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Largest Toothed Pterosaur Skull from the Early Cretaceous Yixian Formation of Western Liaoning, China, with Comments on the Family Boreopteridae

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Abstract: A new pterosaur *Moganopterus zhuiana* gen. et sp. nov. is erected based on a complete skull with lower jaws and anterior cervical vertebrae. It is characterized by much elongated upper and lower jaws with at least 62 total, long, curved teeth with sharp tips, a well developed parietal crest extending posterodorsally, forming an angle of 15 degrees with the ventral margin of the skull, the ratio of length to width of cervical vertebrae greater than 5:1. The skull length is 750 mm, and it is the largest toothed pterosaur found so far in the world. Based on this new pterosaur, the Boreopteridae can be divided into two subgroups: Boreopterinae sub-fam. nov. and Moganopterinae sub-fam. nov., which is also confirmed by the phylogenetic analysis.

Key words: *Moganopterus*, Boreopteridae, Yixian Formation, western Liaoning

1 Introduction

At present, except for the toothless forms *Eopteranodon* (Lü and Zhang, 2005), most reported pterosaurs from the Early Cretaceous Yixian Formation of western Liaoning and its surrounding areas are toothed forms, including small sized and large sized forms. Small sized forms include the pterodactyloid *Ningchengopterus* (Lü, 2009), ctenochasmatid *Beipiaopterus* (Lü, 2003), *Eosipterus* (Ji and Ji, 1997; Lü et al., 2006a), *Cathyopterus* (Wang and Zhou, 2006) and *Gegepterus* (Wang et al., 2007); large sized forms are boreopterids *Boreopterus* (Lü and Ji, 2005), *Feilongus* (Wang et al., 2005), and *Zhenyuanopterus* (Lü, 2010). Among them, *Boreopterus* and *Zhenyuanopterus* are known from almost complete specimens. *Zhenyuanopterus* has been regarded as the most complete, largest pterosaur from the Yixian Formation until now. Herein reported is a new pterosaur *Moganopterus zhuiana* gen. et sp. nov., which is based on a large skull with lower jaws and cervical vertebrae. The skull is much larger than that of *Zhenyuanopterus*, which is also from the Yixian Formation, and it is the largest pterosaur skull found from western Liaoning and its surrounding areas so far. It also represents the largest toothed pterosaur from the world. The discovery of *Moganopterus zhuiana* provides much more osteological information about boreopterids.

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2 Systematic Paleontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Ornithocheiroidea Seeley, 1891 (Sensu Unwin, 2003)
Boreopteridae Lü et al. 2006b
Moganopterus gen. nov. (Figs. 1, 2)

Etymology: Generic name refers to a combination of the first two words of the two famous names of a sword in Chinese History: Moye and Ganjiang. Moye means female and Ganjiang means male, which are never separated from each other. Here it refers to the very long upper and lower jaws, and pterus for wing.

Diagnosis: As for the type and only species.

Moganopterus zhuiana gen. et sp. nov.

Holotype: A complete skull with lower jaws and anterior three cervical vertebrae preserved. The specimen is housed at Henan Geological Museum (41HIII0419).

Type locality and horizon: The specimen was collected from the Yixian Formation of Xiaosanjiazi Village, Lamadong Town, Jianchang County of Liaoning Province (Bureau of Geology and Mineral Resources of Liaoning Province, 1989).

Etymology: The specific name is in honor of Ms. Zhu

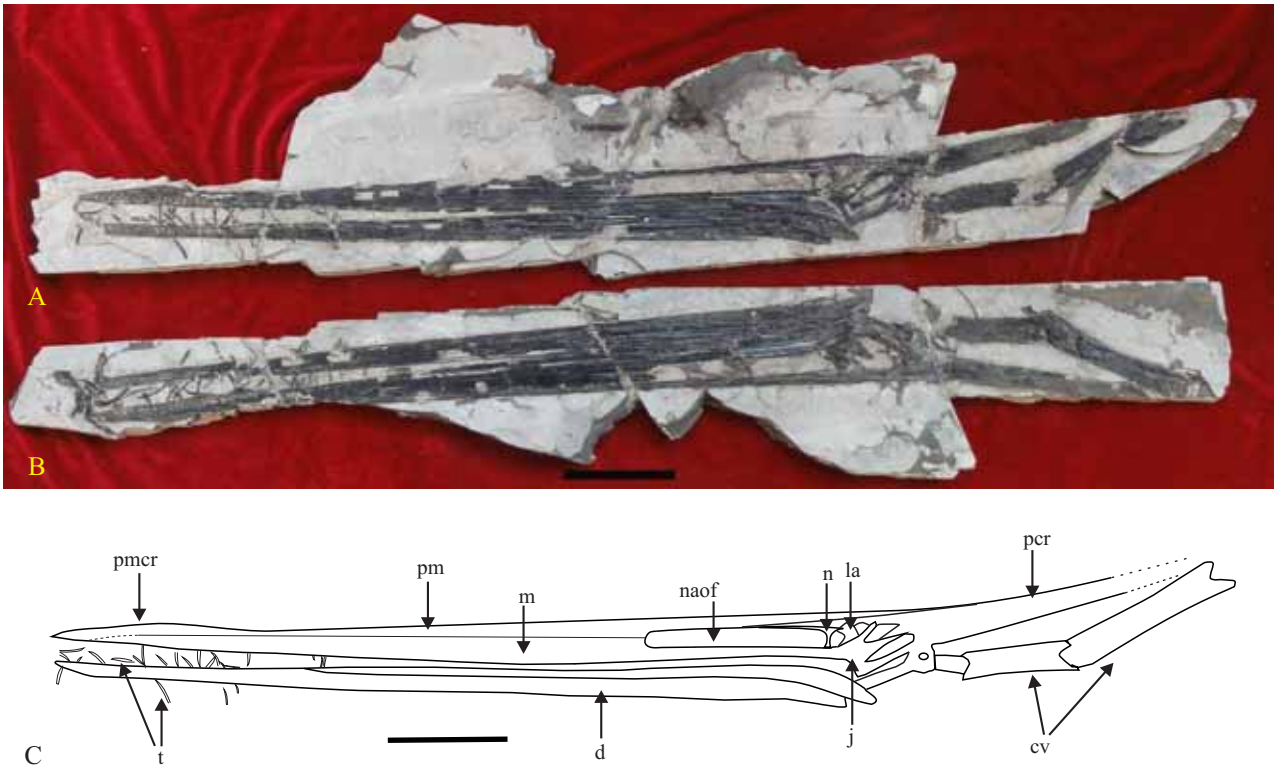

Fig. 1. Holotype of *Moganopterus zhui* gen. et sp. nov. (JPM-10-089), slab (A), counterslab (B) and the outline drawing of the slab (C).
Abbreviations: cv, cervical vertebrae; d, dentary; j, jugal; la, lacrimal; m, maxilla; n, nasal; naof, naso-antorbital opening; pcr, parietal crest; pm, premaxilla; pmcr, premaxillary crest; t, teeth. Scale bar equals 10 cm.

Haifen, who offered the specimen for scientific research.

Diagnosis: Large sized pterosaur bearing the following characters: both the upper and lower jaws much elongated with straight ventral margins, at least 62 long, slender, curved upper and lower jaw teeth with sharp tips; rectangular nasoantorbital fenestra occupies 22% of the upper jaw length; the long, narrow blade-like parietal crest extends posterodorsally, forming an angle of 15 degrees with the ventral margin of the skull, the ratio of length to width of cervical vertebra greater than 5:1, and the ratio of skull length (excluding the parietal crest) to height about 11.5:1.

3 Description

The skull and lower jaws are almost completely preserved (Fig. 1; Table 1). It is preserved as a slab and counter-slab. Unfortunately, the plane of separation between the two slabs was rather uneven, passing through the skull and lower jaws, rather than leaving them on one slab and impressions on the other. Consequently, fragments of each element are preserved on both slabs. Thus, the poor preservation of bones frequently hinders the identification of details, but by combining evidence from both slabs it is possible to determine the general shape of some skull elements.

Table 1 Measurements of *Moganopterus* gen. nov. (cm)

Elements	Length	Height (width)
Skull	75 (without parietal crest) >95 (with parietal crest)	6.5 (vertical to the articular end of the quadrate)
Upper jaw	66.6 (Ventral margin of the upper jaw: from tip to the articular end of the quadrate)	-
Orbit	1	1
Lower jaw	68.5	1 (anterior portion) 2 (posterior portion)
Parietal crest	18.5 (est.)	2
Nasoantorbital Opening	16.5	1.7
Dentition	26 (lower jaw); 23 (upper jaw)	-,-
Cervical vertebra 2	2.5	1
Cervical vertebra 3	11	2 (width)
Cervical vertebra 4	14.5	2 (width)

Notes: est. estimated; -, inapplicable.

Both the ventral margin of the upper jaw and the dorsal margin of the lower jaw are straight. The tip of the upper jaw is pointed. There is a short premaxillary crest located on the anterior portion of the upper jaw (Fig. 2A). The premaxillary crest is 5 cm long and 0.6 cm high. The broken surfaces show cellular structures present within the anterior portion of the jaws. Only the anterior portions,

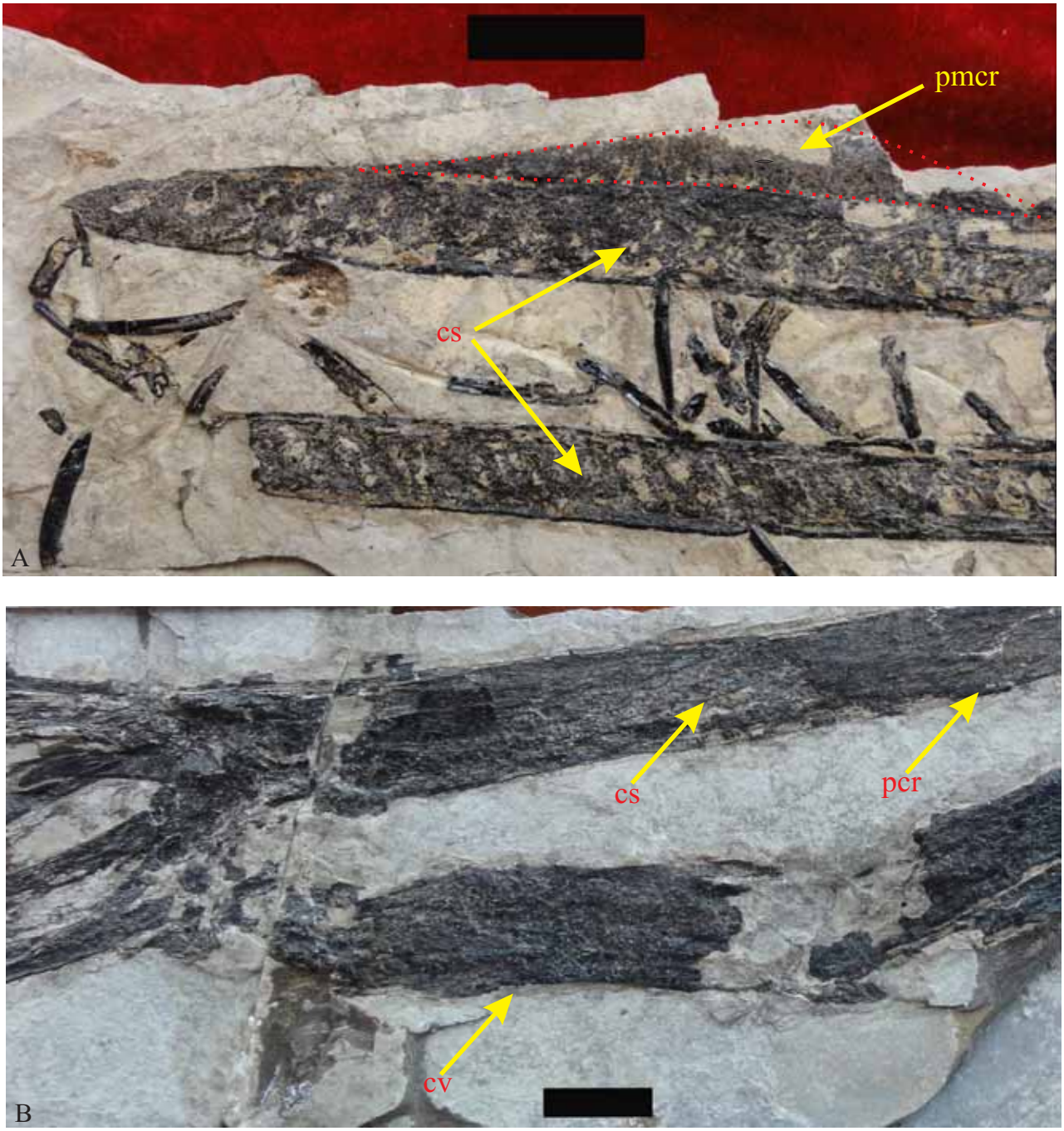

Fig. 2. (A), Close up of the anterior portions of the upper and lower jaws, showing the premaxillary crest and cellular structures within the jaws; (B), Closeup of the parietal crest, showing the cellular structures within it.
Abbreviations: cs. cellular structure; cv. cervical vertebra; pcr. parietal crest; pmcr. premaxillary crest. Scale bar equals 2 cm.

which bear teeth, are filled with cellular structures (Fig. 2A), whilst the posterior portions are solid. The suture between the maxilla and premaxilla is not clear. The dorsal margin of the skull is concave, but not straight as that of *Feilongus* (Wang et al., 2005). The orbit is round and small, and located above the dorsal margin of the nasoantorbital opening. The nasoantorbital opening is rectangular. It occupies 22 % of the upper jaw length. The nasal process contacts with the ventral margin of the nasoantorbital opening. The posterior margin of the nasoantorbital opening is concave. The anterior process of the nasal is long and slender and extends anteriorly. The jugal is a stout bone with three processes. The posterior process extends dorsoposteriorly and contacts with the postorbital bone. Its dorsal process contacts the lacrimal, although their sutures are not clear. The lacrimal is a wide, thin plate-like bone. The anterior process, which contacts the maxilla, is not clear either. The quadrate is obliquely

orientated. The angle between the quadrate and the ventral margin of the upper jaw is about 155 degrees. The parietal crest is long, narrow, and blade-like (or rod-like, which is uncertain because of its preservation). It extends posterodorsally, forming an angle of 15 degrees with the ventral margin of the skull. As the anterior portion of the upper and lower jaws, the cellular structures are developed within the parietal crest (Fig. 2B).

There are about 62 long, curved teeth with sharp tips which scattered near the anterior portions of the upper and lower jaws. There are still some teeth planted in the jaw, and considering that both upper and lower jaws are nearly preserved in their natural articulation, all the teeth (including the teeth falling from the dentition) should be near the jaws and could not lose during burial process. The teeth are confined to between the far anterior jaws and the anterior margin of the nasoantorbital opening. All the longer teeth are distributed anteriorly. Most of them are about 3.1 cm long and 0.3 cm in diameter. The shortest tooth is about 0.3 cm long and 0.1 cm in diameter. Three posterior adjacent teeth which are still planted in the upper jaw show that the distance between adjacent teeth is about 1–1.5 cm. The teeth point ventroposteriorly. The dentition length of the upper jaw is about 23 cm, thus the tooth number is about 23/1.5=15, therefore, the total upper jaw teeth is about 30; the dentition length of the lower jaw teeth is about 26 cm, thus the tooth number is about 26/1.5=17, therefore, the total number of the lower jaw teeth is about 34. So, the total tooth number is 64, which is close to the number (62) we counted.

There are three cervical vertebrae preserved. The second cervical vertebra (axis) is not well-preserved, but its length and width can be measured. The third and fourth cervical vertebrae are very long, and their ratios of length to width are 5.5 and 7.25 respectively. The broken surface of the centra shows that short thin bony struts forming cellular structures.

4 Phylogenetic Analysis

To determine the relationships of boreopterid *Moganopterus*, a phylogenetic analysis was conducted. The data matrix (ingroup 59 taxa and 117 characters) is based on Lü et al. (2010), with the addition of 117 characters coded for *Moganopterus* (Wang et al., 2005) and *Zhenyuanopterus* (Lü, 2010) (Table 2). Phylogenetic analysis was conducted using PAUP* version 4.0b10 (Swofford, 2003). A heuristic search using Branch-Swapping options was performed using the Tree Bisection and Regrafting (TBR) algorithum. The limit of the MaxTree was set up 33500, using the maximum computer memory. Thirty-three thousand and five hundred most parsimonious trees were found (Tree length = 402; CI = 0.4055; HI =0.5945; RI = 0.7837). The 50% Majority-rule consensus of 33500 trees shows that the existence of a monophyletic family Boreopteridae, with two subfamilies (Boreopterinae sub-fam. nov. and Moganopterinae sub-fam. nov.). Boreopteridae is supported by one unambiguous character (24) and two ambiguous characters (37 and 94). Boreopterinae is supported by three unambiguous characters (27, 57 and 68). Moganopterinae is supported by five unambiguous characters (12, 23, 38, 64 and 65) and two ambiguous characters (9, 67). *Moganopterus* is supported by one unambiguous character: 28(4) and one ambiguous character 9(3). The clades (Boreopterinae and Moganopterinae) and Boreopteridae were well supported, with Bootstrap support values of 100% and 82% respectively (Fig. 3).

5 Discussion and Comparison

The skull length of *Moganopterus* is 750 mm, and it is the largest toothed pterosaur skull in the world. The wing-span of *Moganopterus* is estimated to exceed to 7 m. *Moganopterus* is assigned to the Boreopteridae, based

Table 2 Coding of 117 characters of *Zhenyuanopterus* (Lü, 2010), *Moganopterus* gen. nov. and *Feilongus* (Wang et al., 2005) in the data matrix of Lü et al. (2010)

Taxa/Character No.	**1–5**	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**
Zhenyuanopterus	00021	21050	11221	- - - - 1	01101	01000
Moganopterus	00011	21010	11221	- - - - 1	01001	00401
Feilongus	00011	21010	10221	- - - - 1	01001	00011
Taxa/Character No.	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**	**56–60**
Zhenyuanopterus	0001?	0?100	01000	01000	00010	0110-
Moganopterus	?0?1?	0?100	01000	01000	00010	0000-
Feilongus	???1?	21000	01000	01010	00010	0000-
Taxa/Character No.	**61 –65**	**66–70**	**71–75**	**76–80**	**81–85**	**86–90**
Zhenyuanopterus	00111	10011	101?1	1?111	2??10	11011
Moganopterus	00102	112??	?????	?????	?????	?????
Feilongus	00102	112??	?????	?????	?????	?????
Taxa/Character No.	**91–95**	**96–100**	**101–105**	**106–110**	**111–115**	**116–117**
Zhenyuanopterus	11111	10200	101??	?110?	???01	1-
Moganopterus	?????	?????	?????	?????	?????	??
Feilongus	?????	?????	?????	?????	?????	??

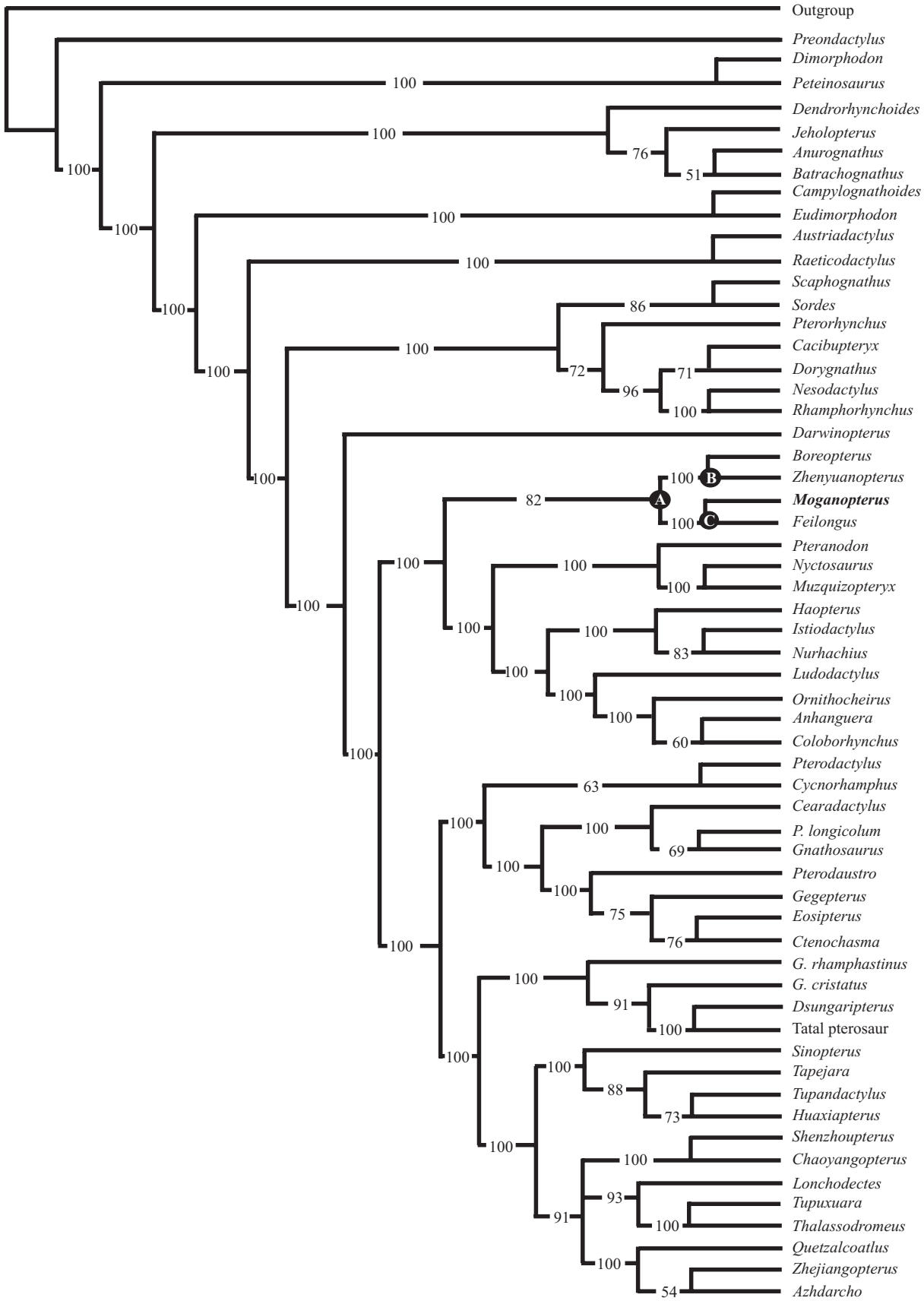

Fig. 3. The 50% Majority-rule consensus of 33500 trees, showing the family Boreopteridae (A); and its two subgroups: Boreopterinae (B) and Moganopterinae (C). The data matrix (ingroup 59 taxa and 117 characters) is based on Lü et al. (2010), with the addition of 117 characters coded for *Moganopterus, Feilongus* (Wang et al., 2005) and *Zhenyuanopterus* (Lü, 2010). Character lists and main data matrix are seen in Lü et al. (2010).

on the following characters: large sized Ornithocheiroidea, skull low and long, extremely elongated rostrum (from the tip to the anterior margin of the fused nasoantorbital fenestra), long curved teeth with sharp tips, anterior teeth varied in size (Lü et al., 2006b).

At present, three taxa are considered part of the Boreopteridae, they are: *Boreopterus* (Lü and Ji, 2005), *Feilongus* (Wang et al., 2005) and *Zhenyuanopterus* (Lü, 2010). All of these are known only from the Early Cretaceous Yixian Formation.

Moganopterus differs from *Boreopterus* (Lü and Ji, 2005) in that in *Boreopterus* teeth are located far back, under the ventral margin of the nasoantorbital fenestra, all the posterior teeth are very small and there is no parietal crest, although the upper jaw tooth numbers are close in both forms, whilst the teeth are confined far anterior to the anterior margin of the nasoantorbital fenenstra, and there is a very long parietal crest in *Moganopterus*. The ratio of length to width of cervical vertebrae is greater in *Moganopterus* than in *Boreopterus*.

Moganopterus differs from *Feilongus* (Wang et al., 2005) in that the skull of *Feilongus* is smaller than *Moganopterus*, but the tooth number is greater (The tooth number is 76) than that of *Moganopterus* (The tooth number is 64). The posterior end of the skull is round in *Feilongus*, but there is a long, developed parietal crest in *Moganopterus*.

Moganopterus differs from *Zhenyuanopterus* (Lü, 2010) in that the posterior teeth are small and distributed under the nasoantorbital fenestra, the parietal crest is large and located above anterior part of the nasoantorbital fenestra, and the cervical vertebrae are short in *Zhenyuanopterus*, whilst the teeth are located more anteriorly in *Moganopterus* and the cervical vertebrae are very elongate.

Comments on the family Boreopteridae: The Boreopteridae were erected by Lü et al. (Lü et al., 2006b), based on the genera *Boreopterus* and *Feilongus*. With the additional discoveries of *Zhenyuanopterus* and *Moganopterus*, the Boreopteridae can be divided into two sub-groups: the Boreopterinae sub-fam. nov. and Moganopterinae sub-fam. nov..

Boreopterinae sub-fam. nov.

Diagnosis: long curved anterior teeth are much larger than the posterior teeth, the posterior teeth located under the nasoantorbital fenenstra; cervical vertebrae short with high, blade-like neural spines, very weak feet.

Included genera *Boreopterus* (Lü and Ji, 2005) and *Zhenyuanopterus* (Lü, 2010).

Moganopterinae sub-fam. nov.

Diagnosis: long, curved teeth confined far anterior to the nasoantorbital fenenstra, the posterior teeth are slightly shorter than the anterior teeth; cervical vertebrae elongated with short neural spine, the ratio of length to width of cervical vertebra greater than 5; two sagittal cranial crests (*Feilongus*), and one very developed parietal crest which extends posteriorly beyond the skull (*Moganopterus*) .

Included genera: *Feilongus* (Wang et al., 2005) and *Moganopterus* gen. nov..

Notes: Wang et al. (2005) listed the following: protruding upper jaw that is about 10% longer than the lower jaw, as one of the diagnostic characters of *Feilongus*. However, from the view of tooth function, this character was questioned by Lü et al. (2006b). Recently, a new collected specimen by Dalian Natural History Museum, which is almost identical to the skull of *Feilongus* (personal observation), shows that both the upper and lower jaw ends are almost at the same vertical level. This means that the upper jaw does not protrude about 10% longer than the lower jaw and it is therefore not the diagnostic for *Feilongus*.

Among the members of boreopterid pterosaurs, *Moganopterus* is much more similar to *Feilongus* than to others in the skull morphology. But *Moganopterus* is much larger than *Feilongus* and more importantly, it has fewer teeth than *Feilongus,* and bears a large long parietal crest which extends posterodorsally. Although the skull-bearing crest is regarded as sexual dimorphism in *Darwinopterus*, other parts of the body, such as the tooth numbers and ratio of long bones are identical in both the male and female individuals (Lü et al., 2011), however, *Moganopterus* (about 75 cm) is much larger than *Feilongus* (about 40 cm) and the teeth are fewer than these of *Feilongus*, which means that *Moganopterus* could not belong to the same species as *Feilongus*. In comparison with *Feilongus*, whose wing span is estimated around 2.4 m (Wang et al., 2005), the wing span of *Moganopterus* may reach more than 5 m. Increasing the body size may be the tendency for boreopterid evolution. Although the parietal crest is not complete in *Moganopterus*, the shape of the basal portion of the parietal crest is reminiscent of the parietal crest of *Nyctosaurus* (Bennett, 2003). However, it is difficult to confirm whether or not *Moganopterus* is related to *Nyctosaurus*.

The large sized reported ornithocheiroid pterosaurs whose lower jaw lengths are greater than 300 mm from the Early Cretaceous include 10 genera and the largest one (606mm) is *Coloborhynchus spielbergi* (see Myers, 2010, table 2), but it is still smaller than *Moganopterus* (750 mm).

The recently reported largest toothed pterosaur skull was thought to be more than 0.75 m long, however, this data was tentatively estimated based on the fragment of the rostrum (Martill and Unwin, 2012). The 750 mm long

skull of *Moganopterus* is the undoubtedly largest toothed pterosaur skull found so far.

Moganopterus bears the longest, sword-like skull and lower jaws. The skull morphology of *Moganopterus* is highly unusual, and its biomechanical analysis would be of great interest, but is beyond the scope of the present work.

6 Conclusions

The phylogenetic analysis of the Boreopteridae confirms the monophyly of the group. Boreopteridae can be divided into two sub-groups: Boreopterinae sub-fam. nov. and Moganopterinae sub-fam. nov.. *Moganopterus* is supported by one unambiguous character: fronto-parietal crest is rod-like and elongate and one ambiguous character premaxillary crest extends from tip of rostrum to apex of skull and confluent with fronto-parietal crest.

Moganopterus gen. nov. represents the largest toothed pterosaur found so far in the world. Increasing the body size and reducing the tooth numbers may be the tendency for the evolution of Moganopterinae. The discovery of *Moganopterus zhuiana* provides much more osteological information about boreopterids, especially the morphologies of the cervical vertebrae between these two subgroups.

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