Holotherian mammals from the Forest Marble (Middle Jurassic of England)

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ABSTRACT
From the Kirtlington Bone Bed of England (upper Bathonian), some 700 mammalian specimens, essentially isolated teeth or fragments, have been recovered by British workers; all orders of mammals known for that period are represented. About two thirds of the holotherian molars studied in this paper are attributed to the genus *Palaeoxonodon* Freeman, 1976, known so far by two lower molars of the type species and a few attributed upper molars. A new species, *P. freemani* n. sp., also based on lower molars, is proposed. A number of additional upper molars are referred to this genus; they indicate that the latter is not a "peramuran" as previously thought, but an amphitheriid, very close to the genus *Amphitherium* Blainville, 1838, itself, also known until now by lower dentitions only. Knowledge of amphitheriid upper molars contributes some new light to the discussion of the phylogenetic relationships of this family. In addition, a new taxon of uncertain ordinal position, *Kennetheredium leesi* n. gen., n. sp., is defined on lower molars. Finally, some teeth could not be precisely identified and are referred to Symmetrodonta indet., Dryolestida indet., Trechnotheria indet. and ?peramurid.

KEY WORDS
Mammalia,
Symmetrodonta,
Dryolestida,
Amphitheriidae,
Peramuridae,
upper Bathonian,
England,
new genus,
new species.

RÉSUMÉ

Mammifères holothériens en provenance de Forest Marble (Jurassique moyen d'Angleterre).

Environ 700 restes mammaliens (essentiellement dentaires) ont été extraits du « Kirtlington Bone Bed » d'Angleterre, Bathonien supérieur, par des chercheurs britanniques. Tous les ordres de mammifères présents à cette époque sont représentés. Deux tiers environ des dents de mammifères holothériens étudiées dans cet article ont été attribuées au genre *Palaeoxonodon* Freeman, 1976, connu jusqu'ici par deux molaires inférieures de l'espèce type et quelques molaires supérieures attribuées. Une nouvelle espèce, *P. freemani* n. sp., est proposée, également sur des molaires inférieures. Un certain nombre de molaires supérieures supplémentaires sont rapportées à ce genre, qui indiquent qu'il ne s'agit pas d'un péramuride, mais d'un amphithériide, très proche du genre *Amphitherium* Blainville, 1838, lui-même, lui aussi représenté jusqu'à maintenant uniquement par des dentures inférieures. La connaissance des molaires supérieures d'amphithériides permet de rediscuter les relations phylogénétiques de ce groupe. En outre un nouveau taxon de position ordinale incertaine, *Kennetheredium leesi* n. gen., n. sp., est décrit sur des molaires inférieures. Finalement, quelques molaires n'ont pu être identifiées avec précision et sont rapportées aux Symmetrodonta indet., Dryolestida indet., Trechnotheria indet. et ?péramuride.

MOTS CLÉS
Mammalia,
Symmetrodonta,
Dryolestida,
Amphitheriidae,
Peramuridae,
Bathonien supérieur,
Angleterre,
nouveau genre,
nouvelles espèces.

INTRODUCTION

The very first Mesozoic mammals ever discovered were those of the Middle Jurassic of Stonefield, England, in the middle of the 19th century. No other mammalian fauna of this age was reported until Waldman & Savage (1972) published a docodont lower jaw from the Bathonian of Scotland. Later, Freeman (1976a, b) announced the discovery of mammal teeth in the upper Bathonian Forest Marble Formation, both in Dorset (Watton Cliff) and in Oxfordshire (Kirtlington). These two sites were further extensively exploited by a team from London University College led by Prof. K. A. Kermack, "with the help of Freeman and David Ward" (Kermack 1988: 91). The sieving of "many tons of matrix" (Kermack 1988: 91) led to the recovery of some 700 mammalian specimens, mostly teeth, along with teeth of a tritylodont and a rich microvertebrate fauna (Evans & Milner 1994). Freeman (1976b; 1979) briefly described three new mammalian taxa and Kermack *et al.* (1987) published a detailed study of a new docodont, and later a new allotherian suborder (Kermack *et al.* 1998). The bulk of the fauna, in which Kermack (1998: 92) had numbered "nine species of therian and non-therian mammals", remained unstudied. Through the intervention of Dr. S. Evans, Prof. Kermack agreed that this fauna, given to The Natural History Museum, London, be entrusted to the author for study. This work is devoted to the analysis of the holotherian component of the fauna.

TERMINOLOGY (Fig. 1)

The terminology of the lower molar cusps does not pose a particular problem, except for the unique cusp of the talonid, interpreted as a hypoconid (Mills 1964; Freeman 1979; Prothero 1981; Butler 1990; Setoguchi *et al.* 1999), more commonly as a hypoconulid (e.g., Kermack *et al.* 1968) or a fused hypoconid and hypoconulid (Martin 2002). The situation observed on the

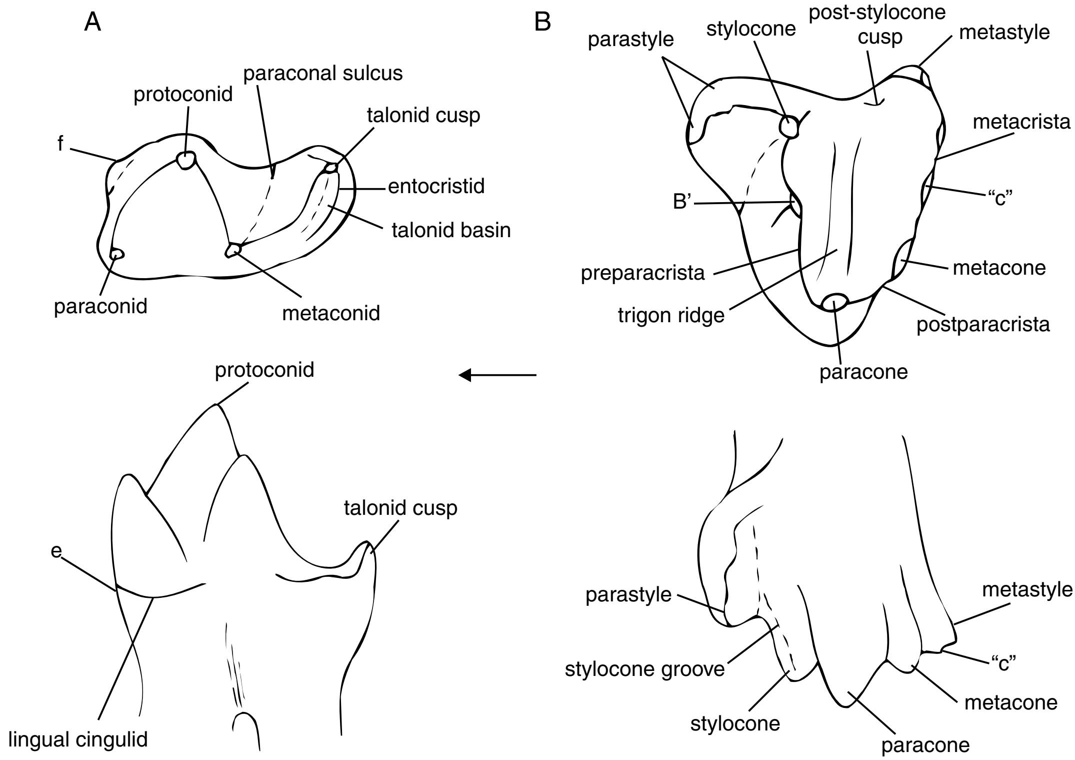

FIG. 1. — Nomenclature of cusps of lower (**A**) and upper (**B**) molars.

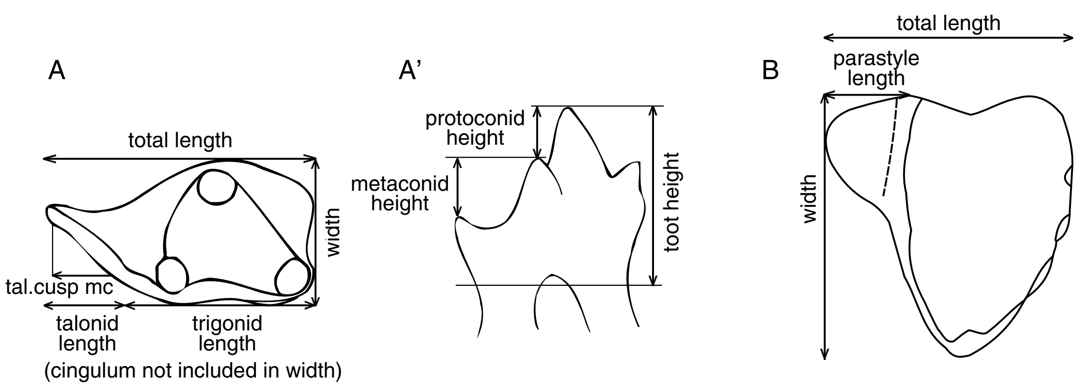

FIG. 2. — Measurements conventions on lower (**A**, **A'**) and upper (**B**) molars.

lower molars of *Peramus* Owen, 1871, as well as the interpretation of the metacone as a primary cusp (Sigogneau-Russell 1999), led me to favour the second interpretation (hypoconulid not yet separated in two cusps, and called here the "talonid cusp"). I use the term "distal metacristid" in the meaning defined by Fox (1985: 423), as a "ridge [which] extends ventrolabially from the apex of the metaconid to the cristid obliqua" and "defines the approximate lingual limits of wear on the posterior wall by the anterior side of the paracone".

For the upper molars, I maintain the term stylocone for the labial cusp linked to the preparacrista, whatever its situation. Posteriorly there most often is, behind the metacone, a cusp "c" (Crompton 1971); this cusp may be doubled and it is sometimes hazardous to distinguish between this feature and the metastyle, which itself can be constituted of a posterior and a labial component. Finally, for the cusp situated in the posterior half of the labial stylar shelf, I use the terms posterior stylar cusp (Fox 1985) (= cusp D in Sigogneau-Russell 1991 = distal stylar cusp in Cifelli & Madsen 1999 = median cusp in Kielan-Jaworwoska *et al.* in press).

ABBREVIATIONS

BMNH M or J	The Natural History Museum, London;
SA	Anoual Syncline, Morocco;
GUI	Guimarota.

MEASUREMENTS (Annexe, Tables 1, 3; Fig. 2)

With exceptions mentioned, measurements were taken by the author with a Wild apparatus MMS 225/235 as shown in Fig. 2. The talonid has been measured in two ways: 1) from the lower part of the metacristid to the distal part of the talonid cusp: T1; and 2) from the tip of the metaconid to the tip of the talonid cusp: T2. All measurements are in mm. Trigonid angles were taken between the tips of the three main cusps in occlusal view.

SYSTEMATICS

Legion CLADOTHERIA McKenna, 1975
Family AMPHITHERIIDAE Owen, 1846

Genus *Palaeoxonodon* Freeman, 1976b

TYPE SPECIES. — *Palaeoxonodon ooliticus* Freeman, 1976b.

REVISED DIAGNOSIS. — Holotherian genus with lower molars having a relatively sharp trigonid, an elongated and incipiently basined talonid with one cusp, a distal metacristid and a more or less concave postero-labial face of the metaconid ("groove that received the paracone", Clemens & Mills 1971: 105). Cusp f well developed; usually no e cusp. Wear facet A present. Roots equal or subequal. Labial alveolar border of lower jaw notably lower than lingual border. Dental formula unknown. Differs from *Amphitherium* Blainville, 1838 by a slightly narrower trigonid with sharper cusps, by the labial face of the metaconid being concave (as in *Peramus* Owen, 1871) whereas it is flat or even convex in *Amphitherium*; also talonid ?more clearly basined and ?not covering distally the adjacent paraconid; cuspule f better individualized. Differs from *Nanolestes* Martin, 2002 by the incipiently basined talonid (see comments on *Nanolestes* below). Differs from *Peramus* by the presence of only one cusp on the talonid rim, the absence of an antero-lingual and forwardly inclined cusp e and the equally lingual position of the para- and metaconid. Differs from *Minimus* Sigogneau-Russell, 1999, with which it may share an anterior lingual cingulum, by the greater extension of the talonid and the absence of an acute antero-lingual cusp (e).

Palaeoxonodon ooliticus Freeman, 1976b

HOLOTYPE. — BMNH M 36508, right lower molar (Fig. 3A; also figured by Freeman 1976b: fig. 1; 1979: pl. 16, 3-7).

ATTRIBUTED SPECIMENS. — BMNH J.59, J.196, ?J.242, M 36507 (figured by Freeman 1979: pl. 17, 1-4; now lost), right lower molars; BMNH ?J.200, J.236, J.619, J.639, J.849, left lower molars.

DISTRIBUTION. — Clay Bands of the Kirtlington Bone Bed, Kirtlington Quarry, Oxfordshire. Forest Marble (upper Bathonian). Survey Grid reference SP 495200.

REVISED DIAGNOSIS. — No lingual cingulum on the lower molars trigonid; paraconid equal to or higher than the metaconid.

DESCRIPTION (Annexe, Table 2; Figs 3-6)

In the following description, we are aware that the terms "rather", "slightly", "usually" do not correspond to an objective appreciation.

Nearly all holotherian lower molars present at Kirtlington are characterized by a more or less elongated talonid, but only nine more teeth cor-

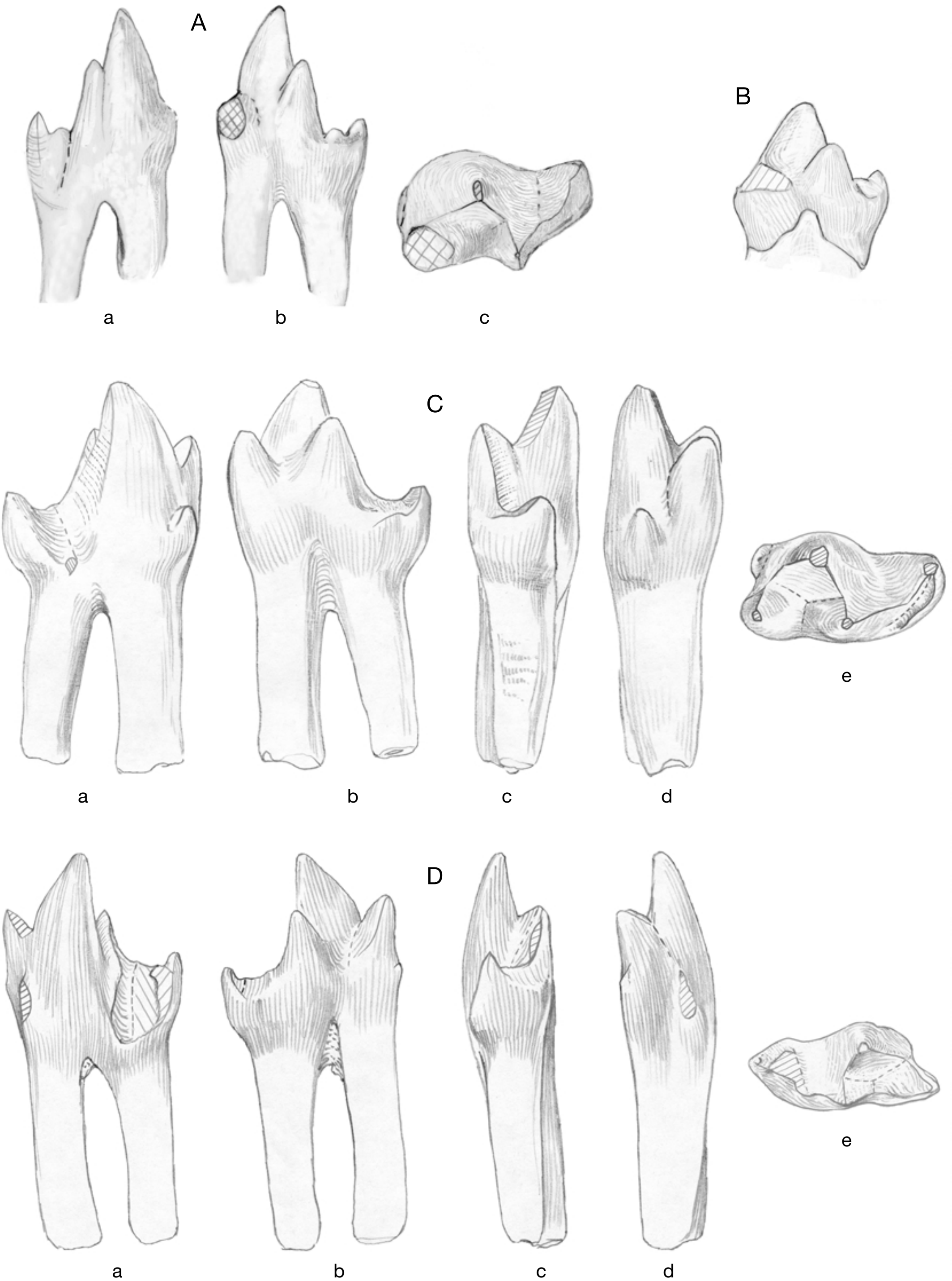

FIG. 3. — Lower molars of *Palaeoxonodon ooliticus* Freeman, 1976b; **A**, holotype BMNH M 36508; **a**, labial view; **b**, lingual view, × 24; **c**, occlusal view, × 33; **B**, BMNH M 36507, lingual view, × 24; **C**, BMNH J.242, × 25; **a**, labial view; **b**, lingual view; **c**, posterior view; **d**, anterior view; **e**, occlusal view; **D**, BMNH J.236, × 27; **a**, labial view; **b**, lingual view; **c**, posterior view; **d**, anterior view; **e**, occlusal view.

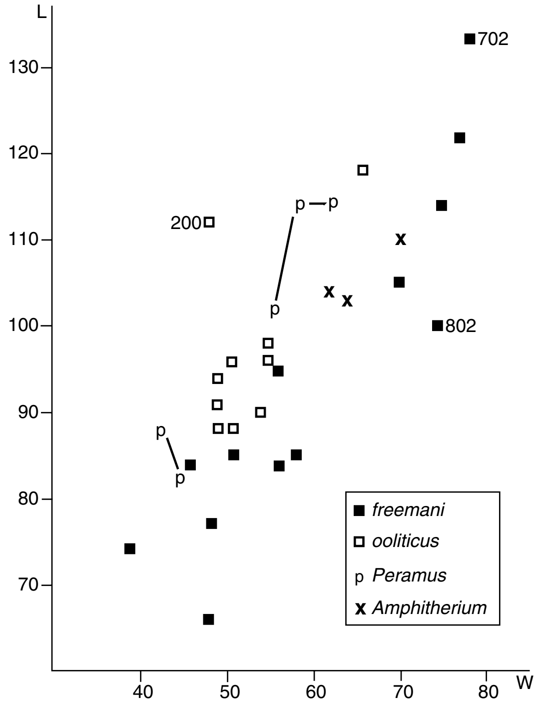

FIG. 4. — Diagram of the width (**W**) versus length (**L**) of the lower molars of *Palaeoxonodon* Freeman, 1976b. Measurements units in 1/100 of mm.

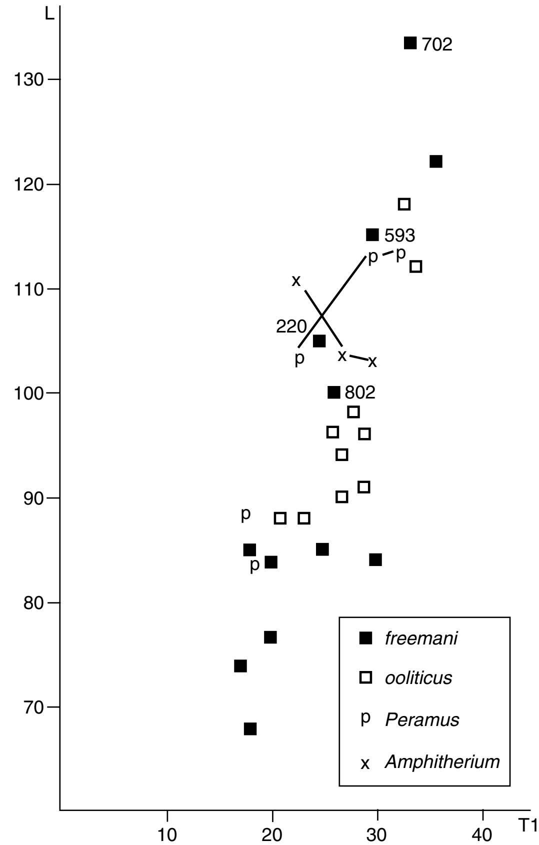

FIG. 5. — Diagram of the length of the talonid (**T1**) versus total antero-posterior length (**L**) of the lower molars of *Palaeoxonodon* Freeman, 1976b. Measurements units in 1/100 of mm.

respond to the morphology of the holotype lower molar of *Palaeoxonodon ooliticus*. The long talonid curves up distally and ends in one sharp cusp; a very narrow basin is enclosed between the metacristid and the entocristid, the latter defined as the lingual crest or ridge between the talonid cusp and the lingual base of the metaconid, limiting lingually the talonid basin. The metaconid is usually hollowed postero-labially, and is situated almost lingually relative to the protoconid (except BMNH J.849), while the paraconid is anterior to the protoconid (except J.639). Cuspule f is present in all cases. Roots are equal, or slightly unequal with a larger anterior root, at least in lingual view where the latter is more extruding.

Even in this small sample of teeth, the variation appears to be considerable: already the previously attributed lower molar BMNH M 36507 (Fig. 3B; FMK/7 in Freeman 1979: pl. 17, 1-3; now lost) differed from the holotype by a much more stocky trigonid, and the talonid surface more inclined lingually. Among the newly attributed specimens are only two complete teeth (BMNH J.236, J.242, Fig. 3C, D), which again appear quite different one from the other, J.236 having a short trigonid with a high protoconid like the holotype, J.242 and other attributed teeth (J.639 excepted) being more like BMNH M 36507. The paraconid (not preserved on the holotype) is equal to or larger than the metaconid. It is straight or slightly forwardly inclined (the same variation occurs in *Amphitherium* or *Peramus*); in two cases (BMNH J.200, J.619), it is straight but situated anteriorly relative to the anterior root. The protoconid can also be straight or posteriorly inclined. The f cusp is more or less strong and is rarely prolonged in an antero-labial cingulum. The talonid basin is oriented either occlusally, linguo-occlusally or completely lingually, this orientation not being directly related to the development of the entocristid. Such variation can also be observed along the dental series in *Peramus* (especially BMNH M 48404, let alone the differences between the various specimens of this genus). The metacristid is slightly irregular in J.849, but no other than the holotype has a step (mesoconid; also present in some specimens of *Peramus* and *Nanolestes*). The entocristid bears a bump in two cases (J.849, J.242). Finally, a slight indication of an e bump is present on only two teeth (J.236, J.639).

Very few specimens are sufficiently well preserved to exhibit wear facets. On some specimens however, facet A (Crompton 1971) is clearly discernible on the posterior face of the paraconid (Fig. 7) (such a facet is still present on the M1 of *Peramus* BMNH M 47339 and of *Amphitherium* M 36822). A frequent ovale facet is the result of wear on cuspule f by the metacone. The anterior and posterior faces of the protoconid can be touched by wear and the latter facet is oriented in a different plane than that which hollows the posterolabial face of the metaconid (this is also the case at least on M3 of *Peramus* BMNH M 47339 and M 48404, though this distinction is not mentioned by Crompton [1971], where both are included in facet 1). The clearest wear facet excavates the paraconal sulcus – almost vertically oriented – between talonid and trigonid; another distinct one can be seen more distally on the labial face of the talonid (BMNH J.200, J.236, facet 3). Finally, there is in some cases (BMNH J.236, J.849) a suspected facet on the **lingual** distal face of the talonid; this could be interpreted as having been produced by the overlapping trigonid of the posterior tooth, as in *Amphitherium*?

Palaeoxonodon freemani n. sp.

HOLOTYPE. — BMNH J.745, left lower molar (Fig. 8A).

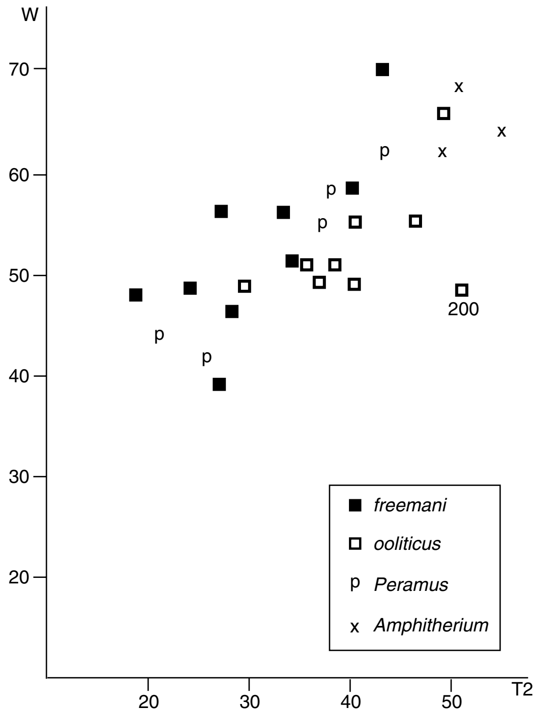

FIG. 6. — Diagram of the length of the talonid (**T2**) versus trigonid width (**W**) of the lower molars of *Palaeoxonodon* Freeman, 1976b. The use of tooth width instead of length is aimed at reducing the effect of variation in the number of molars present in the jaw (suggestion P. M. Butler). Measurements units in 1/100 of mm.

ETYMOLOGY. — *freemani*, after Mr. E. Freeman, who initiated the paleontological work in the Kirtlingon Bone Bed.

ATTRIBUTED SPECIMENS. — BMNH J.197, J.213, J.388, J.530, J.569, J.593, J.715, ?M 44303, right lower molars; BMNH ?J.220, J.?350, J.?618, J.626, J.628, J.657 (in a jaw fragment), J.701, J.727, J.825, J.827, J.837,?M 51823, left lower molars.

HORIZON AND LOCALITY. — Clay Bands of the Kirtlington Bone Bed, Kirtlington Quarry, Oxfordshire. Forest Marble (upper Bathonian). Survey Grid reference SP 495200.

DIAGNOSIS. — Differs from *P. ooliticus* by the presence of an anterior lingual cingulum. Trigonid slightly wider; paraconid equal to or smaller than the metaconid. Talonid cusp slightly more upright. Cusp f tends to be more acute.

DESCRIPTION (Annexe, Table 2; Figs 4-6; 8; 9A, B)
A lingual cingulum occurs below the paraconid; it can be slight, moderate or forming a ledge. In

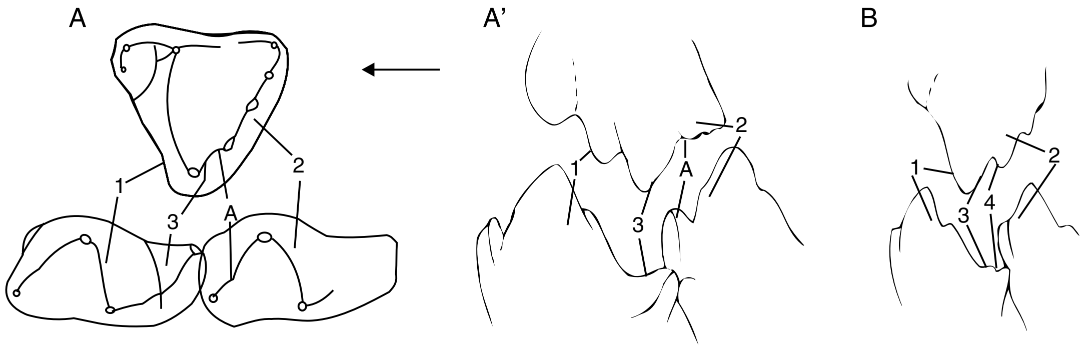

FIG. 7. — Occlusal relationships of upper with lower molars in amphitheriids (**A**, **A'**) and peramurids (**B**). Arrow points anteriorly.

spite of the presence of this cingulum, a tiny cusp e emerges on two teeth only. The paraconid is thus reduced in height though it is equal to, or even larger than, the metaconid in two cases (BMNH J.220, M 51823). Cusp f can be followed by a faint antero-labial cingulum. The protoconid is again straight or, more rarely, posteriorly inclined (three cases); this cusp is generally more slender than in *P. ooliticus* except for the holotype of this species and also J.236 (the shape of the trigonid is also variable in the hypodigm of *Nanolestes* [Martin 2002: fig. 2]). The hollowing of the labial part of the metaconid occurs in only six cases. This cusp is entirely lingual or slightly posterior (BMNH J.350 [Fig. 8B], J.745, J.837) relative to the protoconid. Finally, the holotype J.745 is noteworthy by the presence of a step at the base of the metacristid (mesoconid) and of a bump on the entocristid (such a bump is also visible on J.530 and J.618); this gives the appearance of a three-cusped talonid. J.220 is larger than most. The talonid surface is again variously oriented. The roots are slightly unequal, the anterior one being usually more salient labially (this is not the case for J.745 and J.618, which may be an m1: the same variation occurs along the jaw in *Amphitherium*). J.350 (short and fused stubby roots) and J.618 (long and thin roots) have a blunt trigonid and the lingual cingulum barely reaches the anterior border; their attribution remains uncertain. Moreover, on J.350 and J.220, f is followed by an anterolabial cingulum fading at mid-length of the protoconid.

The same wear facets as those described above for *P. ooliticus* are identifiable on the rare specimens sufficiently well preserved. However, that affecting the metaconid (paracone wear) is more frequently situated on the same plane as that affecting the posterior face of the protoconid (Fig. 7, facet 1); in consequence it is more posterior than labial. That affecting the sulcus between trigonid and talonid is possibly less vertically oriented. On two teeth only (J.388, J.593) could one detect an incipient oval wear facet on f (metacone wear). When the paraconid is sufficiently well preserved, an A facet (anterior side of metacone wear) is discernible.

Palaeoxonodon sp.

MATERIAL EXAMINED. — BMNH J.702, J.290, J.117, right lower molars; BMNH J.802, J.53, left lower molars.

BMNH J.702 (Fig. 10A) is a relatively large tooth with a stocky trigonid and no cingulum beyond a slight crest running lingually between the para- and metaconid. These two characters (trigonid proportions, no lingual cingulum) characterize *Palaeoxonodon ooliticus*; but the paraconid is smaller than the metaconid and the latter is hardly hollowed labially as in the second species. The talonid is elongated and its "basin" occlusally

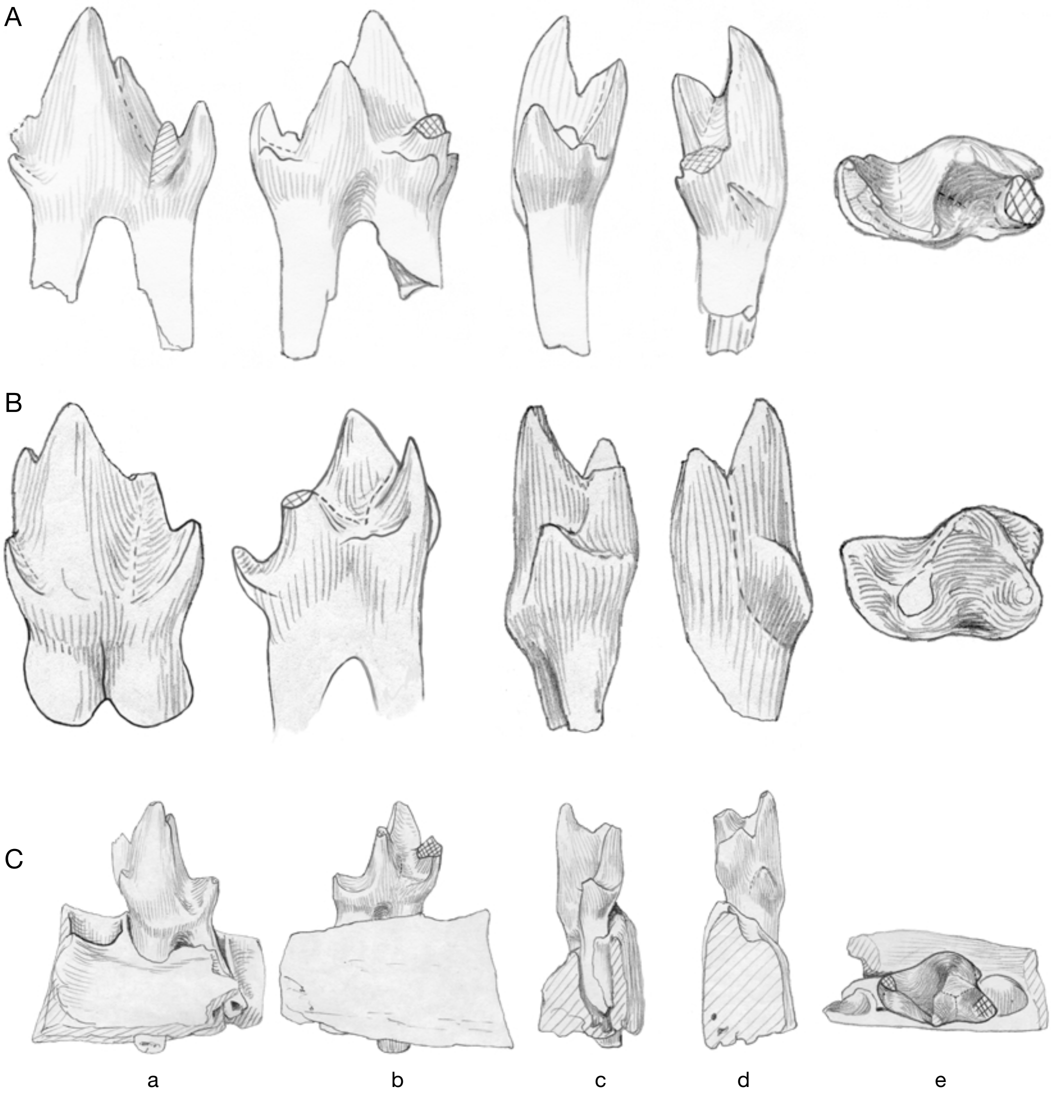

FIG. 8. — Lower molars of *Palaeoxonodon freemani* n. sp.; **A**, holotype BMNH J.745, × 34; **B**, BMNH J.350, × 40; **C**, BMNH J.657, × 17; **a**, labial view; **b**, lingual view; **c**, posterior view; **d**, anterior view; **e**, occlusal view.

oriented. The sharp cusp f is followed by a short antero-labial cingulum more like in *P. freemani* n. sp. Roots are equal.

Wear is present on the anterior face of the protoconid and extends down to the anterior sulcus; facet A (paraconid) is in a slightly different plane. The facets affecting the posterior face of the protoconid and the labial face of the metaconid are nearly aligned as is often the case in *P. freemani* n. sp.; the metacristid is heavily eroded. No wear is clear on the talonid either labially or occlusally. Three teeth display a complete lingual cingulum, as well as a distal metacristid. J.802 (Fig. 10C) is a large tooth; unfortunately the three cusps are broken but the paraconid was smaller than the metaconid. The talonid is of the *Palaeoxonodon* type, even having two cuspules on the metacristid and an undulating entocristid. The posterior face of the metaconid is not hollowed and is situated in the same plane as the posterior face of the protoconid. Anteriorly, cusp f is again followed by a partial labial cingulum, both characters more like *P. freemani* n. sp. There seems to have been an A facet. Otherwise only the paraconal sulcus shows trace of wear. Most characters point to a close affinity to *P. freemani* n. sp.

J.290 is smaller, and very partially preserved, but the lingual cingulum is well marked and so is the distal metacristid. J.53 (a trigonid) is even smaller (size of the *Palaeoxonodon* species) and "only" the paraconid is broken. The anterior cingulum ends in a point (cusp e) but cusp f remains faint; the metaconid is slightly hollowed but there is one single posterior wear facet; anterior facet A is present. The roots are fused proximally. It is tempting to consider these specimens, especially J.802 and J.290 as variants of the *Palaeoxonodon* type. Finally J.117 is a relatively large posterior half of a right tooth, again with a distal metacristid and the paraconal sulcus hollowing the posterolabial face of the metaconid. The paraconid is relatively high, there is no cingulum at least posteriorly, and the talonid (quite rolled) seems to have been shorter than in *Palaeoxonodon*, the occlusal surface not being prolonged by a distal curvature. Roots seem to have been slightly unequal.

Comments

I hesitated to create a second species of *Palaeoxonodon*. In *Guimarotodus inflatus* Martin, 1999, the lower molar lingual cingulum is present only on the posterior teeth (but under the metaconid); it is then conceivable that this was the case in *Palaeoxonodon* and that the two types of teeth – without a lingual cingulum or with a partial lingual cingulum – represent the variation along the jaw. All the more so that some of the other differences cited between the two species suffer exceptions within both groups of specimens, with some uncertain teeth: on BMNH M 51823 and BMNH J.220 (?*P. freemani* n. sp.), the paraconid is at least equal to the metaconid; on J.569, J.618 and J.715 (*P. freemani* n. sp.), the anterior lingual cingulum is very faint. Another possibility is that this cingulum would be one diagnostic criterium of the genus *Palaeoxonodon* versus *Amphitherium*, so that the teeth without cingulum (including the holotype of *Palaeoxonodon*) would represent in fact *Amphitherium*. In the *Amphitherium* jaw BMNH M 36822 (Simpson 1928: fig. 8-1) (Fig. 10) however, on which teeth have no cingulum, the paraconid is equal to or smaller than the metaconid, a character observed here on teeth **with** a cingulum. Finally, a very tempting hypothesis is that "*Palaeoxonodon*" is but a species of *Amphitherium*.

The evaluation of the relations between *Palaeoxonodon* and *Amphitherium* is of importance since the former has been uniformly classified as a Zatheria (e.g., McKenna & Bell 1997), while *Amphitherium* has been considered to be on the dryolestoid side (Prothero 1981; McKenna & Bell 1997; Martin 1999; Butler & Clemens 2001). However, Mills (1964), Kermack *et al.* (1968), Crompton & Jenkins (1968), Hopson & Crompton (1969), Crompton (1971), Freeman (1979) and Sigogneau-Russell (1999) viewed the genus closer to Peramuridae.

When Freeman (1976a) created the genus *Palaeoxonodon*, which he attributed to ?Peramuridae, he diagnosed it on the presence of a cuspule on the metacristid and on the weakly developed antero-buccal cingulum (though both characters can also be found in *Peramus*). He concluded that *Palaeoxonodon* is intermediate between *Amphitherium* (one talonid cusp and no basin) and *Peramus* (two to three cusps and a small basin). But in 1979, when he enriched the mammalian fauna from Kirtlington, he mentioned a partial ?*Amphitherium* left lower molar M 36516, suborder Amphitheria (including Peramuridae, Amphitheriidae and Paurodontidae), which he distinguished from *Palaeoxonodon* by "its larger size, the slightly convex lingual face of the protoconid and a prominent antero-buccal cusp".

Size cannot be considered a generic character. The six molars of the jaw of *Amphitherium* BMNH M 36822 (Fig. 11) have a flat lingual face of the protoconid. The prominence of the antero-buccal cusp (rather an antero-buccal cingulum in fact) as a diagnostic character of *Amphitherium* is weakened by the condition of m1 of the same specimen, where this cuspule is barely perceptible, while it is strong in several *Palaeoxonodon* specimens. Indeed, before going any further, variability along the jaw in *Amphitherium*, already mentioned by Crompton (1971) and Prothero (1981), should be stressed. On the jaw mentioned above (M 36822), the relative length of the talonid as well as its inclination, the distinctness of the metacristid, the relative size (equal to or smaller than the metaconid) and inclination of the paraconid, the extension of the antero-buccal cingulum (very weak cuspule f on m1), the situation of the metaconid relative to the protoconid with individualization of an antero-labial metaconid facet, as well as the proportion of the roots (unequal labially on m3) vary along the dental series.

Later, Prothero (1981) stated that *Palaeoxonodon* shows "further development of the talonid" relative to *Amphitherium*, with an "incipient hypoconulid and entoconid". The first assumption is not confirmed by measurements (see Annexe, Table 1; Figs 4-6). Moreover, in *Palaeoxonodon*, as in *Peramus*, the talonid looks longer than it really is, because of the very sloping posterior face of the metaconid. The second assumption was based on fig. 6, pl. 16 of Freeman (1979); the "entoconid" is an artefact of lighting for photography, which has not been confirmed by scrutiny of the original specimen. The accessory cusps were not present either on the second tooth described by Freeman himself (1979).

Sigogneau-Russell (1999) retained the generic distinction on the basis of the smaller size of *Palaeoxonodon* (again not a generic character), a metaconid better detached from the protoconid, hence a more accentuated posterior hollowing of the metaconid, and the less dorsally recurved talonid. Considering the metaconid situation in the same *Amphitherium* jaw BMNH M 36822, it appears in fact that the first feature varies, with a better detachment of this cusp in the posterior teeth. Similarly the hollowing of the metaconid is less accentuated in *Palaeoxonodon freemani* n. sp. than in *P. ooliticus*, and this character varies along the *Peramus* jaw BMNH M 47339. Finally, as already mentioned, the dorsal curvature of the talonid varies along the series in *Amphitherium*, as well as in the teeth attributed to *Palaeoxonodon*, and so does its posterior extension, though it tends to be more accentuated in *Amphitherium*. Butler & Clemens (2001) consider that in *Palaeoxonodon* as in *Peramus*, the molars are longer and narrower than in *Amphitherium* and that there is no overlap of the talonid-trigonid of adjacent teeth, the former being enclosed between "the lingual basal cusp and the mesio-buccal cingulum" (p. 15). The "lingual basal cusp" (e) is in fact absent on the holotype of *Palaeoxonodon* and is very rarely expressed in the hypodigm; when detectable, it represents only the anterior border of the lingual cingulum and not a real cusp as in *Peramus*, so that the talonid interlocks between the paraconid and f as in *Amphitherium*. As for the extension of this overlapping over the adjacent molar, it was probably variable along the series. It is interesting to add that, in *Amphitherium* and *Palaeoxonodon* and contrary to the condition in *Peramus*, the distal face of the trigonid is not wider than the mesial face. Finally, my maintaining of two distinct genera is mainly based on the ignorance of critical data, including the dental formula.

There remains the question: on which side of the cladogram are amphitheriids situated? I shall discuss the matter after study of the upper molars.

?***Palaeoxonodon*** sp.

One of the difficulties in dealing with isolated molars results from their variability along the jaw. In the absence of associated upper molars for *Palaeoxonodon* and *Amphitherium*, the closest (in time) complete holotherian upper dentitions at our disposal for comparison are those from Guimarota: *Henkelotherium* Krebs, 1991, *Krebsotherium lusitanicum* Martin, 1999 and *Dryolestes leiriensis* Martin, 1999. These confirm the observations made on more recent dryolestoids (Morrison, Purbeck): the main characters (general shape, presence of a trigon ridge, degree of development of metacone, position of stylocone, labial cingulum) are constant along the

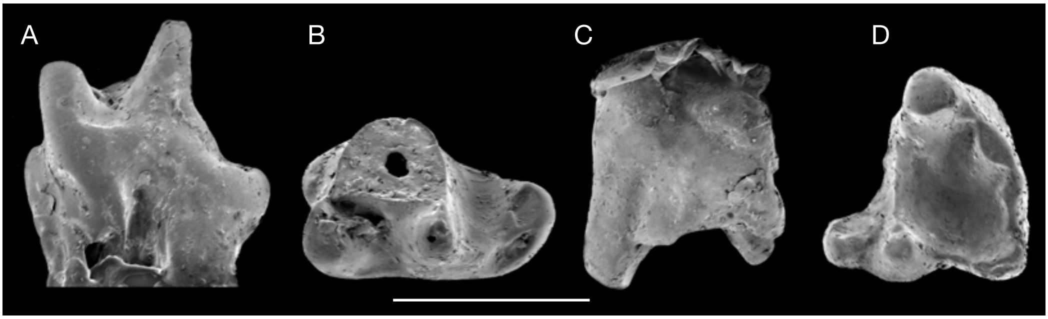

FIG. 9. — SEM photographs; **A**, **B**, *Palaeoxonodon freemani* n. sp., BMNH M 44303 lower molar, lingual and occlusal views; **C**, **D**, ?*Palaeoxonodon* sp., BMNH M 34994 upper molar, posterior and occlusal views. Scale bar: 1 mm.

series. Size and proportions vary, as well as the importance of the parastylar or metastylar lobes.
Among the Kirtlington holotherian upper molars, several groups can be recognized. I tentatively attribute two of these groups, which form the bulk of these molars, to *Palaeoxonodon*, the most abundant form among the holotherian lower molars. All of them have a labio-lingually wide trigon (Annexe, Tables 3, 4; Figs 12; 13).

Group I (Figs 9C, D; 14; 19D)
BMNH J.146, J.524, J.749, J.754, J.792, M 36512 (figured by Freeman 1979: pl. 18, 1-3), right upper molars; BMNH J.137, J.392, J.436, J.636, M 36504 (figured by Freeman 1979: pl. 18, 4-5), left upper molars.
Questionably referred to group I: BMNH J.44, J.231, J.669, M 34994, right upper molars; BMNH M 36526 (figured by Freeman 1979: fig. 2b, pl. 19, 4-6), J.25, left upper molar.
This first group (11 teeth) contains relatively short (antero-posteriorly) teeth with a weak median ridge, a labial parastyle crest oriented rather vertically, a usually straight preparacrista and straight or convex postparacrista+metacrista, both being nearly equal (except on J.749, Fig. 14B). The paracone is sharp, and the metacone well distinct. A well individualized "c" cusp is always present, followed by a poorly defined metastyle. This point needs some clarification: the metastyle is the "cusp fitting against the lingual side of the parastyle of the following tooth" (Butler 1978: 442). In fact, its identification is not easy, beyond *Kuehneotherium* and "*Eurylambda*", where it appears as a sharp point of the posterior cingulum. Prothero (1981) and Martin (1999) figured schematically two small cusps, one posteriorly and one labially on the convex posterior border of the dryolestoid tooth; but on several dryolestoids, what I consider as the metacone is followed not only by "c" (not mentioned by Martin [1999] on his schema, Abb.7) but by a second often shorter but similarly shaped cusp (e.g., *Krebsotherium lusitanicum* M3, *Dryolestes leiriensis* M5, or *Herpetairus* Simpson, 1927 AMNH 101130, middle molar); a third cusp is even present in two cases. Then follows the curved posterior part of the tooth, on which metastyle cusps are more or less clearly projecting. On the sufficiently well preserved teeth from this group I from Kirtlington, the same situation is observed: the metacone is followed by one cusp, lower but wider labio-lingually ("c"), in fact in the shape of a curved crest rather than a cusp; then follows the rounded border of the tooth, bearing one or two cuspules, posteriorly and labially. It can also happen (e.g., J.749) that cusp "c" is shorter but doubled as in the cases mentioned above. The labial shelf bears a detectable individualized posterior stylar cusp only in two cases.
On this general scheme, several more features vary (Annexe, Table 4): a B' formation (Hu *et al.* 1997), again not in the shape of a sharp cusp but of a crestiform bulge projecting inside the trigon (very

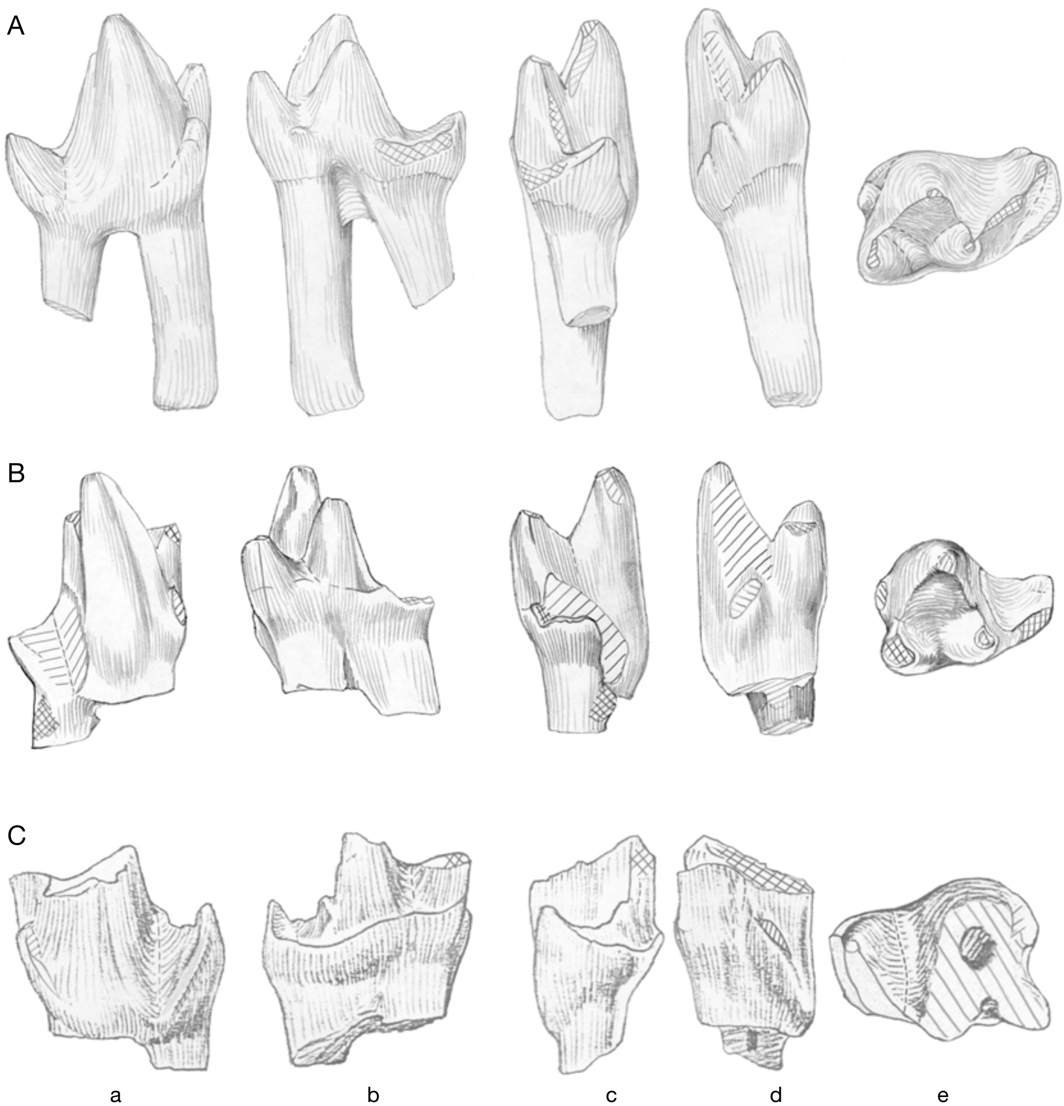

FIG. 10. — Lower molars; **A**, *Palaeoxonodon* sp., BMNH J.702, × 22; **B**, ?*Kennetheredium* sp., BMNH J.515, × 20; **C**, *Palaeoxonodon* sp., BMNH J.802, × 25; **a**, labial view; **b**, lingual view; **c**, posterior view; **d**, anterior view; **e**, occlusal view.

similar to the situation in *Spalacotherium*-"*Peralestes*"), is present in four cases (and identifiable mostly when worn). This cusp is also present, though not named, in *Nanolestes* (see below). The ectoflexus is absent, weak or moderate. The stylocone is well developed, either terminal on the preparacrista or slightly posterior relative to it (but always linked to its labial extremity); it clearly dominates in height the parastyle in labial view. The latter is constituted of one or two elements. As mentioned above, the metastylar extension is variable, probably according to the position of the tooth along the jaw (like in "*Peralestes*"; J.146 is thus probably a last molar). There is only one case of an anterior cingulum (J.636, Fig. 14A). When preserved, three roots can be counted.

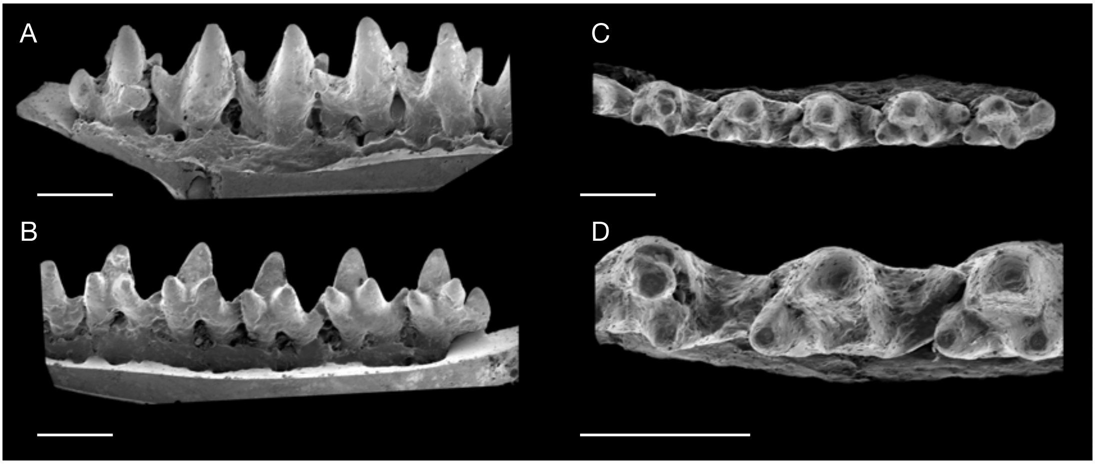

FIG. 11. — SEM photographs of *Amphitherium rixoni* Butler & Clemens, 2001, BMNH M 36822; **A**, labial view of the molar series; **B**, lingual view of the same; **C**, occlusal view of the same; **D**, occlusal view of M1, M2, trigonid of M3. Scale bars: 1 mm.

The posterior face of the tooth is convex posteriorly, so that shear was not transverse; the metacone always has a distinct anterior face even if wear (facet A of Crompton 1971) is rarely detectable (BMNH J.295, J.436, J.392). On the teeth showing wear, the posterior face of the paracone (Fig. 7, facet 3) is the most frequently touched. More facets can be detected on the lateral face of the metacone and of "c", the two (or three) cusps being either united or differently oriented. Only three teeth show wear on the anterior face of the paracone. The parastyle sulcus has the same nearly vertical orientation as the stylocone sulcus, one prolonging the other.

In the questionably attributed sample, J.231 (Fig. 14D) is a larger tooth with a nearly transverse posterior face; M 36526 is very worn, J.44 poorly preserved and J.25 has no preserved parastyle.

On M 34994 (Fig. 9C, D), the ridge is somewhat displaced anteriorly as in group II, but other characters are those of group I. Finally, J.669 also shares some characters with group II.

Group II (Figs 15A, C, D; 16A, B)

BMNH J.99, J.238, J.241, J.458, J.817, M 36532) (figured by Freeman 1976b: fig. 2a-b; 1979: pl. 9, 1-3; fig. 2a), right upper molars; BMNH M 36530, left upper molar.

Questionably referred to group II: J.32, J.506 (milk?), J.508, J.512bis, J.742, J.743, J.788, right upper molars; BMNH J.294, J.627, left upper molars.

This second group contains teeth with an anteriorly situated trigon ridge. The trigon is slightly more open, most often with a relatively lower paracone. Again, the preparacrista is usually straight and the postparacrista+metacrista straight or convex, but the former is clearly shorter than the latter (one exception), and provided in four cases with a distinct B' bulge. The well developed parastyle is usually more lingually oriented. The stylocone remains strong but does not notably exceed the parastyle in height (one exception). The metacone and "c" are sharp cusps rather than crests and the latter is more often doubled than in group I. The metastylar area itself bears, in a few cases, one or two small and sharp cusps. A posterior stylar cusp is individualized in half the specimens. The stylocone and parastyle sulcus are here oriented at an angle. The posterior face of the trigon shows the same morphology as in the first group, not being transverse. When observable, one counts three roots.

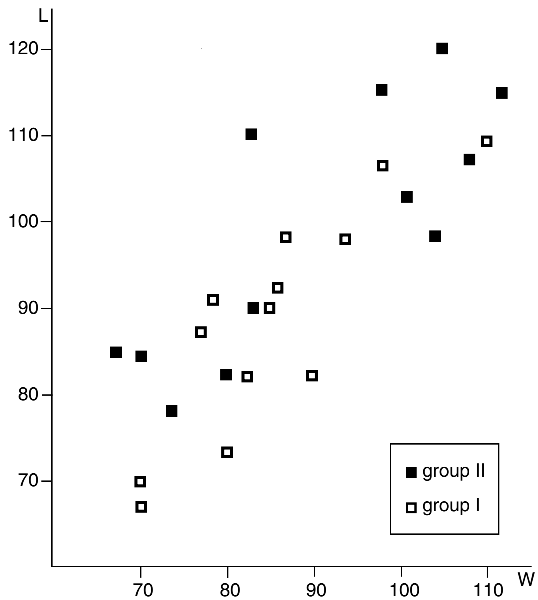

FIG. 12. — Diagram of the width (**W**) versus length (**L**) of the upper molars of ?*Palaeoxonodon* sp. (group I and group II). Measurements units in 1/100 of mm.

As is apparent from the above description, variation is again considerable (Annexe, Table 4): the metastylar lobe is more or less extended, this being certainly related to the position of the teeth in the jaw. The parastyle (simple or double) is followed, in two cases (J.99, [Fig. 15A], and M 36532) by an anterior cingulum fainting lingually. Again, the ectoflexus is modest or strong, the stylocone is either terminal or displaced slightly posteriorly. According to Martin (1999: 7), this position differentiates Dryolestidae from Paurodontidae "stylocon direkt labial der Paracrista"; in fact it is distal on the holotype specimen of *Comotherium* Prothero, 1981 (unlike the figuration by Prothero 1981: fig. 2), a genus however classified by Martin in the Paurodontidae. Finally, several teeth have a short indentation labially between parastyle and stylocone.

Among the questioned teeth, J.742 (Fig. 15C) and J.788 (unlikely to represent the same specific taxon) are large teeth with also an anterior cingulum and a lingual cingulum as well; the stylocone is also slightly displaced lingually relative to the labial rim (this also occurs on J.743). Otherwise the main characters are the same as those mentioned above, with a particular relatively low paracone. All three possess a posterior stylar cusp. J.32 and J.512 are incomplete. J.506 may be a milk molar: it is very worn and has only two

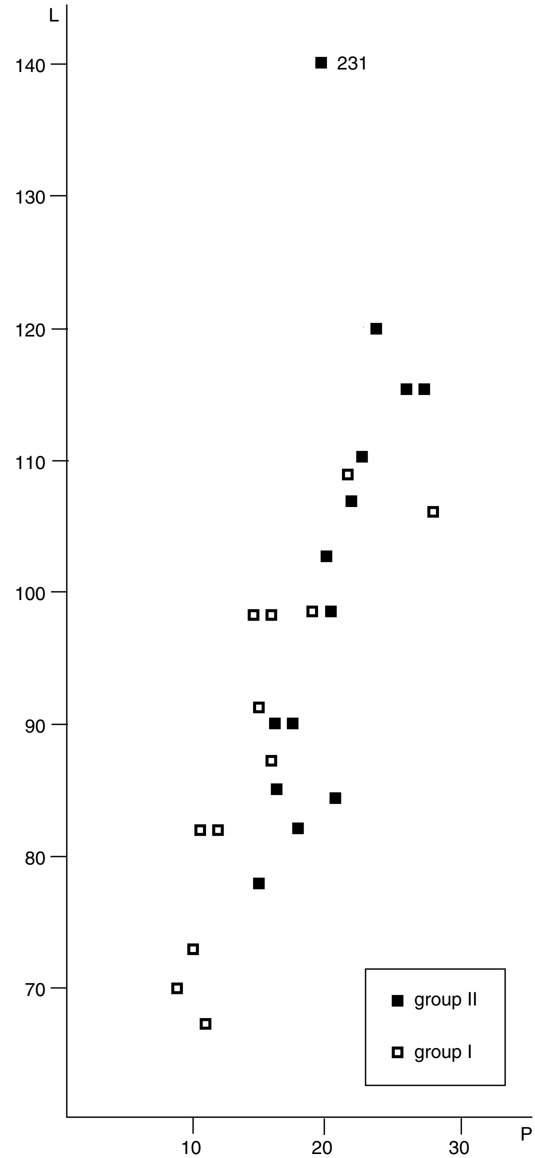

FIG. 13. — Diagram of the length of the parastyle (**P**) versus total length (**L**) of the upper molars of ?*Palaeoxonodon* sp. (group I and group II). Measurements units in 1/100 of mm.

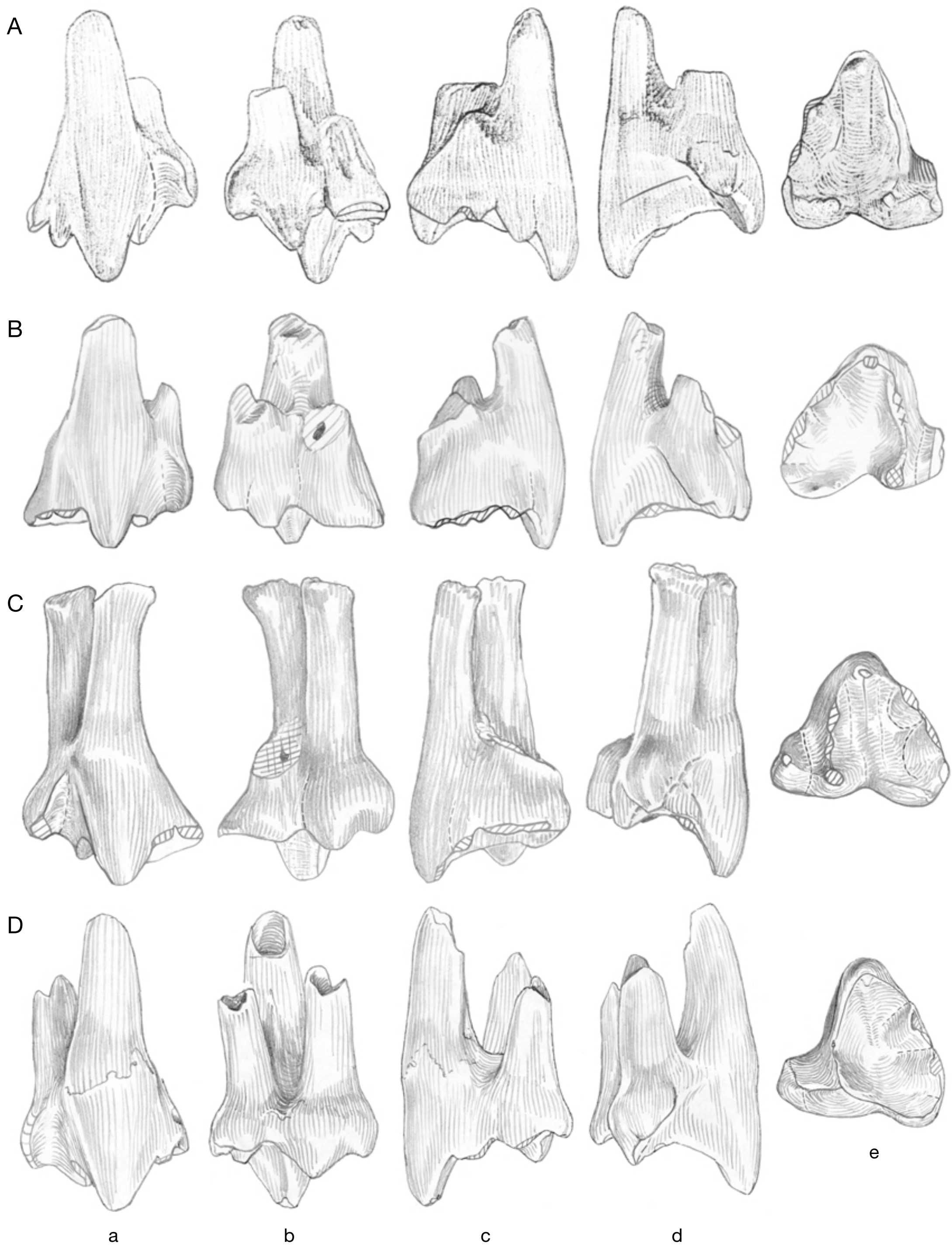

FIG. 14. — Upper molars of *Palaeoxonodon* sp. (group I); **A**, BMNH J.636, × 24; **B**, BMNH J.749, × 30; **C**, BMNH J.792, × 30; **D**, BMNH J.231, × 19; **a**, lingual view; **b**, labial view; **c**, posterior view; **d**, anterior view; **e**, occlusal view.

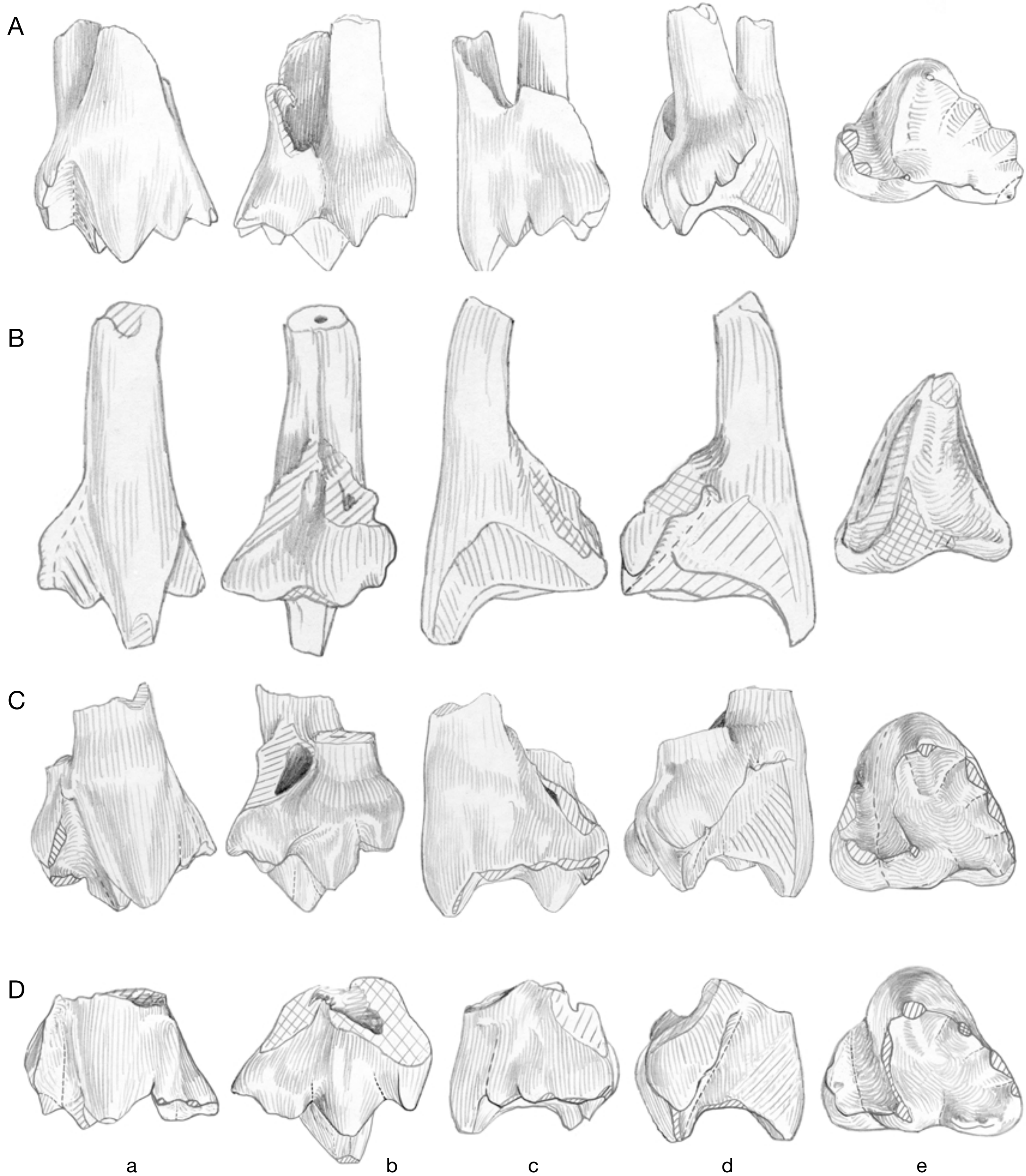

FIG. 15. — Upper molars; **A**, *Palaeoxonodon* sp. (group II), BMNH J.99, × 25; **B**, ?*Kennetheredium* sp., BMNH J.517, × 35; **C**, *Palaeoxonodon* sp. (group II), BMNH J.742, × 22; **D**, *Palaeoxonodon* sp. (group II), BMNH J.743, × 23; **a**, lingual view; **b**, labial view; **c**, posterior view; **d**, anterior view; **e**, occlusal view.

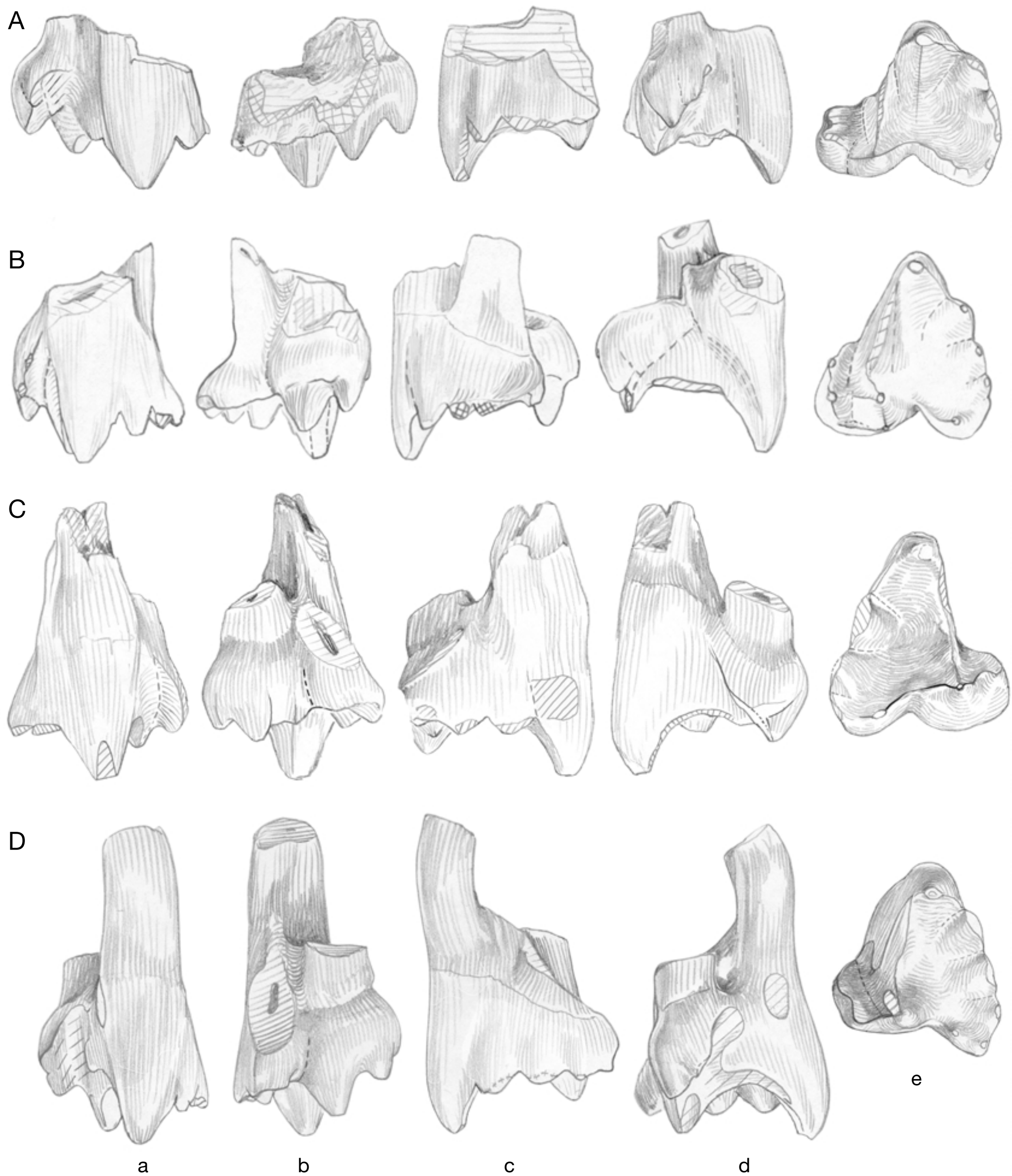

FIG. 16. — Upper molars of *Palaeoxonodon* sp.; **A**, group II, BMNH J.817, × 30; **B**, ?group II, BMNH J.508, × 25; **C**, Trechnotheria indet., BMNH J.698, × 20; **D**, Trechnotheria indet., BMNH J.786, × 25; **a**, lingual view; **b**, labial view; **c**, posterior view; **d**, anterior view; **e**, occlusal view.

roots, the two being fused; but the trigon remains short antero-posteriorly. J.294 fits better with a milk molar; the trigon ridge is short, the posterior lobe extended, the ectoflexus strong and the parastylar wing extended transversely. J.508 (Fig. 16B) has a sharp paracone and narrow parastyle as in group I; but the ridge is not median, the parastylar cusp is relatively high and the metacrista cusps acute; moreover a cingulum overhangs the base of the parastyle and the stylocone. Finally, J.627 is a large tooth with the cristae and paraconal sulcus deeply worn.

The same type of wear as on group I prevails. But, due to a more marked convexity of the posterior face of the trigon, that affecting the posterior face of the metacone is more often distinct from that of "c". Occlusion was thus of a similar type as in the first group (not completely transverse shear) though the rotatory movement must have been more accentuated: the parastyle sulcus is slightly more inclined and is angled downward along the stylocone, so that the tip of the parastyle is not worn and is even isolated by a crest.

Comments

Again the question arises whether these two configurations (supposing the teeth included in each set are homogeneous) correspond to one or two distinct species: Martin (1999) cites the trigon ridge as varying within one unit of dryolestids, but this variation concerns more its expression than its situation. Other intraspecifically variable characters cited by Martin are, beside size and proportions, the stylocone development and the shape of the labial wall, variations also observed here. The length/width plot (Fig. 12) does not reveal two sets of teeth as clearly as the same did for the lower molars: this relation may be more variable along the series than on the lower molars. Even if some teeth are difficult to assign to one or the other group, the differences mentioned above between the two groups seem to be sufficient to correspond to the two identified species of *Palaeoxonodon*. The so-called first group of upper molars may represent *P. freemani* n. sp., in which the masticatory movement would have been more vertical (parastyle sulcus more upright), the second *P. ooliticus*? Incidentally, doubts expressed by Sigogneau-Russell (1999) as to the attribution of BMNH M 36512 and M 36530 to this genus (Freeman 1979) appear now, in the light of this new material, as unjustified.

Crompton (1971) had, after Mills (1964) and Clemens & Mills (1971), tentatively reconstructed the upper molar of *Amphitherium* and the occlusal pattern. If one excludes the relative proportions of the metacone and "c", this reconstruction (Clemens & Mills 1971: fig. 6A-B') fits the material examined above. However, if a wear facet does persist on the anterior face of the metacone, no facet 4 is detectable on the talonid; this upper facet (on the metacone) would thus correspond to facet A and still occlude with that affecting the posterior side of the paraconid (Fig. 7). The latter is in continuity with that detectable on the disto-labial extremity of the talonid of the preceding molar, and disposed at a different angle from facet 3 (labial face of talonid-paracone).

Discussion

We can now come back to the question of the position of *Palaeoxonodon-Amphitherium* within Holotheria. Mills (1964: 129) compared the lower dentition of *Amphitherium* and *Peramus* and proposed that *Peramus* "should be transferred from the Paurodontidae to the Amphitheriidae". Similarly Kermack *et al.* (1968) placed Peramuridae in the suborder Amphitheria as opposed to the order Dryolestoidea. Crompton & Jenkins (1968: 455) argued that "the occlusion in *Amphitherium* was different from that in *Kuehneotherium* on the one hand and dryolestid pantotheres on the other" and concluded with the same classification as Kermack *et al.* (1968), a classification also adopted later by Freeman (1979). Crompton (1971) stated that *Amphitherium* represents a stage preceding the origin of a hypoconid (which would apply as well to *Palaeoxonodon*). On the other hand, Clemens & Mills (1971: 108) concluded from their study of *Peramus* that "*Amphitherium* and *Peramus* are representatives of different lineages"; however, this interpretation was based mostly on the comparison of the last lower premolar of *Amphitherium* with what they considered as the last premolar of *Peramus* but which is now interpreted as the antepenultimate premolar. Prothero (1981) presented several arguments to include *Amphitherium* in Dryolestoidea; these have been discussed at length by Sigogneau-Russell (1999), who proposed that *Amphitherium* be considered the sister group of Zatheria, sharing with the earliest ones the presence of a distal metacristid and of an incipient talonid basin. McKenna & Bell (1997) do not give any argument for including the order Amphitheriida in the Dryolestoidea. Martin (1999) isolated *Amphitherium* from Zatheria (hence supposedly from *Palaeoxonodon*) and linked it with Dryolestida on several lower molar characters: unicuspidate talonid (but so is it on several "peramuran" taxa, admittedly not considered by Martin), presence of six molars, paraconid forwardly inclined (not on M1 and hardly on M2 of *Amphitherium* M 36822), posterior lower molar root smaller than the anterior one (they are equal at least on the first molar of the same jaw); but no upper tooth character defines Martin's Dryolestoidea (Dryolestida plus *Amphitherium*, node 6, p. 4), Finally, Butler & Clemens (2001) implicitely excluded *Amphitherium* from Zatheria, while, in his later paper, Martin (2002: 346) considers *Amphitherium* as a representative of the "stem lineage of Zatheria".

Now, if the upper molars described above are rightly attributed to *Palaeoxonodon* – and the near absence in the fauna of any *Peramus*-like molar sustains such an attribution – one is led to a contradictory situation between lower and upper molars, unless one admits that a long talonid is primitive for Trechnotheria. The lower molars are undoubtedly of a pretribosphenidan type (expanded talonid incipiently basined, distal metacristid, paraconal sulcus on metaconid), though the persistance of a lingual cingulum (as in *Minimus*) and the presence of only one talonid cusp have to be considered as primitive; but the reduction of cusp e is again derived. This very peculiar configuration of the talonid both in amphitheriids and peramurids can hardly be considered as having developed twice (though this would only be one more example of parallel evolution in the dentition of Mesozoic mammals); it thus implies a close relationship between the two. On the upper molars, on the other hand, the presence of a cusp B' was rightly considered as possibly primitive for spalacotheriids (Cifelli & Madsen 1999); it definitely appears as the persistance, in amphitheriids, of a primitive trechnotherian character. Similarly, the "c" cusp is to be considered as a primitive heritage, being shared with some symmetrodonts and dryolestoids as well (that of peramurans may not be homologous). Finally the persistance of a wear facet A is plesiomorphic. But amphitheriid upper molars exhibit what are considered as dryolestoid apomorphies: widened trigon, trigon ridge, three roots, interlocking stylar region (however also present in some spalacotheriids and, for the last two, possibly *Peramus*); these upper molars are at the same time devoid of "peramuran" features usually considered as derived: lingual position of the metacone, reduction of the stylocone, presence of lingual cuspules. This ambiguous situation might require a reconsideration of the polarity of the characters involved. In any case it emphasizes the insight of Blainville (1838) when coining the name *Amphitherium*.

Martin (2002) has recently published a new genus *Nanolestes* which he dubbed "a representative of the stem line of Zatheria". As concerns the lower molars, no anterior or posterior view having been published, some details remain uncertain: did the anterior interlocking involve an e cusp? Does the "abc" cusp represent f? Is there a metacristid rather than a "cristid obliqua"? Moreover, the talonid is described as non basined but fig. 1A shows a double line on the talonid. The stereophoto of the occlusal view of the holotype seems also to show a diffuse lingual part in this area. But Martin wrote (*in litt*. 2002): "What you interpreted as a double line in my fig. 1A is the labial edge of the talonid cusp. There definitely is no incipient basin or double line present".

As concerns the attributed upper molars of *Nanolestes*, Martin's diagnosis (2002: 333) mentions "stylocone comparatively large and paracrista" (= preparacrista) "and metacrista" (= postparacrista+

metacrista) "separated into cusps and cuspules". Large cusp "C (= 'c') between metacone and double-cusped metastyle. Additional cusp with two tips at the anterior border of the trigon near the base of the paracone" (cusp B'). If this doubling and degree of development of cusp B' (a cusp not named by the author) represents undoubtedly an apomorphy of the genus (a smaller cusp B' is also doubled at least on the last molar of "*Peralestes*"), the other features are quite comparable to what is observed in some trechnotheres and especially in *Palaeoxonodon* (especially group II). The two cusps labial to the metacone would represent a unique or double "c" cusp plus a metastyle. However, specific to *Nanolestes* would be the two unnamed cusps figured (Figs 8; 9C) between the paracone and metacone (though Martin's description [2002: 341] says that the metacone follows "immediately" the paracone on the posterior border). Finally, a posterior stylar cusp seems also to have been present ("a small bulge with a tiny enamel cuspule", Martin 2002: 341). The morphology of these upper molars is certainly closer to that of the dryolestoids than to that of Zatheria. The possible inclusion of *Nanolestes* into the amphitheriids rests on the clarification of uncertain points.

Meanwhile, Amphitheriidae may be diagnosed as follows, if one accepts the association proposed above of upper and lower molars: Cladotherian mammals whose lower molars have an elongated and incipiently basined talonid (1) with only one talonid cusp; presence of a distal metacristid (1). Lingual cingulid tends to disappear. Cusp e reduced or absent but a developed cusp f. Two subequal roots with a tendency to the predominance of the anterior root. Lower jaw slender, with an anteriorly situated mandibular foramen, an elongated Meckelian sulcus, a long symphysis. five premolars, five to seven molars. Upper molars relatively wide transversely; trigon ridge; presence of accessory cusps on the anterior and posterior cristae (1); metacone not lingually situated; large stylocone. Three roots. Persistence of facet A during occlusion. (Characters listed (1) are derived relative to Dryolestida).

None of these characters is exclusive to the family. There remains to account for an elongated and incipiently basined talonid in the absence of a corresponding upper cusp (protocone). The elongation encountered in the amphitheriid line at least could have developed as an answer to the elongation of the postparacrista+metacrista (and development of accessory cusps) on the upper molars, thus increasing the efficiency of the shearing function. In dryolestoids, the answer to this elongation of the crista was to increase the transverse dimension of the lower tooth, which also contributed to improving the shearing function of the molars. In the pretribosphenid line, the elongation of the talonid and individualizaton of talonid cusps had its counter part in the lingual situation and role of the metacone, anticipating the grinding function of the teeth.

The remaining holotherian lower molars from Kirtlington again display a rather elongated talonid, but the distal point of the latter does not surpass the level of the posterior root as is the case in amphitheriids; moreover they are devoid of a metacristid and the posterior trigonid face is transverse. Some have a complete lingual cingulum; others lack this feature.

Order indet.
Family indet.

Kennetheredium n. gen.

TYPE SPECIES. — *Kennetheredium leesi* n. gen., n. sp.

ETYMOLOGY. — *heredium* (Latin): heritage from Kenneth A. Kermack.

DISTRIBUTION. — Clay Bands of the Kirtlington Bone Bed, Kirtlington Quarry, Oxfordshire. Forest Marble, upper Bathonian.

DIAGNOSIS. — Holotherian lower molars characterized by a long talonid and a distally sloping lingual cingulum. Trigonid high and slender with sharp cusps; paraconid slightly shorter than metaconid and slightly sloping anteriorly. Extended antero-buccal cusp; buccal cingulum may be present. Talonid with a tiny occlusal surface. Posterior face of trigonid transverse: facet A very reduced.

Kennetheredium leesi n. sp.

HOLOTYPE. — BMNH J.746, left lower molar (Fig. 17A).

ETYMOLOGY. — *leesi*, to acknowledge the essential contribution of Mr A. Lee's drawings to this paper.

ATTRIBUTED LOWER MOLARS. — BMNH J.379, ?J.430, J.514, right lower molars; BMNH J.289, ?J.518, J.824, left lower molars.

LOCALITY AND HORIZON. — Clay Bands of the "Kirtlington mammal bed" (Freeman 1979), Kirtlington Old Quarry, Oxfordshire. Forest Marble (upper Bathonian).

DIAGNOSIS. — As for genus by monotypy.

DESCRIPTION (Fig. 17A, C)
This taxon would be represented by at least seven teeth with a complete and sometimes denticulated lingual cingulum. The latter is quite different from that of the three teeth mentioned above (p. 509), in that it slopes regularly from front to back and ends in a low situated talonid. The trigonid is high with closely grouped cusps. The talonid (preserved on three specimens only) is shorter than that in *Palaeoxonodon* but still relatively elongated and with a short occlusal concavity; it is again labially recurved distally. There is no distal metacristid, only a very short crest at the base of the metaconid limiting labially the talonid surface. Where preserved, the paraconid is slightly inclined forwards and slightly smaller than the metaconid as a consequence of the distally inclined lingual cingulum. The antero-labial cusp (f) is well indicated and occupies the whole anterior base of the protoconid. Moreover, a slight labial cingulum may be present (the type is not preserved low enough). At most, one root is preserved so that the relative proportions of the two roots are uncertain; they were at least subequal if not equal.
The enamel of the holotype tooth not being intact, only the ovale f facet is certain. J.514 has a narrow wear facet on the anterior face of the protoconid which joins that of f and that on the tip of the paraconid, and a wider posterior facet which joins that of the paracone sulcus; the situation is nearly the same anteriorly on J.430. On J.289 the paraconal sulcus goes up to the tip of the metaconid.
This morphology partially resembles that of spalacotheriid symmetrodonts with the notable difference of a longer talonid with a concave occlusal component and the absence of a labial cingulid. Given the fact that the reduction of the talonid is the only apomorphic character of the lower molars recognized for symmetrodonts (Prothero 1981), the ordinal attribution of the new taxon must remain indeterminate.

?*Kennetheredium* sp.

MATERIAL EXAMINED. — BMNH J.428, J.515, J.532, J.801, right lower molars; BMNH J.214, J.846, left lower molars.

Six more lower molars could belong to a closely related taxon: but the low situated talonid is more extended labio-lingually than antero-posteriorly; it is thin and recurved labially in the most complete tooth. The attribution of these teeth to the preceding taxon meets with the other following difficulties.
BMNH J.214 (left) has a barely sloping lingual cingulum which does not underline the whole paraconid, starting only at its posterior end; the paraconid is anteriorly inclined; an f cusp is present; the metacristid may have been present, in which case this particular trigonid would not fit here. On J.428 (right; Fig. 17B) the cingulum is extremely faintly indicated, but the erosion of the enamel might explain this situation; the distal end of the talonid is recurved upwards distally as in ?*Kennetheredium leesi* n. gen., n. sp. J.430; there is a strong cusp f. The roots are slightly unequal at the expense of the anterior root (a situation opposite to that of the amphitheriids). J.801 (right) lacks a lingual cingulum; this may be due again to the absence of enamel. It has a high and narrow trigonid, with a completely transverse posterior face and no distal metacristid, at least in the present state of preservation. An antero-labial cingulum may have been present. Roots were subequal. J.846 (left) is a posterior half of a molar with uncertain charac-

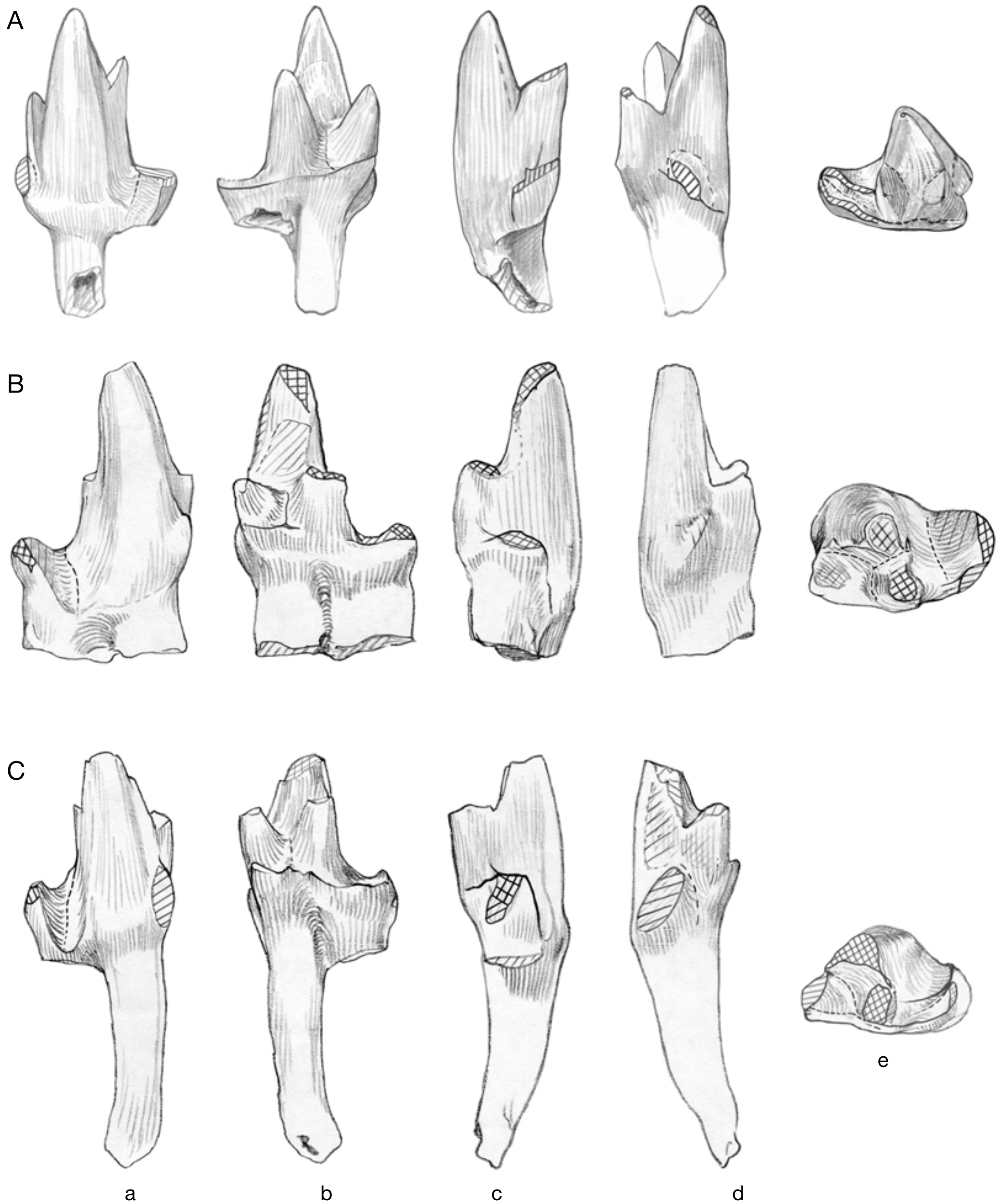

FIG. 17. — Lower molars; **A**, *Kennetheredium leesi* n. gen., n. sp., holotype BMNH J.746, × 25; **B**, ?*Kennetheredium* sp., BMNH J.428, × 26; **C**, ?*Kennetheredium leesi* n. gen., n. sp., BMNH J.430, × 26; **a**, labial view; **b**, lingual view; **c**, posterior view; **d**, anterior view; **e**, occlusal view.

ters except a possible lingual and labial cingulum and the same type of talonid. J.532 (right) might also have had a complete lingual cingulum, now eroded; however it differs from the other teeth considered above by the equally high, parallel, tubular para- and metaconid; and the former is not inclined forwards. Finally J.515 (right; Fig. 10B) is slightly larger and more stocky; the lingual cingulum is very faint and incomplete under the metaconid; cusp f was smaller. There was no metacristid; the talonid, of which the occlusal border is abraded, is recurved labially while the paraconal sulcus is oriented rather vertically. The roots were unequal at the expense of the posterior one. It is clear that these last two teeth, whatever their shared features, cannot belong to the same taxon.

On J.515, there are two independent wear facets posteriorly, one on the metaconid, one on the protoconid; on this same tooth the anterior face of the protoconid is worn; so is f, a cusp less extended than on the *Kennetheredium* n. gen. specimens. The paraconal sulcus as well as the antero-labial face of the talonid are deeply incised.

Cladotheria indet.

MATERIAL EXAMINED. — BMNH J.490, right lower molar.

A posterior half of a right lower molar (BMNH J.490; Fig. 18A, B) represents the largest of the holotherian lower molars of the collection. The protoconid is very high and was probably narrow; there was a wide lingual cingulum forming a shelf and rising in the middle. The talonid is wide transversely, but very short antero-posteriorly; in fact its ledge is hardly wider than the lingual ledge of the cingulum. A very sharp crest crosses the base of the metaconid, which is broken very low, and ends on the distal talonid rim. There is no labial cingulum. The tooth is not worn.

The proportions of the talonid (linguo-labial width, antero-posterior narrowness) are different from those of any symmetrodont, whether tinodontid or spalacotheriid. It is on the contrary surprisingly close to that of *Henkelotherium* (e.g., GUI M 74/74); however, the wide lingual cingulid is not found in any other dryolestoid or even amphitheriid. This, combined with the very tall protoconid, certainly testifies to a different line of Dryolestida.

?Symmetrodonta indet.

MATERIAL EXAMINED. — BMNH J.438, left? lower molariform; BMNH J.253, ?right tooth.

BMNH J.438 (Fig. 18C-E), a left? lower molariform, most probably represents a milk tooth of a symmetrodont. It is complete but the enamel is poorly preserved and there are no remains of roots. The crown is long and low; the lingual cingulum is slightly convex dorsally but not rising in the middle. The ?paraconid is lower and more labial than the ?metaconid. If the tooth is properly oriented (the symmetry of the protoconid cristae makes this orientation uncertain), there is a particularly high e cusp; but is it in fact a d cusp? (NB: the holotype tooth of *Tinodon micron* Ensom & Sigogneau-Russell, 2000, presented as a left tooth, is in fact probably a right). Labially the crown is broken too high to allow a statement about a cingulum. Wear surfaces are uncertain. This tooth evokes the anterior molars or *Tinodon* Marsh, 1879 but differs by a lower crown and a cingulum not being angled in the middle. This morphology also recalls some of the deciduous symmetrodont teeth published by Cifelli (1999: fig. 6A, B, E).

The ?posterior half of a ?right tooth J.253, though of a similar type to J.438, does not have the appearance of a milk tooth; the preserved root is long and vertical. The metaconid is small as is the talonid cusp. The lingual cingulum is straight and there is no labial cingulum. Wear shows on the whole posterior face, creating even a sulcus between proto- and metaconid.

These two badly preserved specimens, whether deciduous molars or not, are the only suggestion of the presence of symmetrodont-like forms in the fauna.

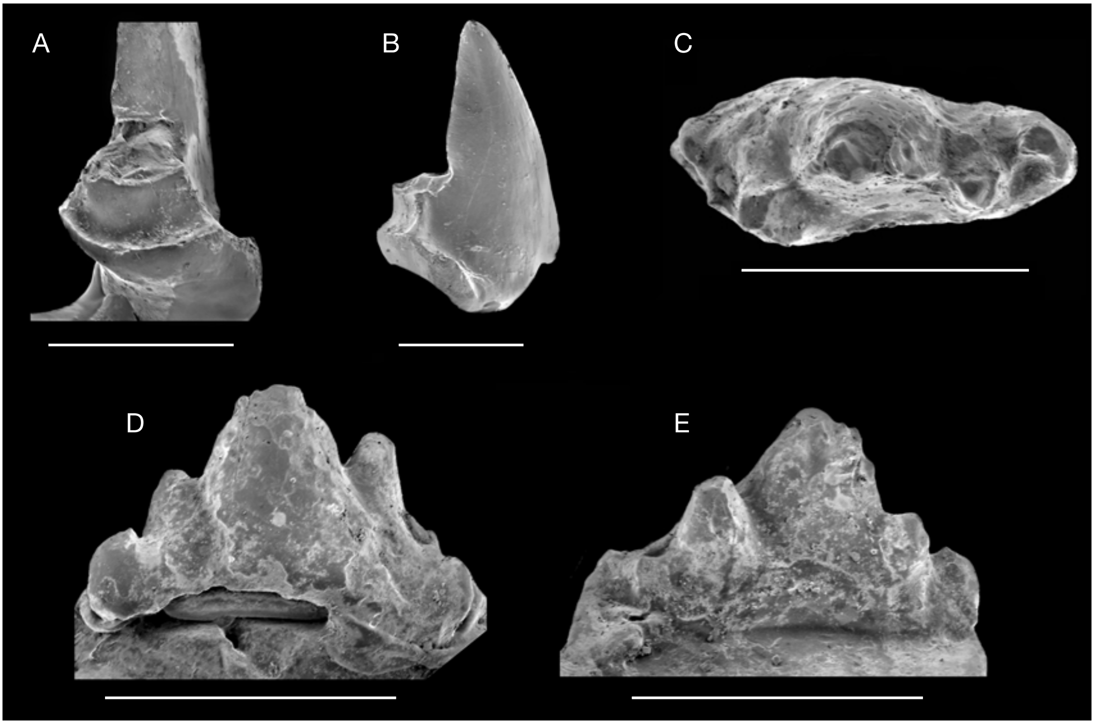

FIG. 18. — SEM photographs of lower molars; **A**, **B**, Cladotheria indet., BMNH J.490, lingual and posterior views; **C**-**E**, ?Symmetrodonta indet., BMNH J.438, oclusal, labial and lingual views. Scale bars: 1 mm.

Trechnotheria indet.

MATERIAL EXAMINED. — BMNH M 51822, J.515, J.653, right lower molars; BMNH M 35004, M 51824, J.429, left lower molars; BMNH J.152, J.295, J.403, J.509, J.510, J.512, J.517, J.519, J.558, J.721, J.786, J.826, right upper molars; BMNH J.21, ?J.95, J.218, J.244, J.698, J.844, left upper molars.

LOWER MOLARS

Two relatively large lower teeth from Watton Cliff (BMNH M 51822, right, incomplete, Fig. 19A-C; M 51824, left, rolled) are characterized by a high trigonid with a tubular metaconid (the paraconid is missing or incomplete). No lingual cingulid or distal metacristid are present, and cusp f is absent or weak. The posterior trigonid face is transverse. The talonid is low situated, ?relatively short (incomplete on both teeth), and wide transversely, occupying the whole width of the tooth. Roots are not preserved, but there is some indication, on M 51824 at least, that the anterior root was more labially disposed than the posterior one.

On M 51822, a wear facet can be seen on the anterior face of the protoconid (paraconid not preserved) and one on the transverse posterior face of the trigonid.

These teeth, with a transverse posterior trigonid face, could be interpreted as representing a dryolestoid, the oldest known so far.

More problems remain, with teeth combining characters and thus transgressing the already fragile taxonomic distinctions. Two more teeth also have a transverse posterior face: J.653 (right) is worn; the trigonid is low; there is no metacristid and the talonid (incomplete) seems to have been of the dryolestoid kind; f cusp is well indicated and roots are subequal. M 35004 (left) is quite

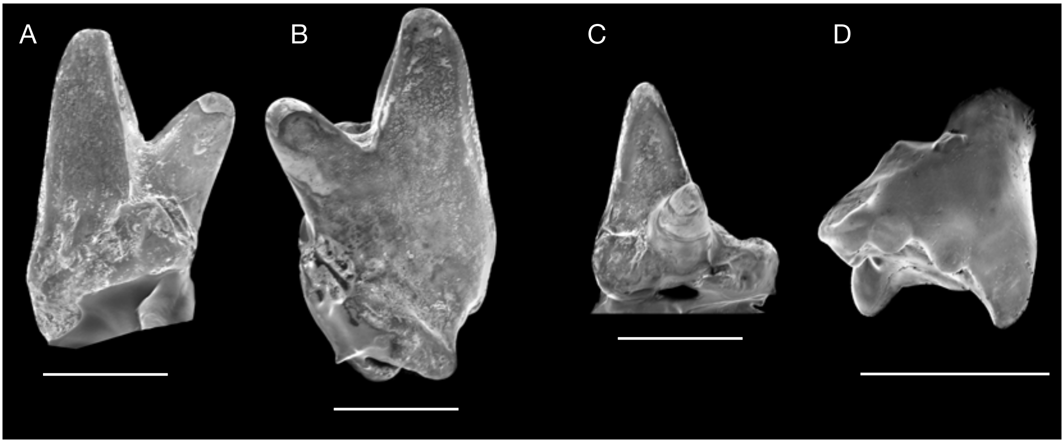

FIG. 19. — SEM photographs; **A**-**C**, lower molar of Trechnotheria indet., BMNH M 51822, anterior, posterior and lingual views; **D**, upper molar of *Palaeoxonodon* sp. (group I), BMNH J.636, posterior view. Scale bars: 1 mm.

similar to J.653 except that the f cusp is very faint.

On J.429, the paraconal sulcus, or rather slit, is deeply incised and vertical but does not affect the metaconid; however, the posterior face is not transverse. All three cusps have been truncated; the trigonid was thick and short, with a possibly low paraconid being underlined by a cingulid; cusp f is strong and the anterior sulcus deep; there is no labial cingulid. The talonid is long and thin and recurves distally; there is no distal metacristid. Roots may have been subequal. J.515 (Fig. 10B) has already been mentioned in two taxonomic units. Finally, half a dozen holotherian tooth fragments are too incomplete to comment upon.

These few teeth lead one to suspect that, besides the dominant amphitheriids, dryolestoids had already individualized in mid-Jurassic times. Prothero (1981) suggested that a large talonid (as well as the postero-ventral deflection of the angular process) seen in *Amphitherium* are to be interpreted as primitive cladothere characters; the Kirtlington holotherian fauna would tend to confirm this view; and also primitive would be a strong antero-buccal cusp f: it is usually present in kuehneotheriids, *Amphitherium* and Zatherians, absent or weak in dryolestoids.

UPPER MOLARS

As in the case for the lower molars, the following upper molars consist of a series of teeth which cannot be included in *Palaeoxonodon*, but their attribution to other taxa cannot be ascertained.

Most of them are very small, worn or badly preserved. The trigon is usually short antero-posteriorly. Some have a faint trigon ridge and a reduced parastyle: BMNH J.21 is only an anterior half with a B' cusp; the stylocone sulcus is present. On J.295, the labial border is abraded, but the parastyle seems again to have been reduced; the posterior cusps are well individualized. On J.519, "c" and the metacone are worn posteriorly in one single facet, but only the crest of the paracone is touched. J.517 (Fig. 15B) has a convex trigon, due to the fact that the cristae have been completely worn off; it clearly shows three roots. Could these teeth represent the upper molars of *Kennetheredium* n. gen.?

On two other teeth, also with a trigon ridge, the parastyle is on the contrary extended at least anteriorly: J.512 is extremely worn; the posterior cusps are hardly distinguishable (two "c" cusps?) and a posterior wear facet, independent from that of the paracone, unites them all. The trigon is short, the parastyle is thin and recurved, the ectoflexus slight. J.721 is very small and eroded; the paracone is very thin but salient; the posterior face is however completely transverse, the parastyle is extended antero-posteriorly but nearly vertical, the ectoflexus weak, the metastylar lobe elongated; the number of roots remains uncertain.

On the following teeth, the trigon is hollow without any ridge. J.218 is the only one to present an extended parastyle, itself prolonged anteriorly by a cingulum. No other cusps are discernible though the posterior face was not transverse; the number of roots is unknown. The remaining four have a reduced parastyle. The latter is not even distinguishable on the very worn J.95, which is wide and extremely narrow and seems to have been supported by one root only; this probably represented a last molar. On J.510, a B' cusp is distinguishable, the metacone is well individualized but it is not clear whether the posterior face (incomplete) was transverse; the parastyle extremely narrow antero-posteriorly is elongated as a crest in the labio-lingual dimension; there may have been only two roots. J.558, complete but without enamel, shows a well developed parastyle and, again, did not have a completely transverse face. Finally, on J.826 the parastyle is not preserved, and the distal face, with well distinct cusps, had probably a small facet A: altogether none seems to have had a perfectly transverse posterior face.

However, the general configuration of these 11 teeth, with a narrow hollow trigon and often vaguely distinct posterior cusps, appears relatively advanced for a Bathonian age. They do not seem to be attributable to an amphitheriid; whether they represent upper molars of *Kennetheredium* n. gen. or a Dryolestida taxon remains uncertain.

Three more small upper molars are worth mentioning. BMNH J.159 is a stubby rolled tooth with rounded cusps. There is no trigon ridge; the metacone is very close to the paracone and nearly as large; anteriorly is a large cusp B', the stylocone is larger (in diameter) than the paracone; the parastyle is wide transversally; there is a lingual cingulum. Facets 3 and A are clearly distinct. No roots are preserved. J.244 has well individualized cusps limiting a very hollow trigon with a high paracone: it shows well individualized metacone, two "c" cusps, metastyle, high stylocone and a two-cusped parastyle; even a B' bump is visible anteriorly. The posterior face of the trigon is not quite transverse; no roots are preserved. These two teeth would seem to have been deciduous premolars. As for J.844, it has all the characteristics of a milk tooth: cusps abraded (paracone, metacone, two "c" cusps, B'), long metastylar lobe, low stylocone, absence of roots.

There finally remains four larger teeth: J.403, J.509, J.698 (left; Fig. 16C), J.786 (right; Fig. 16D) which present a mixture of characters, The trigon is short antero-posteriorly, "c" is present and there is no trigon ridge. On J.698, the metacone is far from the paracone and the parastyle is short transversely; also the parastyle sulcus is vertical and is prolonged on the low stylocone. The ectoflexus is well marked. The posterior face is nearly transverse, with a clear wear facet on the posterior face of the paracone more or less in the same plane as that of the ventral border of the metacone and "c" (most of these features recall *Palaeoxonodon* group I). J.786 is even shorter antero-posteriorly with a particularly strong stylocone; the metacone is here close to the paracone; it is followed by a double "c" cusp; the parastyle extends almost to the half width of the tooth. Again the posterior face is not completely transverse, even if facet A would have been reduced to a minimum. The preparacrista is worn and so is the parastyle sulcus. Most of these features here are those of group II. J.403 looks at first sight very close to J.786 while being slightly smaller, but the parastyle is shorter and narrower. Wear surfaces are not clear, but in any case the stylocone is not touched. The last two teeth have a metastyle salient labio-distally. Finally, J.509 is damaged antero-labially; "c" is double and all posterior cusps are salient. The posterior face is curved. Three roots seem to be the rule.

Some of these teeth could be related to the large lower molars *Palaeoxonodon* sp. BMNH J.702, or "Trechnotheria indet." M 51822 or 51824, or even represent a new amphitheriid species. The uncertainty of these groupings appears however too heavy to risk the creation of new taxa, given the already fragile status of the two *Palaeoxonodon* species.

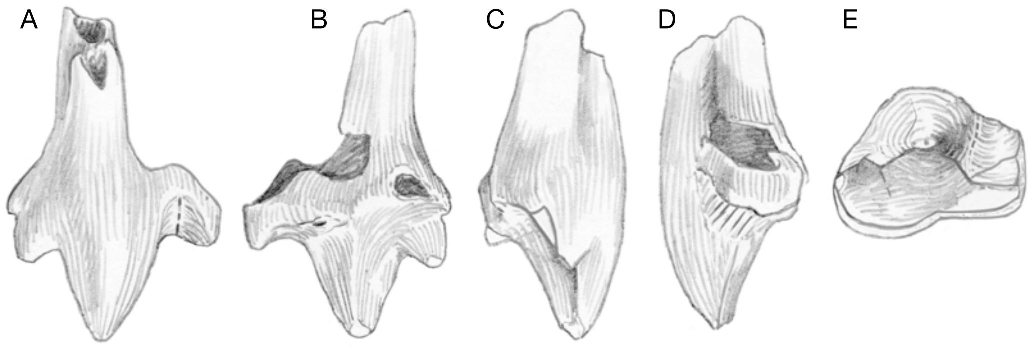

FIG. 20. — ?Peramurid upper molar, BMNH J.752, × 34; **A**, lingual view; **B**, labial view; **C**, posterior view; **D**, anterior view; **E**, occlusal view.

?Peramuridae

MATERIAL EXAMINED. — BMNH J.752, left upper molariform.

One last interesting tooth is the left upper molariform BMNH J.752 (Fig. 20): very small, it has only two roots, the posterior one showing only a sulcus along its length and being dominant lingually. The tooth is very narrow so that there is no trigon basin. The paracone is high, closely followed postero-lingually by a small metacone; there is only a faint indication of a low "c" cusp but the distal labial lobe is not quite complete. A shelf-like labial cingulum leads to a very extensive parastyle. The paracrista crest leading to the tiny stylocone is vertical; from the stylocone a short horizontal crest connects to the parastyle.

The first interpretation is that this tooth would be a milk molar. However, in dryolestids (Martin 1999) DP4 and even more DP3 are longer than a molar; if J.752 is identified as a milk molar of *Palaeoxonodon*, it is too small to be either tooth. Apparently DP2 would be shorter, but none is known in dryolestids: only a fragment is preserved in GUI MAM 34/76; from what is left it can be assumed that the tooth measured slightly more than a half molar; J.752 would then fit in *Paleoxonodon* only as a DP2. The large parastyle extension also fits the deciduous interpretation (though the morphology seems overly complex for a DP2).

But other features do not fit: lingual position of the metacone (no different from that of molars in DP3 and DP4, Martin 1999: fig. 39A), possible presence of a facet 4, reduction of the stylocone (not occuring on DP3 and DP4, Martin 2002: fig. 39A, E-H), vertical preparacrista.

These features are strongly reminiscent of M1 of *Peramus* (in fact J.752 has the morphology and proportions intermediate between the P5 and M1 of this genus). Could it be that the structure of the peramurid upper molars is plesiomorphic (the situation of the metacone and the lingual cingulid have already been suspected of such, Fox [1975], Sigogneau-Russell [1999] but contra Butler & Clemens [2001]), and that the amphitheriid structure is derived from that scheme, which would still show in its DPs? That would also explain the configuration of the talonid similar in both lines.

However, J.752 is smaller than M1 of *Peramus*, has a larger parastyle, and lacks the lingual cuspules. Also the metacone is lower situated relative to the paracone. The Kirtlington tooth appears even closer to SA 37, from the Early Cretaceous of Morocco (*Peramus* sp., Sigogneau-Russell 1999), being only a bit smaller; the metacone is not quite so lingual, and the "c"-metastylar area possibly less developed; unfortunately the parastylar area is not fully preserved on SA 37, which may also represent a milk molar.

In conclusion, if amphitheriids were dominant in this Bathonian fauna, there are some indications that Dryolestida were already individualized, and scant suggestion that "Peramura" had detached from the "stem-lineage of Zatheria". At the same

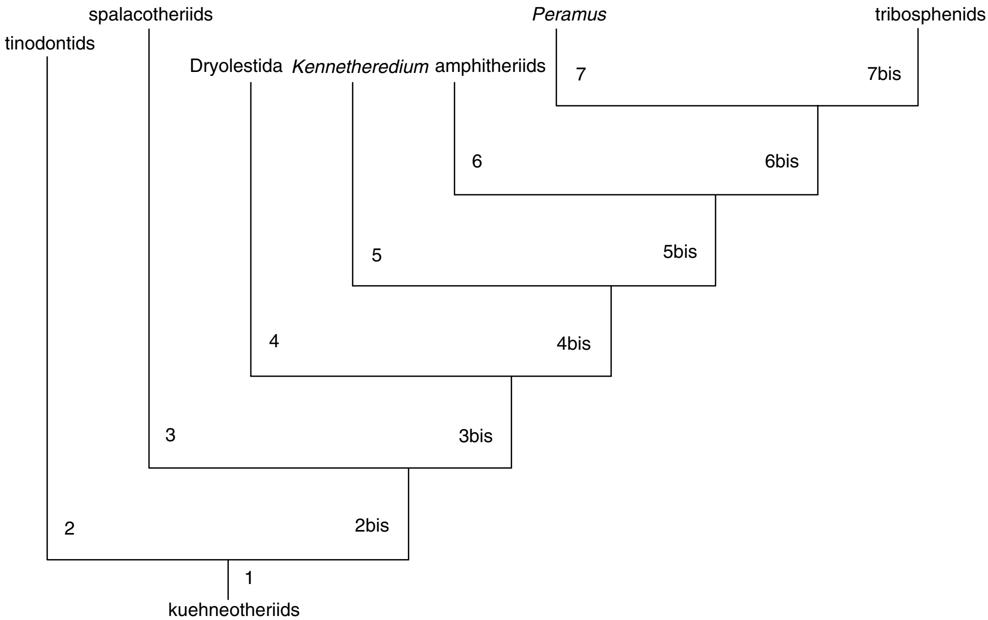

FIG. 21. — Proposed evolution of the molars of the main holotherian taxa (but see p.); **1**, (*Kuehneotherium*) metacone lingual; lingual cingulum; strong stylocone; two roots; facet A present; *narrow trigonid; e, f, present; lingual cingulid; facet A present*; **2**, (tinodontids) lingual cingulum decreases; parastyle increases? stylocone decreases; **2bis**, (Trechnotheria) trigon widens; lingual cingulum decreases; paracone increases; parastyle becomes hooklike; metacone more labial; B' and "c" present; *trigonid angle more acute*; **3**, (spalacotheriids) metacrista cusps tend to disappear; posterior stylar cusp; cusp B' and facet A tend to disappear; *f becomes cingulid; complete cingulid; talonid cusp reduces*; **3bis**, (Cladotheria) trigon ridge; *talonid develops; transverse crest ascends base of metaconid and on talonid isolates lingual component*; **4**, (Dryolestida) B' tends to disappear; posterior stylar cusp; facet A disappears; 3 roots; *lingual cingulid disappears; paraconid inclined forwards and lamellar; talonid widens bucco-lingually; e disappears; f becomes anterior*; **4bis**, *talonid elongates with a protruding talonid cusp*; **5**, (*Kennetheredium* n. gen.) *trigonid taller; e disappears*; **5bis**, (Zatheria) *distal metacristid; lingual cingulid decreases*; **6**, (amphitheriids) posterior stylar cusp; 3 roots; *e reduces; f becomes anterior cingulid*; **6bis**, trigon ridge disappears; B' disappears; lingual cingulum develops; facet 4; *lingual cingulid disappears; hypoconid develops; number of molars decreases*; **7**, (peramurids) stylocone decreases?; **7bis**, (tribosphenids) protocone develops; three roots; facets 5 and 6.

time there also were evolutionary tentatives among holotherians (J.490; *Kennetheredium* n. gen.) which are not so far known in later faunas. Bushiness is a common step in the early evolutionary history of clades, after which natural sorting permits the flourishing of only a limited number of branches. Finally the quasi-absence of symmetrodonts suggests that these forms were direct ecological competitors of amphitheriids, or even of dryolestoids.

CONCLUSION

To help clarify the situation, I present Fig. 21 (not based on a computerized cladistic analysis), but I stress its very limited value as a representation of phylogenetic relationships, given the number of absent data, and of course the frequency of homoplasy.

Are these amphitheriids representatives of a stem lineage of Zatheria or of dryolestoids? Either one admits that a long, "basined" talonid evolved several times: unlikely given the very close configuration in peramurids and some amphitheriids: "the talonids of the molar teeth" (of *Peramus* and *Amphitherium*) "show similarities [...] which contrast more definitely with the remaining Pantotheres" (Mills 1964: 127); or one admits a strong parallelism between amphitheriids and dryolestids (and spalacotheriids) in the upper dentition; a position I tend to subscribe to.

Concerning this talonid, it is interesting to remark that we know all the morphological steps from a single crest and cusp (*Arguimus*), to a very faintly indicated lingual slope (*Nanolestes*), to a flat surface (*Amphitherium*), to an incipient basin (*Palaeoxonodon*), to the two-cusped basined talonid of *Peramus*.

Among the problems encountered in establishing firmer phylogenies of the holotherians, I shall cite the situation of the coronoid angle of the lower jaw: it is very open in *Kuehneotherium* and *Minimus* (unpublished material), still sloping in *Peramus*, but upright in amphitheriids and strongly so in *Tinodon*, the ?peramuran *Tendagurutherium* Heinrich, 1998, in spalacotheriids and Dryolestida. Such a variation is difficult to include in relationships based on the lower dentition. As an additional remark, this angle remains very open in *Zhangeotherium* Hu, Wang, Luo & Li, 1997 (Hu *et al.* 1997); this character, together with others of its lower jaw or dentition (e.g., low number of premolars) contribute to render questionable the spalacotheriid nature of this later taxon (the genus has not been included in Fig. 21 by lack of knowledge on several aspects of the dentition; in particular cusp f seems to be detectable on fig. 2b of Hu *et al.* [1997]).

Another difficulty arises with the position of the dentary condyle in the various lines, a character which cannot be incorporated before reexamination of all specimens concerned.

Similarly the evolution of the dental formula poses a problem: Cifelli & Madsen (1999) states the presence of five molars for *Kuehneotherium*, four for *Tinodon*, six for *Zhangeotherium*, seven for spalacotheriids; nine are known in dryolestids (paurodontids undergo a reduction) and Butler & Clemens (2001) count five to seven molars for *Amphitherium*; *Nanolestes* has five while *Peramus* has only three. The morphological variability found here in the hypodigm of *Palaeoxonodon* suggests the presence of four to five molars.

Moreover, on the upper molars, it remains to be determined whether the limited lingual cingulum of *Peramus* and the lingual situation of the metacone are primitive or derived before using these characters in phylogeny. It should also be proved that the "c" cusp of "peramurans" is homologous to that of the dryolestids and amphitheriids; its configuration seems to be different in the two ensembles. Finally, the question of the homologies of the metacone and "c" cusp remains open.

Still concerning "peramurans", should we "choose" *Peramus* as a representative or its nearly contemporaneous *Afriquiamus* Sigogneau-Russell, 1999? Do the similarities in the teeth of the two taxa at the level of the paracone-metacone express relationships or homoplasy? Is the well developed anterior cusp of the type molar of "*Eurylambda*" homologous to B' or to a stylocone? Does the similarity between the upper molar attributed to *Tinodon micron* (Ensom & Sigogneau-Russell 2000) with the P5 of *Peramus* mean an erroneous attribution (for which the junior author of the paper is sole responsible) or a real relationships between the two forms? (the "c" cusp of *Tinodon micron* is however of the non-peramuran type as on the type molar of "*Eurylambda*"). Again the homology of cusps is at stake.

All these questions should be answered in order to determine polarity, hence phylogenetic relationships. All recent discoveries of Mesozoic mammalian remains testify that we still know very little of their diversity; the latter should be explored before new cladograms are proposed. As a confirmation of this assessment, the present study did not yield the results expected from a Middle Jurassic mammalian fauna: contrary to what was earlier supposed, ancestral peramurids are not present, while the supposed ancestral peramurid *Palaeoxonodon* represents in fact a branch of non tribosphenid holotherians. Nor do we find ascertained primitive dryolestoids or primitive spalacotheriids (unless one admits that the talonid increased and reduced again in that family, which seems unlikely). This holotherian fauna from the Bathonian is thus quite original and not easily linked either to that of the early Jurassic or to that of the late Jurassic of the same area. Such a conclusion was already attained after study of the Kirtlington Allotheria

(Kermack *et al.* 1998). It will be extremely interesting to learn if more mammalian groups from this locality confirm it. If this be the case, paleogeographic and paleoenvironmental data may have to be invoked to explain this discrepancy.

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ANNEXE

TABLE 1. — Measurements (in mm) of the lower holotherian molars considered in this paper. *, figures kindly provided by P. M. Butler. BMNH J.117, J.197 are too incomplete, and J.213 too crushed, for measurements. Abbreviations: **BMNH**, The Natural History Museum, London.

Specimen BMNH	Width	Length	Length	Length	Length	Height	Height	Height	Angle
		Trigonid	Talonid (T1)	Total	Metac.-Tal. cusp (T2)	Metacon.	Protocon.	Total	
J.59	0.49	0.67	0.27	0.94	0.36	0.19?	0.35?	0.91?	-
J.196	0.51	0.70	0.26	0.96	0.38	0.25?	0.33?	0.77	83
J.200	0.48	0.79	0.29	1.08	0.50	0.32	-	-	70
J.236	0.55	0.70	0.28	0.98	0.40	0.31	0.36	1.00	82
J.242	0.66	0.83	0.32	1.15	0.51	0.41	0.27	1.03	66
J.619	0.55	0.67	0.29	0.96	0.46	0.28?	0.30?	0.76	63?
J.639	0.51	0.64	0.24	0.88	0.35	0.32	-	-	56?
J.849	0.49	0.65	0.23	0.88	0.29	0.16	0.31	0.69?	75
M 36507*	0.54	0.63	0.27	0.90	-	-	-	0.80	60?
M 36508	0.49	0.62+	0.26	0.88+	0.40	0.29	0.27	0.82?	-
J.220	0.70	0.80	0.25	1.05	0.43	0.27	-	-	80?
J.350	0.48	0.51	0.15	0.66	0.19	0.15?	0.25?	0.62	78
J.388	0.52	0.65+	-	-	-	0.35+	0.30	0.90	67
J.530	0.56	0.54	0.30	0.84	0.37	0.34?	0.40?	0.97?	45
J.569	0.68	0.69	-	-	-	-	0.40	1.02?	58
J.593	0.75	0.84	0.30+	1.14+	-	-	-	1.04?	50?
J.618	0.48	0.57	0.20	0.77	0.24	0.31	0.23	0.76	52
J.626	0.58	0.67	0.18	0.85	0.40	-	-	-	66
J.628	0.54	0.65+	-	-	-	-	0.35?	-	67
J.657	0.51	0.60	0.25	0.85	0.35	0.40	0.15	0.80	60
J.701	0.56	0.70	0.25+	0.95	0.33	0.47	0.32??	1.09?	61
J.715	0.56	0.62?	-	-	-	-	-	-	65
J.727	0.54	0.66+	-	-	-	-	0.31	0.74?	-
J.745	0.46	0.64	0.20	0.84	0.28	0.35	0.25	0.81?	65
J.825	0.65	0.64	-	-	-	-	-	1.03?	-
J.827	0.83	0.83+	-	-	-	-	-	1.18?	-
J.837	0.57	0.66	-	-	-	0.32	0.36	0.86?	-
M 44303	0.85	0.95	0.30	1.25	0.60	0.30	-	-	-
M 51823	0.39	0.57	0.17	0.74	0.27	0.25	0.31	0.67	-
J.702	0.78	0.97	0.36	1.33	0.65	0.55	0.25	1.13	76
J.802	0.74	0.74	0.26	1.00	0.41	-	-	-	57?
J.53	0.50	0.72+	-	-	-	0.31?	0.27?	0.74	-
J.290	-	0.63	0.26	0.89	0.37	-	-	-	-
M 34985	0.75	0.85	-	-		-	-	-	-
J.289	0.68	0.66	-	-		-	0.43	1.05	66
J.379	0.57	0.62+	-	-		0.50?	0.41	0.96	-
J.430	0.61	0.61	0.20	0.81		-	-	-	56
J.514	0.55	0.55	-	-		0.46?	0.46	0.94	52
J.746	0.68	0.60	0.22	0.84		0.60	0.26	1.00	57
J.824	0.55	0.65	-	-		0.35?	0.25	0.80?	-
J.214	0.65	0.68+	-	-		-	0.22	1.03	48
J.428	0.64	0.70	0.27	0.97		0.43?	0.60?	1.23?	75
J.515	0.86	0.94	0.36	1.30		0.68	0.37	1.22	55
J.532	0.60	0.63	0.23	0.86		0.48	-	-	60
J.801	0.53	0.60	0.24	0.84		0.45	0.26	0.85	54

Specimen BMNH	Width	Length	Length	Length	Length	Height	Height	Height	Angle
		Trigonid	Talonid (T1)	Total	Metac.-Tal. cusp (T2)	Metacon.	Protocon.	Total	
J.490	-	-	-	-		-	-	1.92	-
J.438	0.56	0.66	0.24	0.90				0.78	-
M 51822	0.90	0.80	0.30	1.10+?		0.72	0.38?	1.43	-
M 51824	0.91	0.98	0.22	1.18		0.28	0.28	0.71	-
J.653	0.65	0.85	-	-		0.45?	-	-	66
M 35004	0.53	0.75	-	-		0.32?	-	-	-
J.429	0.60+	0.59	0.21	0.80		-	-	-	55
Peramus									
M 47339	0.42	0.70	0.20	0.90	0.26	0.31?	0.30?	0.84	91
M1	0.44	0.64	0.20	0.84	0.21	0.26	-	-	60
M3									
Peramus									
M 48404	0.55	0.80	0.23	1.03	0.37	0.18	0.46	1.00	75
M1	0.62	0.87	0.27	1.14	0.48	0.23	0.46?	1.02?	69
M2	0.58	0.73	0.33	1.16	0.43	0.18	0.31	0.76?	59
M3									
Amphitherium									
M1	0.64	0.73	0.30	1.03	0.55	0.29	0.37+	0.95+	60 to
M2	0.62	0.80	0.24	1.04	0.49	0.35	0.40	1.05	68*
M3	0.68	0.86	0.24	1.10	0.51	0.37	0.34	0.95?	
M 36516	0.75	0.80+	-	-	-	-	0.32	-	

TABLE 2. — Distribution of the morphologic characters considered above on the lower molars (special mention should be made of the subjectivity in the appreciation of such characters). BMNH J.117 and J.197 are too incomplete; J.213 is too crushed. Abbreviations: **BMNH**, The Natural History Museum, London; **f**, cusp f; **mcd**, metaconid; **pad**, paraconid.

Specimen BMNH	Protoconid	Paraconid	pad/mcd	Talonid basin	mcd labially hollowed	f	Roots
J.59	straight	sloping	>	occlusal	yes	?	?
J.196	sloping	sloping	>?	occlusal	yes	?	?
J.200	straight	sloping?	?	lingual	no	weak	equal
J.236	sloping	sloping	>	lingual	yes	moderate	equal
J.242	sloping	straight	equal	occlusal	slightly	strong	equal
J.619	straight	straight	?	?	?	strong	unequal?
J.639	?	straight	>	ling/occl	yes	moderate	equal
J.849	straight	sloping	equal	lingual	yes	?	?
M 36508	sloping	?	?	occlusal	no	moderate	equal
J.220	?	straight	=	ling/occl	yes	strong	subequal
J.350	straight	sloping	<?	lingual	no	strong	equal
J.388	straight	?	?	?	no	strong	?
J.530	sloping	straight	<	occlusal	no	strong	equal
J.569	sloping	sloping	<	?	no	strong	?
J.593	sloping	?	<?	ling/occl	no	moderate	unequal?
J.618	straight	sloping	<	occlusal	no	strong	equal
J.626	straight	?	?	?	?	weak	?

Specimen BMNH	Protoconid	Paraconid	pad/mcd	Talonid basin	mcd labially hollowed	f	Roots
J.628	straight	sloping	<	?	?	moderate	?
J.657	straight	sloping	<?	occlusal	no	moderate	equal
J.701	straight	straight	<	occlusal	no	moderate	?
J.715	sloping	straight	=	?	?	weak	?
J.727	sloping	?	?	?	yes	weak	?
J.745	straight	?	<	occlusal	yes	moderate	equal
J.825	straight	straight?	<?	?	?	strong	?
J.827	straight	sloping	<	?	?	moderate?	?
J.837	sloping	straight	<	occlusal	no	moderate	?
M 44303	?	sloping	<	occlusal	no	strong	?
M 51823	sloping	straight	>	lingual	yes	very weak	?
J.702	sloping	straight	<	occlusal	no	strong	equal
J.802	?	?	<	lingual	no	strong	?
J.53	straight	?	?	?	no	weak	?
J.290	?	?	<	occlusal	no	?	equal?
M 36822 m1	straight	straight	equal	occlusal	no	very weak	equal
m2	straight	straight	equal	occlusal	no	weak	equal
m3	straight	sloping	<	occlusal	no	moderate	unequal
m4	straight	sloping	<	ling/occl	no	moderate	unequal
m5	straight	sloping	<	ling/occl	no	moderate	unequal
M 36516	straight	sloping	equal	?	no	weak	unequal?

TABLE 3. — Measurements (in mm) of the upper holotherian molars. BMNH J.32 and J.458 are too incomplete for measurements. Abbreviation: **BMNH**, The Natural History Museum, London. *, figures provided from Freeman 1979; **, without parastyle.

Specimen BMNH	Labio-lingual	Antero-posterior (incl. parastyle)	Parastyle
J.25	0.91	0.65**	-
J.44	0.82	0.82	0.12
J.137	0.98	1.06	0.28
J.146	0.96?	-	-
J.392	0.87	0.98	0.16
J.436	0.86	0.92?	0.19
J.524	0.70	0.70	0.09
J.636	1.10	1.09	0.22
J.669	0.85	0.90	0.17
J.749	0.77	0.88	0.16
J.754	0.90	0.82	0.11
J.792	0.78	0.91	0.15
M 34994	1.01	1.03	0.20
M 36504	0.99*	0.84+*	?
M 36512	0.94	0.98	0.20
M 36526	0.98	1.05	0.14
J.99	0.83	1.10	0.23
J.238	0.67	0.85	0.16
J.241	0.80+	0.82	0.18
J.294	0.70+	0.84	0.21
J.506	0.74+	0.78	0.15
J.508	1.04	0.98	0.20
J.512bis	0.65?	0.64**	-

Specimen BMNH	Labio-lingual	Antero-posterior (incl. parastyle)	Parastyle
J.627	1.08	1.14	0.28
J.742	1.12	1.15	0.26
J.743	1.05	1.20	0.24
J.788	0.98	1.15	0.26
J.817	0.83	0.90	0.17
M 36532	1.08	1.07	0.22
M 36530	0.72+	0.74**	-
J.21	0.95	-	0.15
J.95	0.56	0.95	-
J.295	0.80	0.73	0.10
J.510	0.76+	-	0.05
J.512	0.75	0.78	0.20
J.517	0.78	0.71	0.10
J.519	0.66	0.60	-
J.558	0.84	0.75	0.12
J.721	0.52	0.59	0.12
J.826	0.85+?	0.66**	-
J.231	1.28	1.28	0.20
J.403	1.00	0.86	0.12+
J.509	0.81?	0.60**	-
J.698	1.37	1.22	0.22
J.786	1.05	0.96	0.25
J.152	0.76	0.82	0.14
J.218	0.71	0.81	0.20
J.244	0.69	0.98	0.30
J.670	0.95	0.96	0.20
J.752	0.57	0.80	0.19
J.844	0.46	0.64	0.15

TABLE 4. — Distribution of the morphologic characters considered above on the upper molars. BMNH J.44 is too eroded. Abbreviations: **BMNH**, The Natural History Museum, London; **B'**, cusp B_1; **ecf**, ectoflexus; **Post. cusps**, postcrista cusps; **Post. st**, posterior stylar cusp; **st**, stylocone.

Specimen BMNH	Ridge	ecf	st	Postcrista	B'	Roots	Post. st	Post. cusps
J.25	weak	+	shifted	convex	0	?	0	2
J.137	weak?	+	terminal	convex	?	3	0	2?
J.146	moderate	?	shifted	convex	0	?	?	?
J.392	moderate	+	terminal	convex	0	3	0	4
J.436	weak	0	terminal	straight	0	3	+	3
J.524	moderate	0	shifted	straight	0	3	0	3
J.636	strong	+	shifted	straight	+	3	+	3
J.669	moderate	+	terminal	convex	+	3	+	4
J.749	weak	+	terminal	straight	?+	3	0	4
J.754	weak	0	shifted	convex	0	?	+	2
J.792	moderate	0	terminal	straight	+	3	0	2
M 34994	moderate	+	shifted	convex	0	?	0	2
M 36504	moderate	+	shifted	?	0	?	?	?
M 36512	moderate	+	shifted	convex	+	?	0	2
M 36526	strong	+	shifted	straight	+	?	0	3
J.231	weak	0	terminal	convex	0	3	0	2
J.32	moderate	0	terminal	convex	0	?	0	2
J.99	moderate	+	shifted	straight	0	3	+	4
J.238	moderate	0	terminal	convex	0	?	0	2

Specimen BMNH	Ridge	ecf	st	Postcrista	B'	Roots	Post. st	Post. cusps
J.241	weak	+	shifted	convex	0	3?	0	2
J.294	weak	+	terminal	convex	+	?	0	?
J.458	weak	?	terminal	?	+	?	?	?
J.506	?	0	terminal	convex	?	2	0	3
J.508	moderate	+	shifted	straight	+?	3	+	4
J.512bis	moderate	+	?	convex	?	?	0	3
J.627	moderate	+	shifted	straight	+	3	0	2
J.742	moderate	0	shifted	straight	0	3	+	3
J.743	moderate	0	shifted	straight	+	?	+	3
J.788	weak	0	shifted	straight	0	3	+	3
J.817	moderate	+	terminal	convex	+	?	+	3
M 36532	moderate	+	shifted	straight	+	?	+	3?
M 36530	moderate	+	?	convex	0	?	?	?