

**A new species of pterosaur from Liaoning, *Dendrorhynchus
curvidentatus*, gen. et sp. nov.**

by

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Abstract

The text describes a new pterosaur from the Chaomidianzi Fm. near the village of Sihetun, Beipiao Municipality, Liaoning Province. The species is extremely small. It has a wingspan of approximately 40 cm. Its dentition is homodont, the tail is long, the wing metacarpal is extremely short, and pedal digit V is exceptionally well developed. Its characters undoubtedly assign it to the family Rhamphorhynchidae and it is erected as *Dendrorhynchus curvidentatus* gen. et sp. nov. The specimen represents the first record of the family from the Late Jurassic of East Asia and further supports a Late Jurassic age for the sediments at Sihetun, Liaoning Province, which also produce *Sinosauropteryx* and *Confuciusornis*.

Introduction

The first publication of a pterosaur from China was the description of *Dsungaripterus weii* Young 1964 from the Early Cretaceous of the Xinjiang Autonomous Region. In the following decade *Noripterus complicidens* was described from the same region (Young, 1973). To date there are six Chinese pterosaur genera and species that range from the Middle Jurassic to the Late Cretaceous. In addition to the two Early Cretaceous taxa from Xinjiang, there are *Huanhepterus qingyangensis* (Dong, 1982) from the Late Jurassic locality of Sanshilipu, Qingyang Co., Gansu Province; *Angustinaripterus longicephalus* (He et al., 1983) from the Middle Jurassic locality of Dashanpu, Zigong Co., Sichuan Province; *Zhejiangopterus linhaiensis* (Cai and Wei, 1994) from the Late Cretaceous locality of Shangpanzhen, Linhai Co., Zhejiang Province; and *Eosipterus yangi* (Ji and Ji, 1997) from the Late Jurassic locality of Sihetun, Beipiao Co., Liaoning Province. There are also several limb bones diagnosed as pterosaurian from the Early Cretaceous of Laiyang Co., Shandong Province (Young, 1958); Yumen Co., Gansu Province (Niu, 1987); and Ejinhoru, Inner Mongolia (Dong, 1993). With the exception of the primitive rhamphorhynchid *Angustinaripterus* from Zigong, the remaining specimens all represent members of the more derived family, the Pterodactylidae.

In recent years, the Sihetun region of Beipiao Co., western Liaoning, has attracted global attention due to the discovery of a plethora of well preserved vertebrates representing numerous orders (Wang et al., 1998; Chen and Wu, 1998). Of particular scientific value are taxa related to the early evolution of birds including *Sinosauropteryx prima* (Ji and Ji, 1996; Ji and Ji, 1997; Chen et al., 1998), *Protarchaeopteryx robusta* (Ji and Ji, 1997, Ji et al., 1998); *Caudipteryx zoui* (Ji et al., 1998), and *Confuciusornis sanctus* (Hou et al., 1995a, Hou et al. 1995b). The authors of this text described *Eosipterus yangi* from the same region, which was the first documentation of a pterosaur in the Jehol Fauna of western Liaoning (Ji and Ji, 1997). Most recently, another pterosaur specimen was excavated from Sihetun that represents a new genus and species of rhamphorhynchid (Fig. 1) and the first occurrence of the suborder in the Late Jurassic of East Asia. Its occurrence not only supplements the abundant Jehol Fauna of western Liaoning, but also provides further significant evidence for the age of the Fauna in, addition to being extremely significant toward biostratigraphy and paleobiogeography.

Description

Pterosauria Kaup, 1834

Rhamphorhynchoidea Plieninger, 1901

Rhamphorhynchidae Seeley, 1870

***Dendrorhynchus* gen. nov.**

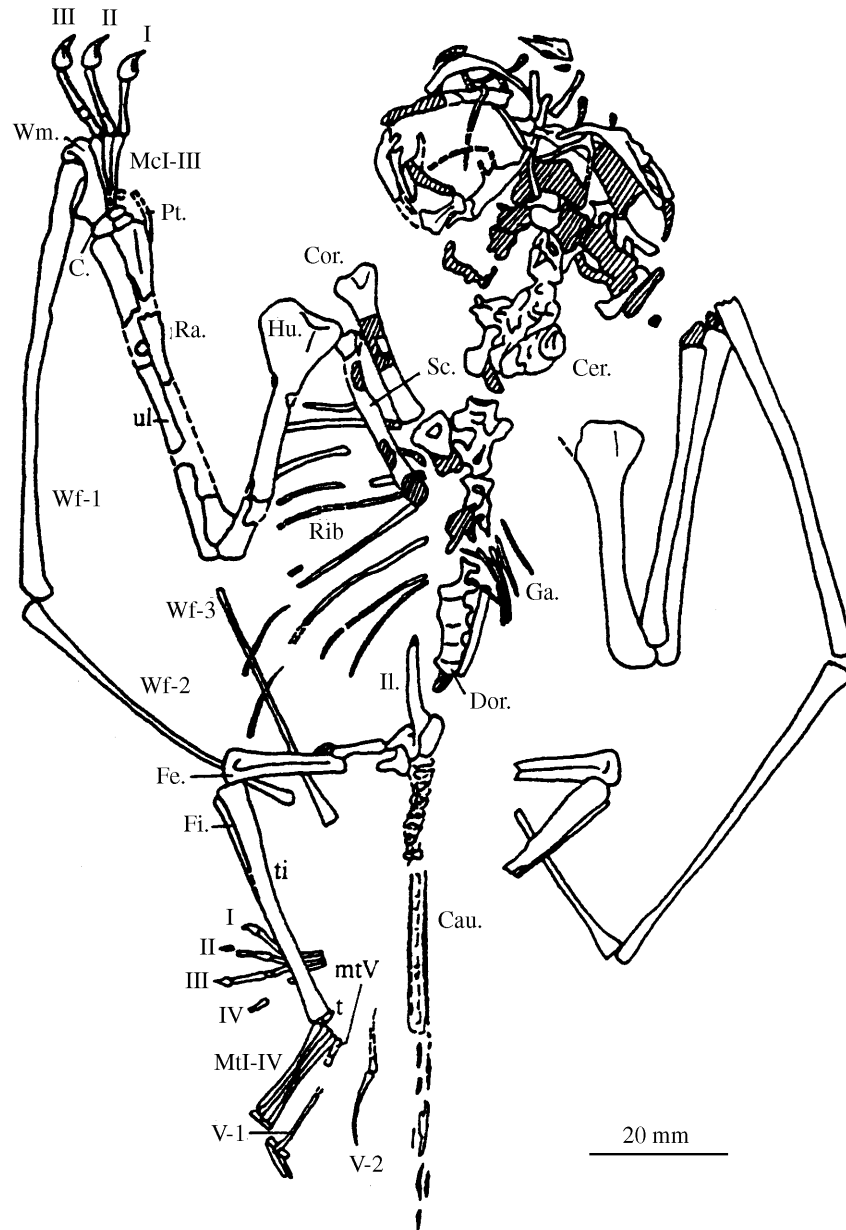


Figure 1. Drawing of *Dendrorhynchus curvidentatus* gen. et sp. nov. skeleton (GMV2128).

C.-carpal; Cau.-caudal vertebrae; Cer.-cervical vertebrae; Cor.-coracoid; Dor.-dorsal vertebrae; Fe.-Femur; Fi.-fibula; Ga.-gastralia; Hu.-humerus; Il.-ilium; McI-III-metacarpal I-III; MtI-IV-metatarsal I-IV; Pt.-pteroid; Ra.-radius; Sc.-scapula; T.-tarsal; Ti.-tibia; Ul.-ulna; Wf1-3-Digits 1-3 of wing finger, Wm.-wing metacarpal; I-IV.-manus or pes digits I-IV; V-1,2.- pes digit V phalanx 1,2

Genus etymology: Dendro-, Gr., tree; -rhynchus, Gr., beak. This indicates the specimen's affinity to *Rhamphorhynchus*.

Genus diagnosis: An extremely small species of rhamphorhynchid with a wing span of only about 40 cm. Tooth crowns are relatively high, acute, and slightly recurved. Cervical

vertebrae are short and thick. Tail is long with distinctly elongated neural spines and haemal arches on the medial and posterior caudal vertebrae. Wing metacarpal is robust with slight posterior curvature and a length only one-quarter that of the radius. Wing finger is slender and long; the first phalanx is distinctly longer than the second phalanx, and the second phalanx is only slightly longer than the radius. Tibia is shorter than the humerus. Fibula is conspicuously present but is slender and weak, and half as long as the tibia. Metatarsals I-IV are nearly equivalent in length but metatarsal V is short and straight. The fifth pedal digit has two extremely well developed phalanges that are two-thirds the length of the metatarsals, and the ungual is curved with an acutely tapered end.

***Dendrorhynchus curvidentatus* gen. et sp. nov.**

Species etymology: The Latin “curvidentatus” alludes to the acutely curved dentition.

Type: A relatively complete skeleton housed in the Chinese Geological Museum (specimen #GMV2128).

Species diagnosis: As for genus (only a single species).

Locality and stratigraphic position: Late Jurassic Chaomidianzi Fm. from the locality of Sihetun, Beipiao Municipality, western Liaoning Province (Ji et al., 1998).

Table 1. *Dendrorhynchus curvidentatus* gen. et sp. nov. measurements (mm).

	Left	Right
Scapula	20.0*	...
Coracoid	17.3	...
Humerus	27.8	27.0
Ulna	35.5	35.6
Radius	34.7	34.3*
Pteroid	5.9	...
Metacarpal I-III	7.0	...
Wing metacarpal	9.3	...
Manus digit I	10.2	...
Manus digit II	11.9	...
Manus digit III	13.1	...
Wing finger phalanx 1	44.5	==
Wing finger phalanx 2	35.6	37.0
Wing finger phalanx 3	==	==
Wing finger phalanx 4
Femur	==	==
Tibia	26.7	==
Metatarsal I-IV	12.1	==
Metatarsal V	3.5*	...
Pes digit V phalanx 1	==	==
Pes digit V phalanx 2	...	8.0*

* Estimate, ... not preserved, == partially preserved

Description: This is an extremely small species of pterosaur (Table 1) with a wing span of approximately only 40 cm, approaching the sizes of the two species *Rhamphorhynchus longicaudus* and *R. intermedius* (Wellnhofer, 1978).

The skull is relatively large but the individual cranial elements are extremely fragmentary due to anteroposterior compressional fracturing, thereupon obliterating the vast majority of cranial elements and leaving the morphology of the cranial fenestrae unknown. The preserved length of the mandible is only 15 mm but what remains is slender, long, and curved. Eleven isolated teeth are scattered within the matrix, six of which are relatively complete with the same morphology of a slightly broadened base and a smooth and glossy 2.5-3.0 mm acute and curved crown.

Cervical vertebrae are procoelous, short, thick, and distinctly more robust than the dorsals. Only the posterior six dorsals are relatively well preserved with procoelous centra that maintain relatively small diapophyses. Sacrals are not preserved. Only the anterior half of the caudals are preserved, the six anterior of which are represented as an impression in the matrix. Because the preserved total length is 50 mm, even with the entire tail length unknown, the species may be recognized as maintaining a long tail. The centra are relatively broad and unfused, the posterior caudals are distinctly slender and elongated with extremely elongated neural and haemal arches that surround and support the centra, a condition commonly documented in the rhamphorhynchids (Wellnhofer, 1978, 1991).

The sternal plate is not preserved. Nine incomplete elongated ribs are present on the left side associated with the dorsal vertebrae. Eight gastralia are present, among which are six in alignment on the right side, indicating there were at least six pair. The gastralia are slender, short, nearly straight, and are determined to be lateral gastralia.

The scapula has a slight curvature and like the coracoid is distinctly slender and elongated. It has an expanded, as opposed to attenuated, distal end. The coracoid is straight and together with the scapula maintains an expanded but shallow glenoid fossa.

The humerus is robust and has a broad and shallow proximal articular fossa, a greatly expanded deltopectoral crest, and a medial process. The humeral shaft is slightly slender and curved. The distal end maintains laterally convex articular processes. The radius and ulna are morphologically similar, slender, long, and in tight proximity. The radius is slightly longer than the ulna and both are distinctly longer than the humerus.

Extremely well preserved carpals, metacarpals, and digits I-III are present on the left side. Three oval carpals are present and a single small spherical carpal lies at the base of the wing finger. The pteroid is slender, weak, short, and slightly curved. Metacarpals I-III are slender, long, and have slightly expanded distal ends. Metacarpal IV, the wing metacarpal, is extremely robust and slightly longer than the other metacarpals; it is one-quarter as long as the radius, and both ends are extremely expanded with convex articular condyles. Its proximal end has a shallow sulcus and its distal end is distinctly posteriorly curved.

The manual digit formula is 2-3-4-4-x. Digit I has two phalanges, the first of which is long and straight, representing the longest phalanx among the digit I-III series, although it is still shorter than the metacarpals. The first ungual is large, recurved, and sharp. Digit II is slightly longer than digit I but shorter than digit III; it has a short proximal phalanx, an elongated medial phalanx, and an ungual that is almost completely consistent in size and morphology with the first. Digit III is composed of a relatively short first phalanx, an extremely short second phalanx, a relatively long third phalanx, and an ungual as an acute talon. The wing finger (digit IV) on the left side is nearly completely preserved. Phalanx 1 is slender and long with a slight curvature, a flat proximal end, and a slightly convex and expanded distal end. Phalanx 2 is relatively well preserved on both sides of the specimen; it is distinctly shorter than the first phalanx, only slightly longer than the radius, curved, and has a relatively flat proximal end but a narrow and convex distal end. Only the relatively broadened proximal end of the third phalanx is preserved. Phalanx 4 is not preserved.

On the ilium, the preacetabular process is narrow and elongated with an approximate length of 11-12 mm. Three fragmentary elements are preserved at the left posterior ilium which should represent elements of the pelvic girdle; however the ischium and pubis are not completely preserved.

The left femur has a damaged proximal end but a relatively well preserved distal end. Its length is estimated to be three-quarters that of the tibia. A shallow groove runs along its shaft and the distal condyles are expanded and project laterally. The tibia has almost no curvature and distally its shaft attenuates sharply. The fibula is distinct, thin, gracile, and in tight contact with the lateral side of the tibia. It is estimated to extend only to the midshaft of the tibia.

The pes is slender and elongated, and has a formula of 2-3-4-?-2. Only a single tarsal is preserved at the distal end of the tibia. Metatarsals I-IV are slender, elongated, and nearly consistent in length, nearly one-half as long as the tibia. The fifth metatarsal is short and straight. The morphology of pedal digits I-IV is distinctly consistent with other rhamphorhynchid pterosaurs (Wellnhofer, 1978, 1991); talons are present on all four digits and their lengths do not exceed those of metatarsals I-IV. But digit five bears two exceptionally well developed phalanges, being two-thirds the length of metatarsals I-IV, and the unguis is not in the shape of a talon although it is gently curved and tapers to a point.

Comparison: The Pterosauria include the primitive Rhamphorhynchoidea which spanned the Late Triassic to Jurassic, and the derived Pterodactyloidea which spanned the Late Jurassic to terminal Cretaceous (Wellnhofer, 1978, 1991; Benton, 1993). The pterosaur described in this text is undoubtedly assigned to the Rhamphorhynchoidea based upon the extremely well developed dentition, extremely short wing metacarpal, elongated tail, and two extremely well developed pedal digit V phalanges. This suborder contains four families and two suspect families. The dentition of the Liaoning specimen both resembles and is distinct from the Late Triassic Eudimorphodontidae and the Late Triassic to Early Jurassic Dimorphodontidae. Its long tail is distinct from members of the Late Jurassic Anurognathidae, *Anurognathus* and *Batrachognathus*.

The Rhamphorhynchidae contains more taxa than any other family in the suborder and spans the entire Jurassic. Several of the genera cannot be compared to the new Liaoning specimen because they are extremely damaged or incomplete. Those genera that are relatively complete include *Campylognathoides*, *Dorygnathus*, *Rhamphorhynchus*, *Scaphognathus*, and *Sordes* (Wellnhofer, 1978, 1991), although cranial characters of the Liaoning specimen cannot be compared because it is so fragmentary. The forelimb length indices of *Dendrorhynchus* (Table 2) are extremely distinct from those of *Dorygnathus*, *Scaphognathus*, and *Sordes*, because its first and second wing phalanges are longer than its radius, whereas on the latter three the radius and ulna are the longest forelimb elements and are distinctly longer than the wing phalanges. Although the wing finger phalanges on *Campylognathoides* are all longer than the radius, it differs from *Dendrorhynchus* in phalanx 1 being shorter than phalanx 2. The *Dendrorhynchus* wing finger condition closely resembles several species of *Rhamphorhynchus* (Wellnhofer, 1978, 1991), although there are distinct discrepancies between the two genera: the deltopectoral crest on the *Dendrorhynchus* humerus is much weaker than on *Rhamphorhynchus*, the second wing finger phalanx on the Liaoning specimen is only barely longer than the radius but on all species of *Rhamphorhynchus* is distinctly longer, and finally, the two pedal digit V phalanges on *Dendrorhynchus* are much more modified than on *Rhamphorhynchus*.

It is evident that the specimen described in this text undoubtedly represents a new genus and species of Rhamphorhynchidae hereby erected as *Dendrorhynchus curvidentatus* gen. et sp. nov., and it shares a close phylogenetic relationship with the genus *Rhamphorhynchus*. A large quantity of specimens assigned to the family are excavated from Western Europe but are also represented in Tanzania, India, and Kazakhstan (Wellnhofer, 1991). In China, another occurrence of the family occurs with *Angustinaripterus* from the Middle Jurassic locality of

Dashanpu, Zigong Co., Sichuan (He et al., 1983). The Late Jurassic occurrence of *Dendrorhynchus* constitutes the second documentation of the suborder in China and the first record of the family in the Late Jurassic of East Asia and is thus extremely significant toward the study of the evolution and biogeography of the Pterosauria.

Discussion of age: *Dendrorhynchus* was excavated from the Sihetun vicinity of Beipiao, western Liaoning, where in recent years, a large assemblage of vertebrates has been produced including fishes, frogs, turtles, lizards, theropods, sauropods, ceratopsians, pterosaurs, birds, and mammals (Wang et al., 1998, Chen and Wu, 1998). The sedimentary units producing these specimens were previously considered by most workers to represent either the basal or lower portion of the Yixian Fm. This study disagrees with the original assessment of the nomenclature and concludes that the sediments represent the newly erected sedimentary unit, the Chaomidianzi Fm. (Ji et al., 1998). Currently, the vast majority of geologists recognizes the age of these sediments as Late Jurassic (Chen, 1988; Wu et al., 1989; Yu et al., 1996; Ren et al., 1997). The unit that produced *Dendrorhynchus* is slightly higher than those that produced *Sinosauropteryx* and *Confuciusornis* and also produces another pterosaur, *Eosipterus* (Ji and Ji, 1997). These two pterosaur taxa provide significant paleontological evidence for the age of the sediments.

Globally, numerous regions produce Late Jurassic pterosaurs, including Solnhofen, Germany; Tanzania, Wyoming in the United States, and Kazakhstan. The pterosaurs produced from these localities constitute characteristically primitive members of the Rhamphorhynchoidea in addition to an early member of the relatively derived Pterodactyloidea (Table 3). *Dendrorhynchus* is assigned to the family Rhamphorhynchidae. The latest occurrence of the family, or for that matter the entire suborder, is recognized as Late Jurassic, because to date there are no Cretaceous records of this group (Wellnhofer, 1978, 1991; Benton, 1993). The contemporaneous *Eosipterus* belongs to the Pterodactyloidea and appears to lie at the same evolutionary level as the German *Germanodactylus* in addition to *Ctenochasma* and *Pterodactylus* from Western Europe, the ages of which are also recognized as Late Jurassic (Wellnhofer, 1978; Benton, 1993). Thus based upon the pterosaur characters at Sihetun, the sediments that produced *Dendrorhynchus*, *Eosipterus*, *Sinosauropteryx*, and *Confuciusornis* are undoubtedly Late Jurassic.

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Table 2. Forelimb indices of Rhamphorhynchidae taxa (humerus = 100).*

	<i>Dendrorhynchus curvidentatus</i> Gen. et sp. nov.	<i>Campylognathoides zitteli</i> (Plieninger, 1985)	<i>Dorygnathus banthensis</i> (Theodori, 1830)	<i>Rhamphorhynchus gemmingi</i> (Meyer, 1846)	<i>Rhamphorhynchus longicaudus</i> (Munster, 1939)	<i>Scaphognathus crassirostris</i> (Goldfuss, 1881)	<i>Sordes pilosus</i> (Sharov, 1971)
Radius	124.8	117.1	157.4	158.4	161.8	175.7	170.0
Wing finger Mc	33.5	42.9	47.5	46.8	60.6	50.5	37.5
Wing finger D1	160.1	264.3	119.7	266.2	224.2	130.8	115.0
Wing finger D2	128.1	298.6	144.3	259.7	192.7	140.2	130.0
Wing finger D3	>101.1	235.7	144.3	235.1	175.2	...	130.0
Wing finger D4	...	173.6	116.4	244.9	196.4	...	82.5

* Data from Wellnhofer, 1978 (with exception of *D. curvidentatus*)

Table 3. Global distribution of Late Jurassic pterosaurs.

	Solnhofen Germany	Tendaguru Tanzania	Como Bluff USA	Karatau Kazakhstan	Beipiao China
Rhamphorynchoidea					
Rhamphorhynchidae					
<i>Rhamphorhynchus</i>	+++	+			
<i>Sordes</i>				+	
<i>Dendrorhynchus</i>					+
Anurognathidae					
<i>Anurognathus</i>	+				
<i>Batrachognathus</i>				+	
Family indet.					
<i>Comodactylus</i>			+		
Pterodactyloidea					
Pterodactylidae					
<i>Pterodactylus</i>	+++	+			
<i>Germanodactylus</i>	+				
Ctenochasmatidae					
<i>Ctenochasma</i>	+				
Family indet.					
<i>Dermodactylus</i>			+		
<i>Eosipterus</i>					+