Docodonts from the British Mesozoic

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This paper deals with new docodont teeth from the upper Bathonian of Forest Marble, collected by Prof. K.A. Kermack and his team, and from the basal Cretaceous of the Purbeck Limestone Group, collected by P. Ensom. Study of this material led to the recognition of three new taxa: *Borealestes mussetti* sp. nov. and *Krusatodon kirtlingtonensis* gen. et sp. nov. from Forest Marble, *Peraiocynodon major* sp. nov. from Purbeck; this makes the Bathonian locality the richest (four species) docodont locality so far known. The possible synonymy of *Cyrtlatherium–Simpsonodon* (Forest Marble) and of *Peraiocynodon–Docodon* (Purbeck-Morrison) suggested by several authors is discussed. In conclusion, phyletic relationships between the known docodont genera are proposed, based on lower molars.

Key words: Mammalia, Docodonta, Bathonian, Berriasian, Forest Marble, Purbeck, Great Britain.

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Introduction

Docodonts are, dentally speaking (as well as cranially, Lillegraven and Krusat 1991), a relatively well known group of Mesozoic mammals (*sensu* Luo et al. 2002), though their dental cusp homologies as well as their relationships to other mammals are still disputed (Butler 1997; Sigogneau-Russell and Godefroit 1997; McKenna and Bell 1997; Kielan-Jaworowska et al. in press). Their molar crowns are characterized by a transverse widening and presence of two longitudinal rows of cusps linked by transverse crests; various complications can be added according to the taxon.

Two Mesozoic levels from Great Britain have yielded docodonts: the Bathonian and the Berriasian. Three genera have been described from the first level (*Borealestes* Waldman and Savage, 1972; *Cyrtlatherium* Freeman, 1979 and *Simpsonodon* Kermack, Lee, Lees and Mussett, 1987), only one from the second (*Peraiocynodon* Simpson, 1928). Two of these taxa have been subsequently thought to represent in fact juveniles: *Cyrtlatherium*, of *Simpsonodon* (Sigogneau-Russell 2001), *Peraiocynodon*, of *Docodon* Marsh, 1881 (Butler 1939 and subsequent authors). New material (isolated teeth) from both levels shows that the situation is in fact more complex. This note is limited to presenting these new data and to discussing the synonymy problem; though the author is well aware of the evolutionary importance of this particular group of mammals, development of such a point would deserve a publication of itself.

Institutional abbreviations.—BMNH M or J., mammals in the Natural History Museum, London, U.K.; BRSUG, Dept of Earth Sciences, Bristol University, U.K.; DORCM GS, Geological Survey, Dorset County Museum of Dorset, U.K.; USNM, United States National Museum of Natural History, Washington D.C., U.S.A. VJ, GUI, specimens in the Institut für Paläontologie der Freien Universität Berlin, Germany.

Nomenclature.—I use here the full name of cusps as in Kielan-Jaworowska et al. in press, based on their respective situation on the tooth (Fig. 1). In order to avoid confusion between lower and upper teeth, names are capitalized for the upper teeth. Whatever the system of nomenclature chosen, I would like to mention that the use of cusp "f" (Butler 1997; Martin and Averianov 2001) at the posterior end of the lower molar is confusing, as this cusp commonly designates the mesio-labial cuspule of the lower molars in "therian" mammals. Again on lower molars, the lingual ridge differs from the lingual cingulum in that it links the two main lingual cusps, while the cingulum is entirely lingual to at least one lingual cusp. Finally, docodont dentition (especially lower molars) is characterized by some kind of "ornamentation" of the enamel; variability of this feature among genera lead me to use various terms, such as furrows, ridges, wrinkling, folding, according to the taxon considered.

Measurements (Tables 1, 2, 3).—All measurements, expressed in mm, were taken by the author with a Wild apparatus MMS 225/235.

Systematic palaeontology

Order Docodonta Kretzoi, 1946

Family Docodontidae (Marsh 1887), Simpson, 1929

Genus *Borealestes* Waldman and Savage, 1972

Type species: *Borealestes serendipitus* Waldman and Savage, 1972.

Revised diagnosis.—Lower molars closest to *Haldanodon* with a high main cusp, and a mesio-lingual cusp notably lower than the disto-lingual. Differs from *Haldanodon* by a slightly better development of the lingual cusps, and by the structure of the lower premolars. A lingual cingulum may be present (absent in *Haldanodon*).

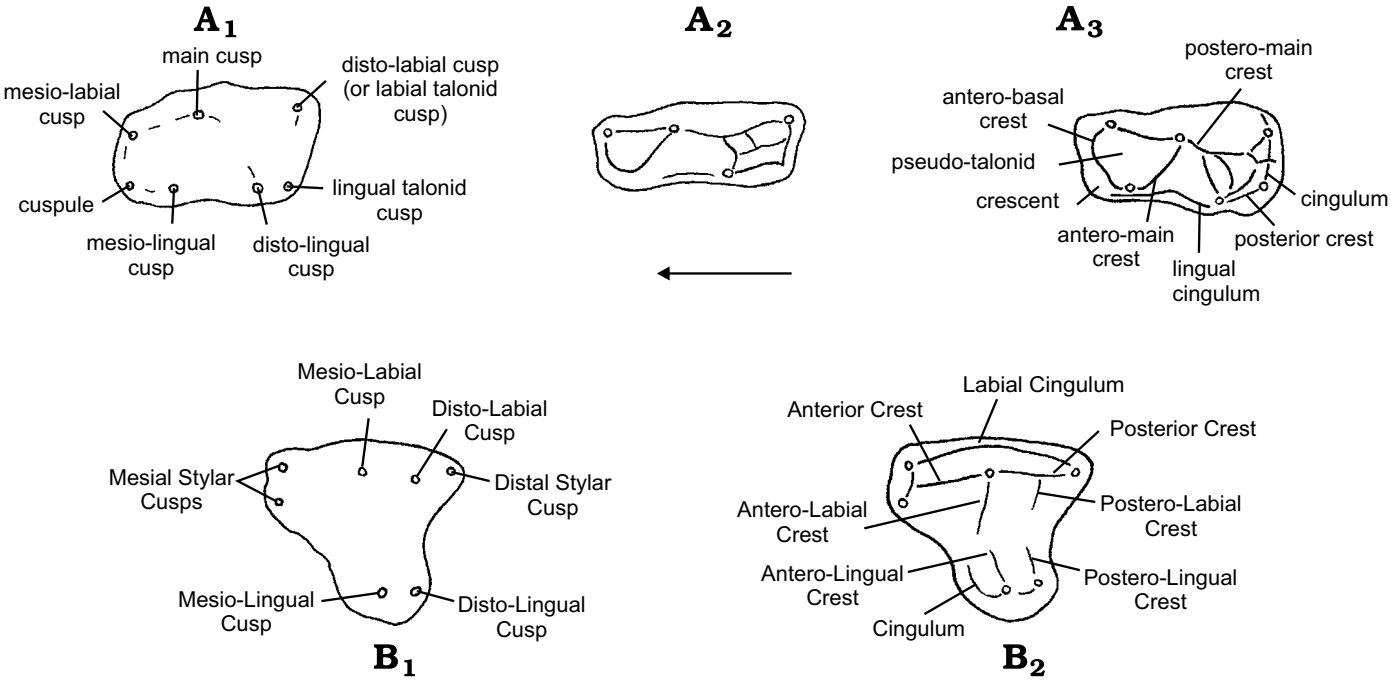

Fig. 1. **A**. Nomenclature of cusps (A_1) and crests (A3) of docodont lower molars; lower molar of *Cyrtlatherium* (A_2). **B**. Nomenclature of cusps (B_1) and crests (B_2) of docodont upper molars. Anterior at left.

Borealestes serendipitus Waldman and Savage, 1972

Fig. 2A, B.

Holotype: BRSUG 20570, left lower jaw with two premolars and four molars.

New molariforms.—BMNH J.58 (right posterior fragment), J.521 (left), J.610 (left), J.791 (left), J.841 (right posterior fragment), M 44301 (left, from Watton Cliff). ?J.39 (right, milk?), ?J.116, (right, milk?), ?J.549, (right posterior fragment), ?J.728 (right anterior fragment), J.869 (right, milk? but main cusp not oblique).

Distribution.—Locality UB 7111, Isle of Skye, Scotland, middle Bathonian; Clay Band, Kirtlington mammal bed in Forest Marble; upper Bathonian.

Revised diagnosis.—Lower molars with antero-basal crest well indicated and vertically oriented. No antero-main crest, hence lingual face of main cusp completely oblique on the axis of the tooth. "Ornamentation" of the enamel limited to a posterior sulcus. Lingual cingulid may be present posteriorly.

Borealestes mussetti sp. nov.

Fig. 2C, D.

Holotype: MNHN J.495, right lower molar.

Derivation of the name: *mussetti*, to acknowledge the major participation of Dr. Frances Mussett in the accumulation of the Kirtlington fauna.

Molariforms.—BMNH J.1 (right posterior fragment), J.239 (right), J.319 (right), J.389 (right posterior fragment), J.401 (right posterior fragment), J.835 (right posterior fragment), J.836 (right), ?J.66 (left posterior fragment), ?J.224, (left anterior fragment), ?J.394 (left posterior fragment), ?J.809 (left anterior fragment).

Distribution.—Clay band, Kirtlington mammal bed in Forest Marble; upper Bathonian.

Diagnosis.—Lower molars differ from those of *B. serendipitus* by being slightly larger; antero-basal crest very weak and horizontally oriented, or even absent. Mesio-lingual cusp slightly more developed. Presence of antero-main crest; hence lingual face of main cusp with two parts, one being parallel to long axis of the tooth. Presence of anterior lingual cingulid. Posterior groove deeper.

Genus *Krusatodon* nov.

Type species: *Krusatodon kirtlingtonensis* sp. nov.

Derivation of name: *Krusatodon*, to honour of the late Dr. George Krusat, whose works have been fundamental for the recent understanding of docodonts.

Diagnosis.—As for the species.

Krusatodon kirtlingtonensis sp. nov.

Fig. 3A, B.

Holotype: BMNH J.526, a right lower molar.

Derivation of the name: *kirtlingtonensis,* provenance of the described material.

Molariforms.—BMNH J.784 (left), J.804 (right), ?J.333 (left); ?J.456 (left, last pm or milk), ?J.778 (left), ?J.796 (left, milk).

Distribution.—Clay Band, Kirtlington mammal bed in Forest Marble; upper Bathonian.

Table 1. Measurements (in mm) of the best preserved of the docodont lower molars from Forest Marble.

	length	width
Peraiocynodon major		
BMNH J.679	2.70	1.30
BMNH J.693	2.15	1.0
Simpsonodon oxfordensis		
BMNH J.688	1.55	0.80
Krusatodon kirtlingtonensis		
BMNH J.526	2.30	1.30
BMNH J.778	1.24	0.81
BMNH J.784	1.68	1.08
BMNH J.804	1.70	–
Borealestes mussetti		
BMNH J.239	1.38	0.64
BMNH J.319	1.41	0.61
BMNH J.495	1.65	0.66
BMNH J.796	1.26+	0.66
BMNH J.836	1.68	0.87
Borealestes serendipitus		
BMNH J.39	0.91	0.43
BMNH J.116	1.35	0.73
BMNH J.521	1.06	0.55
BMNH J.610	1.21	0.63
BMNH J.791	1.30	0.66
BMNH J.869	1.03	0.44
BMNH M44301	1.70	1.20
Docodon victor AMNH 3002 m4	1.88	1.25
Haldanodon exspectatus VJ 1001-155 m4	1.61	1.08
Peraiocynodon inexpectatus type "m1"	1.60	0.80
type "d3"	1.30	0.54

Diagnosis.—Lower molars differ from those of all other docodont genera (?except *Tegotherium* Tatarinov 1974) by the depth of the lingual and distal furrows of the main cusp, and by the posterior crest of the talonid, which bears three cuspules. Mesio-lingual cusp well developed. Moreover, differs from *Simpsonodon*, which also has a high development of lingual cusps, by a relatively higher main cusp, an even wider and deeper pseudo-talonid, and the lack of a lingual cingulum. Differs from *Borealestes* by the development of the mesio-lingual cusp, the pseudo-talonid and the limited extension of the anterior crescent, somewhat of the same extent as in *Docodon*. Differs from *Docodon* by the pseudo-talonid, the development of the mesio-lingual cusp, the lack of antero-posterior compression of the various cusps and the absence of "the complicated pattern of furrows and ridges" (Simpson 1929: 91). Possibly synonymous with *Tegotherium* (see discussion below).

Genus *Peraiocynodon* Simpson, 1928

Type species: *P. inexpectatus* Simpson, 1928

Revised diagnosis.—Differs from all other genera by the relative narrowness of the lower molars and the development and detachment of the disto-labial cusp (labial talonid cusp). Shares with *Docodon* and *Simpsonodon* the presence of furrows and ridges on the enamel. Shares with *Docodon* the absent or weak mesio-lingual cusp, the partial fusion of the lingual talonid cusp and of the disto-lingual cusp; but differs by the less developed lingual ridge, the more posterior situation of the disto-lingual cusp and the more oblique posterior slope. Differs from *Simpsonodon* mainly by the absence of a pseudo-talonid and of a mesio-lingual cusp. Differs from *Borealestes* and *Haldanodon* by the ornamentation of the enamel on the posterior face of the main cusp, by the even more reduced mesio-lingual cusp and the high development of the labial talonid cusp.

Peraiocynodon inexpectatus Simpson, 1928

Fig. 3C.

Holotype: BMNH M 48348, a partial left lower jaw with two premolars and two molars, from the Purbeck Limestone Group; Berriasian.

New molariforms.—BMNH M 51817 (left), DORCM GS 619 (left), 620 (right), 968 (left posterior half), ?800 (left), ?916 (left).

Revised diagnosis.—Lower molars characterized by small size, a marked anterior indentation, the presence of an antero-basal crest and of a lingual ridge.

Peraiocynodon major sp. nov.

Fig. 3D.

Holotype: BMNH J.693, a left lower molariform

Derivation of the name: *major*, L., larger.

Material.—J.679, a right lower molariform.

Distribution.—Clay Band, Kirtlington mammal bed in Forest Marble; upper Bathonian.

Diagnosis.—Differs from *P. inexpectatus* by the much larger size, the anterior narrowness, the absence of an antero-basal crest and the total absence of a lingual ridge. Mesio-lingual cuspule and mesio-labial cusp better individualized; posterior concavity more accentuated.

New material from the Kirtlington mammal bed

Lower molars

The genus *Cyrtlatherium* Freeman, 1979 was based on a lower molariform tooth (Fig. $1A_2$) attributed to Symmetrodonta by its author, but later shown to represent a docodont (Sigogneau-Russell 2001). In the unpublished docodont material (about 40 teeth) from Kirtlington, which appears unexpectedly varied, no tooth similar to that of *Cyrtlatherium* could be found. The posterior half tooth BMNH M 36538, considered by Freeman (1979) as belonging to this taxon,

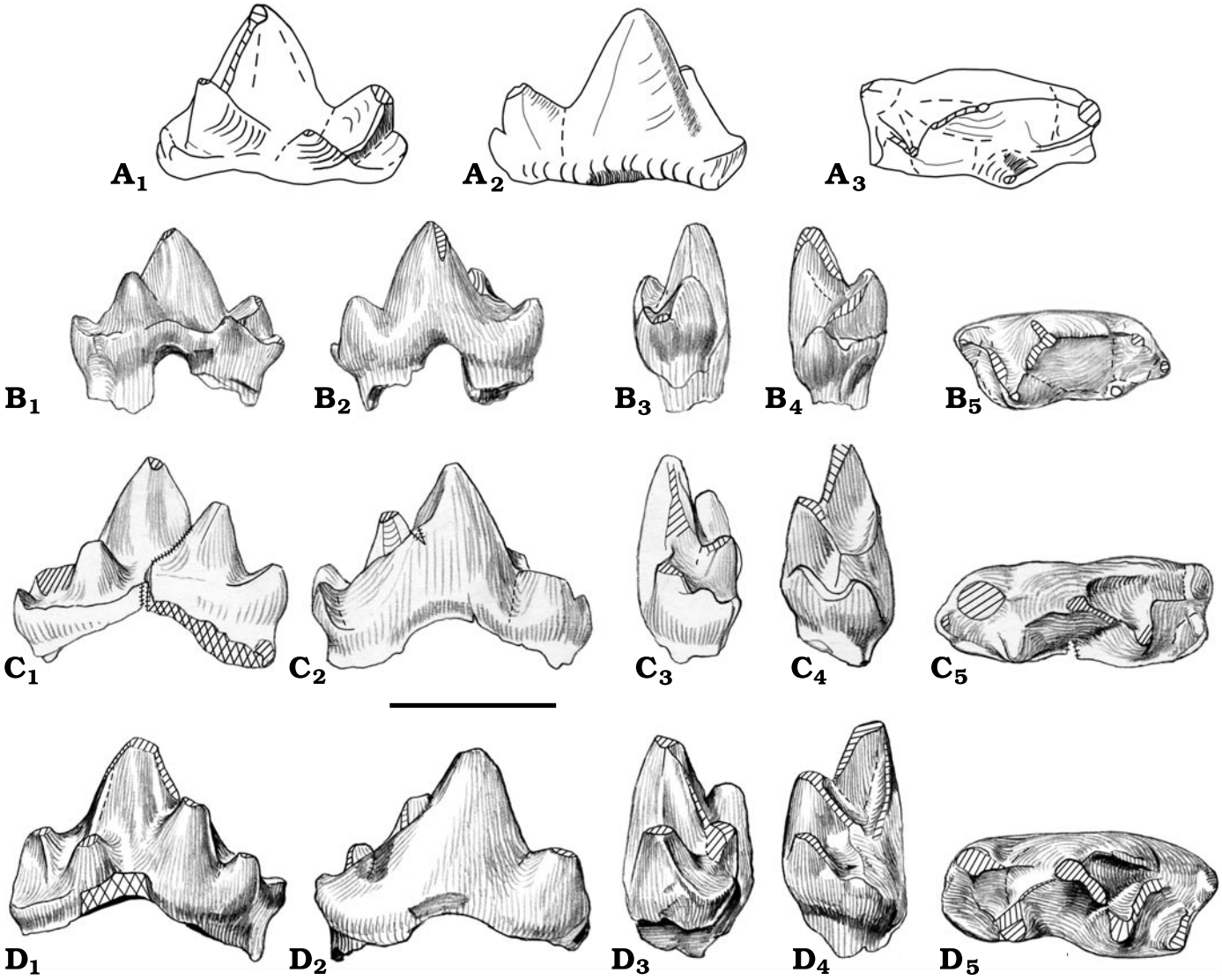

Fig. 2. **A**. *Borealestes serendipitus*, left M3 of the holotype left lower jaw UBGM 20570, in lingual (A_1), labial (A_2), and occlusal (A_3) views. **B**. *Borealestes serendipitus*, left lower molar BMNH J.791 in lingual (B_1), labial (B_2), anterior (B_3), posterior (B_4), and occlusal (B_5) views. **C**. *Borealestes mussetti* sp. nov. holotype right lower molar BMNH J. 495 in lingual (C_1), labial (C_2), anterior (C_3), posterior (C_4), and occlusal (C_5) views. **D**. *Borealestes mussetti* sp. nov. right lower molar BMNH J. 836 in lingual (D_1), labial (D_2), anterior (D_3), posterior (D_4), and occlusal (D_5) views. Scale bar 1 mm.

does not have the posterior slope typical of docodonts; this tooth is more likely a symmetrodont as labelled in Freeman 1976: fig. 2c.

The only other docodont taxon so far described from Kirtlington, *Simpsonodon oxfordensis* Kermack et al., 1987, is represented in the fauna not only by the six lower molariform teeth already published, but also by BMNH J.43 (left anterior half), J.46 (right anterior basin), J.570 (left anterior basin), J.688 (eroded, complete right), and possibly J.785 (right posterior slope) and J.843 (right anterior half). Such material does not add any new data to those brought out by the authors.

Another described Bathonian taxon, *Borealestes serendipitus*, not from Kirtlington but from the Isle of Skye in Scotland, was known by two lower jaws (Waldman and Savage 1972). Their molars differ from those of *Simpsonodon* by several features (Fig. 2). The main cusp is relatively higher and there is no crest from it to the weak mesio-lingual cusp, so that its lingual face is not parallel to the long axis of the tooth, but oblique from front to back and from labially to lingually. This lingual face is convex and not concave as in *Simpsonodon*. The mesio-lingual cusp is much smaller than the disto-lingual and often inclined lingually (it is upright in *Simpsonodon*). The anterior basin is delimited anteriorly by a straight (not arched) and oblique crest crossing the width of the tooth and leaving anteriorly a triangular space, which varies along the series from a wide sulcus to a narrow basin or crescent. There is no ornamentation on the posterior slope of the main cusp other than a slight vertical groove. Moreover, the posterior crest emanating from the disto-lingual cusp is not vertical but oblique, so that the posterior slope is divided in two, that of the disto-lingual cusp being more posterior

than the slope of the main cusp. The talonid basin is reduced to a narrow sulcus delimited posteriorly by a cingulum culminating in two subqual cuspules, one lingually, one labially. In *Simpsonodon*, there is no sulcus: the cingulum abuts directly against the distal slope and culminates in a high labial point while the lingual point is very reduced. Finally, the lingual cingulum is usually more complete in *Simpsonodon*.

It is to be stressed here how close the morphology of the lower molars of *Borealestes serendipitus* is to that of *Haldanodon* Kühne and Krusat, 1972; the main differences between the two concern the premolars.

In the new material from Kirtlington, 11 teeth or fragments can be attributed to *B. serendipitus*. BMNH J.610, a left lower molar, presents the main characters of the holotype. So does J.791, also left (Fig. 2B), except that there is no lingual talonid cusp; but the latter is very small also on m1 of the holotype jaw. On J.521, again left, the talonid cusps are completely missing. On all three teeth, the mesio-lingual cusp is very small, hence not inclined lingually; this is also the case on the m1 of the holotype. M 44301 is slightly larger and stouter, with its mesio-lingual cusp well inclined lingually. On the type jaw, variability concerns the general size, the degree of development of the mesio-lingual cusp, size and shape of the anterior crescent, size of the small pseudotalonid and individualization of the lingual cingulum. On the teeth analyzed here, the same factors vary, and, in one case at least, the length/width relation.

BMNH J.39, J.116 and J.869, smaller and devoid of a mesio-lingual cusp, may represent milk molars of the same taxon.

Thirteen teeth or fragments differ significantly from *Borealestes serendipitus* (Fig. 2C, D). The main cusp remains dominant and the two lingual cusps are well developed, but the former bears two anterior crests, one linking it to the mesio-lingual cusp, the other to the mesio-labial one; so that, as in *Simpsonodon*, an anterior basin, or pseudotalonid, is well delimited posteriorly; however, the basal crest linking together the two mesial cusps is much weaker or absent, so that the basin has no anterior limit. Also as in *Simpsonodon*, the presence of an antero-main crest divides the lingual face of the main cusp into a longitudinal sector and an oblique anterior one. The mesio-lingual cusp is less or not inclined lingually and the disto-lingual cusp is more posterior relative to the main cusp than in *Borealestes serendipitus*. There is a weak or no posterior lingual cingulum, but a more or less distinct anterior one. The posterior sulcus of the main cusp is more accentuated than in the type species and the dominant talonid cusp is the lingual one. Finally, on the holotype and several specimens, the posterior crest does not go straight into the talonid, but angles down as it meets the main cusp's posterior crest; in others, it diverges obliquely toward the labial talonid cusp but remains more accentuated than in the type species. These characters define at least a new species, *B. mussetti* sp. nov.

Due to various factors (poor enamel preservation, inadequate optical apparatus at my disposal), wear facets were rarely detected on the teeth analyzed above and could in no way compare with the detailed accounts of Krusat (1980) and Kermack et al. (1987). On the type jaw of *Borealestes*, abrasion progresses regularly from front to back. On the new specimens, it seems that wear mostly touches the various crests, and occasionally, the antero-labial side of the mesiolabial and main cusps, as well as their postero-labial faces.

The new taxon *Krusatodon kirtlingtonensis* gen. et sp. nov. (Fig. 3A, B) is characterized by its relatively large molars having a main cusp crossed by ribs and deep furrows anteriorly, lingually and posteriorly. The two lingual cusps are well developed with a slight dominance of the distal one and a slightly more lingual position of the mesial one. The talonid, when unabraded, is posteriorly tri-denticulated and is transversely crossed by an horizontal crest which join the vertical crests emanated from the main cusp and from the disto-lingual cusp. There is a particularly wide and deep anterior basin (pseudo-talonid), but the antero-main crest meets the basal crest before reaching the mesio-lingual cusp. The lingual anterior crescent is short. A crest links the mesio-lingual cusp to a sharp anterior cuspule (cusp e of Butler 1997). No lingual cingulum is present. The posterior pattern is more like that of *Borealestes mussetti*, but the horizontal transverse crest mentioned above goes to the middle talonid cusp. In this taxon, size seems to vary in a greater extent than in the previous ones; so does the depth of furrows and the development of the anterior cuspule.

The genus *Tegotherium*, with the species *T. gubini* Tatarinov, 1974, is known by a lower molar that Hopson was the first (1995) to recognize as a docodont. As far as can be told from the figures (Tatarinov 1974; Kielan-Jaworowska et al. 2000) and the description given by Martin and Averianov (2001), it shares with *Krusatodon* a number of characters: the vertical furrows of the main cusp, which are weak or absent in other taxa, proportions of labial and lingual cusps, crest between the mesio-labial cusp and the protruding mesio-lingual cuspule. A generic identity is thus possible, but only direct comparison of the specimens could ascertain it. In any case, these Kirtlington teeth differ from the Mongolian taxon by the absence of a lingual cingulum and a more complex array of crests, especially posteriorly; which would justify at least a specific distinction. Several of the diagnostic characters enumerated above for *Krusatodon* and *Tegotherium* are supposed to define Asiadocodonta Martin and Averianov, 2001; this concept should be reviewed with respect to the new material from Kirtlington and also take into account the individual variability of these teeth.

Wear on J.784 has touched the anterior crest and crescent as well as the talonid rim; on J.778, the talonid itself is worn and most crests are blunted.

The two teeth here referred to as *Peraiocynodon major* sp. nov. (Fig. 3D) have a very unusual configuration in that they possess no mesio-lingual cusp; in that the mesio-labial cusp does not send a crest lingually (= antero-basal crest: such a crest is present in *Docodon* in spite of the absence of a distinct mesio-lingual cusp; the same is true for "m1" of

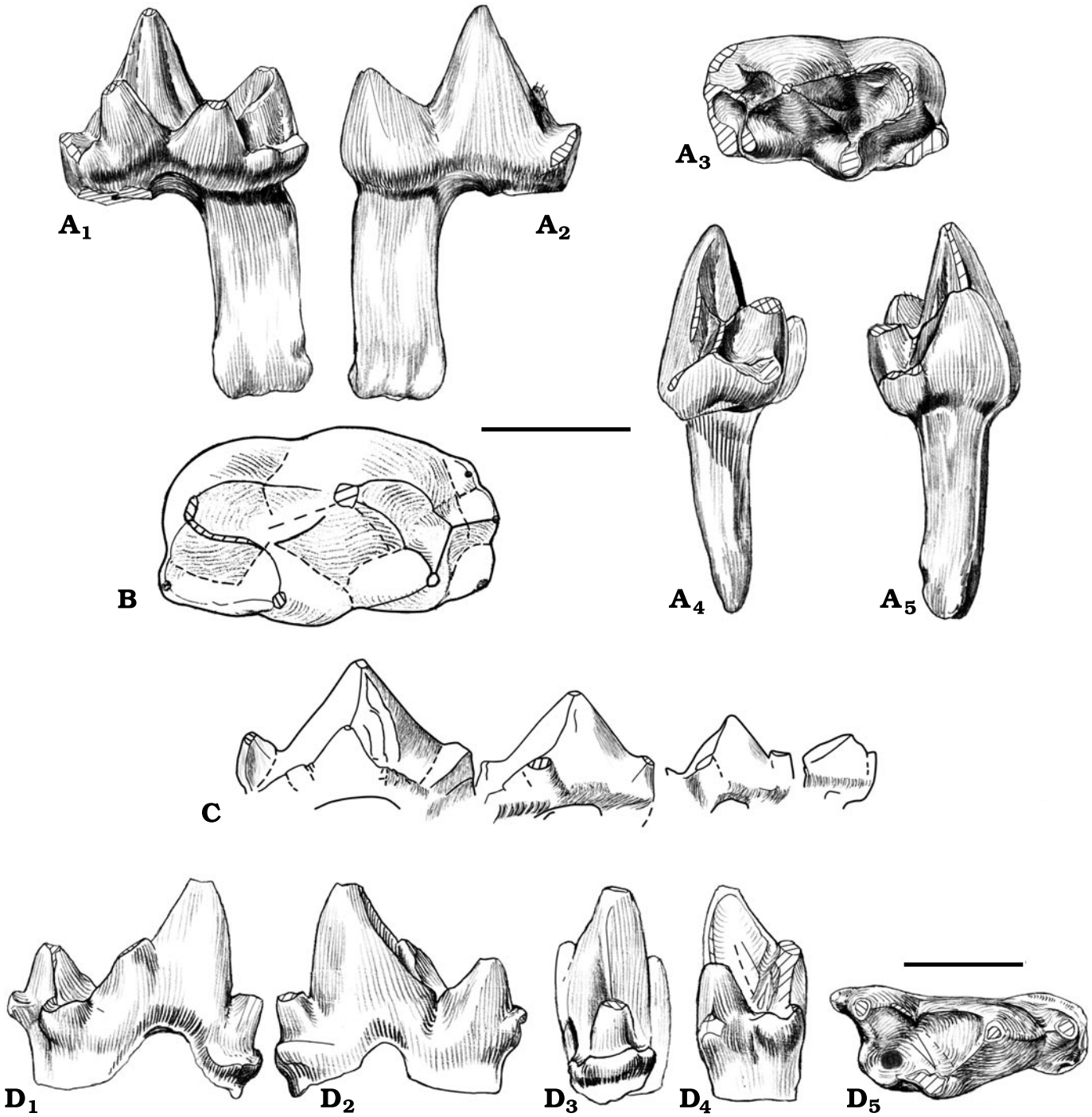

Fig. 3. **A**. *Krusatodon kirtlingtonensis* gen. et sp. nov., left lower molar BMNH J. 784, in lingual (A_1), labial (A_2), occlusal (A_3), anterior (A_4), and posterior (A_5) views. **B**. *Krusatodon kirtlingtonensis* gen. et sp. nov., right lower molar BMNH J. 526, in occlusal view. **C**. *Peraiocynodon inexpectatus*, holotype lower molariforms BMNH M 48248, in lingual view, drawn from cast. **D**. *Peraiocynodon major* sp. nov. holotype left lower molariform BMNH J. 693 in lingual (D_1), labial (D_2), anterior (D_3), posterior (D_4), and occlusal (D_5) views. Upper scale bar is for A–C, lower for D. Scale bars 1 mm.

Peraiocynodon inexpectatus); in the great development of the disto-labial cusp (labial talonid cusp) and of a posterior cingulum; and in the deeply concave posterior slope, crossed by two vertical ridges. The disto-lingual and mesio-labial cusps are nearly equal and weakly detached from the sides of the large main cusp, whose lingual face is very oblique to the longitudinal axis of the tooth. Posteriorly, the disto-labial cusp (labial talonid cusp) is bordered by a small additional cuspule; an indentation separates the latter from the lingual talonid cusp. J.679 is incomplete lingually; its preserved part differs from the holotype in being slightly larger and in having an even more developed disto-labial cusp, crossed by a sharp lingual crest. On both teeth, the postero-lingual crest has been particularly blunted by abrasion.

Several possibilities were envisaged concerning these two teeth. They do not seem to represent the deciduous molars of the large *Krusatodon*: the posterior face is simple and not divided into several cavities, the lingual face of the main cusp is mainly smooth, the mesio-labial cusp is not extended or hollowed to form a large pseudo-talonid. As for representing the premolars of this taxon, they would be extremely different from any docodont lower premolar by the development of the disto-lingual cusp and the wide posterior slope. A third choice was to consider them as deciduous molars of the genus *Docodon,* a genus close to *Peraiocynodon* (see below). In *Peraiocynodon*, deciduous molars differ from the molars mainly by the absence of the mesio-lingual cusp; however, the great development of the disto-labial cusp has no equivalent in *Docodon*, where, moreover, the main cusp is shorter and striated lingually and the posterior slope is much more oblique.

On the contrary, the resemblance of these two molariforms to the much smaller teeth of *Peraiocynodon inexpectatus* from the Purbeck Limestone Group is striking. Apart from the size, they only differ from the preserved teeth of this taxon by the absence of a crest from the mesio-labial cusp. Moreover, they differ from the antepenultimate tooth of *Peraiocynodon inexpectatus* by the more developed disto-labial cusp and from the penultimate tooth by the absence of furrows and ridges on the lingual face of the main cusp. Finally, it is not excluded that they might represent premolars or deciduous premolars rather than molars of the new species *P. major*; comparison with the second preserved tooth on the type jaw of *Peraiocynodon inexpectatus* (considered as deciduous) shows the common absence not only of a mesio-lingual cusp but also of an antero-basal crest; a unique situation among docodont molars (if molars they were). Anyway the similarities with the teeth of this taxon, which include what can be considered as derived characters (great development of the disto-labial cusp, absence of mesio-lingual cusp, ornamentation and concavity of the distal face, disto-lingual cusp weakly detached) lead to the grouping of these two forms into one generic unit; which represents a solid argument for keeping the Purbeck taxon independent from the various species of the genus *Docodon* (see discussion below).

Now, if the genus *Cyrtlatherium* was based on a deciduous tooth (BMNH M 36511), to which of these taxa present in the Kirtlington mammal bed can it be most closely related? Table 4 sums up the situation. The size, relation length/width and the dominance of the main cusp on the only known specimen would suggest *Borealestes*; as would the absence of the mesio-lingual cusp, barely present on the m1 of the holotype of *B. serendipitus.* However, this species is eliminated by the absence of an antero-lingual crest from the main cusp. *B. mussetti* would then be a better possibility, but the structure of the posterior slope in that taxon does not conform to M 36511; moreover, comparison of the latter with J.796, a possible milk molar of *Borealestes mussetti*, clearly shows dissimilarity.

Comparison of the holotype of *Cyrtlatherium* (Fig.1A$_2$) with the molars of *Simpsonodon* (Fig. 1A$_3$), shows that these teeth share a similar enamel ornamentation. In both cases, moreover, the disto-lingual cusp is, in posterior view, situated on the same transverse plane as the main cusp so that there is one single distal slope limited lingually by a near-vertical crest and distally and basally by a cingulum culminating in a high labial cusp. Again in both cases, there is a large anterior basin or pseudo-talonid[1]; the antero-basal crest limiting this basin is convex anteriorly, a unique shape among docodonts. Finally, the lingual face of the main cusp is parallel to the long axis of the tooth and is flat or concave.

On the other hand, *Cyrtlatherium* differs from *Simpsonodon* by its smaller size (length = 0.83 mm. against 1.09 for the smallest molar of *Simpsonodon*), by being relatively narrower bucco-lingually, by the main cusp being relatively higher, by a much fainter lingual cingulum and by the absence of a mesio-lingual cusp; moreover the transverse distal slope is less vertical, the disto-lingual cusp is barely detached from the main cusp and the mesio-labial cusp is relatively lower.

Krusat (1980: figs. 23, 24) has figured and described the d3 of the docodont genus from Guimarota, *Haldanodon*. This tooth differs from the definitive molars precisely by lacking the mesio-lingual cusp, hence its weaker anterior crest. However, in this case, the difference is in degree (for instance, this cusp is very small on the definitive molars of *Haldanodon*); the basal morphology of the teeth is the same; in particular the main cusp is not any higher relatively on d/3. On the contrary, the differences between the type tooth of *Cyrtlatherium* and the molars of *Simpsonodon* are more marked. They could be explained by the holotype of *Cyrtlatherium* being in fact a d2 and not a d3: the contour of a d2 is figured by Krusat (1980: fig. 23) and its length relative to that of an m1 is close to that of BMNH 36511 relatively to an m1 of *Simpsonodon*. But the proportion of the cusps of the former do not "announce" those of a definitive molar of *Simpsonodon*. However, as long as no docodont d/2 is better known, it will be hazardous to confirm or reject this proposed synonymy, though it remains likely that *Cyrtlatherium* is based on a deciduous tooth.

[1] Pseudo-talonid: this term was created by Chow and Rich (1982) "to describe the extensive shelf anterior to the trigonid" on the lower molars of their new genus *Shuotherium*. Kermack et al. (1987: 11) borrowed this term—besides not formally designated on any figure of their paper- to represent the "deep basin" enclosed between the main cusp, the mesio-lingual and the mesio-labial cusps "and the crests connecting them". In *Shuotherium*, however, the concavity is situated completely anterior to the trigonid, lingually to the mesio-labial cusp (a cusp interpreted by Sigogneau-Russell et Godefroit 1997 as f) and it is limited lingually by a simple crest; this is the only real pseudo-talonid, which receives the pseudo-protocone of the uppers. The term seems improper for docodonts, where the homology of cusps involved is not established, and mostly because the "protocone" (Butler 1939 = hypocone of Kermack et al. = Mesio-Lingual Cusp) bites in the posterior slope of the lower molar while it is the hypocone (protocone of Kermack et al. = Disto-Lingual Cusp) that bites into this so-called "pseudo-talonid". I keep the term here for simplicity purposes.

Some comments should be made here about the lower premolars. The lower premolars of *Borealestes* and *Docodon* have a relatively close morphology: the last two at least are long and narrow, encircled by a complete lingual cingulum and an incomplete labial one, and composed of one main cusp (higher in *Docodon*), a small distal one and an even smaller mesial one. In *Haldanodon* (holotype VJ 1001-155), the premolars are more molariform: rectangular, i. e. relatively wider, with a complete lingual and labial cingula forming an anterior ledge; the main cusp has a disto-lingual crest like that leading to the disto-lingual cusp on the molars. This discrepancy between the premolars of *Borealestes* and *Haldanodon* (contrary to Krusat 1980: 51) is surprising since their lower molars appear to be so close morphologically. Finally, it is interesting to note that the last premolar of *Simpsonodon* (Kermack et al. 1987: figs. 5–11) is intermediate in its degree of molarisation between the simple premolars of *Borealestes* and the more complex ones of *Haldanodon*: narrow anteriorly, it presents a disto-lingual cusp with the corresponding crest, and a groove on its posterior slope.

Upper molars

There are about as many upper docodont molariform teeth in the Kirtlington collection as there are lowers, though many are only fragmentary. Four main types could be distinguished.

The first type, composed of: BMNH M 36524 (right; figured by Freeman 1976 and 1979) and "ascribed with great diffidence to *Borealestes*" (Freeman 1979: 160), but recognized by Kermack et al. (1987) as belonging to their new genus *Simpsonodon*); BMNH J.62 (right), J.191 (right), J. 223 (right), J.416 (left), J.434 (right), J.435 (right), J.447 (right), J.480 (right), J.565 (left), J. 665 (right), ?J.798 (right), J.840 (left), J.870 (left) are referable to the described upper molars of *Simpsonodon* (Kermack et al. 1987): low cusped crowns, squarish contour, flat lingual part, occlusal surface crossed by two complete transverse crests of which the posterior one forms the edge of the tooth. BMNH J.252 (left), J.426 (right), J.798 (right) are suspected to be deciduous molars of this genus: the contour is less squarish than in the adult teeth, with a shorter lingual part, but the proportions of the cusps and the configuration of the crests are close. The published tooth J.227 (Kermack et al. 1987:27) may also have been a deciduous molar.

The second type: BMNH J.316 (left lingual part), J.396 (left), J.404 (left), J.445 (right), J.448 (left), J.580 (right), J.871 (left); probably also the labial parts BMNH J.246 (left), J.394 (left), J.400 (left), J.607 (right), could represent the uppers of *Borealestes* (Fig. 4). The most complete teeth have grossly the same morphology as those of *Haldanodon*, with a much shorter lingual part than the labial part, and unequal Labial Cusps; the latter remain aligned, though, as in *Haldanodon*, the posterior crest of the Disto-Labial Cusp (Fig. $1B_2$) is more oblique towards the rear and labially. The crest emanating lingually from the Mesio-Labial Cusp is present on all specimens but one, and so is the cingulum ascending anteriorly from the apex of the Mesio-Lingual cusp; but the dorso-anterior part of the tooth is shorter and the antero-labial cingulum seems to have been less salient anteriorly than in *Haldanodon*. The two parallel Crests of the lingual part are also more accentuated than in this genus. Among these teeth, some (Fig. 4A) are smaller than the uppers of *Haldanodon* and could be assigned to *Borealestes serendipitus* (BMNH J.316, J.396, J.400, J.445, J.580, J.607). The others (Fig. 4B) have a Mesio-Labial Cusp hollowed by a vertical concavity on its lingual face; but mostly, the lingual part shows a supplementary cuspule on the Antero-Lingual Crest and the Mesio-Lingual Cusp tends to become salient lingually. I tentatively assign them to *B. mussetti*. Finally, J.455 (left, Fig. 4C) is interpreted as a milk molar of *Borealestes* sp.: the two Labial Cusps are closely set, a cingulum ascends from the tip of the Mesio-Lin-

Table 2. Measurements (in mm) of the best preserved of the docodont upper molars from Forest Marble.

	labial length	lingual length	width
Haldanodon exspectatus GUI 128/76	1.64	1.00	2.06
Docodon victor USNM 2715 M2	2.10	1.94	2.46
Borealestes serendipitus and *B. musetti*			
BMNH J.228	1.05	0.40	0.71
BMNH J.246	1.32+	–	–
BMNH J.394	1.03+	–	–
BMNH J.396	1.0+	0.6	1.26
BMNH J.400	1.31	–	–
BMNH J.404	–	0.72	–
BMNH J.445	–	0.85	–
BMNH J.448	–	0.45	–
BMNH J.455	1+	0.53	0.83
BMNH J.580	1.30+	0.90	1.58
BMNH J.607	1.26	–	–
BMNH J.871	1.38+	1.10	2.00
Krusatodon kirtlingtonensis			
BMNH J.199	1.89	0.68	1.14
BMNH J.222	1.72	1.15	2.0
BMNH J.437	1.90	1.20	1.94
BMNH J.442	–	1.16	–
BMNH J.454	1.51	0.86	1.15
BMNH J.667	1.56+	1.08	1.68+
BMNH J.803	1.87	–	–
BMNH J.830	1.50+	0.95	1.36
BMNH J.872	1.67	0.93	1.40
Peraiocynodon major			
BMNH J.198	–	1.20+	–
BMNH J.230	2.14	–	–
BMNH J.576	2.65	1.85	2.20
BMNH J.839	2.40	–	–

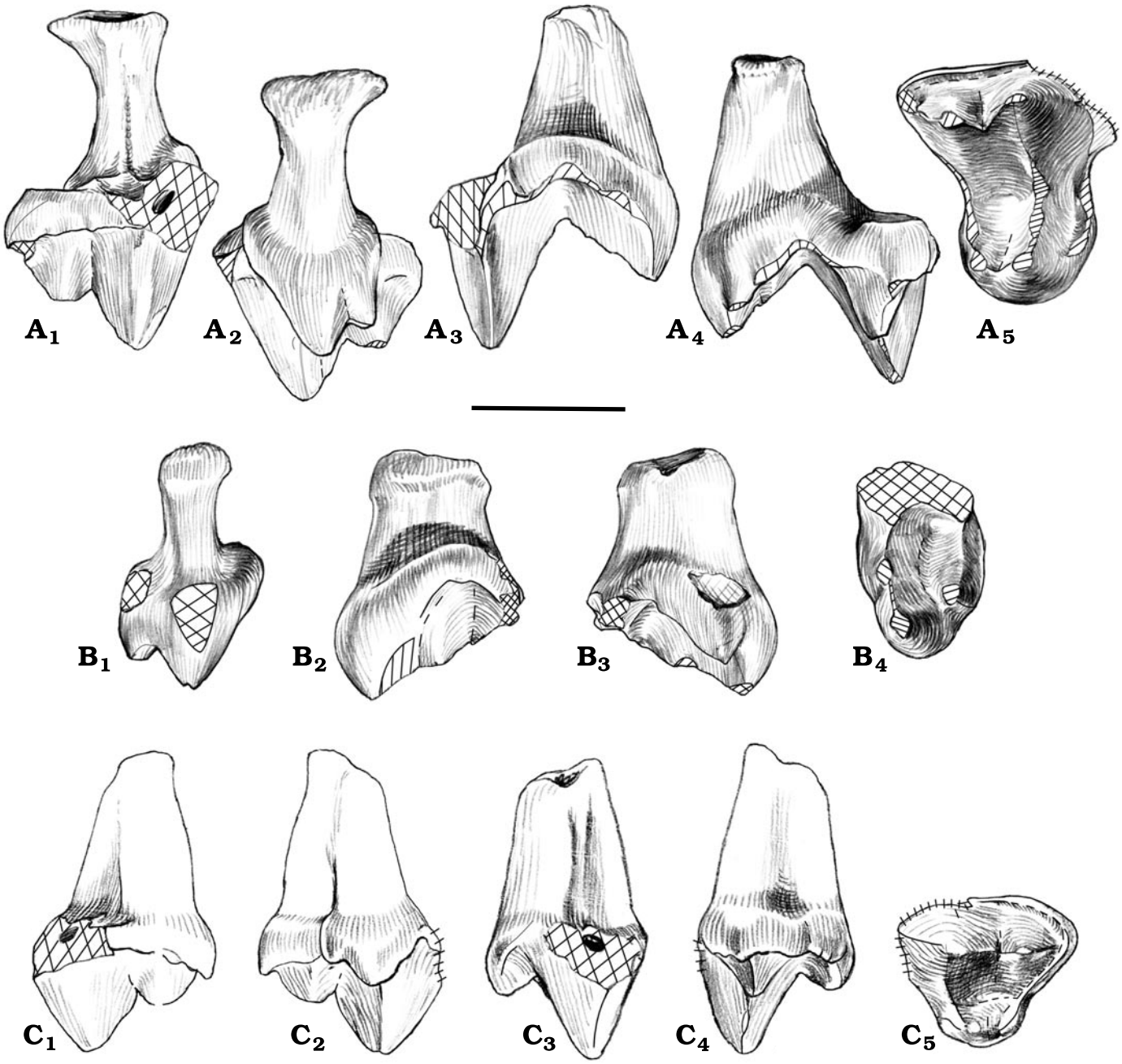

Fig. 4. **A**. *Borealestes serendipitus*, attributed right upper molar BMNH J. 580, in labial (A_1), lingual (A_2), anterior (A_3), posterior (A_4), and occlusal (A_5) views. **B**. *Borealestes mussetti* sp. nov., attributed left upper molar BMNH J.404, in lingual (B_1), anterior (B_2), posterior (B_3), and occlusal (B_4) views. **C**. *Borealestes* sp., left upper molar BMNH J.455, in labial (C_1), lingual (C_2), anterior (C_3), posterior (C_4), and occlusal (C_5) views. Scale bar 1 mm.

gual Cusp, and a crest links the latter to the base of the Mesio-Labial Cusp. It differs from an adult molar mostly by the labio-lingual narrowness (in a similar way to J.798 for *Simpsonodon*).

As mentioned above, wear is rarely detectable: in one case on the anterior face of the Main Lingual Cusp, and in one case on the postero-lingual face of the Mesio-Labial Cusp.

The third type, referred to *Krusatodon*, is represented by larger teeth (Fig. 5), so structurally similar to "tribosphenid" uppers that attribution to sympatric shuotheriids was envisaged, to be dismissed mostly because of a very different lingual part from that of the attributed upper molars of this genus (Sigogneau-Russell 1998; Wang et al. 1998). Like in the above-mentioned molars, the labial half is longer than the lingual half, but the two Labial Cusps are not strictly aligned: the crests linking them form an arch in occlusal view. These Cusps usually bear no Lingual Crest, but the Mesial Cusp shows a concave posterior face. The lingual half of the tooth is rounded, with one dominant Lingual Cusp linked by crests

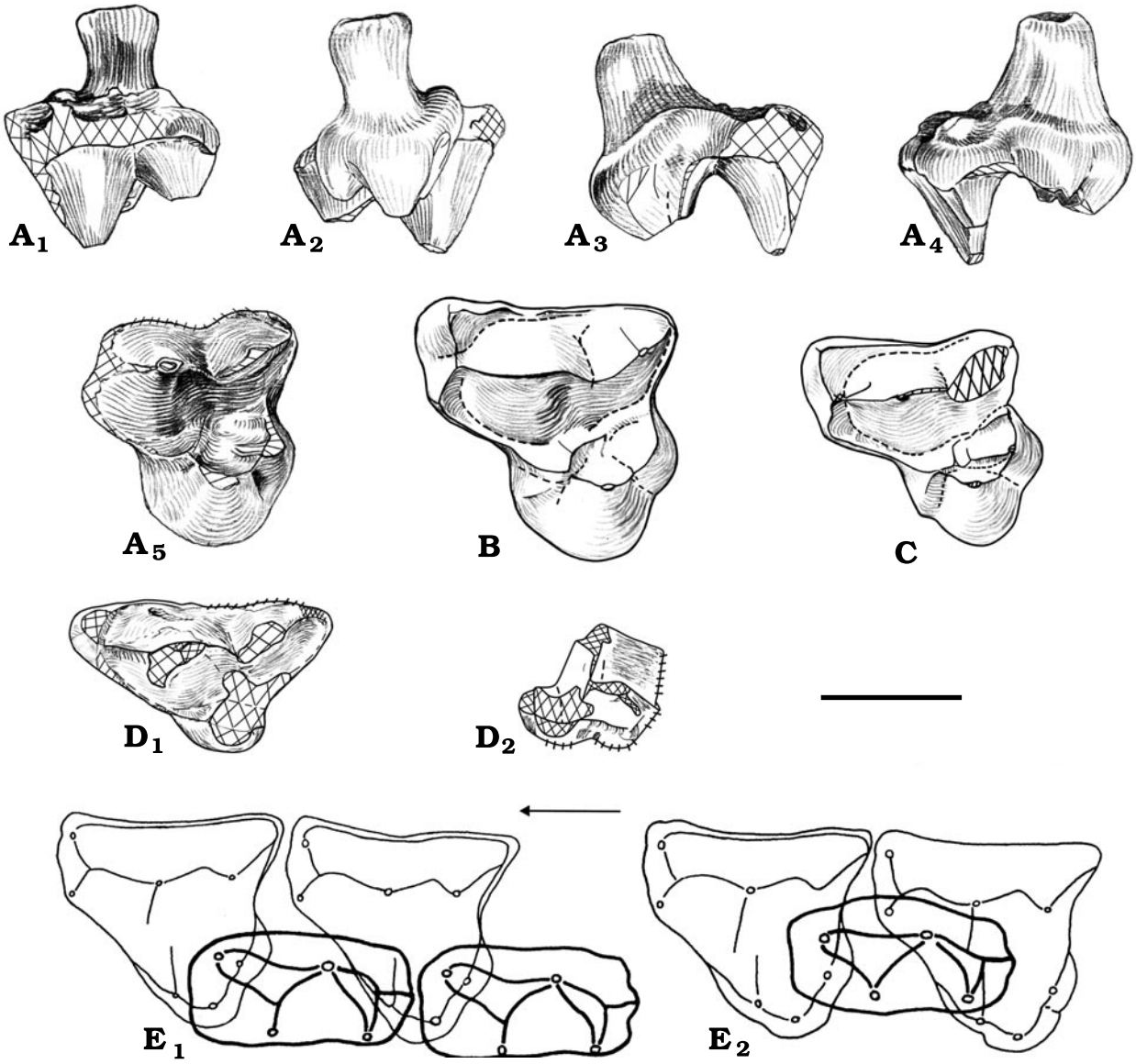

Fig. 5. **A**. *Krusatodon kirtlingtonensis* gen. et sp. nov., attributed left upper molar BMNH J. 667, in labial (A_1), lingual (A_2), anterior (A_3), posterior (A_4), and occlusal (A_5) views. **B**. *Krusatodon kirtlingtonensis* gen. et sp. nov., attributed left upper molar BMNH J. 437, in occlusal view. **C**. *Krusatodon kirtlingtonensis* gen. et sp. nov., attributed left upper molar BMNH J.222, in occlusal view. **D**. ?*Krusatodon kirtlingtonensis* gen. et sp. nov., left upper ?milk molar BMNH J. 199, in occlusal (D_1) and posterior (D_2) views. Scale bar 1 mm. **E**. Tentative occlusion between lower and attributed upper molars of *Krusatodon kirtlingtonensis*; arrow points anteriorly; lingual occlusion (E_1), end of centric occlusion (E_2).

to two smaller lateral protuberances, one Mesial, one Distal, the former being always dominant on the latter. The Mesial Cusp is situated at the crossing of a transverse crest and of a crest-like cingulum joining the anterior border of the tooth. Of these three transverse Crests, the two posterior ones are homologous to the two found in other docodont upper molars. The lingual half is more or less extended transversely and deeply concave occlusally. Finally, inside this lingual basin, faint oblique crests may be detected. A sharp cingulum limits the tooth labially, culminates in two cusps antero-labially and joins anteriorly the Mesio-Lingual cusp. BMNH J.222 (left, Fig. 5C), J.437 (left, Fig. 5B) and J.667 (left, Fig. 5A) are the most complete teeth; J.222 (left) is asymmetrical, probably in relation to its posterior position in the series. J.838 (right) and J.872 (right) have a relatively short (antero-posteriorly) lingual half and may be seen as anterior molars. BMNH J.803 (right) is a labial half, J. 531 (left) and J.442 (left) are large lingual halves. J.457 (right) lacks the posterior half and is thus only tentatively referred here. J.454 (left), a complete and beautifully preserved tooth, is puzzling: it is relatively short and the Labial Cusps are nearly aligned, as on the teeth attributed to *Borealestes*. However, as in *Krusatodon*, the lingual part is rounded, though very narrow, but the additional cuspule of the Antero-Lingual crest is hardly discernible. Finally, the two posterior roots are fused medially. The tooth is not worn and could be inter-

preted as the posteriormost molar. BMNH J.199 (left, Fig. 5D) is interpreted as a premolar though it is less asymmetrical than known upper premolars; its labial half is long and arched, the lingual part is extremely short and narrow; the state of preservation of the latter does not allow the numbering of cusps. As for the lower molars of *Krusatodon*, size of the upper molars listed above varies considerably; also notable is the variation of the linguo-labial width of the lingual part, of the crests inside the lingual basin and the state of individualization of the Mesio-Lingual Cusp.

This molar morphology can be viewed as a step further than that of the *B. mussetti* type, with greater development of the third Cusp mentioned above on the Antero-Lingual crest. In fact I had envisaged the possibility that these teeth did represent *B. mussetti;* on the other hand, no other candidate for *Krusatodon* being present, it is plausible that we have here the uppers of this taxon. Tentative occlusion between lowers and uppers (Fig. 5E) shows that the cusp limiting the pseudo-talonid of the lowers would fit in the lingual basin of the uppers, that the labial crests of each series would cut one against the other, that the two lower lingual cusps would be responsible for wear on the mesial and distal side of the lingual part of the uppers, and that the transverse crests of the uppers would produce the wear facets observed on the mesial and distal ends of the lowers. The function of the faint oblique crest in the lingual basin of the uppers remains elusive. In any case, teeth of this early docodont taxon have achieved the most complete cutting and crushing function. The poorly preserved upper molar published by Nessov et al. (1994) from the middle Jurassic of Kyrgystan, if it belongs to the Asiatic tegotheriids, shows no similarity in its outline to the molars attributed to *Krusatodon*, suspected here to be congeneric with *Tegotherium*; it rather evokes the *Docodon* type.

Wear on the upper molariforms attributed to *Krusatodon* is better exhibited than on the teeth attributed to *Borealestes:* on J.454, the posterior face of the Main Lingual Cusp is flattened, while on J.437 and J.667, it is the anterior face of the lingual part that bears a clear facet; on J. 437 and J.222, so does the labial face of the same lingual part. On J.442, the dorsal border of the lingual part is worn anteriorly; finally, on J.803, it is the Disto-Labial Cusp, which is worn postero-lingually.

The fourth type of upper molars represents an even larger form. The contour of the only complete molar (BMNH J.576, right, Fig. 6A) is at first sight close to that of a *Simpsonodon* molar: squarish (as opposed to rectangular in *Docodon*) though still longer than wide (wider than long in *Docodon*); but the labial half remains longer (antero-posteriorly) than the lingual one (these are about equal in *Simpsonodon* and *Docodon*). The Disto-Labial Cusp forms an angle with the Mesio-Labial one; the latter is deeply hollowed posteriorly by a vertical groove. On the other hand, this tooth shares with *Docodon* a great size discrepancy between the two Lingual Cusps, the ridges and furrows of the enamel, and a sharp crest linking the two Mesial Cusps. The labial cingulum protrudes anteriorly but does not form a high Stylar Cuspule as on the uppers attributed to *Krusatodon*; this cingulum may be interrupted labially. In summary, the lingual part is closer to that of *Docodon*, while the labial part is more like *Simpsonodon*, with the two Cusps deeply separated. Also, contrary to *Docodon*, the lingual and labial parts are not very far apart so that the lower teeth fitting in between would have been relatively narrow. Finally, ornamentation of the enamel evokes not only *Docodon*, but also the lower molariforms of *Peraiocynodon major*; these narrow lower molariform teeth could occlude with such uppers. I tentatively suggest attribution of J.576 to the latter species (though *Krusatodon* should not be excluded). Fig. 6A shows erosion of the crests; moreover, the anterior face of the Mesio-Lingual Cusp is slightly flattened.

BMNH J.839 (right) and J.230 (right) are only labial parts; J.198 (right) a lingual part, J.188 (left) a Mesio-Labial Cusp. Finally, J.212 (left, Fig. 6B) is possibly an upper canine of this taxon: biradiculated, the crown consists of one large cusp compressed anteriorly, widening posteriorly; its labial face is perfectly flat; its lingual face is flat anteriorly, concave distally and crossed with vertical ridges and grooves; one of these ridges leads to a stubby disto-lingual cusp. The enamel is hardly preserved. The upper canine is known in *Haldanodon* and *Docodon*; in the latter it is relatively longer antero-posteriorly, more symmetrical with two small cuspules distally; in *Haldanodon* (Krusat 1980: fig. 16), it is relatively short, with no dorsal cuspule but a com-

Table 3. Measurements (in mm) of the new docodont specimens from the Purbeck Limestone Group. DORCM GS 619, 620, 800, 916, 968, BMNH M 51817, M 45240, M 45242 are attributed to *Peraiocynodon inexpectatus*; DORCM GS 697, 703, 841, 983, BMNH 51813, and 51814 are tentatively attributed to *Docodon* sp.; DORCM GS 1084 remains *incertae sedis*.

Lower molars	length	width
DORCM GS 619	1.40	0.66
DORCM GS 620	1.31	0.70
DORCM GS 697	1.65+	1.13+
DORCM GS 703	1.18+	0.72+
DORCM GS 800	0.93	0.45
DORCM GS 916	1.00	0.53
DORCM GS 968	–	0.60
BMNH M 51817	1.20	0.65
Upper molars	lingual length	width
DORCM GS 841	0.85	–
DORCM GS 983	1.20	–
DORCM GS 1084	0.61	–
BMNH M 45240	0.72 (lab l = 1.28)	1.60
BMNH M 45242	0.72	–
	length	width
BMNH 51813	0.95+	0.55+
BMNH 51814	1.20+	1.00

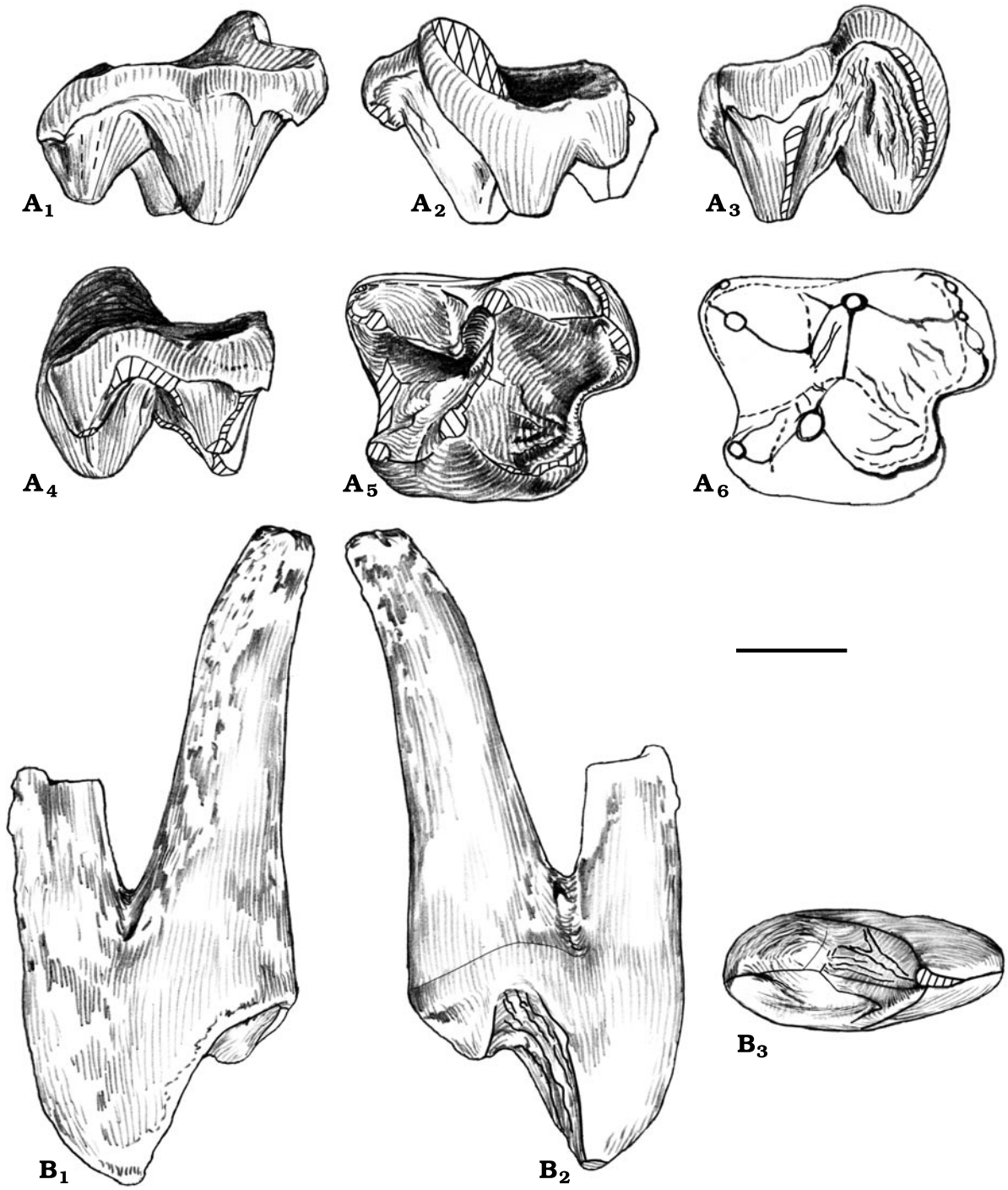

Fig. 6. **A**. *Peraiocynodon major*, attributed right upper molar BMNH J. 576, in labial (A_1), lingual (A_2), anterior (A_3), posterior (A_4), and two occlusal (A_5, A_6) views (one shaded). **B**. *Peraiocynodon major* sp. nov., attributed left upper canine BMNH J.212, in labial (B_1), lingual (B_2), and occlusal (B_3) views. Scale bar 1 mm.

plete cingulum. Size and ridulation of J.212 explain my tentative attribution of this tooth to *Peraiocynodon major*.

Finally, some upper premolars are present in the collection: BMNH J.345 (left) and J.545 (left) are considered as ?P2s, while J.64 (left) and the better preserved J.630 (right) have a P3 morphology. All are asymmetrical with a dominant Labial Cusp, a posterior crest and a more or less expressed Lingual Crest leading to small Cusps. A complete cingulum encircles the P2s; it is incomplete or absent on the P3s. These compare well with P2/ and P3/ of *Haldanodon* VJ 1008-155 (Krusat 1980: fig. 20A. It should be remarked that fig. 20D also illustrates a P3/ whose morphology is different from that of fig. 20A; could fig. 20D correspond to a DP3/?).

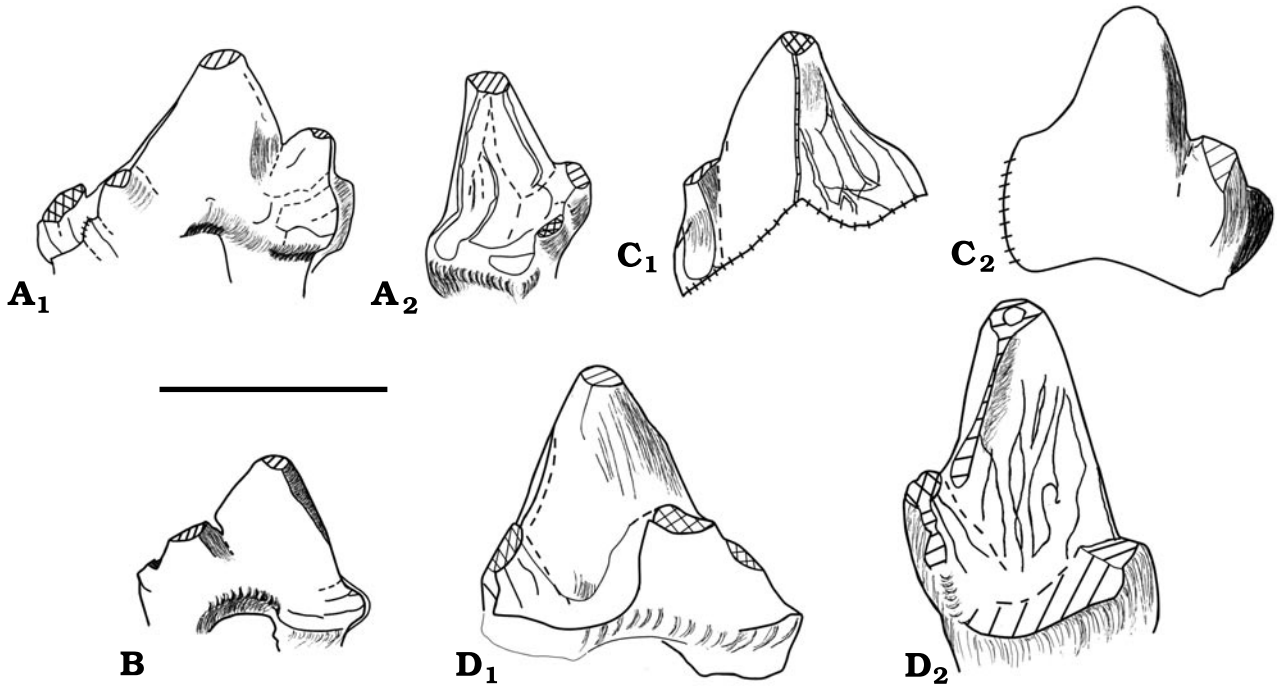

Fig. 7. **A**. *Peraiocynodon inexpectatus*, left lower molar DORCM GS 619, in lingual (A_1) and posterior (A_2) views. **B**. *Peraiocynodon inexpectatus*, left lower molar DORCM GS 800, in lingual view. **C**. *Docodon sp.*, right lower molar DORCM GS 703, in posterior (C_1) and lingual (C_2) views. **D**. *Docodon* sp., right lower molar DORCM GS 697, in lingual (D_1) and posterior (D_2) views. Scale bar 1 mm.

New material from the Purbeck Limestone Group

The only docodont taxon so far described from Purbeck is *Peraiocynodon inexpectatus* Simpson, 1928, known from a single partial lower jaw with four teeth (Fig. 3C). These were interpreted as deciduous premolars of the Morrison genus *Docodon* by various authors, following Butler (1939), but as dm1–3 and m1 by Krusat (1980).

In fact,"m1" of *Peraiocynodon* shows a very close morphology to that of *Docodon victor* (the closest *Docodon* species in size), with the main cusp showing an oblique antero-lingual face and a wide posterior face, the absence of a mesio-lingual cusp and presence of anterior and posterior striae on the main cusp. In both cases also, the lingual talonid cusp is set close to the disto-lingual cusp.

However, it differs by a more elongated trigonid, by the mesio-labial cusp being lower, hence a less vertical anterior crest, by the disto-labial cusp clearly more detached. Moreover, the posterior ornamentation forms a net in *Peraiocynodon* while it consists of vertical furrows and ridges in *Docodon*. Finally, the posterior slope is distinctly less hollow in the former; this discrepancy is even more accentuated with the first molars of *D. crassus* and *D. affinis*. These differences could indeed be attributed to the "m1" of the holotype of *Peraiocynodon* being instead a d/3; unfortunately, to my knowledge, no d/3 of *Docodon* has been published. The smaller "d/3" (*sensu* Krusat 1980) of *Peraiocynodon inexpectatus* is similar to its "m1", except for the absence of lingual striations, the fainter lingual ridge and lower mesio-labial and disto-lingual cusps.

Lower molars

The new material from the Purbeck Limestone Group consists of eight molars or fragments of molars. DORCM GS 619 (left, Fig. 7A), GS 968 (left posterior half) and BMNH M 51817 (left) conform to the *Peraiocynodon* scheme: these teeth are similar to the "m1" of the holotype in size, but to its "d3" in the absence of lingual striations on the main cusp; the anterior indentation is very well marked (the situation is not clear on the cast of *Peraiocynodon*). DORCM GS 620 (right, size of GS 619 and belonging possibly to the same individual) differ from the latter in having a complete ridge linking the disto-lingual cusp to the mesio-lingual edge of the tooth (as in the holotype "m1-d2" and in *Docodon*); this tooth was obviously situated posterior to GS 619 in a jaw. DORCM GS 800 (left, incomplete postero-labially; Fig. 7B) and GS 916 (left, incomplete labially and with no enamel) are of the same general type but clearly smaller.

The remaining two teeth are notably larger: DORCM GS 697 (right, incomplete anteriorly, Fig. 7D) has a shorter talonid and "trigonid" than the above teeth, and a complete arched lingual ridge; all characteristics of *Docodon*; but the lingual and labial faces of the "trigonid" are smooth while the posterior slope has a net of ridges and grooves. GS 703 (right, Fig. 7C) is slightly smaller; the specimen consists essentially in the main cusp, of which the smooth lingual face is

Table 4. Comparison of the main lower molar characters of the docodont taxa. li, lingual; lab, labial; m.c., main cusp; m-l, mesio-lingual cusp.

	Simpson-odon	*Haldan-odon*	*Borea-lestes seren-dipitus*	*Borea-lestes mussetti*	*Cyrtla-therium*	*Krusat-odon*	*Docodon*	*Peraio-cynodon inexpec-tatus*	*Peraio-cynodon major*	*Tego-therium*
mesio-li cusp	+++	+/0	+	++	0	+++	0/+	0	0	+++
disto-li cusp	+++	++	+++	+++	+	+++	+++	+/++	+	+++
crescent	very narrow	narrow	narrow	variable	very nar-row	triangular, cusp	very narrow	none, cuspule	cingulum	sulcus?
anterior crest	convex, sub-horizontal	vertical	straight, vertical	weak, hor-izontal	convex, sub-horizontal	angular	convex	vertical	0	vertical oblique
crest from m.c. to m-li cusp	+	0	0	+	+ (no cusp)	+	0	0	0	+
post. slope	1	2	2	2	1	2	1	1	1	?
tal.cusps	lab > li	lab = li	lab = li	lab = li	lab < li	3	li > lab fused to disto-li cusp	li fused to disto-li cusp	lab > li	?
pseudo-talonid	large	narrow	narrow	narrow	large	very large	0	0	0	large
post.sulcus on m.c.	ridges	weak	weak	deeper	ridges	very deep	ridges	ridges	ridges	?
lingual cingulum	variable	0 or slight	posterior	anterior	faint, median	0	0	0	0	+?
main cusp	low	high	high	high	high	high	high	very high	high	high
main cusp	longitudin. concave	oblique, convex	oblique, convex	longitudin. flat	longitudin. concave	longitudi-nal, ridges	very oblique	oblique	very oblique, convex	longitudin. ridges

particularly short and in fact more anterior than lingual (as in *Docodon*); the anterior part of the tooth was antero-posteriorly compressed, also as in *Docodon*, and the posterior side again crossed with ridges.

It seems unlikely that we would have here six deciduous teeth for two permanent molars of one single taxon. Given that argument, and the morphological features enumerated above, I would interpret the six teeth as permanent molars of *Peraiocynodon* and the two fragments as the remains of a *Docodon* species, differing from the Morrison ones by the absence of striations on the antero-lingual face of the main cusp. Nevertheless, given the shared peculiarities of the two taxa, it would have been tempting to consider *Peraiocynodon* as a smaller species of *Docodon*. However, given the fact that the two large lower molariforms from Forest Marble (J.693 and J.679) described above as *P. major* are clearly closer to *P. inexpectatus* than to *Docodon*, I concluded that the genus *Peraiocynodon* should be kept, with two species. As for the type jaw of *P. inexpectatus*, it should be interpreted as bearing one definitive molar and three deciduous premolars, as suggested by Krusat (1980): the latter are much more molariform than are the definitive premolars of *Docodon* for instance.

Upper molars

There was no complete upper molar in the new Purbeck material; only two labial parts and five lingual ones. The two labial parts M 45240 (right, Fig. 8A) and M 45241 (right) are of about the same size, smaller than the same parts in *Docodon* and consisting typically of two Cusps which are unequal and aligned lingually and labially (they are disposed on a curve lingually in *Docodon*). The Mesial Cusp is divided about equally into an anterior and a posterior face by a sharp transverse crest: the latter is less sharp in *Docodon* and the two faces are more unequal; finally, the anterior face is smooth while it is faintly striated in *Docodon*. The course of the postero-lingual cingulum indicates that the lingual part of the tooth was short (antero-posteriorly). Indeed, one preserved lingual part is very short and seems to fit with the labial part BMNH M45240 (Fig. 8B): it consists of a wide and short part crossed occlusally by a sharp crest, which divides the dominant Mesio-Lingual Cusp into two very steep faces; the Distal Cusp is reduced and high situated relative to the Mesial one. Anteriorly a thick cingulum ascends vertically along this cusp; this extends into a large lip in *Docodon* and *Peraiocynodon major*. A short and compressed root supports this part. M 45242 (right) is slightly larger and possibly striated anteriorly. These three (two after reconstruction of M45240) specimens would likely correspond to *Peraiocynodon inexpectatus*. If such is the case, one is obliged to observe that the uppers of the two species of *Peraiocynodon* as identified in this paper are quite differently structured from each other, labially as well as lingually, though in both cases the Mesio-Lingual Cusp has the same peculiar configuration (steeply sloping posterior face), the same also as in *Docodon*.

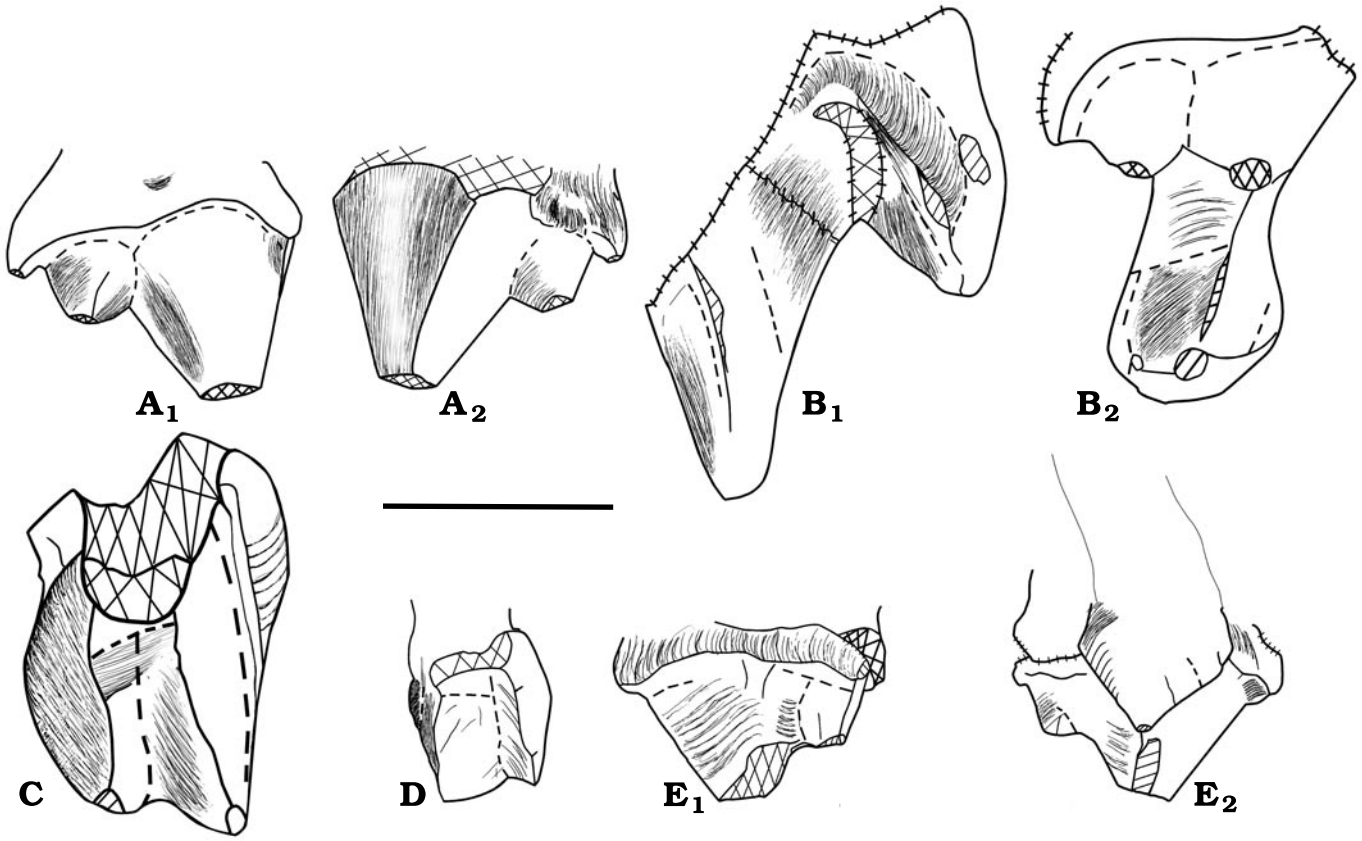

Fig. 8. **A**. ?*Peraiocynodon inexpectatus*, labial part of the upper right molar BMNH M 45240, in labial (A_1) and lingual (A_2) views. **B**. The same reconstructed upper right molar BMNH M 45240, in posterior (B_1) and occlusal (B_2) views. **C**. Lingual part of the right upper molar of *Docodon* sp., DORCM GS 983, in occlusal view. **D**. Lingual part of the docodont indet., left upper molar DORCM GS 1084, in occlusal view. **E**. Upper left P3/ BMNH M 51814, docodont indet., in labial (E_1) and lingual (E_2) views.

GS 983 (right lingual part, Fig. 8C) is even larger than M 45242; moreover, it has a much more extended posterior lip, and the Distal Cusp and crest are better defined; no striation is discernible. This latter tooth can be referred to the unnamed species of *Docodon* recognized on the lower molars; wear has affected the lingual border of the anterior ledge and the posterior side of both cusps. GS 841 (right lingual part) is very small, the crests are less sharp but the two faces of the Mesial Cusp are again steeply inclined and there is an extended anterior lip: could this fragment have belonged to a deciduous molar of the same *Docodon* sp.?

The situation is very different for GS 1084, a smaller (left, Fig. 8D) lingual part where the two crests are equally acute; the posterior slope of the Mesial Cusp is only weakly inclined and the anterior cingulum faint and vertical; the root is of the same type as on M45240. No proposal is made for the identity of this disturbing fragment, closer to the *Haldanodon–Borealestes* morphology.

In any case, these upper molar fragments would confirm the presence of at least two taxa in the Purbeck hypodigm, with a new *Docodon* species (too inadequately represented to be formally diagnosed) and the independence of the genus *Peraiocynodon*.

Finally, BMNH M 51813 and 51814 are two fragments of apparently the same (left) maxillary with roots of C, P1, part of P2 for the former, and ?P3 for the latter. This latter tooth is complete (Fig. 8E), except for a piece of the labial side of the Main Cusp and a break through its posterior base. These premolars are hardly smaller than the corresponding teeth of *Docodon superus* USNM 2715. The morphology of ?P3 however is different, in that it possesses a complete lingual part similar to that of molars—though much narrower— linked to the Labial Main Cusp by a sharp and fully transverse crest; however, the Disto-Lingual Cusp is hardly distinguishable. In *D. superus* (USNM 2715), the last Pm is less molariform, having no real lingual part, only a Disto-Lingual Cusp linked to the Main Labial Cusp by an oblique, fainter crest. These premolars could be those of the new *Docodon* species.

Conclusion

To my knowledge, no attempt for establishing phylogenetic relationships among docodonts has been proposed. Given the ignorance that reigns concerning the origin of their dentition, hence the polarity of characters, it is indeed presumptuous to

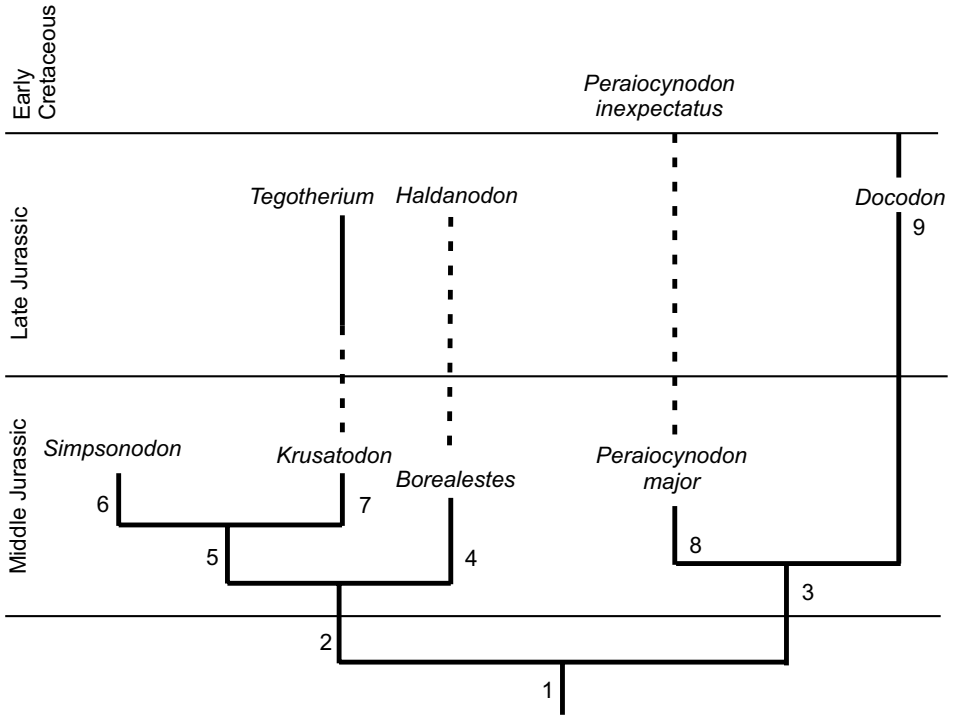

Fig. 9. Suggested relationships of the docodont genera based on lower molars. 1. Transverse widening of molars; formation of transverse crests. 2. Development of an incipient pseudo-talonid (anterior). 3. Reduction of mesio-lingual cusp; development of the real talonid (posterior); folding enamel. 4. Straight anterior crest. 5. Development of mesio-lingual cusp, of pseudo-talonid. 6. Folding of the enamel. 7. Vertical furrows. 8. Enlargment of disto-labial cusp. 9. Tendency to fuse lingual cusps together and labial cusps together.

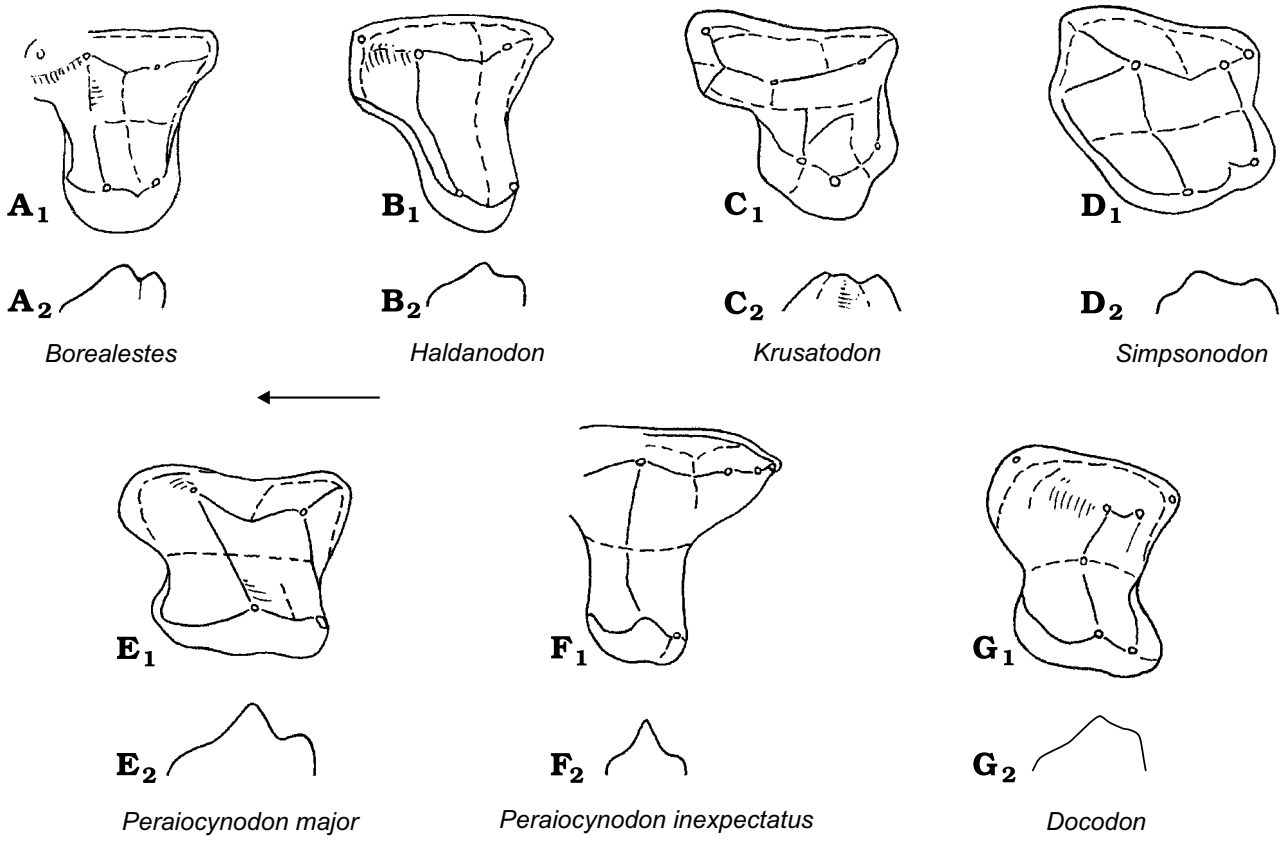

Fig. 10. Occlusal view of the various types of docodont upper molars (A_1–G_1) and longitudinal section of the lingual part (A_2–G_2). Anterior at left. Not to scale.

attempt it. Fig. 9 is merely a suggestion of the possible relationships of the genera, but is not based on a computerized analysis. From the least derived *Haldanodon–Borealestes*, two possible scenarios can be envisaged, whether one considers as a synapomorphy the folding of the enamel, or the development of an anterior pseudo-talonid (both characters already incipient in the two above-mentioned genera). The former of these features concerns only the lower molars in *Simpsonodon* and *Peraiocynodon inexpectatus*; moreover, the second feature has the consequence of suggesting a different type of occlusion, hence my decision to consider it as prominent in determining the affinities.

Some remarks may be added. If—and that is a major if—the mesio-lingual cusp of the lower molar is homologous to cusp g (kuehneocone) (Butler 1997), its presence in docodonts would be primitive (*Borealestes*), and its absence (*Peraiocynodon, Docodon*) or hyperdevelopment (*Tegotherium, Simpsonodon, Krusatodon*) would be specialisations. The lowering of cusp a (main cusp) (*Simpsonodon*) would also be secondary. *Peraiocynodon* has the autapomorphy of the very large disto-labial cusp on the lower molars. In *Krusatodon*, ornamentation of the enamel consists in deep furrows, which testifies to an accentuation of the crushing function (Fig. 10, showing the lingual part of the upper molar in the various docodont genera, illustrates the diversification of the occlusal mode in the order). In any case, *Borealestes–Haldanodon* would represent the most primitive members of a dentally derived and diverse clade. Origin of the latter remains frustratingly elusive; the attempt by Butler (1997) to link it to *Woutersia* or of Sigogneau-Russell and Godefroit (1997) to link it to *Delsatia* appears unsatisfactory.

The Kirtlington docodonts are the earliest representatives of the order, unless the Kota Formation of India is confirmed to be of Early Jurassic age (Prasad and Manhas 2001 and in press). The Purbeck docodonts are the youngest representatives so far known, if one excepts the disputed genus *Reigitherium* Bonaparte, 1990 from the Late Cretaceous of Patagonia (Pascual et al. 2000). Docodonts coexisted with the early representatives of tribosphenids (Sigogneau-Russell et al. 2001), whose teeth had acquired a similar function but whose general specialisations probably surpassed by far the level reached by these "audacious pioneers". What remains surprising is that, in spite of these dental assets, docodonts do not seem to have ever been dominant in the earlier faunas: their teeth represent nine per cent of the mammal teeth found in Guimarota (Martin 2001; but see Martin's remark, 2001: 123), slightly more in Kirtlington. However, as aptly warned by Freeman (1979: 145) "it is a highly dangerous practice to assume that a given Mesozoic mammal fossil assemblage *even approximately* represents the live fauna from which it was derived".

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