Anais da Academia Brasileira de Ciências (2010) 82(4): 1045-1062
(Annals of the Brazilian Academy of Sciences)
ISSN 0001-3765
www.scielo.br/aabc

New long-tailed pterosaurs (Wukongopteridae) from western Liaoning, Chin

XIAOLIN WANG[1], ALEXANDER W.A. KELLNER[2]*, SHUNXING JIANG[1,3], XIN CHENG[1,3], XI MENG[1] and TAISSA RODRIGUES[2]

[1]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology
Chinese Academy of Sciences, PO Box 643, Beijing, 100044, China
[2]Setor de Paleovertebrados, Museu Nacional/UFRJ, Quinta da Boa Vista s/n, São Cristóvão
20940-040 Rio de Janeiro, RJ, Brasil
[3]Graduate University of Chinese Academy of Sciences, Beijing, 100049, China

Manuscript received on August 3, 2010; accepted for publication on October 21, 2010

ABSTRACT

Two almost complete long-tailed pterosaurs from the Linglongta, Jianchang County, western Liaoning, China, a described and represent new taxa referred to the non-pterodactyloid clade Wukongopteridae. *Kunpengopterus sinen* gen. et sp. nov. differs from other members of this clade mainly by the rounded posterior region of the skull, thi lacrimal process of the jugal and lack of a bony premaxillary crest. This species further shows a soft tissue cre above the frontal, a comparatively larger wing finger, and the proximal segment of the second pedal phalanx of t fifth toe shorter than in other wukongopterids. The second new species is referred to the genus *Darwinopteru D. linglongtaensis* sp. nov. based on the posterior region of the skull. It further differs from other wukongopter pterosaurs by the thin lacrimal process of the jugal, foramen on nasal process rounded, and by having the seco pedal phalanx of the fifth toe less curved (115°). Several differences among the Wukongopteridae can be found in t dentition and the feet, suggesting that they might have occupied slightly different ecological niches. The long-tail *Changchengopterus pani* is tentatively referred to this clade and new diagnosis for the wukongopterids *Wukongo terus lii* and *Darwinopterus modularis* is provided.

Key words: Pterosauria, Wukongopteridae, *Kunpengopterus*, *Darwinopterus*, Liaoning, China.

INTRODUCTION

Although the majority of pterosaur specimens consists of incomplete material (e.g., Costa and Kellner 2009, Ibrahim et al. 2010) that in several cases lack detailed stratigraphic data (e.g., Kellner and Campos 1999), there are some areas where complete material of these volant archosaurs have been found in surprisingly large numbers. The main country that has furnished more pterosaur specimens than any other in the last decades is China. This is due to several discoveries from the so called Jehol Biota (e.g., Chang et al. 2003). Pterosaur specimens were collected mainly in the Earl taceous Yixian and Jiufotang Formations (e.g., al. 2004), where 13 and 16 species were reco respectively (e.g., Wang et al. 2005, 2008, Lü 2008, Andres and Ji 2008, Lü 2010), some of have spurred controversy (e.g., Ji et al. 1999, U al. 2000, Wang and Zhou 2006, Lü et al. 2006).

More recently a number of pterosaurs we recovered from older deposits that crop out parti in the Linglongta region of the Jianchang County ern Liaoning. The stratigraphy of these deposits

al. 2010). There are also questions about the age of these deposits, ranging from Middle to Late Jurassic (Zhang 2002, Zhang et al. 2008, Lü et al. 2010) up to the Early Cretaceous (e.g., Wang, Zhou et al. 2005, He et al. 2004).

So far, two pterosaur taxa have been recognized from Linglongta: *Wukongopterus lii* Wang et al. 2009 and *Darwinopterus modularis* Lü et al. 2010. Another species, *Changchengopterus pani* Lü 2009, recovered from a different locality (Mutoudeng Town, Qinglong County), apparently also comes from the same stratigraphic unit (Lü 2009, Wang et al. 2009, Lü et al. 2010).

Here we report two specimens from Linglongta that are also referable to the Wukongopteridae and represent new taxa: *Kunpengopterus sinensis* gen. et sp. nov. and *Darwinopterus linglongtaensis* sp. nov. We also discuss the inclusion of previously described taxa to this unusual non-pterodactyloid clade, providing new diagnoses for them.

Anatomical Abbreviations: car – carpus, cdv – caudal vertebra, cor – coracoid, cs – cristospine, cv – cervical vertebra, d – dentary, dca – distal carpal series, dlca – distal lateral carpal, dpc – deltopectoral crest, dv – dorsal vertebra, f – frontal, fe – femur, fish – fish scales and other elements, fona – foramen nasale, fopn – foramen pneumaticum, gas – gastralia, hu – humerus, hy – hyoid bone, il – ilium, is – ischium, j – jugal, l – left, la – lacrimal, ltf – lower temporal fenestra, m – maxilla, mcI – metacarpal I, mcII – metacarpal II, mcIII – metacarpal III, mcIV – metacarpal IV, n – nasal, naof – nasoantorbital fenestra, obfo – obturator foramen, or – orbit, p – parietal, pel – pelvis, ph1d4 – first phalanx of manual digit IV, ph2d4 – second phalanx of manual digit IV, ph3d4 – third phalanx of manual digit IV, ph4d4 – fourth phalanx of manual digit IV, pl – palatine, pm – premaxilla, pmcr – premaxillary crest, po – postorbital, pph2d5 – second phalanx of pedal digit V, ppu – prepubis, pr – process, prca – proximal carpal, prf – prefrontal, prn – processus nasalis, ptd – pteroid, pu – pubis, q – quadrate, r – right, ra – radius, rapr – retroarticular process, ri – rib, san – surangular, sca

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup 1834

WUKONGOPTERIDAE

Wang, Kellner, Jiang and Meng 2009

Type genus: *Wukongopterus* Wang, Kellner, Jiang and Meng 2009.

Definition: The most recent common ancestor of *Wukongopterus lii* and *Kunpengopterus sinensis* gen. et sp. nov. and all its descendants.

Included taxa: *Wukongopterus lii*, *Darwinopterus modularis*, *Darwinopterus linglongtaensis* sp. nov., *Kunpengopterus sinensis* gen. et sp. nov., and *Changchengopterus pani*.

Synapomorphies: Non-pterodactyloid pterosaurs with confluent naris and antorbital fenestra; maxillary ramus of the jugal long, anteriorly projected and splint-like; free lateral nasal process; quadrate inclined backwards for about 120°; mandibular symphysis short (less than 25% the length of the lower jaw); cervical vertebrae more elongated than in other non-pterodactyloids; cervical ribs reduced; length of the wing metacarpal about half the length of the first wing finger phalanx; first wing finger phalanx shorter than fourth wing finger phalanx (modified from Wang et al. 2009).

Wukongopterus

Wang, Kellner, Jiang and Meng 2009

Type species: *Wukongopterus lii* Wang, Kellner, Jiang and Meng 2009.

Diagnosis: The same as for the species.

Wukongopterus

Wang, Kellner, Jiang and Meng 2009

Emended diagnosis: Wukongopterid pterosaur with the following combination of characters that distinguishes it from other members of this clade (autapomorphies are marked with an asterisk): first two pairs of premaxillary teeth protruding beyond the dentary almost vertical*; dentition formed by short cone-shaped and very pointed teeth; preacetabular portion of the ilium

pedal phalanx of the fifth toe elongated* (modified from Wang et al. 2009).

Darwinopterus Lü, Unwin, Jin, Liu and Ji 2010

Type species: *Darwinopterus modularis* Lü, Unwin, Jin, Liu and Ji 2010.

Included taxa: *Darwinopterus modularis* and *Darwinopterus linglongtaensis* sp. nov.

Emended diagnosis: Wukongopterid pterosaur with the following combination of characters that distinguishes this genus from others of this clade: posterior region of the skull elongated; presence of a bony premaxillary crest that starts about the anterior margin of the nasoantorbital fenestra; dorsal margin of the premaxillary crest serrated; thin nasal process; preacetabular region of the ilium elongated (modified from Lü et al. 2010).

Darwinopterus modularis
Lü, Unwin, Jin, Liu and Ji 2010

Emended diagnosis: Wukongopterid pterosaur with the following combination of characters that distinguishes it from other members of this clade (autapomorphies are marked with an asterisk): posterior region of the skull more elongated than in *Darwinopterus linglongtaensis* sp. nov.; dentition formed by well-spaced spike-like teeth* (modified from Lü et al. 2010, here based only on the holotype).

Darwinopterus linglongtaensis sp. nov.

Etymology: From Linglongta, where the holotype of this new species was discovered.

Holotype: Almost complete and well-articulated skeleton housed in the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences), Beijing, under the number IVPP V16049 (Figs. 1-5).

Locality and horizon: Linglongta, Jianchang County, western Liaoning, China, Daohugou Bed (Formation) or Tiaojishan Formation.

Diagnosis: Wukongopterid pterosaur with the follow-

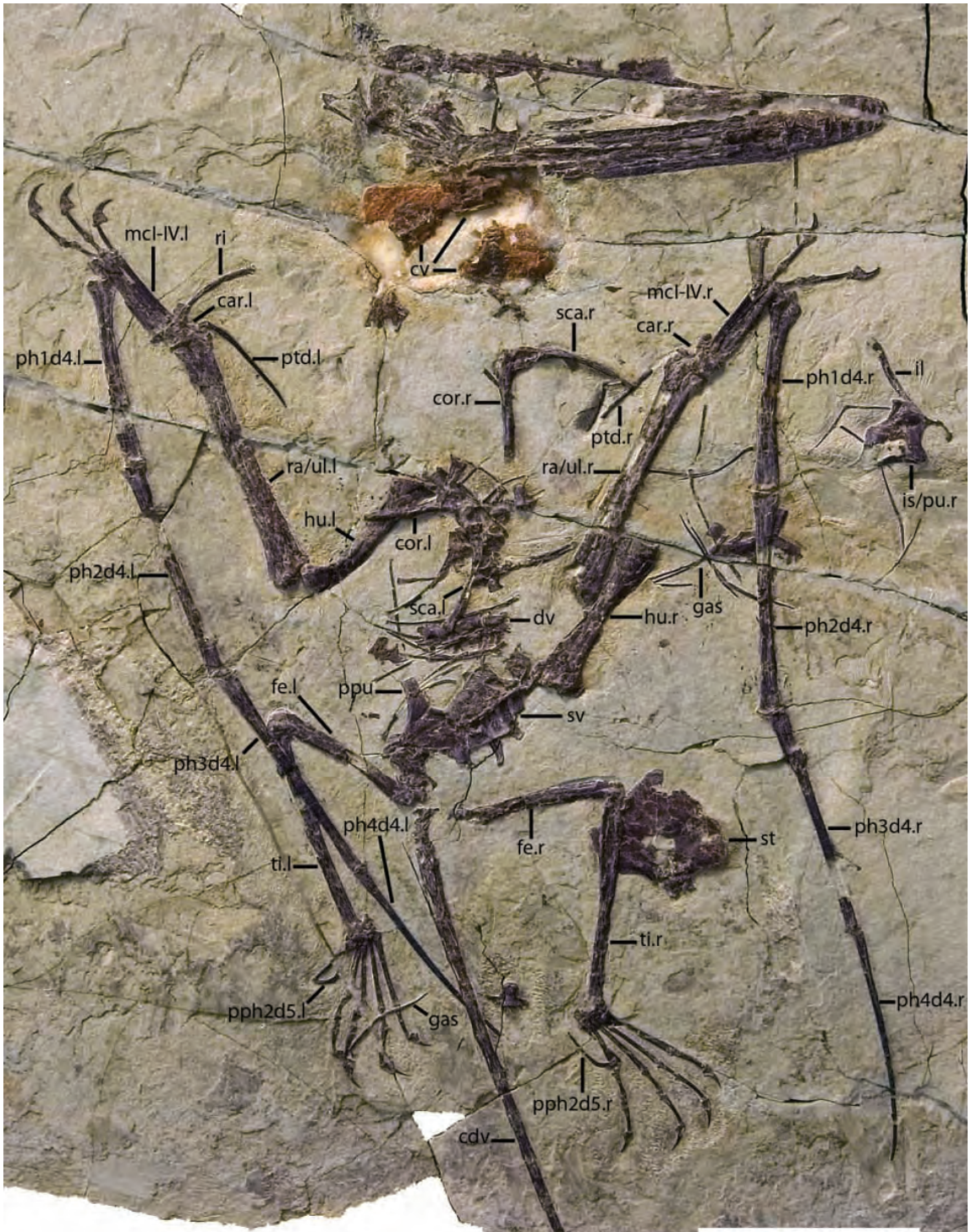
less elongated han in *Darwinopterus modularis*
tion formed by short cone-shaped teeth; lacrim
cess of the jugal comparatively thin*; foramen o
process rounded*; curved second pedal phalanx
fifth toe with an angle between the proximal an
segment about 115°*.

Description: The holotype of *Darwinopterus li*
taensis is preserved in a slab formed by light grey
The specimen is almost completely articulated
for some portions of the vertebral column that
from their natural position as the right pelvic el
(ilium, pubis and ischium) (Fig. 1). Some eleme
missing, particularly from the neck.

The skull of *Darwinopterus linglongtaensis*
V16049) is exposed in right lateral view (Fig. 2
fortunately part of the bone surface on the later
was broken off leaving only an impression on the
However, it is clear that this taxon had a conflu
ternal naris and antorbital fenestra. The length b
the squamosal and the tip of the premaxilla is 119
and, therefore, almost 12% larger than *Kunpeng*
sinensis (IVPP V16047). Also as the former, th
is large and has the ventral margin wider than i
winopterus modularis.

A well-developed premaxillary crest runs
the dorsal margin of the skull reaching about the
region of the orbit and not extending posteriorly
the occipital region. This crest has a serrated
margin (Fig. 3a), which suggests the existenc
horny covering. The nasal has an elongated nas
cess that has a broad dorsal part but gets ventrall
ner (Fig. 3c). A well-developed oval pneumati
men pierces this bone.

The dorsal part of the posterior region of th
is not very well preserved, which impedes the
lishment of the limits of most bones. The postor
triradiated bone, is displaced backwards from it
ral position. The posterior region of the skull,
by the parietal, is slightly extended backwards, al
not to the same degree as observed in *Darwino*
modularis. The jugal has a thin, slightly anteri


mcl-lV.l
ri
car.l
ptd.l
ph1d4.l
cv
sca.r
mcl-lV.r
car.r
ph1d4.r
il
cor.r
ptd.r
ra/ul.l
ra/ul.r
is/pu.r
hu.l
cor.l
ph2d4.l
sca.l
dv
hu.r
gas
ph2d4.r
fe.l
ppu
sv
ph3d4.l
ph4d4.l
fe.r
st
ph3d4.r
ti.l
ti.r
ph4d4.r
pph2d5.l
gas
pph2d5.r
cdv

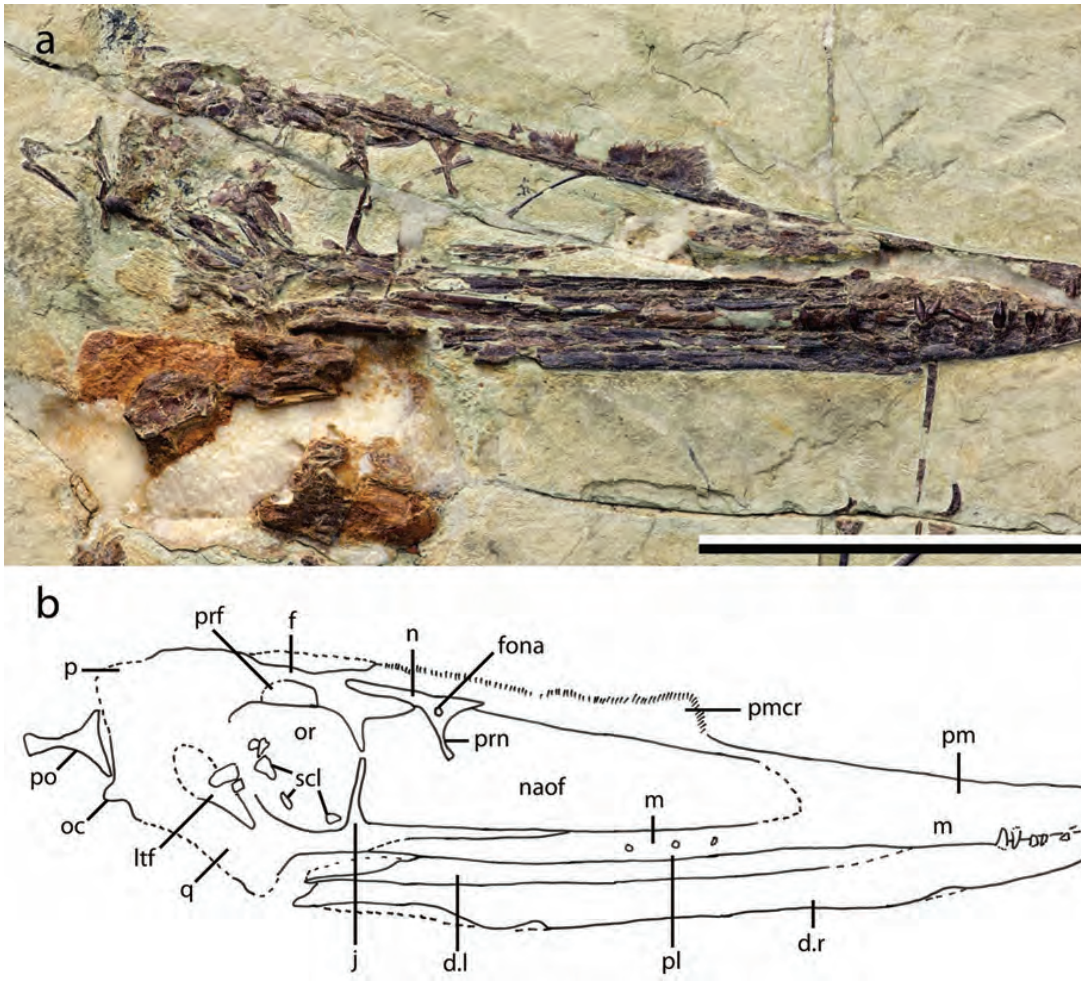


Fig. 2 – *Darwinopterus linglongtaensis* sp. nov. (IVPP V16049). a, skull and b, drawing. Scale bar: 50 mm.

quadrate, also not well preserved, is inclined posteriorly, differing from most other non-pterodactyloid pterosaurs (except for other wukongopterids). A rounded occipital condyle can be observed, directed posteroventrally.

Overall the shape of the skull in *Darwinopterus linglongtaensis* suggests a high skull, particularly at the posterior portion, higher than both *Kunpengopterus sinensis* and *Darwinopterus modularis*. It shares with the latter a bony premaxillary crest and the posterior extension of the skull, albeit less developed. *Darwinop-*

in *Darwinopterus modularis*, was not reported al. 2010).

The postcranial elements of the holotype o *winopterus linglongtaensis* (IVPP V16049) show tinct degree of fusion. Among them, the extens don process of the first wing finger phalanges an elements of the proximal and distal carpal series fused (Fig. 4c), whereas the sacral vertebrae ar (Fig. 5a). In some cases, bones are firmly connec show a distinct suture line indicating that they co-ossified like the scapula with the coracoid (F


a
pmcr
naof
b
la
j
c
n
fona
prn
d
pm
d
e
dv
sca
ri
hu
cor
f
cs
ti
stp
fe

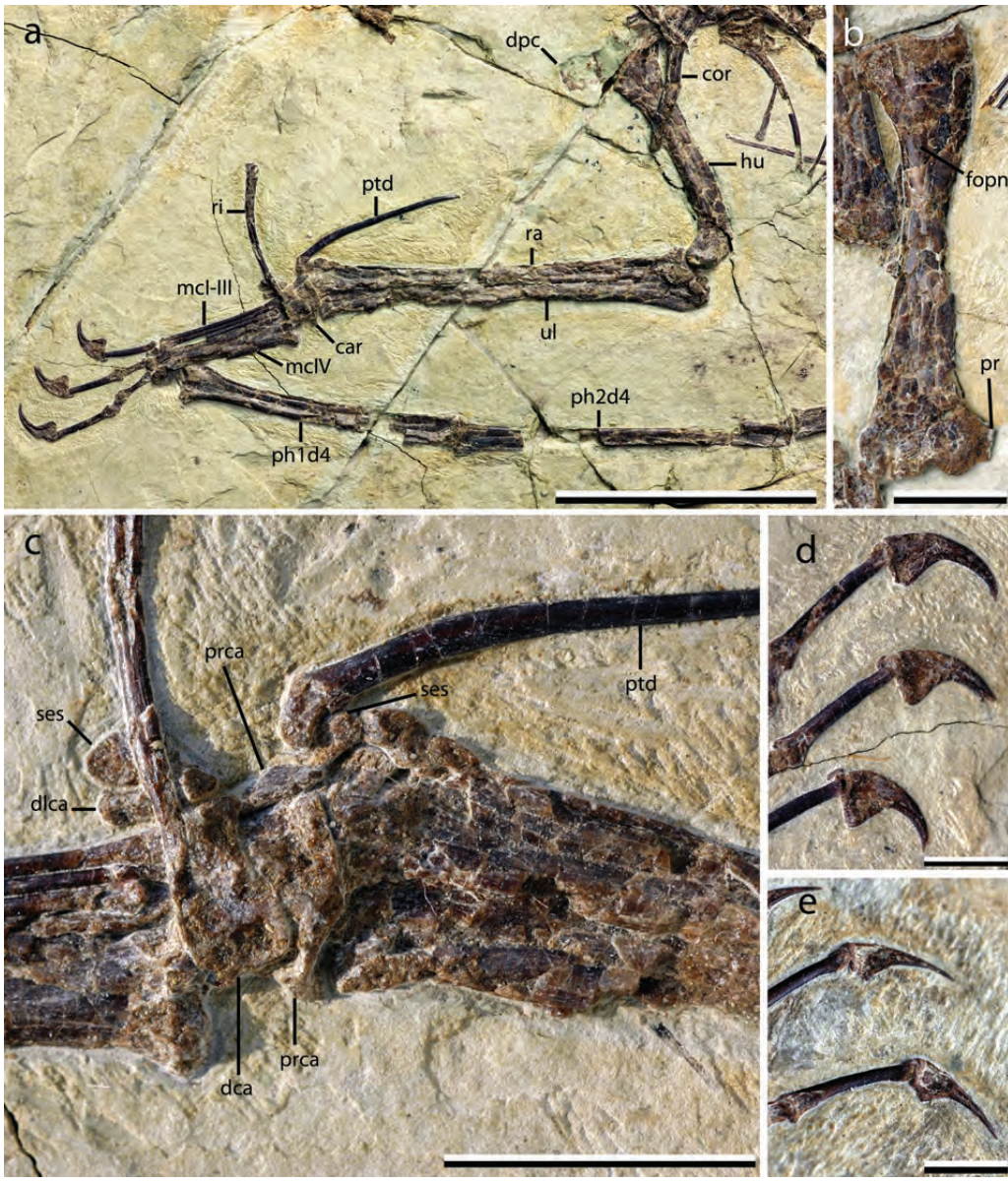


Fig. 4 – *Darwinopterus linglongtaensis* sp. nov. (IVPP V16049). a, part of the left wing; b, right humerus; c, deta of the left carpal region; d, manual unguals; e, pedal unguals. Scale bars: a: 40 mm; b, c: 10 mm; d, e: 5 mm.

represent a juvenile or a very young animal, but rather a sub-adult at the time of death.

The remains of three cervical vertebrae are preserved. The most complete one is observed from vent-

scattered in the matrix. The sacral vertebrae a preserved and formed by five elements, four of are fused with each other by the distal ends transverse processes and the neural spines (Fi

Fig. 5 – *Darwinopterus linglongtaensis* sp. nov. (IVPP V16049). a, detail of sacral vertebrae and prepubis; b, pelvis; c, part of the tail; d, right foot; e, left foot. Scale bars: a, b, d, e: 10 mm; c, 5 mm.

clear whether a caudal vertebra was incorporated to the sacrum. The tail has the first proximal caudal vertebrae short, but the remaining ones are quite elongated and enclosed by rod-like bony structures formed by extensions of the zygapophyses (Fig. 5c). The sternum is almost complete, lacking the cristospine (Fig. 3f). This heart-shaped bone is exposed in dorsal view and has the anterior margin slightly more concave compared to *Kunpengopterus sinensis*. Several elements of the gastralia are found scattered around. They are very thin and curved.

deltopectoral crest was developed (Fig. 4a), but more confined to the proximal portion of the humerus, which is regarded as a plesiomorphic trait within pterosaurs (e.g., Wang et al. 2009). The right humerus is exposed in dorsal view and shows a tiny foramen in the proximal half (Fig. 4b) that might also be a diagnostic feature of this taxon. Such a foramen, which could be either pneumatic or nutrient, has never been reported in a non-pterodactyloid pterosaur before, together with a developed process on the anterior surface of the distal articulation of the humerus. This process, however, is

TABLE I
Measurements of some species of the Wukongopteridae (in mm).

Bones/ taxa	*Wukongopterus lii*	*Darwinopterus linglongtaensis*	*Kunpengopterus sinensis*
sca	34.1 (r) 32.9 (l)	31.1 (r)	~28.8 (r)
cor	~25.3 (r)	24.9 (r) 26.3 (l)	~23.8 (r)
hu	~38.7 (r)	40.4 (r) 39.9 (l)	~36.2 (r)
ul	~62.1 (r)	58.0 (r) 61.2 (l)	~59.2 (l)
mcIV	22.9 (l)	22.5 (r) 23.6 (l)	~ 23 (l)
ph1d4	~45.7 (r)	46.2 (r) 44.4 (l)	54.2 (r)
ph2d4	56.8 (r)	50.7 (r) 52.1 (l)	58.0 (r)
ph3d4	58.3 (r) 59.3 (l)	53.2 (r) 53.7 (l)	59.2 (r)
ph4d4	51.5 (l)	53.6 (r) 53.7 (l)	~48.8 (l)
fe	33.3 (r) 35.6 (l)	39.4 (r) 40.1 (l)	~39.3 (r) ~41.1 (l)
ti	52.8 (r)	49.8 (r) 49.6 (l)	54.5 (l)
mt3	~17.2 (r) 16.8 (l)	17.0 (r)	21.8 (r) 20.7 (l)
mt4	~14.5 (r) 15.0 (l)	14.2 (r) 14.2 (l)	17.9 (r)
pt	+ 7.3 (r)	28.9 (l)	~25.8 (l)

The carpal region of both sides is well preserved. Some elements of the proximal and distal carpal series are unfused (Fig. 4c). In both sides, the distal lateral carpal shows a well-developed sesamoid in the fovea carpalis, and the elongated, slightly curved pteroid is clearly articulated with the proximal carpal series. A sesamoid is present between the proximal portion of the pteroid shaft and the proximal carpal series.

As observed in *Kunpengopterus*, the wing meta-

1.69, right side 1.80) than in other non-pterodact
but shorter compared to pterodactyloids (e.g., I
2003). Metacarpals I-III are thin, subequal in
and articulate with the distal carpal series. As i
wukongopterids, the first phalanx of the wing
has concave anterior and convex posterior marg
spectively. The wing finger phalanges are very w
served and clearly show that the first wing pha
the smallest of all. Compared to *Kunpengopterus*

with the pubis and ischium can be observed in medial view (Fig. 5b), whereas the correspondent bones from the left side are partially covered by the sacral vertebrae. The preacetabular portion of the ilium is rather long, more developed than in *Wukongopterus* and other non-pterodactyloid pterosaurs such as *Dimorphodon* and *Campylognathoides* (see Wellnhofer 1978, Padian 2008b).

The femur is only slightly curved and the femur head (of left side) lies at an angle close to 150° with the shaft. On the left and right sides a thin splint-like fibula that apparently does not reach the tarsus can be observed. The feet (Fig. 5d, e) are well preserved, showing a phalangeal formula of 2:3:4:5:2. Metarsals I and II are the largest, being subequal in size. Metatarsal V is short and has a broad proximal portion, being less elongated compared with *Kunpengopterus* and *Wukongopterus*. It bears two pedal phalanges (a plesiomorphic trait), with the second being boomerang-shaped. The angle between the proximal and distal portions of the latter is about 115°, which is larger than in *Wukongopterus* (Wang et al. 2009) but smaller than in *Kunpengopterus*. Pedal unguals (Fig. 4e) are more elongated, thinner and comparatively smaller than manual unguals (Fig. 4d), a generally common trait within pterosaurs. The curvature of the pre-ungual phalanx of the first and second digits is less pronounced than in *Kunpengopterus*.

Kunpengopterus gen. nov.

Etymology: *Kunpengopterus*, from Kun Peng, an ancient mythological figure from China regarded as being a very strange flying animal, and *pterus*, from the Greek language meaning wing.

Type species: *Kunpengopterus sinensis* sp. nov., type by monotypy.

Diagnosis: The same as for the species.

Kunpengopterus sinensis sp. nov.

Etymology: From the Greek term *sino* meaning pertaining to China, where this new species was discovered.

Academy of Sciences), Beijing, under the number IVPP V16047 (Figs. 6-8).

Locality and horizon: Linglongta, Jianchang County, western Liaoning, China. Daohugou Bed (Formation) or Tiaojishan Formation.

Diagnosis: Wukongopterid pterosaur with the following combination of characters that distinguishes it from other members of this clade (autapomorphies are marked with an asterisk): posterior region of the skull rounded*; dentition composed of short cone-shaped teeth; lacrimal process of the jugal thick; absence of a bony premaxillary crest; presence of a soft tissue crest above the frontal*; broad nasal process*; foramen on nasal process elliptical with main axis subvertical*; curved second pedal phalanx of the fifth toe with an angle between the proximal and distal segments about 137°*; proximal segment of the second pedal phalanx of the fifth toe shorter than in other wukongopterids*.

Description: *Kunpengopterus sinensis* (IVPP V16047) is preserved in a grey shale slab with several bones of the skeleton associated but not articulated (Fig. 6). When collected, the specimen was broken in a few parts and later put together. One mass of dark matter is observed close to the skull. It is not part of the pterosaur, but scales and other fish elements (Fig. 6). Soft tissue formed by elongated dark unbranched fibers similar to the pycnofibers reported in other pterosaurs (Wang et al. 2002, Kellner et al. 2010) is observed above the frontal (Fig. 8a). Although not as well preserved as reported from some other deposits (e.g., Kellner 1996) and differing from the typical structures found in fossilized feathers (e.g., Kellner et al. 1994), this soft tissue is here interpreted as the remains of a soft cranial crest. Such a structure was previously observed in a similar position in the archaeopterodactyloid *Gegepterus* from the Yixian Formation (Wang et al. 2007). Dorsal and anteriorly to this dark mineralized substance (which is possible organic in nature), there are some yellow stains in the matrix. Although no UV photography was taken on this specimen, it would possibly reveal an extensive dorsal projection of the soft portion of the cra-

Fig. 6 – *Kunpengopterus sinensis* gen. et sp. nov., holotype (IVPP V16047). Scale bar: 50 mm.

The skull of *Kunpengopterus sinensis* is complete tral portion (anterior to the external naris; ~40.5

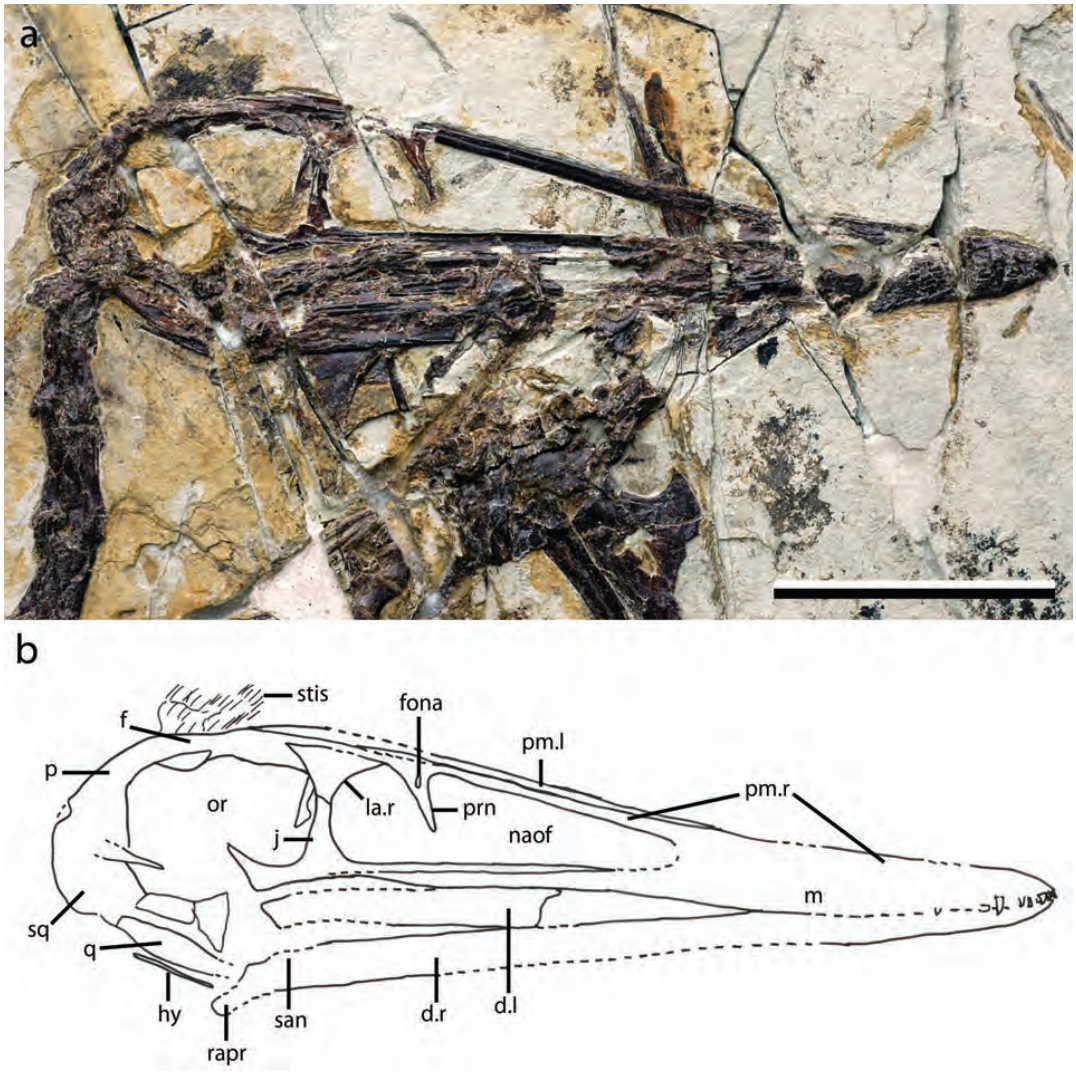


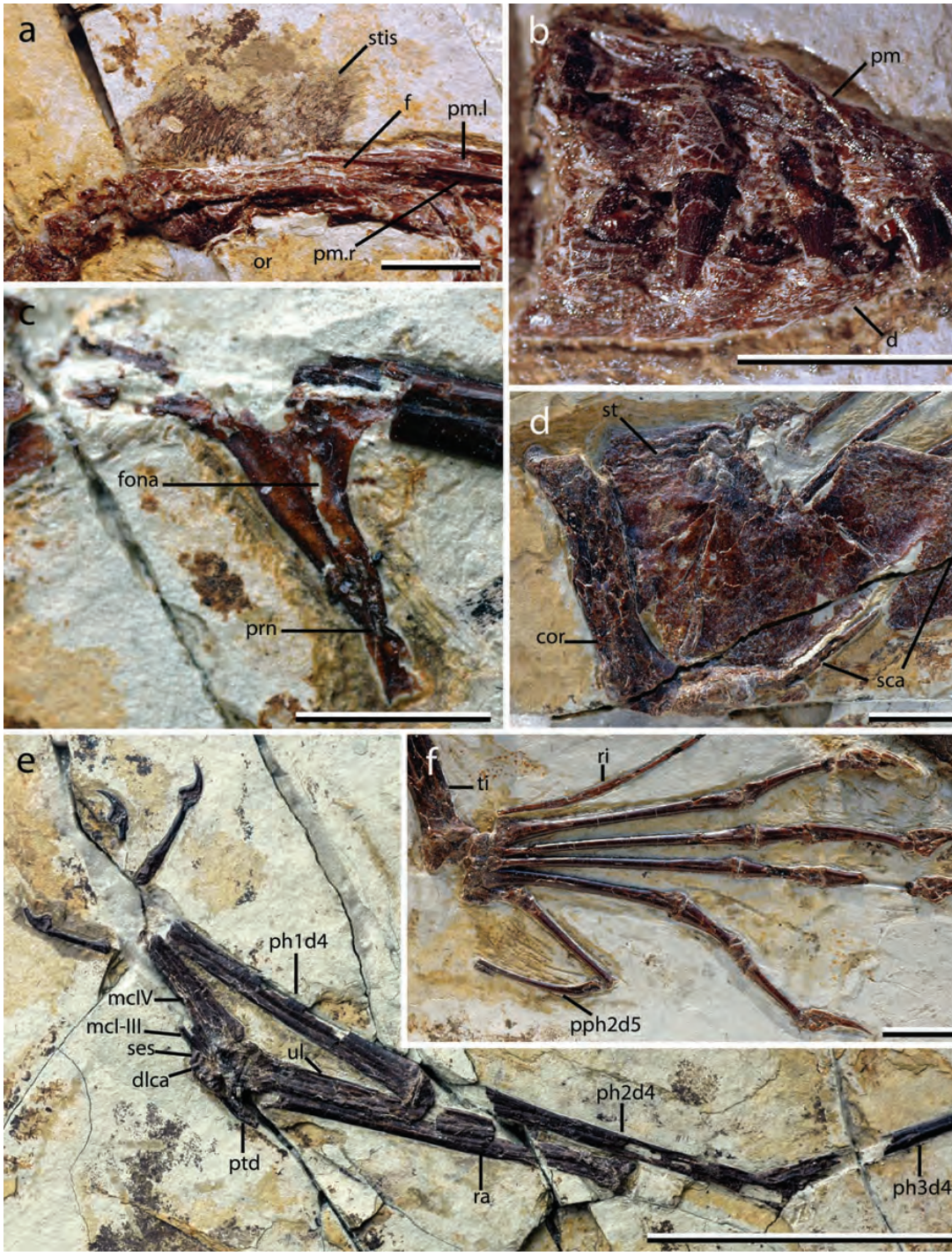
Fig. 7 – *Kunpengopterus sinensis* gen. et sp. nov. (IVPP V16047). a, skull and b, drawing. Scale bar: 50 mm.

large and has the lower margin more rounded compared with *Darwinopterus modularis*. The naris and antorbital fenestra are confluent and form a nasoantorbital fenestra, a rather derived trait within pterosaurs (e.g., Kellner 2003, Unwin 2003). No information about the temporal openings can be retrieved from this specimen.

A low ridge runs over part of the cranial dorsal margin, but does not form a bony premaxillary crest. Nonetheless, as pointed out before, soft tissue is present

tacts the frontal and also does not form a posterior premaxillary bony crest that has been observed in several pterosaurs, particularly in the Pterodactyloidea (e.g., Wellnhofer 1991, Kellner 2003, Unwin 2003), but also in some more primitive non-pterodactyloids (e.g., Dalla Vecchia et al. 2002, Dalla Vecchia 2009).

The nasal has an elongated, broad nasal process (Fig. 8c) that occupies a lateral position and is directed anteroventrally. This process bears an elliptical fora-


a
stis
f
pm.l
or
pm.r
b
pm
d
c
fona
prn
d
st
cor
sca
e
ph1d4
mcIV
mcI-III
ses
dlca
ul
ptd
ra
f
ti
ri
pph2d5
ph2d4
ph3d4

forms the dorsoanterior margin of the orbit. The posterior portion of the skull, which is formed by the parietal (Fig. 7), is rounded and does not extend posteriorly. The jugal has a broad, almost perpendicular lacrimal process and an elongated, anteriorly directed thin (splint-like) maxillary process that forms part of the lower margin of the nasoantorbital fenestra. No information from the palatal and occipital region is available on this specimen.

The lower jaw (length: 90.0 mm) of *Kunpengopterus sinensis* is tightly connected with the skull. The symphysis in this taxon is short, having a maximum estimated length of 22 mm and being, therefore, less than 25% the length of the lower jaw. No evidence of a dentary sagittal crest (made of bone or soft tissue) was observed.

The dentition of *Kunpengopterus sinensis* is composed of cone-shaped, peg-like teeth (Fig. 8b). The exact number of teeth cannot be determined in none of the jaws but, based on the preserved portion, the last tooth was apparently placed anterior to the anterior margin of the nasoantorbital fenestra. If correct, this can be considered another diagnostic feature that further distinguishes this taxon from other wukongopterids.

Compared to other non-pterodactyloid pterosaurs, the skull of *Kunpengopterus sinensis* has a rounded posterior outline, similar to the condition observed in *Rhamphorhynchus* and *Sordes* but differing from *Darwinopterus* (Wellnhofer 1975, 1991, Lü et al. 2010). The thick lacrimal process is also observed in *Darwinopterus modularis*, but absent in *Darwinopterus linglongtaensis* (see below). The nasal process, a feature typical of derived pterosaurs but absent in non-pterodactyloids (e.g., Kellner 2003, Wang et al. 2008), is rather broad, differing from the thinner condition observed in *Darwinopterus*. The symphysis of *Kunpengopterus* displays the primitive condition by being reduced as observed in *Darwinopterus* and *Wukongopterus*, and being less developed than in *Rhamphorhynchus* and *Dorygnathus* (Kellner 2003). The dentition is similar to the one observed in *Wukongopterus lii*, differing only in being less pointed than in the latter. Furthermore, the two anteriormost upper teeth are almost vertical in *Wukongopterus*,

known from *Kunpengopterus sinensis* (IVPP V16047) shows signs of a fully ontogenetically mature individual, having several elements fused such as the scapulocoracoid and the proximal and distal carpal series (Fig. 8e), which at least in derived pterosaurs are normally unfused in subadult or juvenile specimens (e.g., Bennett 1993). Even the proximal tarsal elements (Fig. 8f), also unfused in young derived flying reptiles (Kellner 2004), are strongly connected with the tibia without showing the suture line.

The cervical series is almost complete, consisting of the first five (including the axis and presumably also the atlas, not visible) and the last two cervical vertebrae. Except for the axis and the last cervical element, the others have an elongated centrum, with cervical vertebrae 3 to 5 being the longest (Fig. 7). In some of them a small cervical rib is noted. No pneumatic foramen piercing the lateral surface of the centrum or the neural arch could be observed. The neural spine is blade-like and comparatively low, getting higher in the posterior elements. The dorsal vertebral series is partially preserved and no elements were fused into a notarium. The tail is long, formed by several caudal vertebrae that are elongated and enclosed by long bony rod-like structures formed by the extensions of the zygapophyses, a primitive feature within Pterosauria. The sternum (Fig. 8d) is not well preserved in this specimen. However, it forms a large bony plate with the anterior margin straight and slightly inclined posteriorly.

As pointed out before, the scapula and coracoid are fused. Although not well preserved, it is clear that the scapula is the longer element. The humerus lacks any pneumatic foramen and the deltopectoral crest is not preserved. The diameter of the radius is smaller, but not half of the diameter of the ulna.

Only the carpal region of the left side is preserved (Fig. 8e). All elements of the proximal and distal series are fused. The distal lateral carpal shows a well-developed sesamoid in the *fovea carpalis*. The pteroid is elongated, slightly curved and clearly articulated with the proximal carpals series. The wing metacarpal (metacarpal IV) is more elongated relative to the first wing

Kellner 2003). Metacarpals I-III articulate with the distal carpal series. The anterior margin of the first phalanx of the wing finger is concave and the posterior convex, as observed in the Dsungaripteridae (Wellnhofer 1978, Unwin 2003). This bone is also the smallest relative to the other wing finger phalanx, here regarded as a synapomorphy of the Wukongopteridae.

The femur is rather straight, with the femur head forming an angle between 125° and 130° with the shaft. Tibia is elongated, almost 40% longer than the femur. The feet are well preserved (Fig. 8f), with the metatarsal II being the largest and metatarsals I and III subequal in size, followed by metatarsal IV. Metatarsal V is small and bears two phalanges, with the second one having the proximal portion comparatively short. The angle between the proximal and distal segments is about 137°. Pedal unguals are more elongated, thinner and comparatively smaller than manual unguals. It is interesting to note that the pre-ungual phalanx of the first and second digits is curved. The pedal phalangeal formula is 2:3:4:5:2.

DISCUSSION

As Wang et al. (2009) pointed out, the basic anatomy of *Wukongopterus lii* is quite different from any other pterosaurs' anatomy by uniting plesiomorphic and derived features. These authors did not have a complete skull that could provide evidence of a confluent external naris and antorbital fenestra, but this was suggested by the elongated and thin maxillary process of the jugal. With the description of *Darwinopterus modularis* by Lü et al. (2010), the existence of a non-pterodactyloid pterosaur with a nasoantorbital fenestra was confirmed.

The two new species described here – *Kunpengopterus sinensis* and *Darwinopterus linglongtaensis* – confirm several derived cranial traits in the non-pterodactyloid clade Wukongopteridae, such as the confluent naris and antorbital fenestra and the elongated maxillary process of the jugal. Furthermore, all members of this group show an inclined quadrate and a free nasal process (not united with the maxilla), also unknown in other non-pterodactyloids. The postcranial skeleton also

absent in derived pterosaurs except for the archae
dactyloid *Gegepterus*, in which short cervical r
reported (Wang et al. 2007).

Wukongopterids also show primitive featu
only in the postcranial skeleton. The most consp
one is the rather short mandibular symphysis
shorter than some non-pterodactyloids such as
nathus and *Rhamphorhynchus* (e.g., Kellner 20
dian 2008a). Plesiomorphic postcranial features
the elongated tail enclosed by rod-like bony exte
of the zygapophyses and the relative lengths of t
langes of the wing finger (see also Lü et al. 2010

The relationship of the Wukongopteridae
to the Pterodactyloidea is object of controversy.
in the phylogenetic analysis of Wang et al. (200
clade assumes a rather basal position, the study
et al. (2010) has *Darwinopterus* closely related
Pterodactyloidea. Although the phylogenetic p
of the Wukongopteridae is not the main purpose
paper, it should be noted that there are features
against this relationship. The Wukongopteridae
with the Pterodactyloidea relative to *Rhamphorh*
and *Campylognathoides* a nasoantorbital fene
nasal process, elongated cervical vertebrae, and
paratively larger wing metacarpal, even not rea
proaching the condition observed in basal pte
tyloids (e.g., the Archaeopterodactyloidea). Oth
tures favor a closer relationship of the Rhamph
chidae (e.g., *Rhamphorhynchus*) to the Pterodact
relative to the Wukongopteridae, such as an elo
mandibular symphysis, the diameter of the radiu
tive to the ulna and the proportions of the element
wing finger, with wukongopterids always show
primitive condition (see Wang et al. 2009).

Another question is the phylogenetic relat
of *Changchengopterus pani*, described by Lü
from a different locality of other wukongopteri
regarded from the same deposits. The specimen
sents a rather small long-tailed pterosaur with a
mated wing span of 475 mm. Several unfused el
are observed, such as the extensor tendon pro
the first phalanx of the wing finger, the elements

Some of the posterior cervical vertebrae are preserved and, contrary to the original description, at least one is elongated. Based on the long tail, Lü (2009) referred this taxon to the Rhamphorhynchidae, which appears paraphyletic in his published analysis. Based on the slightly elongated cervical vertebra and the ratio of the wing finger phalanges (with the first one being the smallest), it is tentatively referred to the Wukongopteridae.

The two new species described here show that there is considerable morphological variation within the Wukongopteridae and further raise the question if both specimens attributed to *Darwinopterus modularis* represent the same taxon (see Kellner 2010 for a discussion on the problematic in recognizing pterosaur species). This is particularly of concern since the preparation of the referred (and more complete specimen) was not finished at the time of publication (Lü et al. 2010: Fig. 2f).

Among the most conspicuous differences within wukongopterids is the dentition. While the holotype of *Darwinopterus modularis* shows spike-like teeth (Lü et al. 2010, no information about the dentition of the referred specimen is available), *Wukongopterus lii* has cone-shaped and very pointed teeth. *Darwinopterus linglongtaensis* and *Kunpengopterus sinensis* also have short cone-shaped teeth, which are slightly blunter compared to the one of *Wukongopterus*. These differences suggest that these flying reptiles might have fed to some extent on different items, most likely insects or perhaps small fishes.

There is also significant variation in the feet within wukongopterids, particularly regarding the second phalanx of the fifth toe. Overall they are curved (boomerang-shaped), with the proximal region of this phalanx differing in proportion with the distal portion, changing from very short (*Kunpengopterus sinensis*) to very long (*Wukongopterus lii*) and with different angles relative to the distal portion (see diagnoses). Since this bone is regarded to be the main support of the uropatagium (e.g., Unwin and Bakhurina 1994, Kellner et al. 2010), it is entirely possible that these pterosaurs (and perhaps others) might have had uropatagia with different might have occupied slightly different ecological niches, a subject that deserves more research.

Lastly it should be noted that the new species described here solve a long debate regarding the position of the pteroid in the wrist. Against the proposals that this unique pterosaur bone was attached to the distal lateral carpal, either in the *fovea carpalis* (e.g., Wilkinson et al. 2006) or on the lateral side (Bennett 2007), this bone was attached to the proximal carpal series, as recently proposed by Peters (2009), and directed inward and not outward. It should be noted that, as observed by Bennett (2001) for the first time, there is a well-developed sesamoid inside the fovea carpalis. In *Darwinopterus linglongtaensis* there is another sesamoid positioned posteriorly to the pteroid and anteriorly to the proximal carpal series.

CONCLUSION

The new specimens described in this paper represent two distinct taxa named here *Kunpengopterus sinensis* and *Darwinopterus linglongtaensis*. They confirm the existence in the Wukongopteridae of plesiomorphic and derived traits in both skull and post cranial skeleton and not limited to only one part of them. The previously described *Changchengopterus pani* is based on a very young individual and is tentatively referred to the Wukongopteridae. Despite the discussion about the age and correct stratigraphic placement of the deposits in the Linglongta region, they have provided a large number of long-tailed pterosaurs that show more diversification than previously thought.

ACKNOWLEDGMENTS

We thank Yutong Li for preparing the specimens described here and Wei Gao for some of the photos that illustrate this article. Zhonghe Zhou (Institute of Vertebrate Paleontology and Paleoanthropology Chinese Academy of Sciences, China). Diogenes de Almeida Campos (Museu de Ciências da Terra, Rio de Janeiro), Juliana M. Sayão (Universidade Federal de Pernambuco, Vitória de Santo Antão) and Fabiana R.C. Nunes

tinguished Young Scholars (40825005), National Natural Science Foundation of China (40121202), The Major Basic Research Projects of the Ministry of Science and Technology of China (2006CB806400) – all to XW. AWAK acknowledges the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ no. E-26/102.779/2008) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq no. 307276/ 2009-0) for supporting research in China.

RESUMO

Dois novos pterossauros de cauda longa procedentes de Linglongta, Jianchang County da região oeste de Liaoning, China, são descritos e referidos ao clado Wukongopteridae. *Kunpengopterus sinensis* gen. et sp. nov. difere dos demais integrantes desse clado basicamente pela região mais arredondada da parte posterior do crânio, pelo espesso processo lacrimal do jugal e pela ausência de uma crista óssea premaxilar. Esta espécie apresenta uma crista formada por tecido mole acima da região frontal e possui o dedo alar proporcionalmente maior do que nos demais wukongopterídeos. A segunda espécie é referida ao gênero *Darwinopterus*, *D. linglongtaensis* sp. nov., com base na região posterior do crânio. Difere dos demais pterossauros wukongopterídeos por possuir o processo lacrimal do jugal delgado, o forâmen no processo nasal arredondado e pela condição menos curvada da segunda falange do quinto dígito do pé. As principais diferenças entre os Wukongopteridae são encontradas na dentição e nos pés, o que sugere que estes ocupavam nichos ecológicos ligeiramente distintos. O pterossauro de cauda longa *Changchengopterus pani* também é tentativamente referido a esse clado. Novas diagnoses para os wukongopterídeos *Wukongopterus lii* e *Darwinopterus modularis* são apresentadas.

Palavras-chave: Pterosauria, Wukongopteridae, *Kunpengopterus*, *Darwinopterus*, Liaoning, China.

REFERENCES

ANDRES B AND JI Q. 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of the pterodactyloidea, and convergence in their cervical vertebrae

BENNETT SC. 2001. The osteology and function phology of the Late Cretaceous pterosaur *Pter* Palaeontographica Abt A 260: 1–112.

BENNETT SC. 2007. Articulation and function of the bone of pterosaurs. Jour Vert Paleont 27: 881–89

CHANG M, CHEN PJ, WANG YQ AND WANG Y 2003. The Jehol Biota. Shanghai Scientific & cal Publishers, Shanghai, 208 p.

COSTA F AND KELLNER AWA. 2009. On two p humeri from the Tendaguru beds (Upper Jurassic nia). An Acad Bras Cienc 81: 813–818.

DALLA VECCHIA FM. 2009. Anatomy and system the pterosaur *Carniadactylus* gen. n. *rosenfeld* Vecchia, 1995). Riv Italiana Paleont Strati 115: 1

DALLA VECCHIA FM, WILD R, HOPF H AND REI 2002. A crested rhamphorhynchoid pterosaur f Late Triassic of Austria. Jour Vert Paleont 22: 19

FREY E AND TISCHLINGER H. 2000. Weichteila der Flugsaurierfüsse und Bau der Scheitelkämm Pterosaurierfunde aus den Solnhofener Schichte ern) und der Crato-Formation (Brasilien). Archae 18: 1–16.

HE HY, WANG XL, ZHOU ZH, ZHU F, JIN F, F, DING X AND BOVEN A. 2004. $^{40}Ar/^{39}Ar$ d ignimbrite from Inner Mongolia, northeastern indicates a post-Middle Jurassic age for the o Daohugou Bed. Geophysical Res Letters 31: 1–4

IBRAHIM N, UNWIN DM, MARTILL DM, BAIDDER ZOUHRI S. 2010. A New Pterosaur (Pterodact Azhdarchidae) from the Upper Cretaceous of M PLoS ONE 5(5): e10875. doi:10.1371/journal.pone.0010875.

JI SA, JI Q AND PADIAN K. 1999. Biostratigraphy pterosaurs from China. Nature 398: 573–574.

KELLNER AWA. 1996. Reinterpretation of a remarka preserved pterosaur soft tissue from the Early Cre of Brazil. Jour Vert Paleont 16(4): 718–722.

KELLNER AWA. 2003. Pterosaur phylogeny and co on the evolutionary history of the group. In: BUF E AND MAZIN J-M (Eds), Evolution and Palaeo of Pterosaurs. Geol Soc, London, Special Publ 217: 105–137.

KELLNER AWA. 2004. The ankle structure of tw dactyloid pterosaurs from the Santana Formation

KELLNER AWA AND CAMPOS DA. 1999. Vertebrate Paleontology in Brazil – a review. Episodes 22: 238–251.

KELLNER AWA, MAISEY JG AND CAMPOS DA. 1994. Fossil down feather from the Lower Cretaceous of Brazil. Paleontology 37: 489–492.

KELLNER AWA, WANG X, TISCHLINGER H, CAMPOS DA, HONE DWE AND MENG X. 2010. The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane. Proc Royal Soc B 277: 321–329.

LÜ JC. 2009. A new non-pterodactyloid pterosaur from Qinglong County, Hebei Province of China. Acta Geol Sin 83: 189–199.

LÜ JC. 2010. A new boreopterid pterodactyloid pterosaur from the Early Cretaceous Yixian Formation of Liaoning Province, Northeastern China. Acta Geol Sin 84: 241–246.

LÜ JC, JI S, YUAN C AND JI Q. 2006. Pterosaurs from China. Beijing: Ed. Geological Publishing House, 147 p.

LÜ JC, UNWIN D, JIN X, LIU Y AND JI Q. 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. Proc R Soc B 277: 383–389.

LÜ JC, UNWIN DM, XU L AND ZHANG X. 2008. A new azhdarchoid pterosaur from the Lower Cretaceous of China and its implications for pterosaur phylogeny and evolution. Naturwissenschaften doi: 10.1007/s00114-008-0397-5.

PADIAN K. 2008a. The Early Jurassic pterosaur *Dorygnathus banthensis* (Theodori 1830). Spec Pap Palaeont 80: 1–64.

PADIAN K. 2008b. The Early Jurassic pterosaur *Campylognathoides* Strand, 1928. Spec Pap Palaeont 80: 65–107.

PETERS D. 2009. A reinterpretation of pteroid articulation in pterosaurs. Jour Vert Paleont 29: 1327–1330.

UNWIN DM. 2003. On the phylogeny and evolutionary history of pterosaurs. In: BUFFETAUT E AND MAZIN J-M (Eds), Evolution and Palaeobiology of Pterosaurs. Geol Soc, London, Special Publications 217: 139–190.

UNWIN DM AND BAKHURINA NN. 1994. *Sordes pilosus* and the nature of the pterosaur flight apparatus. Nature 371: 62–64.

UNWIN DM, LÜ J AND BAKHURINA NN. 2000. On the systematic and stratigraphic significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China. Mitt Mus Naturk Berlin, Geowiss R 3: from western Liaoning of China. An Acad Bras Cienc 81: 793–812.

WANG X, KELLNER AWA, ZHOU Z AND CAMPOS DA. 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. Nature 437: 875–879.

WANG X, KELLNER AWA, ZHOU Z AND CAMPOS DA. 2007. A new pterosaur (Ctenochasmatidae, Archaeopterodactyloidea) from the Lower Cretaceous Yixian Formation of China. Cretac Res 28: 245–260.

WANG X, KELLNER AWA, ZHOU Z AND CAMPOS DA. 2008. Discovery of a rare arboreal forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China. Proc Nat Acad Sci 105: 1983–1987.

WANG X AND ZHOU ZH. 2006. Pterosaur assemblages of the Jehol Biota and their implication for the Early Cretaceous pterosaur radiation. Geol J 41: 405–418.

WANG X, ZHOU Z, HE H, JIN F, WANG Y, ZHANG J, WANG Y, XU X AND ZHANG F. 2005. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. Chin Sci Bull 50: 2369–2376.

WANG X, ZHOU Z, ZHANG F AND XU X. 2002. A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and "hairs" from Inner Mongolia, northeast China. Chin Sci Bull 47: 226–230.

WELLNHOFER P. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura Plattenkalke Süddeutschlands I: Allgemeine Skeltettmorphologie. Palaeontographica 148: 1–33.

WELLNHOFER P. 1978. Pterosauria. Handbuch der Palaeoherpetologie, Teil 19. Stuttgart: Gustav Fischer Verlag, Stuttgart, 82 p.

WELLNHOFER P. 1991. The illustrated encyclopedia of pterosaurs. London: Salamander Books, 192 p.

WILKINSON MT, UNWIN DM AND ELLINGTON CP. 2006. High lift function of the pteroid bone and forewing of pterosaurs. Proc R Soc B 273: 119–126.

ZHANG J. 2002. Discovery of Daohugou Biota (Pre-Jehol Biota) with a discussion on its geological age. J Stratigr 26: 173–177.

ZHANG H, WANG M AND LIU X. 2008. Constrains on the upper boundary age of the Tiaojishan Formation volcanic