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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 skeleton (IVPP V15113) representing an individual with an estimated wing span of 730 mm. The specimen was discovered in strata that possibly represent the Daohugou Bed (or Daohugou Formation) at Linglongta, Jianchang, Liaoning Province, China. *Wukongopterus lii* is a non-pterodactyloid pterosaur diagnosed by the first two pairs of premaxillary teeth protruding beyond the dentary, elongated cervical vertebrae (convergent with Pterodactyloidea), and a strongly curved second pedal phalanx of the fifth toe. The specimen further has a broken tibia that indicates an injury occurred while the individual was still alive. Taphonomic aspects provide indirect evidence of an uropatagium, supporting the general hypothesis that at least all non-pterodactyloid pterosaurs show a membrane between the hind limbs. A phylogenetic analysis including most non-pterodactyloid pterosaurs shows that *Wukongopterus lii* gen. et sp. nov. lies outside the Novialoidea, being cladistically more primitive than the Rhamphorhynchidae and *Campylognathoides*. This analysis differs from previous studies and indicates that 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.

INTRODUCTION

Since the description of the first pterosaur from the Early Cretaceous Jehol Biota (Ji and Ji 1997), about 28 species have been recorded, 13 from the Yixian and 15 from the Jiufotang formations, respectively (see Wang, Kellner et al. 2005, 2008, Wang and Zhou 2006, Wang, Kellner et al. 2008, Lü et al. 2006, Lü et al. 2008, Andres and Ji 2008). Among them are primitive taxa such as members of the Anurognathidae (Ji and Ji 1998, Wang et al. 2002, Kellner et al. 2009), a few Archaeopterodactyloidea (e.g., Lü 2003, Wang et al. 2007), and several Dsungaripteroidea (e.g., Wang and Zhou 2003). Although some species have been the object of controversy (e.g., Ji et al. 1999, Unwin et al. 2000) and the actual diversity might be inflated (e.g., Wang and Zhou 2006, Wang, Campos et al. 2008), pterodactyloids by far outnumber non-pterodactyloid species, the latter represented by two anurognathids (Ji and Ji 1998, Wang et al. 2002) and two putative rhamphorhynchids (Czerkas and Ji 2002, Lü 2009). Based on our present under-

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standing of the evolutionary history of pterosaurs the prevalence of pterodactyloids in Cretaceous deposits is expected and, apart from the Anurognathidae, possibly *Pterorhynchus* and the newly described *Changchengopterus*, all non-pterodactyloid flying reptiles went extinct towards the end of the Jurassic (Wellnhofer 1991, Kellner 2003, Unwin 2003a).

Of the non-pterodactyloid pterosaurs associated to the Jehol Biota, two bear an elongated tail. The first is *Pterorhynchus wellnhoferi*, known from a complete skeleton collected from the Daohugou Bed (Czerkas and Ji 2002), whose age 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, Wang, Zhou et al. 2005) 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. According to Lü (2009) that specimen was collected in the Tiaojishan Formation that is regarded middle Jurassic in age. However after a thorough field investigation, *Changchengopterus* was probably collected from the same horizon as the specimen described in this paper (X. Wang, unpublished data).

Here we report another long-tailed flying reptile from a new locality (Linglongta, Jianchang County, Huludao City) of western Liaoning, China (Fig. 1). There is considerable controversy regarding those strata, with local geological map considering the fossil-bearing-bed the Lanqi Formation, which is equivalent to the Tiaojishan Formation. Based on sedimentological and field data, it is likely that the outcrop where the specimen was collected belongs to the Daohugou Bed (Formation) rather than Tiaojishan Formation (X. Wang, unpublished data). Therefore, along with *Pterorhynchus wellnhoferi*, the new find reported here (*Wukongopterus lii* gen. et sp. nov.) is potentially the youngest long-tailed non-pterodactyloid known to date, showing that those primitive pterosaurs were more diverse towards the end of the Jurassic perhaps entering in the Cretaceous. It further highlights the importance of the Jehol Biota that is starting to shape our understanding of the evolutionary history of this group of volant archosaurs.

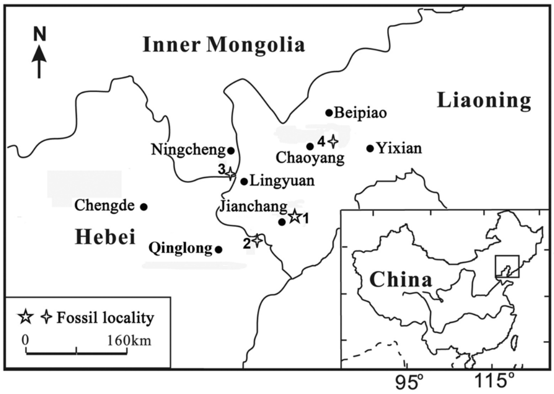

Fig. 1 – Sketch map showing the localities with the occurrence of non-pterodactyloid pterosaurs in northeast China. 1. Linglongta, Jianchang, Liaoning (Daohugou Bed): *Wukongopterus lii* gen. et sp. nov. in this paper; 2. Mutoudeng, Qinglong, Hebei (Tiaojishan Formation, probably Daohugou Bed): *Changchengopterus 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 fictional characters of 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 preparing this and many other Chinese fossils.

Holotype: The specimen consists of an almost complete skeleton, lacking the occipital region and the skull roof, housed at the Institute of Vertebrate Paleontology and Paleoanthropology, CAS in Beijing under the number IVPP V15113 (Figs. 2–3).

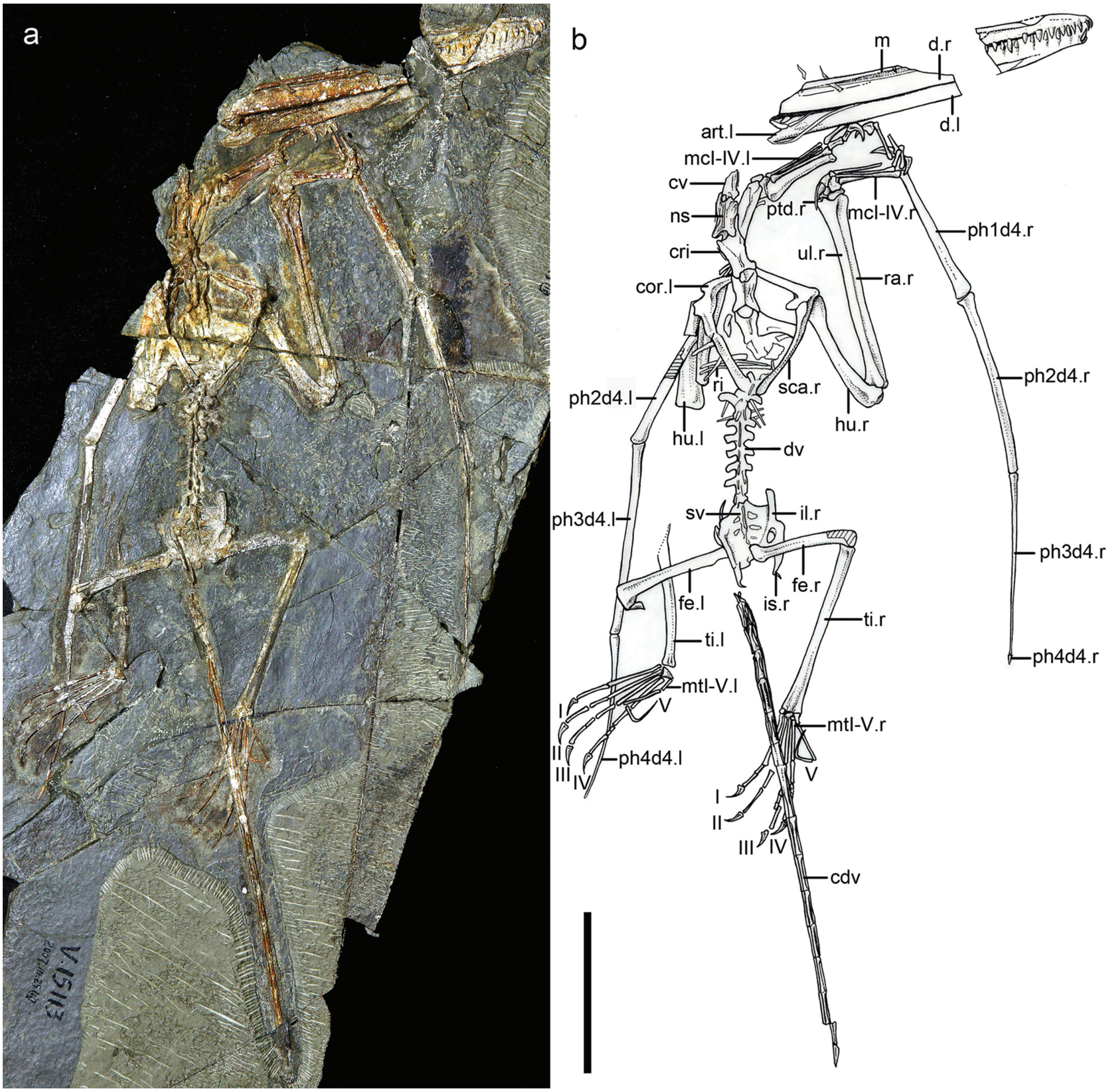

Fig. 2 – *Wukongopterus lii* IVPP V15113, holotype. (a) photo and (b) drawing of the complete skeleton. Note the broken tibia on the left side. Scale bar: 50 mm. art, articular; cdv, caudal vertebrae; cri, cervical rib; cor, coracoid; cv, cervical vertebra; d, dentary; dv, dorsal vertebra; fe, femur; hu, humerus; il, ilium; is, ischium; l, left; m, maxilla; mcI-IV, metacarpal 1-4; ns, neural spine; ph1-4d4, first to fourth phalanx of manual digit IV; mtI-V, Metatarsal 1-5; ptd, pteroid; ra, radius; r, right; ri, rib; sca, scapula; sv, sacral vertebra; ti, tibia; ul, ulna; I-IV, 1-5, first through fifth pedal digits.

Locality and horizon: Linglongta, Jianchang, western Liaoning, China. Daohugou Bed (Formation), ?Late Jurassic-Early 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 protruding beyond the dentary*, at least 16 short peg-like teeth on each side of the upper jaw (convergent with some archaeopterodactyloids), maxillary ramus of the jugal long, anteriorly projected and splint-like*,

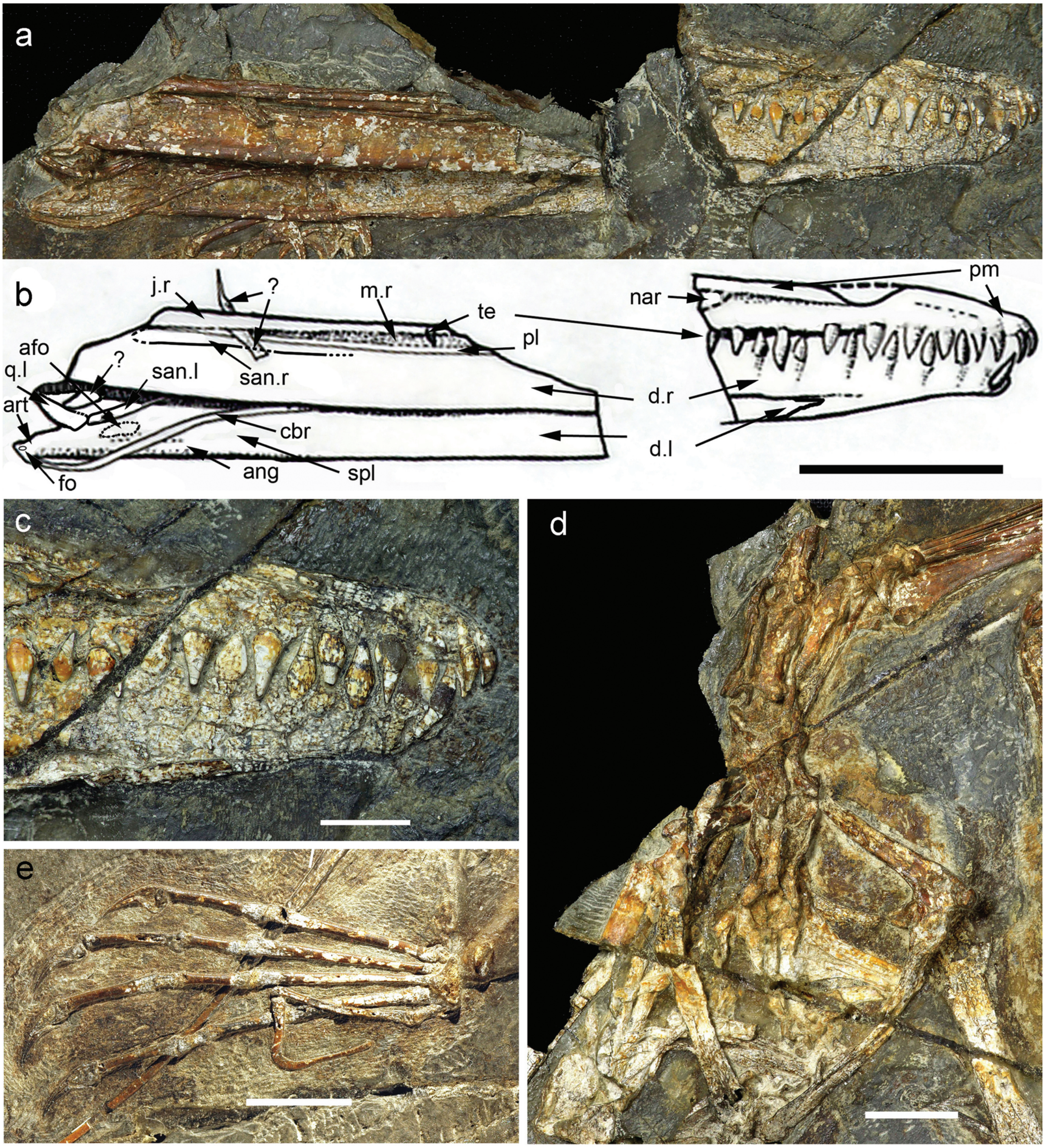

Fig. 3 – *Wukongopterus lii* IVPP V15113. (a) photo and (b) drawing of the skull. Scale bar: 20 mm, c-d details of the skeleton. (c) dentition. (d) cervical vertebrae. (e) left foot. Scale bars: 10 mm. afo, adductor fossa; ang, angular; art, articular; cbr, ceratobranchial; d, dentary; j, jugal; l, left; m, maxilla; nar, external naris; pm, premaxilla; pl, palatine; q, quadrate; r, right; san, surangular; spl, splenial; te, teeth; ?, unknown element.

quadrate inclined backwards for about 120°*, cervical vertebrae more elongated than in any known non-pterodactyloid*, length of wing metacarpal about half the length of the first wing finger phalanx (convergent with the Pterodactyloidea), strongly curved second pedal phalanx of the fifth toe with the angle between 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 skull is exposed on its right side and completely lacks the occipital and dorsal portions as well as part of the middle region, possible broken away during the collecting process. The anterior cervical vertebrae and parts of the left wing are also lacking. Bones tend to be flattened, a common condition of pterosaur material. The specimen is well articulated with almost all elements in their natural position, indicating that the carcass reached the bottom of the water column complete and remained practically undisturbed before final burial. The left wing is partially folded underneath the body and the left manus lies close to the right one. Some patches of soft tissue are preserved near the wing elements, particularly on the left side between the third and fourth wing phalanges. Although not as extremely well preserved as some other specimens from the Daohugou locality, Inner Mongolia, China (Wang et al. 2002, Kellner et al. 2009) and deposits from other countries (e.g., Wellnhofer 1991, Kellner and Campos 1999), the preserved material shows the structural fibers that are typical of the pterosaur wing (e.g., Unwin and Bakhurina 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 with the acetabulum and perpendicular to the body, almost as a mirror image of its right counterpart. The left tibia is broken below the proximal articulation, which is still articulated with the femur. The broken portion of the tibia and the foot, which also remained in anatomical position, are displaced towards the body, underneath the femur. The fracture is not a clean transverse break through the bone, which would have suggested a taphonomic origin, but rather longitudinal and therefore consistent with the rupture of fresh bone. No evidence of scavenging was observed that could have accounted for this breakage. The skeleton is rather undistorted and even small elements, such as the pedal phalanges of both feet, are preserved. Based on those observations it is likely that the breakage of this bone occurred while the animal was still alive. The fact that it is not healed as was observed in pterosaurs before (e.g., Kellner and Tomida 2000), there is a possibility that the broken tibia might be or resulted in the *causa mortis* of this individual. Similar conclusions on broken wing metacarpals were published by Wellnhofer (1970).

Lastly, the fact that the broken part of the left hind limb is still in close contact with the body argues for the presence of an uropatagium in *Wukongopterus lii*, as has been reported in a few primitive pterosaurs (Unwin and Bakhurina 1994, Wang et al. 2002).

DESCRIPTION AND COMPARATIVE ANATOMY

Although not complete, the skull of *Wukongopterus lii* is clearly elongated, a characteristic of non-anurognathid pterosaurs (length quadrate – anterior tip of the premaxillae: 101 mm, estimated length squamosal – tip of premaxillae: 120 mm). The rostral portion anterior to the external nares (32.6 mm) is proportionally shorter than in *Angustinaripterus*, *Rhamphorhynchus* and the Pterodactyloidea (He et al. 1983, Kellner 2003, 2004, Unwin 2003a). There is no evidence of a premaxillary crest that has been reported in some pterodactyloids (e.g., Campos and Kellner 1985), but also in the primitive *Austriadactylus*, *Raeticodactylus*, *Angustinaripterus*, *Harpactognathus*, and *Pterorhynchus* (He et al. 1983, Dalla Vecchia et al. 2002, Czerkas and Ji 2002, Carpenter et al. 2003, Stecher 2008). The ventral margin of the skull is straight as in most pterosaurs and differs from the undulating condition observed in *Harpactognathus* (Carpenter et al. 2003). The premaxillae are not laterally expanded, differing from *Angustinaripterus*. The alveolar margin of the maxilla is thickened, with a marked parallel sulcus running for most of the extension of this bone. The maxillary ramus of the jugal is an anteriorly directed long and very thin bone, clearly indicating that the antorbital fenestra must have been quite large in this pterosaur. The bony bar that forms the ventral margin of the middle portion of the skull (composed of the jugal and maxilla) is remarkably thin for a non-pterodactyloid pterosaur. The preserved part of the maxilla shows no evidence of a bony bar separating the external naris from the antorbital fenestra, and it is possible that *Wukongopterus* possessed a nasoantorbital fenestra. Although only the ventral portion of the left quadrate is preserved, it shows that this bone is inclined posteriorly for about 120° (but not to the same degree as observed in the Archaeopterodactyloidea), differing from anurognathids, *Austriadactylus*, *Cacibupteryx*, and *Dimorphodon* (Wellnhofer 1991, Dalla Vecchia et al. 2002, Gasparini et al. 2004, Bennett 2007). There is no anterior bony projection (formed by the premaxillae) as present in *Rhamphorhynchus* (Wellnhofer 1975a, b). No detailed information of the palatal or occipital regions is available.

The lower jaw (total length: 103.2 mm) is articulated to the skull. The dentary is long and lacks a ventral sagittal crest as the one reported in anhanguerids (e.g., Kellner and Tomida 2000), some tapejarids (Wellnhofer and Kellner 1991, Wang and Zhou 2002), and in the primitive non-pterodactyloid *Raeticodactylus* (Stecher 2008). The anterior tip is straight and not downturned as in *Campylognathoides* and *Eudimorphodon* (Wild 1978, Padian 2008b) and does not show the laterally compressed anterior projection of *Rhamphorhynchus*. The mandibular symphysis is short (estimated length: 20 mm, less than 20% of mandibular length), differing from the longer symphysis of *Rhamphorhynchus*, *Dorygnathus* and pterodactyloids (Kellner 2003). The surangular is elongated and forms part of the dorsal margin of the adductor fossa. This bone also contacts the articular but does not take part in the articulation for the skull. The long angular composes the posteroventral border of the mandibular ramus. The articular is also elongated but not to the same degree as in *Caviramus* and *Raeticodactylus*, in which this bone is ventroposteriorly projected (Fröbisch and Fröbisch 2006, Stecher 2008). The borders of this element are thickened and a prominent opening is present on the dorsal surface. It is not clear if this opening leads to a pneumatic foramen as observed 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 mandibular ramus.

Since the middle portion of the skull and mandible are not preserved, the total number of teeth cannot be established with certainty. Anterior to the broken area there are 10 upper teeth on the right side (anterior to the external naris), and one tooth is preserved on the posterior end of the maxilla right after the breakage. In the lower jaw the ninth tooth is positioned right under the anterior margin of the external naris. Based on the spacing between the alveoli, the total tooth counts estimated 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 tooth count of the new Chinese specimen is higher than in the Anurognathidae, *Sordes*, *Scaphognathus*, and *Rhamphorhynchus* (Wellnhofer 1991).

The first two premaxillary pair of teeth are positioned anterior to the tip of the lower jaw and therefore have no matching mandibular teeth. Such a projection has not been observed in non-pterodactyloids with the exception of *Scaphognathus*, in which the dental margin of the upper jaw is slightly deflected dorsally (Wellnhofer 1991) contrasting to the straight condition of *Wukongopterus*. Within more derived pterosaurs, the archaeopterodactyloid *Feilongus* also has the anterior part of the upper jaw projecting relative to the lower jaw (Wang, Kellner et al. 2005), but is more pronounced than in *Wukongopterus*. The teeth are conical and peg-like, with an oval cross-section. All the teeth are quite short compared with rhamphorhynchids. *Wukongopterus* lacks anteroventrally-projecting fang-like teeth present in *Dorygnathus* and *Angustinaripterus*, and the particular heterodont dentition of *Dimorphodon*. The new species also lacks multicuspid teeth present in several Triassic pterosaurs (Wild 1978, Jenkins et al. 2001, Dalla Vecchia 2003, 2009, Fröbisch and Fröbisch 2006, Stecher 2008) and the finely serrated 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 view. The last one shows morphological similarities with the subsequent dorsal vertebrae but is much larger. All remaining cervical vertebrae bear ribs and are elongated, more than in any other non-pterodactyloid pterosaur and similar to more derived pterosaurs (e.g., Wang et al. 2007). Their length does not reach the condition of some archaeopterodactyloids like *Pterodactylus kochi* or the Azhdarchidae (Howse 1986, Kellner and Langston 1996), but are elongated similar to *Germanodactylus cristatus*. Although mainly exposed in dorsal view, the lateral surface of some can be observed and lacks a pneumatic foramen. The neural spine is blade-like and comparatively low, differing in this respect from other non-pterodactyloids. The complete set of dorsal vertebrae is preserved comprising 12 elements, none being fused into a notarium. The neural spine is high (proportionally higher than in the cervical series) and quadrangular. There are five sacral vertebrae, four original ones showing intercostal fenestrae and a fifth element incorporated from the caudal series, totally fused with the preceding vertebra. This last sacral has the transverse processes bent up and joins the postacetabular portion of the ilium on the medioventral surface. Despite being strongly connected to the ilium, the sacral vertebrae are not fused to this bone. The caudal vertebrae series is almost complete lacking the distal part. Individual vertebrae are difficult to distinguish. Rod-like structures formed likely by the elongation of the zygapophyses (as in most other non-pterodactyloid species except *Austriadactylus* and *Changchengopterus* [Dalla Vecchia 2002, Dalla Vecchia et al. 2002, Lü 2009]) are present indicating that *Wukongopterus lii* had a stiffened tail. Only one free caudal 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 scapula (length: 34.1 mm-32.9 mm) is longer than the coracoid (∼ 25.3 mm) and both elements are not fused. The scapula is elongated and does not form a plate-like structure as in some Triassic pterosaurs (Dalla Vecchia 2003, 2009). This bone is longer relatively to the coracoid compared to *Changchengopterus pani*. The coracoid shows a well developed biceps tubercle but lacks a deep coracoidal flange as reported for *Changchengopterus* (Lü 2009). Although not well preserved, the deltopectoral crest of the humerus (length: 38.7 mm) is positioned proximally and does not extend further down the shaft as in *Raeticodactylus*, *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 (length: 62.1 mm). The carpus is best observed on the right side, the carpals are not fused, with both the proximal and distal series presenting two elements. This number could be higher and more carpal elements have been reported in pterodactyloid pterosaurs (Kellner and Tomida 2000). The pteroid (length: 7.3 mm) is very small and is attached to the proximal carpal series. The ratio of the wing metacarpal (length: 22.9 mm) and some bones (e.g., wing finger phalanges, humerus) suggests that this element is slightly larger compared to other non-pterodactyloid pterosaurs, but does not approach the extreme elongated pterodactyloid condition. Manual unguals are deeper and more curved than pedal unguals. The first wing finger phalanx is the smallest (length: 45.7 mm) followed by the fourth (51.4 mm), second (56.8 mm) and third (58.3–59.3 mm) ones, respectively. The ratio of the first wing finger phalanx and the tibia is similar to "*Eudimorphodon*" *cromptonellus* (see Jenkins et al. 2001) and are 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 pedes are well preserved with metatarsal III (16.8–17.2 mm) being larger than metatarsal IV (14.5–15.0). The phalangeal formula (2.3.4.5.2) is typical for 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 all pterosaurs in being more curved with the distal and proximal portion forming an angle of about 75°. This "boomerang-shaped" last phalanx of pedal digit V is also observed in *Sordes*, *Dorygnathus* and *Scaphognathus*, but all show a larger angle (135°) between the distal and proximal parts (Wellnhofer 1991, Unwin and Bakhurina 1994). The pedal unguals are long, curved with a deep lateral 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 not a member of the Pterodactyloidea. In order to assess the phylogenetic position of the new species, we performed a cladistic analysis using the original data set of Kellner (2003), which is being continuously updated by the inclusion of new characters and taxa, as well as by the review of character states (Kellner 2004, Wang, Kellner, 2005, 2008, see Appendix). The present analysis shows that *Wukongopterus lii* is a primitive non-pterodactyloid placed outside the Novialoidea, but more derived relative to the Anurognathidae, *Austriadactylus*, *Sordes*, *Preondactylus*, and *Scaphognathus* (Fig. 4). *Wukongopterus lii* lacks the synapomorphic features of the Rhamphorhynchinae and also the ones which unite the two species of *Campylognathoides*. These taxa are nested within the Novialoidea.

Although the phylogeny of non-pterodactyloid taxa is beyond the scope of this paper, it is interesting to note that the results that were achieved in the present study differ from previous analyses (e.g., Kellner 2003, 2004, Unwin 2003a, b, Wang, Kellner et al. 2008, Dalla Vecchia 2009). Among the most striking differences is the paraphyly of the Campylognathoididae, having *Eudimorphodon ranzii* forming a monophyletic group with other Triassic pterosaurs instead of *Campylognathoides* as has been previously advocated (e.g., Wild 1978, Kellner 2003, Unwin 2003a, b). The particular position of *Peteinosaurus* as sister-taxon of "*Eudimorphodon*" *cromptonellus* further supports the suspicion that *Eudimorphodon* as presently defined is paraphyletic and there are doubts if all specimens attributed to this taxon do represent the same species or even the same genus (e.g., Kellner 2003, Dalla Vecchia 2003, 2009). Caution is therefore needed before compiling all *Eudimorphodon* specimens in one single terminal taxon as has been done before (Unwin 2003b).

In addition, the search conducted by PAUP (Swofford 2000) with the inclusion of *Harpactognathus*, *Angustinaripterus*, and *Cacibupteryx*, known from cranial material only, and *Changchengopterus*, known from a partial skeleton (lacking cranial elements), resulted in thousands of most parsimonious cladograms. Part of the explanation for this can be attributed to the incompleteness of several species. Due to the fragility of their bones and based on the fact that they are flying animals, pterosaur remains are generally difficult to preserve and are mostly fragmentary (e.g., Dalla Vecchia et al. 2001, Fröbisch and Fröbisch 2006, Calvo et al. 2007, Martill et al. 2008, Costa and Kellner 2009). Even deposits where exceptionally specimens are occasionally found like the Romualdo Formation (e.g., Fara et al. 2005) have yielded incomplete and fragmentary material (e.g., Wellnhofer 1985). Regarding non-pterodactyloid pterosaurs, with the exception of *Campylognathoides*, *Dorygnathus* and *Rhamphorhynchus* (Wellnhofer 1975a, b, Bennett 1995, Padian 2008a, b), all other are based on incomplete or badly preserved specimens (e.g., *Preondactylus*). Even more complete taxa such as *Austriadactylus* and *Raeticodactylus* lack important post-cranial bones that have yielded diagnostic characters of several non-pterodactyloid clades (e.g., Kellner 2003, Unwin 2003b). When only *Changhengopterus pani* is included in the phylogenetic analysis, the consensus cladogram differs even more from all published pterosaur phylogenies so far by having *Austriadactylus* as the most basal pterosaur, the Anurognathidae as the sister group of the Pterodactyloidea, and all remaining non-pterodactyloid united in a monophyletic group (see Appendix). Since we were not able to examine the holotype and only known specimen of *Changhengopterus pani* first hand, this result must be seen with caution.

The present study shows the lack of stability regarding the relationships of non-pterodactyloid taxa and several changes are expected in the future when additional and more complete non-pterodactyloid material comes to light. Until a more stable 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 Daohugou Bed) and *Dendrorhynchoides* (from the Jianshangou Bed of the Yixian Formation), and three putative rhamphorhynchids: *Angustinaripterus* from the Middle Jurassic Xiashaximiao Formation, *Changchengopterus* reported from the Tiaojishan Formation (although we suspect that it comes also from the Daohugou Bed) and *Pterorhynchus* (from the Daohugou Bed). The anurognathid *Dendrorhynchoides* was first thought to possess an elongated tail (Ji and Ji 1998, Ji et al. 1999), which was convincingly dismissed by Unwin et al. (2000). *Angustinaripterus longicephalus* is only known by a skull and lower jaw but, despite its uncertain phylogenetic position, is not a pterodactyloid (e.g., separated external nares and antorbital fenestra). The dentition and the presence of a premaxillary sagittal crest are some fea-

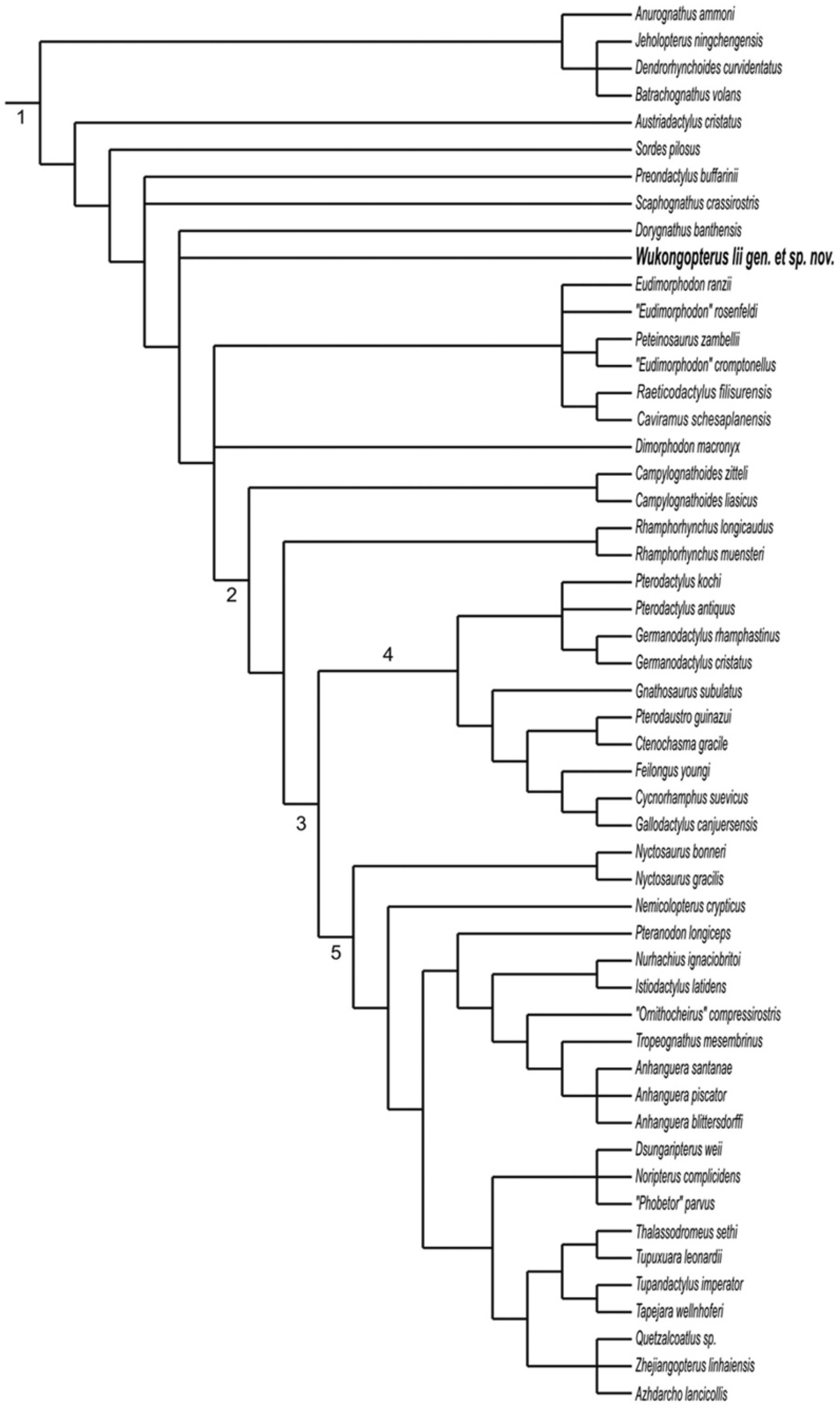

Fig. 4 – Phylogenetic relationships of *Wukongopterus lii*. 1, Pterosauria; 2, Novialoidea; 3, Pterodactyloidea; 4, Archaeopterodactyloidea; 5, Dsungaripteroidea. See appendix for details.

tures that distinguish *Angustinaripterus* from *Wukongopterus*.

The non-pterodactyloid *Changchengopterus pani* is known from a partial skeleton to which we had no access that was only briefly described by Lü (2009). Based on the original publication, *Wukongopterus* differs from *Changchengopterus* by several features, including the presence of elongated pre- and postzygaphophyses, a comparatively larger ulna, and the strongly curved second phalanx of pedal digit V. In the data matrix, Lü (2009) also points out that *Changchengopterus* bears short cervical vertebrae, which contrasts to the elongated condition of those bones in *Wukongopterus*. *Changchengopterus* also appears to have a proportionally smaller tibia, which can be regarded as a potential diagnostic feature of this taxon. Another difference is found in the proportion of the wing finger elements, with *Wukongopterus* having the first wing finger phalanx the shortest of all (including the fourth), while in *Changchengopterus* this bone has the same size of the third wing finger phalanx (Lü 2009).

The only long-tailed pterosaur that comes from the same deposit of *Wukongopterus* is *Pterorhynchus wellnhoferi*, which is based on a nearly complete specimen from the Daohugou Bed that was still unprepared when described (Czerkas and Ji 2002). Unfortunately, we also did not have any access to the specimen (as is apparently the case for other researchers, C. Bennett, pers. comm. 2009). Based on the published illustrations, *Wukongopterus* differs from *Pterorhynchus* by features such as the lack of a premaxillary sagittal crest and the larger number of teeth. *Pterorhynchus* was classified in the Rhamphorhynchidae (Czerkas and Ji 2002) but is unlikely a member of this clade since it lacks cranial rhamphorhynchid synapomorphic features (e.g., Kellner 2004). It would be interesting to make a detailed comparison between *Wukongopterus* and *Pterorhynchus*, particularly regarding 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 pterodactyloids. Those include the thin ventral margin of the skull, suggesting the presence of a large antorbital fenestra, and the inclination of the quadrate. Also some postcranial elements, mainly the elongated cervical vertebrae that have not been reported in any non-pterodactyloid before, are a derived trait of this taxon. The different sizes of the cervical vertebrae in pterosaurs, now also in the non-pterodactyloids, is a quite interesting subject for further research that might try to understand mechanical consequences of such arrangement. Nonetheless the remaining skeleton clearly shows primitive non-pterodactyloid characteristics such as the elongated tail and the developed fifth pedal digit.

Non-pterodactyloid pterosaurs also show considerable variation in the shape of the second (and last) pedal phalanx that can be short (*Campylognathoides*), straight (*Jeholopterus*, *Dimorphodon*), slightly curved (*Rhamphorhynchus*), and strongly curved ("boomerang" shaped) (*Sordes*, *Scaphognathus*, *Dorygnathus*). Although falling into the last category, the angle between the proximal and distal portion of the last phalanx of pedal digit V in *Wukongopterus lii* is strongly curved, with the proximal and distal segment at an angle of lesser than 90°. In *Sordes* the last phalanx of pedal digit V has been demonstrated to be connected with the uropatagium (Unwin and Bakhurina 1994) and it is generally accepted that this was also the case of other pterosaurs (e.g., Wellnhofer 1991). Therefore, the variation of morphology and size of the phalanx of pedal digit V might indicate a variation in the shape of the uropatagium in non-pterodactyloid pterosaurs, a hypothesis that might be explored in the future 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 Daohugou Bed, that might extend into the lower Cretaceous, *Wukongopterus* indicates that long-tailed pterosaurs were more diverse towards the end of the Jurassic than previously thought. This discovery further enhances the importance of the ancient ecosystems of the Jehol Group for the understanding of pterosaur evolutionary history.

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RESUMO

Um novo pterossauro de cauda longa, *Wukongopterus lii* gen. et sp. nov., é descrito baseado em um esqueleto quase completo (IVPP V15113) de um indivíduo com abertura alar estimada em 730 mm. O exemplar foi encontrado nas camadas Daohugou (ou Formação Daohugou) em Linglongta, Jianchang, Província de Liaoning, China. *Wukongopterus lii* é um pterossauro não-pterodactilóide diagnosticado pela presença de dois pares de dentes pré-maxilares posicionados antes do início do dentário, vértebras cervicais alongadas (convergente com os Pterodactyloidea) e a segunda falange do quinto dígito do pé fortemente curvada. Este espécime também apresenta uma tíbia quebrada indicando que a quebra ocorreu com o animal em vida. Evidências tafonômicas apresentam dados indiretos da presença de um uropatágio, corroborando com a hipótese de que pelo menos os não-pterodactilóides possuíam uma membrana entre os seus membros posteriores. Uma análise filogenética incluindo vários pterossauros não-pterodactilóides resulta no posicionamento de *Wukongopterus lii* gen. et sp. nov. fora dos Novialoidea, sendo cladisticamente mais primitivo do que os Rhamphorhynchidae e *Campylognathoides*. Esta nova análise filogenética difere de resultados anteriores, indicando que mais trabalhos são necessários até que uma estabilidade da relação de parentesco entre os pterossauros não-pterodactilóides seja alcançada.

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

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APPENDIX

In order to access the phylogenetic position *Wukongopterus lii* gen. et sp. nov., we performed a phylogenetic analysis using PAUP 4.0b10 for Microsoft Windows (Swofford 2000). The large dataset (3 outgroups + 57 pterosaur taxa, 89 characters, several multistate) dictated the heuristic search option. Characters were given equal weight and treated unordered (ACCTRAN setting). The search conducted by PAUP including all three outgroups (*Ornithosuchus longidens*, *Herrerasaurus ischigualastensis* and *Scleromochlus taylori*) and all 57 pterosaur taxa produced 140.698 of equally parsimonious trees with a length of 233 steps (consistency index = 0.6781, retention index = 0.8806, rescaled consistency index = 0.5971). A second search excluding the outgroup *Scleromochlus* and the pterosaur taxa *Changchengopterus pani*, *Harpactognathus gentryii*, *Angustinaripterus longicephalus* and *Cacibupteryx caribensis*, PAUP found 15893 equally parsimonious trees of 225 steps (consistency index = 0.6933, retention index = 0.8831, rescaled consistency index = 0.6122). A strict consensus cladogram of this last search is shown in Figure 4. See the main text for more details.

CHARACTER LIST (per anatomical region)

SKULL

01. Dorsal margin of the skull:
0 – straight or curved downward; 1 – concave; 2 – only rostrum curved upward

02. Upper and lower jaw:
0 – laterally compressed; 1 – comparatively broad

03. Rostral part of the skull anterior to the external nares:
0 – reduced; 1 – elongated (less than half of skull length); 2 – extremely elongated (more than half of skull length)

04. Rostral end of premaxillae/maxillae downturned:
0 – absent; 1 – present

05. Position of the external naris:
0 – above the premaxillary tooth row; 1 – displaced posterior to the premaxillary tooth row

06. Process separating the external nares:
0 – broad; 1 – narrow

07. Dorsoventrally compressed and elongated naris
0 – absent; 1 – present

08. Naris size relative antorbital fenestra
0 – naris smaller than antorbital fenestra; 1 – naris larger than antorbital fenestra; 2 – both very reduced (slit-like)

09. Naris and antorbital fenestra:
0 – separated; 1 – confluent, shorter than 45% of the skull length; 2 – confluent, longer than 45% of the skull length

10. Antorbital fenestra, shape
0 – eliptical or ovoid; 1 – triangular, with base and height subequal; 2 – triangular with height larger than base;
3 – very elongated anteroposteriorly

11. Orbit comparatively small and positioned very high in the skull:
0 – absent; 1 – present

12. Orbit pear-shaped:
0 – absent; 1 – present

13. Position of the orbit relative to the nasoantorbital fenestra (naris + antorbital fenestra):
0 – same level or higher; 1 – orbit lower than the dorsal rim of the nasoantorbital fenestra

14. Suborbital opening:
0 – absent; 1 – present

CHARACTER LIST (per anatomical region) – (continuation)

15. Premaxillary sagittal crest, position:
    0 – absent; 1 – confined to the anterior portion of the skull; 2 – starting anterior to the anterior margin of the nasoantorbital fenestra, not reaching the skull roof above the orbit; 3 – starting anterior to the anterior margin of the nasoantorbital fenestra, extending beyond occipital region; 4 – starting at about the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit but not extending over the occipital region; 5 – starting close or at the anterior portion of the skull and extended over the occipital region; 6 – starting close or at the anterior portion of the skull, reaching orbit but not extended over the occipital region; 7 – starting at the posterior half of the nasoantorbital fenestra
16. Premaxillary sagittal crest shape:
    0 – striated, low with a nearly straight dorsal margin; 1 – striated, high with a nearly straight dorsal margin; 2 – striated, high, spike-like; 3 – round dorsal margin, bladeshaped; 4 – smooth, moderately expanded anteriorly and forming a low rod-like extension posteriorly; 5 – smooth, very expanded anteriorly and forming a low rod-like extension posteriorly; 6 – smooth, starting low anteriorly and very expanded posteriorly
17. Expansion of the premaxillary tip:
    0 – absent; 1 – present, with premaxillary end high; 2 – present, with premaxillary end dorsoventrally flattened
18. Posterior ventral expansion of the maxilla:
    0 – absent; 1 – present
19. Maxilla-nasal contact
    0 – broad; 1 – narrow; 2 – absent
20. Nasal process:
    0 – absent; 1 – placed laterally, long, straight, and directed ventrally (not fused with maxillae); 2 – placed laterally, reduced; 3 – placed medially, long; 4 – placed medially, reduced; 5 – placed laterally, short and directed anteriorly
21. Foramen on nasal process:
    0 – absent; 1 – present
22. Anterior process of jugal rodlike and deflected dorsally
    0 – absent; 1 – present
23. Lacrimal process of the jugal:
    0 – broad; 1 – thin, subvertical; 2 – thin, strongly inclined posteriorly
24. Bony frontal crest:
    0 – absent; 1 – low and blunt; 2 – low and elongated; 3 – high and expanded posteriorly
25. Bony parietal crest:
    0 – absent; 1 – present, blunt; 2 – present, laterally compressed and posteriorly expanded, with a rounded posterior margin; 3 – present, constituting the base of the posterior portion of the cranial crest
26. Posterior region of the skull rounded with the squamosal displaced ventrally:
    0 – absent; 1 – present
27. Position of the quadrate relative to the ventral margin of the skull:
    0 – vertical or subvertical; 1 – inclined about 120° backwards; 2 – inclined about 150° backwards
28. Position of the articulation between skull and mandible:
    0 – under the posterior half of the orbit or further backwards; 1 – under the middle part of the orbit; 2 – under the anterior half of the orbit
29. Helical jaw joint:
    0 – absent; 1 – present
30. Supraoccipital:
    0 – does not extend backwards; 1 – extends backwards
31. Foramen pneumaticum piercing the supraoccipital:
    0 – absent; 1 – present
32. Expanded distal ends of the paroccipital processes:
    0 – absent; 1 – present
33. Basisphenoid:
    0 – short; 1 – elongated

CHARACTER LIST (per anatomical region) – (continuation)

34. Palatal ridge:
    0 – absent; 1 – discrete, tapering anteriorly; 2 – strong, tapering anteriorly;
    3 – strong, confined to the posterior portion of the palate

35. Maxilla excluded from the internal naris:
    0 – absent; 1 – present

36. Opening between pterygoids and basisphenoid (interpterygoid opening):
    0 – absent or very reduced; 1 – present and larger than subtemporal fenestra; 2 – present but smaller than subtemporal fenestra

37. Large distinct foramina (cup-shaped structures) on the lateral side anterior portion of the dentary
    0 – absent; 1 – present

38. Mandibular symphysis:
    0 – absent or very short; 1 – present, at least 30% of mandible length

39. Anterior tip of the dentary downturned:
    0 – absent; 1 – present

40. Tip of the dentary projected anteriorly:
    0 – absent; 1 – present

41. Dentary bony sagittal crest:
    0 – absent; 1 – blade-like and short, placed anteriorly; 2 – massive and deep

42. Distinctively elongated and posteriorly oriented articular and retroarticular process
    0 – absent; 1 – present

43. Position and presence of teeth:
    0 – teeth present, evenly distributed along the jaws; 1 – teeth absent from the anterior portion of the jaws;
    2 – teeth confined to the anterior part of the jaws; 3 – jaws toothless

44. Largest maxillary teeth positioned posteriorly:
    0 – absent; 1 – present

45. Variation in the size of the anterior teeth with the 5th and 6th smaller than the 4th and 7th:
    0 – absent; 1 – present

46. Teeth with a broad and oval base:
    0 – absent; 1 – present

47. Multicusped teeth:
    0 – absent; 1 – present

48. Teeth finely serrated
    0 – absent; 1 – present

49. Peg-like teeth:
    0 – absent; 1 – present, 15 or less on each side of the upper jaws; 2 – present, more than 15 on each side of the upper jaws

50. Long slender teeth:
    0 – absent or less than 150; 1 – present, more than 150

51. Laterally compressed and triangular teeth
    0 – absent; 1 – present

AXIAL SKELETON

52. Notarium:
    0 – absent; 1 – present

53. Atlas and axis:
    0 – unfused; 1 – fused

54. Postexapophyses on cervical vertebrae:
    0 – absent; 1 – present

55. Lateral pneumatic foramen on the centrum of the cervical vertebrae:
    0 – absent; 1 – present

CHARACTER LIST (per anatomical region) – (continuation)

56. Midcervical vertebrae:
0 – short, sub-equal in length; 1 – elongated; 2 – extremely elongated

57. Cervical ribs on midcervical vertebrae:
0 – present; 1 – absent

58. Neural spines of the midcervical vertebrae:
0 – tall, blade-like; 1 – tall, spike-like; 2 – low, blade-like; 3 – extremely reduced or absent

59. Number of caudal vertebrae:
0 – more than 15; 1 – 15 or less

60. Caudal vertebrae with elongated zygapophyses forming rod-like bony processes
0 – absent; 1 – present

PECTORAL GIRDLE

61. Length of the scapula:
0 – subequal or longer than coracoid; 1 – scapula shorter than coracoid ($1 > \text{sca/cor} > 0.80$);
2 – substantially shorter than coracoid ($\text{sca/cor} \leq 0.80$)

62. Proximal surface of scapula:
0 – elongated; 1 – sub-oval

63. Shape of scapula
0 – elongated; 1 – stout, with constructed shaft

64. Coracoidal contact surface with sternum:
0 – no developed articulation surface; 1 – articulation surface flattened, lacking posterior expansion;
2 – articulation surface oval, with posterior expansion

65. Deep coracoidal flange:
0 – absent; 1 – present

66. Broad tubercle on ventroposterior margin of coracoid:
0 – absent; 1 – present

67 – Cristospine:
0 – absent; 1 – shallow and elongated; 2 – deep and short

FORELIMB

68. Proportional length of the humerus relative to the metacarpal IV (hu/mcIV):
0 – $\text{hu/mcIV} > 2.50$; 1 – $1.50 < \text{hu/mcIV} < 2.50$; 2 – $0.40 < \text{hu/mcIV} < 1.50$; 3 – $\text{hu/mcIV} < 0.40$

69. Proportional length of the humerus relative to the femur (hu/fe):
0 – $\text{hu/fe} \leq 0.80$; 1 – $1.4 > \text{hu/fe} > 0.80$; 2 – $\text{hu/fe} > 1.40$

70. Proportional length of the humerus plus ulna relative to the femur plus tibia (hu+ul/fe+ti):
0 – humerus plus ulna about 0.80% or less of femur plus tibia length ($\text{hu+ul/fe+ti} \leq 0.80$);
1 – humerus plus ulna larger than 0.80% of femur plus tibia length ($\text{hu+ul/fe+ti} > 0.80$)

71. Pneumatic foramen on the ventral side of the proximal: part of the humerus
0 – absent; 1 – present

72. Pneumatic foramen present on dorsal side of the proximal part of the humerus:
0 – absent; 1 – present

73. Deltopectoral crest of the humerus:
0 – reduced, positioned close to the humerus shaft; 1 – enlarged, proximally placed, with almost straight proximal margin;
2 – subrectangular, extending down the humerus shaft for at least 30% of humerus length; 3 – distally expanded;
4 – enlarged, hatchet shaped, proximally placed; 5 – enlarged, hatched shaped, positioned further down the humerus shaft;
6 – enlarged, warped; 7 – long, proximally placed, curving ventrally

74. Medial (= ulnar) crest of the humerus:
0 – absent or reduced; 1 – present, directed posteriorly; 2 – present, massive, with a developed proximal ridge

75. Distal end of the humerus:
0 – oval or D-shaped; 1 – subtriangular

CHARACTER LIST (per anatomical region) – (continuation)

76. Proportional length of the ulna relative to the metacarpal IV (ul/mcIV):
    0 – ulna 3.6 times longer than metacarpal IV ($ul/mcIV > 3.6$); 1 – length of ulna between 3.6 and two times the length of metacarpal IV ($3.6 > ul/mcIV > 2$); 2 – ulna less than two times the length of metacarpal IV ($ul/mcIV < 2$)
77. Diameter of radius and ulna:
    0 – subequal; 1 – diameter of the radius about half that of the ulna; 2 – diameter of the radius less than half that of the ulna
78. Distal syncarpals:
    0 – unfused; 1 – fused in a rectangular unit; 2 – fused in a triangular unit
79. Pteroid:
    0 – absent; 1 – shorter than half the length of the ulna; 2 – longer that half the length of the ulna
80. Metacarpals I-III:
    0 – articulating with carpus; 1 – metacarpal III articulates with carpus, metacarpals I and II reduced;
    2 – not articulating with carpus
81. Proportional length of the first phalanx of manual digit IV relative to the metacarpal IV (ph1d4/mcIV):
    0 – both small and reduced; 1 – both enlarged with ph1d4 over four times the length of mcIV ($ph1d4/mcIV > 4.0$);
    2 – both enlarged with ph1d4 between two and four times the length of mcIV ($4.0 > ph1d4/mcIV \geq 2.0$);
    3 – both enlarged with ph1d4 less than two times the length of mcIV ($ph1d4/mcIV < 2.0$)
82. Proportional length of the first phalanx of manual digit IV relative to the tibiotarsus (ph1d4/ti):
    0 – ph1d4 reduced; 1 – ph1d4 elongated and less than twice the length of ti (ph1d4/ti smaller than 2.00);
    2 – ph1d4 elongated about or longer than twice the length of ti (ph1d4/ti subequal/larger than 2.00)
83. Proportional length of the second phalanx of manual digit IV relative to the first phalanx of manual digit IV (ph2d4/ph1d4):
    0 – both short or absent;
    1 – elongated with second phalanx about the same size or longer than first (ph2d4/ph1d4 larger than 1.00);
    2 – elongated with second phalanx up to 30% shorter than first (ph2d4/ph1d4 between 0.70 – 1.00);
    3 – elongated with second phalanx more than 30% shorter than first (ph2d4/ph1d4 smaller than 0.70)
84. Proportional length of the third phalanx of manual digit IV relative to the first phalanx of manual digit IV (ph3d4/ph1d4):
    0 – both short or absent; 1 – ph3d4 about the same length or larger than ph1d4; 2 – ph3d4 shorter than ph1d4
85. Proportional length of the third phalanx of manual digit IV relative to the second phalanx of manual digit IV (ph3d4/ph2d4):
    0 – both short or absent; 1 – ph3d4 about the same size or longer than ph2d4; 2 – ph3d4 shorter than ph2d4

HIND LIMB

86. Proportional length of the femur relative to the metacarpal IV (fe/mcIV):
    0 – femur about twice or longer than metacarpal IV ($fe/ mcIV \geq 2.00$); 1 – femur longer but less than twice the length of metacarpal IV ($1.00 < fe/mcIV < 2.00$); 2 – femur about the same length or shorter than metacarpal IV ($fe/mcIV \leq 1.00$)
87. Length of metatarsal III:
    0 – more than 30% of tibia length; 1 – less than 30% of tibia length
88. Fifth pedal digit:
    0 – with four phalanges; 1 – with 2 phalanges; 2 – with 1 or no phalanx (extremely reduced)
89. Last phalanx of pedal digit V:
    0 – reduced or absent; 1 – elongated, straight; 2 – elongated, curved; 3 – elongated, very curved (boomerang shape)

DATA MATRIX

Ornithosuchus longidens (Huxley, 1877)									
0000000000	00000-0000	-000000000	0000000000	0000000000	0000000000	0000000000	0000000000	000000000	
Herrerasaurus ischigualastensis Reig, 1963									
0000000000	00000-0000	-0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	00000020	
Scleromochlus taylori Woodward, 1907									
000?0?0000	0?000-0000	-0?00000???	?????0?0?0	000?00?00?	0???00?00?	???????00?	?0???0?0??	????????	
Anurognathus ammoni Döderlein, 1923									
01000100??	?0??0-00?0	-?00???????	????00000	0000001100	0???0??10?	??????011?	?10000?101	1???001?	
Batrachognathus volans Rjabinin, 1948									
?1000100??	????0-00?0	-??0???????	???0?00000	0000001100	??0?0?0???	001????21?	?10???????	????????	
Dendrorhynchoides curvidentatus (Ji and Ji, 1998)									
01000100??	????0-00?0	-??0??????	??????0?00	0000000110	00???00?10	0?0100?021	??1??00?10	1122200??	
Jeholopterus ningchengensis Wang, Zhou, Zhang and Xu 2002									
0100010???	????0-00??	???00??0??	??????0?00	0000000110	00???01?10	000100?021	??1??00?10	112221011	
Austriadactylus cristatus Dalla Vecchia, Wild, Hopf and Reitner, 2002									
0010100100	0000610000	-000?000??	??????????	??00000000	0????00?00	????0?????	??????0???	????1????	
Sordes pilosus Sharov, 1971									
001010000?	00000-00?0	-?000010?0	?0????0000	00000001?0	00?0?00001	000100?011	??10000?10	211110013	
Preondactylus buffarinii Wild, 1984									
0010100?0?	0?000-00?0	-??000?0??	???????000	0?0?00??00	00???0??0?	???????111	??1??10?10	2111100??	
Scaphognathus crassirostris (Goldfuss, 1861)									
0010100000	00000-0000	-000001000	?000010?00	0000000100	00?0000001	0001001111	0010010?10	211110013	
Dorygnathus banthensis (Theodori, 1830)									
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Wukongopterus lii gen. et sp. nov.									
001010????	??????00??	?0????1???	??????0000	0000000120	00??010201	000?0??111	?01??10?10	211111013	
Dimorphodon macronyx (Buckland, 1829)									
0010100102	00000-0010	-0000000?0	?0????0000	0000000100	00?0000001	00010??111	0010011110	211111011	
Raeticodactylus filisurensis Stecher, 2008									
0010100000	0000220000	-00??010??	??????1000	2100001100	00???00???	????????21	??20??????	?1211?0??	
Caviramus schesaplanensis Fröbisch and Fröbisch, 2006									
?0????????	??????????	??????????	??????1000	0100?01100	0?????????	??????????	??????????	?????????	
Peteinosaurus zambellii Wild, 1978									
?0????????	??????????	??????????	??????????	?000?01100	00??????01	0001???111	??10011?10	211110011	
"Eudimorphodon" rosenfeldi Dalla Vecchia, 1995									
?01?1??00?	???????0??	??????????	???????0??	??00001100	00?000????	0???00?111	0????1????	2111100??	
"Eudimorphodon" cromptonellus Jenkins, Shubin, Gatesy and Padian, 2001									
??????????	??????????	???00?????	000???????	?0???011??	00????????	???????111	?????1???0	21211101?	
Eudimorphodon ranzii (Zambelli, 1973)									
0010100000	00000-0000	-0000010?0	?0????0010	0000001100	00?0000?0?	000100?11?	0020011?10	?????1???	
Campylognathoides liasicus (Quenstedt, 1858)									
0010100101	00000-0000	-100001000	?000110010	0000000100	0000000001	0001001111	0020011?10	121221010	
Campylognathoides zitteli (Plieninger, 1894)									
0010100101	00000-0000	-1000010?0	??????0010	0000000100	0000000001	000100?1??	?12??11?10	121220010	
Cacibupteryx caribensis Gasparini, Fernández and Fuente, 2004									
001?100000	00000-?000	-000000000	000010????	??00??????	??????????	??????????	??????????	?????????	
Harpactognathus gentryii Carpenter, Unwin, Cloward, Miles and Miles, 2003									
0010101?0?	????2?0???	??????????	???01?????	??0???????	??????????	??????????	??????????	?????????	
Angustinaripterus longicephalus He, Yan and Su, 1983									
0010101003	000020101?	?00????0??	??????00??	??00000100	0?????????	??????????	??????????	?????????	
Rhamphorhynchus muensteri (Goldfuss, 1831)									
0010100200	00000-0000	-000001100	0000110101	0000000100	0000000001	0001001111	0040011?10	122221012	
Rhamphorhynchus longicaudus (Münster, 1839)									
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Pterodactylus kochi (Wagner, 1837)									
0010100-1-	00000-0021	00000121?0	?0?0??0100	0000000120	0000011210	0001001211	0070021?20	312222020	
Pterodactylus antiquus (Soemmerring, 1812)									
0010100-1-	00000-0021	00000121?0	?0?0??0100	0000000120	0000011210	0001001211	0070021?10	312222020	

DATA MATRIX (continuation)

Germanodactylus cristatus (Wiman, 1925)	0010100-1-	0000400021	0000121?0	?0????0100	0000000120	00???11???	000100?211	??7?021???	3122221??
Germanodactylus rhamphastinus (Wagner, 1851)	0010100-1-	0000400021	0000121?0	??????0?00	0000000120	00???11??0	?001???211	??7?021???	31???2???
Gnathosaurus subulatus Meyer, 1834	0020100-1-	0000202025	0000121?0	?0??020100	0000000100	0?????????	??????????	??????????	?????????
Ctenochasma gracile Oppel, 1862	1020100-1-	0?000-0020	-0?00121?0	?0????0100	0000000101	0??00112?0	?001???211	??7??21???	312??2020
Pterodaustro guinazui Bonaparte, 1970	1020100-1-	00000-0021	0000121?0	?0????0100	0000000101	0???011210	?001???211	??7?02?1??	312222020
Feilongus youngi Wang, Kellner, Zhou and Campos, 2005	1020100-1-	0000100021	0000212?00	?0?0??0?00	0020000100	0?????????	??????????	??????????	?????????
Gallodactylus canjuersensis Fabre, 1974	1010100-1-	0?000-0022	0??02??1??	?0????0??0	0020000100	0?????????	0001??????	??????????	?1222?1??
Cycnorhamphus suevicus (Quenstedt, 1855)	1010100-1-	00000-0022	00002121??	?0?0??0100	0020000100	0?00?112??	0001???210	??70021??0	3122221??
Nyctosaurus gracilis (Marsh, 1876)	0010100-1-	00000-0020	-00000?110	?010120100	0030000100	0111001010	0001001311	1050?21222	3222220??
Nyctosaurus bonneri Miller, 1972	0010100-1-	00000-0020	-00000?1?0	?0????0100	0030000100	01?1?010?0	???????31?	??50?????2	322222???
Nemicolopterus crypticus Wang, Kellner, Zhou and Campos, 2008	0010100-1-	00000-0026	001000?2??	??????0100	0030000100	00??001?10	000?0???11	?17??2????	31?222120
Pteranodon longiceps Marsh, 1876	1020100-1-	00000-0024	0003301210	1010120100	0030000100	0111101110	1101001211	1061121222	322222020
Istiodactylus latidens (Seeley, 1901)	0010100-2-	?0??0-0?20	-?2?????0?	???0???100	0?20000100	11?1?0????	1111002?1?	??611?2???	??1??????
Nurhachius ignaciobritoi Wang, Kellner, Zhou and Campos, 2005	0010100-2-	00000-002?	?02???12??	??????0?00	0020000100	110??011??	1?1?0?2211	0?61?222?1	312??21??
"Ornithocheirus" compressirostris (Owen, 1851)	00101?????	????0-00??	??????????	???1????00	0?00000100	0?????????	??????????	??????????	?????????
Tropeognathus mesembrinus Wellnhofer, 1987	0010100-1-	000013102?	?001101210	1012120100	1000000100	0?????????	??????????	??????????	?????????
Anhanguera santanae (Wellnhofer, 1985)	0010100-1-	0000131023	1001101210	1011120100	?000100100	001110111?	211200????	01611?22?1	?????????
Anhanguera blittersdorffi Campos and Kellner, 1985	0010100-1-	000013102?	?001101210	1011120100	1000100100	0?????????	??????????	??????????	?????????
Anhanguera piscator Kellner and Tomida, 2000	0010100-1-	0000131023	1001101210	101?120100	1000100100	0011101110	2112002211	01611222?1	?????2120
Dsungaripterus weii Young, 1964	2010100-1-	1001310120	-002301211	1111120100	0011010100	0111101010	00010?2200	??7?0211?1	312222120
"Phobetor" parvus (Bakhurina, 1982)	0010100-1-	1001310120	-0023012?1	?1????0100	0011010100	0?????????	??????????	???????1??	?????????
Noripterus complicidens Young, 1973	??????????	??????????	??????????	??????????	????10?00	???11010??	???????200	01720211??	312??2120
Tupuxuara leonardii Kellner and Campos, 1994	0010100-2-	011056002?	?012301211	1113120100	0030000100	01111010??	0001012200	10720211??	313??2???
Thalassodromeus sethi Kellner and Campos, 2002	0010100-2-	0110560024	0012301211	1113120100	0030000100	0?????????	??????????	??????????	?????????
Tapejara wellnhoferi Kellner, 1989	0011100-2-	011055002?	?012301201	1110120100	2030000100	00?11010?0	000101?200	117202112?	31???2120
Tupandactylus imperator (Campos and Kellner, 1997)	0011100-2-	011055002?	?0123012?1	??????????	??30000100	0?????????	??????????	??????????	?????????
Quetzalcoatlus sp.	0010100-1-	00107?0020	-00???121?	???01?0100	0030000100	0110213?0	000110?200	10720211??	313222?20
Azhdarcho lancicollis Nessov, 1984	??????????	??????????	??????????	??????????	??30000100	?1110213??	??????????	107?0?????	?????????
Zhejiangopterus linhaiensis Cai and Wei, 1994	0010100-1-	00100-0020	-000?012?1	??????0?00	0030000100	011??213?0	000?10?200	??7??21?2?	313??2???