

A new species of *Archaeoryctes* from the Middle Paleocene of China and the phylogenetic diversification of Didymoconidae

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ABSTRACT. Didymoconidae are an enigmatic group of Asian endemic insectivorous mammals. We describe the new didymoconid species *Archaeoryctes wangi* sp. nov. from the Upper Member of the Wanghudun Formation (Middle Paleocene). This new species from the Qianshan Basin (Anhui Province, China) forms an interesting geographical intermediate between *A. notialis* from South China and *A. borealis* and *A. euryalis* from the Mongolian Plateau. To better understand the origin and evolutionary diversification of Didymoconidae, we performed a cladistic and stratocladistic study of the Didymoconidae and various outgroups. This study of dental material did not resolve the higher level affinities of Didymoconidae, but confirms the validity of the family and its distinctiveness from the morphologically similar Sarcodontidae. Moreover, our results corroborate the current didymoconid classification with the distinction of three subfamilies: “Ardynictinae”, Kennatheriinae and Didymoconinae; “Ardynictinae” are a paraphyletic stemgroup for the two other subfamilies. Our results suggest three distinct didymoconid radiations: (1) primitive ardynictines appeared in South China from the start of the Nongshanian; their evolution continues on the Mongolian Plateau with (2) the radiation of more evolved ardynictines and kennatheriines at the start of the Middle Eocene Arshantan and (3) the origin of didymoconines at the start of the Late Eocene Ergilian.

KEYWORDS: Ardynictinae, Sarcodontidae, Qianshan Basin, Asia, Evolution, Stratocladistics

1. Introduction

Didymoconidae are a poorly known, enigmatic group of insectivorous mammals, which are strictly endemic to Asia (Lopatin, 2006). They appear at the start of the Nongshanian Asian Land Mammal Age (ALMA, early Middle Paleocene) and persist until the Tabenbulakian ALMA (Late Oligocene) (Wang

et al., 2007; Missiaen, 2011). The specialized Oligocene genus *Didymoconus* was originally referred to Carnivora (Matthew and Granger, 1924), and based on similarities of older, more primitive didymoconids with North American the family has also been linked to Mesonychidae and Wyolestidae (Gingerich, 1981). Based on more recent studies of cranial morphology (Meng et al., 1994; Lopatin, 2001), Didymoconidae are now generally thought



Figure 1. Geographic location of the Qianshan Basin and other principal didymoconid sites. Map of East Asia (modified from Missiaen, 2011). Hexangular marks show localities of Ardynictinae with list of taxa present, diamond indicates Kennatheriinae, and circles indicate Didymoconinae. Squares indicate location of *Hunanictis* and *Mongolotherium* not formally assigned to a specific subfamily here.

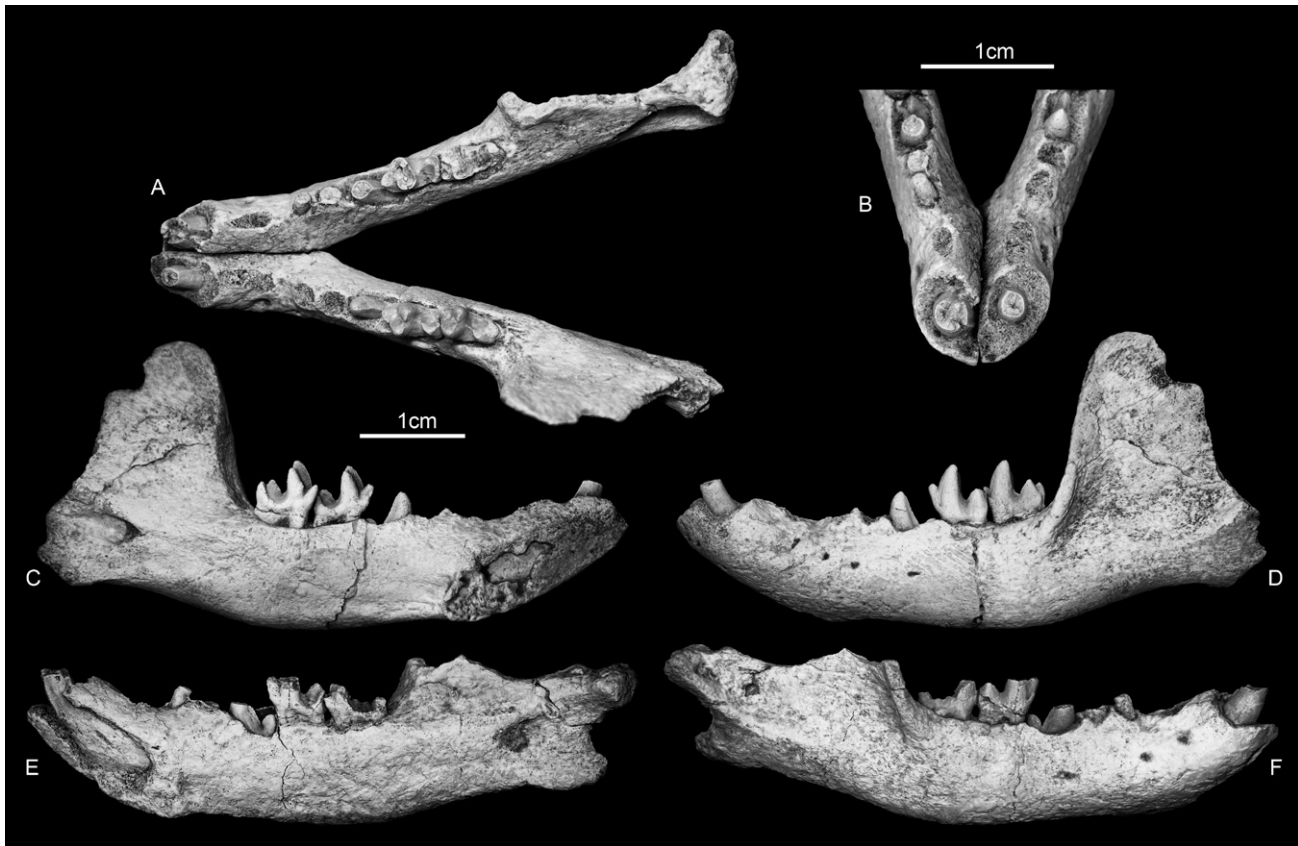


Figure 2. Dental morphology of *Archaeoryctes wangi* sp. nov. Holotype specimen IBCAS QS003 from the Nongshanian Upper Member of the Wanghudun Formation in the Qianshan Basin, Anhui Province, P.R. China in occlusal (A) and anterior (B) view, left dentary in lingual (C) and labial (D) view, and right dentary in lingual (E) and labial (F) view.

to be related to various primitive insectivorous taxa, but overall their suprafamilial affinities remain unclear. Similarly, recent discoveries have led to the recognition of three didymoconid subfamilies, Didymoconinae, Ardynictinae and Kennatheriinae (Lopatin 1997, 2006). Specific details of this classification vary however and the corresponding evolutionary scenarios have never been formally analyzed (Tong, 1997; Lopatin, 1997, 2006). Here we describe a new, well preserved and nearly complete lower jaw of the primitive didymoconid *Archaeoryctes* from the early Nongshanian ALMA of the Qianshan Basin of Anhui Province, China (Fig. 1), and identify it as the new species *Archaeoryctes wangi* sp. nov. Additionally, we perform the first cladistic and stratocladistic study of Didymoconidae and potentially related taxa based on dental morphology in order to better understand the supra- and infrafamilial affinities and the evolutionary history of Asian Paleogene Didymoconidae.

2. Systematic paleontology

Family Didymoconidae Kretzoi, 1943

Sub-family “Ardynictinae” Lopatin, 1997

Genus *Archaeoryctes* Zheng, 1979

Type species: *Archaeoryctes notialis* Zheng, 1979

Included species: *Archaeoryctes borealis* Meng, 1990; *Archaeoryctes euryalis* Lopatin, 2001; *Archaeoryctes wangi* sp. nov.

	C-M ₂		P ₃ -M ₂		P ₃		P ₄		M ₁		M ₂	
	L	L	L	W	L	W	L	W	L	W	L	W
Right Dent	33,0	20,1	(4,6)	-	(4,6)	-	5,53	3,19	5,9	3,3	5,9	3,3
Left Dent	32,7	(20,6)	-	-	(4,5)	-	5,43	3,16	5,9	3,2		

Table 1. Tooth dimensions of the holotype specimen of *Archaeoryctes wangi* sp. nov. (x) = measurement estimated from roots or partially erupted teeth. Abbreviations: L = Length; W = Width.

Distribution: Nongshanian (Middle Paleocene) to Arshantan (Middle Eocene) Asian Land Mammal Age of China and Mongolia

Archaeoryctes wangi nov. sp.

(Fig. 2-3, Table 1)

Type and only specimen: IBCAS QS003, an associated left and right dentary, with C and P₄-M₂ in place on both sides.

Type locality and Horizon: Zhongjialaowu (coordinates: E 116°30'14.83", N 30°35'18.50", altitude 46m), Qianshan County, Anhui Province, Upper Member of the Wanghudun Formation; Middle Paleocene, *Asiostylops* interval zone of Nongshanian Asian Land Mammal Age (following Missiaen, 2011).

Etymology: In honour of Dr. Wang Yuanqing (IVPP, Beijing) who extensively studied the fossiliferous deposits in the Qianshan Basin and who was the first to report the presence of *Archaeoryctes* there.

Diagnosis: Species of *Archaeoryctes* characterized by a relatively narrow trigonids with high, pointed protoconid and metaconid and by a relatively strong entoconid. Similar in size to *A. notialis* but differing by a deeper dentary and relatively smaller M₂. Smaller in size than *A. euryalis* and larger than *A. borealis*, further differing from *A. borealis* by the shallower dentary, by the higher, more gracile P₄ protoconid, and by the lower cristid obliqua on P₄-M₂.

Description: The two dentaries are relatively short and deep (length: 58 mm, depth below M₁: 10 mm). The symphysis is long, robust, and extends below the anterior root of P₃. The thin coronoid crest is vertical and high, and delimits a large, shallow masseteric fossa. The round mandibular condyle is laterally short and positioned at about the same height as the teeth. The angular process is slightly medially deflected. The right dentary has three mental foramina (below P₂, between P₂ and P₃, and below the

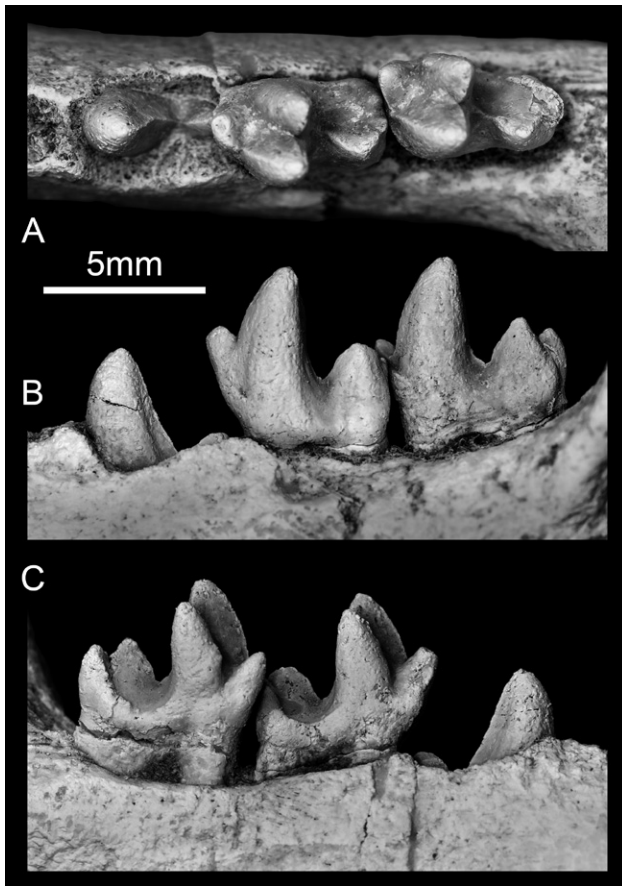


Figure 3. Dental morphology of *Archaeoryctes wangi* sp. nov. Detail of the left cheek tooth portion of the holotype specimen IBCAS QS003 from the Nongshanian Upper Member of the Wanghudun Formation in the Qianshan Basin, Anhui Province, P.R. China in occlusal (A) labial (B), and lingual (C) view.

P_4 trigonid), whereas the left dentary has an additional foramen below P_3 . The mandibular foramen is wide and low.

The area for the incisors, in front of the canine, is very small and suggests the presence of one or two small incisors on each side. The canine is large and curved postero-dorsally, with a massive root. Both dentaries suggest the presence of three premolariform and two molariform teeth. The first premolariform tooth is single-rooted, the second one is two-rooted, and the third one is erupting. The last molariform tooth has a narrower talonid and more posteriorly placed hypoconulid than the preceding tooth, and the molar dentition therefore seems to be complete. This reduced dental formula, with only three premolars and two molars and with P_4 as the last tooth to erupt, is typical for Didymoconidae, to which the specimen described here is referred. Because in this group the DP_2 is not replaced (Lopatin, 2006; p. 308), these postcanine loci are here identified as P_2 (= DP_2), P_3 , P_4 (in eruption), M_1 and M_2 .

P_2 and P_3 are missing on both sides of the specimen. Based on the alveoli, the P_2 seems to be larger posteriorly than anteriorly. On both sides P_4 is erupting, and we can only observe the presence of a distinctly pointed protoconid, and of a narrow, unbasined talonid with single high talonid cusp (= hypoconid?). No metaconid is present on P_4 . The two molars show a high, lingually open trigonid. The protoconid and metaconid are the two largest cusps with the protoconid higher than the metaconid. The paraconid is much lower and shorter. The talonid on M_1 is slightly narrower than the trigonid. The hypoconid, hypoconulid and entoconid are well individualized and unfused, forming a curved arc. The hypoconid is clearly the largest talonid cusp, while the hypoconulid is somewhat higher and more posteriorly placed than the entoconid. The cristid obliqua is obliquely oriented and the talonid basin is open lingually due to the posterior position of the entoconid and the short entocristid, which does not reach the metaconid. On M_2 , the paraconid is lower and the talonid is

longer and narrower than on M_1 , with a more posteriorly located hypoconulid.

Comparison: Specimen IBCAS QS003 differs from most other Asian early Paleogene “insectivores” by the absence of M_3 , a feature typical of the Sarcodontidae and Didymoconidae (Lopatin, 2006, Missiaen and Smith, 2008). This new specimen from Qianshan differs from all Sarcodontidae by the small and reduced incisors, by the loss of the first premolar, by the complete absence of P_4 metaconid, and the absence of carnassial specialization of the molars. The specimen is however clearly similar to Didymoconidae by these characters, as well as by the highly placed first mental foramen, by the diastemata surrounding P_2 , and by the molars with a low paraconid, a high protoconid and metaconid, and a lingually open talonid basin.

The most recent classification of didymoconids involves three subfamilies, kennatheriines, ardynictines, and didymoconines, of which only the two first are recorded in the Paleocene (Lopatin, 2006). Specimen IBCAS QS003 clearly resembles ardynictines by the simple, single-rooted P_2 , by the P_4 without metaconid and only a single talonid cusp, and by molars with a distinct, labiolingually oriented cristid obliqua, and a posteromedially placed hypoconulid. Contrastingly, kennatheriines and didymoconines are characterized by at least partially molarized last premolars, and by talonids where the hypoconulid is lingually displaced against the entoconid or where all cusps form a straight transverse line.

Within ardynictines, the new specimen only matches the genus *Archaeoryctes*, based on the completely unmolarized P_4 , and the molars with a low paraconid and relatively low protoconid and metaconid. Three species of *Archaeoryctes* have been so far described, the contemporaneous *A. notialis* from the Chijiang Formation in Jiangxi Province (Zheng, 1979), the Late Paleocene *A. euryalis* from the Zhigden Member of the Naran Bulak Formation in Mongolia (Lopatin, 2001) and *A. borealis* from the Middle Eocene Arshanto Formation in Inner Mongolia (Meng, 1990). The new specimen described here resembles *A. notialis* but differs by the deeper jaw and by the relatively smaller M_2 that is similar in size to M_1 in *A. wangi* than in *A. notialis*. It differs from *A. borealis* by the much larger size, by the lower dentary, by the higher, more gracile P_4 protoconid, and by the lower cristid obliqua on P_4 - M_2 . It differs from *A. notialis* and *A. borealis* by lower molars with a narrower molar trigonid and less robust protoconid and metaconid and a stronger entoconid. *Archaeoryctes euryalis* is only known from a skull with the upper dentition found in the Gashatan of Naran Bulak and can therefore not be morphologically compared with the new Nongshanian lower jaw from the Qianshan Basin described here. However, because P^4 - M^2 in *A. euryalis* are over 15 percent larger than their counterparts in the *A. wangi*, and because of the considerable temporal and geographical distance between them, it seems unlikely that both specimens represent the same species.

We can therefore conclude that specimen IBCAS QS003 represents a new, previously unknown species of *Archaeoryctes*, for which we propose the new name *Archaeoryctes wangi*. The new material constitutes the oldest and best preserved lower jaw of the genus *Archaeoryctes*, and formally indicates its presence in the early Nongshanian of the Qianshan Basin

3. Phylogenetic analysis

3.1 Cladistic analysis

In order to better understand the origin and evolutionary diversification of Didymoconidae, we built a cladistic data matrix for all didymoconid genera plus a number of relevant outgroup taxa. Because Zalambdalestidae, Leptictidae and insectivores all have been cited as potential relatives of didymoconids (Szalay and McKenna, 1971; Meng et al., 1994; McKenna and Bell, 1997; Lopatin, 2001), *Zalambdalestes* (Zalambdalestidae), *Leptacodon* and *Praolestes* (Nyctitheriidae), and *Gypsonictops* (Leptictida) were included. These specific taxa were chosen based on the availability of well-preserved specimens and their basal position within their respective groups.

In our analysis, we additionally included the sarcodontids *Carnilestes*, *Prosarcodon* and *Sarcodon*. This Asian early

Affinities	Genus	First Appearance	Last Appearance	# char
Eutheria incertae sedis	<i>Prokennalestes</i>	Early Cretaceous	Early Cretaceous	46
Zalambdalestidae	<i>Zalambdalestes</i>	Late Cretaceous	Late Cretaceous	48
Leptictida	<i>Gypsonictops</i>	Late Cretaceous	Late Cretaceous	45
Nyctitheriidae	<i>Leptacodon</i>	Shanghuan	Irдинmanhan	46
Nyctitheriidae	<i>Praolestes</i>	Gashatan	Gashatan	38
Sarcodontidae	<i>Carnilestes</i>	Shanghuan	Shanghuan	43
Sarcodontidae	<i>Prosarcodon</i>	Shanghuan	Shanghuan	47
Sarcodontidae	<i>Sarcodon</i>	Nongshanian - <i>Bothriostylops</i> IZ	Gashatan	41
Didymoconidae	<i>Archaeoryctes</i>	Nongshanian - <i>Asiostylops</i> IZ	Irдинmanhan	46
Didymoconidae	<i>Zeuchtherium</i>	Nongshanian - <i>Asiostylops</i> IZ	Nongshanian - <i>Asiostylops</i> IZ	17
Didymoconidae	<i>Wanolestes</i>	Nongshanian - <i>Bothriostylops</i> IZ	Nongshanian - <i>Bothriostylops</i> IZ	18
Didymoconidae	<i>Hunanictis</i>	Bumbarian - <i>Orientalophus</i> IZ	Irдинmanhan	11
Didymoconidae	<i>Mongoloryctes</i>	Irдинmanhan	Irдинmanhan	9
Didymoconidae	<i>Khaichinula</i>	Irдинmanhan	Irдинmanhan	15
Didymoconidae	<i>Erlitherium</i>	Irдинmanhan	Irдинmanhan	27
Didymoconidae	<i>Kennatherium</i>	Irдинmanhan	Irдинmanhan	45
Didymoconidae	<i>Jiajianictis</i>	Irдинmanhan	Irдинmanhan	14
Didymoconidae	<i>Ardynictis</i>	Irдинmanhan	Ergilian	44
Didymoconidae	<i>Ergilictis</i>	Ergilian	Hsandgolian	28
Didymoconidae	<i>Didymoconus</i>	Hsandgolian	Tabenbulakian	45
Didymoconidae	<i>Archaeomangus</i>	Hsandgolian	Hsandgolian	27
Didymoconidae	<i>Tshotgoria</i>	Tabenbulakian	Tabenbulakian	14

Table 2. Summary table of analysed taxa. Biochronology following Tsubamoto et al. (2004) and Missiaen (2011). # char.: Number of morphological characters scored on a total of 48.

Paleogene family of insectivorous mammals is also characterized by the reduction of their molar dentition (Missiaen and Smith, 2008). No explicit statements have been made about a link between both families, but *Wanolestes* was originally described as a sarcodontid (Huang and Zheng, 2002) and is now considered a didymoconid (Lopatin, 2006). This analysis therefore also serves as a test of the distinctiveness and interrelationships of Sarcodontidae and Didymoconidae.

Finally, we added *Prokennalestes* as the outgroup for the analysis, originally resulting in a total of 22 taxa, of which 21 ingroup taxa and 14 didymoconids.

The cladistic matrix contains 48 morphological, mostly dental, characters (See Appendix). All characters were newly created based on their potential to discriminate between didymoconids, between sarcodontids and between the five ingroup families. Diagnostic characters mentioned in available literature were maximally incorporated, most notably those used by Lopatin (2006) to diagnose didymoconids and sarcodontids, but only robust, clearly visible and informative characters were retained. Cladistic analyses were run in PAUP 4.0b10 (Swofford 2003) using default settings, with all multistate characters treated as ordered.

3.2 Stratocladistic analysis

Didymoconidae have a long, and potentially revealing stratigraphic distribution, with supposedly primitive genera occurring earlier than more derived forms (Lopatin, 2006).

The stratigraphic distribution of all taxa was determined from the available literature and placed in a recent Asian mammal biochronological framework (Tsubamoto et al., 2004; Wang et al., 1998, 2007; Missiaen, 2011). Most significantly, this showed that the primitive didymoconids *Zeuchtherium* and *Wanolestes* are Nongshanian in age (Table 2), rather than Shanghuan and Gashatan respectively (Missiaen, 2011). This information was subsequently converted into a stratigraphic character for analysis, resulting in a total of 12 character states for the stratigraphic character (See Appendix, char 49). All of the stratigraphic stages differ by their faunal content and match the criteria for stratigraphic subdivisions as discussed by Alroy (2002), making this subdivision in 12 states appropriate or even conservative.

We expanded the classical cladistic approach with a stratocladistic study, an analytical method aiming to improve taxonomic resolution by also incorporating stratigraphic data. Stratocladistics further differ from traditional cladistics by also considering potential ancestor-descendant relationships, attempting to reconstruct phylogenetic trees, rather than cladograms which strictly speaking are only “hierarchies based

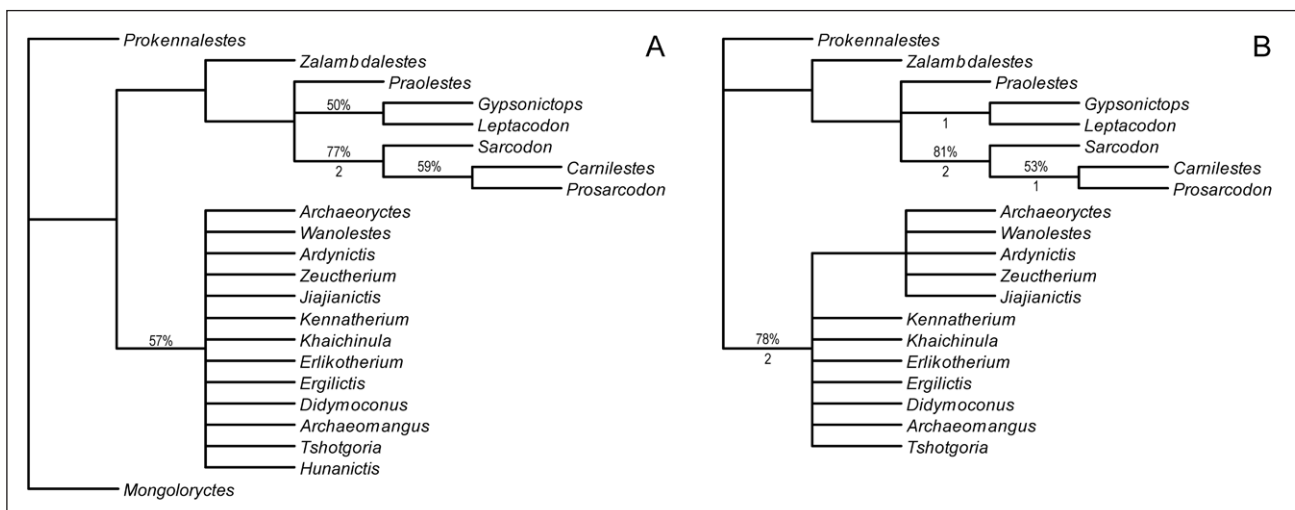


Figure 4. Strict consensus trees of cladistic analysis. A. Full analysis, resulting in 2673 MPTs. B. Analysis excluding *Mongoloryctes* and *Hunanictis*, resulting in 90 MPTs. Percentages indicate bootstrap support values higher than 50% for clades, numbers indicate Bremer support values.

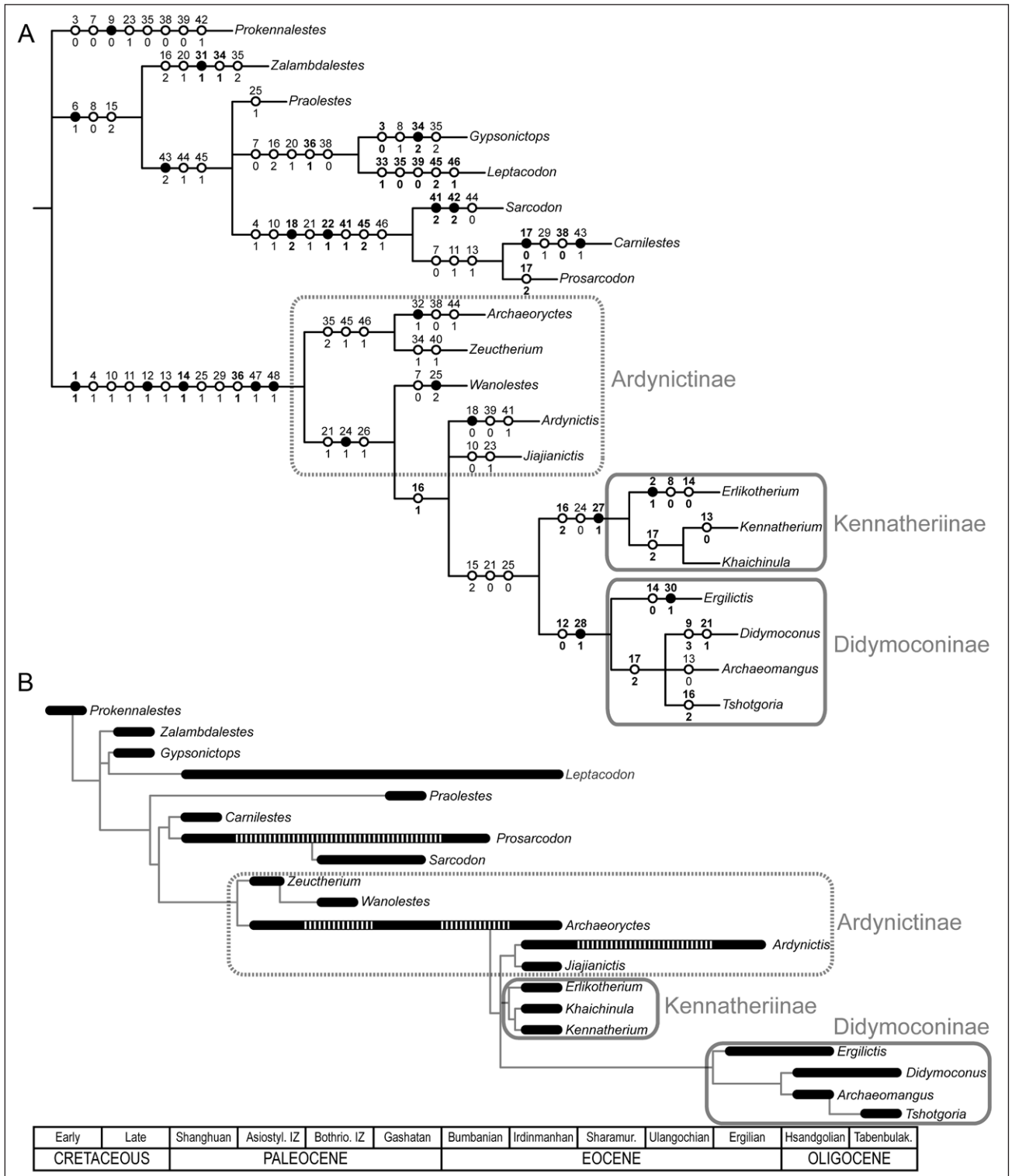


Figure 5. Strict consensus trees of phylogenetic analyses also incorporating stratigraphic data. A. Strict consensus of the 27 MPTs from Fig. 4B that are stratigraphically most parsimonious. Circles indicate unambiguous synapomorphies. Open circles indicating homoplasious characters and filled circles indicating unique synapomorphies. Bold type indicates synapomorphies identically present in Fig. 4B. B. Strict consensus of 4 optimal stratocladistic trees, showing temporal distribution. Hatching indicates periods where genera were supposedly present but have not been recorded. Length of biochrons is not to scale, timing of evolutionary events is approximate.

on homology hypotheses” (Bloch et al., 2001, Brochu, 2001; Marcot & Fox, 2008). Stratocladistic analyses were run in StrataPhy 0.3.5a (Marcot & Fox, 2008) using default settings, with all multistate characters except the stratigraphic character treated as ordered.

3.3 Results and discussion

The initial cladistic analysis of the complete morphological data set resulted in a total of 2673 Most Parsimonious Trees (MPTs) of 132 steps, and a poorly resolved consensus tree (Fig.

4A). Unsurprisingly, the affinities of the Eocene didymoconid *Mongoloryctes* known only from a single isolated M¹ (Van Valen, 1966; Lopatin, 2006) are completely unresolved in the analysis. The strict consensus tree does group all other didymoconid genera in a monophyletic clade, but fails to provide any further information on their internal relationships.

A detailed analysis of these cladistic results indicated that the high number of MPTs was primarily caused by the inclusion of *Mongoloryctes* and *Hunanictis*, for which only 9 and 11 morphological characters could be scored respectively, on a total of 48 morphological characters. These taxa act as unstable

wildcards due to a combination of missing data and character conflicts (Kearney and Clark, 2003), and their removal from the analysis reduces the number of MPTs from 2673 to 90 MPTs of 130 steps. The corresponding strict consensus tree (Fig. 4B) is better resolved and more robust. Most significantly, the consensus tree groups *Archaeoryctes*, *Zeutherium*, *Wanolestes*, *Ardynictis* and *Jiajianictis* together in a monophyletic clade, similar to the didymoconid subfamily Ardynictinae proposed by previous authors (Tong, 1997; Lopatin, 2006).

A better resolved didymoconid cladogram could be obtained by additionally removing *Jiajianictis* and *Tshotgoria*, for which only 14 characters were scored, or by considering less strict consensus techniques. Both solutions however represent poor answers to missing data problems in phylogenetic analyses (Kearney and Clark, 2003). Instead, given the potentially significant stratigraphic distribution of didymoconids, we added these stratigraphic data to our analysis as a simple, ordered character. Of the 90 equally parsimonious morphological trees from figure 3B, 27 trees are stratigraphically shorter than the others, with a total of 141 steps. These same 27 trees are also the most parsimonious results of a new, direct analysis containing the stratigraphic character from the onset. Their strict consensus (Fig. 5A) suggests that the “Ardynictinae” form a paraphyletic stemgroup that gave rise to two monophyletic subfamilies, the Kennatheriinae and Didymoconinae.

The same data were also analysed using the dedicated stratocladistic StrataPhy software (Marcot and Fox, 2008), resulting in 2 optimal topologies and 4 optimal trees. The stratocladistic consensus solution (Fig. 5B) mainly differs from Figure 5A in the rooting of the didymoconid family and the relative position of the most basal didymoconid genera. Otherwise, both are highly similar, suggesting that the older “Ardynictinae” form a stemgroup that after the end of the early Eocene gave rise to the more derived Kennatheriinae and Didymoconinae.

All analyses unambiguously include *Wanolestes* within Didymoconidae and clearly discriminate between Sarcodontidae (*Carnilestes*, *Prosaracodon* and *Sarcodon*) and Didymoconidae (Figs 4 and 5). These results therefore support the inclusion of *Wanolestes* in Didymoconidae and underline the validity of Didymoconidae as a monophyletic natural group (Lopatin, 2006).

Didymoconids are morphologically characterized by a long jaw symphysis, by a reduction of the lower incisors, by large canines and the loss of P¹/₁ and M²/₃, by relatively simple anterior premolars mostly lacking a P³ parastyle and a P₃ paraconid, by a P⁴ with distinct metacone, by upper molars without distinct conules and by lower molars with a simplified talonid structure and posteriorly placed entoconid, leading to lingually open talonid basin. These analyses are generally consistent with existing subdivisions of Didymoconidae into ardynictines, kennatheriines and didymoconines (Tong, 1997; Lopatin, 2006). Primitive ardynictines are characterized by a single rooted P₂, and by a premolariform P₄ with a small to absent metaconid and single talonid cusp. More evolved forms have a reduced number of lower incisors, generally a more stronger P³ metacone, relatively larger last premolars with more distinct metaconid and more complex talonid, and a more longitudinally oriented cristid obliqua on the molars. Kennatheriinae are characterized by a P₄ with three talonid cusps, and a molar hypoconulid that is lingually displaced and closely appressed against the entoconid. Didymoconinae on the other hand are diagnosed by a two-rooted P₂, by a P₄ with two or three talonid cusps, and molar talonids with cusps arranged in a straight transverse line.

The main novelties in this phylogenetic study are the explicit notion that the subfamily Ardynictinae is not a monophyletic clade but a paraphyletic stem group and the newly proposed affinities for *Zeutherium* and *Khaichinula*. Lopatin (2006) identified *Zeutherium* as a kennatheriine based on the reduced molar styles. *Zeutherium* however resembles ardynictines, and *Archaeoryctes* in particular, by the more molarized P³ and the stronger hypocone and hypocone shelf on the molars and is therefore referred to the ardynictine stemgroup here. The poorly known *Khaichinula* has previously been referred to Didymoconinae (Lopatin, 2006), but is placed here in the Kennatheriinae based on the molariform, tricuspid P₄ talonid that we consider typical of kennatheriines and not of didymoconines.

4. Conclusions

Specimen IBCAS QS003 represents a new, previously unknown species of *Archaeoryctes*, described here with the name *Archaeoryctes wangi*. This confirms the presence of the genus in the Nongshanian of the Qianshan Basin already alluded to by Wang et al. (1998), and forms a geographical intermediate between *A. notialis* from South China and *A. borealis* and *A. euryalis* from the Mongolian Plateau.

The discovery of this well preserved specimen makes that both the upper and lower dentition of *Archaeoryctes* is now relatively well known, and we performed a morphologic, cladistic and stratocladistic study of the dental morphology of Didymoconidae and potentially relevant taxa. Our results unambiguously confirm the validity and distinctiveness of Didymoconidae from Sarcodontidae, but we could not unambiguously identify the higher level affinities of the family based on dental information alone. This study generally corroborates the current didymoconid classification of Lopatin (2006) with the distinction of three didymoconid subfamilies, “Ardynictinae”, Kennatheriinae and Didymoconinae, although we show that “Ardynictinae” are a paraphyletic stemgroup for the two other subfamilies. From an evolutionary point of view, our results suggest three distinct didymoconid radiations, with an ardynictine stemgroup evolving in South China from the start of the Nongshanian. At the end of the Nongshanian, didymoconids disappear from southern and central China, but continue to thrive in the Mongolian Plateau with the radiation of more evolved ardynictines and Kennatheriinae at the start of the Middle Eocene Arshantan and the origin of Didymoconinae at the start of the Late Eocene Ergilian.

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3. One
4. Zero, lower incisors absent
10. **Canine size:**
0. Small, canine root smaller than that the roots of P_2
1. Large and massive, canine root larger than that the roots of P_2
11. **Diastema before P_2 :**
0. Absent or indistinct
1. Clearly present
12. **P_2 :**
0. Two-rooted
1. Single-rooted
13. **Diastema between P_2 and P_3 :**
0. Absent or indistinct
1. Clearly present
14. **Paraconid on P_3 :**
0. Present
1. Absent
15. **Metaconid on P_4 :**
0. Absent
1. Poorly developed or indistinct
2. Present and clearly developed
16. **Talonid on P_4 :**
0. One cusp
1. Two cusps
2. Three cusps
17. **P_4 and M_1 length:**
0. P_4 shorter than M_1 ($P_4L/M_1L < 90\%$)
1. P_4 similar in length to M_1 ($90\% < P_4L/M_1L < 110\%$)
2. P_4 longer than M_1 ($P_4L/M_1L > 110\%$)
18. **M_1 and M_2 length:**
0. M_2 shorter than M_1 ($M_2L/M_1L < 90\%$)
1. M_2 similar in length to M_1 ($90\% < M_2L/M_1L < 110\%$)
2. M_2 longer than M_1 ($M_2L/M_1L > 110\%$)
19. **M_2 and M_3 length:**
0. M_3 shorter than M_2 ($M_3L/M_2L < 90\%$)
1. M_3 similar in length to M_2 ($90\% < M_3L/M_2L < 110\%$)
2. M_3 longer than M_2 ($M_3L/M_2L > 110\%$)
20. **M_1 shape in occlusal view:**
0. Trigonid wider than talonid
1. Trigonid narrower than talonid
21. **Lower molar trigonid:**
0. Low
1. High, at least twice as high as the talonid
22. **Lower molar paraconid:**
0. Low
1. High and enlarged, paraconid cusp distinctly higher than the talonid cusps
23. **Lower molar metaconid:**
0. Similar in height to the protoconid
1. Distinctly lower than the protoconid
24. **Orientation of cristid obliqua on $M_{1,2}$:**
0. Oblique, running anteriorly and lingually from the hypoconid
1. Longitudinal, running essentially anteriorly from the hypoconid
25. **M_1 entoconid:**
0. Present and distinct, similar to the hypoconid
1. Reduced, distinctly smaller than the hypoconid
2. Absent
26. **M_1 hypoconulid:**
0. Present
1. Indistinct or absent
27. **M_1 hypoconulid:**
0. Medially placed
1. Lingual, closely appressed to the entoconid
28. **M_1 talonid cusps:**
0. Forming a curved arc
1. Linearly arranged, all three cusp forming a straight, transversal line
29. **M_1 talonid basin:**
0. Closed, with premetacristid reaching the trigonid back wall
1. Open
30. **M_2 talonid:**
0. Longer than M_1 talonid
1. Shorter than M_1 talonid
31. **Upper incisors:**
0. Three
32. **P^2 :**
0. Two-rooted
1. Single-rooted
33. **Parastyle on P^3 :**
0. Present
1. Absent
34. **Metacone on P^3 :**
0. Absent
1. Incipiently present
2. Distinctly present
35. **P^3 protocone:**
0. Absent
1. A small cusp
2. A distinct cusp, its base approaching the size of that of the paracone
36. **Metacone on P^4 :**
0. Absent
1. Present
37. **P^4 hypocone region:**
0. Talon shelf and hypocone absent
1. Talon shelf and hypocone weakly developed
2. Talon shelf and hypocone developed
38. **M^1 Shape:**
0. Not transversely elongated (Centrocrista-Protocone distance/Paracone-Metacone distance $< 150\%$)
1. Transversely elongated (Centrocrista-Protocone distance/Paracone-Metacone distance $> 150\%$)
39. **Stylar shelf on molars:**
0. Wide
1. Narrow, a mere ridge
40. **Molar parastyle and metastyle:**
0. Distinct
1. Reduced
41. **Preparacrista and postmetacrista on M^1 :**
0. Equivalent in development
1. Postmetacrista better developed than preparacrista
2. Postmetacrista strongly developed, preparacrista reduced
42. **Paracone-metacone on M^1 :**
0. Well-separated
1. Poorly separated to partially fused
2. Strongly fused
43. **Upper molar trigon basin:**
0. Conules absent
1. Only conules present
2. Conules and conule wings present
44. **Precingulum on M^1 :**
0. Absent
1. Present
45. **Talon shelf on M^1 :**
0. Absent
1. Present as a narrow ridge
2. Present and extending far postero-lingually
46. **Hypocone on M^1 :**
0. Absent
1. Present
47. **Jugal:**
0. Developed
1. Reduced
48. **Contact between the palatine and lacrimal inside the orbit:**
0. Present
1. Absent
49. **Statigraphic range:**
0. E Cretaceous
1. L Cret
2. Shanghuan
3. Nongshanian - *Asiostylops* zone
4. Nongshanian - *Bothriostylops* zone
5. Gashatan
6. Bumbanian
7. Irdinmanhan
8. Sharamurunian+Ulangochian
9. Ergilian
10. Hsandgolian
11. Tabenbulakia