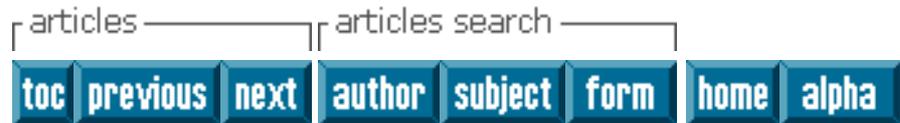


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EARTH SCIENCES

An unusual long-tailed pterosaur with elongated neck from western Liaoning of China

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ABSTRACT

A new long-tailed pterosaur, *Wukongopterus lii* gen. et sp. nov, is described based on an almost complete (V15113) representing an individual with an estimated wing span of 730 mm. The specimen was discov

possibly represent the Daohugou Bed (or Daohugou Formation) at Linglongta, Jianchang, Liaoning Province. *Wukongopterus lii* is a non-pterodactyloid pterosaur diagnosed by the first two pairs of premaxillary teeth, the dentary, elongated cervical vertebrae (convergent with Pterodactyloidea), and a strongly curved second toe. The specimen further has a broken tibia that indicates an injury occurred while the individual was alive. Taphonomic aspects provide indirect evidence of an uropatagium, supporting the general hypothesis that non-pterodactyloid pterosaurs show a membrane between the hind limbs. A phylogenetic analysis including non-pterodactyloid pterosaurs shows that *Wukongopterus lii* gen. et sp. nov. lies outside the Novialoidea, being more primitive than the Rhamphorhynchidae and *Campylognathoides*. This analysis differs from previous studies and more work is needed before a stable picture of non-pterodactyloid pterosaur relationships is achieved.

Key words: Pterosauria, *Wukongopterus*, ?Late Jurassic-Early Cretaceous, Liaoning, China.

RESUMO

Um novo pterossauro de cauda longa, *Wukongopterus lii* gen. et sp. nov., é descrito baseado em um espécime (IVPP V15113) de um indivíduo com abertura alar estimada em 730 mm. O exemplar foi encontrado na Formação Daohugou (ou Formação Daohugou) em Linglongta, Jianchang, Província de Liaoning, China. *Wukongopterus lii* é um pterodactilóide diagnosticado pela presença de dois pares de dentes pré-maxilares posicionados anteriormente às vertebrae cervicais alongadas (convergente com os Pterodactyloidea) e a segunda falange do quinto dedo curvada. Este espécime também apresenta uma tíbia quebrada indicando que a quebra ocorreu com o indivíduo vivo. Evidências tafonômicas apresentam dados indiretos da presença de um uropatágio, corroborando com a hipótese geral de que pterossauros não-pterodactilóides possuíam uma membrana entre os seus membros posteriores. Uma análise filogenética incluindo vários pterossauros não-pterodactilóides resulta no posicionamento de *Wukongopterus lii* fora da Novialoidea, sendo cladisticamente mais primitivo do que os Rhamphorhynchidae e *Campylognathoides*. Esta análise difere de resultados anteriores, indicando que mais trabalhos são necessários até que um quadro estável das relações entre os pterossauros não-pterodactilóides seja alcançada.

Palavras-chave: Pterosauria, *Wukongopterus*, ?Jurássico Superior-Cretáceo Inferior, Liaoning, China.

INTRODUCTION

Since the description of the first pterosaur from the Early Cretaceous Jehol Biota (Ji and Ji 1997), about 13 recorded, 13 from the Yixian and 15 from the Jiufotang formations, respectively (see Wang, Kellner et al. 2003, Zhou 2006, Wang, Kellner et al. 2008, Lü et al. 2006, Lü et al. 2008, Andres and Ji 2008). Among them are members of the Anurognathidae (Ji and Ji 1998, Wang et al. 2002, Kellner et al. 2009), a few Archaeopteryx (Wang et al. 2003, Wang et al. 2007), and several Dsungaripteroidea (e.g., Wang and Zhou 2003). Although some species are the object of controversy (e.g., Ji et al. 1999, Unwin et al. 2000) and the actual diversity might be inflated (e.g., Wang, Campos et al. 2008), pterodactyloids by far outnumber non-pterodactyloid species, the latter represented by anurognathids (Ji and Ji 1998, Wang et al. 2002) and two putative rhamphorhynchids (Czerkas and Ji 2002). Our present understanding of the evolutionary history of pterosaurs the prevalence of pterodactyloid species is expected and, apart from the Anurognathidae, possibly *Pterorhynchus* and the newly described *Changchengopterus pani* pterodactyloid flying reptiles went extinct towards the end of the Jurassic (Wellnhofer 1991, Kellner 2003).

Of the non-pterodactyloid pterosaurs associated to the Jehol Biota, two bear an elongated tail. The first is *wellnhoferi*, known from a complete skeleton collected from the Daohugou Bed (Czerkas and Ji 2002), but is controversial. Although this matter has not been settled yet, there is growing evidences that the layers of the Daohugou Bed (Wang et al. 2000) were formed between Late Jurassic to Early Cretaceous (Zhang 2002, He et al. 2004), instead of Middle Jurassic as previously thought (Chen and Zhang 2004). The second long-tailed pterosaur is *Changchengopterus pani* that is based on a partial skeleton lacking the skull briefly described recently. This specimen was collected in the Tiaojishan Formation that is regarded middle Jurassic in age. How-

investigation, *Changchengopterus* was probably collected from the same horizon as the specimen described by Wang (unpublished data).

Here we report another long-tailed flying reptile from a new locality (Linglongta, Jianchang County, Hebei, Liaoning, China (Fig. 1). There is considerable controversy regarding those strata, with local geological names for the fossil-bearing bed the Lanqi Formation, which is equivalent to the Tiaojishan Formation. Based on stratigraphic data, it is likely that the outcrop where the specimen was collected belongs to the Daohugou Bed (Formally part of the Tiaojishan Formation (X. Wang, unpublished data). Therefore, along with *Pterorhynchus wellnhoferi*, this new locality (*Wukongopterus lii* gen. et sp. nov.) is potentially the youngest long-tailed non-pterodactyloid known. This discovery highlights the importance of the Jehol Biota that is starting to shape our understanding of the evolution of volant archosaurs.

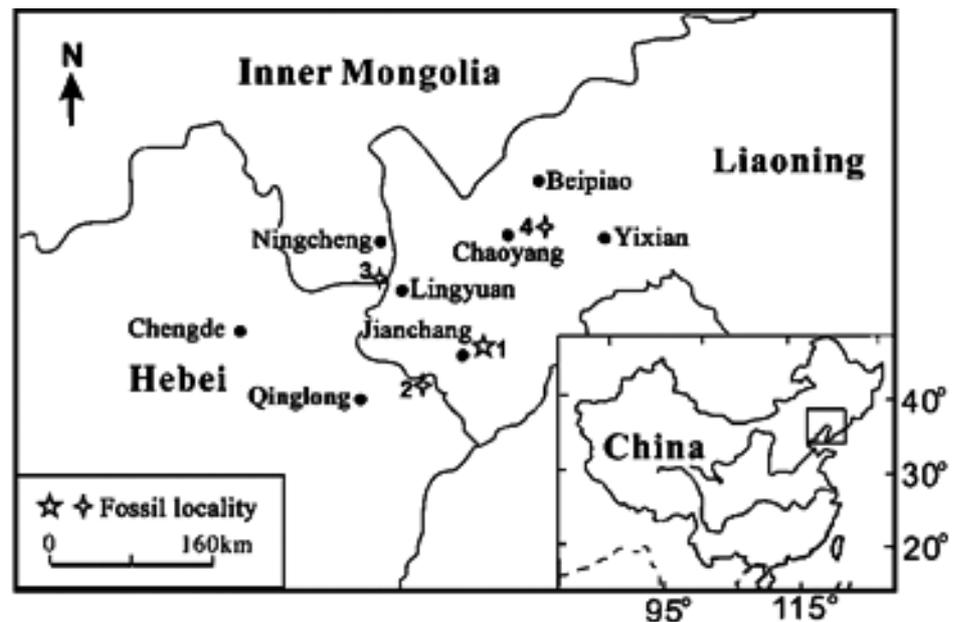


Fig. 1 – Sketch map showing the localities with the occurrence of non-pterodactyloid pterosaurs in northeast China. 1. Linglongta, Jianchang, Liaoning (Daohugou Bed): *Wukongopterus lii* gen. et sp. nov. in this paper; 2. Mutoudeng, Qinglong, Hebei (Tiaojishan Formation, probably Daohugou Bed): *Changchengopterus pani* Lü 2009; 3. Daohugou, Ningcheng, Inner Mongolia (Daohugou Bed): *Jeholopterus ningchengensis* Wang et al. 2002, *Pterorhynchus wellnhoferi* Czerkas and Ji 2002; 4. Zhangjiagou, Beipiao, Liaoning (Jianshangou Bed of the lower Yixian Formation): *Dendrorhynchoides curvidentatus* Ji and Ji 1998.

SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup 1834

Wukongopteridae fam. nov.

Type genus: *Wukongopterus* gen. nov.

Diagnosis: as for the genus.

***Wukongopterus* gen. nov.**

Etymology: *Wukongopterus*, from Sun Wukong (the Monkey King), one of the most famous and beloved characters in the classical Chinese literature "Journey to the West", and *pterus* from the Greek meaning wing.

Type Species: *Wukongopterus lii* sp. nov.

Diagnosis: As for the type and only species.

***Wukongopterus lii* sp. nov.**

Etymology: In honour to Yutong Li, senior preparator of the IVPP in recognition of the excellent work on many other Chinese fossils.

Holotype: The specimen consists of an almost complete skeleton, lacking the occipital region and the skull, collected at Linglongta, Institute of Vertebrate Paleontology and Paleoanthropology, CAS in Beijing under the number IVPP V15113.

Locality and horizon: Linglongta, Jianchang, western Liaoning, China. Daohugou Bed (Formation), ?Late Cretaceous (Zhang 2002, He et al. 2004).

Diagnosis: A non-pterodactyloid pterosaur with the following combination of characters that distinguish it from other pterosaurs (autapomorphies are marked with an asterisk): first two pairs of premaxillary teeth protrude at least 16 short peglike teeth on each side of the upper jaw (convergent with some archaeopterodactyloids), the jugal long, anteriorly projected and splint-like*, quadrate inclined backwards for about 120°, cervical vertebrae elongated than in any known non-pterodactyloid*, length of wing metacarpal about half the length of the third phalanx (convergent with the Pterodactyloidea), strongly curved second pedal phalanx of the fifth toe, and the proximal and distal segments about 75°*.

TAPHONOMY

The specimen (IVPP V15113) is preserved in a grey-dark shale and most elements are exposed in dorsal view. The specimen is broken on its right side and completely lacks the occipital and dorsal portions as well as part of the neck. The skull is broken away during the collecting process. The anterior cervical vertebrae and parts of the left wing are broken. The left wing appears to be flattened, a common condition of pterosaur material. The specimen is well articulated with almost all elements in natural position, indicating that the carcass reached the bottom of the water column complete and remained undisturbed before final burial. The left wing is partially folded underneath the body and the left manus is tucked under the wing. Some patches of soft tissue are preserved near the wing elements, particularly on the left side between the wing phalanges. Although not as extremely well preserved as some other specimens from the Daohugou Formation, Mongolia, China (Wang et al. 2002, Kellner et al. 2009) and deposits from other countries (e.g., Wellnhofer 1999, Campos 1999), the preserved material shows the structural fibers that are typical of the pterosaur wing membrane (Bakurina 1994, Kellner 1996, Sayão and Kellner 2007).

A noteworthy feature of IVPP V15113 is the condition of the left hind limb. The left femur is articulated perpendicular to the body, almost as a mirror image of its right counterpart. The left tibia is broken before the distal end, which is still articulated with the femur. The broken portion of the tibia and the foot, which are in a non-anatomical position, are displaced towards the body, underneath the femur. The fracture is not a clear break through the bone, which would have suggested a taphonomic origin, but rather longitudinal and there is no evidence of rupture of fresh bone. No evidence of scavenging as observed that could have accounted for this breakage is present. The breakage is rather undistorted and even small elements, such as the pedal phalanges of both feet, are preserved. From these observations it is likely that the breakage of this bone occurred while the animal was still alive. The fact that the breakage was observed in pterosaurs before (e.g., Kellner and Tomida 2000), there is a possibility that the breakage resulted in the *causa mortis* of this individual. Similar conclusions on broken wing metacarpals were proposed by

(1970).

Lastly, the fact that the broken part of the left hind limb is still in close contact with the body argues for uropatagium in *Wukongopterus lii*, as has been reported in a few primitive pterosaurs (unwin and Bak 2002).

DESCRIPTION AND COMPARATIVE ANATOMY

Although not complete, the skull of *Wukongopterus lii* is clearly elongated, a characteristic of non-anurognathids (length quadrate - anterior tip of the premaxillae: 101 mm, estimated length squamosal - tip of premaxilla: 101 mm, estimated length rostral portion anterior to the external nares (32.6 mm) is proportionally shorter than in *Angustinaripterus* and the Pterodactyloidea (He et al. 1983, Kellner 2003, 2004, unwin 2003a). There is no evidence of a premaxillary process has been reported in some pterodactyloids (e.g., Campos and Kellner 1985), but also in the primitive *Austriadactylus*, *Raeticodactylus*, *Angustina-ripterus*, *Harpactognathus*, and *Pterorhynchus* (He et al. 1983, Dalla Vecchia et al. 2002, Carpenter et al. 2003, Stecher 2008). The ventral margin of the skull is straight as in most pterosaurs, in contrast to the undulating condition observed in *Harpactognathus* (Carpenter et al. 2003). The premaxillae are not laterally projected from *Angustinaripterus*. The alveolar margin of the maxilla is thickened, with a marked parallel sulcus extending along the extension of this bone. The maxillary ramus of the jugal is an anteriorly directed long and very thin bone. The antorbital fenestra must have been quite large in this pterosaur. The bony bar that forms the ventral portion of the skull (composed of the jugal and maxilla) is remarkably thin for a non-pterodactyloid pterosaur. A part of the maxilla shows no evidence of a bony bar separating the external naris from the antorbital fenestra, but that *Wukongopterus* possessed a nasoantorbital fenestra. Although only the ventral portion of the left maxilla shows that this bone is inclined posteriorly for about 120° (but not to the same degree as observed in non-pterodactyloid Archaeopterygidae), differing from anurognathids, *Austriadactylus*, *Cacibupteryx*, and *Dimorphodon* (Dalla Vecchia et al. 2002, Gasparini et al. 2004, Bennett 2007). There is no anterior bony projection (for example as present in *Rhamphorhynchus* (Wellnhofer 1975a, b)). No detailed information of the palatal or occipital region is available.

The lower jaw (total length: 103.2 mm) is articulated to the skull. The dentary is long and lacks a ventral process as reported in anhanguerids (e.g., Kellner and Tomida 2000), some tapejarids (Wellnhofer and Kellner 1999, 2002), and in the primitive non-pterodactyloid *Raeticodactylus* (Stecher 2008). The anterior tip is straight as in *Campylognathoides* and *Eudimorphodon* (Wild 1978, Padian 2008b) and does not show the laterally directed projection of *Rhamphorhynchus*. The mandibular symphysis is short (estimated length: 20mm, less than the total length), differing from the longer symphysis of *Rhamphorhynchus*, *Dorygnathus* and pterodactyloids (Carpenter et al. 2003). The surangular is elongated and forms part of the dorsal margin of the adductor fossa. This bone also contains a foramen, but does not take part in the articulation for the skull. The long angular composes the posteroventral border of the adductor fossa. The articular is also elongated but not to the same degree as in *Caviramus* and *Raeticodactylus*, in which the articular is ventroposteriorly projected (Fröbisch and Fröbisch 2006, Stecher 2008). The borders of this element are straight. A prominent opening is present on the dorsal surface. It is not clear if this opening leads to a pneumatic space as in some pterodactyloids (e.g., Wellnhofer 1985).

The left ceratobranchial is preserved and forms an elongated rod-like bone running over the medial surface of the maxillary ramus.

Since the middle portion of the skull and mandible are not preserved, the total number of teeth cannot be determined with certainty. Anterior to the broken area there are 10 upper teeth on the right side (anterior to the external nares) and 10 preserved on the posterior end of the maxilla right after the breakage. In the lower jaw the ninth tooth is located at the anterior margin of the external naris. Based on the spacing between the alveoli, the total tooth count for the upper jaw is 16 and for the lower one might be 12, although this last number could be higher. In any case, the number of teeth in this new Chinese specimen is higher than in the Anurognathidae, *Sordes*, *Scaphognathus*, and *Rhamphorhynchus*.

The first two premaxillary pair of teeth are positioned anterior to the tip of the lower jaw and therefore anterior to the mandibular teeth. Such a projection has not been observed in non-pterodactyloids with the exception of *Rhamphorhynchus* in which the dental margin of the upper jaw is slightly deflected dorsally (Wellnhofer 1991) contrasting to

Wukongopterus. Within more derived pterosaurs, the archaeoptero-dactyloid *Feilongus* also has the ant jaw projecting relative to the lower jaw (Wang, Kellner et al. 2005), but is more pronounced than in *W* are conical and peg-like, with an oval cross-section. All the teeth are quite short compared with rhamph *Wukongopterus* lacks anteroventrally-projecting fang-like teeth present in *Dorygnathus* and *Angustinia* heterodont dentition of *Dimorphodon*. The new species also lacks multicuspid teeth present in several (Wild 1978, Jenkins et al. 2001, Dalla Vecchia 2003, 2009, Fröbisch and Fröbisch 2006, Stecher 2008) and a carinae observed in *Austriadactylus* (Dalla Vecchia et al. 2002).

Six cervical vertebrae from the middle and posterior part of the neck are preserved, exposed in dorsal morphological similarities with the subsequent dorsal vertebrae but is much larger. All remaining cervical and are elongated, more than in any other non-pterodactyloid pterosaur and similar to more derived (al. 2007). Their length does not reach the condition of some archaeoptero-dactyloids like *Pterodactylus* Azhdarchidae (Howse 1986, Kellner and Langston 1996), but are elongated similar to *Germanodactylus* mainly exposed in dorsal view, the lateral surface of some can be observed and lacks a pneumatic foramen blade-like and comparatively low, differing in this respect from other non-pterodactyloids. The complete vertebrae is preserved comprising 12 elements, none being fused into a notarium. The neural spine is higher than in the cervical series) and quadrangular. There are five sacral vertebrae, four original ones fenestrae and a fifth element incorporated from the caudal series, totally fused with the preceding vertebrae the transverse processes bent up and joins the post-acetabular portion of the ilium on the medioventral strongly connected to the ilium, the sacral vertebrae are not fused to this bone. The caudal vertebrae are lacking the distal part. Individual vertebrae are difficult to distinguish. Rod-like structures formed like zygapophyses (as in most other non-pterodactyloid species except *Austriadactylus* and *Changchengopterus* Dalla Vecchia et al. 2002, Lü 2009) are present indicating that *Wukongopterus lii* had a stiffened tail. One is preserved, but since the tail has drifted slightly from the pelvis, more might have been originally present.

The sternum is present and well ossified but lies under the body and cannot be described in detail. The humerus (length: 32.9 mm) is longer than the coracoid (~ 25.3 mm) and both elements are not fused. The scapula and humerus form a platelike structure as in some Triassic pterosaurs (Dalla Vecchia 2003, 2009). This bone is longer than the coracoid compared to *Changchengopterus pani*. The coracoid shows a well developed biceps tubercle and a coracoidal flange as reported for *Changchengopterus* (Lü 2009). Although not well preserved, the deltopectoral humerus (length: 38.7 mm) is positioned proximally and does not extend further down the shaft as in *Campylognathoides*, and *Eudimorphodon ranzii* (Wild 1978, Padian 2008b, Stecher 2008).

The radius and ulna are elongated, with the diameter of the radius being sub equal to the one of the ulna. The carpus is best observed on the right side, the carpals are not fused, with both the proximal and distal series of elements. This number could be higher and more carpal elements have been reported in pterodactyloids (Lü and Tomida 2000). The pteroid (length: 7.3 mm) is very small and is attached to the proximal carpal series and the second metacarpal (length: 22.9 mm) and some bones (e.g., wing finger phalanges, humerus) suggests that this bone is larger compared to other non-pterodactyloid pterosaurs, but does not approach the extreme elongated condition. Manual unguals are deeper and more curved than pedal unguals. The first wing finger phalanx (length: 45.7 mm) followed by the fourth (51.4 mm), second (56.8 mm) and third (58.3-59.3 mm) ones, the first wing finger phalanx and the tibia is similar to "*Eudimorphodon*" *cromptonellus* (see Jenkins et al. 2001) with the smallest values within non-pterodactyloid pterosaurs.

The femur (length: 33.3-35.6 mm) is shorter than the tibia (length: 52.8 mm) and has a large head. Both the femur and tibia with metatarsal III (16.8-17.2 mm) being larger than metatarsal IV (14.5-15.0). The phalangeal formula of the foot is similar to non-pterodactyloid pterosaurs that have two elongated phalanges on pedal digit V. The first phalanx of pedal digit V is longer than in some non-pterodactyloids (e.g., *Rhamphorhynchus*). The last phalanx of pedal digit V differs from other pterosaurs by being more curved with the distal and proximal portion forming an angle of about 75°. This "boomerang" shape of pedal digit V is also observed in *Sordes*, *Dorygnathus* and *Scaphognathus*, but all show a larger angle between the distal and proximal parts (Wellnhofer 1991, Unwin and Bakhurina 1994). The pedal unguals are long, curved and have a deep sulcus, and have a broad, flattened ventral surface.

DISCUSSION AND CONCLUSIONS

The long tail, short wing metacarpals and long pedal digit V clearly indicate that *Wukongopterus lii* is non-Pterodactyloidea. In order to assess the phylogenetic position of the new species, we performed a cladistic analysis of the original data set of Kellner (2003), which is being continuously updated by the inclusion of new characters by the review of character states (Kellner 2004, Wang, Kellner, 2005, 2008, see [Appendix](#)). The present position of *Wukongopterus lii* is a primitive non-pterodactyloid placed outside the Novialoidea, but more derived than the Anurognathidae, *Austriadactylus*, *Sordes*, *Preondactylus*, and *Scaphognathus* ([Fig. 4](#)). *Wukongopterus lii* shares several features of the Rhamphorhynchinae and also the ones which unite the two species of *Campylognathoides* within the Novialoidea.

Although the phylogeny of non-pterodactyloid taxa is beyond the scope of this paper, it is interesting that the results that were achieved in the present study differ from previous analyses (e.g., Kellner 2003, 2004, Unwin et al. 2008, Dalla Vecchia 2009). Among the most striking differences is the paraphyly of the Campylognathoides. *Eudimorphodon ranzii* forming a monophyletic group with other Triassic pterosaurs instead of *Campylognathoides* as previously advocated (e.g., Wild 1978, Kellner 2003, Unwin 2003a, b). The particular position of *Peteinosaurus* and *"Eudimorphodon" cromptonellus* further supports the suspicion that *Eudimorphodon* as presently defined is not a monophyletic group. There are doubts if all specimens attributed to this taxon do represent the same species or even the same genus (Kellner 2003, Dalla Vecchia 2003, 2009). Caution is therefore needed before compiling all *Eudimorphodon* specimens into a single terminal taxon as has been done before (Unwin 2003b).

In addition, the search conducted by PAUP (Swofford 2000) with the inclusion of *Harpactognathus*, *Angustinarapterus*, *Cacibupteryx*, known from cranial material only, and *Changchengopterus*, known from a partial skeleton (including the skull elements), resulted in thousands of most parsimonious cladograms. Part of the explanation for this can be the incompleteness of several species. Due to the fragility of their bones and based on the fact that they are small, pterosaur remains are generally difficult to preserve and are mostly fragmentary (e.g., Dalla Vecchia et al. 2006, Fröbisch 2006, Calvo et al. 2007, Martill et al. 2008, Costa and Kellner 2009). Even deposits where exceptionally well preserved fossils are occasionally found like the Romualdo Formation (e.g., Fara et al. 2005) have yielded incomplete and fragmentary specimens (Wellnhofer 1985). Regarding non-pterodactyloid pterosaurs, with the exception of *Campylognathoides* and *Rhamphorhynchus* (Wellnhofer 1975a, b, Bennett 1995, Padian 2008a, b), all other are based on incomplete specimens (e.g., *Preondactylus*). Even more complete taxa such as *Austriadactylus* and *Raeticodactylus* are known from cranial bones that have yielded diagnostic characters of several non-pterodactyloid clades (e.g., Kellner 2003). When only *Changchengopterus pani* is included in the phylogenetic analysis, the consensus cladogram differs from all published pterosaur phylogenies so far by having *Austriadactylus* as the most basal pterosaur, the sister group of the Pterodactyloidea, and all remaining non-pterodactyloid united in a monophyletic group. Since we were not able to examine the holotype and only known specimen of *Changchengopterus pani*, its position should be seen with caution.

The present study shows the lack of stability regarding the relationships of non-pterodactyloid taxa as expected in the future when additional and more complete non-pterodactyloid material comes to light. Until a clear picture of the relationships of non-pterodactyloids is achieved, we refrain from naming nodes.

The only non-pterodactyloid pterosaurs from China are the anurognathids *Jeholopterus* (from the Daxueshan Formation), *Dendrorhynchoides* (from the Jianshangou Bed of the Yixian Formation), and three putative rhamphorhynchids: *Angustinarapterus* from the Middle Jurassic Xiashaximiao Formation, *Changchengopterus* reported from the Daohugou Formation (although we suspect that it comes also from the Daohugou Bed) and *Pterorhynchus* (from the Daohugou Formation). The anurognathid *Dendrorhynchoides* was first thought to possess an elongated tail (Ji and Ji 1998, Ji et al. 2000), but this was convincingly dismissed by Unwin et al. (2000). *Angustinarapterus longicephalus* is only known by a skull fragment. Despite its uncertain phylogenetic position, it is not a pterodactyloid (e.g., separated external nares and absence of a premaxillary sagittal crest and the presence of a premaxillary sagittal crest are some features that distinguish *Angustinarapterus* from *Wukongopterus*).

The non-pterodactyloid *Changchengopterus pani* is known from a partial skeleton to which we had no access. It was briefly described by Lü (2009). Based on the original publication, *Wukongopterus* differs from *Changchengopterus* in several features, including the presence of elongated pre- and postzygophyses, a comparatively larger ulna,

curved second phalanx of pedal digit V. In the data matrix, Lü (2009) also points out that *Changchengopterus* vertebrae, which contrasts to the elongated condition of those bones in *Wukongopterus*. *Changchengopterus* have a proportionally smaller tibia, which can be regarded as a potential diagnostic feature of this taxon found in the proportion of the wing finger elements, with *Wukongopterus* having the first wing finger phalanx (including the fourth), while in *Changchengopterus* this bone has the same size of the third wing finger phalanx.

The only long-tailed pterosaur that comes from the same deposit of *Wukongopterus* is *Pterorhynchus* on a nearly complete specimen from the Daohugou Bed that was still unprepared when described (Czárán et al. 2009). Unfortunately, we also did not have any access to the specimen (as is apparently the case for other recent publications, e.g., 2009). Based on the published illustrations, *Wukongopterus* differs from *Pterorhynchus* by featuring a premaxillary sagittal crest and the larger number of teeth. *Pterorhynchus* was classified in the Rhamphorhynchidae (Czárán and Ji 2002) but is unlikely a member of this clade since it lacks cranial rhamphorhynchid synapomorphies (Czárán et al. 2004). It would be interesting to make a detailed comparison between *Wukongopterus* and *Pterorhynchus* postcranial elements, in order to establish if there is a close relationship among those taxa.

Among the interesting features of *Wukongopterus* are the several traits of the skull that are similar to pterosaurs, including the thin ventral margin of the skull, suggesting the presence of a large antorbital fenestra, and the quadrate. Also some postcranial elements, mainly the elongated cervical vertebrae that have not been reported in pterodactyloids before, are a derived trait of this taxon. The different sizes of the cervical vertebrae in pterodactyloids and non-pterodactyloids, is a quite interesting subject for further research that might try to understand the evolution of such arrangement. Nonetheless the remaining skeleton clearly shows primitive non-pterodactyloid characters, including the elongated tail and the developed fifth pedal digit.

Non-pterodactyloid pterosaurs also show considerable variation in the shape of the second (and last) phalanx of pedal digit V: they can be short (*Campylognathoides*), straight (*Jeholopterus*, *Dimorphodon*), slightly curved (*Rhamphorhynchus*, "boomerang" shaped) (*Sordes*, *Scaphognathus*, *Dorygnathus*). Although falling into the last category, the proximal and distal portion of the last phalanx of pedal digit V in *Wukongopterus lii* is strongly curved, with the distal segment at an angle of lesser than 90°. In *Sordes* the last phalanx of pedal digit V has been demonstrated to be associated with the uropatagium (Unwin and Bakhurina 1994) and it is generally accepted that this was also the case in other pterosaurs (e.g., Wellnhofer 1991). Therefore, the variation of morphology and size of the phalanx of pedal digit V among pterosaurs, and the variation in the shape of the uropatagium in non-pterodactyloid pterosaurs, are hypotheses that might be tested with more findings.

To conclude, most researchers agree that the primitive long-tailed pterosaurs went extinct by the end of the Jurassic (Wellnhofer 1991), some even using them for dating deposits (e.g., Lü 2009). Despite the disputed age of the Jehol Group, that might extend into the lower Cretaceous, *Wukongopterus* indicates that long-tailed pterosaurs were still present at the end of the Jurassic than previously thought. This discovery further enhances the importance of the Jehol Group for the understanding of pterosaur evolutionary history.

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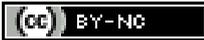
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