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ANALYSIS OF MOLAR STRUCTURE AND PHYLOGENY OF DOCODONT GENERA

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ABSTRACT

Docodonts are a Mesozoic mammal group (Synapsida: Mammaliaformes) with a fossil record from the Middle Jurassic to the late Early Cretaceous. With highly distinctive molars for both shearing and grinding functions, docodonts are inferred to have diverse dietary adaptations, including insectivory, omnivory, and even carnivory. This group also offers the earliest-known case of mammalian swimming adaptation; at least two docodonts are inferred to have occupied a semi-aquatic niche. Here we present a phylogenetic analysis of 31 dental characters of docodonts (12 genera), plus six outgroups, including the taxa considered by some to be close relatives to docodonts. Our analysis recognizes a clade of *Itatodon* and *Krusatodon* and a clade of *Tashkumyrodon* and *Borealestes*, both of the Middle Jurassic. There is also a well-supported Late Jurassic Euroamerican clade (*Dsungarodon, Docodon,* and *Haldanodon*) and an Asiatic clade (*Sibirotherium* and *Tegotherium*). The Late Jurassic and Early Cretaceous clades are nested in a paraphyletic series of plesiomorphic taxa from the Middle Jurassic of Eurasia. Our re-analysis of *Gondtherium* from the Kota Formation of India confirms its docodont affinity and supports a prior hypothesis that this group dispersed to Gondwana during the Middle Jurassic. We hypothesize that docodonts and Late Triassic *Tikitherium* are sister taxa, and that the *Tikitherium*-docodont clade, in turn, is related to the mammaliaforms *Woutersia* and *Delsatia*. Contingent on the current scheme of cusp homology, docodonts are related to some Late Triassic mammaliaforms with triangular molar cusps, a paraphyletic group commonly known as "symmetrodonts."

INTRODUCTION

Docodonts are a mammaliaform group, characterized by very distinctive molars with a complex cusp and crest pattern adapted to both shearing and crushing functions. Their versatile dental functions are supposedly correlated with diverse dietary adaptations, from insectivory to omnivory, and even carnivory. Docodonts have a wide range of body sizes, from mole-sized small mammals to platypus-sized larger mammals. Two docodonts are inferred to have occupied a semi-aquatic niche (Martin and Nowotny 2000; Martin 2005, 2006), and at least one had developed skeletal structures for swimming (Ji et al. 2006).

This group is more primitive than the mammalian crown group, but more closely related to modern Mammalia than *Sinoconodon*, morganucodontans, kuehneotheriids, and haramiyidans, according to several studies of currently available skull and postcranial evidence (Wible and Hopson 1993; Luo 1994; Rougier et al. 1996; Luo et al. 2002; Luo and Wible 2005; Martin 2005). Among mammaliaforms of the Late Triassic to Early Jurassic, the Docodonta used to be considered to be relatives of morganucodonts (Hopson and Crompton 1969; Kermack et al. 1973; Lillegraven and Krusat 1991; Averianov and Lopatin 2006), but more recently, the prevailing hypothesis is that the Docodonta are closely related to some "symmetrodont-like" mammaliaforms (Sigogneau-Russell and Hahn 1995; Butler 1997).

To date, uncontested docodonts have been found from the Middle Jurassic through Aptian-Albian beds of the Cretaceous, and their geographic distribution is in the northern Laurasian continents during the Middle Jurassic to late Early Cretaceous, except for one putative taxon from India (Prasad and Manhas 2001, 2007). They reached their peak diversity in the Middle Jurassic, and only one genus extended into the late Early Cretaceous (Maschenko et al. 2002; Kielan-Jaworowska et al. 2004; Martin and Averianov 2004; Lopatin and Averianov 2005; Pfretzschner et al. 2005; Ji et al. 2006). Although *Reigitherium* from Argentina was previously considered to be a docodont (Pascual et al. 2000), this taxon is now regarded to be a highly transformed dryolestoid (Rougier and Apesteguia 2004).

The cranial anatomy of the Docodonta has been described for only one taxon, *Haldanodon* (Lillegraven and Krusat 1991), and postcranial characteristics are known for *Haldanodon* and *Castorocauda* (Martin 2005; Ji et al. 2006). Most docodonts are represented only by jaws and isolated teeth (Simpson 1928, 1929; Kron 1979; Kielan-Jaworowska et al. 2004). The mandibular structure is very conserved and shows relatively little systematic variation among docodonts (Simpson 1929; Krusat 1980; Lillegraven and Krusat 1991; Averianov et al. 2005; Ji et al. 2006). Accordingly, the phylogenetic relationships of docodont genera must be based on molar characters. Molars of docodonts are so specialized and distinctive from other Mesozoic mammals that there have been some uncertainties about the homology of their molar cusps with respect to those of other Mesozoic mammals. However, Butler's (1997) scheme of docodont molar cusp homology is now generally accepted by other students (Fig. 1). Historical changes in our understanding of the cusp homology of docodonts to those of other Mesozoic mammals are reviewed below.

Molar Cusp Homology

The upper molars of docodonts are characterized by a "T-shaped" pattern, with two or three labial cusps in anteroposterior alignment and a prominent lingual cusp that can form a transverse crest with respect to the labial cusp row (Fig. 1). The lower molars of docodonts are characterized by a labial row of higher cusps and a lingual cingulid row of smaller cusps. The main labial cusp (a) and two cusps on the lingual row can form a triangular pattern. This is best de-

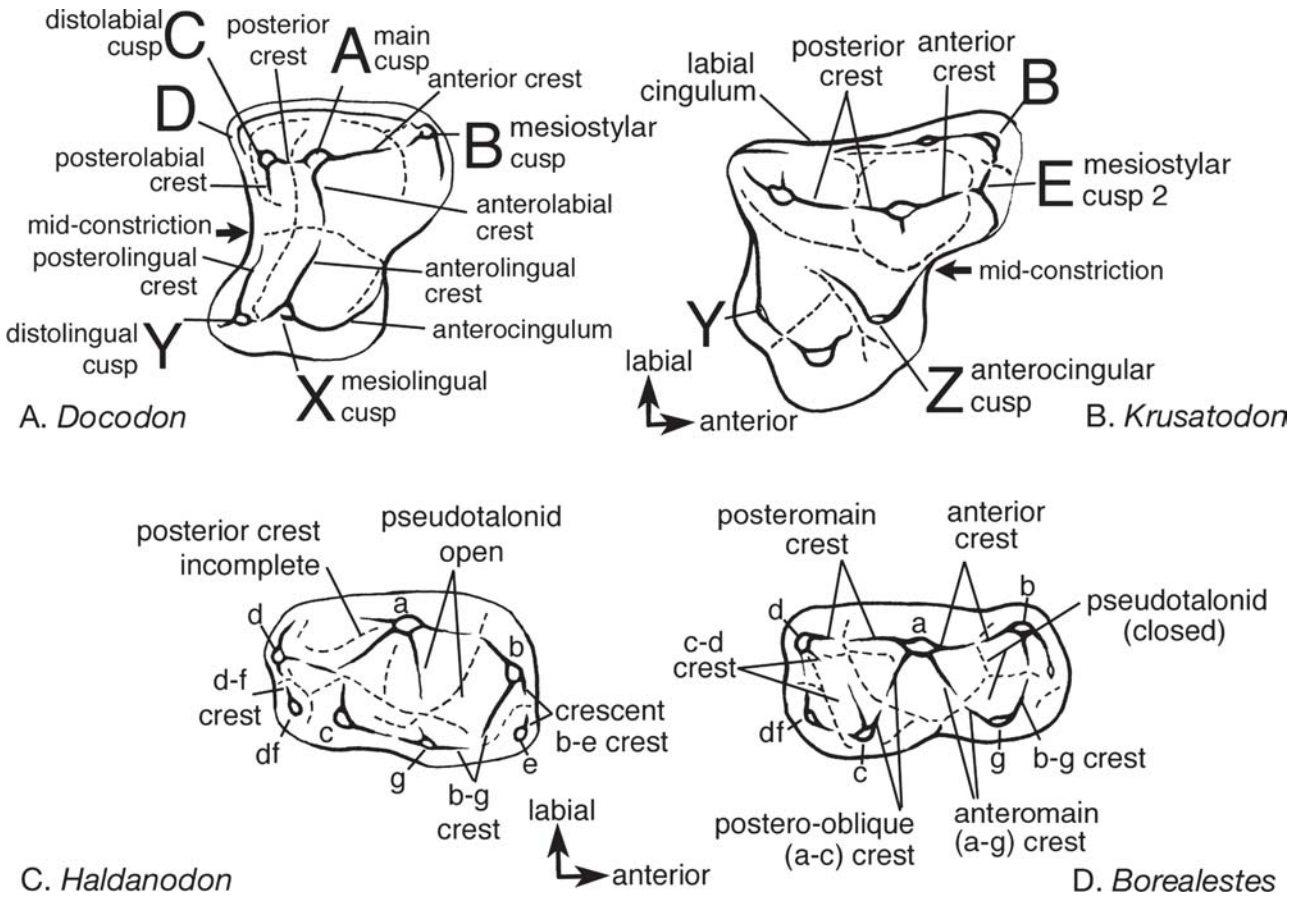

Fig. 1.—Diagrammatic definition of terminology of docodont molar structures. **A**, upper molar of *Docodon*; **B**, upper molar of *Krusatodon* [modified from Sigogneau-Russell (2003)]; **C**, lower molar of *Haldanodon* [modified from Butler (1997)]; **D**, Lower molar of *Borealestes* [modified from Sigogneau-Russell (2003)]. Wherever applicable, the alphabetical designation of molar cusps follows Butler (1997). Descriptive definition of crests and basins follows Sigogneau-Russell (2003), as supplemented by Kielan-Jaworowska et al. (2004) and Pfretzschner et al. (2005). The abbreviated crest designation by connected cusps is developed here.

veloped in Middle Jurassic docodonts, but can be secondarily obscured by the extensive development of smaller ridges and grooves on the occlusal surface in several Late Jurassic taxa. The complex pattern of cusps and crests on the upper teeth does not always correspond in an unambiguous fashion with similar structures on the lower teeth, and this has led to alternative interpretations of their dental function and wear patterns (e.g., Jenkins 1969; Gingerich 1973), and also to entirely different schemes of cusp homology, as discussed below. Among the homology schemes proposed so far, each poses certain problems. In the proposal by Patterson (1956), the lack of any correspondence between the upper molar lingual cusp and a lower molar structure was not explained, and there would be no corresponding structure for the lower docodont cusp c in the morganucodont-like molar structure. The lower cusp c would not correspond to upper cusp C in the proposal by Butler (1997), which is adopted by this study. Both lower cusps c and "b" would lack occlusal correspondence to upper cusps C and B in the proposal by Sigogneau-Russell and Godefoit (1997; also see Kermack et al. 1987). All of the alternative cusp homology schemes of docodonts (Fig. 2), including the one preferred here, have some inherent uncertainty because of the lack of clear correspondence between some upper and lower tooth structures.

In his classic works on docodonts, Simpson (1928, 1929, 1971) emphasized that the upper lingual cusp occludes with (and grinds against) the complex occlusal surface of the lower molar. This bears resemblance to therian mammals. As a result, Simpson (1928, 1929) classified docodonts as belonging to pantotherians, an ancestral group from which the modern therians evolved. However, Simpson (1928, 1929) interpreted the docodont dental pattern only in general terms of overall resemblance, and did not offer any detailed discussion of the cusp pattern, let alone the wear facets associated with cusps.

The first explicit scheme of docodont cusp homology, in the broad context of a wide range of Mesozoic mammals, was proposed by Patterson (1956). The Patterson homology scheme for docodont molars was reviewed by Krusat (1980). This scheme of cusp designation assumes that the labial cusp row on docodont lower molars (cusps a, b, and

d) are homologues of cusps a, b and d on molars of *Morganucodon* (Fig. 2A, E). Under this assumption, the key features of docodont lower molars are in straight alignment, being similar to all mammaliaforms with "triconodont-like" molars, such as those of *Megazostrodon* and *Dinnetherium* (see "traditional scheme" in Fig. 2). The labial row cusps on the upper molars of docodonts (cusps A and C) are considered to be homologues to cusps A and C of *Morganucodon*. The upper lingual cusps X and Y of docodonts (Fig. 1) have no corresponding structures in *Morganucodon*, and are therefore considered to be neomorphic (Patterson 1956; Krusat 1980). This scheme was widely accepted by the majority of Mesozoic mammal workers in the 1970s (Hopson and Crompton 1969; Jenkins 1969; Kermack et al. 1973; Gingerich 1973; Kron 1979).

However, this traditional scheme of cusp homology poses some difficulties, and significant morphological differences remain, even if the labial cusp row of the lower molars of docodonts is homologized with the main cusp row of *Morganucodon*. According to the Patterson (1956) scheme, lower cusp c and upper cusp B of *Morganucodon* have no corresponding structures in docodonts (Fig. 1A, C). If the lower molar labial cusp row of docodonts is supposed to be homologous to the main cusp row of *Morganucodon*, then cusp "c" of *Morganucodon* has no corresponding structure in docodonts, and would have to be lost or somehow "missing" in docodonts (see Fig. 2E). If the labial row on the upper molars of docodonts is supposed to be homologous to the main cusp row of the upper molar of *Morganucodon*, then cusp "B" of *Morganucodon* would have to be regarded as lost or somehow "missing."

Butler (1997; also see Fig. 2 here) designated lower cusp c in both *Morganucodon* and the Late Triassic "symmetrodont-like" mammaliaforms, as exemplified by *Woutersia*, to be the homolog of the distolingual cusp of the docodont lower molar (a cusp formerly known as "g" in the traditional scheme) (Fig. 2F: Butler scheme). Butler's scheme has satisfactorily accounted for the homology of cusp c of morganucodonts in docodonts. It is significantly different from the traditional Patterson scheme (Fig. 2E) in assuming a triangulation of cusps b-a-c. Its triangulated molar cusp pattern is therefore homologous with those of *Woutersia* and other "symmetrodont mammaliaforms" with cusp triangulation (Fig. 2B). Under the traditional scheme of cusp

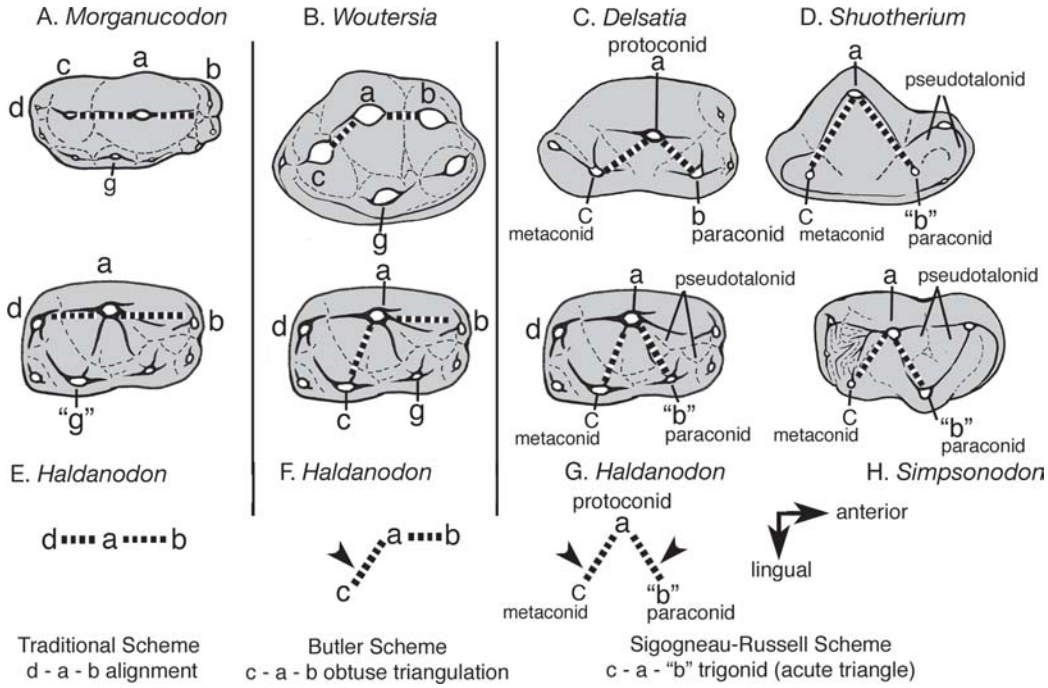

Fig. 2.—Alternative hypotheses of homology of docodont lower molar structures (see Table 1). (**A**, **E**) traditional scheme proposed by Patterson (1956) as illustrated by Krusat (1980), whereby cusps in the labial row of the lower molar of docodonts (**E**) are considered to be homologous to the main cusp row in *Morganucodon* (**A**); the docodont pattern is considered to be fundamentally different from kuehneotheriids. (**B**, **F**) Butler's (1997) scheme, whereby the distolingual cusp c (cusp "g" of Krusat, 1980) of docodonts (**F**) is designated to be homologous to cusp c (metaconid) of mammaliaforms having a triangular molar cusp pattern, as exemplified by *Woutersia* (**B**). Cusps b-a-c form an obtuse triangulation, although not fully equivalent to the trigonid of the acute-triangled symmetrodonts (trechnotherians). The "pseudotalonid" [sensu Martin and Averianov (2004)] in this scheme is not homologous to the pseudotalonid of *Shuotherium*. (**C**, **G**) The homology scheme proposed by Sigogneau-Russell and Godefroit (1997), whereby the mesiolingual cusp "b" (cusp g of Butler) is homologized with the paraconid (cusp b), and the distolingual cusp c is homologized with the metaconid (cusp c) of symmetrodont mammaliaforms. The main difference between the Butler scheme (**B**, **F**) and the Sigogneau-Russell scheme (**C**, **G**) is that the latter considers the triangulated crest a-"b" and crest a-c of docodonts to form an acute triangle that is equivalent to the trigonid of derived symmetrodonts [the trechnotherian clade *sensu* Kielan-Jaworowska et al. (2004)]. In the Sigogneau-Russell scheme, the anterior basin (the area anterior to crest a-"b") in docodonts is homologous to the pseudotalonid of *Shuotherium* (**D**), as first noted by Kermack et al. (1987).

homology (Patterson 1956; Krusat 1980), docodont molars are more comparable to those of *Morganucodon* with "triconodont-like" teeth than "symmetrodont-like" teeth. In the Butler (1997) scheme, however, docodont molars are more comparable to "symmetrodont" teeth with a triangulated molar cusp pattern. By extrapolation, two main shearing crests (crest a-b and crest a-c) of docodonts would be homologous with the triangulated crests a-b and a-c of a symmetrodont-like mammaliaform. Butler's (1997) homology scheme is similar overall to Simpson's (1928, 1929) proposition regarding dental similarity of docodonts and pantotherians. However, Butler (1997) has offered much more detailed justification by matching upper and lower tooth structures.

The resemblance of the cusp-crest pattern in docodont molars to the triangular cusp pattern of "symmetrodont-like" molars was also noted from a different comparative perspective by other students of Mesozoic mammals. Kermack et al. (1987) suggested that *Shuotherium*, a Mesozoic mammal with a triangulated molar cusp pattern, is similar and possibly related to the docodont *Simpsonodon*. Tatarinov (1994) also noted the similarity of *Shuotherium* to the docodont *Tegotherium*. Sigogneau-Russell and Godefroit (1997) observed the similarity between docodont molars and those of the Late Triassic mammaliaform *Delsatia* with triangulated molar cusps. They suggested that docodonts are similar to *Delsatia* in that the docodont molar cusps a, b and c (= former "g") are equivalent to the trigonid in symmetrodont-like molars (Fig. 2C, D, G). The lower cusp "b" is considered to be equivalent to the paraconid, and cusp c is considered to be equivalent to the metaconid of symmetrodonts (Sigogneau-Russell and Godefroit 1997). Key differences between Sigogneau-Russell and Godefroit (1997) and Butler (1997) are in the placement of the paraconid (cusp "b"), and in the nature of the pseudotalonid for docodonts.

Butler's proposed homology on cusp c has been endorsed by all subsequent studies (Sigogneau-Russell and Godefroit 1997; Maschenko et al. 2002; Martin and Averianov 2004; Lopatin and Averianov 2005; Pfretzschner et al. 2005; Ji et al. 2006). In the character analysis of docodont molar structures, we follow the basic cusp homology scheme of Butler (1997) in considering the distolingual cingulid cusp in docodonts to be the homolog of cusp c on the lower molars of *Morganucodon* and mammaliaforms with triangulated molars, such as *Kuehneotherium*, *Woutersia,* and *Delsatia* (as illustrated in Figs. 1 and 2F). In defining systematic characters, we follow the cusp and crest nomenclature as illustrated in Figures 1 and 2F. The overall patterns of dental variations in different times in geological time scale are shown in Figure 3 for the lower molars and Figure 4 for the upper molars.

MATERIALS AND METHODS

Abbreviations

Gui Mam, Guimarota Mammal. The *Haldanodon* specimens from the Guimarota coal mine are currently housed for study at the Institut für Paläontologie of the University of Bonn, Germany under the acronym Gui Mam (Guimarota Mammal) plus specimen number/year of collecting (e.g., Gui Mam 41/75 is mammal specimen number 45 collected in 1975) [see also Lillegraven and Krusat (1991, p. 132)]. VJ 1001–155, a specimen number used in the classic study of Krusat (1980), and listed here for reference. **SGP**, the permanent specimen numbers in the paleontological collection of the former Serviços Geológicos de Portugal (Lisboa) (now Geological Museum), where the corresponding specimens will finally be deposited. **SNP**, specimens of comparative taxa from Saint-Nicholas-de-Port, deposited in the Muséum National d'Histoire Naturelle, Paris.

Taxonomic and Character Sampling

Taxonomic sampling.—In this phylogenetic analysis, we included the following undisputed docodont genera: *Borealestes* (Waldman and Savage 1972; Sigogneau-Russell 2003), *Docodon* (Simpson 1928, 1929), *Castorocauda* (Ji et al. 2006), *Dsungarodon* (Pfretzschner et al. 2005), *Haldanodon* (Krusat 1980; Martin and Nowotny 2000; Nowotny et al. 2001), *Itatodon* (Lopatin and Averianov 2005; Averianov and Lopatin 2006), *Krusatodon* (Sigogneau-Russell 2003), *Sibirotherium* (Maschenko et al. 2002), *Simpsonodon* (Kermack et al. 1987), *Tashkumyrodon* (Martin and Averianov 2004), and *Tegotherium* (Tatarinov 1994). We follow Averianov (2004) in excluding "*Peraiocynodon*" (Simpson 1928; Sigogneau-Russell 2003). We note that *Simpsonodon* is considered to be a junior synonym of *Cyrtlatherium.* "*Cyrtlatherium*" (Freeman 1979) is based on deciduous teeth or juvenile specimens of *Simpsonodon* according to the latest consensus (Sigogneau-Russell 2003; Martin and Averianov 2004; Averianov 2004; Kielan-Jaworowska et al. 2004). Because its permanent teeth are more reliable for character interpretation, we prefer *Simpsonodon* (Kermack et al. 1987) to "*Cyrtlatherium*" here. Dental features on deciduous teeth are less reliable for systematic inference. The South American taxon *Reigitherium* was originally considered to be a dryolestoid (Bonaparte 1990). Pascual et al. (2000) reconsidered *Reigitherium* to be a docodont on the basis of more complete fossils. However, this assignment has been disputed, and *Reigitherium* is not considered to be a docodont here. It is either a dryolestoid (Rougier and Apesteguia 2004) or a taxon of uncertain position in Mammalia (Kielan-Jaworowska et al. 2004).

The definition of the docodont ancestry and the diagnosis of the Docodonta are dependent on their putative sister group. Derived diagnostic features of docodonts can only be established by way of contrast with the plesiomorphic condition in their nearest relatives. It has been proposed that the Docodonta are related to some mammaliaforms of the Late Triassic and Early Jurassic. For example, it was suggested that the Late Triassic mammaliaform *Woutersia* of Europe would be closely related to docodonts (Butler 1997), or that *Delsatia* should be included in Docodonta (Sigogneau-Russell and Godefroit 1997). The Late Triassic mammaliaform *Tikitherium* from the Upper Triassic of In-

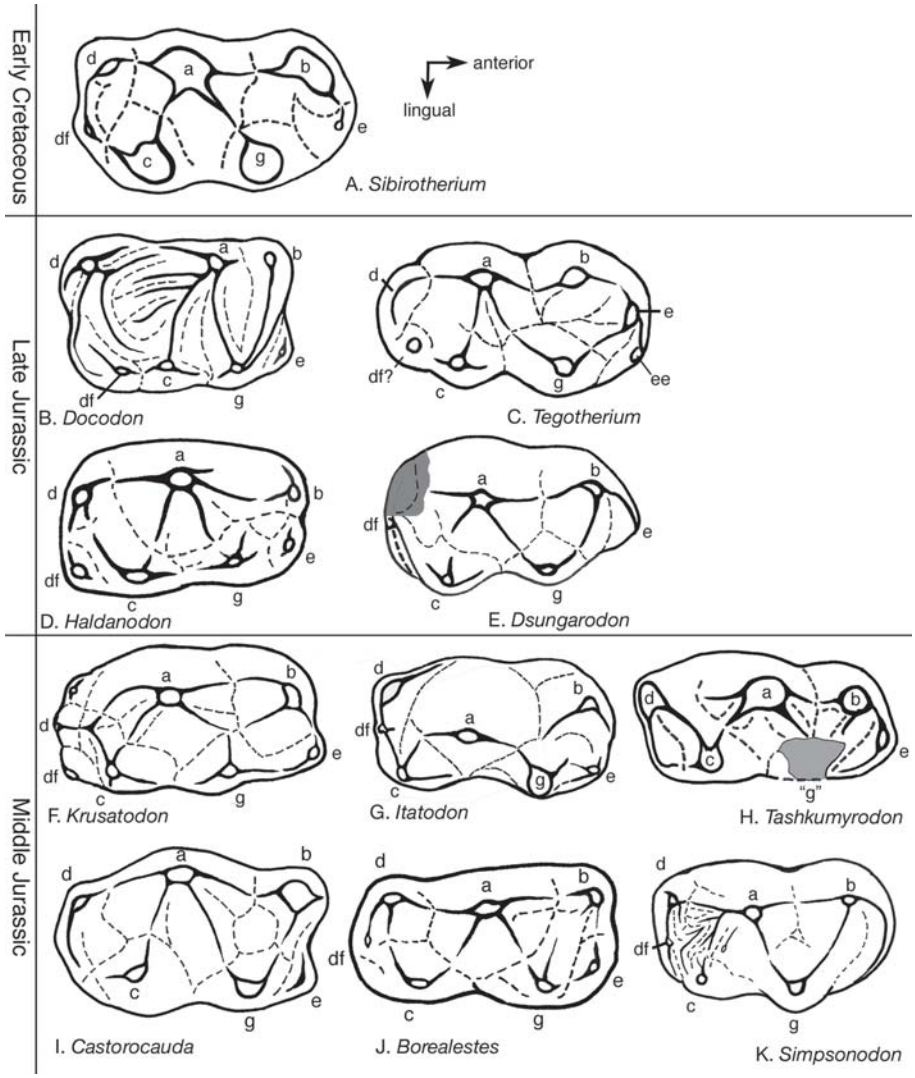

Fig. 3.—Systematic character variation of the lower molar cusps among selected docodontans. **A**, *Sibirotherium* (re-drawn from Maschenko et al. 2002); **B**, *Docodon*. C. *Tegotherium* (redrawn from Tatarinov 1994); **D**, *Haldanodon*; **E**, *Dsungarodon* (redrawn from Pfretzschner et al. 2005); **F**, *Krusatodon* (redrawn from Sigogneau-Russell 2003); **G**, *Itatodon* (redrawn from Averianov and Lopatin 2006); **H**, *Tashkumyrodon* (from Martin and Averianov 2004); **I**, *Castorocauda;* **J**, *Borealestes* (redrawn from Sigogneau-Russell 2003); **K**, *Simpsonodon* (redrawn from Kermack et al. 1987).

dia (Datta 2005) resembles the Docodonta in upper molar morphology; we therefore included *Tikitherium* here for comparison with other putative relatives of docodonts. It should be mentioned that the specimens assigned to *Woutersia* show significant variation in several features (Sigogneau-Russell 1983; Sigogneau-Russell and Hahn 1995). According to Averianov and Lopatin (2006) these differences may reflect gradational variation of morphological features along the tooth row.

In order to develop a balanced reanalysis of the competing views on the mammaliaform sister group of the Docodonta, we included *Tikitherium*, *Woutersia,* and *Delsatia* in the parsimony analysis, and we will discuss the affinities of these taxa to the Docodonta, a posteriori. Because *Tikitherium*, *Woutersia,* and *Delsatia* are previously referred to as "symmetrodonts," more mammaliaforms ought to be selected as outgroups in order to root the tree properly for parsimony analyses; therefore, we selected *Morganucodon*, *Megazostrodon*, and *Kuehneotherium*. It is also necessary to include these outgroups from a morphological point of view. *Morganucodon* is required for this analysis because it is traditionally accepted that the main cusps a, b, and c in straight alignment on *Morganucodon* molars are homologous to the labial series of cusps on the lower molars of docodonts (Patterson 1956; Krusat 1980). *Woutersia* and *Delsatia* were selected for the new scheme of cusp homology for *Woutersia* and docodonts as suggested by Butler (1997) and Sigogneau-Russell and Godefroit (1997), and followed at least in part by other workers (Martin and Averianov 2004; Pfretzschner et al. 2005) (Figs. 1–2).

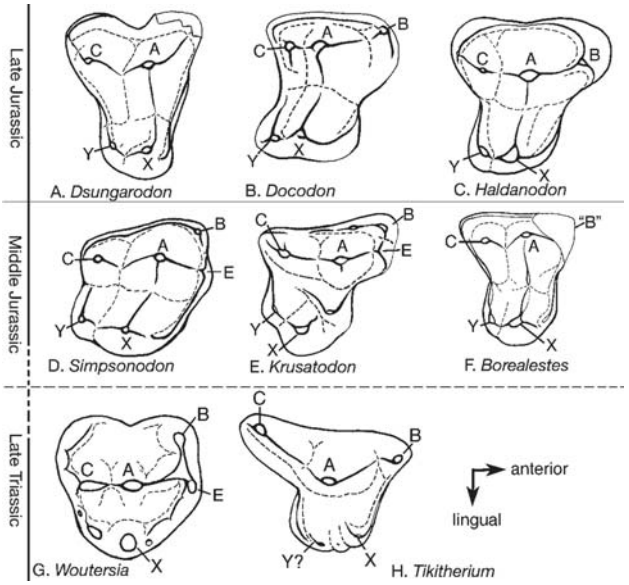

Fig. 4. Systematic variation of upper molar cusp patterns among several docodonts and putative relatives. **A**, *Dsungarodon* (redrawn from Pfretzschner et al. 2005); **B**, *Docodon*, **C**, *Haldanodon;* **D**, *Simpsonodon* (redrawn from Kermack et al. 1987); **E**, *Krusatodon* (redrawn from Sigogneau-Russell 2003); **F**, *Borealestes* (redrawn from Sigogneau-Russell 2003); **G**, *Woutersia* (redrawn from Sigogneau-Russell and Hahn 1995); **H**, *Tikitherium* (reoriented from Datta 2005).

Character sampling.—Besides *Haldanodon* and *Castorocauda*, most docodonts are only represented by teeth and mandibles. Mandibular structure is uninformative for interpreting the relationships of docodont genera because it is remarkably similar among all docodont genera for which the mandibles are known (Simpson 1928, 1929; Krusat 1980; Lillegraven and Krusat 1991; Averianov et al. 2005; Ji et al. 2006). Therefore, dental characteristics become the default source of information for phylogenetic analysis.

With the justification provided above, we followed Krusat (1980) and Butler (1997) in the designation of the molar cusps of docodonts, with some minor modifications. Sigogneau-Russell (2003) developed an extensive and accurate scheme of naming cusps after their topographic locations, with a similar assumption that the main crests (anteromain and posteromain crests of her fig. 1) are triangulated. This has been adopted by Kielan-Jaworowska et al. (2004). The synonymy of these features between Butler (1997; see also Martin and Averianov 2004; Pfretzschner et al. 2005) on the one hand, and Sigogneau-Russell (2003; see also Kielan-Jaworowska et al. 2004) on the other, is illustrated in Figures 1-4 and summarized in Table 1.

We introduced 11 new characters and scored these among docodont genera in this analysis. Many of the lower molar characters of this study are adapted, with modification in some cases, from the character lists of Martin and Averianov (2004) and Pfretzschner et al. (2005). Upper molar characters are adapted with modification from Sigogneau-Russell (2003), Prasad and Manhas (2001), and Datta (2005). The canine character is adopted from Averianov and Lopatin (2006). For definition and description of characters see Appendix 1. The original sources of these characters are listed under each character. Each character state is also illustrated in at least one figure here. Some molar features of docodonts show gradational variation along the tooth row. Because characters are less variable in the anterior molars among individuals of the docodont *Haldanodon exspectatus*, we relied on the anterior molars (M^{1-3}) to define the characters, if such variations occur (discussed below) (Figs. 5 to 9). In total, we scored six outgroup taxa, 12 ingroup taxa of docodonts, and 29 molar characters. The distribution of the systematic characters is presented in Appendix 2. PAUP 4.0b (Swofford, 2000) search parameters are presented with Figure 10 and discussion.

VARIABILITY OF MOLAR CHARACTERS IN *HALDANODON EXSPECTATUS*

Haldanodon exspectatus from the Late Jurassic (Kimmeridgian) of the Guimarota Coal Mine in Portugal is the only docodont for which a large number of upper and lower dentitions are available. It therefore provides an opportunity to evaluate the variability of molar characters that are used in the phylogenetic analysis. Here we document the variation gradient along the tooth row and show that dental characters are less variable on the anterior molars but more so on the posterior molars, especially on the reduced ultimate and penultimate molars.

Upper molars (Figs. 5–6).— *Haldanodon exspectatus* has five upper molars, of which M^5 is vestigial and does not show the typical molar characters (Nowotny et al. 2001). M^4 is smaller than M^{1-3} and is simplified in some specimens (e.g., Gui Mam 41/75 [SGP 6721]), whereas it corresponds in size and shape to M^{1-3} in others (Gui Mam 16/78 [SGP 6724]), or is intermediate (Gui Mam 72/78). In general, a number of characters on our list (Appendices 1 and 2) show a gradational variation, and this is reviewed here.

Character 1 (transverse widening of upper molars) is constantly present in all M^{1-3} and most M^4 among the specimens examined. Character 2 (mesiolingual cusp X of upper molars: wear facets on the labial aspect of the cusp) is well-developed on M^{1-4} of all specimens examined except Gui Mam 41/75 (SGP 6721), in which cusp X on the simplified M^4 has an apical wear facet. Character 3 (transverse mesiolingual and mesiolabial crests between cusp A and cusp X) is present on M^{1-4} of all studied specimens, although it may be obliterated in worn specimens (e.g., Gui Mam 72/78). Character 4 (cusp Y or the upper distolingual cusp) is present, distinctive and in straight anteroposterior alignment only on M^{1-2} of the examined specimens; on M^3 it is reduced in size and shifted somewhat labially; on M^4 it is either vestigial (Gui Mam 16/78 [SGP 6724]) or completely absent (Gui Mam 30/79 [SGP 6726]) (the molar dentition of both specimens is only slightly worn, so this difference cannot be attributed to different degree of dental wear). In more heavily worn specimens (e.g. Gui Mam 41/75 [SGP 6721], 72/78), cusp Y may be vestigial or com-

Table 1. Homology and terminology of molar structure[1].

Butler (1997); Pfretzschner et al. (2005)	Sigogneau-Russell (2003); Kielan-Jaworowska et al (2004)	Molar Structure terminology used in this paper (defined in Fig. 1)	Newly defined molar features and explanations
		Lower Molar	
cusp a	main cusp	cusp a	
cusp b	mesiolabial cusp	cusp b	
cusp c	distolingual cusp	cusp c	
cusp d	distolabial talonid cusp	cusp d	
cusp e	cuspule	cusp e	mesiolingual cingulid cuspule
cusp df[2]	lingual talonid cusp	docodont cusp f	distolingual cingulid cuspule
cusp g	mesiolingual cusp	cusp g	
	anteromain crest	a-g crest	antero-oblique crest
		a-b crest	anterior crest
	anterobasal crest	b-g crest	
	crescent	b-e crest	mesiocingulid crest
	pseudotalonid	pseudotalonid[3]	pseudotalonid[3]
	posteromain crest	a-d crest	
		a-c crest	postero-oblique crest
	posterior crest	c-f crest	posterolingual crest
	cingulum	d-f crest	distal-cingulid crest
		c-d crest	transtalonid crest
	lingual cingulum	lingual cingulid	
		Upper molar	
cusp A	mesiolabial cusp	cusp A	
cusp B	mesial stylar cusp 1	cusp B	
cusp C	distolabial cusp	cusp C	
cusp D	distal stylar cusp	cusp D	
cusp E	mesial stylar cusp 2	cusp E	
cusp X	mesiolingual cusp	cusp X	cusp Z (Datta 2005)[4]
cusp Y	distolingual cusp	cusp Y	
		cusp Z	anterocingular cusp
	anterior crest	A–B crest	
	posterior crest	A–C crest	
	anterolabial crest	anterolabial crest	anterolabial transverse crest
	anterolingual crest	anterolingual T-crest	anterolingual transverse crest
	posterolabial crest	posterolabial T-crest	posterolabial transverse crest
	posterolingual crest	posterolingual T-crest	posterolingual transverse crest
	cingulum	anterocingulum	anterocingulum
	labial cingulum	labial cingulum	

[1]Several molar features show a gradient of variation along the tooth row (see the discussion regarding the variability of molar characters in *Haldanodon exspectatus*). The morphological features on the anterior molars (M_{1-3}) are more conserved than those of posterior molars. We prefer to use the character condition on the anterior molars in case of such morphological variation along the tooth row (see Figs. 5–8).

[2]Lower cusp df stands for the "docodont cuspule f." By accident, this distolingual cusp was designated as cusp f in the terminology of docodont molars (Martin and Averianov 2004, figs. 3, 5). However, it is entirely different from the mesiolabial cingulid cusp f (the "standard cuspule f") that has long been designated for morganucodonts and kuehneotheriids, crown therians, and their near relatives (Crompton 1974; Kielan-Jaworowska et al. 2004). Accordingly, cusp df is meant to be distinguished from cuspule f in other taxa.

[3]The pseudotalonid of this paper follows the same usage employed by Martin and Averianov (2004) and Pfretzschner et al. (2005) (Fig. 2B, F), which differs from the pseudotalonid of Kermack et al. (1987) and Sigogneau-Russell (2003) in its topographical relationship to the a-b crest, due to the different hypotheses regarding homology between lower molar cusps of docodonts and the paraconid cusp b of symmetrodont-like and morganucodont mammaliaforms.

[4]Cusp X in the present paper is the same as cusp Z designated by Sigogneau-Russell and Godefroit (1997) and Datta (2005). The former cusp Z in *Delsatia* (Sigogneau-Russell and Godefroit 1997) and *Tikitherium* (Datta 2005) is renamed here as cusp X and homologized with the mesiolingual cusp X of docodonts.

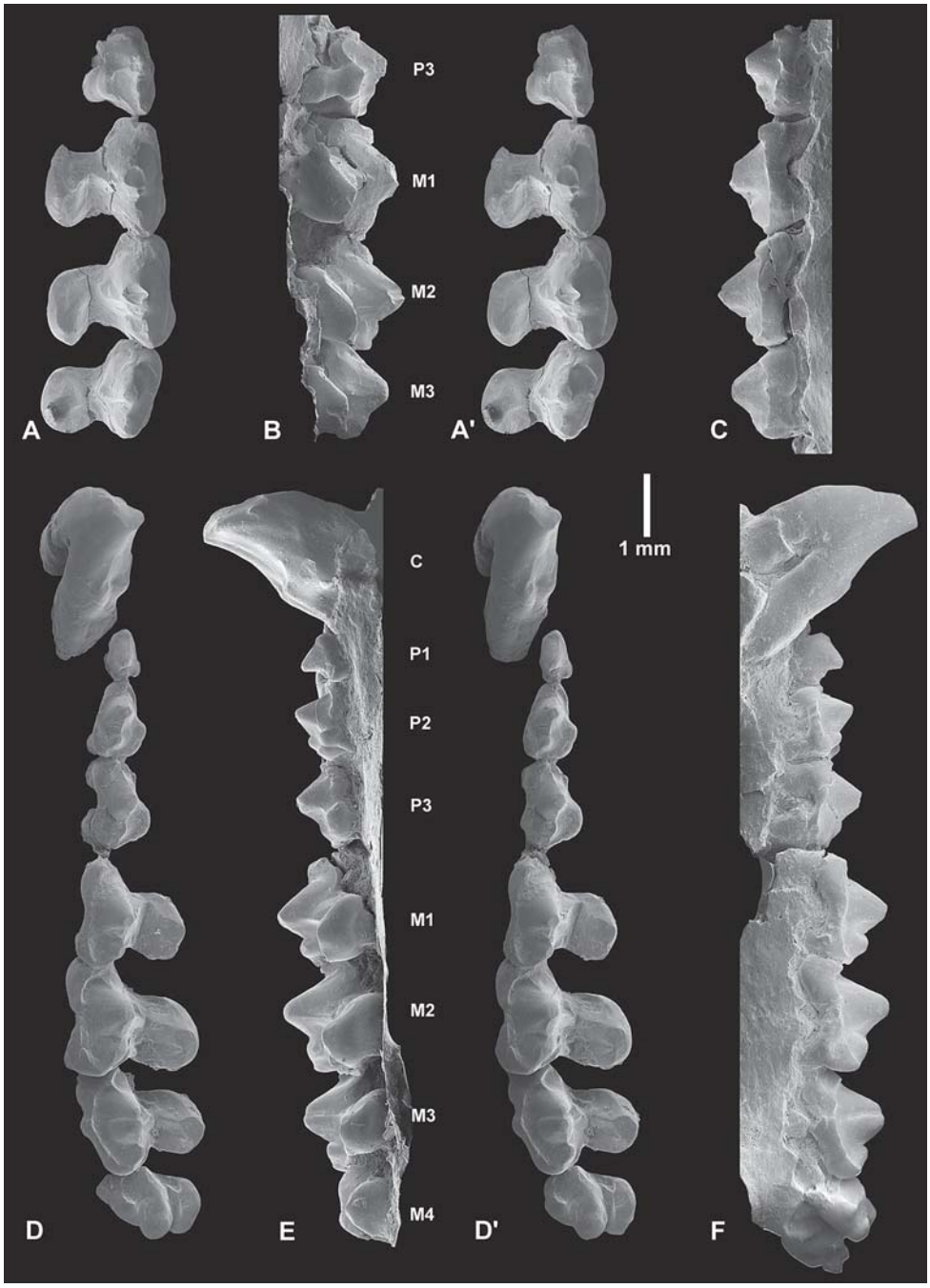

Fig. 5.—Morphological variation in the upper dentition of the docodont *Haldanodon exspectatus*, Late Jurassic (Kimmeridgian) of the Guimarota Coal Mine, Portugal. Upper dentition in occlusal (A, A′ and D, D′, stereopairs), lingual (B, E), and labial views (C, F). **A–C**, Gui Mam 41/75 [SGP 6721], left maxillary dentition with P^4, $M^{1–3}$; **D–F**, Gui Mam 60/76 [SGP 6732], right maxillary dentition with C^1, $P^{1–3}$, $M^{1–4}$ (photos of epoxy casts).

pletely absent. Character 5 (size and development of cusp C or the distolabial cusp; its separation from cusp A or the mesiolingual cusp): cusp C is reduced and twinned with cusp A on $M^{1–4}$ of all studied specimens. Character 6 (posterior transverse crest between distolabial [C] and distolingual [Y] cusps) is present on $M^{1–4}$ of the specimens examined, but it may be removed by wear in teeth with older functional ages (e.g., Gui Mam 41/75 [SGP 6721], 72/78). Character 7 (cusp E, separated from cusp B) is missing on the molars of all studied specimens. Character 8 (constricted waist between the labial part and the lingual part of the upper tooth) is present on $M^{1–4}$ of the studied specimens (except for the simplified and reduced M^4 of Gui Mam 41/75 [SGP 6721]). Due to the vestigial nature of M^5 and vari-

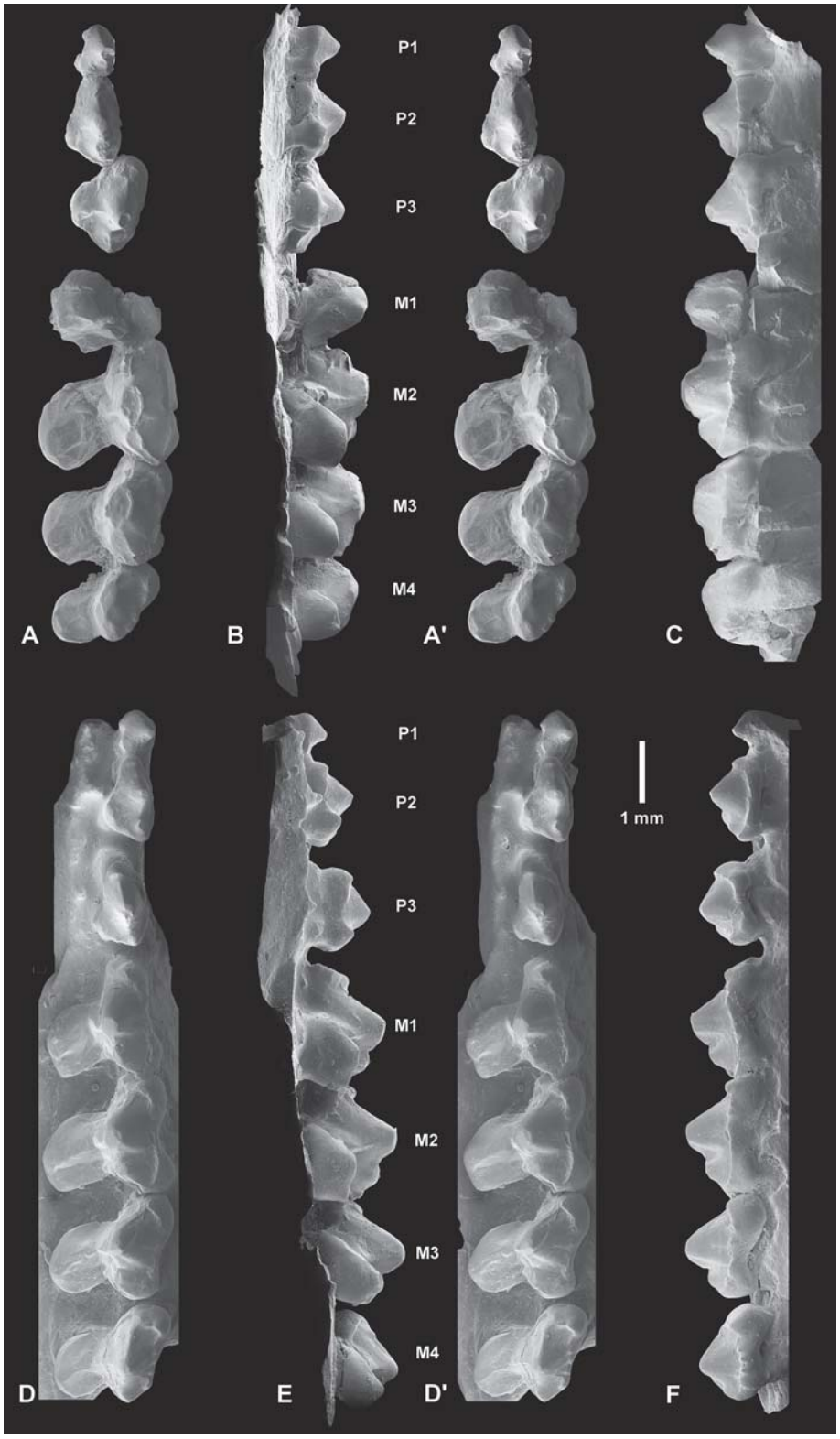

Fig. 6.—Morphological variation of upper dentition in *Haldanodon exspectatus*. Left maxillary dentitions in occlusal (A, A′ and D, D′, stereopairs), lingual (B, E), and labial views (C, F). **A–C**, Gui Mam 72/78, P^{1-3}, M^{1-4}; **D–F**, Gui Mam 72/78, P^{1-3}, M^{1-4} (photos of epoxy casts).

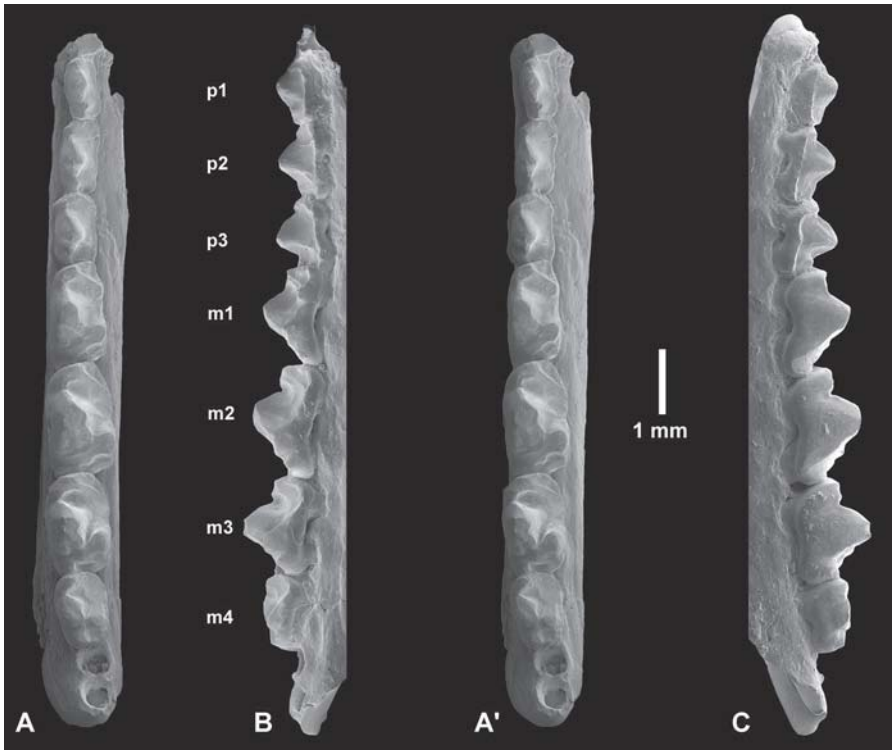

Fig. 7. *Haldanodon exspectatus* , Late Jurassic (Kimmeridgian) of Portugal. VJ 1001–155 (holotype), left lower dentition with P_{1-3}, M_{1-4}, and alveoli for M_5 in occlusal. (A, A′, stereopair), lingual (**B**), and labial views (**C**) (photos of epoxy casts).

able conditions on some M^4, character definitions should be based on $M^{1–3}$ for character analysis of *Haldanodon.*

Lower molars (Figs. 7–9).— *Haldanodon exspectatus* has up to six lower molars, although M_6 occurs only in a few specimens (e.g., Gui Mam 35/75 [SGP 6769]). Dentaries of adult specimens may have four to six molars (Nowotny et al. 2001); M_5 and M_6 are always vestigial, and even M_4 is much smaller than $M_{1–3}$ and is more simplified. Character 9 (cusp c on lingual cingulid and in alignment with mesiolingual cusp g) is present on M_{1-4} (but not on vestigial M_{5-6}) of all studied specimens. Character 10 (cusp c to cusp g size ratio): cusp c is much larger than cingular cusp g on $M_{1–5}$ of all studied specimens. Only on M_{3-4} of Gui Mam 79/75 is the size ratio somewhat closer, although cusp c is still clearly larger than cusp g. Character 11 (a-c crest) is complete and c-notched on $M_{1–5}$ of all specimens studied. Character 12 (presence vs. absence of cusp g): cusp g is largest on M_1, but considerably smaller (although clearly present) on $M_{2–3}$, in which the cusp is not only small in proportion to its tooth, but also more heavily reduced by wear. In the smaller M_{4-6}, cusp g is increasingly vestigial, if present at all. Character 13 (development of pseudotalonid): the pseudotalonid is present and appears lingually open on M_{1-4} of all studied specimens; on vestigial M_{5-6} no pseudotalonid is developed. Character 14 (v-notched a-g crest): this crest is present and incomplete on M_{1-4} of the examined specimens (in more vestigial M_4 it may be indiscernible; e.g., Gui Mam 122/76 [SGP 6796]). Character 15 (c-d crest in the posterior basin) is present and straight on $M_{1–3}$ of the studied specimens and may be missing on M_4 if this tooth is vestigial (e.g., Gui Mam 122/76 [SGP 6796]). Character 16 (placement of cusp d): cusp d is in a labial position on M_{1-4} of all studied specimens. Character 17 (folding of enamel) is not present on any of the molars of the examined specimens. Character 18 (the a-d crest alignment): crest a-d is straight on $M_{1–3}$ of the studied specimens. In vestigial M_4 it may be angled, if cusp d is somewhat shifted lingually (e.g., Gui Mam 122/76 [SGP 6796]). Character 19 (a-d crest): the a-d crest is incomplete on the molars of the examined specimens. Character 20 (the b-g crest) is present and continuous on $M_{1–4}$ of the studied specimens. Character 21 (size of cusp e) is reduced on the molars of all studied specimens (not distinctive from the cingulid). Character 22 (the mesiolingual cingulid extending from cuspule e or an equivalent position) is extending to below cusp g on the molars of all studied specimens. Character 23 (size of cusp b relative to cusp a): cusp b is small and appressed to cusp a on $M_{1–3}$ of all studied specimens. On M_4 cusps b and a are twinned, although cusp a is still larger; on M_{5-6} cusp b is not developed. Character 24 (“docodont cusp f,” posterolingually positioned) is present on $M_{1–3}$ of the studied specimens; on M_4 it may be reduced (e.g., VJ 1001–155 [SGP 6804], Gui Mam 79/75) or present (Gui Mam 3/77). Character 25 (the “standard cuspule f, ” mesiolabially positioned) is absent on the molars of all studied specimens. Character 26 (b-e crest) is absent on the molars of all studied specimens of *Halda-*

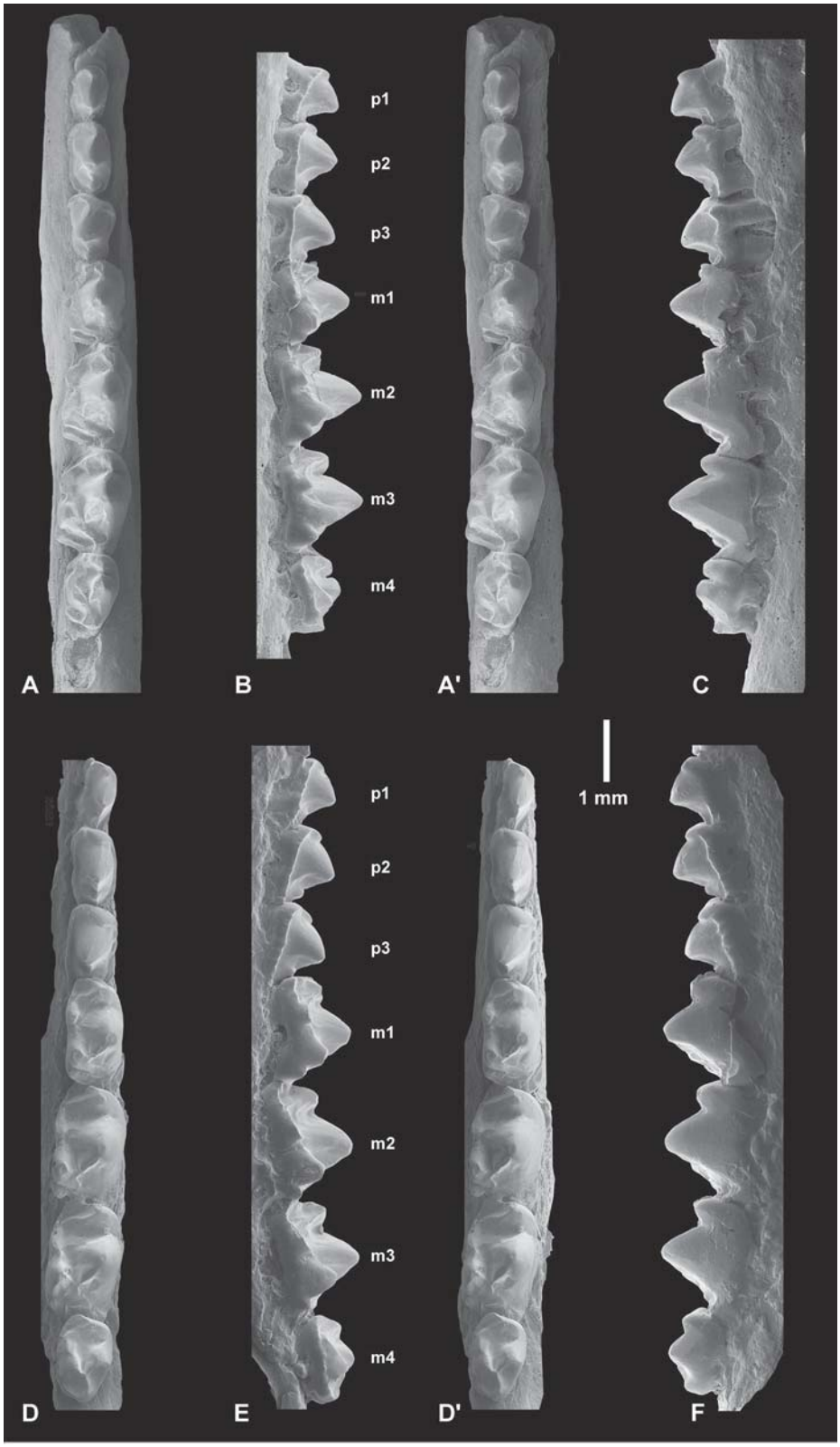

Fig. 8.—*Haldanodon exspectatus*, Late Jurassic (Kimmeridgian) of Portugal. Right lower dentition in occlusal (A, A′ and D, D′, stereopairs), lingual (B, E), and labial views (C, F). **A–C**, Gui Mam 95/75, P_{1-3}, M_{1-4}, and alveoli for M_5; **D–F**, Gui Mam 122/76 [SGP 6796], P_{1-3}, M_{1-4} (photos of epoxy casts).

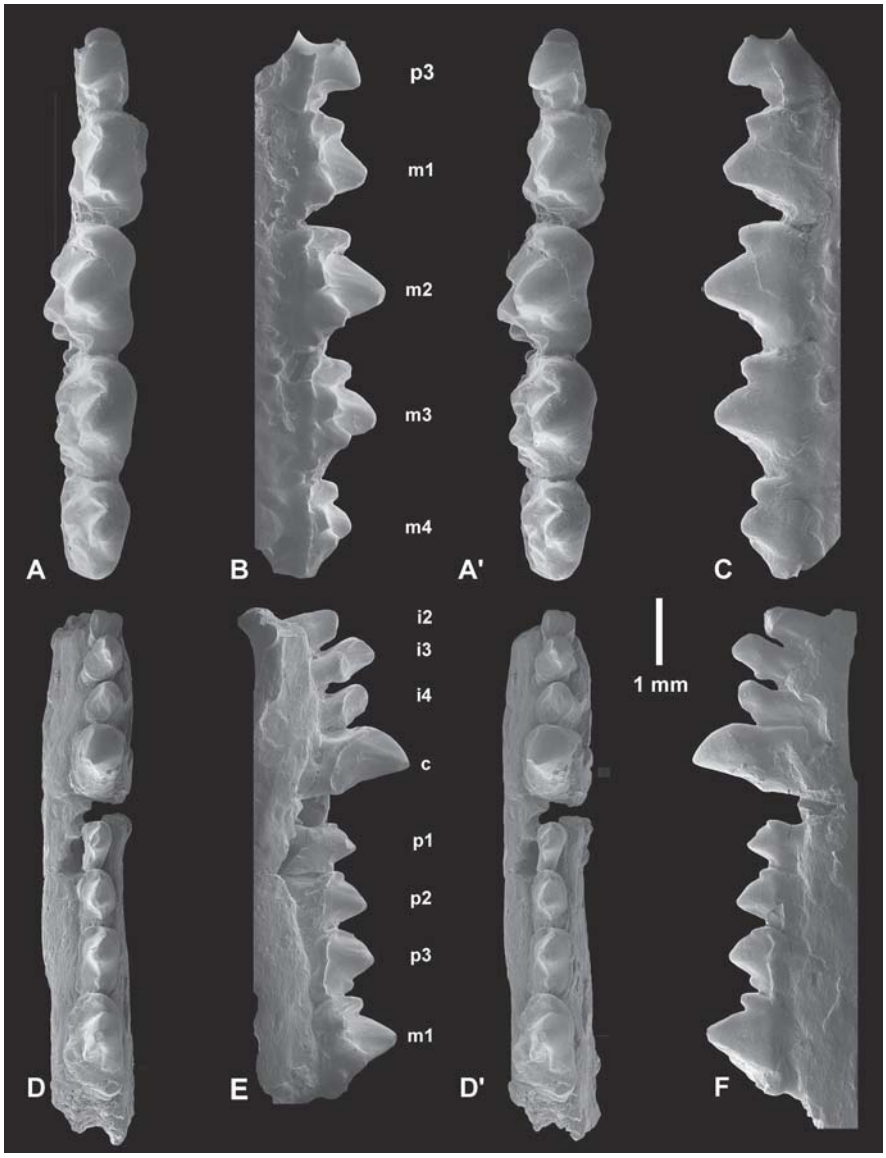

Fig. 9. ~~*H*~~*aldanodon exspectatus* , Late Jurassic (Kimmeridgian) of Portugal. Right lower dentition in occlusal (A, A′ and D, D′, stereopairs), lingual (B, E), and labial views (C, F). **A–C**, Gui Mam 79/75, P_3, M_{1-4}; **D–F**, Gui Mam 30/79 [SGP 6726], I_{2-4}, C_1, P_{1-3}, M_1 (photos of epoxy casts).

nodon. Character 27 (interlock of lower molars): in the molars of all specimens studied there is a d-b overlap present. Character 28 (cusp triangulation): there is a cusp triangulation present between the a-c crest and the a-b crest on the anterior molars of all studied specimens (although missing on some vestigial M_4 and all $M_{5–6}$). Character 29 (placement of lower cusp e): cusp e is placed lingual to the median axis of the lower molar in all specimens examined. Due to the vestigial nature of $M_{5–6}$ and some M_4, for a character analysis of *Haldanodon* M_{1-3} should be considered.

CLADISTIC ANALYSIS AND DISCUSSION

Sister taxon of Docodonta.— A recent consensus is that docodonts are more closely related to the mammalian crown group than *Sinoconodon*, morganucodonts, haramiyidans, and the mammaliaforms with triangulated molars (such as kuehneotheriids) (Wible and Hopson 1993; Luo 1994; Rougier et al. 1996; Luo et al. 2002; Kielan-Jaworowska et al. 2004; Ji et al. 2006; but see Lillegraven and Krusat 1991). However, there has been relatively little discussion about which "non-docodont" mammaliaform group would be most close to docodonts. Two competing hypotheses are: the docodont-morganucodont relationship and the docodont-"symmetrodont-like" mammaliaform relationship.

The docodont-morganucodont relationship was based on Patterson's (1956) scheme of cusp homology of docodonts and *Morganucodon* (see the thorough review by Krusat 1980). From the 1960s through 1980s, most workers

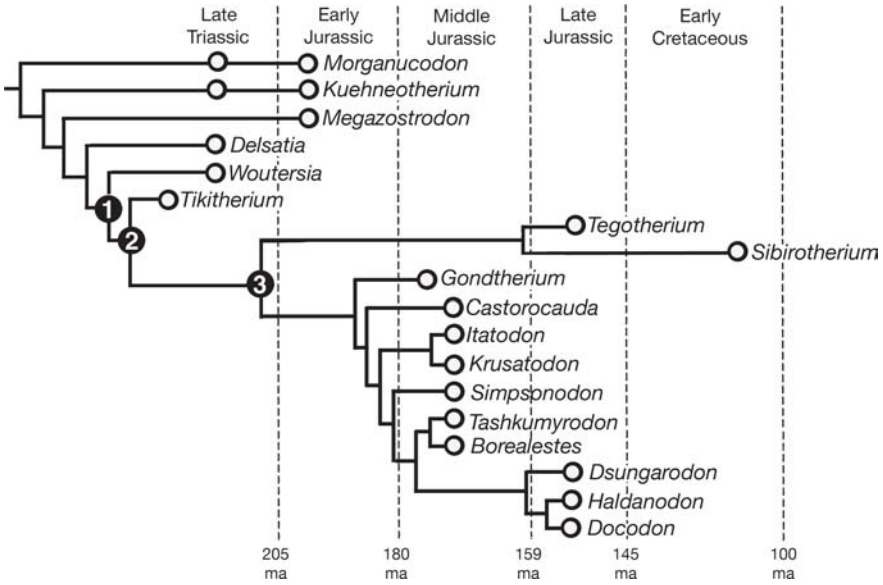

Fig. 10.—Phylogenetic relationships and stratigraphic distributions of docodont genera and their putative relatives. The single most parsimonious tree from branch and bound search of PAUP 4.0b10 (Swofford 2000) of 12 docodont genera plus six outgroups and 31 molar characters is depicted (Appendices 1–2). Tree length = 71 steps; consistency index = 0.606; retention index = 0.77. This topology is based on branch and bound search with multi-state characters treated as unordered. Dental characters are adopted from Butler (1997), Sigogneau-Russell (2003), Martin and Averianov (2004), supplemented by Ji et al. (2006), Averianov and Lopatin (2006), and new observations. Cladogram nodes 1, 2, and 3 are defined in the text.

who had considered this issue agreed that, based on dental features and following Patterson's assumption of cusp homology, docodonts are more closely related to morganucodonts than to any mammaliaforms with triangulated molars (Hopson and Crompton 1969; Kermack et al. 1973; Krusat 1980). Some went so far as to classify docodonts and *Morganucodon* formally in the same taxonomic group (Hopson and Crompton 1969; Kermack et al. 1973). Kemp (1983) pointed out that the straight alignment of the main cusps in "triconodont-like" mammals is a primitive feature that is also present in many pre-mammaliaform cynodonts, rendering it uninformative for inferring phylogenetic relationships among mammaliaforms. In this light, traditional groups supported on the basis of this primitive character, such as the docodont-morganucodont grouping, should be abandoned. The basicranial characteristics of the docodont *Haldanodon* are more derived than those of *Sinoconodon*, *Morganucodon,* and *Dinnetherium* (Wible and Hopson 1993; Luo 1994; Rougier et al. 1996). Docodonts and *Morganucodon* belong to different nodes on the mammaliaform phylogenetic tree.

The docodont-"symmetrodont mammaliaform" relationship is based on the putative cusp homology between docodonts and *Woutersia* or *Delsatia*, both of the latter being mammaliaforms with triangular "symmetrodont-like" molars. The resemblance in upper molars between *Woutersia* and docodonts was first recognized by Sigogneau-Russell and Hahn (1995). However, these authors stopped short of proposing close affinities between docodonts and *Woutersia*, or between docodonts and "symmetrodont" mammaliaforms in general. A more explicit argument for close affinities between docodonts and either *Delsatia* or *Woutersia* was proposed by Sigogneau-Russell and Godefroit (1997) and Butler (1997), although these authors disagreed on certain details.

Sigogneau-Russell and Godefroit (1997) considered *Delsatia* to be either a docodont or a near relative of the Docodonta (Fig. 2C, G). They proposed that the docodont mesiolingual cusp (Butler's cusp g) should be homologized with the paraconid (cusp b) of symmetrodonts. The docodont distolingual cusp (Butler's cusp c) can be homologized with the metaconid (cusp c) of symmetrodonts. Under this scheme of cusp homology, the triangular structure in the central part of the docodont lower molar is entirely comparable to the triangulated cusp pattern of symmetrodont teeth, and can be homologized with the trigonid of all "therians," including those that are now called symmetrodont mammaliaforms. This also implies that the cusps in the middle portion of docodont lower molars form an acute triangle, more so than in the obtuse-triangled symmetrodonts (e.g., kuehneotheriids and tinodontids), and comparable to the trigonids of pseudotribosphenic and tribosphenic mammals.

Sigogneau-Russell and Godefroit (1997) further hypothesized that the basined or ridged area anterior to the trigonid-like structure can be homologized with the pseudotalonid of *Shuotherium* (Chow and Rich 1982). This helped to integrate the newly developed triangular cusp homology on the trigonid-like area in the middle of the lower with the basin for crushing function anterior to the trigonid, thereby establishing the basis for comparing docodonts with *Shuotherium*, a non-docodont taxon with a pseudotalonid basin (for crushing and grinding) anterior to the trigonid (for shearing) (Chow and Rich 1982; Sigogneau-Russell

1998; Wang et al. 1998). This scheme is consistent with a case study on the similarity between the docodont *Simpsonodon* and *Shuotherium* (Kermack et al. 1987).

Butler (1997) offered a slightly different interpretation, and he homologized the docodont distolingual cusp with cusp c (metaconid) of symmetrodont mammaliaforms. In this feature, Butler's scheme is in agreement with Sigogneau-Russell and Godefroit (1997). However, Butler considers the anterior cusp b in *Morganucodon* and symmetrodonts (paraconid of the latter) to be homologous to the anterior cusp b in docodonts, instead of the mesiolingual cusp g of docodont molars as proposed by Sigogneau-Russell and Godefroit (1997). The difference in designating cusp b vs. cusp g would have further implications for interpreting the pseudotalonid. Under Butler's scheme, a true pseudotalonid basin like that of *Shuotherium* would not be present in docodonts: the pseudotalonid of docodonts is lingual to the a-b crest between the protoconid (cusp a) and the "paraconid" (cusp b) on the trigonid (see Fig. 1). In contrast, the pseudotalonid of *Shuotherium* is positioned anterolateral to the a-b crest of the trigonid. Therefore, the pseudotalonid in our scheme (see also Martin and Averianov 2004; Pfretzschner et al. 2005) is different from the pseudotalonid of *Shuotherium*, because of the difference in homologizing the paraconid cusp b [sensu Kermack et al. (1987) and Sigogneau-Russell and Godefroit (1997)]. Nevertheless, Butler's scheme, as adopted here, is still more similar to that of Sigogneau-Russell (Sigogneau-Russell and Godefroit 1997), than to the traditional Patterson scheme. Despite their difference in designating the homologue of the paraconid (cusp b), both Butler and Sigogneau-Russell assume strong overall similarity between docodonts and mammaliaforms with obtuse triangular molar cusp patterns (Fig. 1).

It should be noted that Pascual and Goin (2001) believe the docodont cusp-crest pattern is triangulated. In some aspects, their view is consistent with the consensus of other workers (e.g., Sigogneau-Russell and Godefroit 1997; Butler, 1997). However, a major difference in the argument of Pascual and Goin (2001) is that the oblique shearing crests of docodonts are convergent to those of "symmetrodont" molars, implying that the triangulation of crests (and related cusps) is homoplastic but not homologous in docodonts and "symmetrodonts" including all of kuehneotheriids.

An important issue remains unresolved. The upper molars assigned to *Woutersia mirabilis* and *Woutersia butleri* by Sigogneau-Russell (Sigogneau-Russell 1983; Sigogneau-Russell and Hahn 1995) are highly variable in many features. One specimen (Saint-Nicholas-de-Port [SNP] 719) has better development of lingual cusp X and transverse widening of the upper molar than the rest of the sample, and this tooth is more docodont-like than most specimens in the collection from the Saint-Nicholas-de-Port site. The case to support a close relationship of *Woutersia* to the Docodonta (Butler, 1997) is based on a single and exceptional specimen. Sigogneau-Russell has discussed the possibility that this upper tooth may belong to an as yet unidentified docodont, or to *Delsatia*, which so far is known only from the lower teeth (Sigogneau-Russell and Hahn 1995; Sigogneau-Russell and Godefroit 1997). Averianov and Lopatin (2006) speculated (and we concur) that *Woutersia* might display gradational variation of its molar features. If the wide range of variation of the docodont-like features among the teeth assigned to *Woutersia mirabilis* is treated as polymorphic, this would significantly weaken the status of *Woutersia* as being most similar to docodonts, relative to *Tikitherium*. In our hypothesis of molar character evolution, we selected one specimen of *Woutersia* (SNP 719) as an exemplar of this taxon.

Tikitherium (Datta 2005), a Late Triassic mammaliaform, also displays several docodont-like features of the upper molar. The transversely wide upper molar has a lingual cusp X, and the middle portion of its crown is constricted in occlusal view [see Fig. 4; reinterpreted from cusp Z of Datta (2005)]. Most importantly, the tooth possesses a platform-like area on the lingual side of the upper molar, and there are wear facets on the labial side of its lingual cusp X. These features are previously known only from docodonts among all Triassic and Jurassic mammaliaforms (including mammals) (Jenkins 1969; Gingerich 1973; Butler 1997; Sigogneau-Russell 2003). Sigogneau-Russell (2003) and Pfretzschner et al. (2005) pointed out that the presence of a wear pattern on the labial side of the mesiolingual cusp X is an important difference distinguishing all docodonts from the pseudoprotocone of *Shuotherium* and the protocone of boreosphenidan mammals.

Tikitherium is more similar to docodonts than any other contemporary mammaliaforms. The upper molar of *Tikitherium* has developed an obtuse triangulation of the main cusps A, B, and C (Fig. 4B); this is a primitive feature shared also by symmetrodont mammaliaforms. Overall, *Tikitherium* has some features that are like symmetrodont therians, as described well by Datta (2005), and other features that are similar to those of docodonts.

The lingual cusp X of *Tikitherium* is not so well developed (in terms of both its height and size) and is therefore less comparable to docodonts, than *Woutersia* (Fig. 11). The prominent lingual cusp X that is elevated relative to the main cusp a in *Woutersia* is perhaps the best apomorphy to support a docodont-*Woutersia* sister group relationship (Fig. 11).

Contingent on the prevailing view that the trigonid of symmetrodonts is homologous to the obtuse b-a-c triangular pattern of docodonts (Butler 1997) or the acute b-a-c trianglular pattern advocated by Sigogneau-Russell (2003) (Fig. 2G, H), the sister taxon of docodonts is probably a taxon with a triangulated cusp pattern on the lower molar and a transversely wide upper molar, such as *Woutersia* and *Tikitherium* (Sigogneau-Russell and Hahn 1995; Butler 1997; Sigogneau-Russell and Godefroit 1997).

Our parsimony analysis favors *Tikitherium* as the sister taxon of docodonts (Figs. 10–11: Node 2). The docodont + *Tikitherium* clade is, in turn, related to the mammaliaform *Woutersia* (Figs. 10–11: Node 1). Synapomorphies of *Tikitherium* and docodonts are: (1) presence of wear facets on the labial side of the lingual cusp X (Datta 2005); (2) pres-

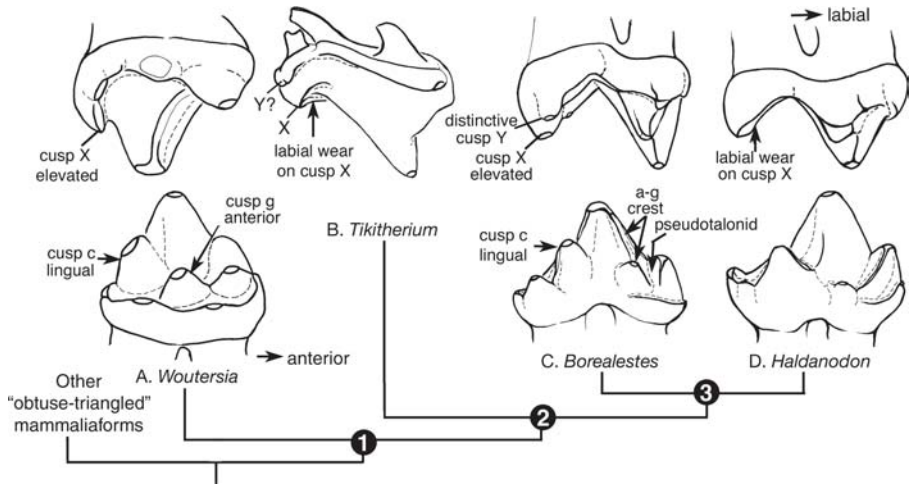

Fig. 11.—Transformation of molar structures between docodonts and their putative mammaliaform relatives of the Late Triassic. **A**, *Woutersia*: right upper molar (top: posterior view) and left lower molar (bottom: lingual view) (from Sigogneau-Russell and Hahn 1995); **B**, *Tikitherium*: right (?) upper molar in posterolingual view (adapted from Datta 2005; tooth has been reoriented); **C**, *Borealestes*: right upper molar (top: posterior view) and left lower molar (bottom: lingual view) (from Sigogneau-Russell 2003); **D**, *Haldanodon*: right upper molar (top: posterior view) and left lower molar (bottom: lingual view). Node 1 apomorphies: anterior placement of lower cusp g; transverse widening of upper molar and cusp X elevated higher than other cingular cuspules. Node 2 (*Tikitherium* + docodont clade) apomorphies: incipient differentiation of cusp Y from cusp X; constricted middle portion of upper molar; development of wear pattern on labial side of mesiolingual cusp X; presence of the third lingual root of upper molar. Node 3 (Docodonta) apomorphies: presence of distinctive cusp Y, development of extensive wear patterns along the posterolingual and anterolingual transverse crests; full development of the a-g crest; presence of the pseudotalonid crushing and grinding area anterior to the a-g crest; presence of c-d rim (although cusps incorporated in this rim may be variable).

ence of a constricted occlusal outline of the upper molar; and (3) incipient development of distolingual cusp Y (Fig. 4). Related to the transverse widening of the upper tooth, *Tikitherium* also has a third lingual root, a derived feature of docodonts (Averianov and Lopatin 2006). However, lingual cusp X is less developed in terms of size and height, and therefore less docodont-like, in *Tikitherium* than in *Woutersia* (Fig. 11).

Monophyly of the Docodonta (Figs. 10–11: Node 3).— Docodonts consist of taxa that are more closely related to *Docodon* and *Simpsonodon* than morganucodonts, *Shuotherium,* and the Late Triassic "symmetrodont" mammaliaforms (such as *Kuehneotherium*, *Woutersia,* and *Tikitherium*) (this definition is modified from Kielan-Jaworowska et al. 2004). This monophyletic group is defined by the common ancestor of the youngest-known *Sibirotherium* and the oldest-known *Borealestes*, *Krusatodon,* and *Simpsonodon* (Fig. 10: Node 3). Docodonta are diagnosed by the following derived characteristics:

(1) Upper molars have developed an anterolingual transverse crest extending from cusp X (Fig. 4). This apomorphy is related to the extensive wear function on the labial side of cusp X in most docodonts, in contrast to the primitive condition of the "symmetrodont" mammaliaforms, all of which lack a distinctive transverse crest. A precursor of this docodont feature occurs in the mammaliaform *Tikitherium.* The triangular molar has a wear facet on the labial side of cusp X [reinterpreted from "cusp Z" of Datta (2005)]; however, *Tikitherium* has no transverse crest as seen in the Docodonta (Fig. 4).

(2) The upper molar is characterized by a distinctive distolingual cusp Y (sensu Krusat 1980; Butler 1997; Pfretzschner et al. 2005), which has a varying degree of wear from occlusal contact with the pseudotalonid of the succeeding lower molar.

(3) Lower molars have developed an extensive pseudotalonid (Sigogneau-Russell 2003; Martin and Averianov 2004). The pseudotalonid is a basin or a relatively flat area that is bounded posteriorly by the a-g crest and anteriorly by either the b-g crest or the b-e-g rim (Fig. 3). This basin may reciprocate cusp Y of the preceding upper molar and its posterolingual transverse crest (if the latter is present). This occlusal contact between upper cusp Y and the lower pseudotalonid is crucial for the derived crushing function of docodont molars, as has been long recognized (Jenkins 1969; Gingerich 1973; Krusat 1980; Butler 1997; Sigogneau-Russell 2003; Pfretzschner et al. 2005).

(4) Lower molars have a basin or flat area ["talonid" of Sigogneau-Russell (2003)] at least partially encircled by a crest from cusp c to cusp d. In most docodonts, the posterior part of this basin or flat area can develop extensive wear from contact with the anterolingual transverse crest of cusp X on the upper molar.

The size of both the pseudotalonid basin and the posterior basin can be variable among docodonts, as are the crests

surrounding these basins. These morphological complexes can each be divided into several independent characters (Appendix 1, characters 12–14, 20–23). It is also noteworthy that only docodonts have consistently developed two-rooted canines (Krusat 1980; Averianov and Lopatin 2006; Ji et al. 2006). This derived feature is absent in most mammaliaforms, except *Hadrocodium* (Luo et al. 2001).

Middle Jurassic groups.—The highest taxonomic diversity of docodonts occurred in the Middle Jurassic. Two pairs of taxa are closely related: *Krusatodon* and *Itatodon*, and *Borealestes* and *Tashkumyrodon*. However, the Middle Jurassic taxa do not form a monophyletic group. Generally, Middle Jurassic docodonts have a posterior basin [talonid of Sigogneau-Russell (2003)] on the lower molars, and this posterior basin is broader than in other docodonts. Lower molars of Middle Jurassic docodonts are also characterized by a crest between cusps c and d (Fig. 3). This c-d crest and other minor ridges and valleys create the appearance that the posterior basin is more corrugated in these taxa [especially in *Simpsonodon* (Kermack et al. 1987)] than is the case in other docodonts. Also Middle Jurassic docodonts have a much better developed anterolabial part of the upper tooth (the upper molar of *Tashkumyrodon* is unknown). We note that the holotype specimen of *Itatodon* from the Middle Jurassic of Russia is nearly identical to the ultimate lower molar of the Middle Jurassic *Castorocauda* from China. However, these features should be considered to be plesiomorphic for docodonts.

Late Jurassic groups.—It has long been recognized that docodonts from the Late Jurassic of Great Britain and the Western Interior of North America are very similar (Simpson 1928, 1929). More recent cladistic analysis has explicitly grouped *Docodon* and *Haldanodon* from the Upper Jurassic of Euroamerica as a clade (Martin and Averianov 2004). The expanded analysis performed here corroborates this observation and adds *Dsungarodon* as the sister group to the *Docodon* + *Haldanodon* clade. This clade is diagnosed by a much higher and more centrally placed upper labial cusp A, and close approximation of upper cusps A and C. On the lower molars, cusp g is smaller and the a-g crest is less developed and even incomplete in *Docodon* and *Haldanodon*, resulting in the medially open pseudotalonid (Fig. 2F), as previously noted by Martin and Averianov (2004).

Our cladistic analysis also shows that the central Asiatic taxa *Sibirotherium* (Maschenko et al. 2002) and *Tegotherium* (Tatarinov 1994; Hopson 1995; Kielan-Jaworowska et al. 2004) form a clade. Both taxa lack a crest between cusps b and g. The crest between cusps e and g is weak to absent. Related to these features, the pseudotalonid basin is open anterolingually. The mesial cusp e is distinctive but located on the median axis of the lower molar. In other taxa with a distinctive cusp e, it is placed more lingually. *Sibirotherium* is represented by relatively good fossils that have been well described, so it can be ruled out that these peculiar features of the pseudotalonid are developmental variations of deciduous teeth. However, *Tegotherium* is represented only by a single tooth (Tatarinov 1994; see re-illustrated tooth in Kielan-Jaworowska et al. 2004). It cannot be excluded that these two taxa are congeneric. In any case, *Sibirotherium* and *Tegotherium* were discovered at geographically nearby sites in Asia, and they are morphologically distinctive from other docodonts. They therefore appear to be endemic Asian docodonts.

The phylogenetic tree presented in Figure 10 is susceptible to alternative treatment of ordered versus unordered multi-state characters. The topology depicted here (Fig. 10) is based on a branch and bound search using unordered multi-state characters. If the multi-state characters are ordered, then the *Tegotherium-Sibirotherium* clade would become the most derived clade, and the *Docodon-Haldanodon* clade would diverge near the base of the docodont tree. The latter topology is more comparable to that produced by Averianov and Lopatin (2006).

The docodont *Gondtherium* from the Kota Formation of India.—Our comparisons corroborate the observations of Prasad and Manhas (2001, 2007) that *Gondtherium* from the Middle Jurassic Kota Formation of India belongs to the Docodonta. The incomplete lower molar of this taxon has a well-developed a-g crest, a key diagnostic feature of the Docodonta. Its a-g crest and g-b crest form a closed pseudotalonid, similar to that of several Middle Jurassic docodonts (Fig. 3). Its upper molar is less docodont-like, but its mesiolabial region is distinctive from the known upper molars of *Shuotherium*. Unless future discoveries of better fossils contradict the present interpretation, *Gondtherium* should be placed in the Docodonta, as originally proposed by Prasad and Manhas (2001). This indicates that the Docodonta enjoyed a wide distribution in the Middle Jurassic.

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APPENDIX 1. List of dental characters and their distribution among docodont genera.

We follow Butler's (1997) homology scheme regarding the designation of the molar cusps of docodonts. The correspondence between this homology scheme and those employed by Sigogneau-Russell (2003) and Kielan-Jaworowska et al. (2004) is illustrated in Figures 1–2, and summarized in Table 1. Lower molar characters are adapted, with modi fication in some cases, from the character lists of Martin and Averianov (2004) and Pfretzschner et al. (2005). Canine and upper molar characters are adapted with modification from Sigogneau-Russell (2003), Prasad and Manhas (2001), Datta (2005), Ji et al. (2006), and Averianov and Lopatin (2006).

Upper Molar Characters

1. Transverse widening of upper molars (Sigogneau-Russell 2003, character 1):
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*;
   (1) Present: *Woutersia*, *Tikitherium*, *Gondtherium*, *Dsungarodon*, *Simpsonodon*, *Krusatodon*, *Haldanodon*, *Borealestes*, *Docodon*;
   (?) Unknown: *Delsatia*, *Tashkumyrodon*, *Sibirotherium*, *Tegotherium*, *Castorocauda*, *Itatodon*.

2. Mesiolingual cusp X of upper molars: wear facets on the labial aspect of the cusp (new character defined in Figs. 1, 11):
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*;
   (1) Wear facets present on the labial side of the lingual cusp: *Tikitherium* (= cusp Z of Datta 2005), *Gondtherium* (Prasad and Manhas 2001), *Dsungarodon*, *Simpsonodon*, *Krusatodon*, *Haldanodon*, *Borealestes*, *Docodon*;
   (?) Unknown: *Delsatia*, *Tashkumyrodon*, *Tegotherium*, *Sibirotherium*, *Castorocauda*, *Itatodon*.

3. Transverse mesiolingual and mesiolabial crests between Cusp A and Cusp X (new character defined in Fig. 1):
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Tikitherium*;
   (1) Present but incomplete: *Gondtherium*, *Krusatodon*;
   (2) Present and complete: *Dsungarodon*, *Simpsonodon*, *Borealestes*, *Haldanodon*, *Docodon*;
   (?) Unknown: *Delsatia*, *Tashkumyrodon*, *Tegotherium*, *Sibirotherium*, *Castorocauda*, *Itatodon*.

4. Cusp Y (= upper distolingual cusp) (new character defined in Fig. 1):
   (0) Absent or indistinct: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Tikitherium*, *Gondtherium*;
   (1) Present and distinct: *Krusatodon*, *Simpsonodon*, *Dsungarodon*;
   (2) Present, distinct, and aligned in anteroposterior line: *Borealestes*, *Docodon*, *Haldanodon*;
   (?) Not preserved: *Delsatia*, *Tashkumyrodon*, *Sibirotherium*, *Castorocauda* (not exposed), *Itatodon*.

5. Size and development of Cusp C (distolabial cusp) and its separation from Cusp A (mesiolingual cusp) (new character defined in Fig. 3):
   (0) Cusp C present and enlarged: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Tikitherium*, *Gondtherium*, *Borealestes*, *Krusatodon*, *Simpsonodon*, *Dsungarodon*;
   (1) Reduced cusp C twinned with cusp A: *Woutersia*, *Haldanodon*, *Docodon*;
   (?) Not preserved: *Delsatia*, *Tegotherium*, *Sibirotherium*, *Tashkumyrodon*, *Castorocauda* (not exposed), *Itatodon*.

6. Posterior transverse crest between distolabial (C) and distolingual (Y) cusps (new character defined in Fig. 1):
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Tikitherium*, *Gondtherium*;
   (1) Present: *Dsungarodon*, *Borealestes*, *Haldanodon*, *Docodon*, *Krusatodon*, *Simpsonodon*;
   (?) Unknown: *Delsatia*, *Tashkumyrodon*, *Castorocauda* (not exposed), *Sibirotherium*, *Itatodon*.

7. Presence of cusp E, separated from cusp B:
   (0) Present: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*;
   (1) Cusp E present and in labiolingual alignment with cusp B: *Woutersia*, *Simpsonodon*, *Krusatodon*;
   (2) Absent: *Tikitherium*, *Gondtherium*, *Borealestes*, *Dsungarodon*, *Docodon*, *Haldanodon*;
   (?) Unknown: *Delsatia*, *Tashkumyrodon*, *Castorocauda*, *Tegotherium*, *Sibirotherium*, *Itatodon*.

8. Constricted waist between the labial and lingual parts of the upper tooth.
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Gondtherium*, *Simpsonodon*;
   (1) Present: *Tikitherium*, *Krusatodon*, *Borealestes*, *Dsungarodon*, *Docodon*, *Haldanodon*;
   (?) Unknown: *Delsatia*, *Tashkumyrodon*, *Castorocauda*, *Tegotherium*, *Sibirotherium*, *Itatodon*.

Lower Molar Characters

9. Cusp c on lingual cingulid and in alignment with mesiolingual cusp g:
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*;
   (1) Present: *Woutersia*, *Delsatia*, *Gondtherium*, *Docodon*, *Haldanodon*, *Tashkumyrodon*, *Sibirotherium*; *Simpsonodon*, *Krusatodon*, *Borealestes*, *Castorocauda*, *Itatodon*;
   (?) Unknown: *Tikitherium*.

10. Cusp c to cusp g size ratio (new character):
   (0) Cusp c much larger than cingular cusp g (if the latter is present): *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Haldanodon*, *Docodon*;
   (1) Cusp c subequal in size to the mesiolingual cusp g: *Woutersia*, *Delsatia*, *Docodon*, *Sibirotherium*, *Tegotherium*, *Simpsonodon*, *Krusatodon*, *Borealestes*, *Castorocauda*, *Itatodon*;
   (?) Unknown: *Tikitherium*, *Tashkumyrodon* (incomplete preservation), *Gondtherium* (incomplete preservation).

11. The a-c crest (posteromain crest of Sigogneau-Russell 2003):
   (0) Complete and v-notched: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Haldanodon*, *Sibirotherium*, *Simpsonodon*, *Krusatodon*, *Borealestes*, *Castorocauda*, *Itatodon*;
   (1) Weakly developed or incomplete: *Docodon*, *Dsungarodon*;
   (?) Unknown: *Tikitherium*, *Gondtherium*.

12. Presence or absence of cusp g (mesiolingual) (Sigogneau-Russell 2003, character 5; Martin and Averianov 2004, character 2):
   (0) Small or absent: *Megazostrodon*, *Morganucodon*, *Kuehneotherium*;
   (1) Distinct, opposite primary cusp a: *Woutersia*, *Delsatia*;
   (2) Distinct, anteriorly placed (more anteriorly placed than primary cusp a): *Gondtherium*, *Docodon*, *Haldanodon*, *Tashkumyrodon*, *Sibirotherium*, *Borealestes*, *Dsungarodon*;
   (3) Anteriorly placed and hypertrophied (the same size as, or larger than cusp c): *Krusatodon*, *Simpsonodon*, *Castorocauda*, *Itatodon*, *Tegotherium*;
   (?) Not preserved: *Tikitherium*.

13. Development of pseudotalonid (Martin and Averianov 2004, character 2):
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*;
   (1) Present and bordered by b-g crest: *Gondtherium*, *Dsungarodon*, *Itatodon*, *Borealestes* (Fig. 1D), *Castorocauda*, *Krusatodon*, *Simpsonodon*;
   (2) Present and bordered by b-e crest: *Tashkumyrodon*, *Sibirotherium*, *Tegotherium*;
   (3) Present and b is much taller than g, so that the pseudotalonid appears to be lingually open: *Docodon*, *Haldanodon* (Fig. 1C);
   (?) Unknown: *Tikitherium*.

14. V-notched a-g crest (new character defined in Fig. 1):
   (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Delsatia*, *Woutersia*;
   (1) Present and incomplete: *Haldanodon*, *Docodon*;
   (2) Present and complete: *Gondtherium*, *Itatodon*, *Tashkumyrodon*, *Tegotherium*, *Sibirotherium*, *Dsungarodon*, *Borealestes*, *Castorocauda*, *Krusatodon*, *Simpsonodon*;
   (?) Not preserved: *Tikitherium*.

15. The c-d crest in the posterior basin (new character):
   (0) Absent: *Castorocauda*, *Tegotherium*, *Sibirotherium*, *Dsungarodon*;
   (1) Present, c-d crest or c-f-d crests straight: *Haldanodon*, *Docodon*, *Itatodon*, *Tashkumyrodon*;
   (2) Present, c-d crest angled: *Borealestes*, *Krusatodon*;
   (?) Not applicable: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Simpsonodon*; not preserved: *Tikitherium*, *Gondtherium*.

16. Placement of cusp d (modified from Sigogneau-Russell 2003, character 7; assuming homology of the morganucodont cusp d and docodont cusp d):
   (0) Labial position (in alignment with a-b crest, or nearly so): *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Borealestes*, *Castorocauda*, *Simpsonodon*, *Tashkumyrodon*, *Sibirotherium*, *Haldanodon*, *Docodon*;
   (1) Median placement (nearly halfway along the transverse width of posterior crown): *Krusatodon*, *Dsungarodon*, *Tegotherium*;
   (0/1) Polymorphism: *Itatodon* [scored "0" for labial position of cusp d in one tooth referred to this taxon (Averianov and Lopatin 2006); scored "1" for lingual position of cusp d in the holotype (Lopatin and Averianov 2005)];
   (?) Not preserved: *Tikitherium*, *Gondtherium*.

17. Folding enamel (on either upper or lower) (Sigogneau-Russell 2003, character 5):
   (0) Absent or weakly developed: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Tikitherium*, *Borealestes*, *Haldanodon*, *Tegotherium*, *Tashkumyrodon*, *Sibirotherium*, *Gondtherium*, *Itatodon*, *Castorocauda*, *Dsungarodon*;
   (1) Present: *Docodon*, *Simpsonodon*, *Krusatodon*.

18. Alignment of posterior crest of cusp a toward cusp d (posteromain crest of Sigogneau-Russell 2003; defined here in Fig. 1):
    (0) Present and straight: *Docodon*, *Tegotherium*, *Castorocauda*, *Itatodon*, *Simpsonodon*, *Sibirotherium*, *Haldanodon*, *Dsungarodon*;
    (1) Present and angled: *Borealestes*, *Krusatodon*, *Tashkumyrodon*;
    (?) Not applicable: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Delsatia*, *Woutersia*; not preserved: *Tikitherium*, *Gondtherium*.

19. The a-d crest:
    (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Delsatia*, *Woutersia*;
    (1) Incomplete: *Haldanodon*, *Docodon*, *Dsungarodon*;
    (2) V-notched: *Tegotherium*, *Castorocauda*, *Itatodon*, *Simpsonodon*, *Sibirotherium*, *Borealestes*, *Krusatodon*, *Tashkumyrodon*;
    (?) Not preserved: *Tikitherium*, *Gondtherium*.

20. The b-g crest (crest between the mesiolabial cusp and mesiolingual cusps; Sigogneau-Russell 2003, character 8; Martin and Averianov 2004, character 7):
    (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Tegotherium*, *Sibirotherium*;
    (1) Present, low, and broken (v-valley): *Gondtherium*, *Borealestes*, *Krusatodon*, *Castorocauda*, *Simpsonodon*;
    (2) Present and continuous: *Haldanodon*, *Docodon*, *Dsungarodon*;
    (?) Not preserved: *Tikitherium*; inapplicable: *Itatodon*; incomplete: *Tashkumyrodon*.

21. Size of cusp e (Martin and Averianov 2004, character 3):
    (0) Present and distinct: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Gondtherium*, *Krusatodon*, *Tashkumyrodon*, *Sibirotherium*, *Tegotherium*;
    (1) Reduced: *Castorocauda*, *Itatodon*, *Borealestes*, *Simpsonodon*, *Dsungarodon*, *Docodon*, *Haldanodon*;
    (?) Not preserved: *Tikitherium*.

22. Mesiolingual cingulid extending from cuspule e or an equivalent position (new character defined in Fig. 2):
    (0) Connected to cusp g: *Morganucodon*, *Megazostrodon*, *Woutersia*, *Delsatia*;
    (1) Extending to below cusp g: *Itatodon*, *Borealestes*, *Krusatodon*, *Tashkumyrodon*, *Haldanodon*;
    (2) Absent or limited to the mesial part of the tooth: *Docodon*, *Castorocauda*, *Simpsonodon*, *Dsungarodon*, *Tegotherium*, *Sibirotherium*;
    (?) Not preserved: *Tikitherium*, *Gondtherium*, *Kuehneotherium* (inapplicable).

23. Cusp b relative to cusp a (Martin and Averianov 2003, character 1):
    (0) Large, well separated by a notch from cusp a: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Castorocauda*, *Simpsonodon*, *Krusatodon*, *Itatodon*, *Tashkumyrodon*, *Sibirotherium*, *Tegotherium*, *Dsungarodon*;
    (1) Small, closely approximated to cusp a: *Borealestes*, *Docodon*, *Haldanodon*;
    (?) Not preserved: *Tikitherium*, *Gondtherium*.

24. The "docodont cusp f" (posterolingually positioned as defined by Martin and Averianov 2004, figs. 3, 5; differs from mesiolabially positioned cusp f):
    (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Dsungarodon*;
    (1) Present: *Castorocauda*, *Borealestes*, *Haldanodon*, *Docodon*, *Simpsonodon*, *Itatodon*, *Tashkumyrodon*, *Sibirotherium*, *Tegotherium*;
    (?) Not preserved: *Tikitherium*, *Gondtherium*.

25. The "standard cuspule f" (mesiolabially positioned, as defined by Kielan-Jaworowska et al. 2004, fig. 5.9: "mesiolabial cusp." Please note that this cusp is different from cusp g in posterolingual position in Figs. 1–2 here):
    (0) Absent: *Morganucodon*, *Dsungarodon*, *Itatodon*, *Castorocauda*, *Borealestes*, *Haldanodon*, *Docodon*, *Simpsonodon*, *Tashkumyrodon*, *Sibirotherium*, *Tegotherium*;
    (1) Present: *Kuehneotherium*, *Delsatia*, *Woutersia*, *Megazostrodon*;
    (?) Unknown: *Tikitherium*, *Gondtherium*.

26. The b-e crest (crescent of Sigogneau-Russell 2003; Martin and Averianov 2004, character 6):
    (0) Absent: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*, *Delsatia*, *Haldanodon*, *Docodon*;
    (1) Present and continuous from cusp b to the cingulid: *Itatodon*, *Gondtherium*, *Borealestes*, *Krusatodon*, *Simpsonodon*, *Castorocauda*, *Tashkumyrodon*, *Dsungarodon*;
    (2) Present, as a part of the pseudotalonid rim: *Tegotherium*, *Sibirotherium*;
    (?) Not preserved: *Tikitherium*.

27. Interlock of lower molars (new character):
    (0) d-b-e interlock: *Morganucodon*, *Tashkumyrodon*, *Dsungarodon*, *Castorocauda*;
    (1) d-"standard f"-e interlock: *Kuehneotherium*, *Delsatia*, *Woutersia*, *Megazostrodon*;
    (2) d-"f"-e interlock: *Borealestes*, *Krusatodon*, *Simpsonodon*, *Itatodon*, *Tegotherium*, *Sibirotherium*;
    (3) d-b overlap: *Docodon*, *Haldanodon*;
    (?) Not preserved: *Tikitherium*, *Gondtherium*.

28. Cusp triangulation (cusp triangulation between the a-c crest and the a-b crest following Butler 1997; Sigogneau-Russell and Godefroit 1997):
    (0) Absent: *Morganucodon*, *Megazostrodon*;
    (1) Present: *Kuehneotherium*, *Woutersia*, *Delsatia*, *Tikitherium*, *Gondtherium*, *Castorocauda*, *Tashkumyrodon*, *Tegotherium*, *Sibirotherium*, *Dsungarodon*, *Borealestes*, *Haldanodon*, *Docodon*, *Itatodon*, *Simpsonodon*.

29. Placement of lower cusp e:
    (0) Lingual position (lingual to the median axis of the lower molar): *Megazostrodon*, *Kuehneotherium*, *Delsatia*, *Woutersia*, *Gondtherium*, *Castorocauda*, *Itatodon*, *Krusatodon*, *Haldanodon*, *Docodon*;
    (1) Median placement of cusp e: *Simpsonodon*, *Borealestes*, *Tashkumyrodon*, *Dsungarodon*, *Tegotherium*, *Sibirotherium*;
    (?) Unknown: *Tikitherium*.

30. Number of upper molar roots (Averianov and Lopatin 2006, character 4):
    (0) Two: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*, *Woutersia*;
    (1) Three: *Tikitherium*, *Castorocauda*, *Sibirotherium* (scored from Averianov and Lopatin 2006), *Krusatodon*, *Borealestes*, *Simpsonodon*, *Haldanodon*, *Docodon*;
    (?) Unknown: *Delsatia*, *Gondtherium*, *Itatodon*, *Tashkumyrodon*, *Tegotherium*.

31. Number of lower canine roots (Ji et al. 2006; Averianov and Lopatin 2006: character 11):
    (0) One: *Morganucodon*, *Megazostrodon*, *Kuehneotherium*;
    (1) Two: *Haldanodon*, *Docodon*, *Castorocauda*, *Krusatodon*, *Sibirotherium*;
    (?) Unknown: *Woutersia*, *Delsatia*, *Gondtherium*, *Borealestes*, *Simpsonodon*, *Dsungarodon*, *Itatodon*, *Tashkumyrodon*, *Tegotherium*.

Appendix 2. Character matrix for phylogenetic analysis.

Morganucodon	00000	00000	0000?	00?00	00000	000?0	0
Megazostrodon	00000	00000	0000?	00?00	00001	11000	0
Kuehneotherium	00000	00000	0000?	00?00	0?001	01100	0
Delsatia	?????	???11	0100?	00?00	00001	1110?	?
Woutersia	10001	01011	0100?	00?00	00001	11100	?
Tikitherium	11000	021??	?????	?0???	?????	??1?1	?
Gondtherium	11100	02?1?	?221?	?0??1	0???0	1?10?	?
Tashkumyrodon	11210	1??1?	02211	0012?	01010	1011?	?
Castorocauda	?????	???11	03210	00021	12010	1010?	1
Tegotherium	?????	???11	03210	10020	02010	2211?	?
Sibirotherium	?????	???11	02210	00020	02010	22111	1
Dsungarodon	11210	12111	02110	10012	12000	10111	?
Borealestes	11210	12111	02112	00121	11110	12111	?
Haldanodon	11211	12110	12211	00012	11110	03101	1
Docodon	11211	12110	12211	01012	02110	03101	1
Itatodon	?????	???11	03211	1002?	11000	1010?	?
Krusatodon	11110	11111	03212	11121	11010	12101	1
Simpsonodon	11210	11011	0321?	01021	12010	12111	?