第48卷 第4期
2010年10月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp.336-347
figs.1-18

“假磨楔式”:一个概念的发展历史

Thomas H. RICH[1,2] Patricia VICKERS-RICH[2,1]

(1 澳大利亚维多利亚博物馆 墨尔本 3001)

(2 澳大利亚莫纳什大学地球科学学院 克莱顿 3128)

摘要:大多数情况下古生物学是事后解释的科学,也就是说,在大多数情况下它的中心任务是解释存在的资料。古生物学成为预测科学的一个罕见的实例见诸于“假磨楔式”这个概念的发展历史中。根据一个假磨楔式哺乳动物的单个齿骨上的下臼齿结构,推测出当时尚不知道的上臼齿结构。随后,被认为很可能属于假磨楔式哺乳动物的单个上臼齿以及更晚的一件具有咬合在一起的上下臼齿的标本的发现证实了最初的假设。磨楔式臼齿结构作为哺乳动物历史中一个关键的创新结构,本身相当复杂。假磨楔式概念的被接受在认识磨楔式臼齿结构方面具有重要意义,这个结构可能发生不止一次。“假磨楔式”这个术语最初提出之后,随着它的使用,一些后来的研究者的用法严重偏离了它的本义。这一术语既被用来描述并不以原始定义的假磨楔式方式咬合的柱齿兽类牙齿,也被用于描述明显属于原始定义的磨楔式而不是假磨楔式牙齿。结果是古生物学界对其定义的理解变得更不准确,这个概念的实用性因此大大削弱。所以,回归最初的定义是合适的。

关键词:中生代,哺乳动物,进化,平行演化,磨楔式

中图法分类号:Q915.873 **文献标识码**:A **文章编号**:1000-3118(2010)04-0336-12

PSEUDOTRIBOSPHENIC: THE HISTORY OF A CONCEPT

Thomas H. RICH[1,2] Patricia VICKERS-RICH[2,1]

(1 *Museum Victoria* PO Box 666, Melbourne, Victoria 3001, Australia trich@museum.vic.gov.au)

(2 *School of Geosciences*, *Monash University*, Clayton, Victoria 3128, Australia pat.rich@monash.edu)

Abstract Palaeontology is for the most part a postdictive science. That is, its central task is for the most part to explain existing data. A rare instance of palaeontology being a predictive science is to be found in the history of the development of the pseudotribosphenic concept. Based on the structure of the lower molars in a single dentary of a pseudotribosphenic mammal, the structure of the then unknown upper molars was hypothesized. The subsequent discovery first of an isolated upper molar regarded as likely to be a pseudotribosphenic mammal and later, a specimen of a pseudotribosphenic mammal with its upper and lower molars in occlusion, rigorously corroborated the original hypothesis.

The acceptance of the pseudotribosphenic concept was instrumental in the recognition that the tribosphenic condition, a key innovation in the history of mammals, could well have arisen more than once, despite its complexity.

Living languages evolve through time. As the term “pseudotribosphenic” was utilised after being originally coined, its usage by some subsequent workers departed significantly from the original concept. The term has been used both to describe teeth of docodonts which do not occlude in the pseudotribosphenic manner as originally defined as well as teeth that were clearly tribosphenic as that term was originally

收稿日期:2009-07-04

defined rather than pseudotribosphenic. As a result, its definition as understood by the paleontological community became less precise, and thus the utility of the concept was significantly reduced. Consequently, a return to the original definition would be appropriate.

Key words Mesozoic, Mammalia, evolution, parallelism, tribosphenic

The Concept George Gaylord Simpson (1936) proposed the term tribosphenic to describe the occlusal pattern in molars of marsupials and placentals which combined a dual function of slicing and crushing. The crushing function is carried out by the protocone of the upper molars, acting as a pestle when occluding with a basin on the lower molars, the talonid, located behind the trigonid. The slicing function is accomplished by crests associated with the paracone and metacone on the upper molars sliding past the labial surfaces of the trigonid and talonid on the lower molars. All living mammals, save monotremes (Pascual et al., 2002; Woodburne, 2003), are thought to either retain this condition or to be descended from ancestors that once had it.

The pseudotribosphenic pattern has much the same function, except that rather than having a talonid located posterior to the trigonid, there is a pseudotalonid which is located anterior to the trigonid rather than behind it. Occluding with the pseudotalonid was a pseudoprotocone on the upper molars. This arrangement had the same combination of slicing and mortar-and-pestle interactions of structures on the upper and lower molars present in tribosphenic teeth, but

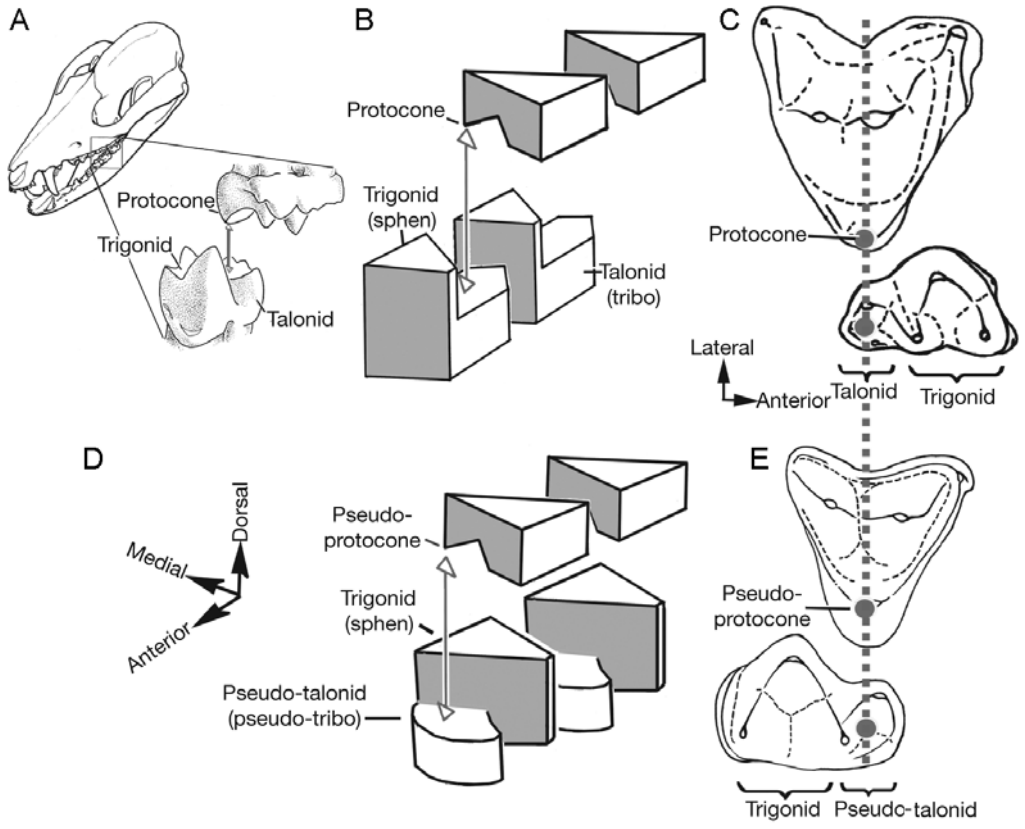

Fig. 1　Figure 3 in Luo et al., 2007 comparing tribosphenic and pseudo-tribosphenic molars

A. Skull of the marsupial *Didelphis virginiana* with its 'true' tribosphenic molars; B. Schematic illustration of the upper-lower occlusion of tribosphenic molars (trigonid anterior to talonid); C. *Kielantherium* as [an] example of the ancestral tribosphenic pattern; D. Schematic illustration of the upper-lower occlusion of pseudo-tribosphenic molars (trigonid posterior to pseudo-talonid); E. Shuotheriids as an example of pseudo-tribosphenic molars (based on *Pseudotribos*); dashed line shows the protocone-talonid occlusion and the pseudoprotocone-pseudotalonid occlusion

were back to front in the sense that the crushing function was anterior to the slicing function on the lower molars of pseudotribosphenic mammals rather than the reverse (Fig. 1).

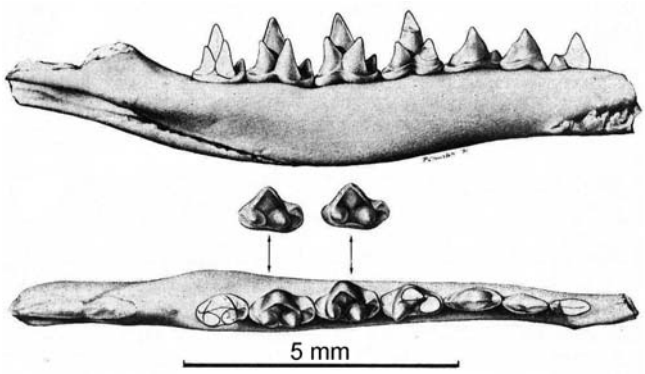

Fig. 2 Holotype of *Shuotherium dongi* Chow & Rich, 1982 in lingual view above and occlusal view below

Recognition 1982 The term pseudotribosphenic was coined to describe the condition in the lower molars of the holotype of the mammal *Shuotherium dongi* Chow & Rich, 1982 from the Middle to Late Jurassic Shaximiao Formation, Sichuan Province of China (Kielan-Jaworowska et al., 2004) (Fig. 2). Chow and Rich (1982) realised that the basin they observed positioned anterior to the trigonid functioned in an analogous manner to the talonid located behind the trigonid in therian mammals, a hallmark of the tribosphenic condition (Fig. 3). For this reason, the arrangement in *Shuotherium dongi* was given the name pseudotribosphenic.

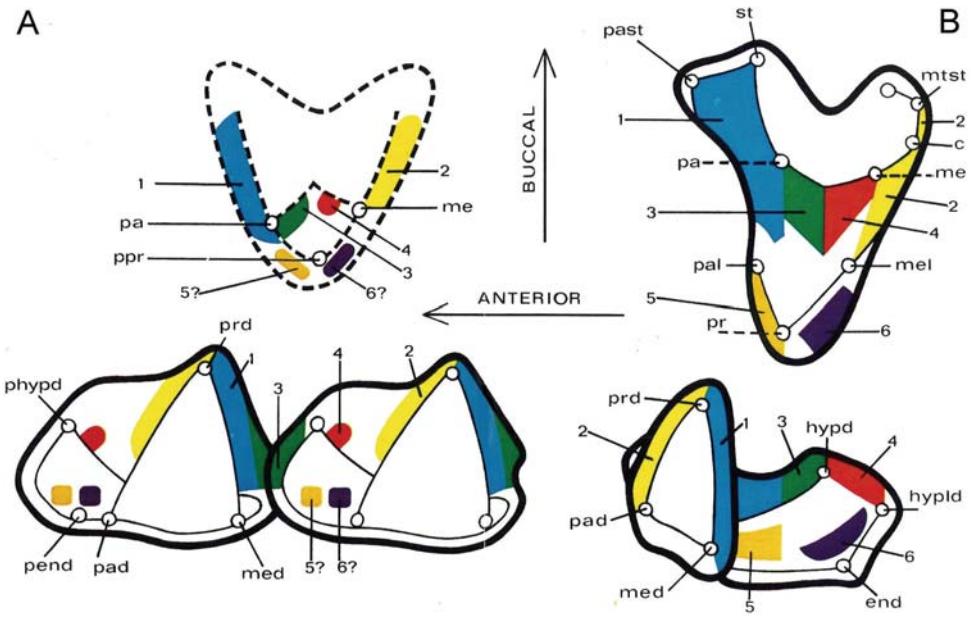

Fig. 3 Figure 6 in Chow and Rich (1982) comparing A, the upper hypothetical molar of *Shuotherium dongi* (above) and the known lower molars of that species (below) to B (= fig. 3A in Crompton, 1971), the upper molar (above) of the tribosphenic *Pappotherium pattersoni* and a lower molar (below) tentatively referred to that species (the corresponding wear facets on the upper and lower molars have the same number and colour) Abbreviations: end. entoconid; hypd. hypoconid; hypld. hypoconulid; me. metacone; med. metaconid; mel. metaconule; mtst. metastyle; pa. paracone; pad. paraconid; pal. paraconule; past. parastyle; pend. pseudoentoconid; phypd. pseudohypoconid; ppr. pseudoprotocone; pr. protocone; prd. protoconid; st. stylocone

Controversy 1983–1997 An alternative reconstruction of the upper molars of *Shuotherium dongi* was offered by Hopson (1995), which amongst other things, did away with the pseudoprotocone (Fig. 4).

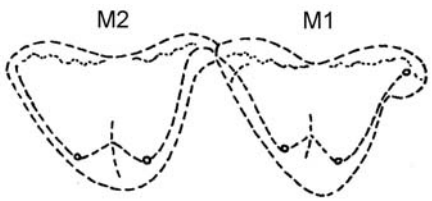

Fig. 4 Alternative hypothetical upper molars of *Shuotherium dongi* (Hopson, 1995)

Corroboration 1998–2007 The discovery of the upper molar of *Shuotherium shilongi* Wang et al., 1998 from the same locality as the holotype of *Shuotherium dongi* lent

significant support to the validity of the pseudotribosphenic concept (Fig. 5).

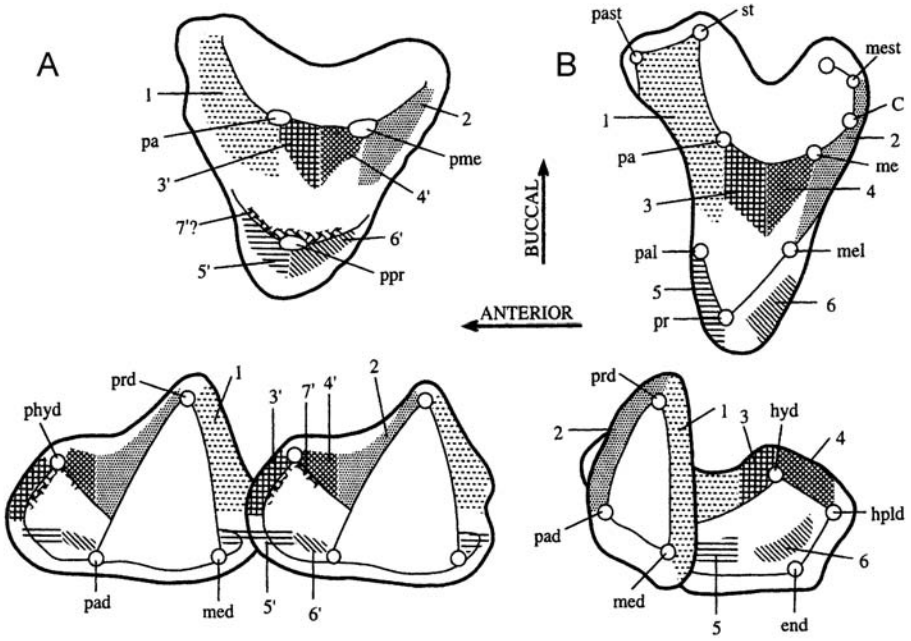

Fig. 5　Figure 6 in Wang et al. (1998), comparing A, the actual upper molar of *Shuotherium shilongi* (above) and the known lower molars of *Shuotherium dongi* (below) to B, the upper molar (above) of the tribosphenic *Pappotherium pattersoni* and a lower molar (below) tentatively referred to that species (the corresponding wear facets on the upper and lower molars have the same number)

Abbreviations: end. entoconid; hpld. hypoconulid; hyd. hypoconid; me. metacone; med. metaconid; mel. metaconule; mest. metastyle; pa. paracone; pad. paraconid; pal. paraconule; past. parastyle; phyd. pseudohypoconid; pme. pseudometacone; ppr. pseudoprotocone; pr. protocone; prd. protoconid; st. stylocone

In the same year that Wang and colleagues described *Shuotherium shilongi*, Sigogneau-Russell (1998) identified three isolated upper and five isolated lower molars that she referred to *Shuotherium* from the Middle Jurassic Forest Marble Formation of England.

However, it was a later find which confirmed beyond all doubt that the pseudotribosphenic condition was real and unique. This was the discovery of pseudotribosphenic upper and lower molars in occlusion present in *Pseudotribos robustus* reported by Luo et al. (2007) from the Middle Jurassic Jiulongshan Formation of Nei Mongol (Inner Mongolia) (Fig. 6).

Extension 1987 – 2007　Kermack et al. (1987) were the first to apply the term pseudotalonid to the teeth of docodonts, namely for *Simpsonodon* from the Forest Marble, Middle Jurassic, Oxford, England. They went so far as to apply this term to basins both anterior and posterior to a triangular structure present on the lower molars of those teeth. Subsequent usage of the term with regards to docodont lower molars has been restricted to basins located on the anterior moiety of those teeth. The term pseudotalonid has been applied to teeth in the following three other docodont taxa, also from the Forest Marble, Middle Jurassic, Oxford, England: *Cyrtlatherium*, *Krusatodon* and *Borealestes* (Sigogneau-Russell, 2001, 2003). Other docodonts to which the term pseudotribosphenic has been applied are *Tegotherium* from the Late

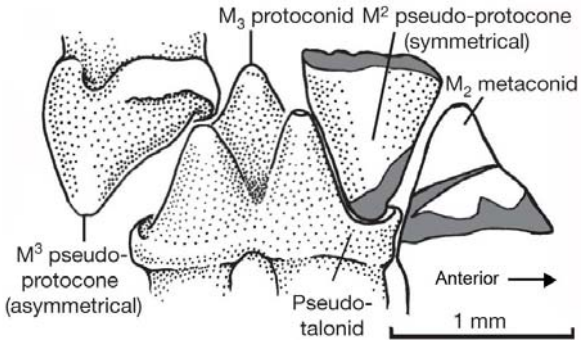

Fig. 6　Upper and lower pseudotribosphenic molars of *Pseudotribos robustus* found in occlusion (fig. 2e in Luo et al., 2007)

Jurassic of Mongolia (Tatarinov, 1994), *Itatodon*, *Simpsonodon* and *Hutegotherium* from the Middle Jurassic of Western Siberia (Averianov and Lopatin, 2006; Averianov et al., 2010), *Dsungarodon* from the Qigu Formation, Junggar Basin, China, early Late Jurassic (Pfretzschner et al., 2005) and *Krusatodon* Luo (2007). In describing *Tashkumyrodon* from the Middle Jurassic Balabansai Formation of Kyrgyzstan, Martin and Averianov (2004) made an implied distinction between the use of the term pseudotalonid in *Shuotherium* and docodonts. In the case of docodonts, the term was put in quotation marks immediately after they had referred to what they termed the anterior basin of the lower molars, while there were no quotation marks setting off the word pseudotalonid in the instance where *Shuotherium* was mentioned. In the case of the description of *Sibirotherium* from the Early Cretaceous Ilek Formation of Western Siberia by Maschenko et al. (2002), they also designated the anterior basin of the lower molars of that docodont as the pseudotalonid in quotation marks. When Lopatin et al. (2009) referred to the same genus, the word pseudotalonid was not set off by quotations marks and yet the word pseudotribosphenic was. Luo and Martin (2007) utilized the term pseudotalonid in a review paper on the dentition of docodonts and noted that various workers applied the term to somewhat different parts of the anterior region of the lower molars of that group. They further noted that some if not all of these variants of that term described structures on the lower molar of docodonts that were not homologous with the pseudotalonid of *Shuotherium*. Thus there appears to be an inconsistent application of the pseudotribosphenic terminology in docodonts since Kermack et al. (1987).

Despite the presence of a prominent cusp or cusps in the lingual region of upper molars of docodonts, no one using the pseudotribosphenic terminology has proposed that a mortar-and-pestle occlusal relationship existed between these structures on their upper and lower molars (Figs. 7–9). Therefore pseudotribosphenic terminology does not seem appropriate with regard to docodont tooth morphology. The mortar-and-pestle relationship between upper and lower molars was fundamental to the original definition of the tribosphenic condition (Simpson, 1936). When Chow and Rich (1982) proposed the term pseudotribosphenic, this same relationship was fundamental to their concept, a back-to-front alternative arrangement of the tribosphenic condition. If an alternative name is to be proposed for the various structures that has been called a "pseudotalonid" on docodont lower molars, we suggest that whatever term is chosen, "talonid" should not be the suffix for the simple reason that functionally these structures in docodonts did not act as a basin in which crushing occurred. "Anterior basin" as used by some workers would seem to be an appropriate alternative.

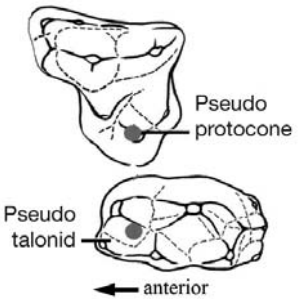

Fig. 7 Upper and lower molars of the docodont *Krusatodon* (modified from fig. 4 in Luo, 2007)

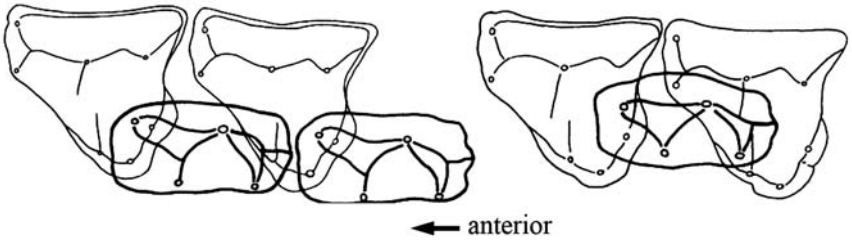

Fig. 8 Two hypothetical stages in the occlusion of upper molars (lighter lines) with the lower molars (darker lines) of the docodont *Krusatodon kirtlingtonensis*
In neither stage is there a mortar-and-pestle relationship shown between the cusps of the upper molars and the pseudotalonid of the lower molars (modified from fig. $5E_{1-2}$ in Sigogneau-Russell, 2003)

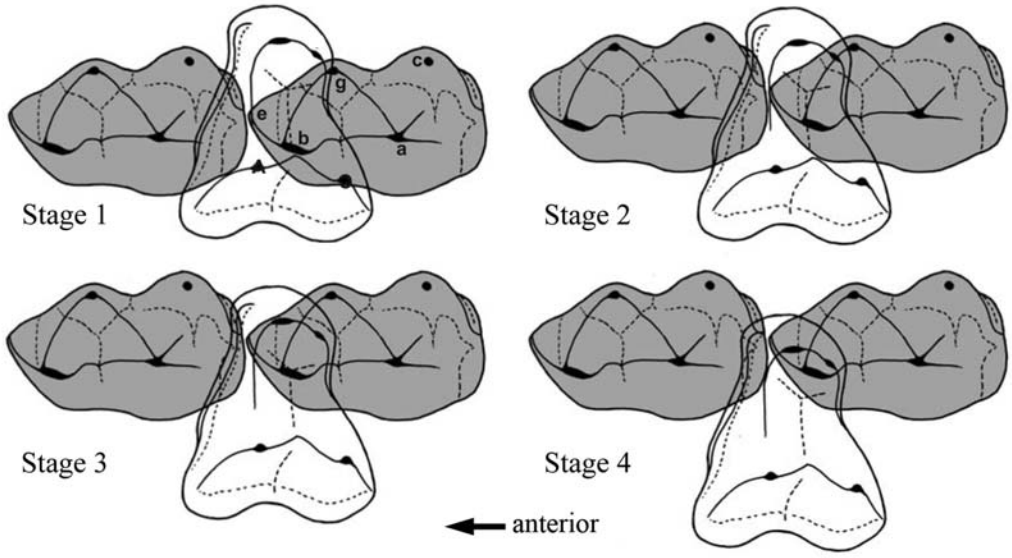

Fig. 9　Four stages in the occlusion of the docodont *Dsungarodon zuoi* starting with initial contact in Stage 1 Again, as in the case of *Krusatodon*, there is no mortar-and-pestle relationship suggested in this reconstruction of the occlusion of this docodont. Dark teeth are lower molars, the lighter tooth is an upper molar. Modified from fig. 5 in Pfretzschner et al. (2005)

A further extension of the original concept of pseudotribosphenic was implied by Martin and Rauhut (2005) when considering various alternatives for the possible occlusal relationship of the lower molars of *Asfaltomylos* from the Middle Jurassic of Argentina. Their figure 5C (Fig. 10 here) depicted an hypothesis showing a pseudoprotocone of an upper molar of *Shuotherium* occluding with the talonid of a known lower molar of *Asfaltomylos*. In their figure, the area of the tooth around the pestle-like cusp on the upper molar was labelled the distolabial bulge on pseudoprotocone. Because it is located posterior to the trigonid rather than anterior to it, the basin into which the pseudoprotocone is shown occluding is clearly the talonid rather than the pseudotalonid on *Asfaltomylos*. Evidently, Martin and Rauhut felt it necessary to identify the cusp on the upper molar as the pseudoprotocone in order to maintain consistency with the Australosphenidian hypothesis of Luo et al. (2001), who regarded shuotheriids with their pseudotribosphenic molars as closely allied with the Australosphenida. As well as *Asfaltomylos*, no other australosphenidans have pseudotalonids on their lower molars, but all also have talonids, namely *Ambondro* (Flynn et al., 1999), *Ausktribosphenos* (Rich et al., 1999), *Bishops* (Rich et al., 2001), and *Henosferus* (Rougier et al., 2007). This extension of the pseudotribosphenic concept by Martin and Rauhut (2005) seems to imply that the evolutionary development of a pestle-like cusp in the upper molars was not functionally linked to the development of a mortar-like cusp in the lower molars, for the pseudoprotocone in their usage could occlude with either a talonid or pseudotalonid.

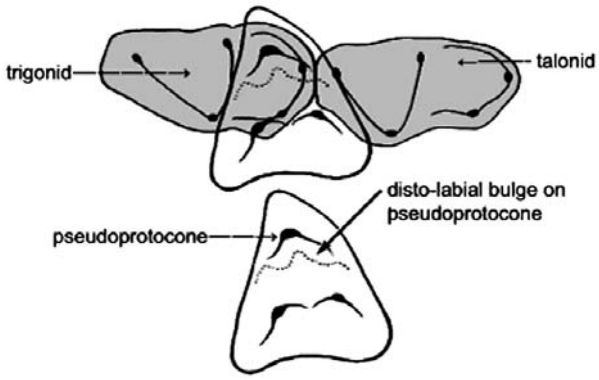

Fig. 10　Hypothesized occlusal relationship between the pseudoprotocone of *Shuotherium* and the talonid of *Asfaltomylos* posterior to the trigonid (Modified from fig. 5C in Martin and Rauhut, 2005)

Luo (2007) dealt with this problem of nomenclature of the cusps in the Australosphenida somewhat differently. He explicitly

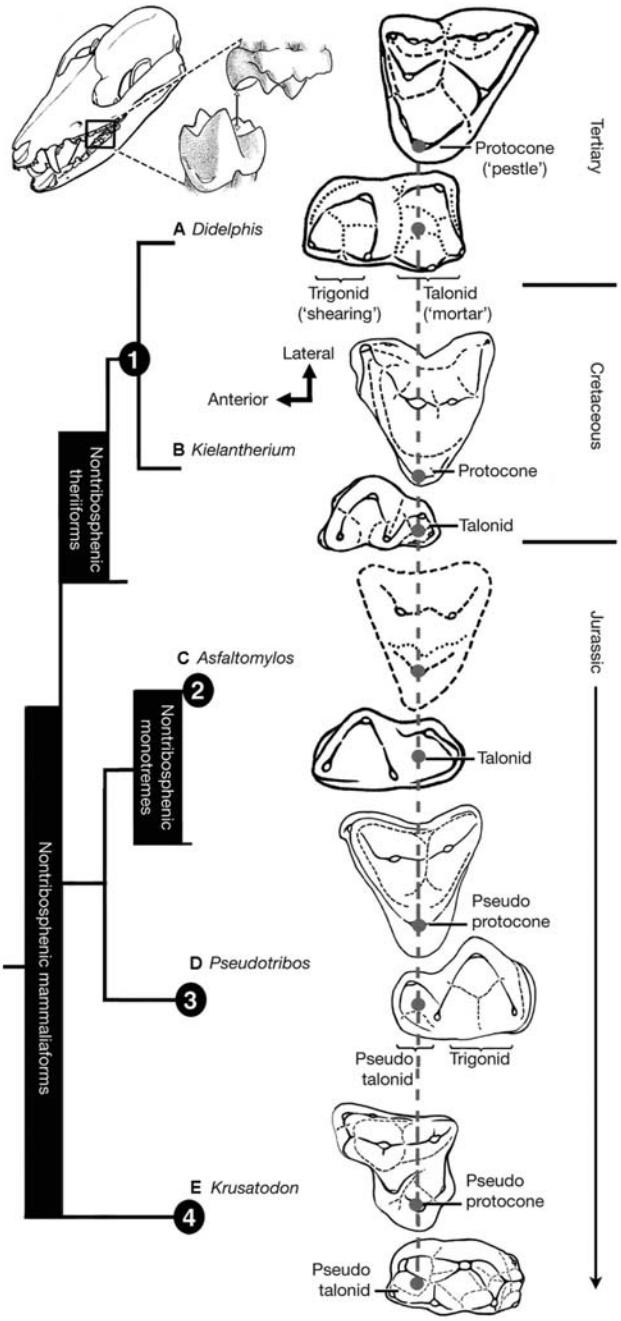

Fig. 11 Hypothesis of Luo regarding the identification of molar structures in various groups of mammals (fig. 4 in Luo, 2007)

regarded the dentition of *Asfaltomylos* as non-tribosphenic, although in his fig. 4 (Fig. 11 here), he employs the term talonid on the lower molar of that genus. He does not identify the lingual upper cusp on the hypothetical molar of *Asfaltomylos* as either a protocone or pseudoprotocone, although he labels the corresponding cusp of all the other upper molars in his fig. 4 one way or the other.

Molar Enumeration 1982–2007 Originally, Chow and Rich (1982) favoured regarding the four most posterior teeth in *Shuotherium dongi* as lower molars (Fig. 12). On the basis that the most anterior of these teeth lacks a pseudotalonid, Kielan-Jaworowska et al. (2002) favoured regarding that tooth as the most posterior premolar instead (Fig. 13). Shortly thereafter, Averianov (2002) analysed the occlusal relationships between the upper and lower molar series of *Shuotherium*. On that basis, he concluded that *Shuotherium* had four lower molars rather than three. In describing *Pseudotribos robustus*, Luo et al. (2007) regarded it as having three lower molars.

Phylogeny 1982 – 2007 Chow and Rich (1982) initially divided the Trechnotheria into two taxa they proposed, the Yinotheria and Yangotheria, *Shuotherium dongi* belonging to the former, the remaining trechnotheres being the Yangotheria and the sister group of the former (Fig. 14). The Yangotheria were equated to the Cladotheria McKenna, 1975 by McKenna and Bell (1997), although the former taxon included the Symmetrodonta and the latter, excluded them.

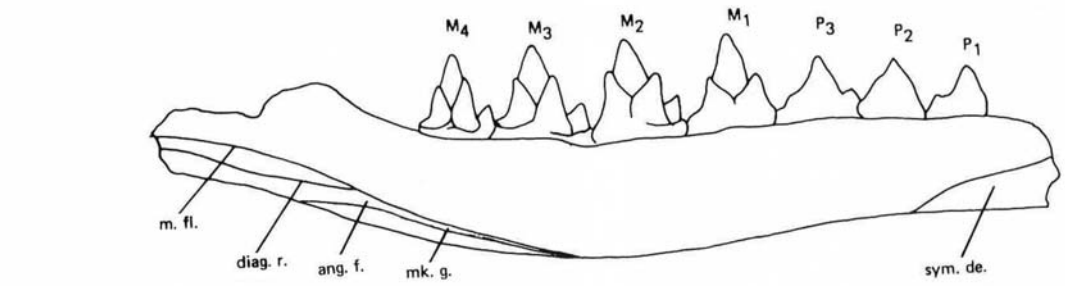

Fig. 12 Four molars attributed to *Shuotherium dongi* in holotype description (modified from fig. 5C in Chow and Rich, 1982)

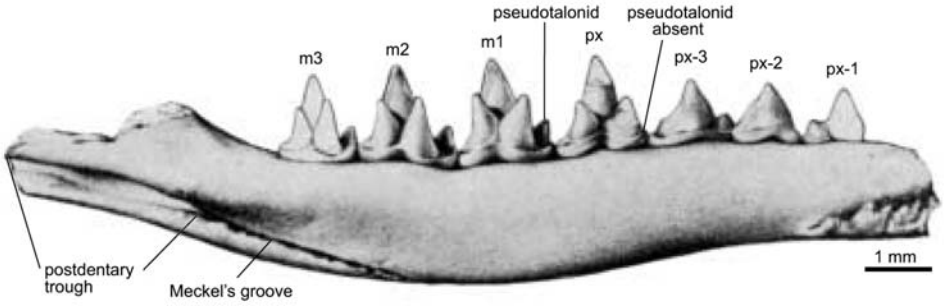

Fig. 13　Three molars attributed to *Shuotherium dongi* in Kielan-Jaworowska et al. (2002)

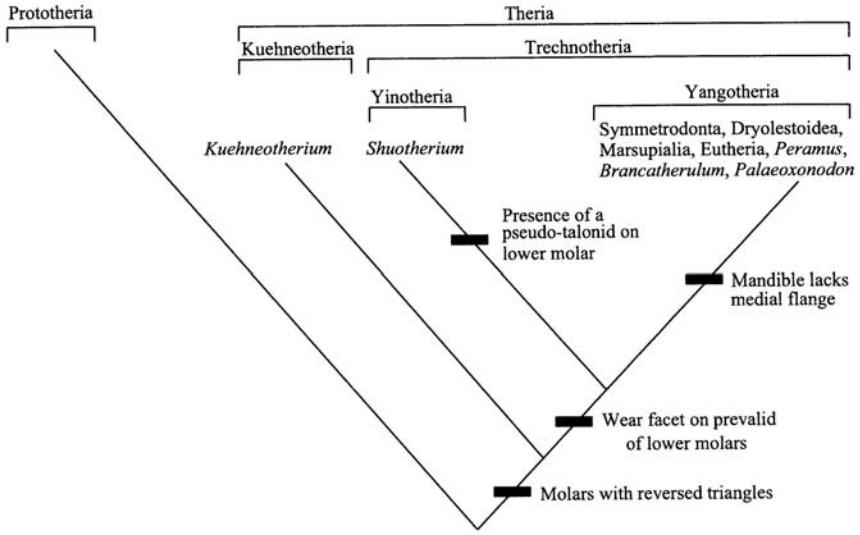

Fig. 14　Initial phylogenetic hypothesis of Chow and Rich (1982)
A fundamental tenet of this hypothesis was that the common ancestor of the tribosphenic and pseudotribosphenic mammals was a triconodontan which did not have the rudiments of either a talonid or pseudotalonid on the lower molars nor did it have a protocone or pseudoprotocone on the upper molars. The Prototheria, as used in 1982, included the monotremes

Prior to the description of an upper molar of *Shuotherium*, *S. shilongi* by Wang et al. (1998) validating the pseudotribosphenic concept, Kermack et al. (1987) tentatively allocated the genus to the docodonts, Hopson (1995) regarded it as, "…a basal 'therian', but its systematic position is otherwise uncertain…," McKenna and Bell (1997) placed the genus in the Symmetrodonta, Sigogneau-Russell (1998) recognised the Shuotherida as a separate order but did not indicate where the order should be placed within the Mammalia, and Sigogneau-Russell and Ensom (1998) dismissed the hypotheses that it was either a symmetrodont or a "basal" therian while accepting it as a therian.

Beginning with Wang et al. (1998), the Shuotheridae have either again been re-

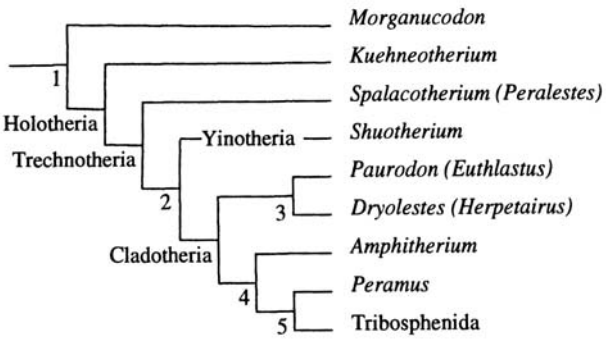

Fig. 15　Cladogram showing the position of *Shuotherium* that was published in the paper where the upper molar of *Shuotherium shilongi* was described (Wang et al., 1998) Generated using Paup, it differs in only one significant respect from the manually drawn cladogram which appeared in Chow and Rich (1982), namely in the position of the symmetrodonts as represented by *Spalacotherium* (*Peralestes*)

garded as a group of mammals near the base of the Theria (Figs. 15–16) or allied with a group of otherwise Southern Hemisphere forms grouped in the Australosphenida (Fig. 17–18). Those southern forms are the monotremes and Gondwanan Mesozoic tribosphenic taxa.

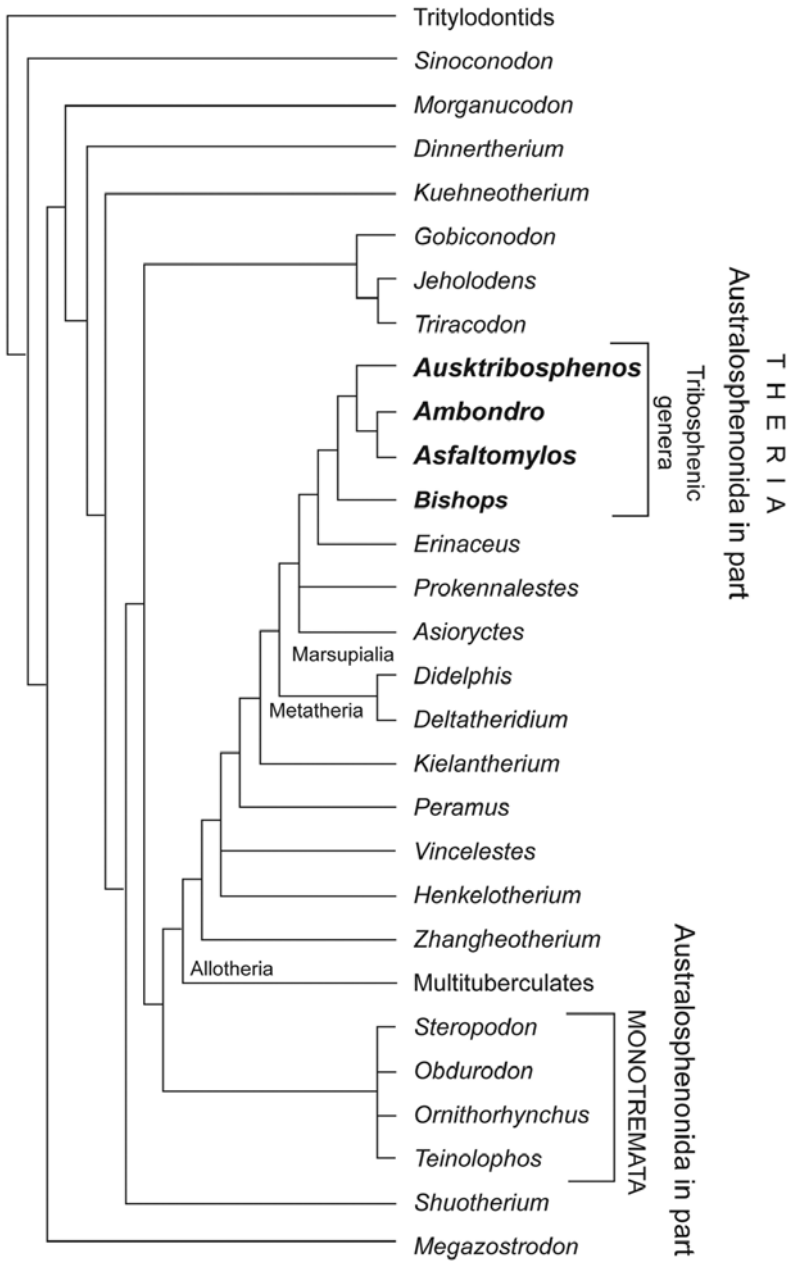

Fig. 16 Hypothesis of Woodburne et al. (2003)
The genera allocated to the Australosphenida *sensu* Luo et al. (2001) are divided into two groups. The pseudotribosphenic *Shuotherium* is not remotely related to either cluster of australosphenidians. Following the hypothesis of Chow and Rich (1982), the common ancestor of the tribosphenic and pseudotribosphenic mammals is regarded as a triconodontan

Significance When Chow and Rich (1982) originally introduced the pseudotribosphenic concept, they noted that its greatest significance was the demonstration that the tribosphenic condition could well have arisen a number of times, rather than being such a complicated phenomenon that it could only have arisen once. This theme has been taken up subsequently and elaborated a number of times by others (Kielan-Jaworowska et al., 2002; Luo et al., 2001, 2007; Woodburne, 2003). This concept was fundamental to the hypothesis establishing the Boreosphenida and Australosphenida (Luo et al., 2001).

During the Mesozoic Era, many groups of Mammalia arose that thrived for a time and then became extinct without issue (Luo, 2007). One example of these "failed evolutionary experiments" was the Yinotheria with their pseudotribosphenic dentition that stands well apart from other mammals.

An appreciation Zhou Mingzhen fervently advocated the importance of international interchange of ideas and data amongst vertebrate palaeontologists. We were amongst the beneficiaries of this enlightened view as well as experienced his warm, personal friendship as a consequence of his having that generous attitude. That the historical account which is the subject of this paper would be quite different had it not been for Mingzhen and his outlook is obvious. It is thus most fitting that we can express our heartfelt thanks to him here in this volume dedicated to his memory.

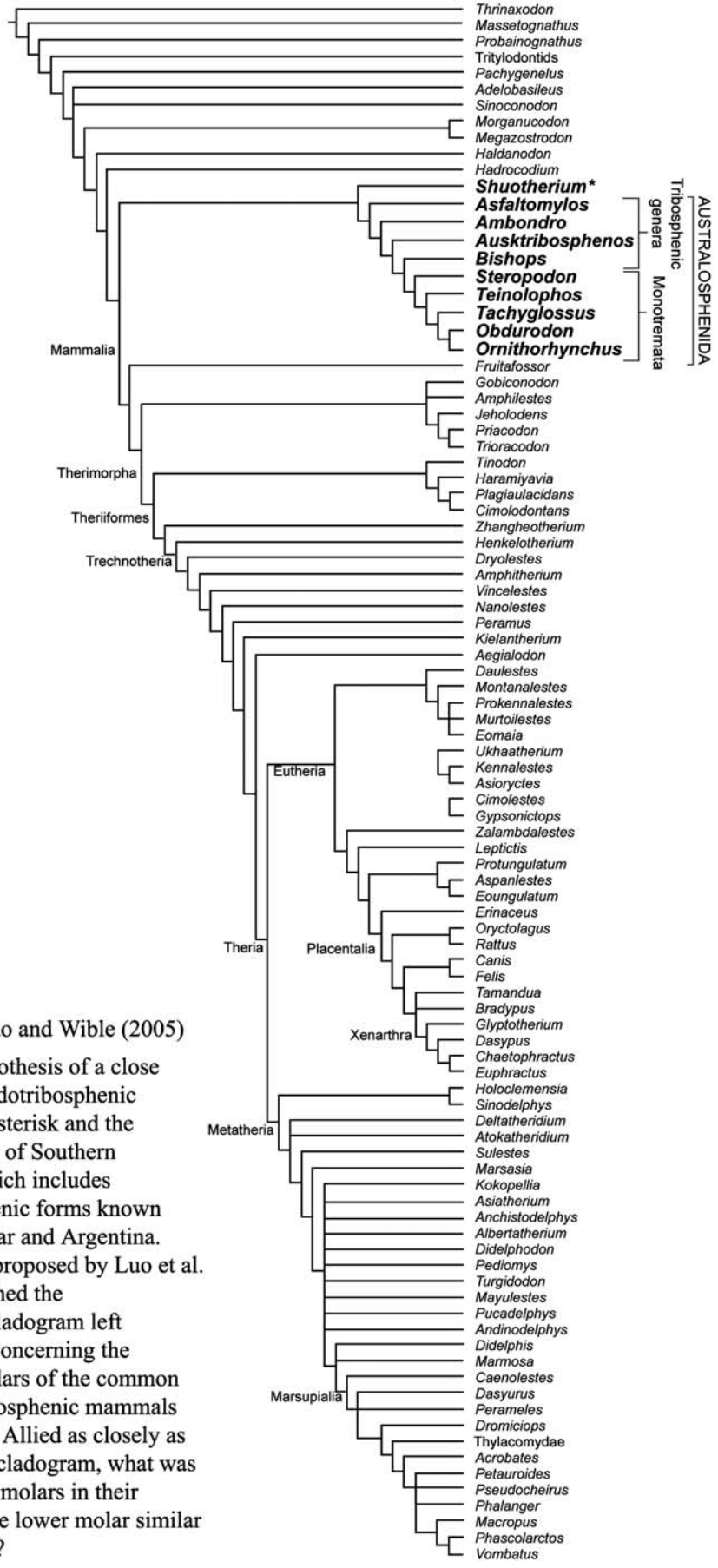

Fig. 17　Hypothesis of Luo and Wible (2005)

This is a variant of an hypothesis of a close relationship between pseudotribosphenic mammals denoted by an asterisk and the Australosphenida, a group of Southern Hemisphere mammals which includes monotremes and tribosphenic forms known from Australia, Madagascar and Argentina. This hypothesis was first proposed by Luo et al. (2001) when they established the Australosphenida. Their cladogram left unanswered the question concerning the condition of the lower molars of the common ancestor of the pseudotribosphenic mammals and the Australosphenida. Allied as closely as the two groups are in this cladogram, what was the condition of the lower molars in their common ancestor? Was the lower molar similar to that of a symmetrodont?

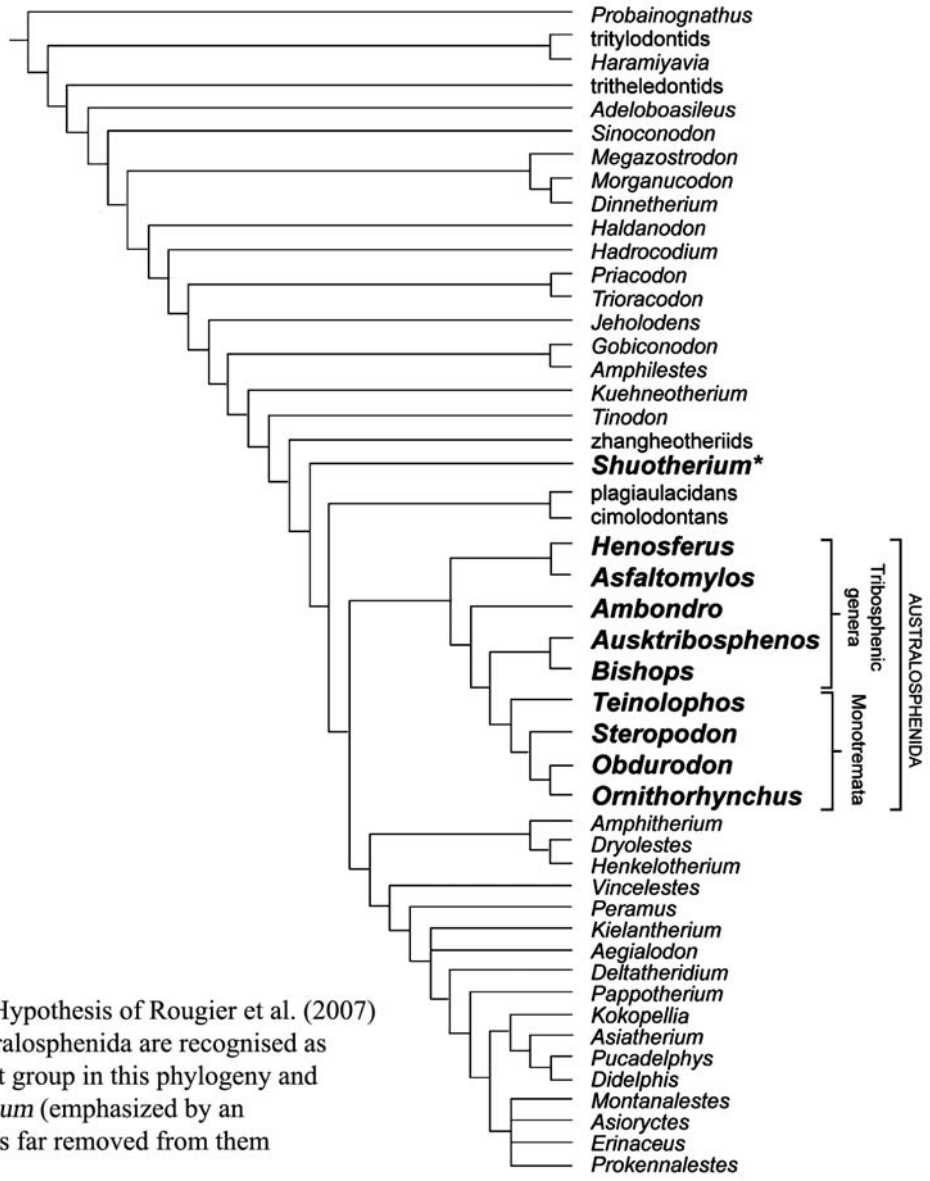

Fig.18 Hypothesis of Rougier et al. (2007) The Australosphenida are recognised as a coherent group in this phylogeny and *Shuotherium* (emphasized by an asterisk) is far removed from them

References

Averianov A O, 2002. Early Cretaceous "symmetrodont" mammal *Gobiotheriodon* from Mongolia and the classification of "Symmetrodonta". Acta Palaeont Pol, **47**: 706–716

Averianov A O, Lopatin A V, 2006. *Itatodon tatarinovi* (Tegotheriidae, Mammalia), a docodont from the Middle Jurassic of Western Siberia. Paleont J, **40**: 668–677

Averianov A O, Lopatin A V, Krasnolutskii S A et al., 2010. New docodontans from the Middle Jurassic of Siberia and reanalysis of Docodonta relationships. Proc Zool Inst Russ Acad Sci, **314**: 121–148

Chow M, Rich T H V, 1982. *Shuotherium dongi*, gen. et sp. nov., a therian with pseudotribosphenic molars from the Jurassic of Sichuan, China. Aust Mammal, **5**: 127–142

Crompton A W, 1971. The origin of the tribosphenic molar. In: Kermack D M, Kermack K A eds. Early Mammals. Zool J Linn Soc Lond, **50**(Suppl 1): 65–87

Flynn J J, Parrish J M, Rakotosamimanana B et al., 1999. A Middle Jurassic mammal from Madagascar. Nature, **401**: 57–60

Hopson J A, 1995. The Jurassic mammal *Shuotherium dongi* "pseudo-tribosphenic therian," docodontid, or neither? J Vert Paleont, **17**(Suppl 3): 53A

Kermack K A, Lee A J, Lees P M et al., 1987. A new docodont from the Forest Marble. Zool J Linn Soc, **89**: 1-39

Kielan-Jaworowska Z, Cifelli R, Luo Z-X, 2002. Dentition and relationships of the Jurassic mammal *Shuotherium*. Acta Palaeont Pol, **47**: 479-486

Kielan-Jaworowska Z, Cifelli R, Luo Z-X, 2004. Mammals from the Age of Dinosaurs - Origin, Evolution and Structure. New York: Columbia University Press. 1-630

Lopatin A V, Averianov A O, Maschenko K N et al., 2009. Early Cretaceous mammals of western Siberia: 2. Tegotheriidae. Paleont J, **43**: 453-462

Luo Z-X, 2007. Transformation and diversification in early mammal evolution. Nature, **450**: 1011-1019

Luo Z-X, Cifelli R, Kielan-Jaworowska Z, 2001. Dual origin of tribosphenic mammals. Nature, **409**: 53-57

Luo Z-X, Ji Q, Yuan C-X, 2007. Convergent dental adaptations in pseudo-tribosphenic and tribosphenic mammals. Nature, **450**: 93-97

Luo Z-X, Martin T, 2007. Analysis of molar structure and phylogeny of docodont genera. Bull Carnegie Mus Nat Hist, **39**: 27-47

Luo Z-X, Wible J R, 2005. A Late Jurassic digging mammal and early mammalian diversification. Science, **308**: 103-107

Martin T, Averianov A O, 2004. A new docodont (Mammalia) from the Middle Jurassic of Kyrgyzstan, central Asia. J Vert Paleont, **24**: 195-201

Martin T, Rauhut O W M, 2005. Mandible and dentition of *Asfaltomylos patagonicus* (Australosphenida, Mammalia) and the evolution of tribosphenic teeth. J Vert Paleont, **25**: 414-425

Maschenko E N, Lopatin A V, Voronkevich A V, 2002. A new genus of the tegotheriid docodonts (Docodonta, Tegotheriidae) from the Early Cretaceous of West Siberia. Russ J Theriol, **1**: 75-81

McKenna M C, 1975. Toward a phylogenetic classification of the Mammalia. In: Luckett W P, Szalay E S eds. McGraw-Hill Encyclopedia of Science and Technology. New York: McGraw-Hill Book Co. 21-46

McKenna M C, Bell S K, 1997. Classification of Mammals Above the Species Level. New York: Columbia University Press. 1-631

Pascual R, Goin F J, Balarino L et al., 2002. New data on the Paleocene monotreme *Monotrematum sudamericanum*, and the convergent evolution of triangulate molars. Acta Palaeont Pol, **47**(3): 487-492

Pfretzschner H-U, Martin T, Maisch M W et al., 2005. A new docodont mammal from the Late Jurassic of the Junggar Basin in Northwest China. Acta Palaeont Pol, **50**(4): 799-808

Rich T H, Flannery T F, Trusler P et al., 2001. A second tribosphenic mammal from the Mesozoic of Australia. Rec Queen Victoria Mus, **110**: 1-9

Rich T H, Vickers-Rich P, Constantine A et al., 1999. Early Cretaceous mammals from Flat Rocks, Victoria, Australia. Rec Queen Victoria Mus, **106**: 1-34

Rougier G W, Forasiepia A M, Martinelli A et al., 2007. New Jurassic mammals from Patagonia, Argentina: a reappraisal of Australosphenidan morphology and interrelationships. Am Mus Novit, (3566): 1-53

Sigogneau-Russell D, 1998. Discovery of a Late Jurassic Chinese mammal in the Upper Bathonian of England. C R Acad Sci Paris, Earth Planet Sci, **327**: 551-576

Sigogneau-Russell D, 2001. Docodont nature of *Cyrtlatherium*, an upper Bathonian mammal from England. Acta Palaeont Pol, **46**(3): 427-430

Sigogneau-Russell D, 2003. Docodonts from the British Mesozoic. Acta Palaeont Pol, **48**(3): 357-374

Sigogneau-Russell D, Ensom P, 1998. *Thereuodon* (Theria, Symmetrodonta) from the Lower Cretaceous of North Africa and Europe, and a brief review of symmetrodonts. Cret Res, **19**: 445-470

Simpson G G, 1936. Studies of the earliest mammalian dentition. Dent Cosmos, **78**: 791-800, 940-953

Tatarinov L P, 1994. An unusual mammal tooth from the Jurassic of Mongolia. Paleont J, **28**: 121-131

Wang Y Q, Clemens W A, Hu Y M et al., 1998. A probably pseudo-tribosphenic upper molar from the Late Jurassic of China and the early radiation of the Holotheria. J Vert Paleont, **18**: 777-787

Woodburne M O, 2003. Monotremes as pretribosphenic mammals. J Mammal Evol, **10**: 195-248

Woodburne M O, Rich T H, Springer M, 2003. The evolution of tribospheny in Mesozoic mammals. Mol Phylogenet Evol, **28**: 360-385