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辽西早白垩世九佛堂组两种新的翼手龙类化石[1)]

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摘要 简要报道了辽西热河群上部九佛堂组两件新的翼手龙类化石,即夜翼龙科(Nyctosauridae)的张氏朝阳翼龙(新属、新种) *Chaoyangopterus zhangi* gen. et sp. nov. 和古魔翼龙科(Anhangueridae)的顾氏辽宁翼龙(新属、新种) *Liaoningopterus gui* gen. et sp. nov.。前者为保存较完整的化石骨架,后者为一大型翼龙的头骨和部分头后骨骼化石。朝阳翼龙是夜翼龙科在亚洲大陆的首次确切的化石记录,也是层位最低和保存最完整的化石骨架。朝阳翼龙具有 4 节翼指骨,手指爪粗大弯曲,这些发现补充和修正了前人认为的夜翼龙科只有 3 节翼指骨,手指爪退化缺失等一些重要的形态学特征。朝阳翼龙与该科的 *Nyctosaurus gracilis* 头后骨骼相比,具有许多不同的特征,如胫骨特长,远长于股骨,翼掌骨和第 1 翼指骨相对较短,肩胛骨短于乌喙骨等。辽宁翼龙是我国已发现的个体最大的翼龙化石,发育前上颌骨和齿骨弧形脊突这一古魔翼龙科的重要鉴别特征。与该科的其他成员相比,辽宁翼龙上、下颌的牙齿较少,仅分布在其前部,齿列约占上、下颌长度的 1/2。上颌第 1、3 齿小,第 2、4 齿巨大,其中第 4 齿最大,为已知翼龙中最大的牙齿。牙齿具有明显的替换现象。夜翼龙科的成员仅分布于美洲大陆的晚白垩世地层中,而古魔翼龙科的成员则是南美巴西早白垩世 Santana 组(Aptian/Albian)最重要的翼龙类群之一。九佛堂组新的翼龙化石的发现,进一步证明了热河群存在下部义县组和上部九佛堂组两个不同的翼龙化石组合,下部组合以进步的翼手龙亚目的成员为主,同时也发现了少量比较原始的喙嘴龙亚目的分子,与 Solnhofen 灰岩(Tithonian)的翼龙组合具有一定的相似性。上部翼龙组合均为翼手龙亚目的成员,该组合与巴西 Santana 组的具有非常相似的组合特征,Santana 翼龙组合中最重要的两大类群,即无齿的古神翼龙科(Tapejaridae)和具齿的古魔翼龙科的成员在九佛堂组均已发现。九佛堂组(Aptian)的时代可能略早于 Santana 组。

关键词 辽宁朝阳,早白垩世,九佛堂组,热河群,翼手龙亚目,夜翼龙科,古魔翼龙科
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TWO NEW PTERODACTYLOID PTEROSAURS FROM THE EARLY CRETACEOUS JIUFOTANG FORMATION OF WESTERN LIAONING, CHINA

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Abstract In this paper we report two new pterodactyloid pterosaurs from the Jiufotang Formation in

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western Liaoning Province of northeast China. They are *Chaoyangopterus zhangi* gen. et sp. nov. (Nyctosauridae) and *Liaoningopterus gui* gen. et sp. nov. (Anhangueridae). The former not only represents the first such record in Asia but also the earliest record and most complete skeleton of the family. Some revisions of the family are made, such as having four wing digits and well-developed manual digits I~ III. *Liaoningopterus* is the largest pterosaur ever discovered in China; its teeth also represent the largest known from any pterosaurs. Discoveries of two more pterosaurs from the Jiufotang Formation further show that two pterosaur assemblages could be recognized in the Jehol Group, represented by the Yixian Formation and Jiufotang Formation, respectively. The pterosaur assemblage of the Jiufotang Formation shows a lot resemblance to that of the Early Cretaceous Santana Formation (Aptian/Albian) such as the Tapejaridae and Anhangueridae. The age of the Jiufotang Formation (Aptian) is slightly older than the Santana Formation.

Key words Chaoyang, Liaoning, Early Cretaceous, Jiufotang Formation, Jehol Group, Pterodactyloidea, Nyctosauridae, Anhangueridae

In recent years pterosaurs have been discovered from the Jiufotang Formation, representing the second horizon of the Jehol Group preserving pterosaurs. One of them has been published and named *Sinopterus* referable to the pterodactyloid family Tapejaridae (Wang and Zhou, 2002). These fossils are associated with beautifully preserved birds (Zhou and Zhang, 2001, 2002 a, b) and feathered dinosaurs (Xu et al., 2000). This paper will report two more new genera of pteryodactyloid pterosaurs from the Jiufotang Formation in Chaoyang, western Liaoning Province. The materials are represented by incomplete skeletons and are referred to the Nyctosauridae and Anhangueridae, respectively.

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Nyctosauridae Nicholson et Lydekker, 1889
Chaoyangopterus gen. nov.
Chaoyangopterus zhangi gen. et sp. nov.

(Fig. 1; Table 1)

Diagnosis Medium to large-sized pterodactyloid. Wingspan about 1. 85m. Skull long and low, with a pointed rostrum. Edentulous. Manual digits I~ III robust, wing claws large and curved. Wing digit comprising 4 phalanges, progressively shorter toward the distal end. Wing metacarpal and first phalanx of the wing digit relatively short compared to *Nyctosaurus gracilis*. Ratios of tibia of femur and tibia to humerus 1. 5 and 2. 2, respectively, compared to 0. 5 and 1. 5 in *N. gracilis*. Ratio of forelimb (humreus+ ulna+ wing metacarpal) to hindlimb (femur+ tibia+ metacarpal III) is 1. 1 compared to 1. 5 in *N. gracilis*.

Holotype An incomplete skeleton including anterior skull, a nearly complete lower jaw, most cervical vertebrae, pectoral girdle, forelimb, pelvis, and hindlimb. Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V 13397.

Locality and horizon Gonggao, Dapingfang, Chaoyang, Liaoning Province; Jiufotang Formation, late Early Cretaceous (Aptian).

Etymology Generic names is derived from the locality "Chaoyang"; species name is dedicated to Mr. Wanlian Zhang, a senior reporter of the Chaoyang Daily, who has contributed a lot to the protection of the fossil localities and the expedition of the Liaoxi Project of the IVPP in Chaoyang.

Description The skull is laterally preserved, with a preserved length of 195mm, the estimated total length of the skull is 270mm. The premaxilla is fused with the anterior maxilla. Teeth are absent on the jaws. The anterior part of both the upper and lower jaws are long and pointed. The anterior half of the lower jaw has a straight ventral margin but curves upward near the middle point. The ventral margin of the premaxiall is straight; the dorsal margin progressively becomes higher posteriorly until the nasopreorbital where it becomes deep.

There are about 7~ 8 cervical vertebrae. They are robust and long. The 3rd through 7th (or 4th to 8th) cervicals are in articulation; their length are 27mm, 40mm, 42mm, 42mm and 42mm,

respectively. Compared to *N. gracilis* (Williston, 1903) the vertebrae are long. The estimated total length of the neck is about 230mm. Two isolated dorsal vertebrae are preserved; the centrum is small while the neural crest is large. One caudal vertebra is preserved, neural crest is not preserved, and its length is about the width (7.5mm).

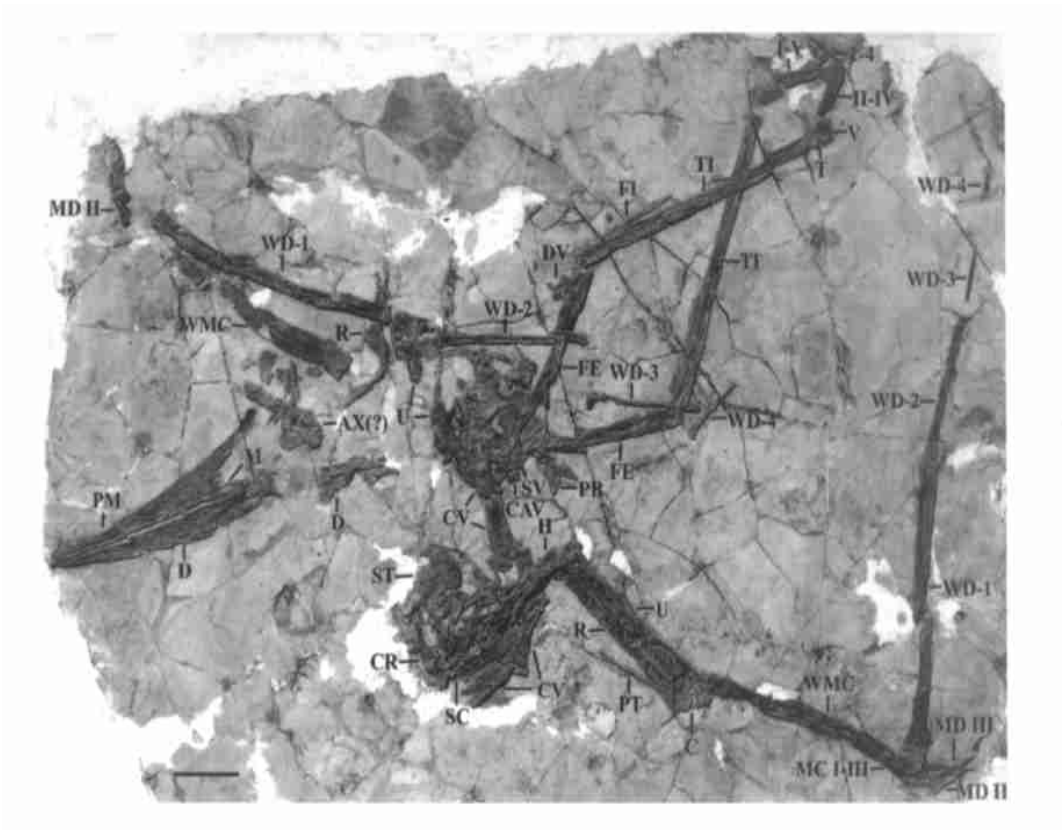

图 1 张氏朝阳翼龙(新属、新种)正型标本(IVPP V 13397),比例尺 5cm

Fig. 1 *Chaoyangopterus zhangi* gen. et sp. nov. (holotype, IVPP V 13397), scale bar 5cm

AX, axis 枢椎; C, carpals 腕骨; CAV, caudal vertebra 尾椎; CR, coracoid 乌喙骨; CV, cervical vertebra 颈椎; D, dentary 齿骨; DV, dorsal vertebra 背椎; FE, femur 股骨; FI, fibula 腓骨; H, humerus 肱骨; M, maxilla 上颌骨; MC Ⅰ ~ Ⅲ, metacarpals Ⅰ ~ Ⅲ 第Ⅰ ~ Ⅲ掌骨; MD Ⅰ ~ Ⅲ, manual digits Ⅰ ~ Ⅲ 第 1~3 指骨; PB, prepubis 前耻骨; PM, premaxilla 前上颌骨; PT, pteroid 翅骨; R, radius 桡骨; SC, scapula 肩胛骨; ST, sternum 胸骨; SV, sacral vertebra 荐椎; T, tarsals 跗骨; TI, tibia 胫骨; U, ulna 尺骨; WD-1~4, 1~4 phalanges of wing digit 第 1~4 翼指骨; WMC, wing metacarpal 翼掌骨; Ⅰ ~ Ⅴ, metatarsals Ⅰ ~ Ⅴ 第 1~5 骨; 1~4, pedal digits 1~4 第 1~4 趾骨

The sternum is small and longer than wider; it is fan-shaped but incomplete; the keel is long and low, similar to that of *N. gracilis* (Williston, 1903).

The scapula and coracoid are incompletely fused. The scapula is slightly longer than the coracoid. Both bones are curved with expanded extremities.

The humerus, ulna, wing metacarpal and the first phalanx of the wing digit are progressively shorter. Phalanges of the wing digit also become shorter distally. The ratios of the ulna, wing metacarpal and first phalanx of wing digit to humerus are 1.4, 2 and 2.1, respectively. The second phalanx of the wing digit is shorter than the ulna. Ratio of forelimb (humreus + ulna + wing metacarpal) to hindlimb (femur + tibia + metacarpal Ⅲ) is about 1.1. The length of the wing digit is 4.8 and 2.4 times that of the humerus and the wing metacarpal, respectively.

表 1　张氏朝阳翼龙(新属、新种)(IVPP V 13397)主要骨骼测量

Table 1　Measurements of major skeleton elements of the holotype (IVPP V 13397) of *Chaoyangopterus zhangi* gen et sp. nov.　(mm)

	Left(左)	Right(右)
Scapula 肩胛骨	—	63*
Coracoid 乌喙骨	—	50*
Humerus 肱骨	—	93
Ulna 尺骨	—	133
Radius 桡骨	—	129
Pteroid 翅骨	71*	—
Wing metacarpal 翼掌骨	160**	185
Metacarpals Ⅰ – Ⅲ第Ⅰ – Ⅲ掌骨	—	135**
First phalanx of manual digit Ⅰ 第Ⅰ指第 1 指节	15**	17
Second phalanx of manual digit Ⅰ 第Ⅰ指第 2 指节(爪)	16**	18
First phalanx of manual digit Ⅱ 第Ⅱ指第 1 指节	23	24
Second phalanx of manual digit Ⅱ 第Ⅱ指第 2 指节	19	18
Third phalanx of manual digit Ⅱ 第Ⅱ指第 3 指节(爪)	18.5	18
First phalanx of manual digit Ⅲ第Ⅲ指第 1 指节	—	23
Second phalanx of manual digit Ⅲ 第Ⅲ指第 2 指节	—	6
Third phalanx of manual digit Ⅲ 第Ⅲ指第 3 指节	—	17
Fourth phalanx of manual digit Ⅲ 第Ⅲ指第 4 指节(爪)	—	18
First phalanx of wing digit 第 1 翼指骨	199	200
Second phalanx of wing digit 第 2 翼指骨	120	82**
Third phalanx of wing digit 第 3 翼指骨	78	34**
Fourth phalanx of wing digit 第 4 翼指骨	48**	12**
Femur 股骨	131	133
Tibia 胫骨	208	205
Fibula 腓骨	67**	76
Metatarsal Ⅰ 第Ⅰ 骨	46	—
Metatarsal Ⅱ 第Ⅱ 骨	52	44**
Metatarsal Ⅲ第Ⅲ 骨	44	43
Metatarsal Ⅳ第Ⅳ 骨	32**	42.5
Metatarsal Ⅴ 第Ⅴ 骨	—	15**
First phalanx of pedal digit Ⅰ 第Ⅰ趾第 1 趾节	10**	—
Second phalanx of pedal digit Ⅰ 第Ⅰ趾第 2 趾节(爪)	—	—
First phalanx of pedal digit Ⅱ 第Ⅱ趾第 1 趾节	10	—
Second phalanx of pedal digit Ⅱ 第Ⅱ趾第 2 趾节	5**	—
Third phalanx of pedal digit Ⅱ 第Ⅱ趾第 3 趾节(爪)	—	—
First phalanx of pedal digit Ⅲ第Ⅲ趾第 1 趾节	9**	—
Second phalanx of pedal digit Ⅲ第Ⅲ趾第 2 趾节	—	—
Third phalanx of pedal digit Ⅲ 第Ⅲ趾第 3 趾节	—	—
Fourth phalanx of pedal digit Ⅲ 第Ⅲ趾第 4 趾节(爪)	—	—
First phalanx of pedal digit Ⅳ 第Ⅳ趾第 1 趾节	12**	—

* indicates estimated or approximate value; ** indicates preserved length.

The ulna is straight, robust and slightly longer than the radius; it is markedly longer than the humerus. Two proximal carpals appear to be fused. The pteroid is robust and consistent throughout its length. Metacarpals are extremely long, but slightly shorter than the first phalanx of wing digit. Wing metacarpal is strong. Metacarpals Ⅰ~ Ⅲ are more slender and shorter than the wing metacarpal and more slender than manual digits. Wing claws are extremely long, sharp and pointed. Compared to the radius, the first phalanx of the wing digit is very long, the second phalanx is slightly shorter, and the third and fourth ones are significantly shorter.

The prepubic bone is foot-shaped. The hindlimb is long; especially the tibia is about 1.6 times the length of the femur. The fibula is slightly over one third the length of the tibia. Metatarsals Ⅰ–Ⅳ are straight and parallel to each other; among them, the second is the longest, the first is relatively short, and the third and fourth about the same length but are shorter than the first and second. Metatarsal Ⅲ is about 23.5%, 33% and 21% the length of the wing metacarpal, femur and tibia, respectively. Metatarsal Ⅴ is significantly reduced. Two free tarsals are preserved.

Anhangueridae Campos et Kellner, 1985

***Liaoningopterus* gen. nov.**

***Liaoningopterus gui* gen. et sp. nov.**

(Fig. 2)

Diagnosis Large-sized pterodactyloid. Estimated skull length 610mm, wingspan about 5m. Skull low and long. Premaxilla and dentary equipped with sagittal crest. Teeth only restricted to the proximal part of the upper and lower jaws. Toothed portion of the jaws does not extend posteriously to one third of the nasopreorbiotal; it is about half the length of the skull. Teeth near the rostal end of the jaws are huge in size. The fourth tooth of the premaxilla is the largest, and the first and third are much smaller than the second and the fourth ones.

Holotype An incomplete skull including premaxilla, maxilla, jugal, quadrate, lower jaw, most teeth and some postcranial bones such as cervicals and wing digit bone. Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V13291.

Locality and horizon Xiaoyugou, Lianhe, Chaoyang, Liaoning Province; Jiufotang Formation, later Early Cretaceous (Aptian).

Etymology Generic name is derived from "Liaoning"; species name is dedicated to Prof. Zhiwei Gu, a distinguished Chinese invertebrate paleontologist, for his pioneering contribution to the study of the Jehol Biota.

Description The skull is low and long, its estimated length is 610mm. Teeth are extremely large, representing the largest ever known from pterosaurs. The anterior premaxilla has a well-developed sagittal crest. The premaxillary sagittal crest is long and low, and the anterior and posterior margins are symmetrical. The crest begins from the 5th tooth of the premaxilla, reaches its highest point at the 9th tooth and ends at the 12th tooth, with a total length of 120mm and maximum height of 17mm. The maxilla is toothed and has a straight ventral margin.

The jugal has a slender anterior process, which is nearly perpendicular to the ascending process; the posterior process of the jugal is robust and directed upward. The quadrate is long. The lower jaw is fractured in the middle, missing some segments, yet most of the teeth are preserved. The anterior lower jaw has a ventral sagittal crest.

Teeth are only found in the anterior half of the upper and lower jaws. The toothed portion of the jaws does not extend past one third of the nasopreorbital. There are about 20 teeth on the upper jaw and only 13-14 on the lower jaw. Teeth on the anterior jaws are extremely large in size while the posterior teeth are small. The 4th tooth of the upper jaw is the largest; it is about 81mm, being the largest known pterosaur tooth. The maximum tooth of the lower jaw is 41mm. Teeth generally become smaller posteriorly. The 1st and 3rd teeth are smaller than the 2nd and 4th teeth of the upper jaw. Posterior teeth are robust, posteriorly curved. Small replacement teeth are also preserved in the upper jaw, they are numbered 3rd, 5th, 7th, 9th and 11th.

Only one cervical vertebra is preserved; the centrum is about 46mm long and 34mm high. One phalanx recognized as the first phalanx of the wing digit is robust; it is about 500mm long.

Comparisons and discussions Members of the Nyctosauridae have previously been known only in the Late Cretaceous of America (Williston, 1902, 1903; Price, 1953; Wellnhofer, 1978, 1991a), while those of the Anhangueridae have been known in the Early Cretaceous Santana Formation(Aptian/Albian) in Brazil and other Cretaceous deposits (Wellnhofer, 1991a, b; Kellner

and Tomida, 2000).

图 2　顾氏辽宁翼龙(新属、新种) 正型标本(IVPP V 13291), 比例尺 5cm
Fig. 2　*Liaoningopterus gui* gen. et sp. nov. (holotype, IVPP V 13291), scale bar 5cm
J, jugal 颧骨; L, lacrimal 泪骨; PMC, premaxillary crest 前上颌骨弧形脊突;
Q, quadrate 方骨; RB, rib 肋骨; TE, teeth 牙齿(for other abbreviations see Fig. 1)

Chaoyangopterus represents the second edentulous pterosaur from the Jehol Biota. It can be easily distinguished from such big edentulous forms as the Pteranadontidae and Azhdarchidae. It can be referred to the Nyctosauridae, representing the lowest occurrence of the family. Currently, this family comprises only one genus and 2 species (Wellnhofer, 1991a): *Nyctosaurus lamegoi* (Price, 1953) and *N. gracilis* (Marsh, 1876; Williston, 1903; Miller, 1972), the former is represented only by an incomplete humerus. The postcranial bones of *Chaoyangopterus* can be distinguished from that of *N. gracilis* by its extremely long tibia, relatively short wing metacarpal and first phalanx of wing digit, scapula shorter than coracoid etc.

Chaoyangopterus is smaller than other members of the Nyctosauridae. For instance, *N. lamegoi* has an estimated humerus length of 165mm and wingspan of 3. 5m. The humerus of *N. gracilis* is 87mm long, with a wingspan of 2. 4- 2. 9m(Wellnhofer, 1978), compared to 93mm and 1. 85m, respectively in *Chaoyangopterus*.

The wing digit of *Chaoyangopterus* has 4 phalanges, and the wing claws are large and curved.

Although it has been proposed that the wing digit of Nyctosauridae has only 3 phalanges (Brown, 1986), there is yet no convincing evidence supporting this conclusion, and the discovery of *Chaoyangopterus* shows that the small number was most likely due to lack of complete preservation.

Liaoningopterus can be easily referred to the family Anhangueridae by the sagittal crest on the maxilla and dentary. Teeth are present only on the anterior half of the jaws of *Liaoningopterus*. Currently this family comprises 4 genera and 9 species. The 4th tooth of *Liaoningopterus* is about 1.3 times the largest tooth of *A. piscator* (Kellner and Tomida, 2000) although the skull of the latter is larger. *Liaoningopterus* has replacement teeth, suggesting the replacement of teeth is common and probably continues throughout the development. The size change of the teeth of *Liaoningopterus* is also similar to that of *Anhanguera* (Kellner and Tomida, 2000).

The first phalanx of the wing digit of *Liaoningopterus* is very robust, and about 500mm long. The estimated wingspan of this pterosaur is about 5m, probably representing the largest known pterosaur from China.

Both *Chaoyangopterus* and *Liaoningopterus* are probably piscivorous as indicated by the long and pointed snout, as in *Sinopterus* (Wang and Zhou, 2002), *Tapejara wellnhoferi* (Wellnhofer and Kellner, 1991) and *Thalassodromeus* (Kellner and Campos, 2002). Abundant fossil fishes such as *Jinanichthys*, *Peipiaosteus*, *Protopsephurus* and *Sinamia* from the locality provide further evidence for this. Further, aquatic reptiles might also be fed by these pterosaurs.

The discovery of two more pterosaurs from the Jiufotang Formation also has important implications for the discussion of the biostratigraphy of this region. In particular, the Jiufotang Formation shares with Santana Formation members of both the Anhangueridae and Tapejaridae, the two most important pterosaur groups of the Santana Formation, suggesting that they share a similar pterosaur assemblage.

Until now, two pterosaur assemblages can be clearly recognized from the Jehol Group. The upper one is represented by the Jiufotang Formation and comprises only advanced pterodactyloids including *Sinopterus* (Wang and Zhou, 2002), *Chaoyangopterus* and *Liaoningopterus* described above; the lower one is represented by the Yixian Formation and comprises mainly pterodactyloids such as *Haopterus* (Wang and L , 2001) and *Eosipterus* (Ji and Ji, 1997) of the Pterodactylidae and only a very few rhamphorhynchoids as *Dendrorhynchoides* (Ji and Ji, 1998; Ji et al., 1999) and *Jeholopterus* (Wang et al., 2002). The age of the lower assemblage has been dated as 125Ma (Smith et al., 1995; Swisher et al., 1999, 2002; Wang et al., 2001). The lower pterosaur assemblage is probably a transition between that of the Solnhofen and the Santana Formation while the upper assemblage is basically comparable to the Santana pterosaur assemblage, but is probably slightly older (Wang and Zhou, 2002).

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