected at Condé-en-Brie, the youngest locality where this taxon is recorded. These data clearly indicate a reduction of the last molar; this agrees with the simplification of its morphology.

The taxon recorded at Mutigny, Avenay and Condé-en-Brie has slightly more square-shaped molars than *Merialus* spp. The ratios of L/W for m1, m2 and m3 of

the new species are generally closer to 1 than those of *Merialus martinae* and *M. bruneti* (Table 4) – only the ratio for the m3s from Avenay and m2s from Condé-en-Brie differ in being higher than that in *Merialus* spp. (Table 4).

The new fossils differ morphologically from those of *Merialus* by the reduction of the precingulid, the common cusplation of the posteristid and entocristid, more closely situated paraconid and metaconid resulting in a distinctly less ‘V’-shaped trigonid (in occlusal view), less pronounced groove between the paraconid and metaconid, a development of the metastylid, lower and less developed trigonid on m3, less mesiodistally elongated talonid on m3, and a lesser difference in height between the trigonid and talonid on the molars.

The dental features of the lower molars of *Fratrodon* (e.g. closely approximated paraconid and metaconid, poorly mesiodistally elongated talonid on m3) are

similarly observed in *Spaniella carezi*. However, the fossils from Mutigny, Avenay and Condé-en-Brie are smaller than those of *S. carezi* (Fig. 4). The ratio L/W of m2 and m3 in *Spaniella* are higher than in *Fratrodon tresvauxi* (Table 4). These values, which are also higher than in *Merialus martinae*, indicate a mesiodistal elongation of the molars in the Spanish paroxyclaenid; however, one can note that these values are close to those of *M. bruneti*.

Therefore, the lower molars of *Fratrodon* are more square-shaped than those of most other paroxyclaenids: only *Pugiodens mirus* have values for the L/W ratio close to those of *Fratrodon* (Table 4). *Fratrodon* also differs morphologically from the Spanish fossils by a more important difference in height between the trigonid and talonid, less reduced paraconid on molars (notably on m3), the presence of a metastylid, and a higher hypoconid – although the hypoconid is still the highest talonid cusp, the talonid cusps of the molars of *S. carezi* are generally more homogeneous in size (height and width). Finally, as noticed by Rich (1971), fossils of *Fratrodon* from Avenay, Mutigny and Condé-en-Brie differ in having a longer trigonid relative to the talonid; the trigonid is highly mesiodistally compressed in *Spaniella*. These features are probably distinctive of the oldest merialines. M2 is the only upper molar that can be compared between the two taxa. All of the M2s of *Fratrodon* differ from the M2 of *Spaniella* by a slightly more developed stylar shelf, more oblique labial edge on M2, and the presence of a crest (i.e. the preparaconule crista) between the paraconule and labial cingula. One can note that the values of the ratio L/W for the upper molars of the merialines *Fratrodon*, *Spaniella* and *Paraspaniella*, and the paroxyclaenine *Kopidodon* are close (Table 4).

To conclude, the fossil *Fratrodon* from the Paris Basin is morphologically different from the other merialines *Merialus* and *Spaniella* (e.g. square-shaped lower molars) in spite of sharing common overall morphology. *Fratrodon*, moreover, displays features that are unknown in the two latter taxa (e.g. the presence of a metastylid). Its discovery thus increases the morphological diversity of the paroxyclaenids and implies the existence of several different morphological ‘subgroups’ among merialines.

Because of the sum of unique characters, the fossils cannot be referred to one of these genera: we therefore erect a new genus and species, *Fratrodon tresvauxi* gen. et sp. nov.

Genus *Paraspaniella* gen. nov.

Type species. *Paraspaniella gunnelli* sp. nov.

Diagnosis. As for the type species.

Derivation of name. ‘Pará’ meaning next to (Latin) and *Spaniella*.

Paraspaniella gunnelli sp. nov.
(Fig. 7)

Diagnosis. Merialine that differs from *Merialus*, *Spaniella* and *Fratrodon* by a high entoconid (as high as the hypoconid), a high entocristid, shallow trigonid and talonid basins, and the absence of a precingulid. Differs from *Merialus* and *Fratrodon* by much reduced difference in height between the trigonid and talonid, much-reduced paraconid, paracristid and protocristid on lower molars, the absence of a groove between the paraconid and metaconid, and reduced para- and metastylar areas on upper molars. Differs from *Spaniella* by flat trigonid and talonid basins, less closely located paraconid and metaconid, less reduced paraconid on m2, trigonid and talonid almost the same in height, higher entoconid, and reduction of the precingulid.

Derivation of name. In memory of Gregg F. Gunnell (1954–2017) who greatly contributed to our knowledge of Cenozoic mammals.

Type locality. Prémontré (Aisne, France), Ypresian (MP10).

Other locality. Grauves (Marne, France), Ypresian (MP10).

Holotype. MNHN.F.SLP-29-PE1327, left m1.

Referred specimens from Prémontré. MNHN.F.SLP-29-PE1209, right m1; MNHN.F.SMP-29-PE-1558, left DP4; MNHN.F.SLP-PR-29-2097, right M1; MNHN.F.SLP-29-PE-885, right M1.

Referred specimens from Grauves. MNHN.F.GR7601, right m2; MNHN.F.GR7874, right m2.

Measurements. See Table 5.

Description. The DP4 is triangular in occlusal view. The parastyle and postmetacrista are projected mesially and distally, respectively. The stylar shelf is short, the ectocingulum is developed and the ectoflexus is deep. The paracone and metacone are separated and mesiodistally elongated. The apexes are broken, preventing determination of their respective heights. The paraconule and metaconule are well defined and large. The metaconule is larger than the paraconule. The preparaconule crista joins the ectocingulum. A short postparaconule crista is present. The protocone is wide and long; its apex is mesially inclined. No lingual cingulum is visible.

Table 5. Length (L) and width (W) data (in mm) for the teeth of *Paraspaniella gunnelli* gen. et sp. nov. from Prémonté and Grauves (France; MP10, Ypresian). **Abbreviations:** M, mean; n, number of teeth.

Locus		n	Observed range	M
DP4	L	1	3.67	–
	W	1	4.01	–
M1	L	2	3.24–3.91	3.58
	W	2	4.83–5.44	5.14
m1	L	2	4.25–4.34	4.3
	W	2	3.13–3.27	3.2
m2	L	2	3.66–3.68	3.67
	W	2	2.87–3.07	2.97

We consider that the two upper molars from Prémonté (MNHN.F.SLP-PR-29-2097 and MNHN.SLP-29-PE-885) are M1s based on their sizes. The M1 is subrectangular in occlusal view. They are completely separated and linked by a thin centrocrista. The paracone is distinctly larger and higher than the metacone. The stylar shelf is short, notably labially to the paracone; the ectocingulum is high and covered by numerous small cuspules. The para- and metastylar areas are much reduced. The ectoflexus is distinguishable on MNHN.F.SLP-29-PE-885, but absent on MNHN.F.SLP-PR-29-2097. The protocone is large and mesially inclined (as a result the preprotocrista is shorter than the postprotocrista). The protocone is almost as high as the paracone and metacone. The metaconule and paraconule are high and well defined; they are close to the paracone and metacone, respectively. The paraconule is linked to the ectocingulum by the preparaconule crista. No lingual cingulum is visible.

Two m1s are known from Prémonté and two m2s from Grauves. The m1s are clearly longer than the m2s (Table 5); moreover, they display a larger paraconid. The trigonid is only slightly higher than the talonid. The trigonid is mesiodistally compressed. The protoconid is the highest trigonid cusp, but only very slightly. The paraconid is lower than the metaconid. The paraconid is lingually located. The para- and postcrisid are only slightly acute. There is no groove between the paraconid and metaconid. The trigonid basin is almost flat. The paracristid is mesially curved (visible in occlusal view); a distinguishable additional cusp is present on this crisid on MNHN.F.SLP-29-PE1209; it is less prominent on MNHN.F.SLP-29-PE1327 (Fig. 7B). No notch is present on either the protocrisid or the paracristid. The talonid is short; it is as wide as the trigonid. The hypoconid and entoconid are the largest and highest talonid cusps; they are almost equal in height. The hypoconulid is present but less developed than the two other cusps. The crisid obliqua is oblique (distally shifted labially). The crisid obliqua and entocrisid are high, closing the talonid

basin labially and lingually. The talonid basin is shallow, a metastylid is present and the precingulid is absent. The hypoflexid is deep and distinctly separates the protoconid from the hypoconid.

The m2s are morphologically similar to the m1s: they display the mesiodistal compression of the trigonid, the shallow trigonid and talonid basins, the closely located paraconid and metaconid, the short and wide talonid, the high entoconid and hypoconid, and the deep hypoflexid. They are, however, smaller than m1s and differ in their lower trigonid.

Variability. The sample is small (seven isolated teeth representing four loci) but provides information concerning variability within this species. MNHN.SLP-29-PE-885 (M1) shows a deeper ectoflexus than MNHN.F.SLP-PR-29-2097 (M1). MNHN.F.SLP-29-PE1209 (m1) has a more distinct accessory cusp on the paracristid. MNHN.F.GR7874 (m2) has a more mesiodistally compressed trigonid; it also appears more transversely enlarged (a variation already noted in *Fratrodon tresvauxi*). A tiny precingulid is visible on GR7601 (m2) but is less developed than in specimens of *F. tresvauxi* from Avenay, Mutigny and Condé-en-Brie. To conclude, this variation recalls that observed in *F. tresvauxi* and *Merialus bruneti*.

Comparison. The presence of a DP4 is interesting because the deciduous molars of paroxyclaenids are rare: this type of tooth is currently known only for *Kopidodon* and (more doubtfully) *Paravulpavoides* (Koenigswald 1983; Hooker 1986; Harrison 2009). The tooth is similar to, but smaller than, the DP4 of *Kopidodon* (Koenigswald 1983, fig. 4). However, the sole presence of merialine teeth and the dimensions of this tooth, which fit with the permanent molars, lead us to consider this tooth as merialine. It is worth mentioning that the presence of deciduous teeth is common in artiodactyls, rodents and pantolestids at Prémonté (Sudre & Erfurt 1996; Escarguel 1999; R. Smith 2001).

There are similarities between the M2 of *Kopidodon* and the M1s of the new taxon described herein (MNHN.F.SLP-PR-29-2097 and MNHN.SLP-29-PE-885): a reduced stylar shelf, reduced para- and metastylar areas, and subrectangular morphology. However, compared to *Kopidodon*, the upper molars are close in size to the DP4 (3.24 and 3.91 mm vs 3.67 mm); in *Kopidodon* the M1 is as long as the DP4, while the M2 is distinctly shorter than the DP4. When comparing the M1s from Prémonté and the M1 of *Kopidodon*, the upper molars from Prémonté differ by reduced para- and metastylar areas, a reduced metacone with respect to the paracone, and the absence of an ectoflexus.

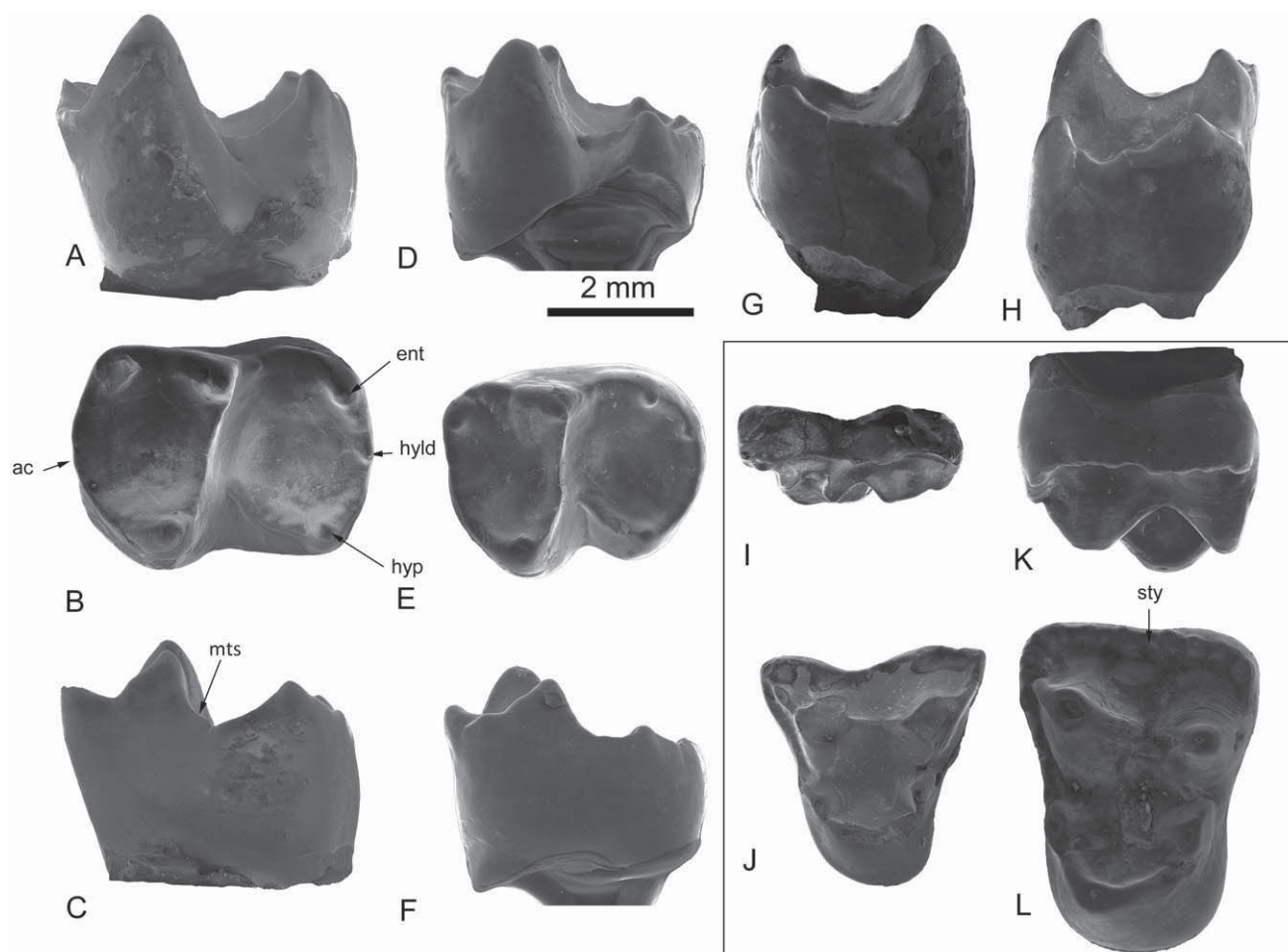


Figure 7. *Paraspaniella gunnelli* gen. et sp. nov. **A–C**, MNHN.F.SLP-29-PE 1327 (holotype), left m1: **A**, labial view; **B**, occlusal view; **C**, lingual view. **D–F**, MNHN.F.GR 7601, right m2: **D**, labial view; **E**, occlusal view; **F**, lingual view. **G, H**, MNHN.F.SLP-29-PE 1327 (holotype), left m1: **G**, mesial view; **H**, distal view. **I, J**, MNHN.F.SLP-29-PE 1558, left DP4: **I**, labial view; **J**, occlusal view. **K, L**, MNHN.F.SLP-PR-29 2097, right M1: **K**, labial view; **L**, occlusal view. Reversed views: C, D, E, K, L. **Abbreviations:** ac, accessory cusp; ent, entoconid; hyp, hypoconid; hyld, hypoconulid; mts, metastylid; sty, stylar shelf.

The reduction of the para- and metastylar areas on MNHN.F.SLP-PR-29-2097 and MNHN.SLP-29-PE-885 agrees with the transversal orientation of the para- and protocristid on the m1s discovered at Prémontré. The reduction of the metacone on the upper molars also fits with the poor development of wear facet 4 on the m1s (compared to the large wear facets 1 and 3). Consequently, we consider that the upper and lower teeth discovered at Prémontré and Grauves belong to the same taxon.

The fossils discovered at Prémontré and Grauves differ from those of *Fratrodon tresvauxi* from Mutigny, Avenay and Condé-en-Brie by a lesser difference in height between the trigonid and talonid. In this regard, it recalls the Spanish species *Spaniella carezi*. No cusplation is observed on the molars from Prémontré and Grauves, unlike in those of *F. tresvauxi*; on the contrary,

the entoconid is well individualized and is as high as the hypoconid; moreover, the entoconid and hypoconid are close in height to the paraconid and metaconid on the m1. The entoconulid, present on the molars of *F. tresvauxi*, is absent on the molars from Prémontré and the trigonid and talonid basins are shallower on the molars of the new taxon. The latter feature represents a tendency that is visible in few specimens of *F. tresvauxi*. The upper molars of the new taxon also differ importantly from those of *F. tresvauxi* by the reduction of the metastylar and parastylar areas, and the reduction of the separation between the metaconule and protocone. All of the features that characterize the lower molars also distinguish the new taxon from *M. martinae* and *M. bruneti*.

Some of these features are present in *Spaniella* (e.g. reduced and lingually located paraconid, reduced para-

and metastylar areas, subrectangular upper molars). However, the fossils from Prémontré differ from the Spanish merialine by the flat trigonid and talonid basins, the less closely located paraconid and metaconid, the less reduced paraconid on m2, the trigonid and talonid being similar in height, the higher entoconid, and the reduction of the precingulid; moreover, the trigonid basin seems longer on the m2s from Grauves than in those from Barranc de Forals (MP10).

The teeth from Prémontré and Grauves also seem to share with those from Spain a less square morphology in comparison with specimens of *F. tresvauxi* (Table 4). However, the L/W values for the m2s (the only values that can be compared between the two species) are lower than those of *Spaniella* (Table 4). It is worth noting that the L/W values for the m2s from Grauves are close to that of *Merialus martinae* (Table 4).

Subfamily **Paroxyclaeninae** Weitzel, 1933

Genus *Sororodon* gen. nov.

Type species. *Sororodon tresvauxae* sp. nov.

Diagnosis. As for the type species.

Derivation of name. ‘Soror’ = sister (Latin) and ‘odon’ = tooth (Greek); in reference to the fact that Mr Frédéric Tresvaux du Fraval and Mrs Marie Tresvaux du Fraval are brother and sister.

Sororodon tresvauxae sp. nov.

(Fig. 8)

1971 cf. *Paroxyclaenus*; Rich: 58–61, fig. 16b–e (*partim*).

Diagnosis. Differs from other paroxyclaenines (*Kopidodon*, *Vulpavoides*, *Paroxyclaenus*, *Paravulpavoides*) in possessing a more mesially located paraconid (resulting in a greater distance between the paraconid and metaconid) and a wider talonid on molars.

Derivation of name. Dedicated to Mrs Marie Tresvaux du Fraval (1990–) for her help and support to the first author (FS) over many years.

Type locality. Mutigny (Marne, France), Ypresian (MP8 + 9).

Other localities. Avenay (Marne, France), Ypresian (MP8 + 9); Condé-en-Brie (Aisne, France), Ypresian (MP8 + 9).

Holotype. MNHN.F.CEB 521, right m1.

Referred specimens from Mutigny (Rich 1971). MNHN.F.Mu5947, left m1; MNHN.F.Mu6385, right m1.

Table 6. Length (L) and width (W) data (in mm) for the teeth of *Sororodon tresvauxae* gen. et sp. nov. from Mutigny (France; MP8 + 9, Ypresian), Avenay (France; MP8 + 9, Ypresian) and Condé-en-Brie (France; MP8 + 9, Ypresian). Partially based on Rich (1971, table 30). **Abbreviations:** M, mean; n, number of teeth.

Locus		n	Observed range	M	
Mutigny	m1	L	2	4–4.1	4.05
		W	2	2.5	2.5
Avenay	m1	L	3	4.3–4.78	4.57
		W	3	2.56–2.8	2.72
	m2	L	1	4.14	–
		W	1	2.35	–
Condé-en-Brie	m1	L	4	3.99–4.12	4.07
		W	4	2.41–2.63	2.54
	m2	L		3.98	–
		W		2.35	–

Referred specimens from Avenay (Rich 1971). MNHN.F.Av5909, right m1.

Referred specimens from Avenay. MNHN.F.Av7712, left m1; RBINS Cast-Vert-32468-2247 (Av-1000-Ph), right m1; MNHN.F.Av4561, left m2.

Referred specimens from Condé-en-Brie. MNHN.F.CEB525, left m1?; MNHN.F.Levé.Condé.924, right m1?; MNHN.F.MCB365, right m1; RBINS Cast-Vert-32468-2248 (CB-12-Ph), right m2.

Measurements. See Table 6.

Description. The m1 is characterized by a mesiodistally elongated trigonid and a wide separation between the paraconid and metaconid. The paraconid is mesiolingually located; the paracristid is oblique and convex. The paraconid is smaller than the metaconid; the protoconid is the highest cusp of the trigonid. The metaconid is more distally located than the protoconid. Notches are present on the para- and protocristid. The metaconid is mesiodistally elongated in lingual view. A metastylid is present; its size varies from one specimen to another. A small cusp is present on the postparacristid of several specimens. The talonid is shorter than the trigonid (Table 7), but is as wide as the latter structure. The hypoconid is large. The entoconid and hypoconulid are not distinguishable on all the specimens because they are replaced by a very thin cusplation on the postcristid and entocristid. The postcristid and entocristid are fused and are more or less convex depending on the specimen. The cristid obliqua is strongly oblique. The hypoflexid is deep. The talonid basin is closed lingually by a high entocristid. A notch is sometimes present between the entocristid and metastylid. A faint precingulid is visible

Table 7. Ratio of talonid length (LTalo)/trigonid length (LTrigo) of the m1, m2 and m3 for several paroxyclaenid species. The minimum, maximum and mean ratios are provided, with the number of specimens following in parentheses.

	m1	m2	m3
<i>Merialus bruneti</i>	–	0.89–1.17/1.03 (2)	–
<i>Fratrodon tresvauxi</i>	0.91–1.19/1.04 (6)	0.73–1.36/1.05 (16)	0.55–1.1/0.95 (10)
<i>Paraspaniella gunnelli</i>	0.58–0.87/0.71 (2)	0.91–0.99/0.95 (2)	–
<i>Sororodon tresvauxae</i>	0.50–0.93/0.71 (9)	0.67–0.85/0.76 (2)	–

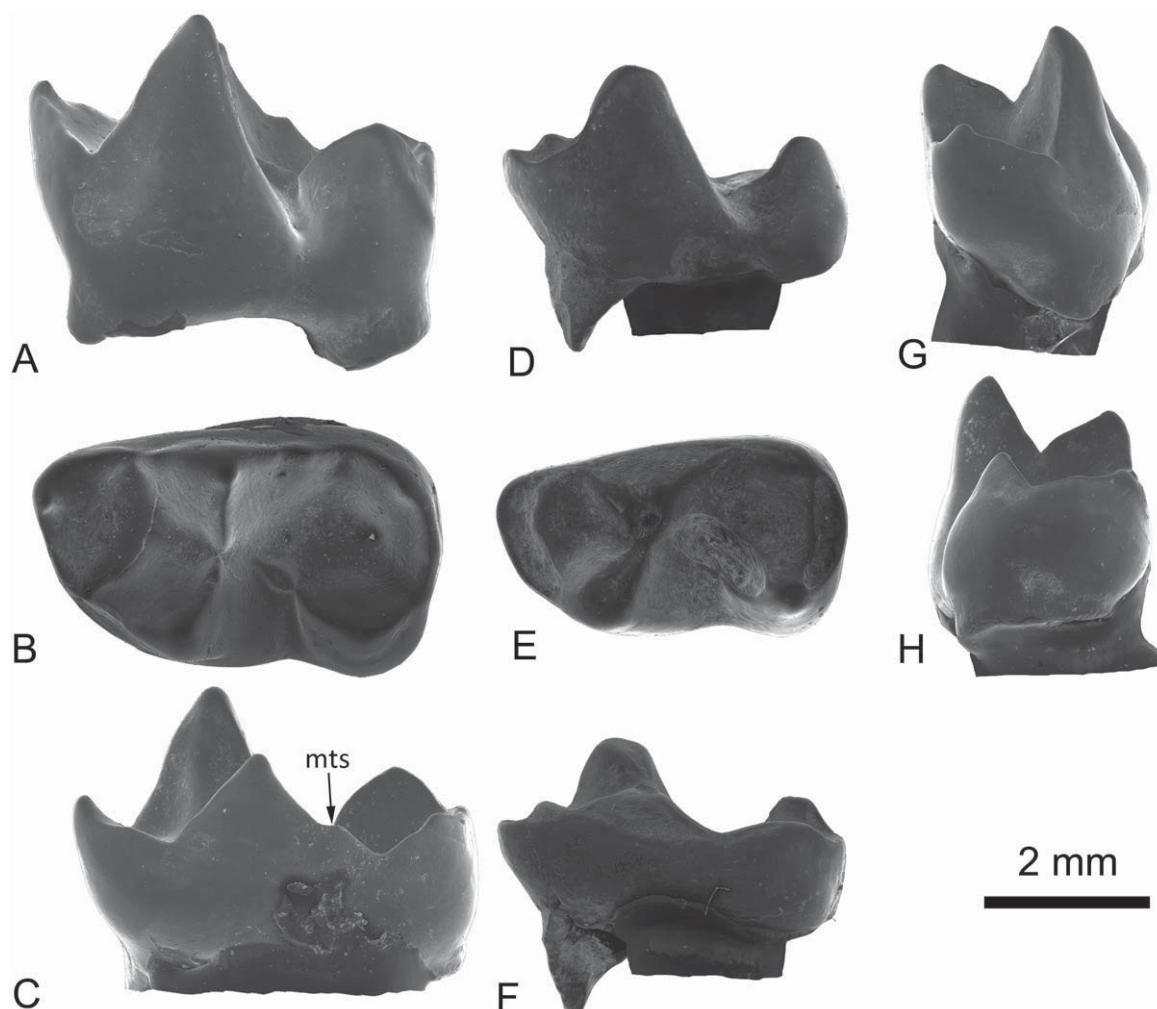


Figure 8. *Sororodon tresvauxae* gen. et sp. nov. **A–C**, MNHN.F.CEB 521 (holotype), right m1: **A**, labial view; **B**, occlusal view; **C**, lingual view. **D–F**, MNHN.F.Av4561, left m2: **D**, labial view; **E**, occlusal view; **F**, lingual view. **G, H**, MNHN.F.CEB 521 (holotype), right m1: **G**, mesial view; **H**, distal view. Reversed views: A, B, F–H. **Abbreviation:** mts, metastylid.

on the mesiolabial facet of the paraconid on several specimens; the other specimens (Fig. 8A) do not have a precingulid.

The m2 is slightly smaller (Table 6) than the m1, but the two molars are similar in morphology. The paraconid is less mesially located and the talonid is slightly longer relatively to the trigonid on m2 than on m1 (Table 7). These differences between the m1 and m2 are also observed in the Lutetian paroxyclaenine

Kopidodon. It is, however, hard to distinguish between the two loci because the two m2s of the present sample are worn (especially the metaconid, hypoconulid and cristid obliqua), so our determination of the m2s should be regarded as uncertain. Moreover, some of the m1s are close in size to the m2s (Fig. 4), but their morphology better agrees with that of an m1 than an m2 (this is notably the case for MNHN.F.CEB525 and MNHN.F.Levé.Condé.924).

Variability. The specimens of paroxyclaenines discovered at Mutigny, Avenay and Condé-en-Brie display less variability than those of other merialines from the same localities. However, this could be due to the poor sample size (only 11 specimens). Only the cusplation of the entocristid and postcristid and the presence of an accessory cusp on the postparacristid vary within the sample.

Comparison. The fossils of the present taxon are only slightly smaller, but distinctly narrower, than those referred to *Fratrodon tresvauxi* (Fig. 4), and the two species are recorded in the same localities. These two taxa share moderately high-crowned molars, cusplation of the entocristid and postcristid, the presence of a meta-stylid, a high entocristid that lingually encloses the talonid basin, a small difference in height between the trigonid and talonid, the shallow depth of the notches on the trigonid, the wide talonid, and the small size of the lingually located paraconid.

The two samples of isolated teeth differ in the less appressed apices of the paraconid and metaconid: the paraconid is clearly more mesially and less lingually located than in the merialine *F. tresvauxi*. As a result, the protoconid part of the paracristid is longer and mesiodistally oriented (it is transversely oriented in merialines); due to this morphology, the trigonid is more 'V'-shaped than in *F. tresvauxi*. Even if the morphology of the talonid recalls merialines, the wider separation of the paraconid and metaconid apices and the position of the paraconid allow referral of the lower molars to Paroxyclaeninae rather than Merialinae. The teeth from Mutigny, Avenay and Condé-en-Brie grouped within this second sample are more mesiodistally elongated (Table 4).

Consequently, Rich (1971) was correct to erect two distinct taxa from among the fossils from Avenay and Mutigny. He was also right to conclude that one taxon is morphologically close to the merialine *Spaniella* (cf. Paroxyclaenidae in Rich 1971, but *Fratrodon tresvauxi* in the present paper), and that the other taxon is close to the paroxyclaenine *Paroxyclaenus* (cf. *Paroxyclaenus* in Rich 1971, *Sororodon tresvauxae* in the present paper). We disagree, however, with Rich (1971) in regarding MNHN.F.Mu6385 and MNHN.F.Mu5947 as possible m1s (Rich 1971 considered these two teeth to be m2s).

It is important to note that several molars, such as MNHN.F.Av4561 (Fig. 8D–F), display peculiarly severe wear on the lingual side, as noticed by Tobien (1969) and Koenigswald (1983) in *Kopidodon* and *Paroxyclaenus* (see Discussion, below).

Among paroxyclaenines, only *Kopidodon*, *Paravulpavoides*, *Pugiodens*, *Paroxyclaenus* and *Vulpavoides vanvaleni* are represented by lower molars;

however, the holotype and sole specimen of *Pugiodens* has been missing since the 1960s and the lower dentition of *V. vanvaleni* consists only of the m3. The new taxon differs from *Paravulpavoides* and *Paroxyclaenus* by its more mesially located paraconid, less rounded but longer paracristid, and also (possibly) by a wider talonid relative to the trigonid (this feature has, however, to be quantified in the future for all paroxyclaenid species). The general morphology of the molars found at Mutigny, Avenay and Condé-en-Brie is more similar to that of *Kopidodon*, the oldest paroxyclaenid found prior to this work (Fig. 1), than to *Paravulpavoides* and *Paroxyclaenus*. It is noteworthy that the lower molars of all paroxyclaenines are morphologically very similar (see Koenigswald 1983).

The new taxon from Mutigny, Avenay and Condé-en-Brie differs from *Kopidodon* in its smaller size (35% when considering the length of the m1). It also differs in its less appressed paraconid and metaconid (the paraconid is more mesially located in the fossils from the Paris Basin than in *Kopidodon*), its longer paracristid and its wider talonid on molars, based on comparisons with the illustrations of *Kopidodon* (Koenigswald 1983, fig. 4).

Fossils of *S. tresvauxae* are less abundant than those of *F. tresvauxi* (11 vs 34 specimens). This poor abundance might explain the absence of paroxyclaenines in localities that yield very few paroxyclaenids (i.e. Pourcy, Grauves and Prémontéré). However, the very similar morphology of the two subfamilies also suggests that they were ecologically close; therefore, they might have co-occurred and the presence of merialines could have influenced the presence of paroxyclaenines.

Discussion

The cases of *Euhookeria hopwoodi* and *Kiinkerishella zaisanica*

Russell & Godinot (1988) referred *Euhookeria hopwoodi* from the Priabonian (Upper Headon beds, Lignite beds) to Merialinae. This species, which is represented by a mandible bearing the canine, p1–p4 and m3 (NHMUK PV M26052; holotype), one isolated p1 (NHMUK PV M26054) and one isolated m1 (NHMUK PV M26053), is interesting because (1) it would be the last representative of Paroxyclaenidae, and (2) its reference to Merialinae implies a very large gap in the fossil record for this subfamily (i.e. the entire middle Eocene, 47.8–38 Myr) (Fig. 1). Russell & Godinot (1988) considered, however, that the m1 should be referred to another taxon.

In their preliminary results of their study on the pantolestans from the Zaysan Basin (Kazakstan; upper Eocene), Lucas & Emry (2000) noted a close relationship between *Euhookeria* and *Oboia argillaceous*, which is considered to be a pantolestine (Lucas & Emry 2004).

Harrison (2009) compared the fossils of *Paravulpavoides* – the youngest paroxyclaenine (Fig. 1) – to those of *E. hopwoodi* (including a new isolated lower molar, HZM 1.19050). He concluded that “the paroxyclaenid affinities of *Euhookeria hopwoodi* appear rather uncertain, but it is clearly not closely related to *Paravulpavoides*” (Harrison 2009, p. 34). He remarked that the m1 of *E. hopwoodi* possesses a small projecting precingulid (a feature absent from *Paravulpavoides cooperi*), a talonid that is not reduced and that bears three distinct cusps, a small but distinct hypoconulid, and a low crestiform entoconid. The development of the precingulid is also visible on m3 of the holotype, and thus seems to be characteristic of *Euhookeria*. The hypoconulid is well developed on m3; the entoconid is crestiform, as on the possible molars (e.g. HZM 1.19050 and NHMUK PV M26053) referred to *Euhookeria*.

The referral of *Euhookeria* to Merialinae is based mainly on the closely appressed paraconid and metaconid (Russell & Godinot 1988). This feature clearly distinguishes *Euhookeria* from Dyspterninae (a subfamily of Pantolestidae), including the genera *Dyspterna* and *Cryptopithecus*. *Euhookeria* also shares with merialines the presence of a simple p4 (i.e. no metaconid) and the reduction of the entoconid on molars. However, this is also the case in Dyspterninae (Cray 1973; Heissig 1977; Russell & Godinot 1988).

However, several features of *Euhookeria* are inconsistent with the morphology of merialine teeth:

1. The upper half of the canine is triangular with sharp antero-internal, internal and postero-external crests; this morphology is observed in the dyspternines *Dyspterna* and *Cryptopithecus*, but not in *Spaniella* (Merialinae); the morphology of the canine in the paroxyclaenine *Kopidodon* is also different from that of *Euhookeria*.
2. The premolars of *Euhookeria* display a mesiolingual groove; this groove is not present on the premolars of *Merialus* and *Spaniella*. The latter genus possesses very simplified premolars with respect to those of *Merialus*.
3. The precingulid is well developed in *Euhookeria* but is extremely reduced in *Merialus*, *Fratrodon* and *Spaniella* and is absent in *Paraspaniella*.
4. The entoconid is reduced/absent in *Euhookeria* as also occurs in merialines (except in *Paraspaniella*),

but the hypoconid and entoconid of the latter are replaced by a cusplation and therefore are not as distinguishable as in *Euhookeria*; in *Merialus*, the entoconid is poorly individualized and the hypoconulid is tiny.

5. The talonid basin is distinctly lingually opened on the m3 of *Euhookeria* whereas all merialine molars have a high entocristid that reaches the metaconid, enclosing the talonid basin.
6. The hypoconid is much higher than the entoconid and hypoconulid in *Euhookeria*; this is not the case in merialines, but this is the case in Dyspterninae.

Based on all of these differences, the closely appressed paraconid and metaconid appear to be of little importance. Moreover, the morphology of the teeth of *Euhookeria* (triangular canine, mesiolingual groove on premolars, precingulid on molars, lingually opened talonid basin, distinguishable hypoconid and entoconid, high hypoconid) fits better with that of Dyspterninae than Merialinae. It is worth noting that the paraconid is not well developed in Dyspterninae, but as noted by Russell & Godinot (1988), it is generally more medially placed, which is not the case on the m3 of the holotype of *Euhookeria*, but is the case on the two isolated molars (NHMUK PV M26053 and HZM 1.19050) doubtfully referred to *Euhookeria*.

Consequently, it appears that *Euhookeria* should be included in Dyspterninae; its inclusion in Merialinae would imply numerous important modifications of the canine, premolars and molars that do not fit with the observed evolution of merialines during the Ypresian. This new attribution would solve the problem of the gap in the merialine fossil record and implies that merialines inhabited Europe only during the Ypresian.

Kiinkerishella zaisanica from the upper Eocene (Ergilian Asian Land Mammal Age) of the Zaysan Basin (Kazakhstan) was considered to be a condylarth (Gabuniya & Biryukov 1978) or a paroxyclaenid close to *Paroxyclaenus* (Russell & Godinot 1988; Lucas & Emry 2000), but was referred to Dyspterninae by Dashzeveg & Russell (1992). The recent study of Lucas & Emry (2004) concluded that *Kiinkerishella* is morphologically close to *Gobiopithecus* and *Dyspterna* and should be included within Dyspterninae.

This species was the sole potential paroxyclaenid known from outside Europe. Its reference to pantolestan dyspternines thus implies that paroxyclaenids were endemic to Europe. Moreover, because of the dyspternid affinities of *Euhookeria* and *Kiinkerishella*, as discussed above, it appears that paroxyclaenids went extinct before the late Eocene.

Principal component analysis

We performed a PCA on all of the complete lower molars in order to discriminate the four new

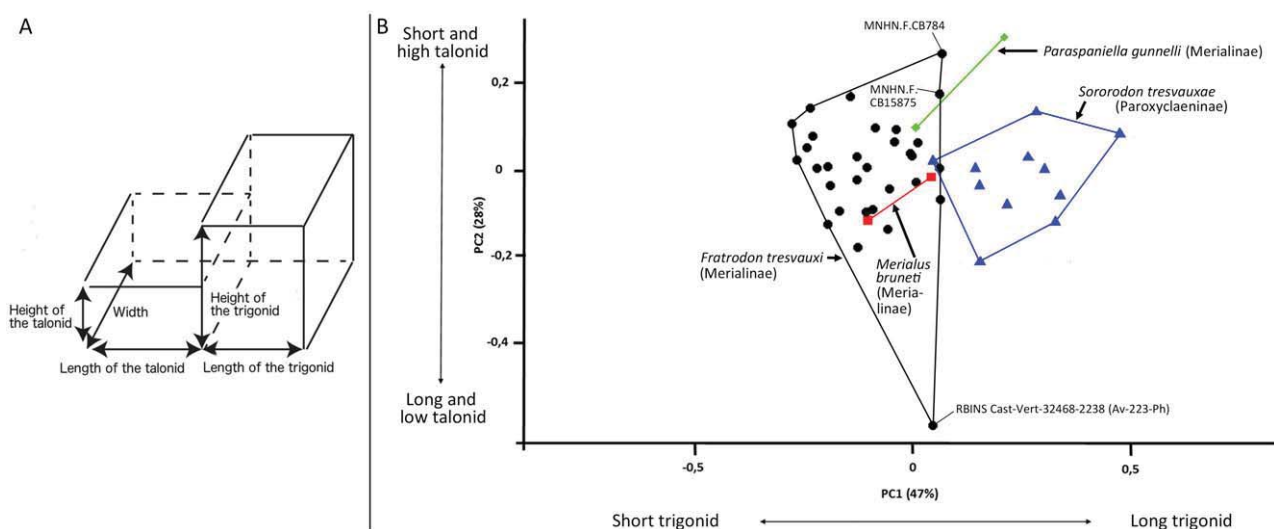


Figure 9. Principal component analysis (PCA) on all the complete lower molars ($n = 46$). **A**, illustration of the five measurements used for the PCA. **B**, biplot of the first two components of the PCA. Circles: *Fratrodon tresvauxi*; diamonds: *Paraspaniella gunnelli*; squares: *Merialus bruneti*; triangles: *Sororodon tresvauxae*.

paroxyclaenid species described herein. We used five measurements taken on the lower molars (Fig. 9A; Supplementary material, File 1). The first two principal components (PCs) represent 75% of shape variation ($PC1 = 47\%$; $PC2 = 28\%$). $PC1$ accounts mainly for the variability in the length of the trigonid, while $PC2$ expresses variability in the length and height of the talonid. The distribution along $PC1$ and $PC2$ clearly separates the different subfamilies (Fig. 9B).

A clear separation is observed between *Sororodon tresvauxae* and *Fratrodon tresvauxi* along $PC1$ (Fig. 9B). The teeth of *Sororodon tresvauxae* are located on the positive side of $PC1$ (i.e. their teeth are narrow with a long trigonid). Conversely, the teeth of *Fratrodon tresvauxi* are located on the negative side of $PC1$ (i.e. their teeth are broad with a short trigonid). The importance of trigonid morphology, notably the position of the paraconid and metaconid (i.e. closely appressed or not), for discriminating between merialines and paroxyclaenines was highlighted by Russell & Godinot (1988) when they erected Merialinae. As the relative positions of the paraconid and metaconid directly influence the length of the trigonid, our PCA supports the importance of this character in paroxyclaenid systematics.

The other two species, *Paraspaniella gunnelli* and *Merialus bruneti*, occur within the morphospace created by specimens of *Fratrodon tresvauxi* (Fig. 9B). However, the former two taxa are represented by two specimens only (two m2s for *M. bruneti* and two m1s for *P. gunnelli*). Moreover, *Paraspaniella gunnelli* is located on the positive side of $PC2$ with a talonid that is high but short. By contrast, *Merialus bruneti* is on the

negative side of $PC2$ with a talonid that is lower but longer. This agrees with the general evolution observed in Merialinae (see below).

A large disparity is observed for *Fratrodon* specimens along $PC2$ (Fig. 9B). This variability involves high variation in the height of the talonid. Some of the individuals have very high but short talonids, while the others have low but long talonids. Three specimens stand out from the other teeth: MNHN.F.CB784 (m2?), MNHN.F.CB15875 (m3) and RBINS Cast-Vert-32468-2238 (Av-223-Ph, m3) (Fig. 9B). MNHN.F.CB784 differs from other m2s in having a very high trigonid, being similar to m1s in this structure, but the other measurements are similar to those of m2s. RBINS Cast-Vert-32468-2238 (Av-223-Ph) differs from other m3s by its very small width and trigonid and talonid heights; the tooth seems to be vestigial when compared to other m3s. MNHN.F.CB15875 differs from other m3s in the shortness of the talonid; however, the separation between the talonid and trigonid is not marked clearly in this specimen, which may have influenced the measurement of talonid length. Consequently, we think that the important variability in the *Fratrodon* teeth, which may be due to reduction of the functional importance of the m2 and m3 relative to the m1, could explain this distribution (see below).

Specimens of *Sororodon* cluster in the centre of $PC2$ (Fig. 9B), which suggests reduced variation of the shape and size of the talonid. Conversely, tooth variation in *Sororodon* takes place at the level of the trigonid (i.e. along $PC1$).

General evolution of paroxyclaenids

The exclusion of *Euhookeria* and *Kiinkerishella* from Paroxyclaenidae and the description of four new species leaves 13 valid species within the family ranging from the Ypresian to Bartonian (MP7 to MP16) (Fig. 1). The oldest fossils that can be referred to Paroxyclaenidae lived in the early Ypresian in the south of France (Palette; MP7) and the Paris Basin (Pourcy; MP7, PE III biozone *sensu* Hooker 1996, 1998). They both belong to Merialinae.

As indicated above, the Pourcy fauna is probably aged between 56–55 Myr and that of Palette is considered close to 55 Myr (Table 1). It is noteworthy that paroxyclaenids are unknown from Dormaal (~56 Myr) although this fossiliferous locality provides numerous teeth that are similar in size to those of the oldest paroxyclaenids (i.e. *Merialus*). Consequently, paroxyclaenids seem to have appeared in Europe during the early Ypresian, shortly (500,000–1,000,000 years) after the Paleocene–Eocene Thermal Maximum (PETM).

As mentioned above, merialines (*Merialus bruneti* and *M. martinae*) are the earliest paroxyclaenids recorded in Europe. Paroxyclaenines (represented by *Sororodon tresvauxae*) make their first appearance later at Mutigny (between 54–52 Myr). This corroborates the recent hypothesis of Hooker (2015) that the Mammal Dispersal Event (MDE; Fig. 1), which resulted in a renewal of the European mammal fauna around the PETM event, can be separated into at least two phases.

The sudden appearance of paroxyclaenines is intriguing because *S. tresvauxae* displays a trigonid on its lower molars that is completely different from that of merialines: the trigonid is not as compressed mesiodistally, the paraconid and metaconid are not closely appressed, the paraconid is more mesially located and individualized, and the protoconid part of the paracristid is longer and mesiodistally oriented (whereas it is transversely oriented in merialines). This distinction is supported by our PCA. Consequently, the molars of paroxyclaenines are clearly different from those of merialines. The morphology of the talonid (hypoconulid and entoconid reduced, cusplation of the entocristid) and the wear facets are, however, generally similar. Paroxyclaenines can be distinguished from merialines also by the molarized morphology of the p4 (Russell & Godinot 1988). Unfortunately, the p4s of the paroxyclaenids from Mutigny, Condé-en-Brie and Avenay are unknown; this prevents reconstructing the evolution of this tooth. This aspect of the dentition of paroxyclaenines indicates that they potentially separated from merialines a long time before their first record (at Mutigny

and that they might have lived in a presently unexplored province of Europe during the early Ypresian. As a consequence, paroxyclaenines may be found in localities close to the MP7 reference level.

The presence of two distinct subfamilies early in paroxyclaenid history, as well as the rapid and wide distribution of its earliest representatives (i.e. merialines in the Paris Basin and southern France), may imply that paroxyclaenids originated during the Paleocene. The presence of two distinct morphotypes among the earliest paroxyclaenids and the difficulty of deriving a paroxyclaenine from a merialine indicate that the two subfamilies may have separated well before their appearance in the fossil record. An origination in the Paleocene (probably rapidly) followed by diversification in the late Paleocene thus seems reasonable.

It is important to remark that the paroxyclaenids are very rare in Palette and Pourcy: one mandible has been found in Palette and three isolated teeth at Pourcy. Surprisingly, the samples from Mutigny, Avenay and Condé-en-Brie, which are larger than those from Pourcy and Palette, show that merialines and paroxyclaenines are both recorded in the three localities. Because paroxyclaenines are less abundant than merialines, one can imagine that the absence of paroxyclaenines in Pourcy and Palette could only be due to sampling bias: paroxyclaenines are indeed only present in the fossil record in localities where merialines are abundant. This reasoning could be applied to the case of Prémontré. However, one might also hypothesize that because the two subfamilies were ecologically very close, the presence of merialines could have influenced the presence/absence of paroxyclaenines; consequently, merialines may have been genuinely absent from localities such as Pourcy, Palette and Prémontré.

The presence of more than one paroxyclaenid species in a locality is very rare: the only other locality that records two paroxyclaenids is Geiseltal obere Mittelkohle (Germany, Lutetian; MP13), where *Pugiodens* and *Vulpavoides germanica* were found. However, these two taxa are close in size and belong to Paroxyclaeninae (Fig. 1) – Van Valen (1965) even synonymized these two taxa. The merialine species in the Paris Basin localities is slightly heavier than the paroxyclaenine one (1.5 vs 1 kg) (Supplementary material, File 2). This difference may suggest that they belonged to two distinct ecological guilds. However, this size difference does not seem significant enough to explain the presence of two very similar mammals in the same localities.

Merialines disappear rapidly from Europe: the last occurrence of this subfamily is the very large *Spaniella* from the late Ypresian of northern Spain (Barranc de

Forals; MP10) and *Paraspaniella* from the late Ypresian of the Paris Basin (Prémontré and Grauves; MP10). *Spaniella* is the largest paroxyclaenid ever found (reaching 3.7 kg) (Fig. 1; Supplementary material, File 2).

As observed for merialines, paroxyclaenines reached maximal body mass around the Ypresian–Lutetian transition (Fig. 1). *Kopidodon* from the Messel pit (MP11) weighed 2.8–3.0 kg based on the dentition (3–5 kg based on postcranial elements) (Supplementary material, File 2).

In contrast to the merialines, paroxyclaenines diversified during the Lutetian. This diversity is concomitant with the first intra-Eocene mammal turnover evidenced by Franzen (2003) (Fig. 1). At least four species are known in localities close to the MP13 reference level: *Vulpavoides germanica*, *Pugiodens mirus*, *Paroxyclaenus lemuroides* and *Vulpavoides vanvaleni*. The two taxa from Geiseltal obere Mittelkohle (MP13), *V. germanica* and *Pugiodens*, are very close in size, while *Paroxyclaenus* (from Mémerlin and Cuzal, France) and *V. vanvaleni* (from Bouxwiller, France) are smaller than the former and have sizes that recall those of the taxa from Mutigny, Avenay and Condé-en-Brie; these differences in size support the specific distinctions and probably result from differences in ecology.

As mentioned above, Van Valen (1965) synonymized *Vulpavoides germanica* and *Pugiodens*. Russell & Godinot (1988), following Tobien (1969), rejected this synonymy, noting the difference in the relative size of the molars. The unreduced m3 of *Pugiodens* (see below), as logically noted by Russell & Godinot (1988), does not fit with the reduced M3 seen in *Vulpavoides germanica* (and other paroxyclaenines). Moreover, based on the measurements provided by Matthes (1952), its lower molars are more square-shaped than those of the other paroxyclaenines. Therefore, we conserve the separation of *V. germanica* and *Pugiodens*. Consequently, *Pugiodens* appears to be unique among paroxyclaenines, which implies the existence of several different morphological ‘subgroups’ among paroxyclaenines during the Lutetian.

The important diversity observed in localities close to the MP13 reference level (Geiseltal obere Mittelkohle, Bouxwiller, Cuzal) is the last record of diversity among paroxyclaenids. Indeed, only one taxon – *Vulpavoides simplicidens* – is recorded in Egerkingen (Switzerland, Lutetian, MP14; the exact locality – α , β or γ ? – is unknown). This taxon is morphologically close to *V. germanica* from Geiseltal obere Mittelkohle and *V. simplicidens* from Bouxwiller (Van Valen 1965; Russell & Godinot 1988).

The last representative of the paroxyclaenids is *Paravulpavoides cooperi* from Creechbarrow (England; Bartonian, MP16) (Hooker 1986; Harrison 2009) (Fig. 1). This species corresponds to a new genus as discussed recently by Harrison (2009) and Harrison *et al.* (2012). This taxon is among the smallest paroxyclaenids ever recorded (~1 kg) (Supplementary material, File 2). This taxon is original among Paroxyclaenidae in possessing an unreduced m3; this feature recalls *Pugiodens*.

The disappearance of paroxyclaenids is related to a profound modification of European mammal faunas. According to Franzen (2003), this modification, which he named the second intra-Eocene faunal turnover, occurred mainly at the Bartonian–Priabonian boundary, between the MP16 and MP17 (Fig. 1). This turnover led to a considerable replacement of taxa, particularly among palaeotheres and artiodactyls. On one hand, several large and primitive species of *Palaeotherium* (Perissodactyla) disappeared. On the other, *Palaeotherium* species of modern aspect, with molarized premolars and cheek teeth that exemplified the development of hypsodonty, appeared suddenly (Legendre *et al.* 1991; Franzen 2003). At the same time, lophiodonts, once abundant in Europe, vanished completely. Among Artiodactyla, Legendre *et al.* (1991) noted the acquisition of fusion between the cuboid and navicular in several lineages around the MP16 and MP17 boundary. Concerning ‘insectivorous’ mammals, the disappearances of Adapisoricidae (MP16) and Pantolestidae (MP17) (Legendre *et al.* 1991) happened at almost the same time as that of Paroxyclaenidae. All of these modifications to the mammal fauna likely resulted from climatic changes to increasing aridity and seasonality in European ecosystems (Franzen 2003; Mosbrugger *et al.* 2005).

Ecology of paroxyclaenids and the evolution of body mass

The skeleton of *Kopidodon* is well known thanks to the discovery of several almost-complete specimens in the Messel pit. These fossils provided crucial elements for understanding the ecology of paroxyclaenids. The skull of *Kopidodon* is rather short, with a broad muzzle and distinct sagittal and nuchal crests. The skeleton is robust: limb bones are stout and the humerus bears prominent deltopectoral and supinator crests. The mobile elbow joint allowed substantial supination of the forearm and the ankle was very flexible. The feet were plantigrade, with divergent first digits, and the claw-bearing terminal phalanges were short, deep and laterally compressed (Koenigswald 1983; Rose 2006; Koenigswald *et al.* 2018). The long caudal series and the outline of soft tissues preserved in one of the

Messel skeletons (Specimen 8; Clemens & Koenigswald 1993) suggest that *Kopidodon* had a long, bushy tail. All of the postcranial features showed by the specimens from Messel indicate that *Kopidodon* was an arboreal mammal.

Specimen 8 of *Kopidodon* stands out because of the material contained within its stomach or intestinal tract. This material corresponds to unidentifiable seeds and fruit tissue; the remains of leaves are rare. As a result, Clemens & Koenigswald (1993) concluded that *Kopidodon* was either an omnivore or a herbivore. This hypothesis agrees with the robust morphology of the teeth and the peculiar pattern of attrition seen on the teeth (Koenigswald 1983; see below). As noted by Teilhard de Chardin (1922), enlarged canines were present in *Paroxyclaenus*; the upper ones are particularly massive and straight. Harrison (2009) argued that the canines might have been used to pluck fruit from branches; he remarked that the dentition of fruit bats (Megachiroptera, such as *Pteropus*) is similar to that of *Paroxyclaenus* in having large canines and in the weak, flattened and widely spaced cheek teeth.

Numerous elements discussed above are unknown for the majority of paroxyclaenids. Only *P. lemuroides*, *K. macrogathus*, and *V. germanica* are represented by fragmentary cranial elements; these fossils are very similar (i.e. morphology of the canines, short rostrum, position of the infraorbital foramina, and distinct sagittal and nuchal crests). Unfortunately, only *Kopidodon* is represented by postcranial elements.

Based on these similarities, and because the dental elements of the paroxyclaenids discovered until now do not show important modifications to their morphology through time – the dentition of the earliest representatives already displays the typical features of the family – one can hypothesize that the diet of paroxyclaenids was maintained during the Eocene. The same can be hypothesized for locomotion. However, it is worth remembering that no postcranial material is known for paroxyclaenids other than *Kopidodon*. Because *Kopidodon* is one of the largest paroxyclaenids known (Supplementary material, File 2), its ecology (i.e. locomotion and diet) could have been very different from that of other paroxyclaenids and *Kopidodon* might have occupied a different ecological niche to other paroxyclaenids.

What about the evolution of body mass? The estimated body masses are given in the Supplementary material, File 2. Previously, Clemens & Koenigswald (1993) estimated the body mass of *Kopidodon* based on measurements taken from postcranial elements (Supplementary material, File 2) and used the BODYMASS program designed by Gingerich (1990).

The estimated body masses that we found using the method of Legendre (1986) are all above 500 g, except for *Merialus bruneti* (355 g), when using the parameters established for all the mammals (Supplementary material, File 2). The values found when using the parameters defined for all mammals range from 355 g to 2.5 kg; those found when using the parameters set for large mammals range from 688 g to 3.6 kg; and those found when using the parameters defined for herbivores are clearly the highest ones, ranging from 835 g to 5.1 kg. The values found by Clemens & Koenigswald (1993) range from 3 to 5.4 kg for *Kopidodon* and are thus closer to the latter estimated values.

As discussed by Legendre (1986) and Gingerich (1989), 500 g represents a break point (or threshold) in the distribution of mammal size. Gingerich (1989) noted that it corresponds to ‘Kay’s threshold’ in the distribution of primate body mass: smaller primates derive their protein primarily from insects, while the source of protein is primarily leaves in larger primates.

Therefore, the diet reconstructed for *Kopidodon* (i.e. predominance of vegetable material) agrees with its body mass as reconstructed based on the methods of Legendre (1986) and Gingerich (1990) (i.e. above 500 g). Moreover, because all species used here have a body weight that is above ‘Kay’s threshold’ (except in *M. bruneti* for one of the three parameters; see above), we believe that all paroxyclaenids were frugivores/granivores (or omnivores).

The evolution of body mass of the paroxyclaenids is interesting to analyse (Fig. 1). *Merialus bruneti* from Pourcy (MP7) is the smallest (average body mass around 626 g). The second oldest paroxyclaenid, *Merialus martinae* from Palette, already weighed around 1.4 kg (average body mass). *Fratrodon tresvauxi* weighed only 1.5 kg, while *Paraspaniella gunnelli* is slightly lighter than *F. tresvauxi*, indicating a small decrease in the body size among the species recorded in the Paris Basin. Therefore, these new species do not indicate an important increase in merialine body weight during the Ypresian. However, *Spaniella* is considerably larger than *Paraspaniella*, and a similar difference in body mass (i.e. Spanish mammals heavier than those from the Paris Basin) has been noted among mesonychids (Solé *et al.* 2017). To conclude, there is no clear trend for body mass evolution among merialines.

Concerning paroxyclaenines, the oldest taxon – *Sororodon tresvauxae* – is one of the smallest representatives of this subfamily (Fig. 1; Supplementary material, File 2); but two Lutetian taxa are close in weight to *S. tresvauxae*. *Kopidodon* is distinctly heavier than *S. tresvauxae* (Fig. 1; Supplementary material, File 2). However, the taxa that are younger than *Kopidodon*

evolved smaller body mass (Fig. 1; Supplementary material, File 2). The weight range of paroxyclaenines, especially during MP13, is quite high (Fig. 1; Supplementary material, File 2). Moreover, it is interesting to note that the latest paroxyclaenine – *Paravulpavoides cooperi* – is one of the smallest (Supplementary material, File 2). To conclude, as for the merialines, no trend can be clearly defined for paroxyclaenines.

As indicated above, the largest representatives of paroxyclaenids are found around the Ypresian/Lutetian boundary. This occurred in the two subfamilies: the merialine *Spaniella* from the latest Eocene (MP10) weighed around 3.7 kg (mean of the three estimated body masses; Supplementary material, File 2), while the paroxyclaenine *Kopidodon* from the earliest Lutetian (MP11) weighed around 2.8 kg (mean of the three estimated body masses; Supplementary material, File 2).

As previously mentioned, the body mass of *Kopidodon* is very different from those of other paroxyclaenids. Its ecology may thus have been very different. The same hypothesis can be envisaged for *Spaniella* because the other merialines have a small weight range (0.6–1.5 kg), even the penecontemporaneous *Paraspaniella* (1.2 kg). Consequently, *Kopidodon* and *Spaniella* might represent outliers among Paroxyclaenidae, probably because of an ecological shift.

The possibility for paroxyclaenids to develop large body mass around the Ypresian/Lutetian transition was probably triggered by the Early Eocene Climatic Optimum (EECO), which is one of the warmest periods of the past 70 myr (about 53–51 Myr; Zachos *et al.* 2008). A recent mean annual temperature (MAT) estimate for the mid-latitude marginal marine Belgian Basin during the EECO – based on otolith $\delta^{18}\text{O}$ compositions of four non-migratory species belonging to the teleost families Congridae and Ophidiidae – equals 27.5 °C (Vanhove *et al.* 2011). However, incremental analyses revealed a ~ 9.5 °C mean annual range of temperatures, similar to modern seasonality (Vanhove *et al.* 2011).

The warm climatic conditions during the EECO may have favoured the large body mass of several paroxyclaenids. Moreover, the increase in body mass through the Ypresian of Europe has recently been evidenced for the carnivorous mammals Proviverrinae (Solé *et al.* 2014, 2015) and Mesonychidae (Solé *et al.* 2018). However, these observations do not support a clear causal connection, and deeper studies (such as statistical analyses) still have to be done to affirm that the EECO is responsible for the body mass increase of some paroxyclaenids (among other mammals).

The Paris Basin experienced tropical conditions and reduced seasonal contrasts during the Ypresian, but transient cooling is recorded within this warm period during the deposition of the Sables de Cuisse Formation, to which the fossiliferous locality of Grauves, where *Paraspaniella* is recorded, belongs (Huyghe *et al.* 2012, 2015). This may explain the smaller size of this merialine with respect to *Fratrodon*.

Two diversity maxima considering body weight can be defined: MP10 witnessed the largest variation range between two species (two merialines in this case; Fig. 1), while the variation recorded by the MP13 localities (four paroxyclaenines; Fig. 1) is comparatively smaller than in MP10 but larger than in the other periods. The body mass diversity seen in MP13 corresponds to a peak of species diversity among paroxyclaenids. However, the highest estimated body masses in MP13 are lower than those of the taxa from the Ypresian–Lutetian transition.

The Lutetian is characterized by long-term cooling that follows the EECO and continues until the Oligocene, except during the Middle Eocene Climatic Optimum (MECO; ~ 40 Myr; Zachos *et al.* 2008). However, during the Lutetian, there were tropical climatic conditions in Europe with an increase in seasonality (especially in temperature) in Central Europe (Mosbrugger *et al.* (2005). Moreover, an important cooling – ‘Lutetian cooling’ (~ 46 – 42 Myr) (Huyghe *et al.* 2015, fig. 7) – occurred before the MECO. This cooling period corresponds to the ‘Intra-Eocene Mammal Turnover 1’ (\sim MP12–13) proposed by Franzen (2003). After this turnover, paroxyclaenids are less diversified (Fig. 1). Following the MECO, the Bartonian is characterized by cooling that lasts until the Eocene–Oligocene boundary (Huyghe *et al.* 2012, 2015).

Although the Lutetian and Bartonian paroxyclaenids are smaller than the largest paroxyclaenids recorded around the Ypresian–Lutetian boundary (i.e. *Spaniella* and *Kopidodon*), they are more numerous than during the previous periods until the Intra-Eocene Mammal Turnover 1 (Fig. 1). It is presently hard to determine the reasons for such increases and decreases in diversity: numerous factors can be envisaged besides the cooling of global climate, such as competition, predation, etc.

The same remarks also apply to the presence of large paroxyclaenids around the Ypresian/Lutetian boundary, the decrease in paroxyclaenid body size during the Lutetian and their disappearance during the Bartonian: one can hypothesize that the continuous decrease in temperatures coupled to an increase of seasonality after the Ypresian/Lutetian boundary (see Mosbrugger *et al.* 2005), and thus a modification of the flora, might be responsible for both phenomena. However, the

explanation is surely more complex. Indeed, most of the paroxyclaenines from the Lutetian and Bartonian have body masses close to those of the Ypresian merialines *Sororodon*, *Paraspaniella* and *Merialus martinae*, yet the temperatures and seasonality were different.

Hypothesized faunal events in the Ypresian of Europe

The period encompassing Pourcy-Palette (MP7 and PE III biozone *sensu* Hooker 1996, 1998) and Mutigny (MP8 + 9 and PE IV biozone *sensu* Hooker 1996, 1998) is characterized by numerous modifications to the mammal faunas: disappearances of Oxyaenodonta, Sinopaninae (Hyaenodonta), *Coryphodon* (Pantodonta) and *Pachyaena* (Mesonychidae); the first appearance of the ‘miacid’ *Quercygalie*; dispersals from the Southern Province to the Northern Province of Proviverrinae (Hyaenodonta) and *Lophiaspis* (Perissodactyla); and dispersal from the Northern Province to the Southern Province of *Plesiesthonyx* (Tillodontia) (D. E. Savage *et al.* 1966; Lucas 1998; Laurent *et al.* 2010; Solé *et al.* 2013, 2014, 2018; Solé 2014). To these previous observations, we can now add the appearance of paroxyclaenines in the Paris Basin around this time.

Because this period of turnover is now well documented, we propose to name it the ‘Intra-Ypresian Mammal Turnover’ (Fig. 1) – however, this event must be extensively studied in future in order to be fully characterized. As mentioned above, the appearance of the paroxyclaenines may be due to dispersal from an unknown region into the Paris Basin during this period of faunal modification and interchanges.

The disappearance of the merialines at the end of the Ypresian is intriguing. One can note that this disappearance affected both the Paris Basin and the Iberian Peninsula. Badiola’s (2004) analysis of the palaeoecological conditions of the Mazaterón and Zambrana mammal assemblages (Western Iberian Bioprovince) suggests that the change from a complex forest habitat to a more open environment that occurred in the late Eocene in several regions of Europe could have started earlier in the Western Iberian Bioprovince, influencing its faunal composition. Moreover, some dental features observed in perissodactyls and rodents could be interpreted as representing adaptations to chewing tough plants associated with the increasingly arid conditions in this region (Franzen 2003; Badiola 2004). Because paroxyclaenids were probably arboreal animals with an omnivorous or herbivorous diet (see below), one can therefore imagine that the reduction of forest habitat had a strong impact on the merialines. However, the data presented here corresponds to the Iberian Peninsula, not the Paris Basin. If the disappearance of *Spaniella* is

understandable, based on palaeoenvironmental data, that of *Paraspaniella* is less clear.

The disappearance of the merialines contrasts with the radiations of the perissodactyls, artiodactyls, pantolestids and hyaenodonts around the MP10 reference level as evidenced by the fossils from Prémontré (D. E. Savage *et al.* 1966; Sudre & Erfurt 1996; R. Smith 2001; Solé *et al.* 2014).

Conversely, Solé *et al.* (2018) recently reported the disappearance of mesonychids at the end of the Ypresian. Like the merialines, mesonychids were recorded from the whole of Europe; they are known from MP10 localities in the Paris Basin (Cuis), southern France (Mas de Piquet), and the north-eastern Iberian Peninsula (Corsà II, Castigaleu). The disappearances of merialines and mesonychids are thus concomitant. They are also partially similar in that these disappearances occurred in two European provinces: north-western and south-western Europe.

However, they are not entirely similar: the mesonychids all belonged to the same genus (*Dissacus*) despite their difference in size (Solé *et al.* 2018), while the MP10 merialines represent two distinct genera (*Paraspaniella* and *Spaniella*). Moreover, as discussed above, *Spaniella* is, like *Kopidodon*, clearly heavier than the other paroxyclaenids and thus may have occupied a particular ecological niche.

Nevertheless, these disappearances suggest that a poorly known faunal turnover took place at the end of the Ypresian in Europe, which we term the ‘Ypresian-Lutetian Mammal Turnover’ (Fig. 1). It is potentially noteworthy that a transient cooling is recorded at the end of the Ypresian in the Paris Basin (Huyghe *et al.* 2015).

These disappearances occurred after the EECO. In North America, this warming is reflected in an increase in mammal diversity (Woodburne *et al.* 2009). Floras associated with the EECO in western Wyoming indicate a sharp increase in MAT to 23 °C, with wet, paratropical conditions at its beginning followed by a retreat to more seasonally dry conditions, but with the MAT still at megathermal levels (*c.* 20 °C). Subsequent climatic deterioration, from 50–47 Myr, resulted in major diversity loss (Bridgerian Crash; Woodburne *et al.* 2009). No similar diversity loss has been found in European ecosystems, but the cases of the Merialinae and Mesonychidae point out the necessity to focus on this period in the future to determine whether or not a limited ‘crash’ occurred in Europe.

Morphology of the premolars and molars

All of the paroxyclaenids have molars that decrease in size from M1/m1 to M3/m3. The M3 and m3 are

sometimes particularly reduced: the merialines *Fratrodon tresvauxi* and *Spaniella carezi* clearly show a reduction in size and alteration of the morphology of the m3 (the tooth is single-rooted in these taxa). However, this trend is not constant among paroxyclaenids. As mentioned above, *Pugiodens* is characterized by a poorly reduced m2 and m3 when compared to m1; however, the m3 is only represented by its two alveoli in the holotype and only specimen of this taxon. Unfortunately, study of *Pugiodens* is now impossible because the holotype has been missing since the 1960s (Van Valen 1965; Russell & Godinot 1988). The weak reduction of the m3 is also found in *Paravulpavoides* – it is one of its distinctive features, as noted by Harrison (2009).

As indicated above, a particularity of the paroxyclaenine dentition is the tendency to enlarge and molarize the third and fourth upper and lower premolars: all of these paroxyclaenids display a p4 that has a metaconid – unfortunately, the p4 of the newly described *Sororodon tresvauxae* is unknown. The p3 also tends to molarize: the p3 of *Kopidodon* is simpler than that of *Pugiodens*, *Paroxyclaenus* and *Paravulpavoides* and *Kopidodon* is older than these three taxa, which is why it has a less-molarized p3. Harrison (2009, pp. 32–33) summarized the implications of this dental tendency and, based on these data, hypothesized that paroxyclaenids were frugivores/granivores that ate hard fruits ('tough-skinned fruits' according to Koenigswald *et al.* 2018, p. 230): "The enlarged and variably molarised posterior premolars suggest a transfer of maximal crushing power forwards in the tooth row, which appears to support such a dietary regime. [...] The enlarged posterior premolars of the paroxyclaenines seem well adapted to produce a 'nutcracker' effect for a relatively hard dietary regime."

Russell & Godinot (1988) noted that merialines differ from paroxyclaenines in the absence p3 and p4 molarization. The premolars of *Spaniella* (only the p2 and p3 have been discovered) are simpler than those of *Merialus* in the disappearance of the small tubercle present in the mesial part of the teeth of the latter. Merialines thus seem to have experienced a simplification of the premolars, a tendency that is opposite to that of paroxyclaenines. Moreover, these differences indicate that *Spaniella* may have had a very different ecology from *Merialus*.

Merialines are characterized by a closely appressed paraconid and metaconid. As mentioned above, the first merialines already show a very close paraconid and metaconid. However, this tendency increases through time: the paraconid is closer to and less separated from the metaconid in *Spaniella* and *Paraspaniella* than in

Merialus and *Fratrodon*. The paroxyclaenines also show this tendency; as mentioned above, the protoconid part of the paracristid is more mesially elongated and the paraconid is mesially located and less lingually located in *Sororodon tresvauxae* than in the youngest paroxyclaenines (Fig. 10). The protocristid and paracristid are also less acute and the notches on these crests are not distinguishable on the youngest paroxyclaenids. Another tendency visible on the lower molars is the reduction of the hypoconid and, to a lesser extent, the entoconid. A cusplation of the posteristid and entocristid is visible in several paroxyclaenids (*Fratrodon*, *Sororodon*, *Spaniella*). This evolution of the talonid cusps occurred together with a shortening of the talonid combined with an increase of the height of the talonid in Merialinae – this is supported by the PCA (see above). Finally, the precingulid also tends to get reduced over time in Paroxyclaenidae.

Concerning the upper molars, paroxyclaenines and merialines clearly differ due to a squarer morphology (in occlusal view) in Merialinae, while paroxyclaenines have more transversely elongated molars over time (Fig. 10; Table 3); however, this transverse elongation is less marked in *Kopidodon* than in younger paroxyclaenines such as *Paroxyclaenus*, *Vulpavoides* and *Paravulpavoides*. As on the lower molars, there is a decrease in the individualization of the structures of the upper molars, both in Merialinae and Paroxyclaeninae. This concerns the reduction of the paraconule and metaconule visible in the Ypresian, Lutetian and Bartonian paroxyclaenids, though the metaconule is actually individualized and very bulbous in *Fratrodon*. On the upper molars, one can observe a reduction of the metastylar and parastylar area, and more generally of the labial shelf (Fig. 10). Therefore, the upper molars have lost the triangular pattern that characterized the tribosphenic molar. This highlights the decreasing importance of the paraconid through time.

The transverse elongation of the upper molars is probably related to a peculiar feature of paroxyclaenines: their unusual dental wear pattern. Indeed, when studying the abrasive wear in *Kopidodon* and *Paroxyclaenus*, Koenigswald (1983) noted that this wear develops notably on the lingual aspects of the lower molars; this affects particularly the paraconid, metaconid and entoconid (Fig. 10). This pattern results from heavy wear due to the presence of an atypical occlusion between the protocone and talonid: in addition to the normal position, in which the protocone occludes with the talonid basin, there is a second position, in which trigon basin and protocone overlap the talonid lingually (i.e. the entocristid and distal wall of the metaconid) (Koenigswald 1983). This second position is mechanically possible due to the long distance between the

		Ypresian			Lutetian			Bartonian		
		MP7	MP8+9	MP10	MP11	MP13	MP14	MP16		
Merlialinae		<i>Merialus bruneti</i> *	<i>Merialus martinae</i>	<i>Fratrodon tresvauxi</i>	<i>Paraspaniella gunnelli</i>	<i>Spaniella carezi</i> *				
Paroxyclaeninae			<i>Sororodon tresvauxae</i>		<i>Kopidodon macrogathus</i>	<i>Vulpavoides vanvaleni</i>	<i>Vulpavoides germanica</i>	<i>Paroxyclaenus lemuroides</i>	<i>Vulpavoides simplicidens</i>	<i>Paravulpavoides cooperi</i>

Figure 10. Comparisons of the left M1 and m1 of merlialines and paroxyclaenines. *Pugiodens mirus* is not illustrated because we did not have access to suitable illustrations. We illustrated the m2 for *Merialus bruneti* and the m2 and M2 for *Spaniella carezi*. The teeth are not to scale. *Merialus martinae* after Russell & Godinot (1988, fig. 1). *Spaniella carezi* after Crusafont-Pairo & Russell (1967, figs 1, 2). *Kopidodon macrogathus* after Koenigswald (1983, fig. 4). *Vulpavoides vanvaleni* after Russell & Godinot (1988, fig. 2). *Vulpavoides germanica* after Van Valen (1965, fig. 1). *Paroxyclaenus lemuroides* after Teilhard de Chardin (1922, fig. 38). *Vulpavoides simplicidens* after Van Valen (1965, fig. 2). *Paravulpavoides cooperi* after Harrison (2009, figs 1, 4).

protocone and the labial cusps (paracone and metacone) in the upper molars and the oblique labial wall of the hypoconid on the lower molars. The inclination of the hypoconid is notably marked in those paroxyclaenids that have a talonid as wide as the trigonid (i.e. *F. tresvauxi*, *S. tresvauxae*, *M. martinae*); it is less marked in younger paroxyclaenids probably because the talonid of the molars is less transversely elongated (Fig. 10). Importantly, the paroxyclaenine *S. tresvauxae* differs from Ypresian paroxyclaenids as it already displays wear facets that are typical of paroxyclaenines such as *Kopidodon* (Fig. 8E). Despite the inclination of the hypoconid, *F. tresvauxi* and *M. martinae* do not display the peculiar wear facets of paroxyclaenines. This unusual molar occlusion would allow for a hard diet (seeds? tough-skinned fruits?) and represents high nutritional specialization (Koenigswald 1983). This supports observations on the evolution of the premolars.

Origin of Paroxyclaenidae

The sudden appearance of paroxyclaenids in the European record combined with the existence of two

distinct subfamilies since almost the first occurrences of this group raises questions about the origin of these mammals. Previous authors have considered the group to be creodonts (Teilhard de Chardin 1927), ‘insectivores’ (close to *Procerberus*; Van Valen 1965), mioclaenid ‘condylarths’ (Teilhard de Chardin 1927; Russell & McKenna 1961) or arctocyonid ‘condylarths’ (Tobien 1969). Since the work of Russell & Godinot (1988), Paroxyclaenidae has been included among pantolestans (Clemens & Koenigswald 1993; McKenna & Bell 1997; Rose 2006; see also Koenigswald *et al.* 2018).

Pantolestans probably originated in North America; the oldest pantolestans is *Propalaeosinopa* from the late Puercan (Cifelli *et al.* 1995; Rose 2006). McKenna & Bell (1997) grouped the Pantolestidae, Pentacodontidae, Ptolemaiidae and Paroxyclaenidae among Pantolesta. However, recent studies concluded that Ptolemaiidae might be included within Afrotheria (Nishihara *et al.* 2005; Cote *et al.* 2007; Seiffert *et al.* 2007; Gunnell *et al.* 2010). Rose (2006) indicated that pantolestans have low-crowned molars with rounded cusps, upper molars with a narrow styler shelf, lower molars with low trigonids and wide-basined talonids, and larger

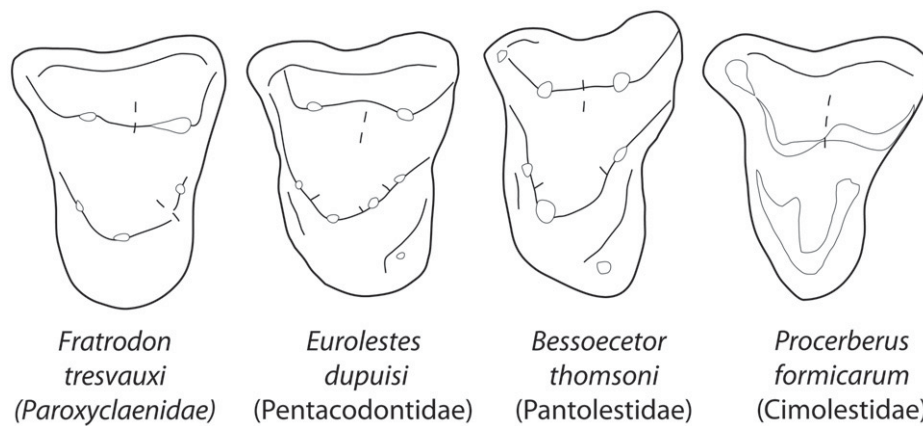


Figure 11. Comparison of the M1 between the paroxyclaenid *Fratrodon tresvauxi* (RBINS Cast-Vert-32468-2240 [AV-1002-Ph]), the pentacodontid *Eurolestes dupuisi* (redrawn from De Bast & Smith 2017, fig. 9), the pantolestid *Bessoecetor thomsoni* (redrawn from Simpson 1936, fig. 4) and the cimolestid *Procerberus formicarum* (redrawn from Lillegraven 1969, fig. 32). The teeth are not to scale.

premolars. The skulls of pantolestans known so far are moderately robust, with large canines, wide snouts and broad, well-developed occipital regions. The infraorbital foramen is large: this indicates that the maxillary nerve, which innervated a sensitive snout with tactile vibrissae, was large. Finally, the skeleton is robust with a long, well-developed tail. It is important, however, to remember that the skeletons of the paroxyclaenid *Kopidodon* and pantolestid *Buxolestes* show major differences (Clemens & Koenigswald 1993).

The referral of paroxyclaenids to Pantolestia is difficult to refute, and the pantolestids and pentacodontids are the most similar mammals to paroxyclaenids presently known. In addition to the features listed by Rose (2006), these mammals share a separated paracone and metacone, a high protocone, and a large paraconule and metaconule on the upper molars; and a hypoconulid lower than the entoconid and hypoconid, and a small paraconid on the lower molars.

Pantolestids and pentacodontids differ from paroxyclaenids by the presence of wide pre- and postcingula (the latter often bearing a distinct hypocone cusp). These features are already visible in the earliest pantolestids such as *Propalaeosinopa* and *Bessoecetor* (Fig. 11). Pantolestids and pentacodontids also differ in the weak extension of the labial shelf. The upper molars discovered at Avenay and Condé-en-Brie show that the earliest paroxyclaenids have a developed labial shelf; moreover, there is no trace of pre- and postcingula on the upper molars.

Paroxyclaenids share with pentacodontids the relative size of the molars (i.e. they decrease in size posteriorly). Pantolestids clearly differ from pentacodontids and paroxyclaenids by possessing an m1 that is generally smaller than m2 and m3.

Because paroxyclaenids are endemic to Europe, it is essential to look at the fossil record of pantolestans in Europe. The first pentacodontid outside North America – *Eurolestes dupuisi* – was recently described from the (most likely) late Danian locality of Hainin (De Bast & Smith 2017; Fig. 11). Like all pentacodontids, its m3 is smaller than its m1 and m2. It also shares with paroxyclaenids a preprotocrista that is shorter than the postprotocrista and a shallow and symmetrical ectoflexus. This species, like all pentacodontids, differs from the earliest paroxyclaenids by the presence of pre- and postcingula, a short labial shelf, the presence of an accessory cusplule between the protocone and the metaconule, a rounded molar outline, a less pronounced difference in height between the trigonid and talonid, a smaller and less lingually located paraconid, a bulbous entoconid and low entocristid, and a developed precingulid.

Consequently, evolution from *Eurolestes* to paroxyclaenids would necessitate an increase in paraconid height; lingual elongation of the paracristid; reduction of the entoconid; increase in entocristid height; reduction of the precingulid; expansion of the styler shelf; reduction of the pre- and postcingula; and disappearance of the accessory cusplule between the protocone and metaconule. These transformations do not seem impossible because some are consequences of crushing adaptations (e.g. modifications of the entoconid and entocristid). Moreover, the time span between *Eurolestes* and the earliest paroxyclaenids covers the Selandian, Thanetian and beginning of the Ypresian (c. 6 Myr). However, the increase of the importance of the styler shelf and paraconid (two structures that are related due to occlusion) is problematic and implies a phase of development of these structures (from *Eurolestes* to the earliest paroxyclaenids) before a regression (in the youngest

paroxyclaenids). As noticed by Koenigswald (1983), transverse elongation seems to have been crucial for occlusion in paroxyclaenids; consequently, one can imagine that the importance of the paracristid and labial shelf (including the para- metastylar areas) might have increased transversely between *Eurolestes* and the earliest paroxyclaenids. This transformation does not seem improbable.

The oldest European pantolestid is *Pagonomus dionysi* from the Cernaysian fauna (Russell 1964) – the species *Nosella europaea* described by López-Martínez and Peláez-Campomanes (1999) has been recently considered a possible adapisoriculid (Jehle *et al.* 2012). This species differs from the earliest paroxyclaenids by the presence of a large hypocone, very reduced stylar shelf, reduced ectoflexus, reduced trigon basin, smaller paraconid, medially located paraconid and the presence of a precingulid. Because of these differences, it appears difficult to derive paroxyclaenids from *P. dionysi*. Moreover, unlike the pentacodontid *Eurolestes*, *Pagonomus* is first recorded in the Thanetian (MP6a) of Cernay-lès-Reims (see Hooker & Russell 2012 for a discussion concerning the localities of Cernay and Berru).

Russell & Godinot (1988) envisaged a relationship (that “merits reflection”, p. 328) between Merialinae and Ptolemaiidae. This family is known only from Africa (Gunnell *et al.* 2010). It has been provisionally placed within Pantolestina (Bown & Simons 1987; McKenna & Bell 1997; Rose 2006), but recent studies indicate that these mammals might be closer to Afroinsectiphilia (especially Macroscelidea and Tubulidentata) and thus regarded as afrotherians (Nishihara *et al.* 2005; Cote *et al.* 2007; Seiffert *et al.* 2007; Miller *et al.* 2015). Paroxyclaenids appeared in Europe at approximately the same time as Hyaenodonta (i.e. around the Paleocene–Eocene boundary), a group that possibly originated in Africa (Solé *et al.* 2015; but see Borths *et al.* 2016 for a different opinion); hyaenodonts and paroxyclaenids are, for example, both recorded in Palette. The ptolemaiids are first recorded in the late Eocene, but this material has not yet been described (Gunnell *et al.* 2010). *Ptolemaia lyonsi* (from the early Oligocene Jebel Qatrani Formation, Quarry A) is therefore the oldest well-described ptolemaiid (Osborn 1908; Simons & Gingerich 1974; Gunnell *et al.* 2010); a second species from the early Oligocene, *P. grangeri*, has been described by Bown & Simons (1987). A second genus, *Cleopatrodon* (containing two species) is also known from the early Oligocene (Bown & Simons 1987). A third genus, *Kelba* (one species) is known from the early and middle Miocene (R. J. G. Savage 1965; Cote *et al.* 2007).

As noted by Russell & Godinot (1988), *Ptolemaia* shares with paroxyclaenids a large p3 and p4, and with paroxyclaenines the presence of a metaconid on p4. However, they also noted that the molars of ptolemaiids are much higher than those of paroxyclaenids. The two groups share the presence of a protocone on P3, which is shifted far posteriorly in ptolemaiids (Cote *et al.* 2007); the separation of the paracone and metacone; and the closely appressed metaconid and paraconid. Some of the typical features of ptolemaiids that are not found in paroxyclaenids are the large protocone and well-developed buccal cingulum, and the absence of preparacrista (Cote *et al.* 2007). Another difference is the weak development of the labial shelf and its asymmetry in Ptolemaiidae. The dental features of Ptolemaiidae are clearly different from the morphology of paroxyclaenids. Concerning the skull, Cote *et al.* (2007) listed, as characteristic features of the Ptolemaiidae, the anterior opening of the infraorbital canal above P3 and a retracted nasal aperture (seen in lateral view) with the premaxilla extending far ventrally relative to its dorsal margin. These two features also distinguish Ptolemaiidae from Paroxyclaenidae.

Crusafont-Pairo & Russell (1967) rejected the similarity between the cimolestans *Procerberus* (Didelphodonta, Cimolestidae) and paroxyclaenids that was underlined by Van Valen (1965), primarily on the basis of the morphology of the labial shelf, which is not symmetrical in Paroxyclaenidae (Crusafont-Pairo & Russell 1967 based their hypothesis on *Spaniella*, which was the earliest paroxyclaenid known at that time). The newly described fossils from the Paris Basin show that the oldest paroxyclaenids have a wide stylar shelf that is symmetrical in occlusal view. Moreover, these fossils recall the cimolestans *Procerberus* in the absence of a hypocone: as discussed above, the presence of this derived structure is typical of Pentacodontidae and Pantolestidae. Therefore, the earliest paroxyclaenids (both the merialines and paroxyclaenines) are closer in some features to the cimolestans such as *Procerberus* than to the pantolestans. The paroxyclaenids described in the present paper also share with some cimolestids a higher and more developed paraconid than in pantolestans, as well as the important difference in height between the trigonid and talonid. However, it is worth highlighting that these similarities concern a number of dental features, but not the whole dentition. Regarding this problem, it should be noted that the premolars of the paroxyclaenids and *Procerberus* are quite different.

Consequently, one can hypothesize that the similarities (e.g. narrow stylar shelf on upper molars, lower molars with low trigonids and wide basined talonids) between several paroxyclaenids and pantolestans may be due to convergence. To conclude, the hypothesis of Van

Valen (1965) should not be entirely rejected and must be kept in mind when analysing the origin and evolution of paroxyclaenids.

Conclusions

Russell & Godinot (1988) noted that they aimed to study the paroxyclaenids from the Ypresian of the Paris Basin based on material discovered since Rich's (1971) study, but this work was not concluded. However, they noted that both subfamilies (i.e. Paroxyclaeninae and Merialinae) were present in the Ypresian of the Paris Basin.

The present study describes four new paroxyclaenid species, all from the Ypresian. These new species considerably increase the diversity of paroxyclaenids from the Ypresian and their study confirms the suggestion of Russell & Godinot (1988) that the radiation of paroxyclaenids (i.e. the split between merialines and paroxyclaenines) took place no later than the early Ypresian.

These species provide important information on the molar morphology in the earliest representatives of this group. The molar morphology described in the present paper is closer to that of cimolestids in several dental features, casting doubt on the hypothesis of a close relationship with pantolestans, as had been suggested since the 1970s, and leaves open the questions of paroxyclaenid relationships and origins.

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Supplementary material

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