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A new scaphognathid pterosaur from western Liaoning, China

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A partial skeleton of a new pterosaur, *Jianchangnathus robustus* gen. et sp. nov. from western Liaoning, China, is described. The specimen (IVPP V16866) was collected near Linglongta, Jianchang County, whose deposits have a disputed age that range from Middle Jurassic to Early Cretaceous. The new species shares several features with the non-pterodactyloid *Scaphognathus* from the Late Jurassic deposits of southern Germany, such as a deep anterior end of the lower jaw, a piriform lower temporal fenestra with the ventral margin broader than the dorsal one and the interalveolar spacing of the maxillary teeth about three alveolar spaces, allowing its allocation to the Scaphognathidae. The main diagnostic features of *J. robustus* include the large maxillary process of the jugal, the convex alveolar margin of the lower jaw and the procumbent disposition of the first three pairs of dentary teeth. The new Chinese taxon also differs from *Fenghuangopterus lii*, which comes from the same deposit and is here regarded as Scaphognathidae *incertae sedis*, mainly by the lower number of teeth and several proportions of the wing elements. The discovery of *J. robustus* demonstrates a larger diversity in the pterosaur fauna of the Linglongta region so far dominated by the non-pterodactyloid clade Wukongopteridae.

Keywords: Pterosauria; Scaphognathidae; *Jianchangnathus*; Liaoning; China

Introduction

In the last 15 years, the research of Chinese pterosaurs has made remarkable contributions to the study of those flying reptiles. Several new taxa, mostly coming from the Yixian and Jiufotang formations of western Liaoning, were found enhancing our understanding of the whole group (e.g. Lü and Ji 2005; Wang et al. 2008). More recently, an older deposit that outcrops in the region of Linglongta at the Jianchang County, also located in western Liaoning, has furnished some pterosaur material as well (Figure 1).

There is still an ongoing debate about the correct stratigraphic placement and consequent age of those deposits. Some researchers advocate that those layers represent the Daohugou Bed (Formation), whereas others regard them as part of the Tiaojishan Formation that has been assigned to the Middle Jurassic (Chen et al. 2004; Ji et al. 2005; Liu et al. 2006; Lü, Fucha et al. 2010; Lü, Unwin et al. 2010), Late Jurassic (Zhang 2002; He et al. 2004; Zhang et al. 2008; Zhou et al. 2010) or Late Jurassic-Early Cretaceous (Wang et al. 2005, 2009, 2010).

Independent of this debate, pterosaur specimens are starting to be found at Linglongta and surrounding areas in an increasing number. The most important material represent the clade Wukongopteridae whose members combine non-pterodactyloid features with some derived characteristics thought previously to be restricted to the pterodactyloids (Wang et al. 2009, 2010; Lü, Unwin et al. 2010).

Beside wukongopterids, only *Fenghuangopterus lii* has been described from those deposits so far and was regarded to be a member of the Scaphognathinae (Lü, Fucha et al. 2010). Here, we report another pterosaur from Linglongta, *Jianchangnathus robustus* gen. et sp. nov., which can be unequivocally referred to clade Scaphognathidae (Hooley 1913). We also discuss the scaphognathid affinities of taxa previously referred to this group including *Fenghuangopterus*.

Systematic paleontology

Pterosauria Kaup 1834
Scaphognathidae Hooley 1913
Jianchangnathus gen. nov.

Etymology: *Jianchangnathus*, from Jianchang County, where the specimen was collected, and *gnathus*, from the Greek meaning jaw.

Type species: *J. robustus* gen. et sp. nov.

Diagnosis: The same as for the species.

J. robustus sp. nov.

Etymology: From *robustus*, the Latin word meaning strong in allusion to the powerful jaws of this species.

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Figure 1.   Sketch map showing the locality where the holotype of *J. robustus* gen. et sp. nov. was recovered.

Holotype: Partial skeleton with complete skull and lower jaw, housed in the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences), Beijing, China, under the number IVPP V16866 (Figures 2–5).

Locality and horizon: Linglongta, Jianchang County, western Liaoning, China. Daohugou Bed (Formation) or Tiaojishan Formation, Late Jurassic-Early Cretaceous (Wang et al. 2005, 2009, 2010; Lü, Fucha et al. 2010; Lü, Unwin et al. 2010).

Diagnosis: Scaphognathid pterosaur with the following combination of characters that distinguish it from other members of this clade (autapomorphies are marked with an asterisk*): external naris smaller and antorbital fenestra longer compared to *Scaphognathus*; premaxillary sagittal ridge extended further posteriorly than in *Scaphognathus*; upper teeth inclined anteriorly; maxillary process of the jugal extending as long as two-thirds of the length of the lower margin of antorbital fenestra*; five teeth on each side of the dentary; alveolar margin of the anterior portion of the dentary convex in lateral view*; anterior teeth (teeth 1–3) of the dentary procumbent*; diameter of metacarpal II the smallest of the metacarpus.

Description

The holotype (IVPP V16866) of *J. robustus* is preserved in a slab of light grey shale (Figures 2 and 3). The specimen is composed of a partial skeleton with the skull and the lower jaw that lacks most of the vertebral column (except for part of the neck and a few caudal vertebrae), portions of the wings and most of the hind limbs (apart from for the feet). Humerus, shoulder girdle and pelvis are very incomplete. The specimen came to the IVPP split in the middle and was glued back before preparation. The material suffered from compaction that has broken most of the bone surface,

a common condition of specimen from western Liaoning, particularly pterosaurs.

The skull of *J. robustus* is nearly complete, missing part of the dorsal margin above the naris and the antorbital fenestra. It was compressed dorsoventrally and shifted slightly to the left lateral side, which resulted in the exposition of some elements of the right side. Most of the cranial elements described here are from the left side that is the main exposed part of the skull (Figures 3 and 5).

Although the bones that form the orbit are displaced due to taphonomy, the dorsal and the ventral margins are preserved showing that it was rounded and the largest cranial opening. The naris suffered from compression with the dorsal and the posterior margins difficult to be reconstructed. In any case, it is comparatively small and anteroventrally elongated. The antorbital fenestra is also anteroposteriorly elongated and larger than the naris. The lower temporal fenestra is pear shaped, with the ventral margin wider than the dorsal, apparently a unique feature of the Scaphognathidae (see Discussion).

The premaxilla and maxilla are fused with the suture between them completely obliterated. The dorsal margin of the premaxillae is very thick on the anterior end and extends between the frontals as a low ridge than can be regarded as a rod-like premaxillary crest. The middle part of this bone was broken and pushed ventrally inside the skull.

The maxilla comprises most of the anterior lateral surface of the skull. It forms the ventral margin of the naris and sends a long nasal process posteriorly that shapes most of dorsal margin of the antorbital fenestra.

The nasal is not very well preserved in this specimen. It is an elongated flat bone that forms the posterior margin of the external naris but does not take part in the antorbital fenestra. This bone is not swelled as the one in *Scaphognathus crassirostris*.

The supraorbital is displaced inside the orbit. The medial part, which is in the original anatomical position contacting the frontal, is straight and marked by a thickening of the bone. The lateral (or ventrolateral) margin that forms the anterior border of the orbit is also thickened.

By far the largest element of the skull roof, the frontal is partially overlain by the posterior processes of the premaxillae. The suture with the parietal, a bone that is very compressed taphonomically in this specimen, is straight.

The lacrimal is partially overlain by the nasal. The jugal process is thick and inclined ventroposteriorly. No ventral lacrimal foramen as the one present in *Sc. crassirostris* is observed. A small thick and broken bone posterior to the lacrimal is what was left of the prefrontal.

Very flattened and displaced ventrally from its original anatomical position, the postorbital participates in the posterior margin of the orbit. Together with the squamosal,
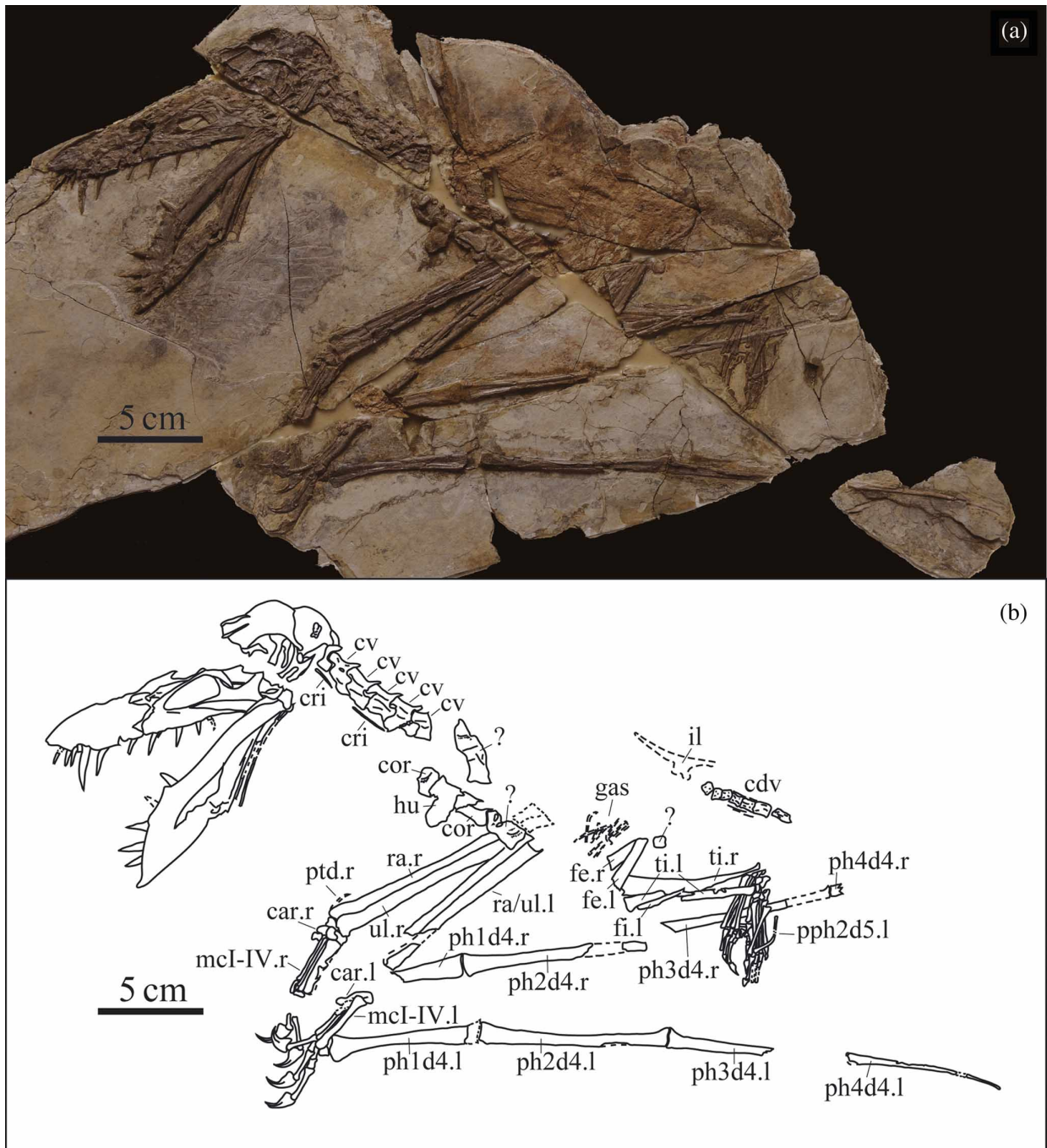
Figure 2. *J. robustus* gen. et sp. nov., holotype (IVPP V16866). (a) Photo and (b) drawing of the nearly complete skeleton. Abbreviations: car, carpus; cdv, caudal vertebra; cor, coracoid; cri, cervical rib; cv, cervical vertebra; fe, femur; gas, gastralia; hu, humerus; il, ilium; mcI-IV, metacarpal 1-4; ph1-4d4, first to fourth phalanx of manual digit IV; pph2d5, second phalanx of pedal digit V; ptd, pteroid; ra, radius; ti, tibia; ul, ulna; l, left; r, right; ?, unknown element.

this bone forms the bony bar that separates the upper and the lower temporal fenestrae. It only takes part in the anterior (but not dorsal) margin of the lower temporal opening.

The jugal is displaced dorsally inside the antorbital fenestra. It bears four processes, with the maxillary process very long, rod-like and anteriorly directed, forming at least two-thirds of the lower margin of the antorbital fenestra. The lacrimal process is rather stout while the postorbital and the posterior processes are both broad and blade-like.

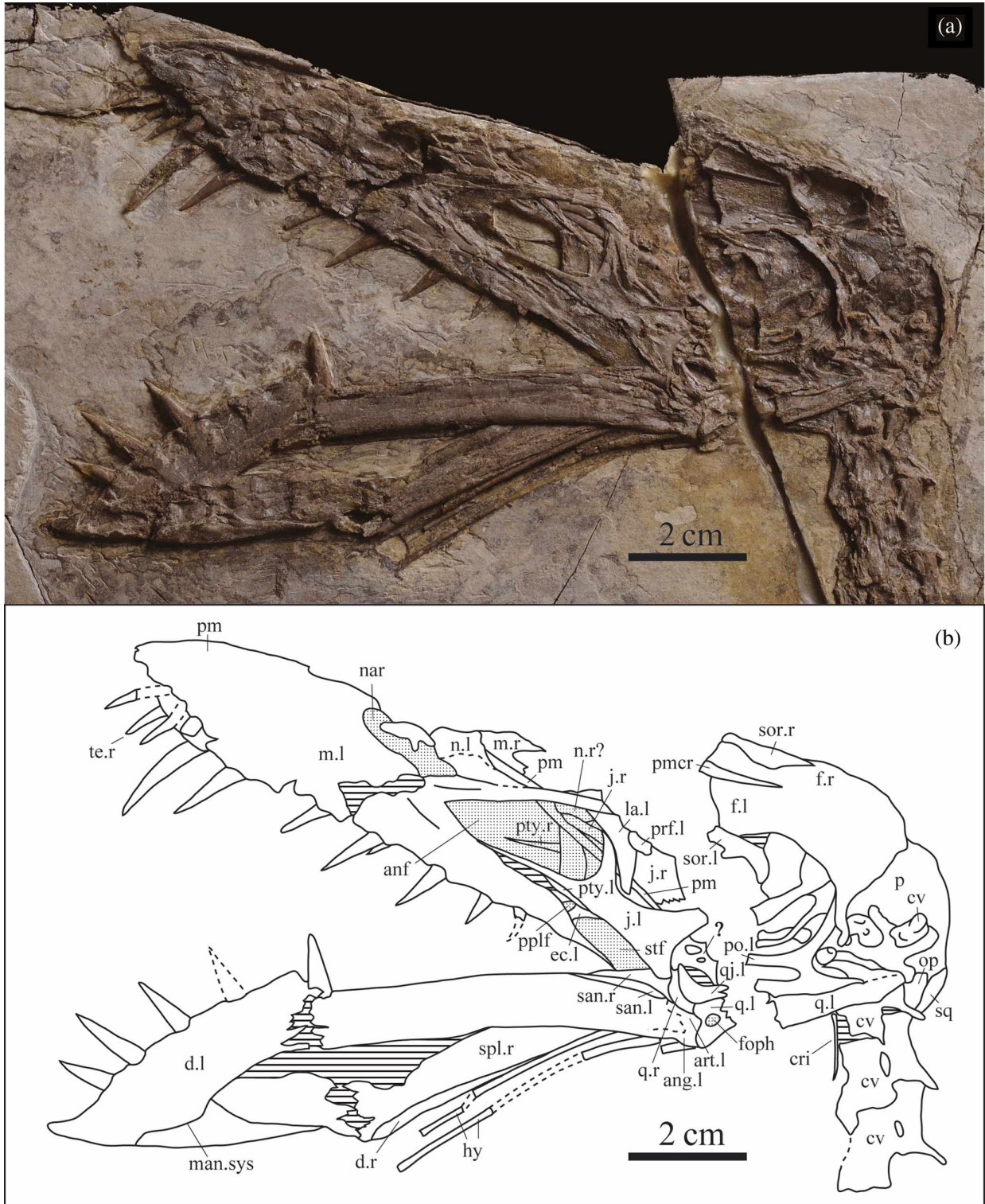The region of the cranio-mandibular articulation is very fragmented and compressed forming a mishmash of

Figure 3. *J. robustus* gen. et sp. nov. (IVPP V16866). (a) Photo and (b) drawing of the skull. Abbreviations: anf, antorbital fenestra; ang, angular; art, articular; cri, cervical rib; cv, cervical vertebra; d, dentary; ec, ectopterygoid; f, frontal; foph, foramen pneumaticum; hy, hyoid; j, jugal; la, lacrimal; m, maxilla; man.sys, mandibular symphysis; n, nasal; nar, external naris; op, opisthotic; p, parietal; pm, premaxilla; pmcr, premaxillary crest; po, postorbital; pplf, postpalatinal fenestra; prf, prefrontal; pty, pterygoid; q, quadrate; qj, quadratojugal; san, surangular; sor, supraorbital; spl, splenial; sq, squamosal; stf, subtemporal fenestra; te, tooth; l, left; r, right; ?, unknown element.
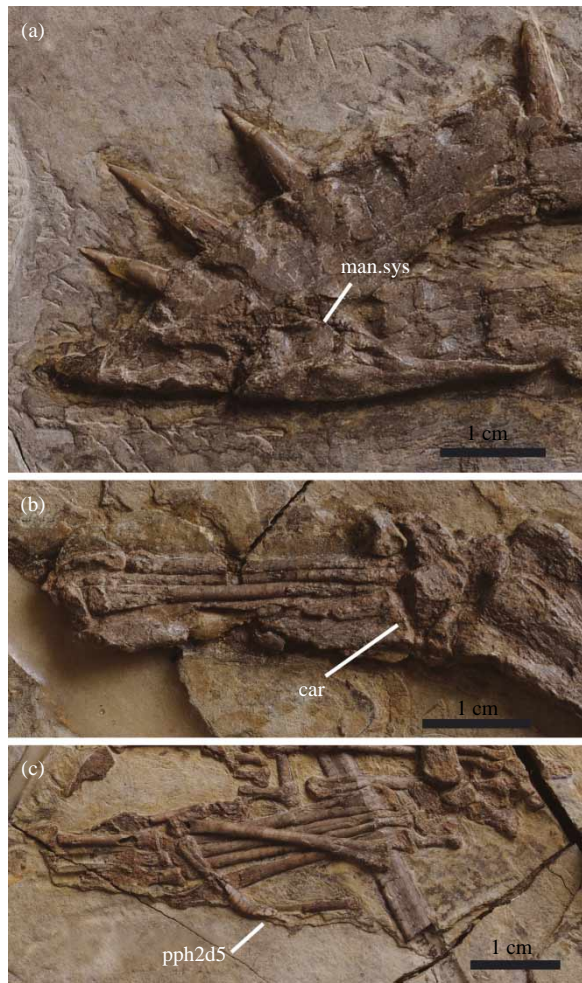
Figure 4. *J. robustus* gen. et sp. nov. (IVPP V16866). (a)–(c) Details of the skeleton: (a) tip of lower jaw, (b) right carpus and (c) left foot. Abbreviations: car, carpus; man.sys, mandibular symphysis; pph2d5, second phalanx of pedal digit V.

broken bones whose interpretation is rather difficult. Both quadrates can be identified with the left one being more complete. It is robust and has a well-developed medial
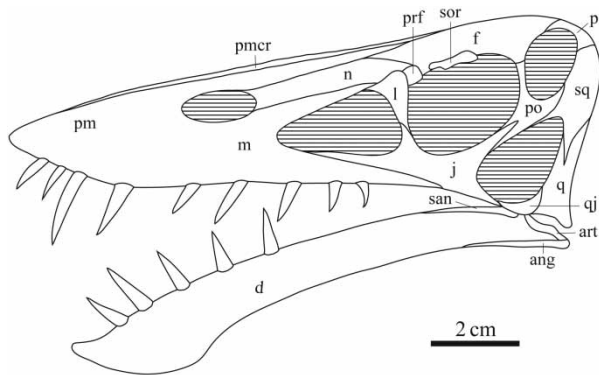

Figure 5. *J. robustus* gen. et sp. nov., holotype (IVPP V16866), reconstruction of the skull. Abbreviations as in Figure 3.

flange. There seems to be a pneumatic foramen close to the lateral condyle. A small, rather blade-like element with a thick margin, presumably taking part in the lower temporal fenestra, is interpreted as the quadratojugal.

As other bones in the posterior region of the skull, the squamosal is very compressed laterally. It forms the dorsal margin of the lower temporal opening and has a ventrally oriented process that overlies the quadrate.

There is not much information available for the palatal region and some unidentifiable elements can be observed through the antorbital fenestra. Among those, a thin slightly twisted rod-like bone that tapers proximally. This element is interpreted as the anterior process of the right pterygoid. Part the left ectopterygoid is observed ventral to the left jugal. This bone is broad and forms the anterior margin of the subtemporal fenestra and the posterior margin of a comparatively smaller postpalatinal fenestra. An anteriorly tapering bone is identified as the left pterygoid.

No details regarding the occipital region and the braincase can be observed due to taphonomy. In the posterior region of the skull, the internal portion of the supraoccipital and the opisthotic from the right side are visible as is part of the medial margin of the postemporal fenestra.

The lower jaw is exposed mostly in lateroventral view. The mandibular rami are broken and overlap partially.

As common for pterosaurs, the dentary is the largest element of the lower jaw. Anteriorly, it has a small anterodorsally inclined projection, much smaller than the one of *Rhamphorhynchus* and *Dorygnathus*. Although ventrally flattened, it can be established that this region of the lower jaw is deeper than the mandibular rami. The anterior portions of both dentary are fused, forming a mandibular symphysis that is rather short, around 25% of the mandibular length (Figure 4(a) and Table 1). The exact posterior extension of the dentary is unknown and the limits between the angular and articular are not discernible.

The surangular of both sides can be observed. This bone takes part in the cranial articulation but its exact extend is unknown. The anterior dentary process of this bone is very long and overlies the dentary for at least one-third of the lower jaw length.

The right mandibular ramus is preserved in medial view and exposes the splenial. The latter is thin-walled and bounded dorsally and ventrally by the dentary. The limits with the angular or prearticular cannot be established.

Two elongated elements preserved ventral to the dentary are interpreted as the hyoid bones. As in other pterosaurs, they are rod-like and very long.

There are nine essentially straight teeth on each side of the upper jaw. All show smooth enamel, lacking carinae or ridges. They are of moderate size, thin and have pointed tips. Some are slightly displaced from the alveoli and one

Table 1.   Measurements of *J. robustus* gen. et sp. nov. (in mm).

Bones	Length
Skull length (tip of premaxillae to posterior end of squamosal)	148.9
Rostrum	40.8
Maximum length of naris	18.8
Maximum length of the antorbital fenestra	32.8[a]
Maximum height of the antorbital fenestra	15.0[a]
Height of the anteriomost point of the external naris	10.6
Lower jaw	113.4[b], 120.0[a]
Mandibular symphysis	28.4
Ulna and radius	103.5[b], 114.0[a] (r)
Metacarpal IV	31.5 (l)
Wing finger phalanx I (with extensor tendon process)	78.2 (r)
Wing finger phalanx II	89.4 (r)
Wing finger phalanx IV	73.2[c] (r)
Metatarsal III	25.9 (l)
Metatarsal IV	22.3 (l)
First phalanx of pedal digit V	24.6 (l)

Notes: r, right; l, left. [a]Estimated length. [b]Preserved length. [c]Minimum length.

tooth from the right side can be observed between the first two teeth of the left side. The first two teeth are shorter and followed by a fang-like tooth (18 mm) that is the largest, being more than three times higher than the last one. The remaining teeth decrease in size towards the posterior end with the last tooth (the smallest) reaching about the middle portion of the antorbital opening. There is a small replacement tooth located posteriorly to the sixth. Except for the last tooth, all teeth are inclined forward. Starting with the fourth tooth, the interalveolar spacing is rather high and reaches about three times the alveolus size of the preceding tooth.

The lower teeth show the same morphology of the upper. There are a total of five teeth on the left side which, except for the forth (very fragmentary), are well preserved. The first three (possible also the fourth) teeth are procumbent and the last one is vertical. The dentition is restricted to the anterior half of the lower jaw. Although the spacing between the teeth is also large, it is smaller than the interalveolar spaces observed in the maxilla.

Seven articulated cervical vertebrae, all exposed in ventral view, can be recognized, the first two of which are overlain by the posterior end of the skull. They are procoelic, robust and subequal in size. The postzygaphyses are quite strongly built with distinct ventrolaterally oriented processes that are set apart from the postzygapophyseal articulation surface. The centrum is not perforated by a pneumatic foramen, but one exists on the contact with the neural arch, similar to what is observed in *Rhamphorhynchus* (Wellnhofer 1975a).

The remains of seven caudal vertebrae can be identified. They suffered distortion during the fossilization process and are very flattened and not well preserved. Nevertheless, they show elongated zygapophyses forming rod-like processes as typically found in non-pterodactyloid pterosaurs.

A few cervical ribs are preserved, some displaced from their original anatomical position. They are elongated and taper posteriorly, reaching half the centrum of the succeeding vertebra.

Some elements of the gastralia are preserved essentially as 'V'-shaped impressions in the matrix, with most of the bone lost. No evidence of stomach content could be identified.

The pectoral girdle and the humerus are very incomplete and some parts were invaded by resin during the preparation process, making interpretations difficult. One elongated bone ($\sim 44\,mm$) that overlies the shaft of the humerus and has the proximal articulation slightly concave is interpreted as the coracoid. In close contact with the latter is another bony element (overlying the right radius and ulna) that has an elaborated surface with ridges, depressions and foraminae. In this area, one expects to find the sternum, but due to poor preservation this element cannot be identified with certainty.

Part of the shaft and the deltopectoral crest of the left humerus could be recognized but are not sufficiently preserved to allow the establishment of the original morphology of this bone. In any case, the deltopectoral crest seems to be directed subperpendicular to the shaft and not deflected proximally as has been observed in some specimens (e.g. Costa and Kellner 2009).

Radius and ulna from both sides are preserved with the left one lacking proximal and distal articulations. The diameter of the radius is slightly less than the diameter of the ulna.

The carpus of the right side is complete and exposed in ventral view. There are at least two elements in the proximal and the distal series, all unfused. The lateral distal carpal is a small, stout triangular bone. The right pteroid is very small, preserved as an impression close the proximal carpal series to which it likely was articulated as observed in other pterosaurs (e.g. Wang et al. 2010). From the left carpus, only some fragments of the distal carpal series are discernible.

The metacarpus of both sides can be observed with the right one better preserved. Metacarpals I to III are straight rod-like bones and articulate with the carpus. Distally, there is a difference in length between those bones that decrease in length from metacarpal III to I, the latter being about 11% shorter that the wing metacarpal. This size difference has not been reported in other pterosaurs such as *Rhamphorhynchus* (Wellnhofer 1975a) and *Dorygnathus* (Padian 2008: 44). The diameter of metacarpal II is the smallest, also an unusual feature within non-pterodactyloid flying reptiles.

The manus of both wings are partially preserved with the left one more complete. The phalangeal formula is 2:3:4:4:0 – like in all non-pterodactyloid pterosaurs. Manual unguals are strong and deep with a marked lateral sulcus.

The first phalanx of the left wing finger has the extensor tendon process unfused. No pneumatic foramen could be observed. The first phalanx of the wing finger is smaller than the third and might have been slightly larger or subequal to the fourth that is incomplete in this specimen.

The pelvic region is poorly preserved. Although there are bone particles scattered around the surface where the pelvis was preserved, the only element that can be confidently identified is the impression of an ilium, possibly from the right side. The preacetabular portion is more developed and longer than the postacetabular part.

The hind limbs are very incomplete and cross each other with the left one above the right. The middle portion of the shaft of both femora and the right tibia are preserved and do not provide any relevant anatomical detail. The distal part of the left tibia shows a rounded articulation with the proximal tarsals not fused to this bone. Part of the left fibula's shaft is also preserved and indicate that it has a comparatively large diameter (~ 1.6 mm).

The feet are well preserved with the left one more complete than the right. The phalangeal formula is 2:3:4:5:2, typical for non-pterodactyloid pterosaurs. The second phalanx of pedal digit V is curved, boomerang shaped, having the proximal and distal part subequal in length and diverging from each other at an angle of about 135° (Figure 4(c)).

Comparison and discussion

Although the ontogenetic variation within pterosaurs including non-pterodactyloid taxa is poorly known, the holotype of *J. robustus* shows indication that it was a young animal when it perished. This is based on the fact that several bones that tend to be fused in ontogenetic mature animals (e.g. Bennett 1993, 1995; Kellner and Tomida 2000) are not fused in IVPP V16866: the elements of the proximal and the distal carpal series, the extensor tendon process of the first wing phalanx and the proximal tarsals with the tibia. The new species is easily excluded from the Pterodactyloidea and the Wukongopteridae based on several cranial (e.g. separated naris and antorbital fenestrae) and postcranial (e.g. short cervical vertebrae) features (e.g. Wang et al. 2010).

Within non-pterodactyloid pterosaurs, *J. robustus* shares several traits with *Sc. crassirostris* (see below), a non-pterodactyloid from the early Tithonian (Late Jurassic) deposits of southern Germany (Goldfuss 1831; Wagner 1861; Wellnhofer 1975b, 1975c). *Scaphognathus* has been referred to the Scaphognathidae (or Scaphog-

nathinae), which was first introduced by Hooley (1913). Since then the monophyly and phylogenetic content of this group has been the subject of debate.

Unwin (2003) and Carpenter et al. (2003) considered the Scaphognathinae as part of the Rhamphorhynchidae, composed of *Sc. crassirostris*, *Sordes pilosus* and *Harpactognathus gentryii*. A monophyletic grouping of *Sc. crassirostris* and *So. pilosus* (but not closely related to *Rhamphorhynchus*) was recovered by Dalla Vecchia (2009a, 2009b), who did not include *H. gentryii* in his analysis. However, none of the more comprehensive phylogenetic studies recovered a sister-group relationship between *Sc. crassirostris* and *So. pilosus* (Kellner 2003, 2004; Wang et al. 2005, 2009; Andres et al. 2010). This also includes the study of Lü, Unwin et al. (2010), where *Sordes* and *Scaphognathus* were recovered in a polytomy with other non-pterodactyloid pterosaurs. The most extreme result was obtained by Andres et al. (2010: 178), where all three taxa (*Sc. crassirostris*, *So. pilosus* and *H. gentryii*) came out in very distinct places on the consensus tree.

As mentioned, *J. robustus* shares several features with *Sc. crassirostris* such as anterior end of the dentary deeper than mandibular rami; sagittal region of the premaxillae forming a thick ridge that extends posteriorly (which can be regarded as a premaxillary crest); lower temporal fenestra piriform with the ventral margin broader than the dorsal one; interalveolar spacing of maxillary teeth about three alveolar spaces; boomerang-shaped second phalanx of pedal digit V with proximal and distal portions subequal in length and length of metacarpals decreasing distally from metacarpal IV to I (mcIV > mcIII > mcII > mcI). Those features might be regarded as synapomorphies of the Scaphognathidae.

J. robustus and *Sc. crassirostris* also share a low number of teeth in the upper (18, nine on each side) and lower (10, five on each side) jaws, which is also reported in the Anurognathidae, where the spacing between the teeth is also large (Wellnhofer 1978).

Among the most conspicuous differences between *J. robustus* and *Sc. crassirostris*, the Chinese species shows a longer maxillary process of the jugal, a convex alveolar margin of the dentary and the first three pairs of dentary teeth procumbent. Furthermore, in *Jianchangnathus* the majority of the upper teeth are inclined anteriorly while in *Scaphognathus* they tend to be subvertical. Although the dorsal portion of the skull in *Jianchangnathus* shows some deformation that affected the sizes of the cranial openings, it is clear that in the new species the external naris is smaller and the antorbital fenestra is longer than the respective openings in *Scaphognathus*. Both taxa also show similar postcranial proportions (see Table 2). The main difference is the diameter of metacarpal II that in the Chinese taxon is the smallest of the metacarpus while in

Table 2.   Postcranial bone ratios of *J. robustus* gen. et sp. nov. and other pterosaurs.

Bones/taxa	*J. robustus* gen. et sp. nov.	*Sc. crassirostris* (Maxberg specimen)	*Sc. crassirostris* GPIB	*F. lii*	*So. pilosus* PIN 2585/3
hu/ul	–	0.61	0.57	0.74	0.62
hu/mcIV	–	2.00	1.98	1.80	2.61
hu/ph1d4	–	0.79	0.76	0.50	0.85
hu/ph2d4	–	0.73	0.71	0.84	0.81
hu/fe	–	1.03	0.97	1.10	1.20
hu/ti	–	0.92	*X*	0.63	0.87
hu + ul/fe + ti	–	1.28	*X*	0.94	1.31
ul/mcIV	3.29[a], 3.62[b]	3.27	3.48	2.43	4.19
ul/ph1d4	1.32[a], 1.46[b]	1.29	1.34	0.68	1.37
ul/fe	–	1.69	1.71	1.49	1.92
ul/ti	–	1.51	*X*	0.85	1.39
ph1d4/mcIV	2.48	2.53	2.59	3.57	3.06
ph2d4/ph1d4	1.14	1.08	1.07	0.60	1.05
ph4d4/ph1d4	0.94	0.97	*X*	–	0.67
ph1d4/fe	–	1.31	1.27	2.19	1.40
ph1d4/ti	–	1.17	*X*	1.25	1.02
fe/ti	–	0.89	*X*	0.57	0.73
fe/mcIV	–	1.93	2.04	1.63	2.18
ti/mcIV	–	2.17	*X*	2.86	3.01
Source	This paper	Wellnhofer (1975c)	Wellnhofer (1975c)	Lü, Fucha et al. (2010) and Lü, Unwin et al. 2010	Unwin et al. (2000)

Notes: Sources for metric data are indicated in last line. fe, femur; hu, humerus; mcIV, metacarpal 4; ph1d4, first phalanx of manual digit IV; ph2d4, second phalanx of manual digit IV; ti, tibia; ul, ulna. [a]Based on preserved length. [b]Based on estimated length.

Sc. crassirostris the diameter of metacarpals I to III is about the same.

Regarding *So. pilosus*, unlikely a member of the Scaphognathidae (e.g. Kellner 2003; Wang et al. 2009; Andres et al. 2010), *J. robustus* differs for all in the dentition. While *So. pilosus* is reported to have a low number of widely spaced teeth – total of 14 in the upper and 12 in lower jaw, respectively (Wellnhofer 1978; Unwin 2003) – they are peg-like and much smaller than in the Chinese taxon (Wellnhofer 1991: 102). Other differences can be seen in the proportions of several wing elements (see Table 2), particularly the size of the wing metacarpal that is smaller relative to the ulna and the first phalanx of the wing finger. There is also a marked difference in the proportion of the last and the first phalanx of the wing finger, with the former comparatively smaller in *So. pilosus* (Unwin et al. 2000). *So. pilosus* also has a boomerang-like second phalanx of the fifth toe, but if the reconstruction provided by Unwin and Bakhurina (1994) is correct, the proximal part is longer than the distal, apparently a unique feature of this taxon and another difference from *Jianchangnathus*.

The only feature supporting a close affinity between *H. gentryii* and the Scaphognathidae (or Scaphognathinae *sensu* Unwin 2003) is the spacing of the upper alveoli. Unfortunately, the taxon from the Morrison Formation is very incomplete and lacks teeth and the lower jaw (although one was illustrated by Carpenter et al. 2003: 50). As implied by the phylogenetic result obtained by Andres et al. (2010), this taxon is quite distinct from *Scaphognathus* (and the Scaphognathidae, here including *Jianchangnathus*) by having a very elongated and dorsoventrally compressed naris. The premaxillary sagittal crest is apparently also higher in *H. gentryii* than in *Sc. crassirostris* and the ridge-like sagittal structure present in *Jianchangnathus*. The new Chinese species also lacks the scalloped lateral surface of the premaxilla and the maxilla, and the undulating and deeply emarginated ventral profile of the dental margin below the external nares, regarded as diagnostic for *H. gentryii* (see Carpenter et al. 2003). A further difference is in the spacing of the anterior three pairs of upper teeth (likely belonging to the premaxilla), which is larger in *H. gentryii* than in *J. robustus*. If the latter also has an antorbital fossa anterior to the antorbital fenestra as reported in *H. gentryii* by Carpenter et al. (2003), cannot be established due to preservation.

Another supposed scaphognathid pterosaur recently reported is *Fenghuangopterus lii*, from the same locality of *J. robustus*. Only briefly described, this species was considered a scaphognathine by Lü, Fucha et al. (2010: 265) based on the following features: proportionally short skull with a blunt tip, large antorbital fenestra, and widely spaced and vertically oriented teeth. Unfortunately, there is no interpretative drawing of the skull of *F. lii* or any indication in the published pictures of individual bones except for the position of the teeth, what restricts the comparisons with *J. robustus*. Most of the dorsal part of the skull of *F. lii* is apparently not preserved including the tip and it is difficult to establish if the anterior part of the skull ends as a blunt tip. The dorsal margin of the antorbital

fenestra is not preserved and therefore its size and height are difficult to be determined. Regarding the dentition, as pointed out by Lü, Fucha et al. (2010), the anteriomost teeth are not particularly widely spaced. In fact, if the positions of the teeth provided in the original description are correct, the interalveolar distances do not reach the three (or four) alveolar spaces regarded as diagnostic for the group (Carpenter et al. 2003; Unwin 2003). Furthermore, the number of teeth is not particularly reduced (11 are reported in the left side of the upper jaw, implying a total of 22 instead of the 18 present in *Sc. crassirostris*). Those observations cast some doubts about the scaphognathid nature of *F. lii*.

Despite being from the same locality, or even the same horizon, there are obvious differences between *Jianchangnathus* and *Fenghuangopterus*, which cannot be attributed to taphonomic reasons, as occasionally happens with pterosaur material from different areas, including China (Kellner 2010). *J. robustus* differs from *F. lii* by having lesser number of teeth in the upper jaw (18 against 22), which are inclined anteriorly and not subvertically. From the published pictures, it seems also that the teeth of *F. lii* are more curved posteriorly, differing from the straight condition observed in *J. robustus*. The location of the last tooth in the upper jaw, which has been regarded as diagnostic for *F. lii*, is about the same in both taxa.

Although not clear in the published pictures, apparently *F. lii* also lacks the convex outline of the lower jaw alveolar margin and the procumbent condition of the first three pairs of the dentary teeth observed in *J. robustus*.

The proportion of several wing elements also is quite different in *J. robustus* and *F. lii* and diverge in all cases where comparisons are possible, for all in the ratio between the first and second wing phalanges and the ratio of several bones and the wing metacarpal (see Table 2). Although proportions of wing elements might vary during ontogeny (e.g. Bennett 1995; Sayão 2003), the variations found in those specimens indicate that they belong to distinct taxa. Actually the ratio of several elements of *F. lii* and both specimens attributed to *Sc. crassirostris* are also surprisingly distinct (see Table 2), not only those related to the first wing phalanx and the wing metacarpal, but also regarding the tibia.

Still concerning the measurements provided for *F. lii*, Lü, Fucha et al. (2010) pointed out that the coracoid was longer than the scapula, and if the published values are correct, the ratio of scapula/coracoid is 0.80. However, only in the members of the derived pterodactyloid clade Pteranodontoidea the coracoid is larger than the scapula (e.g. Bennett 1994; Kellner 2003). Although difficult to establish in the published pictures, the scapula seems to be much longer than the coracoid (see Lü, Fucha et al. 2010, Figure 1(a)) and most likely *F. lii* shows the normal condition observed in non-pterodactyloids.

In terms of size, although not all bones of *J. robustus* are preserved, the wingspan of the holotype can be estimated as being around 116.8 cm. When direct comparisons of the size of postcranial bones between the holotype of the new taxon and the one of *F. lii* are made, some of *Jianchangnathus* are larger (e.g. ulna, ph2d4) while others are smaller (e.g. wing metacarpal, first phalanx of the wing finger). This contrasts with the length of the skull that in the holotype of *J. robustus* is almost the double that of *F. lii*. If only the postcranials are considered, it seems that both have similar wingspans.

Notwithstanding, the holotype of *J. robustus* shows sign of ontogenetic immaturity while, according to Lü, Fucha et al. (2010), the scapula and coracoid are apparently fused in *F. lii* suggesting that the holotype of the latter might represent an adult individual at time of death. This indicates that likely *J. robustus* could still grow and might have attained a larger wingspan than *F. lii*. If this assumption is correct, *J. robustus* is only smaller to *H. gentryii* within the Scaphognathidae, if the latter indeed turns out to be a member of that group.

Conclusions

Based on a series of combination of distinctive features, a new genus and species, *J. robustus* from the Linglongta region (western Liaoning) is established and regarded as a member of the clade Scaphognathidae. *J. robustus* and *Sc. crassirostris* share several features mainly observed in the skull, lower jaw and dentition. Among the main differences between those taxa is the shape of the alveolar margin of the lower jaw that shows the first three pairs of teeth distinctly procumbent. *J. robustus* also differs from the disputed scaphognathid *H. gentryii* mainly by the particular shape of the alveolar margin of the upper jaw present in the latter. It also differs from *So. pilosus* (unlikely a member of the Scaphognathidae) by having more and larger teeth and distinct bone ratios.

The sole other taxa supposed to have scaphognathid affinities from the Linglongta region is *F. lii* that lacks most of the scaphognathid features previously established for this group (Carpenter et al. 2003) and is here regarded as Scaphognathidae *incertae sedis* pending a more accurate description of the holotype. Nonetheless, dental features present in *J. robustus* such as the lesser number of teeth in the upper jaw (18 against 22), which are inclined anteriorly and not subvertically, and the procumbent condition of the first three pairs of the dentary teeth are quite distinct from *F. lii*. The same happens regarding the proportion of several wing elements that differ in those taxa in all cases where comparisons are possible for all in the ratio between the first and the second wing phalanges and the ratio of several bones and the wing metacarpal (see Table 2).

The fossil deposits from the Linglongta and neighbouring areas have recently provided several pterosaur

materials. The main represented clade is the Wukongo-peridae (Wang et al. 2009, 2010; Lü, Unwin et al. 2010), which based on the number of specimens and described species apparently dominated this pterosaur fauna. *J. robustus* increases the diversity of flying reptiles from this region, indicating a large potential of those deposits for the study of non-pterodactyloid flying reptiles that lived comparatively close or at the Jurassic–Cretaceous boundary.

Acknowledgements

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