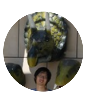
A new boreopterid pterosaur from the Lower Cretaceous of western Liaoning, China, with a reassessment of the phylogenetic relationships of the Boreopteridae

Article *in* Journal of Paleontology · July 2014

DOI: 10.1666/13-068



Shunxing Jiang

Chinese Academy of Sciences

A new boreopterid pterosaur from the Lower Cretaceous of western Liaoning, China, with a reassessment of the phylogenetic relationships of the Boreopteridae

Author(s): Shun-Xing Jiang, Xiao-Lin Wang, Xi Meng, and Xin Cheng
Source: Journal of Paleontology, 88(4):823-828. 2014.
Published By: The Paleontological Society
DOI: http://dx.doi.org/10.1666/13-068
URL: http://www.bioone.org/doi/full/10.1666/13-068

Journal of Paleontology, 88(4), 2014, p. 823–828

0022-3360/14/0088-823$03.00
DOI: 10.1666/13-068

A NEW BOREOPTERID PTEROSAUR FROM THE LOWER CRETACEOUS OF WESTERN LIAONING, CHINA, WITH A REASSESSMENT OF THE PHYLOGENETIC RELATIONSHIPS OF THE BOREOPTERIDAE

SHUN-XING JIANG,[1,2] XIAO-LIN WANG,[1] XI MENG,[1] AND XIN CHENG[1,2]

[1]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, China, <wangxiaolin@ivpp.ac.cn>; and [2]University of Chinese Academy of Sciences, Beijing, 100049, China

ABSTRACT—A new species of boreopterid pterosaur from the new fossil locality, Heichengzi, Beipiao, western Liaoning, China allows a reassessment of the Boreopteridae. In this new analysis, three species, *Boreopterus cuiae*, *Boreopterus giganticus* n. sp., and *Zhenyuanopterus longirostris*, are included within the Boreopteridae united by the autopomorphic occurrence of two main tooth morphologies, an equal length of the tibia and femur, and weak feet. Other taxa previously placed within the Boreopteridae are not in a monophyletic group with the former three species. *Boreopterus* has fewer teeth and a shorter tooth row than that in *Zhenyuanopterus*. This new *Boreopterus* species has a large size, a piriform orbit, an extensively fenestrated lacrimal, and a posteriorly directed lacrimal process, that differs from *Boreopterus cuiae*.

INTRODUCTION

During the last decade, many different vertebrate taxa have been reported from Mesozoic deposits in the western part of Liaoning Province in China, including fishes, amphibians, reptiles, birds, and mammals (Chang et al., 2003; Zhou, 2004). Since the description of the first pterosaur *Eosipterus yangi* from these sediments, more than 30 additional pterosaur species have been described in Jehol Biota (Ji and Ji, 1997; Wang et al., 2012; Lü et al., 2012). The Jehol Biota derives from fossiliferous strata in the Jehol Group, which is comprised of the Yixian and Jiufotang formations.

One of the pterosaur groups known from the Jehol Biota is the Boreopteridae. Based on *Boreopterus cuiae* and *Feilongus youngi*, the Boreopteridae was established with the diagnosis of being large-sized ornithocheiroid pterosaurs that have a low skull with an extremely elongated rostrum, having long and sharp teeth, having anterior teeth different from each other in size, and having leg proportions where the femur is equal to the tibia in length (Lü et al., 2006). The skull crest is present in some but not all boreopterids (Lü et al., 2006), and it does not help to distinguish among boreopterid taxa. Lü (2010) considered *Zhenyuanopterus longirostris* as the third species of boreopterids and changed the diagnostic character from anterior teeth different from each other in size to anterior teeth longer than posterior teeth.

The Boreopteridae have been divided into two sub-families, the Boreopterinae and Moganopterinae (Lü et al., 2012). At present, *Moganopterus zhuiana* and *Feilongus* are placed within the Moganopterinae, and *Boreopterus* and *Zhenyuanopterus* have been assigned to the Boreopterinae (Lü et al., 2012). That taxonomic arrangement is based on their phylogenetic analysis, but when we duplicated the analysis, the results were different (see Appendix 1 for our result). Hence, the classification of two sub-families appears to be incorrect.

Herein, we described a new specimen of boreopterid pterosaur, *Boreopterus giganticus* n. sp. The holotype is from Heichengzi, a new fossil locality, where no vertebrate fossil has been reported previously. Heichengzi is in the north of Beipiao, near the border with Fuxin (Fig. 1). We performed a phylogenetic analysis of boreopterid pterosaurs, including this new species, and reassess the phylogenetic relationships among members of the Boreopteridae.

SYSTEMATIC PALEONTOLOGY

Order PTEROSAURIA Kaup, 1834
Suborder PTERODACTYLOIDEA Plieninger, 1901
Superfamily ARCHAEOPTERODACTYLOIDEA Kellner, 1996
Family BOREOPTERIDAE Lü et al., 2006

Diagnosis.—Medium- to large-sized archaeopterodactyloids with the following autapomorphies: two distinct tooth morphologies, the slender anterior teeth much larger than the triangular posterior teeth; femur and tibia that are equal in length; and weak feet. In addition, the following characters in combination diagnose this clade: tooth rows extending at least to the middle of the nasoantorbital fenestra; relatively short cervical vertebra, with a high neural spine (modified from Lü et al., 2006, 2012).

Type genus.—*Boreopterus* Lü and Ji, 2005.

Included taxa.—*Boreopterus cuiae, Boreopterus giganticus* new species, and *Zhenyuanopterus longirostris*.

Occurrence.—Yixian Formation, Early Cretaceous (Aptian); Beipiao and Yixian, western Liaoning, China.

Remarks.—These diagnoses are combinations of the diagnoses of the Borepteridae (Lü et al., 2006) and Boreopterinae (Lü et al., 2012). The weak foot is a unique character. Although the postcranial is not preserved in the new specimen, we checked the condition of the published pterosaurs. We found the ratios of metatarsal III to tibia are 13/82=0.159 in *Boreopterus cuiae* (Lü and Ji, 2005) and 2.6/20=0.13 in *Zhenyuanopterus* (Lü, 2010), respectively. These ratios are smaller than all pterosaurs found in China (the smallest ratios are in *Sinopterus* whose ratios are more than 0.2, Wang and Zhou, 2003a).Two original supposedly diagnostic characters have been omitted: one is the elongated skull that is found in some other archaeopterodactyloids, and the other one is skull crest that does not aid in distinguishing taxa.

Genus BOREOPTERUS Lü and Ji, 2005

Diagnosis.—Boreopterid pterosaurs with the autapomorphy the first nine of the anterior teeth larger than the other more posterior teeth in the per-side of the upper and lower jaws. In addition, the following characters in combination diagnose the clade: less than

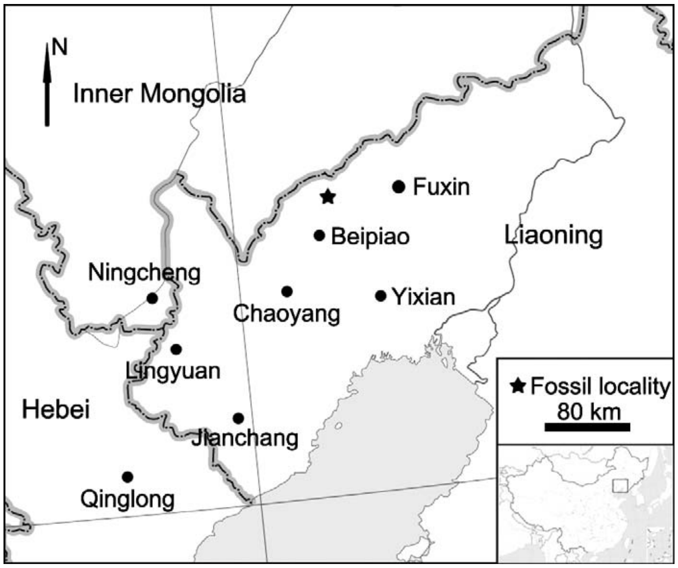


FIGURE 1—Locality map of the new fossil site, Heichengzi Town, Beipiao County, western Liaoning, China.

120 teeth, much fewer than *Zhenyuanopterus* (174), and tooth rows just reaching the middle of nasoantorbital fenestra, much shorter than that in *Zhenyuanopterus* (modified from Lü and Ji, 2005).

Type species.—*Boreopterus cuiae* Lü and Ji, 2005.

Included species.—*Boreopterus cuiae* Lü and Ji, 2005 and *Boreopterus giganticus* n. sp.

Occurrence.—Yixian Formation, Early Cretaceous (Aptian); Beipiao and Yixian, western Liaoning, China.

Remarks.—The diagnoses concerning tooth number and the tooth rows are new. The equal length of the tibia and the femur is shared by *Zhenyuanopterus*. The other potential characters in diagnosis are not preserved in *B. giganticus*. Thus, they are considered as diagnostic of only *B. cuiae* at the moment.

BOREOPTERUS CUIAE Lü and Ji, 2005

Diagnosis.—Medium-sized *Boreopterus* with following character combination: circular orbits; the third and the fourth of the anterior teeth are the largest; and the ratio of the length of mandibular symphysis to the lower jaw length ~65 percent (modified from Lü and Ji, 2005).

Occurrence.—Yixian Formation, Early Cretaceous (Aptian); Yixian, western Liaoning, China.

Remarks.—The circular orbit is a newly recognized diagnosistic character. The other characters are part of the original diagnosis of *Boreopterus*, but are not preserved in *B. giganticus*. The character of "humerus slightly shorter than femur" is common in many pterodactyloids, so it is omitted.

BOREOPTERUS GIGANTICUS new species

Diagnosis.—Large-sized *Boreopterus*, with the autapomorphy extensively fenestrated lacrimal. In addition, the following characters in combination diagnose this species: piriform orbit and a lacrimal process directing posteriorly.

Description.—See text below.

Etymology.—*Giganticus* from the Greek word *gigantikos*, referring to its larger size than *Boreopterus cuiae*.

Holotype.—The skull and mandible are housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (IVPP V14588; Figs. 2–4).

Occurrence.—Yixian Formation, Early Cretaceous (Aptian); Heichengzi, Beipiao, western Liaoning, China.

Genus ZHENYUANOPTERUS Lü, 2010

Type species.—*Zhenyuanopterus longirostris* Lü, 2010.

Diagnosis.—As for the species.

ZHENYUANOPTERUS LONGIROSTRIS Lü, 2010

Diagnosis.—Large-sized boreopterids with the following character combination: a large number of teeth (i.e., 172); the tooth rows extend beyond the middle of the nasoantorbital fenestra; an elongated nasal process that nearly reaches the ventral margin of the nasoantorbital fenestra; the length of the dorsal and sacral vertebrae nearly half of the skull length; the length ratio of the humerus to metacarpal IV is ~91 percent; and the third wing phalanx, humerus, and femur are equal in length (modified from Lü, 2010).

Remarks.—Long tooth rows and an elongated nasal process are two new diagnostic characters, that differ from character states in *Boreopterus* (Lü and Ji, 2005). We exclude one of the supposed diagnostic characters from the original diagnosis, "the longest teeth more than 10 times longer than the smallest", because it is present also in *B. giganticus* and *Guidraco* (Wang et al., 2012), and it is similar in *B.cuiae* (Lü and Ji, 2005, table 1, the ratio is 9.5). The other excluded character, "the feet especially small", is not only present in *B. cuiae,* and is considered rather as diagnostic of the Boreopteridae.

DESCRIPTION AND COMPARISON

The holotype and only known specimen of *Boreopterus giganticus* (IVPP V14588) preserves a nearly complete skull and mandible. The posterior part of the skull exposed in dorsal view, and the other portion is compressed laterally. The fusions of both frontals and maxilla and premaxilla were found; they are the first skull elements to fuse (Kellner and Tomida, 2000). Hence, this specimen cannot represent a very early stage of development. The skull is elongated, and the length from the anterior tip to the articulation of the upper and lower jaws is ~392.4 mm long. The estimated length of the skull (from the anterior tip to the posterior margin of the squamosal) is ~477.5 mm. The rostrum, 279.8 mm in length, is extremely elongated and occupies the 58.6 percent of the skull length. The orbit is not complete, and obscured by other bones covering it. Therefore, the shape of the orbit is uncertain, but it is appears to be piriform, because of the sharp angle formed by two processes of the jugal. This condition is not present in *Boreopterus cuiae* (Lü and Ji, 2005) and most other archaeopterodactyloids such as *Feilongus* (Wang et al., 2005), *Gegepterus* (Wang et al., 2007), and *Pterodaustro* (Chiappe et al., 2000).

The nasoantorbital fenestra is the most complete opening in the skull. The fenestra is piriform, 103.2 mm in length, and 37.3 mm in height. Thus, the fenestra occupies 21.6 percent of the skull's length. The posterior margin of the fenestra is concave, and is similar to the condition observed in some archaeopterodactyloids, such as *Feilongus* (Wang et al., 2005) and *Ctenochasma* (Jouve, 2004). However, it differs from the straight posterior margin in *Pterodaustro* (Chiappe et al., 2000).

The right premaxilla is low and elongated. It extends dorsally to the orbit, beyond the anterior margin of the orbit. The anterior parts of the premaxilla and maxilla are fused together, and the posterior part of the suture can be seen. There is no crest on the premaxilla.

The maxilla forms most of the lateral side of the skull and the anterior margin of the nasoantorbital fenestra. The maxilla extends posteriorly to at least half the length of the nasoantorbital fenestra. The posterior surface of the maxilla is smooth, and can be distinguished from the premaxilla.

The lacrimal is a triradiate bone, and both lacrimals are exposed in medial view (Fig. 3). The anterior process of lacrimal is slightly

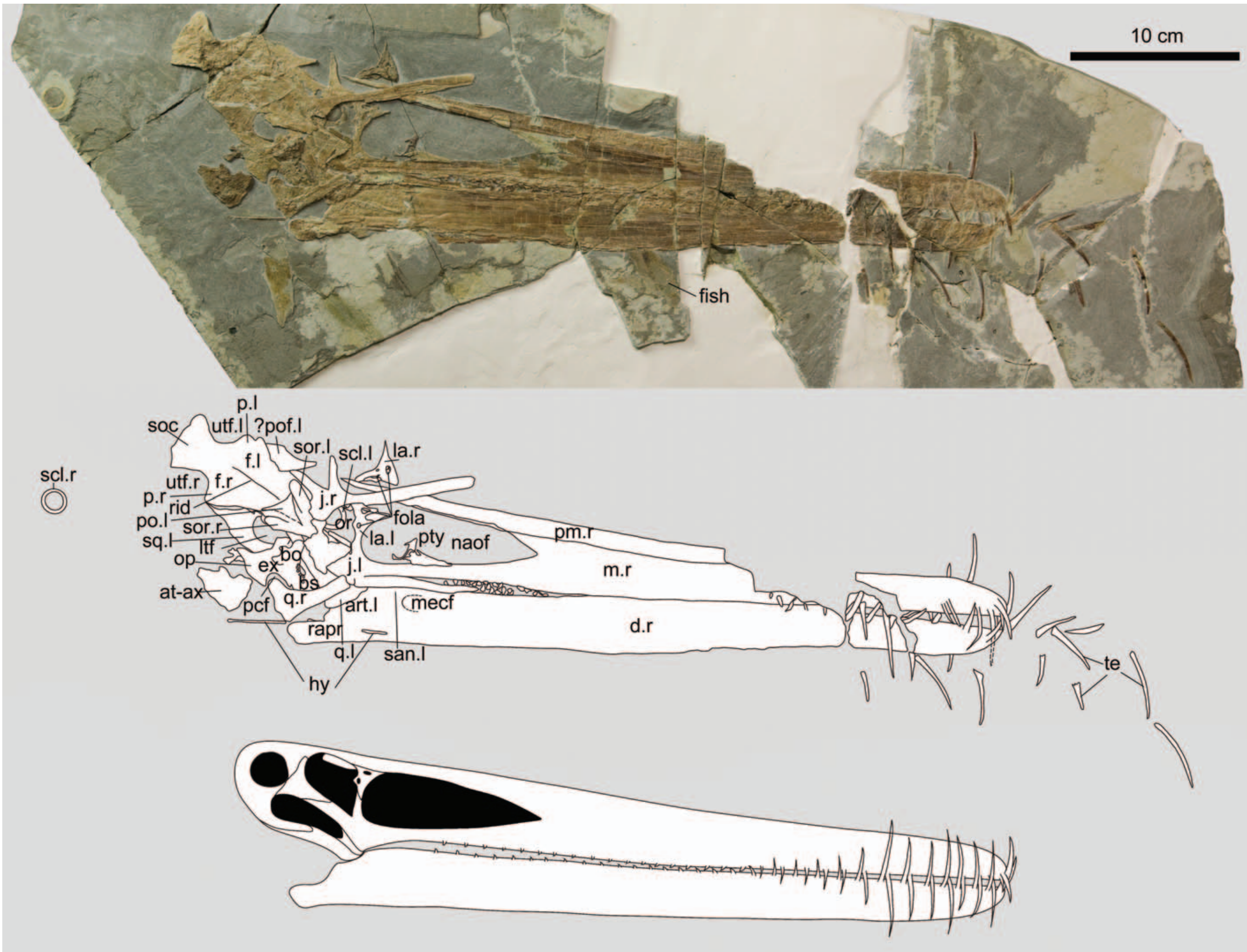


FIGURE 2—Photo, line drawing and skull reconstruction of the holotype of *Boreopterus giganticus* n. sp. (IVPP V14585). Abbreviations: art=articular; at-ax=atlas-axis; bo=basioccipital; bs=basisphenoid; d=dentary; ex=exoccipital; f=frontal; fola=foramen lacrimale; hy=hyoid bone; j=jugal; la=lacrimal; ltf=lower temporal fenestra; m=maxilla; mecf=Meckelian fossa; naof=nasoantorbital fenestra; op=opisthotic; or=orbit; p=parietal; pcf=posterior cranial fenestra; pm=premaxilla; po=postorbital; pof=postfrontal; pty=pterygoid; q=quadrate; rapr=etroarticular process; rid=ridge; sar=surangular; scl=slerotic ring; soc=supraoccipital; sor=supraorbital; sq=squamosal; te=teeth; utf=upper temporal fenestra; l=left; r=right; ?=uncertain.

longer and thinner than the posterior one, although the former one is still short. The lacrimal is extensively fenestrated with two of the foramina being elliptical, and larger than the others. One of the large foramina is near the dorsal margin of the lacrimal, and it contains two other small foramina. The other large foramen is at the posterior position, just like the lacrimal foramen in some other pterosaurs, such as *Feilongus* (Wang et al., 2005) and *Gegepterus* (Wang et al., 2007). On the posterior side of this foramen position, an apparently unique process directed posteriorly in the orbit is present. A lacrimal spine in *Ludodactylus*, which is more slender than the process of this specimen, was the only similarity the process in *B. giganticus* (Frey et al., 2003a). The condition of an extensively fenestrated lacrimal has been reported only in some tapejarids, such as *Tapejara wellnhoferi* (Kellner, 1989), *Sinopterus dongi* (Wang and Zhou, 2003a), and *Tupandactylus navigans* (Frey et al., 2003b).

The left jugal is in its original position, and almost fused with the lacrimal (Fig. 3). The right jugal is exposed in lateral view. The jugal is triradiate. The maxillary process is long and terminates before the anterior margin of the nasoantorbital fenestra. The lacrimal and maxillary processes form a right angle with a round corner, and it forms the posteroventral margin of the nasoantorbital fenestra. The postorbital and lacrimal processes make a 60° angle with two straight edges. It makes the orbit a ventrally facing sharp corner. The lateral ridge of the jugal cannot be observed because of its crushed surface.

The left quadrate is covered by many elements, and it is at least 53.8 mm long because it is not complete. The left quadrate and the ventral margin of the skull form a 130° angle. That angle is different from many archaepterodactyloids who have a strongly inclined quadrate relative to the ventral margin of the skull (Kellner, 2003; Unwin, 2003; Wang et al., 2012). This condition could be the result of crushing of the left quadrate relative to the skull. The right quadrate is displaced with the anterior portion exposed in ventral view. The morphology indicates that the quadrate has a helical joint with the lower jaw.

Both frontals and parietals are exposed in dorsal view; their sutures are difficult to discern. The frontal is a triangular bone, and it is the biggest element, forming most of the skull roof. The frontals are fused with each other medially, and a small ridge can be distinguished. The surfaces of parietals are crushed badly, and no details can be seen.

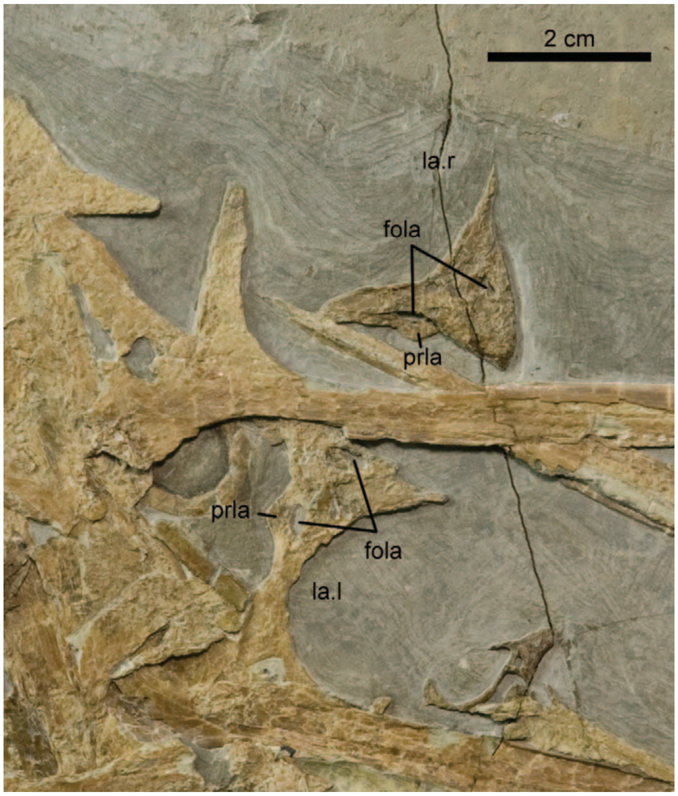


FIGURE 3—Details of both lacrimals in *Boreopterus giganticus* n. sp. Abbreviations: fola=foramen lacrimale; prla=process of lacrimal; la=lacrimal.

The supraorbital is a small laminar bone with nearly parallel lateral and medial margins. The supraorbital is fused with frontal, but only the posterior suture is visible.

There is a big break in the frontal, and the postorbital can been seen within the break. The postorbital should be a triangular bone, and dorsally faced the angle can be observed. The dorsal margin of the lacrimal is overlain by the frontals, and this margin makes the frontals have a small ridge. The posteroventral margin of lacrimal is not clear.

The preserved squamosal is the left one because it is overlain by the elements of the occipital region. The squamosal is exposed in the medial view, and connects with the postorbital, forming the posterior margin of the lower temporal fenestra and the anteroventral margin of the upper temporal fenestra.

The sclerotic ring comprises a few small, thin laminar bones, and the outline of each ossicle is undistinguishable. The outer diameter of the ring is 15.7 mm, and the width of the ossicle is only 2.6 mm.

Near the right quadrate are the likely elements of occipital region. Although the individual bones are difficult to distinguish, it seems that the right exoccipital and opisthotic are fused together, forming the posterior margin of the left postcranial fenestra. The condyle should be the basioccipital. The posterior part of the basisphenoid is preserved, and it forms the medial margin of the postcranial fenestra. There is a bone with several struts forming foramina near the basisphenoid. We interpret that bone as the interorbital septum, and that septum should be a vertical lamina and separating the right and left eyes. The supraoccipital is exposed in posterior view and is fused with parietals. The surface of this element is crushed. Along with the parietals, it forms the medial margins of the upper temporal fenestra.

The mandible is low and long, with a length of 418.5 mm (from the anterior tip to the posterior margin of the mandible). Most elements of the mandible are crushed, and individual bones are not discernible.

There are 29 upper and 28 lower teeth per side on the upper and lower jaws (Fig. 4). The tooth rows of the upper and lower jaws extend from the anterior tip of the skull to a position under the middle part of the nasoantorbital fenestra. That condition is also present in *B. cuiae* (Lü and Ji, 2005), *Zhenyuanopterus* (Lü, 2010), and some archaeopterodactyloids, like *Pterofiltrus* (Jiang and Wang, 2011), and *Ctenochasma* (Bennett, 2007). However, a different state occurs in *Feilongus* (Wang et al., 2005) and *Gegepterus* (Wang et al., 2007).

Two main distinct tooth morphologies can be indentified in *B. giganticus*. The first nine pairs of teeth on the upper jaw are much larger than the posterior ones. The anterior teeth have ratios of length to width from 7.09 to 14.22. They are similar to those of *B. cuiae* (Lü and Ji, 2005) and Ctenochasmatidae (Wang et al., 2007; Bennett, 2007). The anterior teeth of *Guidraco* (Wang et al., 2012) and *Liaoningopterus* (Wang and Zhou, 2003b) have ratios from 2.84 to 7.83 and from 2.28 to

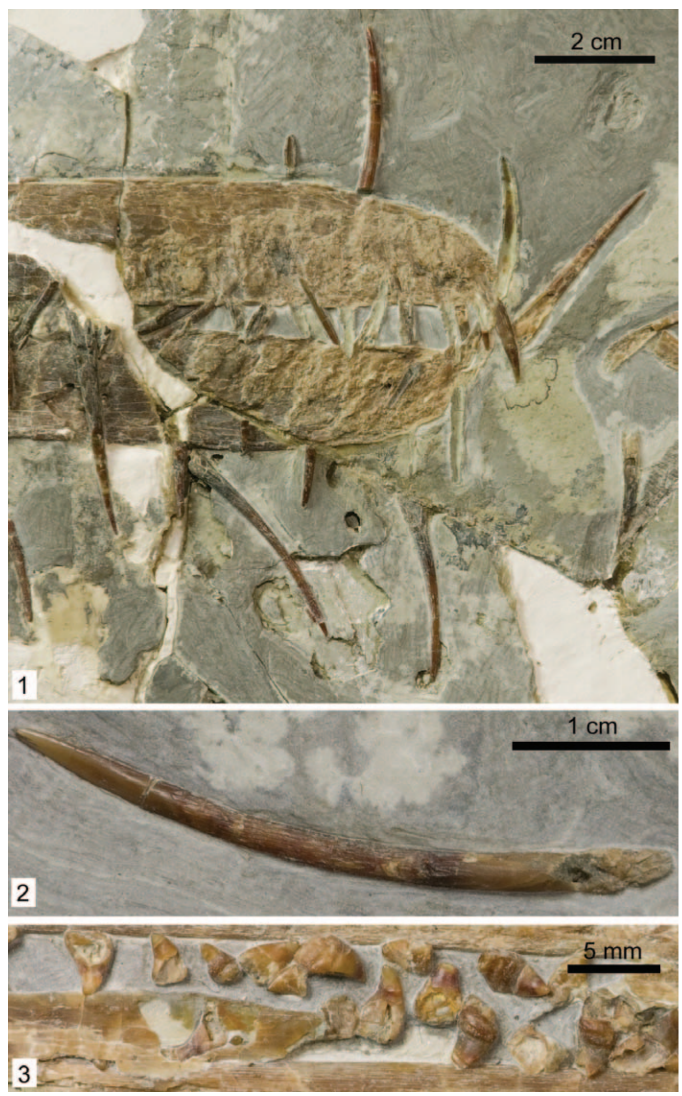


FIGURE 4—Details of the two tooth morphologies in *Boreopterus giganticus* n. sp. *1*, *2*, the anterior teeth, which are slender and slightly curved; *3*, the posterior teeth, which are short and triangular laterally.

4.55, respectively. Therefore, the anterior teeth are much more slender than those in *Guidraco*, and *Liaoningopterus*.

The larger teeth are slender, and slightly curved. The enamel surface of the tip is smooth, and some striations are present near the root. The slender teeth are almost perpendicular to the upper and lower jaws, although they incline slightly distally. The first eight teeth extend beyond the dorsal margin of the skull and the ventral margin of the lower jaw, respectively, similar to the condition in *B. cuiae* (Lü and Ji, 2005) and *Zhenyuanopterus* (Lü, 2010). The eighth tooth is the largest one in its alveolus, with a length of 39.6 mm. Some isolated anterior teeth also have a similar length. The teeth decrease in size posteriorly starting with the ninth one. The first, second, and eighth teeth have replacement teeth.

The posterior teeth exhibit a second tooth morphology. They are not in their alveoli, and are much smaller than the anterior ones. The teeth are compressed in a triangular shape, without an apparent base, and curve slightly. Their surfaces also are smooth.

The isolated vertebral elements near the skull likely are the fused atlas and axis, but their surfaces are crushed obscuring any osteological details. It appears that the axis is short and that it has a high neural spine, which is slightly taller than the centrum.

PHYLOGENETIC ANALYSIS AND DISCUSSION

In order to access the phylogenetic position *Boreopterus giganticus* n. sp. among pterosaurs, we performed a phylogenetic analysis using PAUP 4.0b10 for Microsoft Windows (Swofford, 2003) using the TBR heuristic searches performed using maximum parsimony. Characters were given equal weight. Twenty-two (22) characters (26, 31, 40, 41, 70, 72, 77, 86, 87, 94, 95, 97–105, 107, 108) were treated ordered and others unordered. This analysis is based on previous studies (e.g., Kellner, 2003; Wang et al., 2005, 2009, 2012; Andres and Ji, 2008). The search conducted using PAUP included three outgroups (*Rhamphorhynchus muensteri, Wukongopterus lii,* and *Kunpengopterus sinensis)* and produced 1483 of equally parsimonious trees with a length of 276 steps (consistency index=0.543; retention index=0.771; rescaled consistency index=0.419). A strict consensus tree is shown (Fig. 5) (see Appendix 2 for details). In addition, we duplicated the phylogenetic analysis performed by Lü et al. (2012). The resulting 50 percent major consensus tree using their data matrix is very different from the one they published. In their tree, *Feilongus* and *Moganopterus* are sister taxa. We did not recover that relationship in our analysis. Additionally, the Boreopteridae is not monophyletic in our result. Therefore, their data matrix does not support their reported phylogenetic result, and the resulting taxonomic classification of Lü et al. (2012) is questionable.

In our own strict consensus tree, the new species and *B. cuiae* are sister taxa. Those two *Boreopterus* species and *Zhenyuanopterus* comprise a monophyletic group that we refer to as the Boreopteridae. Two unambiguous synapomorphies of this clade are combination of slender and long anterior teeth and short posterior teeth (ch 64.1), and femur and tibia equal in length (ch 108.0). *Feilongus* and *Moganopterus* are not in this Boreopteridae clade, but comprise a supported monophyletic group along with *Gallodactylus* and *Cycnorhamphus*. Members of this group share three ambiguous synapomorphies, including the concave posterior margin of nasoantorbital fenestra (ch 9.1), the parietal crest (ch 37.1), and teeth confined to the anterior part of the jaws (ch 57.2).

In the original diagnoses of the Boreopteridae, the presence of two tooth morphologies and the equal length of the tibia and

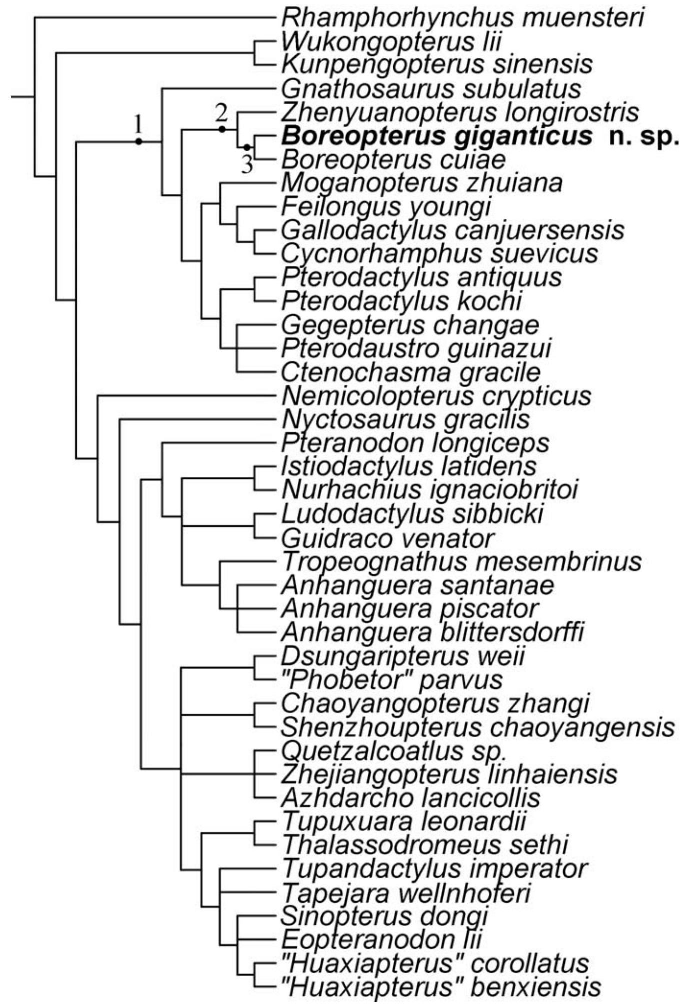


FIGURE 5—Strict consensus tree of 1483 parsimonious trees with a length of 276 steps. *1*, Archaeopteroidae; *2*, Boreopteridae; *3*, *Boreopterus*.

femur are two unambiguous synapomorphies. Both *Feilongus* and *Moganopterus* only have anterior slender teeth and no small posterior teeth (Wang et al., 2005; Lü et al., 2012). Some new specimens preserving the postcranial of *Feilongus* have been found in western Liaoning. Although they are still undergoing preparation, it is clear that *Feilongus'* tibia is longer than the femur. Meanwhile, the tibia and femur are not preserved in *Moganopterus* (Lü et al., 2012). From our analysis and the absence of these two unambiguous synapomorphies of the Boreopteridae, *Feilongus* and *Moganopterus* should not be placed in Boreopteridae.

The stratigraphic distribution of these taxa would also seem to support our reassessment of the relationships among the Boreopteridae. *Zhenyuanopterus*, *B. cuiae*, and *B. giganticus* were all collected from the Yixian Formation (Lü and Ji, 2005; Lü, 2010) and they share the same stratigraphic horizon. *Moganopterus* is considered to have been collected in the deposits of Yixian Formation, in Xiaosanjiazi locality (Lü et al., 2012). However, this locality only has outcrops of Jiufotang Formation, where we have worked for nearly a month. Considering the color of the bones, we surmise that *Moganopterus* likely is from the Jiufotang Formation rather than the Yixian Formation. The first specimen of *Feilongus* was found in the deposits of Yixian Formation (Wang et al., 2005). However, we found some additional unpublished specimens in the

Jiufotang Formation. As a result, *Zhenyuanopterus*, *B. cuiae*, and *B. giganticus* (that comprise the Boreopteridae), have only been found in Yixian Formation. The other taxa that have been allocated to that clade occur in the Jiufotang Formation suggesting a temporal separation among the taxa.

The skull of *B. giganticus* has a length of 477.5 mm, slightly smaller than that of *Zhenyuanopterus longirostris* (545 mm; Lü, 2010, p. 242), but more than twice of that of *B. cuiae* (235 mm; Lü and Ji, 2005, p. 159). The tooth rows of *B. giganticus* and *B. cuiae* reach the middle of the nasoantorbital fenestra, occupying 69.2 percent and 72.3 percent of the skull, respectively. The tooth rows of *Zhenyuanopterus longirostris* exceed the middle of the nasoantorbital fenestra with a larger ratio (80.7%) than those of the other Boreopteridae members. Likewise, *Zhenyuanopterus longirostris* has more teeth (172) than *B. giganticus* (114) and *B. cuiae* (108). *Boreopterus cuiae* has a small and circular orbit, while *B. giganticus* and *Zhenyuanopterus longirostris* both have piriform-shaped orbits. *Zhenyuanopterus longirostris* has a long nasal process, nearly reaching the ventral margin of the skull. A nasal process is not present in *Boreopterus*. The lacrimal of *B. giganticus* is special because it is extensively fenestrated, and has a posterior process, which can be distinguished from the other species.

SUMMARY

We erect a new species, *Boreopterus giganticus* as a sister taxon of *B. cuiae*. This new species is over twice as large as *B. cuiae*, has a piriform orbit, and has an extensively fenestrated lacrimal, with a posterior process. According to our phylogenetic analysis and the discussion above, the Boreopteridae are comprised of two genera *Boreopterus* and *Zhenyuanopterus*, united by the synapomorphic characters that two tooth morphologies are present, tooth rows that reach at least the middle of nasoantorbital fenestra, the femur and tibia equal being in length, and weak feet. Both the phylogenetic analysis and new specimens of *Feilongus* show that *Feilongus* and *Moganopterus* do not belong in the Boreopteridae, but though they group with *Cycnorhamphus* in our analysis, they probably are not gallodactylids.

ACKNOWLEDGMENTS

We thank Drs. L. Codorniú and A. W. A. Kellner for discussion about this specimen. We thank Dr. C. Bennett and an anonymous referee for reviewing the manuscript, and Dr. T. Stidham for polishing our writing. We also thank Y.-F. Guo for preparing the specimen and W. Gao for photographing. This study was supported by the National Science Fund for Distinguished Young Scholars (40825005), the Major Basic Research Projects of the Ministry of Science and Technology of China (2012CB821900), and the Hundred Talents Project of CAS.

REFERENCES

ANDRES, B. AND Q. JI. 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. Palaeontology, 51:453–469.

BENNETT, S. C. 2007. A review of the pterosaur *Ctenochasma*: taxonomy and ontogeny. Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen, 245:23–31.

CHANG, M.-M., P.-J. CHEN, Y.-Q.WANG, Y. WANG, AND D.-S. MIAO. 2003. The Jehol Biota, the Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants. Shanghai Scientific and Technical Publishers, Shanghai, 208 p.

CHIAPPE, L. M., A. W. A. KELLNER, D. RIVAROLA, S. DAVILA, AND M. FOX. 2000. Cranial morphology of *Pterodaustro guinazui* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of Argentina. Natural History Museum of Los Angeles County. Contributions in Science, 483:1–19.

FREY, E., D. M. MARTILL, AND M.-C. BUCHY. 2003a. A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur, p. 55–63. *In* E. Buffetaut and J.-M. Mazin (ed.), Evolution and Palaeobiology of Pterosaurs. Special Publication 217, Geological Society, London.

FREY, E., D. M. MARTILL, AND M.-C. BUCHY. 2003b. A new species of tapejarid pterosaur with soft-tissue head crest, p. 65–72. *In* E. Buffetaut and J.-M. Mazin (eds.), Evolution and Palaeobiology of Pterosaurs. Geological Society of London Special Publication, vol. 217.

JIANG, S.-X. AND X.-L. WANG. 2011. A new ctenochasmatid pterosaur from the Lower Cretaceous, western Liaoning, China. Academia Brasileira de Ciências, 83:1,243–1,249.

JI, S.-A. AND Q. JI. 1997. Discovery of a new pterosaur from western Liaoning, China. Acta Geologica Sinica, 71:1–6. (In Chinese)

JOUVE, S. 2004. Description of the skul of a *Ctenochasma* (Pterosauria) from the latest Jurassic of eastern France, with a taxonomic revision of Europian Tithonian Pterodactyloidea. Journal of Vertebrate Paleontology, 24:542–554.

KAUP, J. J. 1834. Versuch einer Eintheilung der Saugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. Isis, 3:311–315. (In German)

KELLNER, A. W. A. 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeast Brazil. Academia Brasileira de Ciências, 61:439–446.

KELLNER, A. W. A. 1996. Description of new material of Tapejaridae and Anhangueridae (Pterosauria, Pterodactyloidea) and discussion of pterosaur phylogeny. Ph.D. thesis, Columbia University.

KELLNER, A. W. A. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group, p. 105–137. *In* E. Buffetaut and J.-M. Mazin (ed.), Evolution and Palaeobiology of Pterosaurs. Special Publication 217, Geological Society, London.

KELLNER, A.W.A. AND Y. TOMIDA. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian–Albian), Northeastern Brazil. National Science Museum Monographs, 17:1–135.

LÜ, J.-C. 2010. A new boreopterid pterodactyloid pterosaur from the Early Cretaceous Yixian Formation of Liaoning Province, northeastern China. Acta Geologica Sinica, 84:241–246.

LÜ, J.-C. AND Q. JI. 2005. A new ornithocheirid from the Early Cretaceous of Liaoning Province, China. Acta Geologica Sinica, English edition, 79:157–163.

LÜ, J.-C., S.-A. JI, C.-X. YUAN, AND Q. JI. 2006. Pterosaurs from China. Geological Publishing House, Beijing, 147 p. (In Chinese)

LÜ, J.-C., H.-Y. PU, L. XU, Y.-H. WU, AND X.-F. WEI. 2012. Largest toothed pterosaur skull from the Early Cretaceous Yixian Formation of western Liaoning, China, with comments on the Family Boreopteridae. Acta Geologica Sinica, English edition, 86:287–293.

PLIENINGER, F. 1901. Beiträge zur Kenntniss der Flugsaurier. Pälaeontographica, 48:65–90. (In German)

SWOFFORD, D. L. 2003. Paup*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sunderland, Sinauer Associates.

UNWIN, D.M. 2003. On the phylogeny and evolutionary history of pterosaurs, p. 139–190. *In* E. Buffetaut and J.-M. Mazin (eds.), Evolution and Palaeobiology of Pterosaurs. Special Publication 217, Geological Society, London.

WANG, X.-L. AND Z.-H. ZHOU. 2003a. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. Chinese Science Bulletin, 48:16–23.

WANG, X.-L. AND Z.-H. ZHOU. 2003b. Two new pterodactyloid pterosaurs from the Early Cretaceous Jiufotang Formation of western Liaoning, China. Vertebrata PalAsiatica, 41:34–41.

WANG, X.-L., A. W. A. KELLNER, S.-X. JIANG, AND X. CHENG. 2012. New toothed flying reptile from Asia: close similarities between early Cretaceous pterosaur faunas from China and Brazil. Naturwissenschaften, 99:249–257.

WANG, X.-L., A. W. A. KELLNER, S.-X. JIANG, AND X. MENG. 2009. An unusual long-tailed pterosaur with elongated neck from western Liaoning of China. Academia Brasileira de Ciências, 81:793–812.

WANG, X.-L., A. W. A. KELLNER, Z.-H. ZHOU, AND D. A. CAMPOS. 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. Nature, 437:875–879.

WANG, X.-L., A. W. A. KELLNER, Z.-H. ZHOU, AND D. A. CAMPOS. 2007. A new pterosaur (Ctenochasmatidae, Archaeopterodactyloidea) from the Lower Cretaceous Yixian Formation of China. Cretaceous Research, 28:245–260.

ZHOU, Z.-H. 2004. Vertebrate radiations of the Jehol Biota and their environmental background. Chinese Science Bulletin, 49:754–756.

ACCEPTED 3 OCTOBER 2013