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A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy*

WANG Xiaolin & ZHOU Zhonghe

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
Correspondence should be addressed to Wang Xiaolin (e-mail: xlinwang@263.net)

Abstract **In this article we describe a new and exceptionally well-preserved pterodactyloid pterosaur, *Sinopterus dongi* gen. et sp. nov. from the Jiufotang Formation in western Liaoning Province of northeast China. The new species is referred to the family Tapejaridae, representing its first record outside Brazil. It also represents the earliest occurrence as well as the most complete skeleton of the family. Some revisions are made about the family according to the morphological observations of the postcranial bones of *Sinopterus*. Two pterosaur assemblages appear to have existed in the Jehol Group, represented by the lower Yixian Formation and upper Jiufotang Formation, respectively. The lower pterosaur assemblage shows some resemblance to that of the Late Jurassic in Solnhofen (Tithonian) by sharing members of the Pterodactylidae and Anurognathidae. The upper one shows more resemblance to that of the Early Cretaceous Santana Formation (Aptian/Albian) by comprising only pterodactyloids such as the Tapejaridae. The age of the Yixian Formation is younger than that of the Solnhofen lithographic limestone, and the age of the Jiufotang Formation (Aptian) is slightly older than the Santana Formation.**

Keywords: Pterodactyloidea, Tapejaridae, *Sinopterus*, Jiufotang Formation, Jehol Group, biostratigraphy, Chaoyang, Liaoning.

The Early Cretaceous Jehol Group, which comprises the Yixian and Jiufotang formations, has yielded not only exceptionally well-preserved early birds[1—3], feathered dinosaurs[4,5], mammals[6,7] and angiosperms[8,9] but also many beautifully preserved pterosaurs such as *Eosipterus*[10] and *Haopterus*[11] of Pterodactyloidea, and *Dendrorhynchoides*[12] and *Jeholopterus*[13] of Rhamphorhynchoidea from the Yixian Formation.

In the past two years a number of pterodactyloid pterosaurs have been discovered from the Jiufotang Formation, which represents the second horizon of the Jehol Group preserving pterosaurs. In this paper we will report a complete skeleton of a new pterodactyloid pterosaur from the Jiufotang Formation in Dongdadao of Chaoyang, western Liaoning Province. The fossil is referred to the family Tapejaridae. Members of the Tapejaridae have previously been known only in the late Early Cretaceous Santana Formation (Aptian/Albian) of Brazil[14,15]. *Sinopterus* represents the earliest record of this family.

Two pterosaur assemblages appear to be present in the Jehol Group, represented by taxa from the lower Yixian Formation and the upper Jiufotang Formation, respectively. These two pterosaur assemblages are more or less comparable to those of the Solnhofen and the Santana pterosaur assemblages. The age of the Jehol pterosaur assemblages is between the Solnhofen lithographic limestone (Tithonian) and the Santana Formation (Aptian/Albian).

1 Systematic paleontology

Order Pterosauria Kaup, 1834
Suborder Pterodactyloidea Plieninger, 1901
Family Tapejaridae Kellner, 1989
Genus *Sinopterus* gen. nov.
Sinopterus dongi gen. et sp. nov.
(Figs. 1 and 2; Tables 1 and 2)

Diagnosis. Medium-small sized pterodactyloid. Wingspan about 1.2 m. Skull length about 170 mm. Rostrum slender and pointed, edentulous, with a horny beak. Skull long and low. Sagittal crest of premaxilla and dentary low and small. Posterior crest of the premaxilla curved upward, separate from the skull, and parallel to the parietal crest. Nasopreorbital fenestra large and long (length about 2.5 times the height), exceeding one-third the total length of the skull. Radius, wing metacarpal and first phalanx of the wing digit about 1.5, 1.6 and 2 times the length of the humerus, respectively. Carpals large and unfused. Scapula strongly curved. Coracoid expanded at the articulation to the scapula. Tibia about 1.4 times the length of the femur. Metatarsals Ⅰ through Ⅳ progressively shorter. Metatarsal Ⅲ about 22.1% the length of the wing metacarpal, and metatarsal Ⅴ is less than 1/5 the length of metatarsal Ⅰ.

Holotype. A nearly completely articulated skeleton. Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) V13363.

Locality and horizon. Lamagou, Dongdadao, Chaoyang, Liaoning Province; Jiufotang Formation, late

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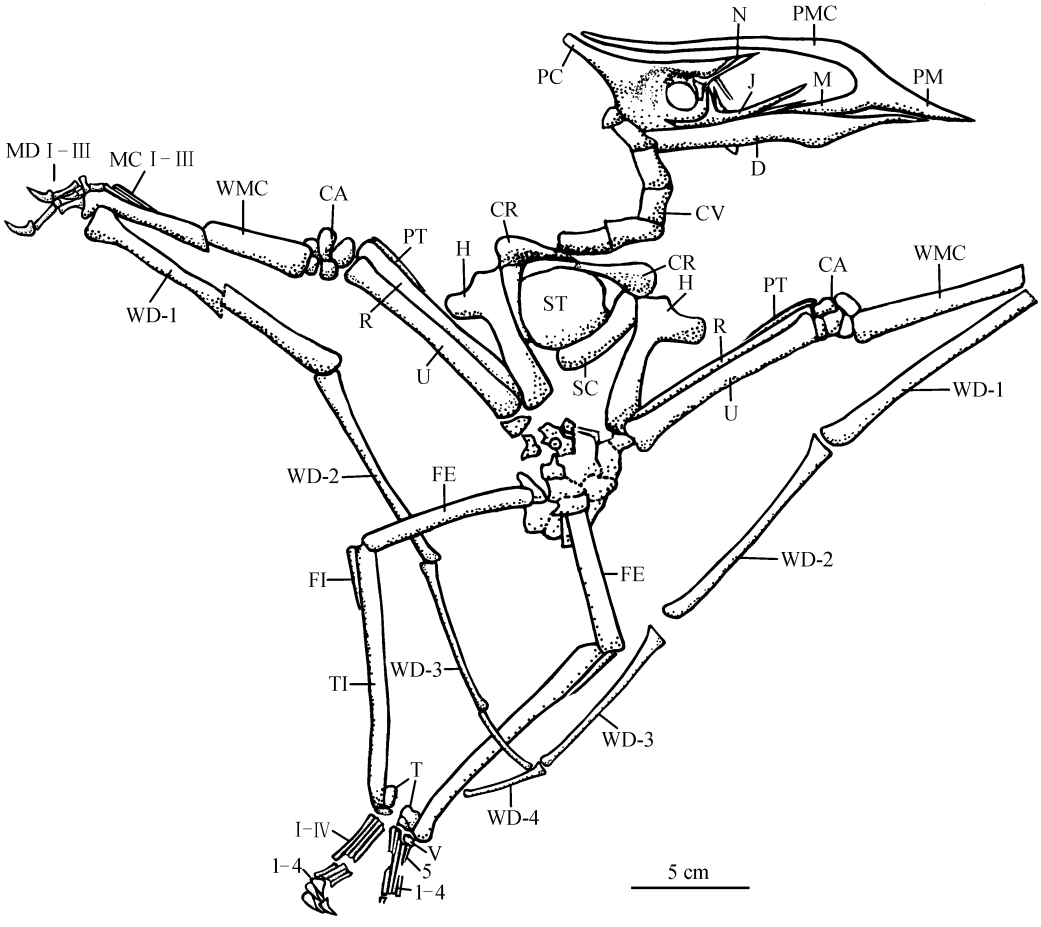

Fig. 1. Line drawing of *Sinopterus dongi* gen. et sp. nov. holotype (IVPP V 13363). CA: Carpal; CR: coracoid; CV: cervical vertebra; D: dentary; FE: femur; FI: fibula; H: humerus; J: jugal; M: maxilla; MC Ⅰ—Ⅲ: metacarpals Ⅰ—Ⅲ; MD Ⅰ—Ⅲ: manual digits Ⅰ—Ⅲ; N: nasal; PC: parietal crest; PM: premaxilla; PMC: premaxillary sagittal crest; PT: pteroid; R: radius; SC: scapula; ST: sternum; TI: tibia; U: ulna; WD 1—4: first through fourth phalanges of the wing digit; WMC: wing metacarpal; Ⅰ—Ⅴ: metatarsals Ⅰ—Ⅴ; 1—5: pedal digits Ⅰ—Ⅴ.

Table 1 Measurements (length) of the skull of *Sinopterus dongi* gen. et sp. nov. (IVPP V 13363) (mm)

Skull (tip of premaxilla to end of the parietal crest)	170
Tip of premaxilla to squamosal	146
Anterior margin of nasopreorbital fenestra to squamosal	101
Tip of premaxilla to anterior margin of nasopreorbital fenestra	48
Skull height (at the quadrate)	30
Skull height (at the highest point of premaxilla)	32
Parietal crest	35
Nasopreorbital fenestra	61
Nasopreorbital fenestra height	25
Diameter of the orbit	15[a)]
Horny beak	13[a)]
Dentary	125
Dentary height (at the highest point of the dentary crest)	14

a) Approximate or estimated value.

Early Cretaceous (Aptian).

Etymology. Sinae (Latin), China; pterus (Greek), wing; species name is dedicated to Chinese dinosaurologist Dong Zhiming.

Skull and mandible. The skull is laterally preserved and edentulous. The premaxilla is fused with the maxilla anteriorly. The anterior premaxilla is long and pointed, with a horny beak. Both the premaxilla and the parietal have a narrow crest. The premaxillary sagittal crest is anteriorly low and flat; it extends horizontally backwards until the posterior margin of the skull. The parietal crest is isolated from that of the premaxilla. The crest of the premaxilla starts to be separated from the rest of the skull from the middle of the nasopreorbital fenestra; it is relatively thick ventrally and thin dorsally, similar to that of *Tapejara wellnhoferi*[14,16]; bony sheath and its impression are observable near the outer margin of the crest for the protection of the crest as suggested earlier[16]. The maxilla has a straight ventral margin, and forms an obtuse angle with the ventral margin of the premaxilla, which is

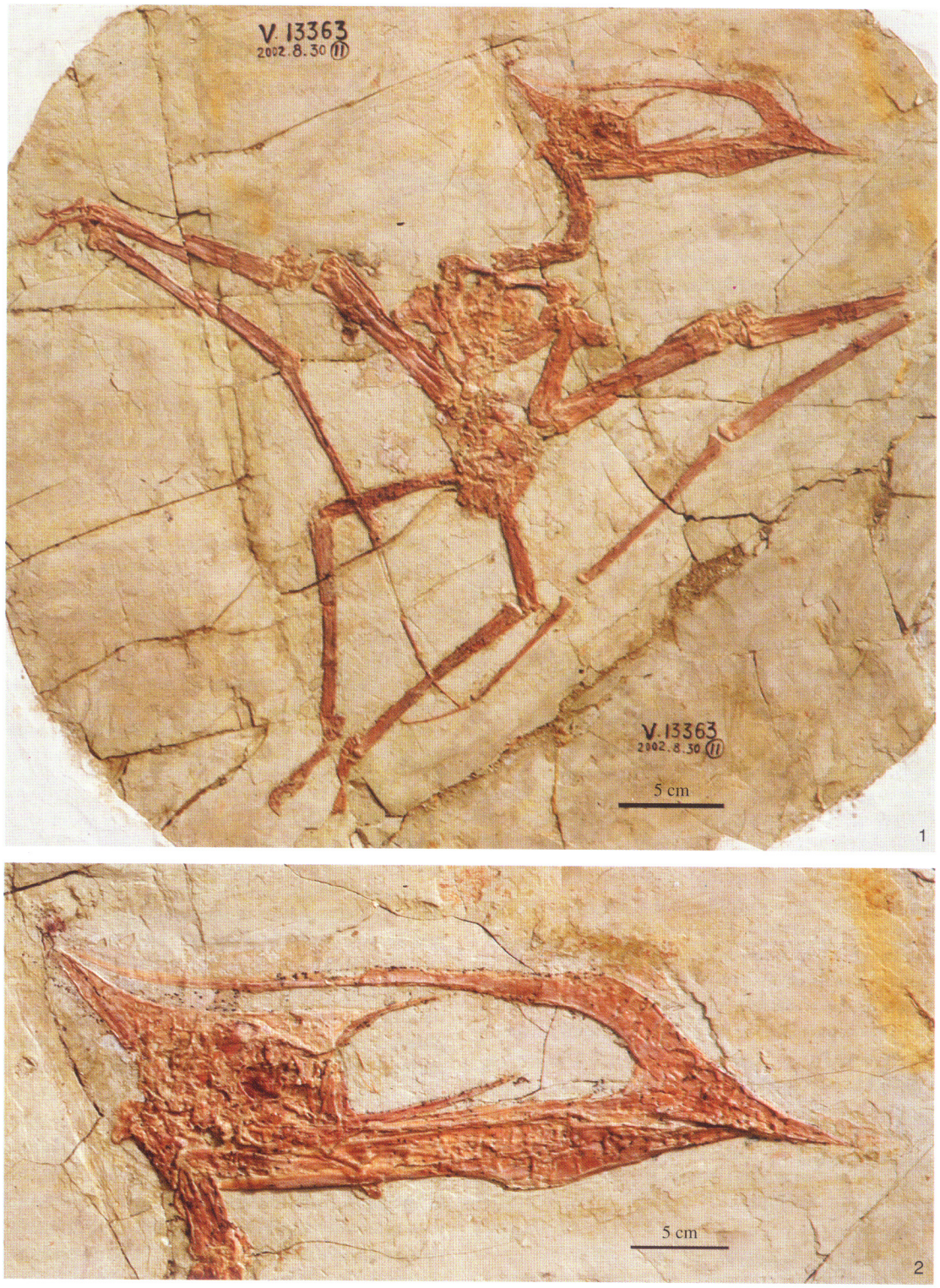

Fig. 2. Holotype *Sinopterus dongi* gen. et sp. nov. (IVPP V 13363). 1, Skeleton; 2, skull.

Table 2 Length (mm) of postcranial bones of *Sinopterus dongi* gen. et sp. nov. (IVPP V 13363)

	Left	Right
Scapula	40	39[a)]
Coracoid	35	36
Humerus	59	58
Ulna	88	87.5
Radius	84	85
Pteroid	29[b)]	38
Wing metacarpal	77[b)]	95
Metacarpals Ⅰ—Ⅲ	–	93[a)]
First phalanx of manual digit Ⅰ	–	12.5
Second phalanx of manual digit Ⅰ	–	8[a)]
First phalanx of manual digit Ⅱ	–	7.5
Second phalanx of manual digit Ⅱ	–	12.5
Third phalanx of manual digit Ⅱ	–	10
First phalanx of manual digit Ⅲ	–	12.5
Second phalanx of manual digit Ⅲ	–	3
Third phalanx of manual digit Ⅲ	–	12
Fourth phalanx of manual digit Ⅲ	–	4[b)]
First phalanx of wing digit	105.5[b)]	121
Second phalanx of wing digit	91	88
Third phalanx of wing digit	65.5	63
Fourth phalanx of wing digit	33	32
Femur	74[a)]	74
Tibia	104	104
Fibula	20	20
Metatarsal Ⅰ	25	24.5
Metatarsal Ⅱ	23	23.3
Metatarsal Ⅲ	20.5	21[a)]
Metatarsal Ⅳ	19	19
Metatarsal Ⅴ	–	4.5
First phalanx of pedal digit Ⅰ	2[b)]	10.5
Second phalanx of pedal digit Ⅰ	–	6
First phalanx of pedal digit Ⅱ	–	–
Second phalanx of pedal digit Ⅱ	–	6.5[a)]
Third phalanx of pedal digit Ⅱ	–	7.5
First phalanx of pedal digit Ⅲ	–	7[a)]
Second phalanx of pedal digit Ⅲ	–	–
Third phalanx of pedal digit Ⅲ	–	10
Fourth phalanx of pedal digit Ⅲ	–	7
First phalanx of pedal digit Ⅳ	–	–
Second phalanx of pedal digit Ⅳ	–	–
Third phalanx of pedal digit Ⅳ	–	–
Fourth phalanx of pedal digit Ⅳ	–	–
Fifth phalanx of pedal digit Ⅳ	–	–
First phalanx of pedal digit Ⅴ	–	8[b)]

a) Approximate or estimated value; b) preserved length.

also similar to the situation in *T. wellnhoferi*[14,16] and *Thalassodromeus*[15].

The nasopreorbital fenestra is large and elliptic in shape; its length is about 2.5 times its height, exceeding one-third the length of the skull. The orbit is relatively small and situated below the level of the upper margin of the nasopreorbital fenestra, as in other species of the family[14—17].

The nasal is long and unfused with the premaxilla and jugal; it has a needle-shaped ventral process. The nasal extends towards the premaxilla anteriorly for about one-third the length of the nasopreorbital fenestra.

The frontal and parietal are fused, without obvious suture. The frontal is an inverse triangle-shaped. The parietal has a posteriorly lifted crest; the crest is better developed than in *T. wellnhoferi*[14,16], and it is also more curved upwards. The ascending process of the jugal contacts the nasal. The anterior process of the jugal is long and slender; it lies near the ventral margin of the nasopreorbital fenestra, and is about two-thirds the length of the nasopreorbital fenestra.

The lower jaw is completely preserved and edentulous; it is robust; its ventral sagittal crest is straight posteriorly but pointed anteriorly. Bones of the lower jaw appear to be well fused.

Compared to other members of the Tapejaridae, the skull of *Sinopterus* is low and long, the skull length (from the tip of the premaxilla to the posterior margin of the parietal crest) is about 170 mm, which is about 5 times its height (excluding the height of the lower jaw). The nasopreorbital fenestra is large and more than one-third the length of the skull.

Vertebral column. There are 7 cervical vertebrae preserved in articulation; they are long and robust. The length of the third through seventh cervicals are 15.5 mm, 19.5 mm, 20.5 mm, 21 mm and 19 mm, respectively. The neck is over 100 mm long. The dorsal vertebrae are disarticulated in preservation. The estimated number of the dorsals is 11—12; the centrum is often isolated from the neural spine; it is about 5—7 mm long and procoelous. The number of the sacral vertebrae is unclear; two sacral are fused with a combined length of 14 mm. Only 4 caudals are preserved, probably indicating a short tail.

Rib and sternum. Dorsal ribs are rarely preserved; a few gastralia are observable, and 3—4 pairs of gastralia are "V"-shaped. The sternum is nearly semicircular, and wider than long; the keel is well-developed.

Pectoral girdle and forelimb. The scapula and coracoid are fused, and form a "U"-shaped scapulocoracoid. The scapula is curved; it is about 9 mm wide throughout its length. The coracoid is straight and robust; its articulation with the scapula is expanded and fan-shaped. The scapula is slightly longer than the coracoid as typical of the Tapejeridae.

The forelimb is robust. The ulna, wing metacarpal and the first phalanx of the wing digit are 1.5, 1.6 and 2 times the length of the humerus, respectively. The four phalanges of the wing digit become progressively shorter distally. The second phalanx of the wing digit is about the same length of the ulna. The length of the humerus + ulna + wing metacarpal is about 1.2 times that of the femur +

tibia + metatarsal Ⅲ. The length of the wing digit is about 5.2 times that of the humerus and 3.2 times that of the wing metacarpal.

The humerus is a robust and straight, with a well-developed delto-pectoral process. The radius is slightly shorter than the ulna; both are straight and a lot longer than the humerus. Five carpals are preserved; they are approximately the same size. Two proximal carpals and three distal carpals are unfused. The pteroid is slender, and about 45% the length of the radius. Metacarpals are long; compared to the phalanges of the wing digit, they are only shorter than the first phalanx. The wing metacarpal is robust; metacarpals Ⅰ—Ⅲ are very slender, and slightly shorter than the wing metacarpal. The phalanges of digits Ⅰ—Ⅲ are relatively long, with large, curved and pointed claws.

Compared with the radius, the first phalanx of the wing digit is longer; the second is about the same length, the third and fourth are shorter. The second, third and fourth phalanges of the wing digit are about 74%, 53.3% and 26.9% the length of the first phalanx, respectively. The wing phalanges are expanded proximally; the fourth phalanx is curved with an expanded distal end.

Hindlimb. The hindlimb bones are slender. The femur and tibia are both straight; the tibia is about 1.4 times the length of the femur. The fibula is reduced and less than 1/5 the length of the tibia. Metatarsals Ⅰ—Ⅳ are well-preserved; they are straight and parallel to each other. Among the four major metatarsals, metatarsal Ⅰ is the longest, Ⅱ the second, Ⅲ is shorter than Ⅱ, and Ⅳ is the shortest and about 3/4 the length of Ⅰ. Metatarsal Ⅲ is about 22.1%, 27.7% and 19.7% the length of the wing metacarpal, femur and tibia, respectively. Metatarsal Ⅴ is very reduced, and less than 1/5 the length of metatarsal Ⅰ.

The phalangeal format of the pedal digit is "2-3-4-5-1". Digit Ⅴ is very short, and the claw is not preserved. Other four pedal digits all preserved curved claws. Distal phalanges appear longer than proximal ones, indicating the arboreal adaptation.

Impressions of the wing fibers are only weakly preserved in the specimen.

2 Comparison and discussion

In the Pterodactyloidea, the Tapejaridae, Pteranodontidae, Nyctosauridae and Azhdarchidae are all edentulous and from the Cretaceous[18]; most members of these families are from the Late Cretaceous except Tapejaridae and some members of the Pteranodontidae that are known from the late Early Cretaceous. Nearly all of these edentulous pterosaurs are known from America. For instance, the Tapejaridae is only known from Brazil, Nyctosauridae is known only from Brazil and the United States. Except a few members from Europe and Asia, the Pteranodontidae and Azhdarchidae are mainly from North America[18].

Sinopterus can be easily distinguished from other edentulous pterodactyloids. For instance, the Pteranodontidae has a huge body size; and it is also characteristic of a sword-shaped long snout, a huge crest from the posterior frontal and a curved delto-pectoral process of the humerus. The Azhdarchidae also comprises large sized members; they are characteristic of a huge nasopreorbital fenestra and crest of the nasal and frontal, and a very short fourth phalanx of the wing digit.

Sinopterus can be referred to the Tapejaridae by its small size, expanded nasopreorbital fenestra, orbit below level of upper margin of the nasopreorbital fenestra, scapula longer than coracoid, and the premaxillary sagittal crest extending to the posterior end of the skull. The discovery of *Sinopterus* represents the first occurrence of this family outside South America; it is also the earliest record of the family.

Members of the Tapejaridae are previously only known from the Santana Formation of Brazil including 3 genera and 5 species: 2 species of *Tapejara*[14,17], 2 species of *Tupuxuara*[19,20] (referred to Azhdarchidae by some other workers[21]) and 1 species of *Thalassodromeus*[15]. *Sinopterus* is distinguishable from them by the small size, low and long skull, more pointed snout, small premaxillary sagittal crest, and flatted nasopreorbital fenestra. It also represents the most complete known skeleton of the family.

The skull of *Sinopterus* is most similar to that of *Tapejara wellnhoferi*[14,16] in the premaxillary sagittal crest and the separation of the crest from other skull bones starting from the middle of the nasopreorbital fenestra; however, the sagittal crest of the premaxilla and lower jaw of *Sinopterus* is less well developed than in *T. wellnhoferi*. The premaxillary sagittal crest of *Tupuxuara* is low, but extends more posteriorly. The same crest of *Thalassodromeus* is low, but extends further more posteriorly and the posterior margin of the crest is "V"-shaped[15].

The centrum of the dorsal vertebra is unfused with the neural spine in the holotype of *Sinopterus*, and the extremities of the long bones are less well defined, probably indicating a subadult individual.

Like *T. wellnhoferi*[16], *Sinopterus* is probably an omnivorous animal. It could probably feed on both fishes and seeds. Piscivorous pterosaurs usually have long and pointed jaws as in *T. wellnhoferi* and *Thalassodromeus*[15,16]. The abundant fishes associated with *Sinopterus* in the Jiufotang Formation provide circumstantial support for its piscivorous habit.

Sinopterus is similar to *Tapejara* in size. The small sized *Tapejara* was proposed to be a frugivorous pterosaur[16]. *Sinopterus* has a more pointed snout, similar to the horny beak of birds; it also has robust lower jaw and cervical vertebrae, strong forelimbs and claws, all sug-

gesting the seed-eating capability. The recognition of seed-eating pterosaurs (including fruit-eating birds such as *Jeholornis*[3]) may provide further support for the hypothesis of the co-evolutionary relationship between pterosaurs and early angiosperms, i.e., pterosaurs might have been involved in the early radiation of angiosperms in the Cretaceous[22].

3 Pterosaur assemblages of the Jehol Group and discussions on biostratigraphy

Two pterosaur assemblages appear to be present in the Jehol Group (Table 3). The lower assemblage from the Yixian Formation comprises *Eosipterus*[10,23,24] and *Haopterus*[11] belonging to Pterodactyloidea, and *Dendrorhynchoides*[12,23] and *Jeholopterus*[13] belonging to the rhamphorhynchoid Anurognathidae. Among the several dozens of pterosaur specimens known from this assemblage, most are pterodactyloids, and only a few of them are rhamphorhynchoids. The upper pterosaur assemblage comprises pterosaurs from the Jiufotang Formation. Until now all the pterosaurs from this formation are pterodactyloids, and *Sinopterus* represents the first taxa described.

The pterosaur assemblage of the Yixian Formation is associated with the *Confuciusornis* avian-fauna including early birds such as *Confuciusornis*, *Liaoningornis*, *Eoenantiornis*, *Liaoxiornis* and *Protopteryx*. Associated dinosaurs are also abundant, including feathered theropods *Sinosauropteryx*, *Beipiaosaurus*, *Sinornithosaurus*, *Protarchaeopteryx* and *Caudipteryx*, the iguanodontid *Jinzhousaurus*[25], the ankylosaurid *Liaoningosaurus*[26], etc. These fossils are mainly from the Jianshangou Bed, Dawangzhangzi Bed and Jingangshan Bed[27,28], with isotope dating ranging between 121 Ma[29]—125 Ma[30—32]. The Lujiatun Bed[33] of the lower Yixian Formation also produced some important dinosaurs such as *Sinovenator*[34], *Incisivosaurus*[35], *Liaoceratops*[36] and *Jeholosaurus*, but no pterosaur yet. The Daohugou bed[27], which is equivalent or lower than the Lujiatun Bed (note: it is still a debatable issue as to whether this bed should be referred to the Yixian Formation[37]) produced *Jeholopterus*[13,37] (note: the pterosaur labeled as a pterodactyloid in reference[37], plates Ⅱ—Ⅲ from the same bed and locality can in fact be referred to *Jeholopterus*). The basalt overlying the Lujiatun Bed was dated as 128 Ma with $^{40}Ar/^{39}Ar$ method[38]. Although currently there is no precise age for this bed, we estimate that it cannot be older than 139 Ma[31], the $^{40}Ar/^{39}Ar$ age of the upper Tuchengzi Formation.

Members of the Anurognathidae include *Anurognathus* from the Solnhofen lithographic limestone and *Batrachognathus* from the Karabastau Formation of Kazakhstan (Oxfordian-Kimmeridgian[39]). Pterodactylids have been discovered from the Late Jurassic deposits in Europe (Germany, France and England) and Tanzania of Africa. The Yixian pterosaur assemblage shows some resemblance to the pterosaurs from the above mentioned localities. For instance, it shares with the Solnhofen assemblage two pterosaur families. However, the Yixian assemblage also shows obvious differences from the Solnhofen assemblage; the latter assemblage comprises 4 genera and 8 species of rhamphorhynchoids and 5 genera and 13 species of pterodactyloids[18]. Overall, the Solnhofen assemblage is more primitive and is older than the Yixian assemblage. The pterosaur assemblage of the Karabastau Formation contains the rhamphorhynchoid *Sordes*[40,41], yet until now no pterodactyloid has been reported; its age is much older than the Yixian Formation. We believe that the Yixian pterosaur assemblage is evolutionarily between those of the Solnhofen and Santana formations[11]; this conclusion is consistent with those based on the isotope dating[30—32] as well as biostratigraphic comparisons of birds and dinosaurs.

Although the age and correlation of the *Jeholopterus*-bearing Daohugou bed in Ningcheng, Inner Mongolia is still controversial[13,27,37,42], it is regarded as the lowest deposit of the Yixian Formation in this paper based on the sedimentary features, lithostratigraphic sequence, the maniraptoran dinosaur *Epidendrosaurus*[43] and the similarity between *Jeholopterus*[13] and *Dendrorhynchoides*[12,23] from the Jianshangou Bed of the Yixian Formation. The Daohugou bed probably represents the earliest stage of the Yixian pterosaur assemblage as well as the earliest appearance of the Jehol Biota. Its age is tentatively regarded as Berriasian (?)-Barremian rather than the Middle Jurassic as proposed by some other workers[37].

The Jiufotang pterosaur assemblage comprises *Sinopterus* described in this paper as well as some unpublished pterodactyloids. No rhamphorhynchoid has been discovered from the over dozen specimens known from the Jiufotang Formation. This pterosaur assemblage is associated with the *Cathayornis* avian-fauna that includes birds such as *Cathayornis*, *Sinornis*, *Boluochia*, *Chaoyangia*, *Longipteryx*, *Yixianornis*, *Yanornis*, *Sapeornis* and *Jeholornis*. Associated dinosaurs include the dromaeosaurid *Microraptor*. The basalt overlying the Jiufotang Formation in Inner Mongolia was dated as 110 Ma[44], therefore, the temporal distribution of this formation is probably 110—120 Ma (Aptian).

The Jiufotang pterosaur assemblage shows some resemblance to that of the Santana Formation in sharing the occurrence of the Tapejaridae, one of the most important components of the Santana assemblage. *Sinopterus* is more primitive than *Tapejara* in morphology, which is consistent with the conclusion that the age of the Jiufotang Formation (Aptian) is slightly older than the Santana Formation (Aptian/Albian).

Table 3 Comparison of the pterosaur assemblages of the Jehol Group in Asia and other regions

		Europe	Asia	South America
Early Cretaceous	Alb			Santana Formation Pterodactyloidea Tapejaridae Anhangueridae Ornithocheiridae Ceradactylidae
	Apt		Jiufotang Formation Pterodactyloidea Tapejaridae	
	Bar		Yixian Formation Rhamphorhynchoidea Anurognathidae	
	Hau		Pterodactyloidea Pterodactylidae	
	Val			
	Ber			
Late Jurassic	Tth	Solnhofen lithographic limestone Rhamphorhynchoidea Rhamphorhynchidae Anurognathidae Pterodactyloidea Pterodactylidae Ctenochasmatidae Gallodactylidae Germanodactylidae		
	Kim		Karabastau Formation Rhamphorhynchoidea Rhamphorhynchidae	
	Oxf		Anurognathidae	

The two pterosaur assemblages of the Jehol Group represent two important pterosaur radiations; they fill up both the evolutionary and temporal gaps between the Late Jurassic pterosaur assemblages of Europe and the late Early Cretaceous of South America, with the Yixian assemblage showing more resemblance to that of the Solnhofen and the Jiufotang assemblage more similar to that of the Santana Formation. A complete understanding of the evolutionary, biostratigraphic and paleogeographic implications of the Jiufotang pterosaurs await to be further explored with the description of more pterosaur taxa from this formation in the near future.

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