RECONSIDERATION OF THE SYSTEMATIC POSITION OF THE MIDDLE JURASSIC MAMMALIAFORMS *ITATODON* AND *PARITATODON*

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Two Middle Jurassic mammaliaforms, *Itatodon* Lopatin *et* Averianov, 2005 and *Paritatodon* Martin *et* Averianov, 2010 have been considered to be members of the Docodonta. Detailed comparison of their dental morphologies with that of typical docodonts shows clearly the differences in cusp pattern and cusp-crest relationship of their lower molar crowns. In docodonts, four crests, originating from the apex of cusp a, extend respectively toward cusps b, g, c, and d, and meet the crests therefrom; all the major crests point to the center of cusps. In contrast, in *Itatodon* and *Paritatodon*, only two crests from cusp a extend to cusps g and c, and all the crests reconcile to the anterior or posterior cusp surface. Such differences suggest that the docodont molars function mainly by cutting and crushing, whereas those of *Itatodon* and *Paritatodon* have a clear shearing function. Both the morphological features and possible molar occlusal function of *Itatodon* and *Paritatodon* distinguish them from the typical docodonts and indicate their shuotheriid affinities. Moreover, the term "pseudotalonid" is used in describing the non-homologous dental features, representing different occlusal relationships, in Shuotheridia and Docodonta. It should thus better be restricted in the description of lower dentition of Shuotheridia, as proposed by the original study.

Key words: *Itatodon*, *Paritatodon*, Middle Jurassic, pseudotalonid, Docodonta, Shuotheridia.

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INTRODUCTION

Studies on Mesozoic mammals (*sensu* Kielan-Jaworowska *et al.* 2004) have achieved great progress since 2004, when Zofia Kielan-Jaworowska, Richard L. Cifelli, and Zhe-Xi Luo published their comprehensive review book entitled *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. The progress has significantly expanded our knowledge of Mesozoic mammals in various aspects, such as taxonomy, phylogeny, biogeography, and biochronology, etc. Meanwhile, the systematic position of some taxa and the usage of a few concepts need to be clarified. Here we present a reconsideration of taxonomic status of two genera, *Itatodon* Lopatin *et* Averianov, 2005 and *Paritatodon* Martin *et* Averianov, 2010, and a discussion on the usage of the term "pseudotalonid", a concept proposed by Chow and Rich (1982) and reviewed by Rich and Vickers-Rich (2010).

Itatodon is a monotypic genus of Middle Jurassic mammaliaformes. It was originally proposed, with type species *I. tatarinovi*, by Lopatin and Averianov (2005) on the basis of an isolated right lower molar from the upper part of the Itat Formation of Krasnoyarsk Territory in West Siberia, Russia. Additional specimens referred to the species include another right lower molar (Averianov and Lopatin 2006) and a left dentary fragment with a premolar, the first lower molar, and the alveoli for three premolars and m2 (Averianov *et al.* 2010) from the same quarry. The genus was first considered as a member of the family Tegotheriidae in Docodonta (Averianov and Lopatin 2006; Lopatin and Averianov 2005), which was followed by Martin and Averianov (2010), but it was excluded from the Tegotheriidae later (Averianov *et al.* 2010; Hu *et al.* 2007; Luo and Martin 2007). Even so, its docodont affinity has not been questioned since the first report of *Itatodon* in 2005.

Sigogneau-Russell (1998) referred two lower molars from the Middle Jurassic Forest Marble Formation of Kirtlington, Oxfordshire, England to the shuotheriid genus *Shuotherium* and named a new species *S. kermacki*. However, when they reported the fossil mammals from the Middle Jurassic (Callovian) Balabansai Formation in northern Fergana Depression, Kyrgyzstan, Martin and Averianov (2010, p. 859) considered that the holotype of *S. kermacki* is similar to a lower molar of the docodont *Itatodon tatarinovi* Lopatin *et* Averianov, 2005. They proposed a new genus *Paritatodon* for the holotype of *S. kermacki* and referred a left ultimate lower molar to *Paritatodon* sp. However, detailed comparison of dental morphology reveals some differences between *Itatodon* and other docodonts, and requires a reconsideration of the systematic position of *Itatodon* and *Paritatodon*.

Institutional abbreviations. — CqMNH, Chongqing Museum of Natural History, Chongqing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PM TGU, Paleontological Museum of Tomsk State University, Tomsk, Russia; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

Acknowledgments. — We dedicate this paper to the late Professor Zofia Kielan-Jaworowska, a well-known vertebrate paleontologist, who made a great contribution to the study of Mesozoic mammals and whose papers on Mesozoic mammals, frequently cited in our studies, are among the most valuable references. We are greatly in debt to Richard L. Cifelli (University of Oklahoma, Norman, OK, USA) and Łucja Fostowicz-Frelik (Institute of Paleobiology PAS, Warsaw, Poland) for inviting us to contribute to this Festschrift volume in honor of Zofia. We appreciate Jin Meng (American Museum of Natural History, New York, NY, USA) and Zhe-Xi Luo (University of Chicago, USA) for useful discussion. We also appreciate in particular the kindness of Alexander Averianov (Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia) for sending us the digital images of *Itatodon tatarinovi* and *Hutegotherium yaomingi* we use in the paper. Thanks also go to Wending Zhang and Fangyuan Mao (both Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China) for help in taking SEM photos of the cast of *Shuotherium dongi* holotype. We are grateful to Thomas Martin (Universität Bonn, Germany) and Thomas H. Rich (Museum Victoria, Melbourne, Australia) for their helpful review comments. This work was supported by the Major Basic Research Projects of MST of China (2012CB821900).

DIAGNOSTIC MOLAR FEATURES OF DOCODONTA

Docodonta is a mammalian group, uncontestably ranging from the Middle Jurassic to Early Cretaceous (Kielan-Jaworowska *et al.* 2004). Docodonts are characterized by distinctive molars with a complex cusp and crest pattern. The terminology and homology of the molar structures, especially the cusps, have been contro-

versial for many years (*e.g.*, Butler 1939, 1988, 1997; Jenkins 1969; Krusat 1980; Patterson 1956; Sigogneau-Russell 2003; Sigogneau-Russell and Godefroit 1997). Most later researchers generally followed the framework of docodont molar homology established by Butler (1997), with their own modification (*e.g.*, Averianov *et al.* 2010; Hu *et al.* 2007; Ji *et al.* 2006; Lopatin *et al.* 2009; Luo *et al.* 2015; Luo and Martin 2007; Martin and Averianov 2010; Martin *et al.* 2010; Maschenko *et al.* 2002; Meng *et al.* 2015; Pfretzschner *et al.* 2005; Rougier *et al.* 2015). For the sake of convenience in discussion, the terminology of docodont molar cusps and crests is labeled on a diagrammatic illustration (Fig. 1). We largely accepted Butler's (1997) terminology with one exception in designation of the distal lingual cusp (cusp f of Butler 1997) as cusp dd following Hu *et al.* (2007). Using Butler's terminology in the present study does not mean we agree with his homologous designation for all cusps in a docodont molar. The homology of docodont cusps with other mammals will not be discussed here because it is beyond the scope of the paper and we would like to simply focus on the dental morphology of related forms.

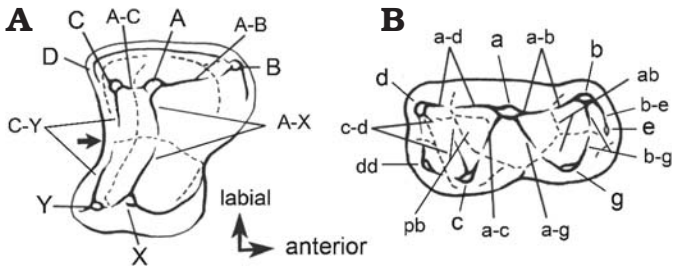

Fig. 1. Diagram showing the terminology of docodont upper (**A**, based on *Docodon*) and lower (**B**, based on *Borealestes*) molars (modified from Luo and Martin 2007). Arrow on the upper molar indicates the mid-constriction between the labial and lingual parts. Single letters represent cusps, and two letters with hyphen represent crest linking cusps. Both the anterior basin (ab) and posterior basin (pb) are used following the definition of Hu *et al.* (2007).

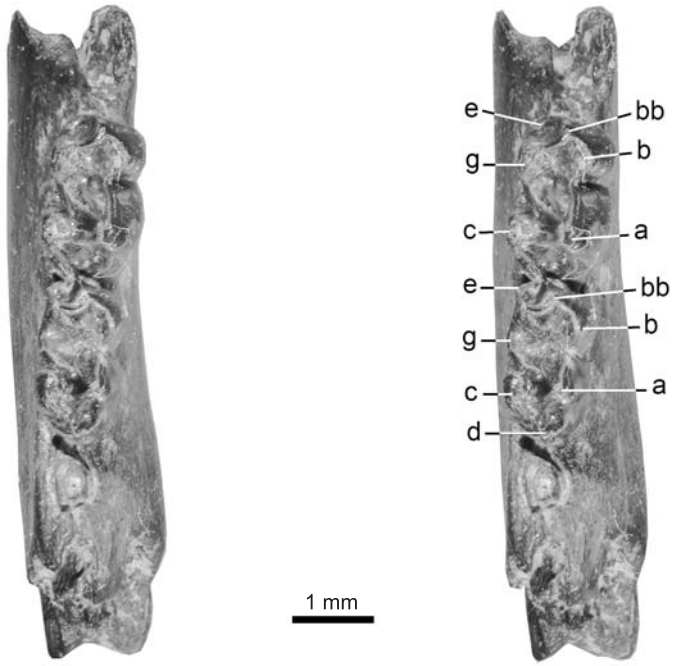

Fig. 2. Dorsal view (stereopair) of a right dentary fragment of *Hutegotherium yaomingi* (PIN 5087/8) from the Middle Jurassic Itat Formation (Bathonian) of West Siberia, Russia (fossil images courtesy of A.O. Averianov).

The complex cusp and crest pattern of docodont molars is unique in mammaliaforms. On the upper molars of docodonts, the crests A-X and C-Y connect the labial cusps A and C to the lingual cusps X and Y, respectively. The pattern is even more complicated on the lower molars, where nearly all cusps are connected by crests to the nearby cusps. Unlike in other mammals, where the crests or ridges connect the cusps by reconciling with either anterior or posterior surface of cusps, the crests on docodont molars run toward the middle of cusps. Most notably on the lower molars, four crests, originating from the top of cusp a, form respectively a part of the crests a-b, a-g, a-c, and a-d, with concave areas in between except for crests a-b and a-d. In most docodont genera, three crests connect cusp b to other cusps: a (a-b), g (b-g), and e (b-e). The exceptions are absence of crest b-g in *Tegotherium*, *Sibirotherium*, and *Hutegotherium* (Lopatin *et al.* 2009; Martin *et al.* 2010; Maschenko *et al.* 2002; Tatarinov 1994). However, the function of crest b-g may be substituted by crest bb-g connecting cusp g to cusp bb (a neomorphic cusp) (Fig. 2).

DENTAL FEATURES OF *ITATODON* AND *PARITATODON*

The dental features of *Itatodon* were only known from the two isolated right lower molars and a left dentary fragment with a premolar and the first molar (Averianov *et al.* 2010). With the description of the left dentary fragment (PIN 5087/7), Averianov *et al.* (2010) revised the diagnosis of the type and only species, *I. tatarinovi* (Fig. 3), and hence of the genus as follows:

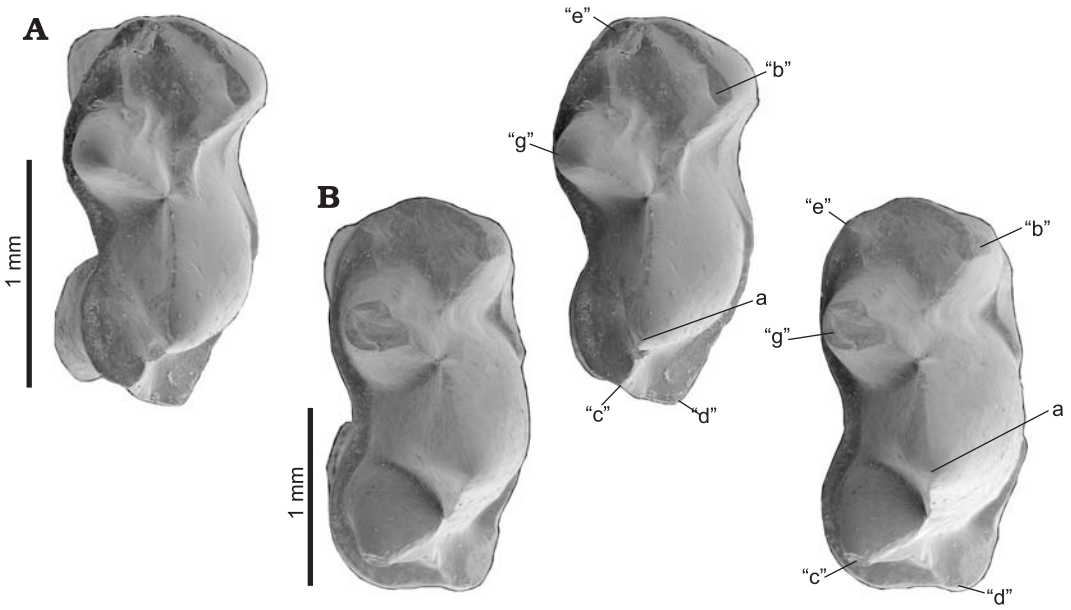

Fig. 3. Occlusal view (stereopairs) of right lower molars of *Itatodon tatarinovi* Lopatin *et* Averianov, 2005 from the Middle Jurassic Itat Formation (Bathonian) of West Siberia, Russia (fossil images courtesy of A.O. Averianov). **A**. Holotype PIN 5087/2. **B**. PM TGU 200/3-BR-7. Cusps labeled with quotation marks means that they occupy the same topographic position but may not be homologous with the respective cusps in docodont molars.

"*Itatodon* is unique among docodontans in having cusp b reduced to the cingular cusp, crests a-g and a-b diverging at the base of cusp a, no pseudotalonid basin on the first lower molariform tooth (absent also on the highly modified m1 of *Castorocauda*), and having the cingular cusp e incorporated into the wall of the pseudotalonid basin on the more posterior molariform teeth. Additionally, it differs from Docodontidae by having cusp b smaller than cusp c and well separated from cusp a, and a narrow mesiolingual cingulid; from Simpsonodontidae fam. nov. by presence of cusp e, a narrow mesiolingual cingulid, and lack of enamel folding; from Tegotheriidae by lack of cusp bb. Among docodontans *incertae familiae* it additionally differs from *Castorocauda* by the first lower non-sectorial molariform tooth, a large cusp g which is almost equal to cusp c, absence of crests b-g and a-d, presence of crest c-d, and the presence of cusp c on the lower molariform tooth; from *Castorocauda* and *Tashkumyrodon* by presence of a lingual cingulid and lack of the cusp dd and the crest c-dd" (Averianov *et al.* 2010, p. 124).

Of these diagnosing features, absence of crests "b"-"g" and a-"d" cannot only distinguish *Itatodon* (and *Paritatodon*) from *Castorocauda*, but the other docodonts as well, except *Tegotherium*, *Sibirotherium*, and *Hutegotherium*, which also lack crest b-g but have bb-g instead. Averianov *et al.* (2010) also stated that the pseudotalonid basin (= anterior basin) is absent on the first molar of *Itatodon* and *Castorocauda*. Unlike the other genera, however, the first two molars of *Castorocauda* are laterally compressed (Ji *et al.* 2006). It is possible that both teeth are highly specialized molars or could be alternately interpreted as premolars.

In addition to all the above-mentioned characters of *Itatodon*, a significant feature clearly distinguishing *Itatodon* from docodonts is that only two crests originate from the top of cusp a on *Itatodon* lower molars, extending to cusps "g" and "c" respectively. Both crests reconcile the anterior and/or posterior surface of the three cusps in *Itatodon*, which is similar to the cusp-crest connection pattern in the lower molars of obtuse-angled symmetrodonts (*e.g.*, *Tinodon*; see Crompton and Jenkins 1967; Simpson 1925) and, to a certain extent, of some cladotherians. This type of cusp-crest pattern suggests an occlusal relationship of the upper and lower molars different from that of docodonts, and can usually well perform a shearing function. No crest links cusp a and cusp "b", but a short crest from cusp "b" extends posterolingually to a point below the notch between cusp a and "g".

Martin and Averianov (2010) named *Paritatodon* for the holotype (a left lower molar) of *Shuotherium kermacki* Sigogneau-Russell, 1998 from the Middle Jurassic Forest Marble Formation (Bathonian) of England, but left the referred specimen (a broken right lower molar) as a shuotheriid. However, the comparable parts of both lower molars are not clearly different from each other according to the description and figures. They are probably from the same species. Martin *et al.* (2010, p. 859) considered that the holotype of

S. kermacki is extremely similar to a lower molar of *Itatodon tatarinovi* Lopatin *et* Averianov, 2005 from the Itat Formation at Berezovsk Quarry, Western Siberia, Russia. They also listed some morphological features that distinguish *Paritatodon* from *Itatodon*. In *Paritatodon*, the labial arms of crests a-c and a-g are almost longitudinal, whereas their lingual arms are more transverse, forming the angles between the labial and lingual arms approximating 90°. The labial cingulid is less pronounced than in *Itatodon* (Martin and Averianov 2010). Apparently, all the differences of *Itatodon* from docodonts are totally applicable to *Paritatodon*.

SHUOTHERIID AFFINITIES OF *ITATODON* AND *PARITATODON*

The above-mentioned morphological features of the lower molars of both *Itatodon* and *Paritatodon* not only separate them from true docodonts, but are similarities to those of *Shuotherium dongi* Chow and Rich, 1982 from the Late Jurassic Upper Shaximiao Formation, Sichuan, China. *S. dongi* is the type species of *Shuotherium*, the type genus of Shuotheriidae that is a peculiar mammalian group with pseudotribosphenic molar pattern (Chow and Rich 1982). The most striking dental feature of Shuotheriidae is a talonid-like structure (pseudotalonid) present anterior to trigonid; a point of contrast to tribosphenic mammals that have a talonid posterior to trigonid. When they reported *Shuotherium dongi*, Chow and Rich (1982) hypothesized that its upper molars possess a protocone-like lingual cusp (named pseudoprotocone) that occluded with the pseudotalonid of the lowers, and further proposed the pseudotribosphenic concept in describing such kind of occlusal pattern. After controversial discussion for many years (see Hopson 1995; Kermack *et al.* 1987; Tatarinov 1994), the validity of the pseudotribosphenic concept received support from referral to *Shuotherium* of some isolated triangular tricuspid upper molars from the same site as *S. dongi* and from the Middle Jurassic of England (Sigogneau-Russell 1998; Wang *et al.* 1998), and it was further confirmed by the discovery of *Pseudotribos robustus* with occluded upper and lower dentition from the Middle–Late Jurassic Daohugou biota of Inner Mongolia, China (Luo *et al.* 2007; see also Sullivan *et al.* 2014).

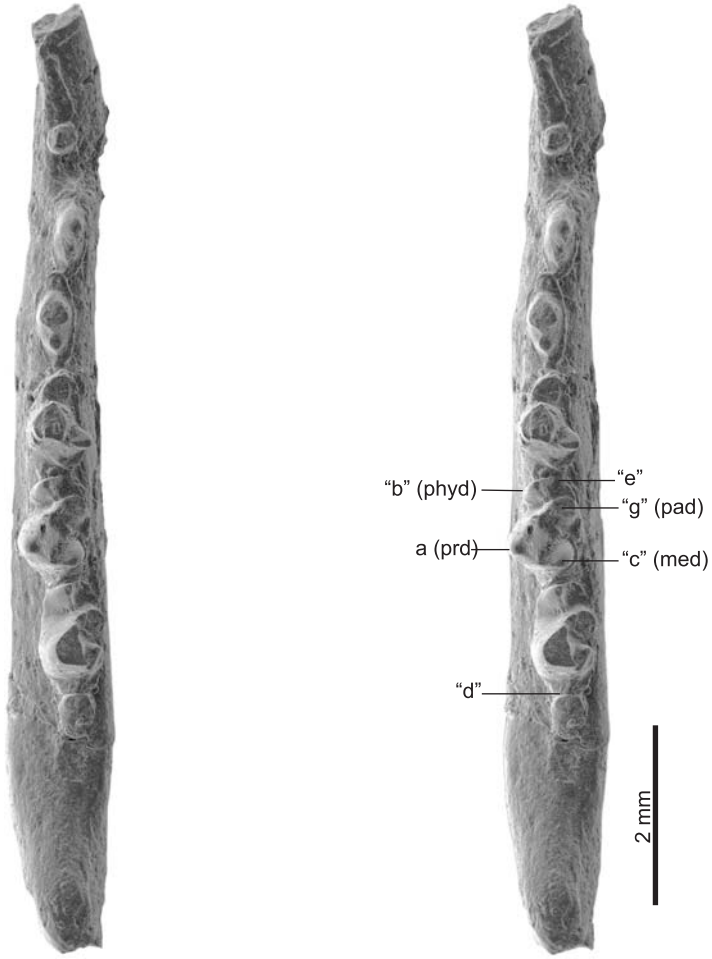

Fig. 4. Left dentary fragment in dorsal view (stereopair) of *Shuotherium dongi* Chow *et* Rich, 1982 (IVPP CV 6448, cast of the holotype, CqMNH V.729[1]) from the Late Jurassic Upper Shaximiao Formation (Oxfordian–Kimmeridgian) of Sichuan, China (modified from Chow and Rich 1984). Cusps labeled with quotation marks means that they occupy the same topographic position but may not be homologous with the cusp in docodont molars. The designation of cusps in pseudotribosphenic molars is given in parentheses. Abbreviations: hyd, hypoconid; med, metaconid; pad, paraconid; phyd, pseudo-hypoconid; prd, protoconid.

The morphology of shuotheriid lower molars was best documented by the type specimen of *Shuotherium dongi* (Fig. 4). The cusp a (protoconid) has two crests ex-

[1] Chow and Rich (1982) originally used IVPP catalogue number V6448 for the holotype of *Shuotherium dongi*, but the specimen was recatalogued after it was returned to the Chongqing Museum of Natural History, Chongqing, China.

tending to cusp "g" (paraconid) and cusp "c" (metaconid) respectively. Both crests a-"g" and a-"c" reconcile with the anterior and/or posterior surface of three cusps, forming the shearing structure. Crests "b"-"g", a-"b" and a-"d" are absent. A distinct crest (pseudo-cristid obliqua), directed posterolingually from the cusp "b" (pseudo-hypoconid), terminates at the base of the prevallid, the notch between cusp a (protoconid) and "g" (paraconid). Similar to *Itatodon tatarinovi*, the first lower molar (m1) does not have the pseudotalonid (Chow and Rich 1982).

The dental features mentioned above are all shared by *Shuotherium* with *Itatodon* and *Paritatodon*, and clearly suggest a close relationship between *Shuotherium* and *Itatodon* plus *Paritatodon*. The major differences of *Itatodon* and *Paritatodon* from *Shuotherium* include more longitudinal labial arms and more transverse lingual arms of the crests a-"c" and a-"g", with wider angle between these arms. Such differences are also applicable in distinguishing *Itatodon* and *Paritatodon* from docodonts and do not support a relationship to docodonts.

Although they mentioned the possibility that the first lower molar of *Shuotherium dongi* may be the last premolar, Chow and Rich (1982) considered the dental formula of the lower cheek teeth as p3m4. Kielan-Jaworowska *et al.* (2002) argued that *Shuotherium dongi* has a dental formula of four (or more) premolars and three molars, on the basis of the differences of previous m1 from the other molars in lacking a pseudotalonid and having a wider opened trigonid, which Chow and Rich (1982) had noted. However, as Chow and Rich (1982: p. 132) stated, "the sharpest change in the form of adjacent post-canine teeth occurs between the simple, somewhat blade-like P_3 and the highly molariform M_1". Compared with trechnotherians, the lack of pseudotalonid and wider opened trigonid do not indicate the tooth is a premolar, and it is not necessary for the first molar to have a pseudotalonid (Averianov 2002). The absence of a pseudotalonod in the first lower molar of *Itatodon* and *Shuotherium* shows that it is a common characteristic of Shuotheridia.

Shuotheriids are known from the Middle to Late Jurassic of China and the Middle Jurassic of England (Chow and Rich 1982; Luo *et al.* 2007; Sigogneau-Russell 1998; Wang *et al.* 1998). Those two places are widely separated. The reallocation into the Shuotheriidae of *Itatodon* from West Siberia, Russia and *Paritatodon* from Kyrgyzstan greatly narrows the biogeographic gap of shuotheriids between England and China.

DEFINITION OF PSEUDOTALONID

When they described the peculiar *Shuotherium dongi*, Chow and Rich (1982) realized that the basin in front of the trigonid functioned in an analogous manner to the talonid posterior to the trigonid in therians with tribosphenic molar pattern. They thus named the basin pseudotalonid. They further proposed the pseudotribosphenic concept describing the occlusal pattern of the pseudoprotocone in the upper molars with the pseudotalonid in the lowers. It is clear that the term pseudotalonid was originally associated with the pseudotribosphenic occlusal pattern. Later studies on shuotheriids followed Chow and Rich's original definition of pseudotribosphenic and pseudotalonid (Luo *et al.* 2007; Sigogneau-Russell 1998; Wang *et al.* 1998), but the term pseudotalonid was extended in description of docodont lower molars.

Kermack *et al.* (1987) first applied the term pseudotalonid to the lower molars of docodonts when they reported *Simpsonodon* from the Forest Marble of Kirtlington Quarry in Oxfordshire, England. Subsequently, pseudotalonid was widely used in describing lower molars of docodonts, *e.g.*, *Tegotherium* (Martin *et al.* 2010; Tatarinov 1994), *Krusatodon* and *Borealestes* (Sigogneau-Russell 2003), *Tashkumyrodon* (Martin and Averianov 2004), *Dsungarodon* (Martin *et al.* 2010; Pfretzschner *et al.* 2005), *Castorocauda* (Ji *et al.* 2006), *Haldanodon* (Luo and Martin 2007), *Sibirotherium* (Lopatin *et al.* 2009), *Simpsonodon* (Averianov *et al.* 2010; Martin and Averianov 2010), *Hutegotherium* (Averianov *et al.* 2010), *Docofossor* (Luo *et al.* 2015), and *Agilodocodon* (Meng *et al.* 2015). At first, some researchers described the anterior part of docodont lower molars as pseudotalonid, mostly because they considered that *Shuotherium* is a docodont (*e.g.*, Kermack *et al.* 1987) or the described docodont taxon is closely related to *Shuotherium* (*e.g.*, Tatarinov 1994). Later use of pseudotalonid in docodonts mainly followed the previous work or kept the term for the purposes of simplicity (Sigogneau-Russell 2003, p. 363). Some researchers designated the anterior basin of docodont lower molars as the pseudotalonid in quotation marks or used the term in association with anterior basin (Ji *et al.* 2006; Martin and Averianov 2004; Maschenko *et al.* 2002; Pfretzschner *et al.* 2005), implying the uncertainty on homology of the pseudotalonid in *Shuotherium* to that in docodonts. In addition, the definition of

the docodont "pseudotalonid" varied in different papers as noted by Luo and Martin (2007) in a review paper on the dentition of docodonts.

Although some researchers argued or accepted that the docodont molars are capable of shearing and grinding (or crushing) function (*e.g.*, Butler 1988; Gingerich 1973; Hu *et al.* 2007; Jenkins 1969; Kermack *et al.* 1987; Kielan-Jaworowska *et al.* 2004; Luo and Martin 2007; Pfretzschner *et al.* 2005), the morphology of docodont molars is clearly different from that of tribosphenic molars of therian mammals, which have both shearing and grinding function. Compared to the occlusal patterns of the nontherian mammaliaforms, the tribosphenic pattern of therian mammals is most efficient in food processing. Its shearing function is performed by the precise occlusion of both paracrista-preprotocrista on the upper molars to protocristid on the lower molars and metacrista-postprotocrista on the uppers to paracristid on the lowers, whereas the occlusion of protocone within the talonid performs its grinding function. The cusp-crest pattern of docodont molars does not clearly indicate the presence of precise shearing occlusion similar to that in tribosphenic therians, which may suggest that the docodont molars may have had less shearing function. Given that potential for grinding function in the docodont *Haldanodon* molar is much less than in the tribosphenic molar (Brinkkötter *et al.* 2014), it is clear that the docodonts had much lower efficiency in food processing than therian mammals. Unlike the shuotheriid molars, the molars of docodonts probably did not function in a reversed manner analogous to tribosphenic molars. Therefore, to use pseudotalonid in describing the anterior basin of docodonts "seems improper for docodonts, where the homology of cusps involved is not established" (Sigogneau-Russell 2003, p. 363). For the sake of precise use of the term pseudotalonid, it is appropriate to return to its original definition, restricted in the shuotheriid lower molars as explicitly advocated by Rich and Vickers-Rich (2010). Meanwhile, "anterior basin" is a proper name in describing the anterior part of docodont lower molars, as used by some researchers (*e.g.*, Hu *et al.* 2007; Ji *et al.* 2006; Lopatin *et al.* 2009; Martin and Averianov 2004; Maschenko *et al.* 2002; Pfretzschner *et al.* 2005; Sigogneau-Russell 2003).

CONCLUSIONS

The topographic distribution of cusp and the crest pattern of molars are the basic features for the comparison of dental morphology in mammaliaforms, especially for those groups whose cusp homology has not been well established. Docodonts are clearly distinguished from other mammaliaforms in having a unique and complex cusp and crest pattern. Among the taxa previously referred to Docodonta, *Itatodon* and *Paritatodon* have a cusp and crest pattern that is significantly different from that of true docodonts and very similar to that of shuotheriids, to which we accordingly refer them. The attribution of *Itatodon* and *Paritatodon* to the Shuotheriidae extends the shuotheriid record to West Siberia and central Asia, narrowing the geographic gap between China and England.

The extended usage of pseudotalonid in the description of docodont lower molars has varied in different studies, without either a clear definition or conformation to the original definition. It is better to restrict the use of pseudotalonid to shuotheriids, and to instead use the term anterior basin in docodonts.

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