NOTES

# A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and "hairs" from Inner Mongolia, northeast China

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**Abstract** **We report a new and nearly completely articulated rhamphorhynchoid pterosaur, *Jeholopterus ningchengensis* gen. et sp. nov., with excellently preserved fibres in the wing membrane and "hairs" in the neck, body and tail regions. Many of its characteristics such as a short neck, short metacarpals and distinctively long fifth pedal digit are characteristic of rhamphorhynchoids. The new species can be further referred to the 'strange' short-tailed rhamphorhynchoid family Anurognathidae. It is much more complete than the other known members of the family, namely, *Anurognathus* from Solnhofen, Germany, *Batrachognathus* from Karatau, Kazakhstan, and *Dendrorhynchoides* from Beipiao, Liaoning Province, China. The new pterosaur also shows that the wing membrane is attached to the ankle of the hind limb. The pedal digits are webbed. Furthermore, the "hair" of *Jeholopterus* bears some resemblance to the hair-like integumental structures of the feathered dinosaur *Sinosauropteryx* although there is yet no direct evidence to argue for or against their homology.**

**Keywords: Anurognathidae, Jeholopterus, Wing membrane, "hair", Yixian Formation, Inner Mongolia,**

The lacustrine Yixian Formation deposit from western Liaoning and neighboring areas in northeast China is famous for its beautiful preservation of feathered dinosaurs, early birds, mammals, and angiosperms. Wing membrane and other soft tissues were rarely completely preserved in pterosaurs[1~3], The new species represents the most complete individual of a poorly known pterosaur family, Anurognathidae[4]. The preservation of the wing membrane and "hair" is among the best of all known pterosaurs. The holotype was collected from the deposits in Ningcheng, Inner Mongolia. The deposits presumably represent the lowest level of the Yixian Formation, which is equivalent to the Dabeigou Formation in Hebei Province[5] and is lower than the Jianshangou Bed of the Yixian Formation that contains abundant *Confuciusornis* and feathered dinosaurs in western Liaoning Province.

## 1 Systematic paleontology

Order Pterosauria Kaup, 1834

Suborder Rhamphorhynchoidea Plieninger, 1901

Family Anurognathidae Kuhn, 1937

*Jeholopterus ningchengensis* gen. nov.

*Jeholopterus ningchengensis* gen. et sp. nov.

(Plates Ⅰ and Ⅱ; fig. 1)

**Etymology.** The generic name is derived from the famous type specimen-bearing Jehol Group; the species name is from the Chinese spelling of the locality Ningcheng County of Inner Mongolia.

**Holotype.** A nearly completely articulated skeleton with excellent preservation of wing membrane and "hairs"; Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) collection number V 12705.

**Locality and horizon.** Daohugou, Ningcheng, Inner Mongolia, China. Lower Yixian Formation; Early Cretaceous[6].

**Diagnosis.** *Jeholopterus* can be distinguished from *Dendrorhynchoides* and other taxa of the Anurognathidae by its nearly twice body size (wing span 90 cm long), much more robust and longer first phalanx of fifth pedal digit (first phalanx of fifth pedal digit robust and as long as metatarsals Ⅰ—Ⅳ), and straight second phalanx of fifth pedal digit. Skull wider than long. Wing metacarpal less than one quarter the length of lower arm. Among the four phalanges of wing digit, the first is longer than the radius, the second is close to the radius, and the third and fourth remarkably shorter. Wing claws extremely long, and about one and half as long as the pedal claws. Fifth pedal digit long and about one and half the length of the third digit.

**Description.** The type of *Jeholopterus* is a nearly complete specimen with the skull and nearly all postcranial bones preserved in articulation. It is a small to medium-sized pterosaur with a wingspan of about 90 cm (table 1). Fibers and "hairs" were preserved (Plates Ⅰ and Ⅱ; fig. 1). The scapula and the coracoid are fused, indicating that it is an adult or subadult individual.

**Skull.** The skull is ventro-dorsally preserved; it is generally similar to that of *Anurognathus*[7,8], *Batrachognathus*[9] and *Dendrorhynchoides*[10,11], but is shorter and wider. The length of the skull of *Jeholopterus* is about 28 mm. It is wider than its length and is shorter than most other pterosaurs, with a frog-like jaw. The teeth are generally short. The teeth on the premaxilla are longer and more curved than those on the maxilla. The maxilla has a slender and vertical dorsal process, indicating that the skull is high. The dentary is toothed too.

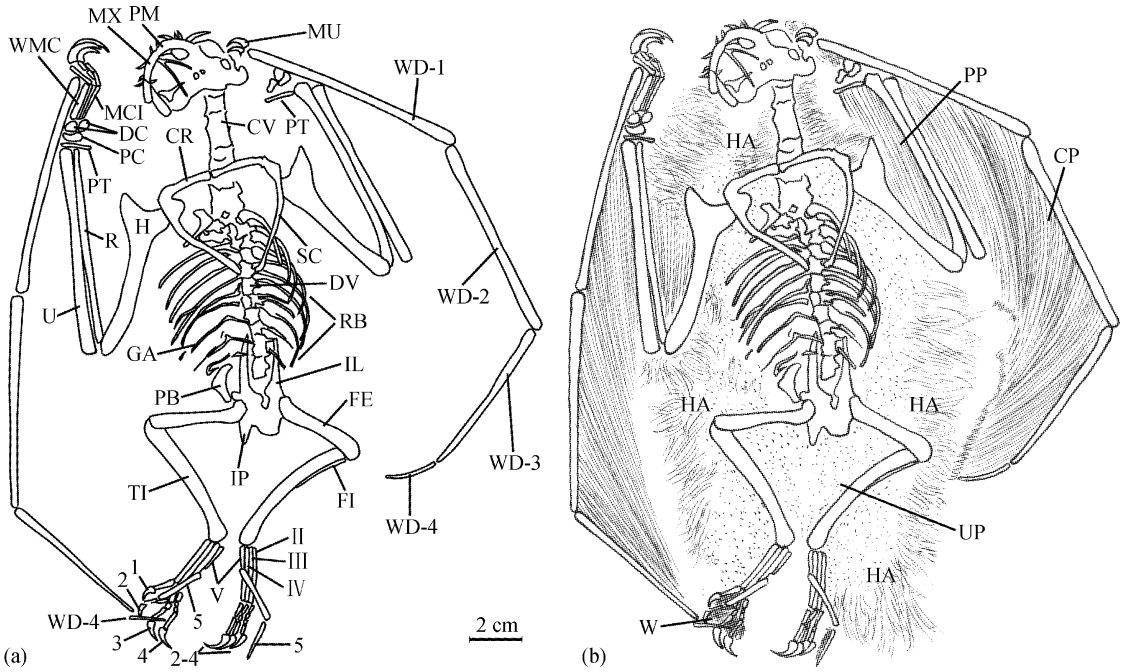


Fig. 1. (a) Composite line drawing of the skeleton of part and counterpart specimens, and (b) reconstruction of the attachment of various parts of the wing membrane to the skeleton and the distribution of "hairs" of *Jeholopterus ningchengensis* gen. et sp. nov. (IVPP V12705). CP, cheiropatagium; CR, coracoid; CV, cervical vertebra; DC, distal carpals; DV, dorsal vertebra; FE, femur; FI, fibula; GA, gastralia; H, humerus; HA, "hair"; IL, ilium; IP, ischiopubis; MC I, metacarpal I; MX, maxilla; MU, manual unguals; PB, prepubis; PC, proximal carpal; PM, premaxilla; PP, propatagium; PT, pteroid; R, radius; RB, rib; SC, scapula; TI, tibia; U, ulna; UP, uropatagium; W, web; WD 1—4, first through fourth phalanges of the wing digit; WMC, wing metacarpal; Ⅰ—Ⅴ, metatarsals Ⅰ—Ⅴ; 1—5, first through fifth pedal digits.

Table 1 Lengths (mm) of major skeletal elements of *Jeholopterus ningchengensi*s gen. et sp. nov. (IVPP V 12705)

| | left | right |
|---|---|---|
| Scapula | 49* | 49 |
| Coracoid | 25* | 24* |
| Humerus | 57+ | 62 |
| Ulna | 82+ | 89 |
| Radius | 81 | 82 |
| Wing metacarpal | | 19* |
| Metacarpals Ⅰ—Ⅲ | | 18* |
| First phalanx of wing digit | 83+ | 93 |
| Second phalanx of wing digit | 79 | 82 |
| Third phalanx of wing digit | 61 | 60 |
| Fourth phalanx of wing digit | 18 | 16 |
| Femur | 38* | 40 |
| Tibia | 50 | 50 |
| Metatarsals Ⅰ—Ⅳ | | 22* |
| Metatarsal Ⅴ | 10 | 10 |
| Total length of first pedal digit | | 14 |
| Total length of second pedal digit | | 22 |
| Total length of third pedal digit | | 26 |
| Total length of fourth pedal digit | | 26 |
| First phalanx of pedal digit Ⅴ | 23 | 20+ |
| Second phalanx of pedal digit Ⅴ | 16 | |

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

**Vertebral column.** The neck is composed of 7 or 8 cervical vertebrae; it is shorter than the spinal column between the neck and the tail as typical of rhamphorhynchoid pterosaurs. The cervical vertebra is short and robust. There exist short and slender cervical ribs. There are 12—13 dorsal vertebrae. The sacrum is composed of three sacral vertebrae. No caudal vertebrae are preserved, but the tail is probably short as in *Anurognathus* based on the preservation of the "hairs" presumably in the tail region (Plates Ⅰ and Ⅱ-3). Five rows of gastralia were preserved; each is composed of a "V"-shaped central piece and two slender, thin and curved sidepieces. The gastralia become progressively shorter caudally.

**Pectoral girdles.** The scapula and the coracoid are fused as in most pterosaurs. The two scapulae meet at an angle of about 60° in a "V" shape. The scapula is relatively long and about twice as long as the coracoid.

**Forelimbs.** The forelimb is long. The total length of the humerus+ulna+wing metacarpal is about one and half that of the femur+tibia+metatarsal Ⅱ. The wing digit is about 6.3 times as long as the femur.

The humerus is robust. The deltoid-pectoral process is short and broad, with a pointed proximal end. The shaft is slightly bow-shaped. Both the ulna and radius are straight and are significantly longer than the humerus.

Two proximal carpals seem to be fused into one. There are two distal carpals. The pteroid is slender; its total length is unknown because it has not been completely exposed for the sake of the preservation of fibres around this area; it is directed towards the body.

The metacarpals are extremely short. They are less than one quarter the length of the radius. The wing metacarpal is much more robust than the other three. Claws of the first three digits are extremely long and about one and half as long as the pedal claws; the claws are sharp and curved. The wing digit is about 4 times as long as the humerus, and about 11.4 times that of the wing metacarpal. It is composed of four elongated phalanges; among them, the first is the longest and is much longer than the radius, the second is close to the radius, the third is shorter than the radius, and the fourth phalanx is the smallest and only about one fifth the length of the radius.

**Pelvic girdles.** The pelvis is articulated with the hindlimb and was dorso-ventrally preserved. The ilium is narrow; it is extended posteriorly and tapers slightly toward the anterior end. The ischium appears to be fused with the pubis and forms the ischiopubis, which is strap-shaped and tapers posteriorly. The prepubis is characteristic of rhamphorhynchoid pterosaurs in being long, slender and bar-shaped. The prepubis is not articulated with the pubis. Since only the left prepubis was preserved, it is unclear how it was held together with the right prepubis.

**Hindlimbs.** The hindlimb is robust. The femurs are straight and were preserved nearly vertical to the vertebral column. The tibia is as robust as the femur. The fibula is reduced and is less than half the length of the tibia. Metatarsals Ⅰ—Ⅳ are straight and parallel to each other; they are nearly equal in length and are less than half the length of the tibia. Metatarsal Ⅴ is short and less than half the length of metatarsals Ⅰ—Ⅳ.

The phalangeal format of the foot digits is "2-3-4-5-2" as is typical of rhamphorhynchoids. The fifth pedal digit is long and about one and half the length of the third digit. The fifth pedal digit is reflected medially. It is composed of two long phalanges. They form a distinctive angle as is typical of rhamphorhynchoids. The first phalanx is robust; it is about as long as metatarsal Ⅱ. The second phalanx is straight and tapers distally; it is slender and slightly shorter than the first phalanx. The fifth pedal digit lacks the claw (Plate Ⅰ-1). The other four digits all possess well developed claws; they are long, sharp and strongly curved. In digit Ⅱ the second phalanx is longer than the first phalanx. In digit Ⅲ the third phalanx is longer than the first phalanx; the second phalanx is much shorter than the first and third phalanges. In digit Ⅳ the fourth phalanx is the longest, the first phalanx is second in length, the second and third phalanges are much shorter than the other two. Therefore, in pedal digits Ⅱ—Ⅳ, the distal phalanges are longer than the basal phalanges.

**Wing membranes.** The wing membrane represents one of the most distinctive features of the new pterosaur. The propatagium, cheiropatagium and the uropatagium of the wing membrane can well be recognized (Plate Ⅰ; fig. 1(b)). It can be clearly seen that the cheiropatagium attaches to both sides of the legs as far as the ankle. The fibers of the cheiropatagium are generally straight and long (Plates Ⅰ and Ⅱ-1). The uropatagium is between the two legs and composed of fibres that are shorter than those of the cheiropatagium.

It is also noteworthy that short fibres were also preserved associated with the pedal digits, including the fifth digit, which indicates that the foot was webbed (Plate Ⅱ-4).

**"Hairs".** In addition to the straight structural fibres of the wing membranes, there exists another type of fibre-like integumentary structures that are present all over the body (Plates Ⅰ—Ⅱ). They are generally shorter, wavy and more curved. Further more, they usually form clusters, presumably another line of evidence for being recognized as "hairs". They taper distally.

## 2 Discussions

*Jeholopterus* was collected from a locality in Ningcheng, Inner Mongolia, which is about 130 km northwest of the famous Sihetun locality in Beipiao, Liaoning Province in northeast China[5]. Associated with the pterosaur are abundant conchostrachans and insects. The faunal assemblage of this locality is unique in having unusually abundant amphibians[12] but lacking fish fossils.

The skeletal bones were nearly completely preserved, thus providing important information for the discussion of its systematic position. The cervical vertebrae are short and robust; their combined length is remarkably shorter than the vertebral column between the neck and the tail as typical of Rhamphorhynchoidea. In addition to a short neck, many of its other characteristics such as short metacarpals, distinctively long fifth pedal digit with two long phalanges and slender bar-shaped prepubis are also characteristic of rhamphorhynchoids. Pterodactyloids usually have a reduced and very short fifth pedal digit comprising no more than one phalanx. *Jeholopterus* appears to have a short tail as indicated by the position and the outline of the "hairs" in the tail region.

The skull of *Jeholopterus* was not completely preserved; it is short, wide and deep as in *Dendrorhynchoides, Anurognathus* and *Batrachognathus*; the latter three are referred to the peculiar short-tailed rhamphorhynchoid family Anurognathidae[13]. As in *Anurognathus* the first wing phalanx is much longer than the ulna; in *Sordes*[14] the reverse is true. But in *Rhamphorhynchus* and *Pterodactylus* the first and second wing phalanges are much longer than the ulna. Besides, the fifth pedal digit of *Jeholopterus* is significantly long. As in *Anurognathus* the

first phalanx of the fifth pedal digit is approximately as long as metatarsal Ⅱ in *Jeholopterus*. In *Rhamphorhynchus*, the first phalanx of the fifth pedal digit is much shorter than metatarsal Ⅱ. *Jeholopterus* also shares with *Anurognathus* and *Batrachognathus* extremely large claws on the first three manual digits. Therefore, it is obvious that *Jeholopterus* should be referred to the family of Anurognathidae.

Most of the pterosaurs from the Yixian Formation are referred to Pterodactyloidea[15,16]. The only reported rhamphorhynchoid from northeast China is *Dendrorhynchoides* from western Liaoning Province[10,11,13]. It has been correctly identified as a rhamphorhynchoid in its first report; however, it has also been later argued that its "long tail" was doctored rather than natural[13,17]. *Dendrorhynchoides* is much smaller than *Jeholopterus*; the former has a wingspan of only about 40 cm compared to about 90 cm in the latter. However, these two pterosaurs share many features: a short skull, a short neck, extremely short metacarpals, wing metacarpal about one third the length of the humerus, first wing phalanx longer than the ulna, second wing phalanx nearly as long as the radius, metatarsal Ⅱ about 44% the length of tibia, fifth pedal digit long, first phalanx of the fifth pedal digit extends distally past the distal end of metatarsal Ⅱ. Many of characteristics and nearly identical skeletal proportions shared by *Jeholopterus* and *Dendrorhynchoides* confirm the suggestion that the latter be referred to the family Anurognathidae[13].

*Batrachognathus* is now represented by two individuals[14,18,19], the wingspan of which is about 75 cm, which is slightly larger than that of *Anurognathus* (50 cm). Besides, a small sized pterosaur specimen from Mongolia has been proposed to be a possible member of the family of Anurognathidae[18]. Therefore, *Jeholopterus* represents the largest member of this family. *Dendrorhynchoides* is, however, the smallest known member of the family (the wing span is about 40 cm).

*Jeholopterus* is different from other taxa of the family Anurognathidae by several characters: first, the first phalanx of the fifth pedal digit is more robust and as long as metatarsals Ⅰ—Ⅳ, it is slightly shorter than metatarsals Ⅰ—Ⅳ in *Anurognathus*, and it is even proportionally shorter in *Dendrorhynchoides*; second, the second phalanx of the fifth pedal digit is straight, but it is curved in *Anurognathus* and *Dendrorhynchoides*.

*Jeholopterus* appears to be most similar to *Dendrorhynchoides* in Anurognathidae. They share a much wider and shorter skull than *Anurognathus* and *Batrachognathus*.

Anurognathidae is not only a unique and the "strangest" group of pterosaurs, it also preserved many primitive characteristics except for a short tail as in pterodactyloids, it is generally believed to have been derived from a primitive clade of pterosaurs at an early stage of pterosaur evolution[2]. The discovery of *Jeholopterus* also shows that Anurognathidae had not only survived to the Early Cretaceous but also experienced more morphological differentiations than previously assumed.

Due to frequent volcanic activities and widely distributed lake environments soft tissues and protofeathers were often particularly well preserved with articulated skeletons in various vertebrate fossils such as the feathered dinosaurs *Sinosauropteryx*[20], *Sinornithosaurus*[21] and *Caudipteryx*[22] from the Early Cretaceous Yixian Formation in western Liaoning and its neighboring areas. *Jeholopterus* represents one of the best preservations of wing membrane and hair-like structures in pterosaurs. Several important conclusions about the wing membrane and other soft tissues of pterosaurs can be drawn from the observation of the new fossil.

First, it has been a debated issue as to how the wing membrane is attached to the rest of the body. It has been proposed that the wing might have been attached to the trunk, the femur or the ankle of the leg, respectively[23~28]. The new pterosaur shows evidence that the wing has a narrow tip, and although the attachment of the wing with the rest of the body may be different in various pterosaurs, at least in *Jeholopterus* it is attached to the ankle of the leg (Plate Ⅰ; fig. 1(b)).

Second, *Jeholopterus* clearly preserved an uropatagium (Plates Ⅰ and Ⅱ-3), a structure that had been strongly doubted but was evident in *Sordes pilosus* from the 'Late Jurassic' of middle Asia[24, 29]. An elongate fifth toe is present as in *Anurognathus*. The fifth toe is reflected medially, its two phalanges also form a distinctive angle, presumably for the attachment of the uropatagium, which is used for maneuvering and braking. The hind limbs also show a comparable positioning to that in *Sordes*: the femur is almost perpendicular to the spinal column.

Third, whether pterosaurs are warm-blooded and "haired" vertebrates has been a controversial question. *Sordes pilosus* has been argued to possess the best evidence of "hairs" in pterosaurs[18, 25]. The putative differences between "hairs" and fibers in *Sordes pilosus* include: (1) they are present in regions of the body remote from the wing membrane such as the posterior margin of the skull; (2) they are markedly thicker than those of the wing membrane; (3) they taper from the base to the tip; (4) they are often curved in very tight arcs; and (5) they lack internal structure. In *Jeholopterus*, "hairs" are short, thicker and more curved; they also taper from the base to the tip; and they are associated with the whole body from the neck to the tail region. Functionally, the "hairs" of pterosaurs could be used for thermoregulation, flight or reducing noises during flight. It should be noted that fibres of the cheiropatagium also taper toward the distal end. Therefore, it cannot be used to distinguish "hairs" from

fibres.

Fourth, the distal toes of the foot of *Jeholopterus* are longer than the basal ones in digits Ⅱ—Ⅳ as in *Anurognathus*. The presence of clearly preserved fibres associated with the toes indicates that the foot was webbed and the web was probably reinforced or supported by fibres, which functioned in a similar way as the fibres in the wing (Plate Ⅱ-4). Similar structures were also present in a Crato Limestone pterosaur[30]. It may also indicate that *Jeholopterus* could live near the water. The wing is extremely long, indicative of powerful flight capability. The mouth is broad and short; teeth are generally short and peg-like, suggesting that *Jeholopterus* was probably mainly insectivorous as *Batrachognathus*. However, some teeth are long and curved, indicating that it could also prey on other animals such as fishes.

Fifth, the fiber-like integuments in pterosaurs have been generally called "hairs"; however, most workers admit that they are not the same structures of mammalian hairs, and it has thus been suggested that bristle is used to replace "hair" to avoid confusion with the mammalian "hairs"[3]. The "hairs" of *Jeholopterus* bear some resemblance to the hair-like integumental structures of the feathered dinosaur *Sinosauropteryx* and *Beipiaosaurus*. The integuments in the latter two dinosaurs are fibre-like, with no branching structure. Besides, they are distributed along the full body. Based on phylogenetic result, it is now generally agreed that the fibre-like integuments in these dinosaurs may represent protofeathers[21]. Although no one has proposed that pterosaurs might have protofeathers there is, however, no direct evidence to argue for or against the homology between the "hairs" of pterosaurs and the fibre-like integuments in *Sinosauropteryx*.

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