Discovery of a rare arboreal forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China

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A previously undescribed toothless flying reptile from northeastern China, *Nemicolopterus crypticus* gen. et sp. nov., was discovered in the lacustrine sediments of the Early Cretaceous Jiufotang Formation, western Liaoning, China. The specimen consists of an almost complete articulated skeleton (IVPP V14377) and, despite representing an immature individual, based on the ossification of the skeleton, it is not a hatchling or newborn, making it one of the smallest pterosaurs known so far (wing span ≈250 mm). It can be distinguished from all other pterosaurs by the presence of a short medial nasal process, an inverted "knife-shaped" deltopectoral crest of the humerus, and the presence of a well developed posterior process on the femur above the articulation with the tibia. It further shows the penultimate phalanges of the foot curved in a degree not reported in any pterosaur before, strongly indicating that it had an arboreal lifestyle, more than any other pterodactyloid pterosaur known so far. It is the sister-group of the Ornithocheiroidea and indicates that derived pterosaurs, including some gigantic forms of the Late Cretaceous with wingspans of >6 m, are closely related to small arboreal toothless creatures that likely were living in the canopies of the ancient forests feeding on insects.

Early Cretaceous | pterosaur | western Liaoning | Jiufotang Formation | Jehol Biota

Fig. 1. Sketch of a map of China with the indication of a new locality.

Regarded as the first vertebrate group fully adapted to a powered flight (1, 2), pterosaurs show a rather sparse record that is strongly biased toward ancient coastal environments, and true habitants of inland regions are extraordinarily rare (3, 4). One exception is the Jehol Group, whose fossil deposits have revealed a magnificent quantity of well preserved material that is shaping our understanding of the evolution of several groups of vertebrates (5, 6). Divided into the Yixian and Jiufotang Formations and as indicated by radiometric datings, those terrestrial ecosystems existed between 125 and 120 million years ago (7, 8). With respect to pterosaurs, extensive collecting in those deposits (Fig. 1) shows that their diversity already rivals that of other important *lagerstätten* such as the Upper Jurassic Solnhofen Limestone (1) and the Lower Cretaceous Santana Formation (2). Here, we report on a previously undescribed pterosaur that provides some insight on inland living pterosaurs.

Background

Systematics. The systematics are as follows: Pterosauria Kaup, 1834; Pterodactyloidea Plieninger, 1901; Dsungaripteroidea Young, 1964; *Nemicolopterus crypticus* gen. et sp. nov.

Etymology. *Nemicolopterus crypticus* comes from the Greek language as follows: *Nemos*, "forest" and *ikolos*, "dweller," plus *pteros*, "wing," and *kryptos*, "hidden," the full meaning being "hidden flying forest dweller."

Holotype. An almost complete skeleton has been deposited at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing (IVPP V-14377; Figs. 2 and 3).
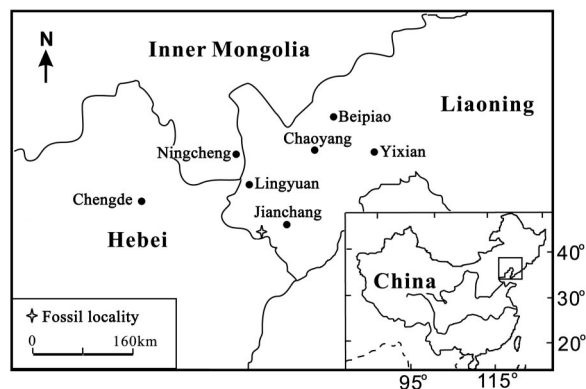
The horizon and locality are as follows: Jiufotang Formation [120 million years, Aptian (7)] at the locality Luzhougou, Ya-olugou Town, Jianchang County, Huludao City, western Liaoning Province.

Diagnosis. *Nemicolopterus crypticus* represents the smallest dsungaripteroid pterosaur known so far, with the following unique characters: nasal with a short but not knob-like medial nasal process; humerus with the distal margin of the deltopectoral more elongated than the proximal portion, giving it an inverted "knife-shaped" appearance; well developed posterior process on the femur above the articulation with the tibia; penultimate pedal phalanges strongly curved ventrally; fourth pedal digit with penultimate phalanx longer than the first (convergent with anurognathids).

Description. The specimen is preserved in a slab of sedimentary rock formed by intercalating siltstones and mudstones. The material is largely complete but lacks most of the left wing and the distal and proximal portion of the right wing metacarpal and first wing phalanx, respectively. Except for the skull, which drifted slightly away from its original position (≈17 mm), the skeleton is articulated with nearly all bones in correct anatomical position. The skull and mandible lie on their left sides whereas most of the postcranial skeleton is exposed dorsally. All bones

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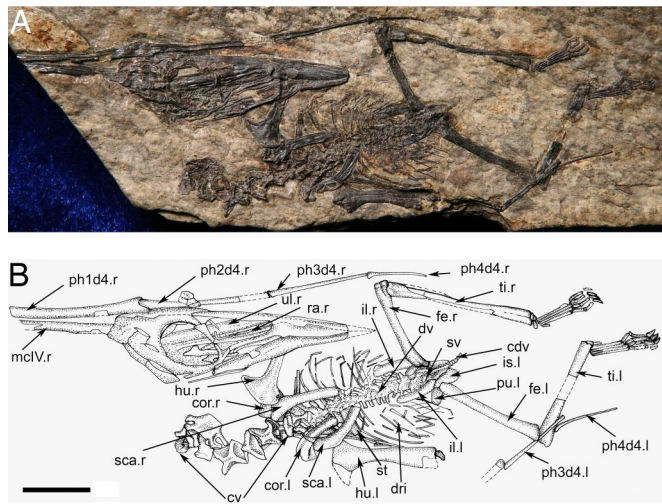
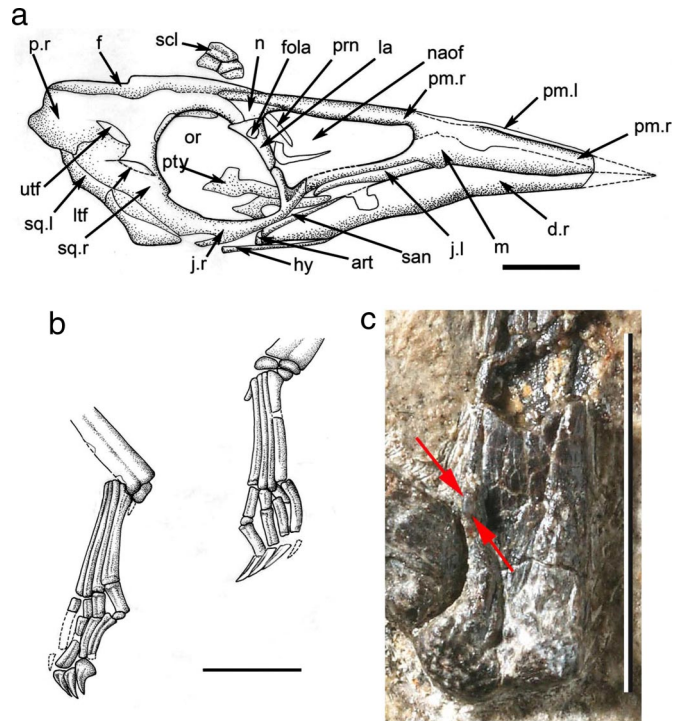**Fig. 2.** *Nemicolopterus crypticus* gen. et sp. nov., a basal dsungaripteroid from the Jiufotang Formation, Liaoning Province, China. (*A*) Photograph. (*B*) Drawing of the complete skeleton. (Scale bar: 1 cm.) cdv, caudal vertebrae; cor, coracoid; cv, cervical vertebrae; dri, dorsal ribs; dv, dorsal vertebrae; fe, femur; hu, humerus; il, ilium; is, ischium; mcIV, metacarpal 4; ph1d4, first phalanx of manual digit IV; ph2d4, second phalanx of manual digit IV; ph3d4, third phalanx of manual digit IV; ph4d4, fourth phalanx of manual digit IV; pu, pubis; ra, radius; sca, scapula; st, sternum; sv, sacral vertebrae; ti, tibia; ul, ulna; l, left; r, right.

have been compressed to different degrees, a common feature in pterosaur specimens (1, 2), but the bone surface is overall well preserved. No soft tissue is preserved, but in some parts along the bones and particularly in the region of the gastralia, there are portions of yellow colored matrix occasionally forming rounded structures (one large portion preserved close to the right femur). Although their true nature cannot be established here, the yellow material could be remains of decomposed soft tissues or amorphous stomach contents.

Nemicolopterus crypticus is a toothless pterosaur with an estimated wingspan of 250 mm. The skull is elongated with a maximum length of 40.3 mm [tip of premaxilla to squamosal (pm-sq) is 37.8 mm]. The orbit is oval (maximum diameter 9.3 mm) and has a similar shape to that of the species classified in the Archaeopterodactyloidea (9) (e.g., *Pterodactylus*, *Germanodactylus*). The nasoantorbital fenestra is relatively small (25.4% of the pm-sq length), being only larger than that of *Pteranodon* and the Ctenochasmatidae (*Pterodaustro* plus *Ctenochasma*). The rostrum occupies ≈40% of the skull (pm-sq) length. The nasal forms the dorsoposterior margin of the nasoantorbital fenestra and bears a short medial nasal process. The lacrimal forms the upper posterior margin of the nasoantorbital fenestra and has a well developed rounded lacrimal foramen. The jugal is a triradiate element with a comparatively thin maxillary process that makes up most of the ventral border of the nasoantorbital fenestra. The lacrimal process of the jugal is mainly directed dorsally. No evidence of a sagittal cranial crest is recognized. The occipital region is compacted, and bones cannot be easily identified. Part of the occiput is displaced from the skull and remains connected with the cervical vertebrae and the remaining parts of the skeleton (Fig. 2). Some thin bony plates that form the sclerotic ring are also preserved and were shifted from their original anatomical position dorsal to the skull roof, above the right first wing phalanx. One long and rod-like element preserved ventral to the lower jaw is interpreted as a hyoid bone (Fig. 3).

The lower jaw (length 26.3 mm) is tightly connected with the skull, and the craniomandibular articulation is situated under the

Fig. 3. *Nemicolopterus crypticus* gen. et sp. nov. details of the skeleton. (*a*) Drawing of the skull. (*b*) Distal part of the tibiae and feet. (*c*) Detail of the posterior process of the femur (arrow). (Scale bar: 5 mm.) art, articular; d, dentary; f, frontal; fola, foramen lacrimale; hy, hyoid bone; j, jugal; la, lacrimal; ltf, lower temporal fenestra; m, maxilla; n, nasal; naof, nasoantorbital fenestra; or, orbit; p, parietal; pm, premaxilla; prn, processus nasalis; pty, pterygoid; san, surangular; scl, sclerotic ring; sq, squamosal; utf, upper temporal fenestra; l, left; r, right.

anterior half of the orbit. The mandibular symphysis is long, occupying ≈46.0% of the lower jaw length. It lacks a mandibular crest such as the one present in *Tapejara wellnhoferi* (9), anhanguerids (10, 11) and *Sinopterus dongi* (12).

The postcranial skeleton of *Nemicolopterus crypticus* is almost complete. The cervical vertebrae are short, those of the middle series subequal in size, and there is no evidence of cervical ribs. Dorsal vertebrae are not fused into a notarium. There are at least eight sacral vertebrae, but they are not fused into a synsacrum. Four caudal vertebrae are present, suggesting that this animal had a short tail. The first two ribs are larger and stronger than all others. The gastralia are slender and flattened elements, with some showing a "V-shaped" structure.

The scapula and coracoid are not fused. The scapula (11.5 mm) is longer than the coracoid (8.3 mm) and shows an elongated scapular blade with parallel borders. The coracoid shows a ventral distal expansion but lacks the coracoid flange of azhdarchids (9). On the right side, a developed pneumatic foramen pierces the dorsal margin of this bone, close to the glenoid articulation surface. Although the sternum cannot be observed in detail, the lateral portions are visible close to the proximal ends of the scapulae, clearly showing that this bone was well ossified and apparently wider than long.

The pelvic region is crushed, but some general anatomic information can be obtained. The ilium has a long preacetabular blade and the postacetabular portion is very short. The pubis is a laterally compressed bone forming the anterior (and likely also the ventral) part of the acetabulum. The anteroventral part for the prepubis (not preserved in this specimen) is ventrally expanded, making the ventral margin of this bone unusually concave (in lateral view). The ischium is also a laterally com-

pressed bone with the posteroventral portion distinctly rounded. It is not clear whether those elements are fused.

Both humeri are present but preserved in different conditions (Fig. 2). The left one has a complete shaft, but the deltopectoral crest is broken. An epiphysis is present on the distal articulation, slightly displaced from its natural position. The length of this bone is ≈15.2 mm. The right humerus has a well preserved proximal part, and the distal end is partly covered by the skull (Fig. 2). It shows a peculiar deltopectoral crest, with the distal margin rather straight and the dorsal margin distinctly curved, giving this structure an inverted "knife-shaped" appearance. A small pneumatic foramen is present on the dorsal side of the proximal articulation of the humerus. Only the radius and ulna (length ≈20 mm) from the right side are preserved, and they are covered by the skull, impeding any detailed information. The first wing metacarpal is only partially preserved on the right side; nevertheless, it is an elongated bone, a typical feature of the Pterodactyloidea (9, 10). The third wing phalanx (length: 16.2 mm) is smaller than the first (with a preserved and estimated length 20.8 mm and 22.5 mm, respectively) and the second (length: 20.9 mm), a trend established by *Campylognathoides*, a basal Novialoidea (9) (Fig. 4).

The hindlimbs are complete with the femora directed outward and slightly backward relative to the pelvis. Both femora have a straight shaft. The left one is severely compressed, with the distal articulation completely flattened, artificially increasing its length (preserved: 18.5 mm; estimated: 16.5 mm). The right one (length: ≈16 mm) is better preserved with the distal portion almost three-dimensional, showing a distinct posterior process, close to the medial margin (Fig. 3c). Neither tibia is well preserved. Besides being flattened, the right one was compressed taphonomically along its major axis, resulting in crushing, overlapping, and loss of some portions. The right one is better preserved (length 23.1 mm), showing a more three-dimensional outline, but some parts were broken possibly during the collecting process. The feet are also complete and show the penultimate phalanges curved ventrally, particularly on the first and fourth digits. The penultimate phalanx of the fourth digit is longer than the first. The unguals are laterally compressed and dorsoventrally expanded with a well developed flexor tubercle, likely the insertion point of flexor muscles.

Discussion

This recently discovered pterosaur species can be referred to the Pterodactyloidea based on several features such as the confluent naris and antorbital fenestra, a long wing metacarpal, a reduced tail, and the pedal digit V lacking elongated phalanges and reduced to a tiny metatarsal (length 0.8 mm) (9, 10). To establish the phylogenetic position of *Nemicolopterus crypticus*, we performed a cladistic analysis using the dataset published by Wang *et al*. [ref. 4; see supporting information (SI) *Appendix*]. The result was rather surprising, because the most extraordinary aspect of this species is the absence of the synapomorphic features of the main pterodactyloid clades. Regarding the Archaeopterodactyloidea (Fig. 4), *Nemicolopterus crypticus* lacks the rounded posterior region of the skull and the elongated midcervical vertebrae that diagnose this group. It has the posterior part of the skull elongated but lacks any crest such as the laterally compressed parietal crest present in *Feilongus* and the Gallodactylidae (4, 9). *Nemicolopterus crypticus* shows a nasal process, but this structure differs from the archaeopterodactyloid condition by being placed medially but not laterally. The nasal process of *Nemicolopterus* seems to be unique by being much shorter than the medial nasal process as reported in *Anhanguera* (1, 11) and *Sinopterus dongi* (12) and longer than the knob-like structure present in *Thalassodromeus sethi* (13) and *Pteranodon* (14). Last, *Nemicolopterus*
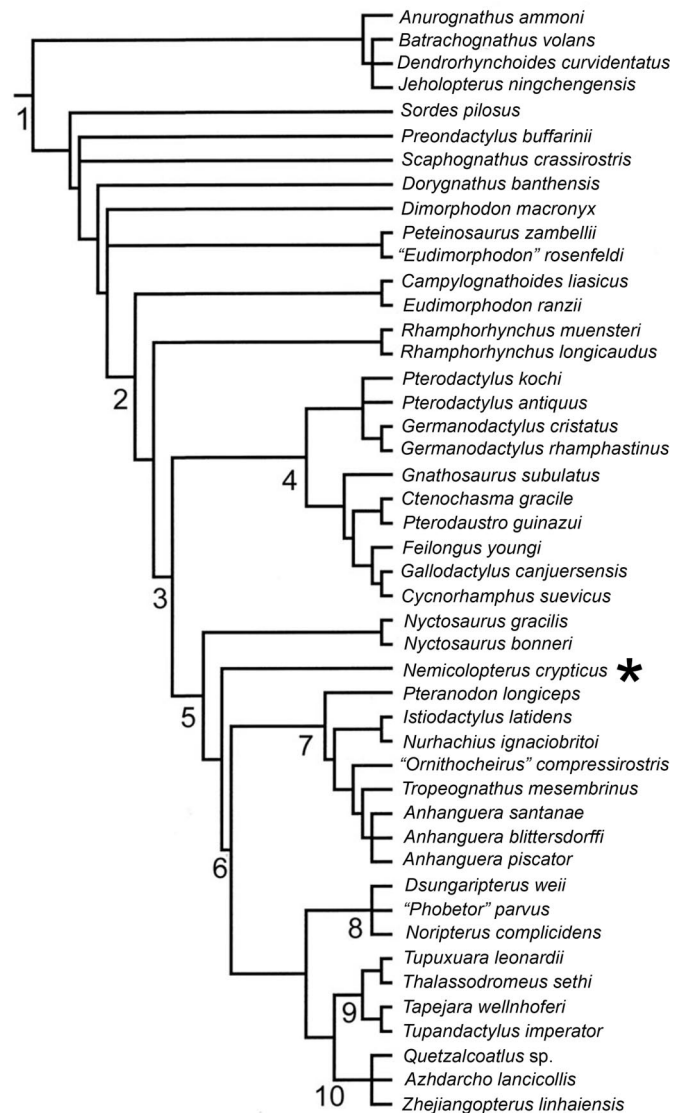
Fig. 4. Cladogram showing the phylogenetic position of *Nemicolopterus crypticus* gen. et sp. nov. (see *SI Appendix*). 1, Pterosauria; 2, Novialoidea; 3, Pterodactyloidea; 4, Archaeopterodactyloidea; 5, Dsungaripteroidea; 6, Ornithocheiroidea; 7, Pteranodontoidea; 8, Dsungaripteridae; 9, Tapejaridae; 10, Azhdarchidae. ∗, Phylogenetic position of *Nemicolopterus crypticus*.

crypticus is toothless, and all members of the Archaeopterodactyloidea bear teeth.

The toothless condition is widespread among the Dsungaripteroidea. *Nemicolopterus crypticus* also shares with dsungaripteroids the presence of a dorsal pneumatic foramen on the proximal articulation of the humerus (Fig. 2).

The cladistically more basal dsungaripteroid pterosaur group is the Nyctosauridae, characterized by having a long wing metacarpal more than double the length of the humerus (15). Although the wing metacarpals are not completely preserved in *Nemicolopterus crypticus*, the length ratios between the humerus and the second and third wing phalanges differ remarkably from that of *Nyctosaurus*, which has longer phalanges, and allows us to confidently infer that the Chinese taxon lacks the extremely elongated wing metacarpal condition. *Nemicolopterus crypticus* also does not show the particularly hatched-shaped deltopectoral crest of the humerus that is displaced further down the shaft as observed in nyctosaurids.

Some authors further argued that *Nyctosaurus* has only three wing phalanges (15). If correct, this feature would be another difference from the plesiomorphic condition (e.g., four wing phalanges) as observed in *Nemicolopterus*.

Nemicolopterus is more closely related to the Ornithocheiroidea (a clade that groups all more derived pterodactyloids) relative to the Nyctosauridae by possessing the articulation between the skull and mandible positioned under the anterior half of the orbit, which in other pterosaurs is displaced further backwards. *Nemicolopterus*, however, lacks several ornithocheiroid features such as a parietal crest and a pneumatic foramen on the lateral side of the cervical vertebral centrum. Moreover, the Chinese taxon lacks the diagnostic features of the Pteranodontoidea, such as the warped deltopectoral crest and the scapula shorter than the coracoid (9).

Nemicolopterus crypticus also does not display the diagnostic features of the Dsungaripteridae such as the small rounded orbit that is positioned very high in the skull, the presence of a suborbital opening, the posteroventral expansion of the maxilla and the characteristic dentition of *Dsungaripterus* and "*Phobetor*" (1, 16). It also cannot be regarded as a member of the Azhdarchidae, which show extremely elongated midcervicals with reduced neural spines (17, 18) and a deep coracoidal flange (19). It shares with the Tapejaridae the presence of a thin and apparently subvertical lacrimal process but lacks the large premaxillary sagittal crest, the large nasoantorbital fenestra, the distinct pear-shaped orbit, and the broad tubercle at the ventroposterior margin of the coracoid (20).

Nemicolopterus crypticus shows some particular morphological features not reported in pterosaurs before. Among those is the presence of a well developed posterior process on the femur, situated above the articulation with the tibia (Fig. 3c). This process has a triangular shape and likely supported tendons or muscles that connected the femur and tibia (possibly reaching the foot), strengthening the movement of the lower part of the leg (and foot). The penultimate phalanges of the foot are curved ventrally to a degree not reported in any other pterosaur, particularly on the first and fourth digits. This species also shows that the penultimate phalanx of the fourth digit is longer than the first, a feature previously unknown in the Pterodactyloidea and only reported in the anurognathids *Jeholopterus* (21) and *Anurognathus* (22). The unguals are laterally compressed and dorsoventrally expanded with the flexor tubercle deeper and larger than in some primitive pterosaurs such as *Rhamphorhynchus* (22), archaeopterodactyloids [e.g., *Pterodactylus* (1, 23)] and in the more derived *Anhanguera* (11) and *Pteranodon* (14). Despite not having a reversed hallux like birds or the odd, hallux-like pedal digit present in drepanosaurids [Triassic diapsid reptiles (24)], the odd curved condition of the penultimate phalanges, which are the largest in the foot, is strongly indicative of arboreal habits of *Nemicolopterus crypticus*. This interpretation is corroborated with studies of phalanges of extinct sloth lemurs that concluded that arboreal species have more strongly curved phalanges than their terrestrial relatives (25). Furthermore, having the penultimate pedal phalanges longer than their neighboring proximal phalanges is a feature typically associated with arboreal capacity in birds (e.g., ref. 26) and also strengthens the present arboreal hypothesis for this flying reptile. Although other pterosaurs, particularly the more primitive anurognathids (e.g., *Jeholopterus*), were also regarded as having an arboreal lifestyle, *Nemicolopterus* is the pterodactyloid pterosaur to present the best adaptation for developing this lifestyle.

The wing span of the holotype and only known specimen of *Nemicolopterus crypticus* is estimated to be ≈250 mm, making it one of the smallest flying reptiles recovered so far. This small size raises the question about its ontogenetic age. Although the growth pattern of this previously undescribed species is not known, there are some comparisons that can be made with other pterosaurs known by more complete ontogenetic series, mainly the archaeopterodactyloid species from the Solnhofen Limestone, Southern Germany. This deposit has yielded the smallest flying pterosaurs recorded in the literature so far and are considered juveniles of the genus *Pterodactylus* (and related taxa). The smallest specimen has a wingspan of only 180 mm and is regarded as a hatchling that was a few weeks old when it died (1). The skeleton of that specimen is very delicate with several parts not ossified, such as the sternum and some pedal phalanges. Other juvenile specimens of *Pterodactylus* were also found in the Solnhofen Limestone and differ from more mature individuals by the lack of ossification in some parts of the skeleton, particularly the pedal phalanges and the tarsal elements (9). This lack of ossification was also observed in one juvenile specimen tentatively referred to as *Germanodactylus cristatus* (27) and seems to have been widespread in at least the Solnhofen pterodactyloid fauna. Although showing signs of immaturity with several cranial and postcranial elements unfused, which are indicative of juvenile pterosaurs (11, 28), *Nemicolopterus crypticus* has all skeletal elements well ossified, including the pedal phalanges, the tarsal elements, and the epiphyses of long bones (e.g., humerus). Furthermore, the gastralia and the sternum, which tend to be fragile and badly preserved in juveniles, are well ossified in this specimen (Figs. 2 and 3). Therefore, it can be concluded that the sole specimen of this small pterosaur represents a young individual, but not a hatchling that had just left the egg. How much it might have grown is not clear, but in any case, it is the smallest pterosaur specimen recovered from the Liaoning deposits (and Asia) so far, even smaller than the embryo of a toothed pterodactyloid recently found in the Yixian Formation, whose wing span was estimated to be 270 mm (29).

Nemicolopterus crypticus presents the best adaptations for an arboreal lifestyle found in any pterosaur, particularly in the Pterodactyloidea. It is very likely that this pterosaur represents a lineage of arboreal creatures that lived and foraged for insects in the gymnosperm forest canopy of Northeast China during the Early Cretaceous.

Another interesting aspect of this animal is its phylogenetic position. *Nemicolopterus crypticus* is undoubtedly a basal dsungaripteroid and in the sister-group relationship with the Ornithocheiroidea. The latter includes the most derived pterosaurs (9), some reaching gigantic sizes with wingspans of >6 m [e.g., *Pteranodon* (1)] and also *Quetzalcoatlus* (30), which has a wingspan of ≈10 m and is regarded as the largest flying animal of all time. The phylogenetic position of *Nemicolopterus crypticus* suggests that the Ornithocheiroidea originated from crestless and toothless small insectivorous arboreal forms. Although not conclusive, the fact that this primitive dsungaripteroid is found in Asia suggests that this continent could have played a major role in the evolution of the derived pterosaurs constituting the Ornithocheiroidea.

Last, because of its arboreal lifestyle, *Nemicolopterus crypticus* can be considered a rarity among pterosaurs, and its preservation further demonstrates the uniqueness of the fossil *lagerstätten* that constitute the Jehol Biota.

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