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Discovery of a pterodactylid pterosaur from the Yixian Formation of western Liaoning, China

WANG Xiaolin[1,2] & LÜ Junchang[1,3]

1. Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China;
2. College of Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China;
3. Department of Geological Sciences, Southern Methodist University, Dallas, TX 75275, USA

Abstract **A well-preserved pterosaur with nearly complete skull is described from the Lower Cretaceous Yixian Formation at Sihetun in western Liaoning. It is characterized by a low and long crestless skull, slender and pointed teeth, long metacarpal, nearly equal length of metatarsals I—III and short pedal digit V. It is referred to a new genus and species of the family Pterodactylidae: *Haopterus gracilis* gen. et sp. nov. This is the first pterosaur with a nearly complete skull from the Jehol Biota; it also represents the first non-controversial fossil record of Pterodactylidae in Asia. *Haopterus* is more derived than *Pterodactylus* from the Late Jurassic Solnhofen in Germany. This discovery extends the distribution of the family Pterodactylidae from Europe and Africa to Asia and its latest occurrence from the Late Jurassic to the Early Cretaceous. The discovery of *Haopterus gracilis* provides further evidence for the study of the origin and radiation of the Jehol Biota; it also sheds new light on the evolution and distribution of pterosaurs in the late Mesozoic.**

Keywords: western Liaoning, Early Cretaceous, Yixian Formation, Pterodactylidae.

Western Liaoning Province is most notable for the excellent preservation of the famous Jehol Biota. Recently, a lot of important vertebrate fossils[1,2] including the primitive bird *Confuciusornis*[3] and various feathered dinosaurs[4—6] have been discovered from the lacustrine deposits of the third member of the Early Cretaceous low Yixian Formation at Sihetun, Beipiao, Chaoyang[1,2]. These fossils form a unique vertebrae assemblage from the terrestrial lake deposits in the Mesozoic and represent an important biological radiation event in the Early Cretaceous[2]; it provides important evidence for the study of the origin and early radiation of major vertebrate groups such as birds.

A total of more than 10 individual pterosaurs have recently been discovered from the lower Yixian Formation in Sihetun areas, western Liaoning Province. Most of them were referred to *Eosipterus*[7] and *Dendrorhynchoides*[8], respectively; others remain unnamed. None of these specimens preserved the skull, therefore their phylogenetic position remain controversial[7,8]. A new specimen of pterosaur was collected during the field season of the IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) in 1998, it contains a nearly complete skull and most of the postcranial bones. It is the first indisputable remains of the family Pterodactylidae from Asia, and extends the distribution from Europe and Africa to Asia and its latest occurrence from the Late Jurassic to the Early Cretaceous. The discovery of *Haopterus gracilis* gen. et sp. nov. provides further evidence for the study of the evolution and distribution of pterosaurs in the late Mesozoic.

1 Systematic paleontology

Order Pterosauria Kaup, 1834
Suborder Pterodactyloidea Plieninger, 1901
Family Pterodactylidae Bonaparte, 1838
Genus *Haopterus* gen. nov.
Species *Haopterus gracilis* gen. et sp. nov.

Diagnosis. Small to medium-sized pterosaur. Maximum wingspan 1.35 m. Skull length 145 mm. Skull low and long; rostrum pointed; crest absent at the rear of the skull; nasopreorbital opening elongate and elliptical. 12 pointed and posteriorly inclined teeth in both upper and lower jaws. Teeth of the premaxilla (first 3 teeth of the upper jaw) slender. Fourth and more posterior teeth constricted at the base. Teeth extend posteriorly toward the middle of the nasopreorbital opening, about 66.4% of the lower jaw equipped with teeth. Forelimb robust. Humerus short, robust and straight, delto-pectoral crest expanded

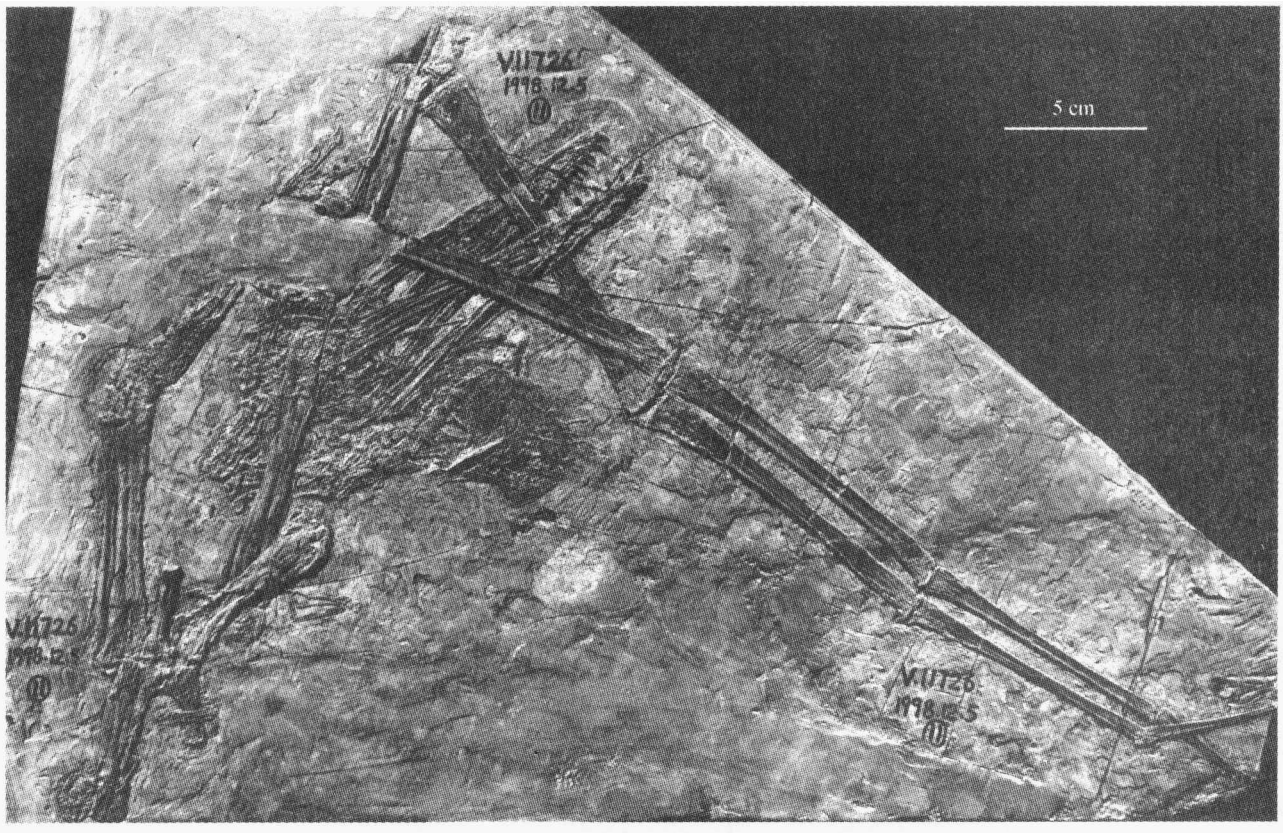

Fig. 1. *Haopterus gracilis* gen. et sp. nov. (IVPP V11726, holotype).

and semicircular. Wing metacarpal long and about 1.3 times that of the humerus. Phalanges I—III of the wing digit longer than wing metacarpal. Ulna and phalanx I of wing digit 1.1 and 1.4 times that of the wing metacarpal, respectively. Metatarsals reduced; Metatarsals I—III of nearly equal length; metatarsals IV and V reduced and short; Length of metatarsal I about 18.7% that of wing metacarpal. Sternum fan-shaped; its length equals its width; keel well-developed.

Holotype. A nearly complete skeleton that contains a complete skull and pectoral girdle, forelimbs, sternum, cervical, dorsal, metatarsals and digits. Institute of Vertebrate Paleontology and Paleoanthropology specimen number: IVPP V11726 (figs. 1 and 2).

Etymology. The genus name is dedicated to Prof. Yichun Hao, a distinguished Chinese paleontologist who has contributed significantly to the study of the Jehol Biota; the species name reflects both the beautiful preservation and the tiny metatarsals of the holotype.

Horizon and locality. Locality 1 at Sihetun, Shangyuan, Beipiao, western Liaoning; Jianshangou Bed of the lower Yixian Formation[1,2], late Valanginian (age of Jurassic/Cretaceous boundary is 135 Ma) or Barremian (Jurassic/Cretaceous boundary is 144 Ma) of the Early Cretaceous.

Description. A nearly complete subadult individual with skull but lacks pelvis, femur, tibia, fibula, caudal and sacral. Both ends of long bones are less well ossified. Measurements of major skeletal elements are listed in table 1.

Table 1 Measurements of skeletal elements of the holotype (IVPP V11726) of *Haopterus gracilis* gen. et sp. nov.

Name	Left/mm	Right/mm
Humerus	70	60+
Ulna	101	102
Scapula	30	–
Coracoid	34	–
Wing metacarpal	89	91
First phalanx of wing digit	141	138
Second phalanx of wing digit	119	119
Third phalanx of wing digit	95	96
Fourth phalanx of wing digit	44+	45+
Pteroid	–	34
Metatarsal I	17	17
Metatarsal II	17	17
Metatarsal III	17	17
Metatarsal IV	13	13
Metatarsal V	5	–
Sternum	45 (length)	46 (width)
Skull	145	
Lower jaw	128	85 (with dentition)

Skull. The skull is lateroventrally preserved. It is

low and 145 mm long. The rostrum is pointed. The crest is absent at the rear of the skull. There are 12 teeth in both the upper and lower jaws. The 5 front teeth are slender, more posterior teeth are constricted at the base. Teeth number is less than that of *pterodactylus*[9].

The premaxilla and the maxilla are fused; no suture is recognizable between these two bones. Teeth extend from the anterior end to the middle of the nasopreorbital opening. Teeth are pointed and posteriorly inclined. Teeth of the premaxilla (first 3 teeth of the upper jaw) represent tiny replaceable teeth. The nasopreorbital opening is elongate and elliptical and 40mm long, which is 27.6% that of the skull length. The nasal is small and nearly vertical near the dorso-posterior margin of the nasopreorbital opening. The nasal overlaps the adlacrimal. The frontal is missing. Most of the bones of the posterior skull are crushed and undistinguishable, but the left squamosal and jugal are recognizable.

The posterior part of the lower jaw is toothless. The lower jaw with dentation is 85 mm long, which is 66.4% of the total length of the lower jaw. The teeth of the lower jaw are similar to those of the upper jaw in size, shape and pattern; the first tooth is slightly inclined anterolaterally. The angular and the surangular are tightly attached to the

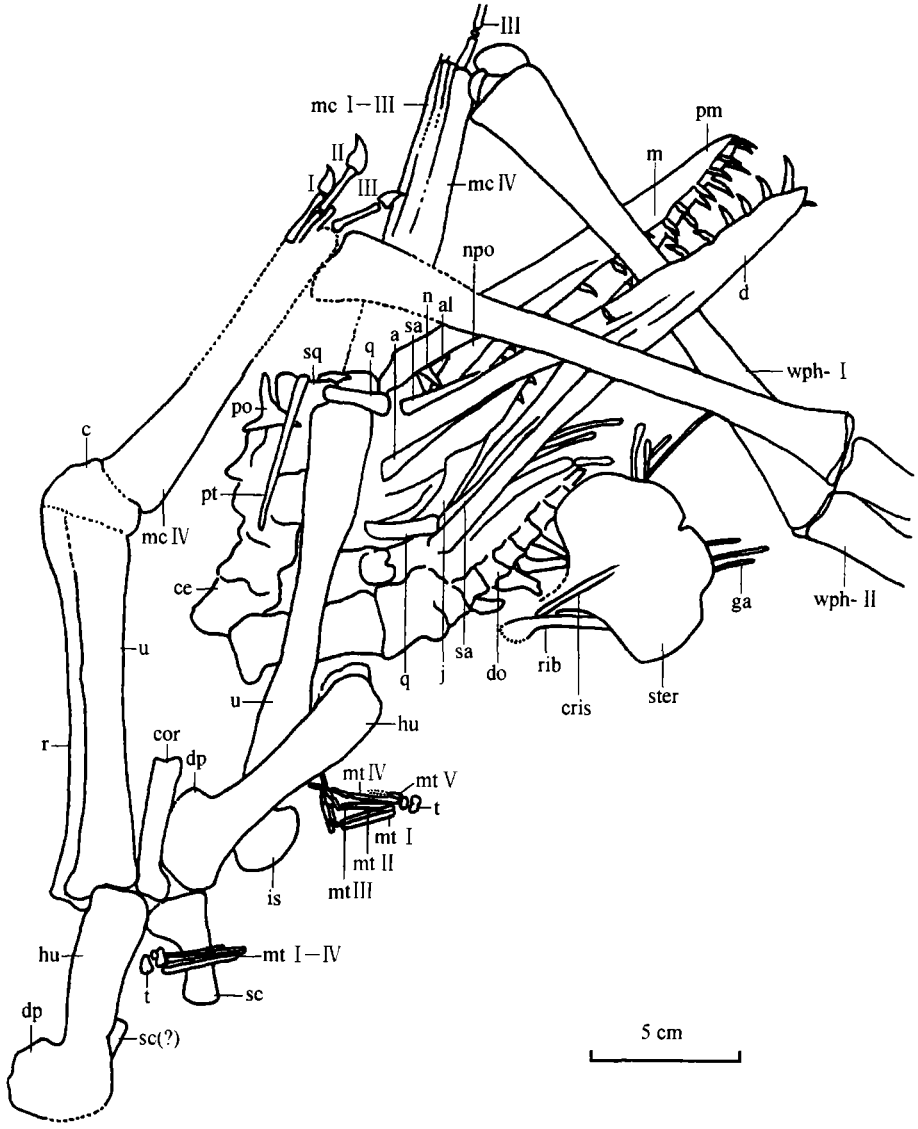

Fig. 2. The outline of the skeleton of *Haopterus gracilis* gen. et sp. nov. (IVPP V 11726, holotype). a, Angular; al, adlacrimal; c, carpal; ce, cervical vertebrae; cor, coracoid; cris, cristospine; d, dentary; do, dorsal vertebrae; dp, delto-pectoral crest; ga, gastralia; hu, humerus; is, ischium; j, jugal; m, maxilla; mc I—IV, metacarpals I—IV; mt I—IV, metatarsals I—IV; n, nasal; npo, nasopreorbital opening, pm, premaxilla; po, postorbital; pt, pteroid; q, quadrate; r, radius; ri, rib; sa, surangular; sc, scapula; sq, squamosal; ster, sternum; t, tarsal; u, ulna; wph I—IV, wing phalanges I—IV; I—III, fingers I—III.

dentary. The quadrate is long, plate-shaped and slightly curved dorsally. The hyoid is slender and 52 mm long.

Vertebral column. Cervical and dorsal vertebrae are preserved, but sacrals and caudals are missing. Cervical vertebrae are crushed together with the posterior skull bones. The anterior 8 dorsal vertebrae are preserved, their combined length is 52 mm. The dorsal vertebra is procoelous. The anterior dorsals are short and become progressively elongate distally. Some incomplete ribs and isolated gastralia are preserved.

Pectoral girdle and forelimb. The left pectoral girdle is ventrally preserved while the right side is dorsally preserved. The left coracoid is completely preserved; it is rod-like, straight and thick-walled; the proximal end is robust with a procoracoid process in articulation with the scapula; distally it is not expanded, and has an obvious articulation with the sternum; ventrally it has a longitudinal groove which becomes wider distally. The left scapula is complete; it is thin, plate-shaped; its length is about 88.2% that of the scapula; distally the scapula is expanded and robust.

Both the left and right humeri lack the proximal end. The humerus is straight; the delto-pectoral crest is semicircular and expanded laterally; the left humerus is in articulation with the coracoid and scapula.

The right radius, ulna and the left ulna are well preserved and in articulation with the humerus and the carpals. The radius and the ulna are straight, thin-walled and expanded at both ends. The radius is slender and slightly longer than the ulna.

The carpals are small; left carpals are crushed together with the posterior skull bones and cervical vertebrae. The left pteroid is well preserved; it is slender and straight but does not taper toward the distal end.

The metacarpals are not completely preserved. Metacarpals Ⅰ—Ⅳ are nearly of equal length, they are slightly longer than the humerus but are shorter than the ulna. Metacarpals Ⅰ—Ⅲ are slender; they are parallel and tightly attached to metacarpal Ⅳ. Metacarpal Ⅳ (wing metacarpal) is robust; it is proximally expanded and in close contact with the carpals; distally it is in articulation with the wing digit. The wing metacarpal is 1.3 times the length of the humerus. The ulna is 1.1 times as long as the wing metacarpal.

The digits are completely preserved. Digits Ⅰ—Ⅳ are completely preserved on the right side and digits Ⅲ—Ⅳ are preserved on the left side. Digits Ⅰ—Ⅲ are slender, the distal phalanges are short and the unguals are sharp. Digit IV is long and preserved all 4 phalanges; they are all robust, straight and thin-walled; they are expanded at both ends, with the proximal end wider than the distal end. The fourth phalanx of the wing digit tapers distally although its distal extremity is missing. The length of the phalanges of the wing digit decreases toward to the distal end; the first three phalanges are longer than wing metacarpal; the first phalanx is 1.4 times as long as the wing metacarpal. The phalangeal format of the hand is 2-3-4-4.

To compare the length of the major elements of the forelimb, we list them in progressively decreasing order as follows: first phalanx of the wing digit, second phalanx of the wing digit, ulna, third phalanx of the wing digit, wing metacarpal, humerus, fourth phalanx of the wing digit.

The sternum is fan-shaped. The keel is well developed and extends anteriorly to one third of the sternal plate; it is about half as long as the sternum. The sternum is thin; its length equals the width. Ventrally it is most similar to that of *Gallodactylus* and *Nesodactylus*[9].

Pelvic girdle and hindlimb. Only the posterior margin of the left ischium is preserved, it is semicircular and thin, with the dorsal margin thickened. It is most similar to the ischium of *Pterodactylus*[9].

Most of the hindlimb elements are missing. Tarsals, metatarsals and a few pedal digits are preserved. Proximal tarsals are large and the distal tarsals are small and fused. Compared to the forelimbs, the metatarsals and digits are extremely reduced and small. Metatarsals Ⅰ—Ⅲ are of equal length; Ⅳ is slightly shorter; Ⅴ is shorter than Ⅳ. The length of metatarsal Ⅰ is only about 18.7% that of the wing metacarpal. Digits Ⅰ and Ⅱ also preserved the unguals. Digit Ⅴ has only one short phalanx and preserved its impression. The pedal phalangeal format is 2-3-4(?)-5(?)-1.

2 Comparisons and discussions

Among the two suborders of Pterosauria the Rhamphorhynchoidea occurred from the Late Triassic to the Late Jurassic and is characterized by the presence of a long tail while the short-tailed Pterodactyloidea has been known from the Late Jurassic to the Late Cretaceous. *Haopterus gracilis* gen. et sp. nov. is characterized by a low and long crestless skull, a unified nasopreorbital opening, short teeth in both the upper and lower jaws, short pedal digit Ⅴ and long wing metacarpal. These characters show that *Haopterus* should be referred to the Pterodactyloidea. Based on the character of the nearly complete skull including the dentition, it can be compared with the known members of different families of Pterodactyloidea.

Pterodactyloidea comprises 15 families[10], among them are the Late Cretaceous toothless Pteranodontidae, Nyctosauridae, Azhdarchidae from North America and the Tapejaridae from the Early Cretaceous of Brazil and An-

hangueridae, Criorhynchidae, Germanodactylidae and Dsungeripteridae that possess both teeth in the jaws and a crest on the skull[10—12]. Among the families that possess teeth but lack a skull crest are Ctenochasmatidae from the Late Jurassic of Germany, France and the Early Cretaceous of China[13] and Pterodaustridae form the Early Cretaceous of Argentina and Chile; these groups possess several hundred dense teeth in both the upper and lower jaws. Some members of the family Ctenochasmatidae also have a skull crest[9,10], which can be easily distinguished from *Haopterus*. Cearadactylidae from the Early Cretaceous Santana Formation in Brazil comprises large-sized pterosaurs that have a small skull with especially long and robust teeth[10]. Ornithodesmidae from the Early Cretaceous (Wealden) of England has short and robust teeth and a duck-bill-shaped rostrum[10]. Both of these families are distinguishable from *Haopterus*. Besides, the family Ornithocheridae, which is widely distributed in the Early Cretaceous to the Late Cretaceous deposits in Europe, Africa, South America and Australia, comprise large-sized pterosaurs which have a low and slender skull, and the teeth are short, pointed and densely distributed. A few members of this family also possess a skull crest[10].

Haopterus is a small to medium sized pterosaur. Its skull characters are most similar to those of the Late Jurassic Pterodactylidae and Gallodactylidae from Europe[9,10]; the later two families are distinguishable from each other by both the teeth morphology and the postcranial characters. Gallodactylidae has slender teeth, which are only distributed in the anterior jaws and a short crest at the rear of the skull. The dentition of *Haopterus* as well as other characters is most similar to that of Pterodactylidae, therefore *Haopterus* is referred to the family Pterodactylidae.

Pterodactylidae is composed of one genus (*Pterodactylus*) and 13 species[10]. *Haopterus* can be clearly distinguished from *Pterodactylus* by the following character: fewer teeth, fusion between the premaxilla and the maxilla, fusion of the tarsals, sternum with a well-developed carina, well-developed pectoral girdle, more expanded deltopectoral crest of the humerus, well-developed procoracoid, more developed wing digit, the first three phalanges of the wing digit longer than the wing metacarpal. All these characteristics are related to more powerful flying capability. In addition, *Haopterus* also has very reduced metatarsals, Metatarsals I —III are of equal length and less than one fifth of the length of the wing metacarpal while *Pterodactylus* has more developed hindlimbs. Compared with *Pterodactylus*, *Haopterus* is probably more adapted to flight than terrestrial life.

Pterosaurs were believed to be more adapted to bipedal locomotion based on its forelimb and pectoral girdle structure[14]; however, further work on large pterosaur *Anhanguera* from the Early Cretaceous Santana Formation of Brazil indicates that they probably lived a quadrupedal life[15]. The extremely reduced hindlimb of *Haopterus* indicates that it cannot be bipedal; small to medium-sized pterosaurs were probably quadrupedal most of the time.

Haopterus has a large skull and a pointed rostrum; the front teeth are sharp and slender, suggesting a piscivorous feeding habit. It probably has strong flight capability and the body was suspended by the hindlimb in resting position.

Eosipterus from the same horizon as *Haopterus* did not preserve the skull; the limb bones were not completely preserved. It can be easily distinguished from the latter by the following characters: the ulna is as long as the first phalanx of the wing digit, but is 1.3 times as long as the wing metacarpal, metatarsals are relatively long, metatarsal I is about 57.5% of the length of the wing metacarpal. *Eosipterus* was recently referred to the Pterodactylidae[16,17]. Since it lacks the skull character we believe that more material is needed to discuss its phylogenetic position. The discovery of *Haopterus* represents the first uncontroversial pterodactylid pterosaur in Asia, it also extends the distribution of this family to the Early Cretaceous.

Dendrorhynchoides is another pterosaur that has been described from the lower Yixian Formation at the same locality as *Haopterus* in western Liaoning. It preserved a very crushed skull containing no diagnostic characters. It was referred to Rhamphorhynchoidea[8]. Although it still preserved a few primitive characteristics such as the short metacarpals it also has many more derived characteristics such as the long wing digit, etc. Its phylogenetic position remains a mystery[2].

Haopterus was collected from the Jianshangou Bed of the lower Yixian Formation, it is the lower fossil-bearing bed of the Jehol Biota. Associated with this pterosaur are important fossil vertebrates[1,2,18] including *Lycopterus*, *Psittacosaurus*, several feathered theropods[4—6], and *Confuciusornis*[3]. $^{40}Ar/^{39}Ar$ dating of the single crystal sanidine from the horizon resulted in an age of (124.6 ± 0.3) Ma — (124.6 ± 0.2) Ma[19], therefore it should be referred to the late Valanginian (age of Jurassic/Cretaceous boundary is 136 Ma) or the middle Barremian (Jurassic/Cretaceous boundary 144 Ma)[2]. The vertebrate assemblage also suggests an Early Cretaceous age[2,20].

Among the pterosaurs known from the Jianshangou Bed of the lower Yixian Formation in Sihetun areas,

western Liaoning, *Dendrorhynchoides* was collected at the Zhangjiagou locality, which is the lowest fossil-bearing horizon of the lower Yixian Formation, *Haopterus* was collected from 18(6) of the excavation section[1,2] of locality 1 of Sihetun which is about 5.5m higher than *Dendrorhynchoides*, *Eosipterus* was collected from the Tuanshanzi locality, the horizon of which is higher than the Sihetun locality[2].

The pterosaur assemblage in the lower Yixian Formation is more advanced than that of the Late Jurassic (Tithonian) in Solnhofen, Germany. It, however, bears a lot resemblance to that of the Early Cretaceous (Aptian-Albian) Santana Formation in Brazil[11]. We believe that the Valanginian or Barremian age derived from isotope dating[2,19] is consistent with the pterosaur assemblages as well as other vertebrate assemblages of the lower Yixian Formation.

Pterodactyloid pterosaurs occurred abundantly in the Early Cretaceous deposits in northern China, Mongolia and former Russia[13,21,22]. Most notable among them are *Huanhepterus* of the Huanhe Formation from the Ordos Basin[13] and *Dsungeripterus* of the Tugulu Group from the Junggar Basin of Xinjiang[21]and Tsagantsab Formation from Mongolia[22]. These Early Cretaceous pterosaurs belong to Pterodactyloidea.

In summary, members of the Pterodactylidae are previously known only in the Late Jurassic (Kimmeridgian-Tithonian) in Europe and Africa[10]. *Haopterus* represents the first occurrence of an non-controversial pterodactylidae in the terrestrial Early Cretaceous deposit in Asia. Therefore this family had existed longer than previously known. The discovery of *Haopterus* also provides new evidence for the study of the global stratigraphic correlations of the Late Jurassic and Early Cretaceous deposits.

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