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New Material of *Feilongus* (Reptilia: Pterosauria) from the Lower Cretaceous Jiufotang Formation of Western Liaoning

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Abstract: Based on a new nearly naturally preserved skull and four cervical vertebrae of the pterosaur *Feilongus* sp. from the lower Cretaceous Jiufotang Formation of Beipiao, western Liaoning province, northeastern China, the diagnosis of *Feilongus* is amended. The revised diagnosis notes long, curved, needle-shaped teeth that are confined to the jaw far anterior to the nasoantorbital fenestra; posterior teeth that are slightly smaller than the anterior teeth; cervical vertebrae elongated with a ratio of length to width greater than 5; tooth number of about 78; and two cranial sagittal crests.

Key words: pterosaur, amended diagnosis, Jiufotang Formation, Aptian, western Liaoning

1 Introduction

Abundant pterosaur specimens have been discovered from western Liaoning and the surrounding areas in China in the last two decades (Ji and Ji, 1997; Ji et al, 1999; Wang and Lü, 2001; Wang and Zhou, 2002, 2003, 2004; Wang et al., 2002, 2005; Wang and Zhou 2006; Lü, 2003, 2009, 2010; Lü and Hone, 2012; Lü and Ji, 2005; Lü et al., 2006a, 2006b, 2011, 2012). This has greatly extended our understanding of pterosaur evolution, classification, morphology and behavior. *Feilongus youngi* was the first reported pterosaur in which the wingspan reached greater than 2 meters (Wang et al., 2005). The type specimen included an almost complete skull and mandible (Fig. 1), which was discovered from the lower Yixian Formation at Beipiao, western Liaoning.

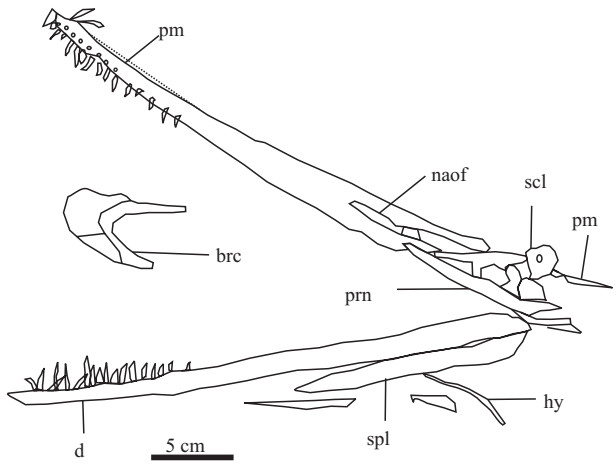

Fig. 1. Line drawing of the holotype of *Feilongus youngi* Wang et al., 2005 (After Wang et al., 2005).

The diagnostic characteristics of the genus *Feilongus* have been questioned since it was first published (Lü et al., 2006a, 2012). However, the debates were based on tooth function and those of other genera closely related to *Feilongus*. Recently, a new specimen, DNHM-D3068, of the genus was collected by the Dalian Natural History Museum from a locality at Chaoyang in the lower Cretaceous Jiufotang Formation, in western Liaoning, and this specimen sheds new light on this debate. DNHM-D3068 was preserved in a nearly natural condition, including a partially complete skull and four cervical vertebrae. It can be assigned to *Feilongus* sp. based on its rostrum and tooth characters. The new discovery expands the stratigraphic range of *Feilongus* from the lower Yixian Formation to the overlying Jiufotang Formation (Aptian, ~120 Ma) (He et al., 2004).

Importantly, the naturally preserved condition shows that the upper and lower jaws are nearly the same length and that their anterior tips could meet when the jaws were closed, which allows us to amend the diagnosis of *Feilongus*.

Institutional abbreviations-DNHM, Dalian Natural History Museum, Dalian, Liaoning Province, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

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2 Systematic Paleontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Ornithocheiroidea Seeley, 1891 (*sensu* Unwin, 2003)
Boreopteridae Lü et al. 2006
Moganopterinae Lü et al. 2012
Feilongus Wang et al. 2005

Holotype: *Feilongus youngi* Wang et al., 2005 (IVPP V12539)

Referred specimen: DNHM-D3068, a partially complete skull and four cervical vertebrae (Fig. 2). The specimen is deposited in the Dalian Natural History Museum, Dalian City, Liaoning Province, China.

Locality and horizon of the referred specimen: Gonggao, Dapingfang Town, Chaoyang City, Liaoning Province; Jiufotang Formation, Aptian, Early Cretaceous (He et al., 2004).

Amended diagnosis: long, curved, needle-shaped teeth confined far anterior to nasoantorbital fenestra; posterior teeth are slightly smaller than the anterior teeth; cervical vertebrae elongated with the ratio of length to width greater than 5; tooth number is about 78; two sagittal cranial crests (after Lü et al., 2012).

Fig. 2. Photograph of *Feilongus* sp. (DNHM-D3068)

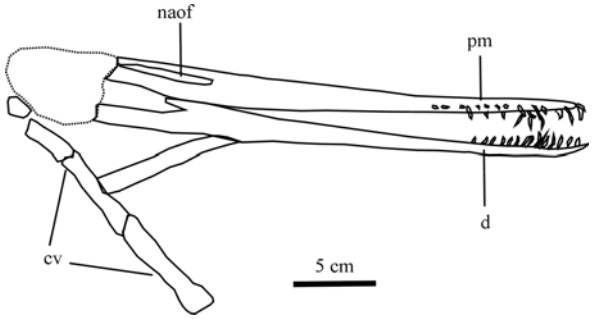

Fig. 3. Line drawing of *Feilongus* sp. (DNHM-D3068).
Abbreviations: brc, braincase; cv, cervical vertebrae; d, dentary; hy, hyoid bone; naof, nasoantorbital fenestra; prn, premaxilla; prn, processus nasalis; scl, sclerotic ring; spl, splenial. Scale in centimeters.

3 Descriptions

The new specimen (DNHM-D3068) consists of a partially complete skull and four cervical vertebrae. The skull is very low and long, with a total length of 32 cm as preserved. The rostrum is extremely elongated. The length from the anterior margin of the nasoantorbital fenestra to the tip of the skull is 22 cm. The nasoantorbital opening is elongated, which is 5.88 cm long. The braincase portion is missing. The dorsal part of skull is too badly preserved to determine exact anatomical structures and characteristics. No sagittal crest or crest impression can be observed.

The naturally preserved condition of DNHM-D3068 shows that both the upper and lower jaws are nearly at the same level; their anterior tips could have met when the jaws were closed. Both the upper and lower jaws are straight and become narrower anteriorly. The upper jaw is slightly shorter than the lower jaw. The dorsal margin of the upper jaw is concave. A distinct ridge is presented on the ventral surface of the upper jaw. Along the ridge are weak grooves on both sides. The mandible is straight and slightly upwards dorsally. The length of the mandibular symphysis is 15 cm. The height of the part of the mandible bearing the dentition is 0.7 cm and that of the upper jaw is 0.9 cm. The dentition occurs along 10 cm of the premaxilla and maxilla with 18 slender teeth (including tooth sockets) at each side of the upper jaw. About 21 teeth are on each side of the lower jaw. The anterior teeth are larger than the posterior ones in both the upper and lower jaws. All the teeth are not perpendicular to the dental margin and confined far anterior to the nasoantorbital fenestra. The teeth extend anteroventrally in the upper and anterodorsally in the lower jaw. The ventral margin of the upper jaw is at an angle of about 60º with the dentition (Fig. 2, 3). The preserved longest tooth is 9.71 mm long and 1.26 mm wide. The details of tooth width and dentition space are seen in Figure 4 and listed in Table 1.

There are four cervical vertebrae preserved, including the atlas. The atlas is short and rectangular, 2.0 cm long and 1.1 cm wide. The second cervical is partially preserved and articulated with the third cervical distally. The length as preserved is 3.5 cm, and the width is 1.1 cm. The third and fourth cervical vertebrae are preserved relatively completely and well articulated. Both of them are very elongated and constricted at the middle parts, with lengths of 6 and 7 cm and widths of 1.0 and 1.1 cm, respectively. The ratio of length to width of the third and fourth cervical vertebrae is greater than 5.

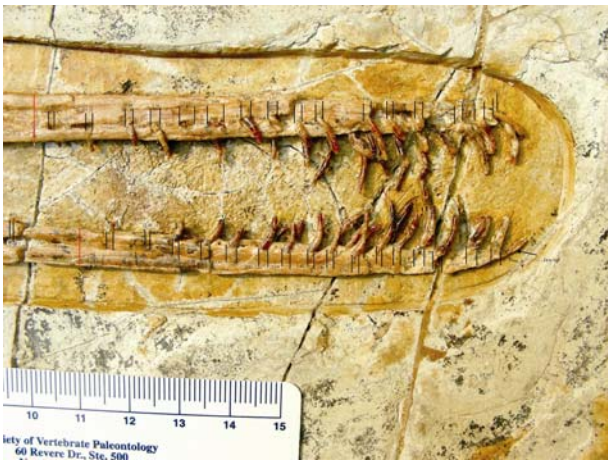

Fig. 4. Detailed photograph of *Feilongus* sp. (DNHM-D3068), with red lines representing the measured parts of upper and lower jaws bearing the dentition.

A weak ridge on the long axis of the dorsal surface of each vertebra is the vestige of the neural spine. There is no pleurocoel on the lateral surface of the cervical vertebra.

4 Comparison and Discussion

Early Cretaceous pterosaurs from western Liaoning and its surrounding areas mostly are toothed, including small- and large-sized forms. Larger forms are boreopterid *Boreopterus* (Lü and Ji, 2005), *Feilongus* (Wang et al., 2005), *Zhenyuanopterus* (Lü, 2010) and *Moganopterus* (Lü et al., 2012). DNHM-D3068 can be assigned to the Boreopteridae based on the following characters: skull long and low, rostrum (from the tip of the skull to the anterior margin of the nasoantorbital fenestra) extremely elongated, strongly recurved teeth, long and with sharp tips (Lü et al., 2005).

The Boreopteridae has been divided into two sub-families: Boreopterinae and Moganopterinae (Lü et al., 2012). The former currently includes only two genera: *Boreopterus* and *Zhenyuanopterus*. The typical characteristic of members of the Boreopterinae is that the posterior teeth are located under the nasoantorbital fenestra. The teeth of DNHM-D3068, however, are confined far anterior to the nasoantorbital fenestra and so DNHM-D3068 can be excluded from Boreopterinae, and be better assigned to the Moganopterinae based on the following characters: long, curved teeth confined far anterior to the nasoantorbital fenestra; the posterior teeth are slightly shorter than the anterior teeth; the ratio of length to width of cervical vertebra is greater than 5.

The Monganopterinae includes two genera: *Feilongus* and *Moganopterus*. The skull lengths of *Feilongus* and *Moganopterus* are 390~400 and 750 mm, respectively, while the skull length of DNHM-D3068 is 320 mm. The tooth numbers of *Feilongus* and *Moganopterus* are 76 and 64, respectively, and the tooth number of DNHM-D3068 is 78. Considering the well-fused skull bones and articulated cervical vertebrae of DNHM-D3068, it could be an adult or sub-adult. Furthermore, tooth number and morphology varied little during the growth period of reptiles. Therefore, DNHM-D3068 differs from *Moganopterus* by having a much shorter skull and more teeth, whereas it is similar to *Feilongus* in having a similar skull size and tooth number (Table 2).

Feilongus has only one species, *Feilongus youngi*, until now. According to Wang et al. (2005), the diagnosis of *Feilongus youngi* includes the combination of two sagittal cranial crests, a parietal crest with a rounded posterior margin, and a protruding upper jaw that is about 10% longer than the lower jaw. The presence of sagittal cranial crests is an important diagnostic characteristic for *Feilongus youngi*, but no clues of cranial crest can be observed in DNHM-D3068. The specimen was probably damaged during the preparation process because the sediments along the upper jaw of DNHM-D3068 had been deeply cut down and totally taken off. On the other hand, if DNHM-D3068 does not in fact possess any cranial crest, then the presence of cranial crests in *Feilongus youngi* could be an expression of sexual dimorphism, like that of *Darwinopterus* (Lü et al., 2011, 2012). As to the other diagnostic characteristic, a "protruding upper jaw

Table 2 Comparison of skull length and tooth number between DNHM-D3068, *Feilongus youngi* (Wang et al., 2005) and *Moganopterus zhuiana* (Lü et al., 2012)

Taxa	Skull length (mm)	Tooth number
DNHM-D3068	320	78
Feilongus youngi	390~400	76
Moganopterus zhuiana	750	64

Table 1 Measurements of teeth width and dentition spaces in *Feilongus* sp. (DNHM-D3068) (in mm)

No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Teeth width (mm)	1.34 (U)	1.84 (U)	1.99 (U)		1.79 (U)	1.79 (U)	1.91 (U)	1.92 (U)	2.04 (U)	2.06 (U)	1.83 (U)	2.34 (U)	3.09 (U)	2.17 (U)	2.39 (U)	1.38 (U)	1.23 (U)	1.05
	1.74 (L)	2.71/2 (L)	1.69 (L)	1.89 (L)	1.23 (L)	1.45 (L)	1.93 (L)	1.54 (L)	1.32 (L)	1.70 (L)	2.01 (L)	1.67 (L)	1.45 (L)	1.60 (L)	1.40 (L)	1.37 (L)	0.71 (L)	(U)
Dentition Spaces (mm)	2.85 (U)	2.33 (U)	7.04 (U)			3.95 (U)	2.66 (U)	6.54 (U)	3.96 (U)	3.06 (U)	2.86 (U)	3.94 (U)	2.80 (U)	3.01 (U)	3.36 (U)	6.94 (U)	5.28 (U)	
	3.29 (L)	3.24 (L)	2.33 (L)	1.84 (L)	2.14 (L)	2.72 (L)	3.58 (L)	1.47 (L)	3.47 (L)	3.19 (L)	4.67 (L)	3.15 (L)	4.86 (L)	3.97 (L)	5.97 (L)	19.56 (L)		

Notes: U, upper jaw; L, lower jaw.

that is about 10% longer than the lower jaw", this also is not observed in DNHM-D3068. Contrarily, the upper jaw and the lower jaw of DNHM-D3068 are almost the same length and their anterior tips could have met when the jaws were closed.

Even now DNHM-D3068 cannot be assigned to *Feilongus* according to the diagnosis given by Wang et al. (2005). However, DNHM-D3068 is most closely related to *Feilongus* in that both the skulls are low and long, and of a similar size; the rostrums are extremely elongated; the curved needle-shaped teeth are long and sharp and confined far anterior to the nasoantorbital fenestra with a similar number; the posterior teeth are slightly smaller than the anterior teeth. Both *Feilongus youngi* and DNHM-D3068 were preserved only with skulls and mandibles or several cervical vertebrae. It is hard to determine whether there are different characteristics between their poscranial skeletons. Therefore, DNHM-D3068 can be taken as a new individual of a species of *Feilongus*.

Then we can discuss further one of the diagnostics listed by Wang et al. (2005), the "protruding upper jaw that is about 10% longer than the lower jaw", based on the naturally preserved condition of DNHM-D3068. Is it the fact that the toothed upper jaw is about 27 mm longer than the lower jaw? What is the function of the extra part of upper jaw since it bears long, curved needle-shaped teeth? Considering the teeth morphology and teeth number of *Feilongus youngi*, it should be a predator. Could the extra part of the upper jaw catch prey with its single sided teeth? How could it eat its prey if the extra part of the upper jaw caught the prey? It is difficult to explain the function of this kind of jaws as described. A reasonable explanation would be that is not a correct interpretation and instead, the holotype was probably caused by the preservation condition. That means that the upper jaw was probably elongated during the fossilization process since the surrounding bones of the braincase are preserved between the upper and lower jaws far anteriorly. Therefore, the nature of the jaws is not suitable here to be one of the generic diagnostic characteristics of *Feilongus.*

No cervical vertebrae have been preserved in the type specimen of *Feilongus youngi*, whereas four cervical vertebrae are preserved in DNHM-D3068, and the ratio of their length to width is greater than 5, which is closely in accordance with the diagnosis of the Moganpterinae (Lü et al., 2012). Therefore, the state of the cervical vertebrae can be added to the diagnostic characters of *Feilongus*.

5 Conclusions

Specimen DNHM-D3068 is more similar to *Feilongus* than to any other pterosaurs, and represents a new smaller individual of this genus with similarities to *F. youngi*.

Based on the new specimen and its natural preservation, the generic diagnosis of *Feilongus* can be amended as follows: long, curved, needle-shaped teeth confined far anterior to the nasoantorbital fenestra; the posterior teeth are slightly smaller than the anterior teeth; cervical vertebrae elongated with the ratio of length to width greater than 5; tooth number is about 78; two sagittal cranial crests. It further approves that the "protruding upper jaw that is about 10% longer than the lower jaw" is not one of the diagnostic characters of *Feilongus* (Lü et al., 2006a, 2012). So, this characteristic should not be used as one of the diagnostic of *Feilongus*. Furthermore, the new specimen provides important cervical vertebrae diagnostic characters for *Feilongus*.

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