



PALEONTOLOGY

An early juvenile of *Kunpengopterus sinensis* (Pterosauria) from the Late Jurassic in China

SHUNXING JIANG, XIAOLI WANG, XIAOTING ZHENG, XIN CHENG, JUNQIANG ZHANG & XIAOLIN WANG

Abstract: The Wukongopteridae is a transitional clade between the long- and short-tailed pterosaur groups, and at least ten specimens have been studied without a determined juvenile specimen. Here, we described a small-sized *Kunpengopterus sinensis*, less than half the size of the holotype, which is the smallest specimen in wukongopterids. Based on unossified small elements, unfused cranial and postcranial elements, and grooves on the bone surface, this specimen is thought to be at least an early juvenile or even a late hatchling. By comparing the juvenile and subadult specimens of *K. sinensis*, we have found that the mid region of the upper and lower jaws had a higher growth rate than the anterior part, and that the growth rates were similar in most postcranial elements except for a higher rate in the caudal vertebrae. We revised the previous diagnosis of *K. sinensis* and specified that two characteristics, nasoantorbital fenestra approximately 40% of the skull length and a thin and relatively short maxillary process of the jugal, should be diagnostic in subadult or adult specimens. We have also found that pedal features are stable during ontogeny and can be diagnostic in juvenile, subadult or adult specimens in *K. sinensis*.

Key words: *Kunpengopterus sinensis*, early juvenile, ontogeny, Late Jurassic, China.

INTRODUCTION

Pterosaurs were the first vertebrates to fly on Earth. Few complete specimens exist, however, because of the fragility of their bones. As a consequence, most species are represented by only one or two specimens (e.g., Cheng et al. 2014, Wang et al. 2017a), except for fewer than ten taxa with a large number of specimens, e.g., *Hamipterus* (Wang et al. 2014), *Caiuajara* (Manzig et al. 2014), *Pterodaustro* (Codorníu et al. 2013, 2016), *Pteranodon* (Bennett 2001), *Pterodactylus* (Wellnhofer 1970), and *Rhamphorhynchus* (Bennett 1995). This is the cause of one of the main problems in the systematic studies of pterosaurs, that is, determining the ontogenetic stage of a particular specimen. Although bone

histology is an efficient tool to access the growth patterns in pterosaur fossils (Sayão 2003, Steel 2008, Chinsamy et al. 2009, Wang et al. 2017b), it is a destructive process and thus impossible to carry out in unique specimens of some taxa. Generally, more mature individuals should be larger; however, body size can be influenced by several factors (such as food supply, climate, gender), and so it is not a good criterion to determine the ontogenetic stage in pterosaurs (Bennett 1993). Size-independent criteria have been proposed to separate different stages of development, such as the texture of the bone surface, the degree of ossification, and the fusion of particular ossified elements (Wellnhofer 1970, Bennett 1993, Kellner & Tomida 2000, Codorníu & Chiappe 2004, Kellner 2015).

Wukongopterid pterosaurs are transitional forms that fill the gap between primitive, long-tailed non-pterodactyloids and derived short-tailed pterodactyloids (Wang et al. 2009, 2010, Lü et al. 2010). At least ten specimens of this group have been studied in China since the first publications approximately ten years ago (Wang et al. 2009, Lü et al. 2010). They have been classified into three genera and five species (Wang et al. 2009, 2010, Lü et al. 2010, 2011b, Cheng et al. 2017a), except for three undetermined specimens (Lü et al. 2011a, Wang et al. 2015, Cheng et al. 2016, 2017b). However, no juvenile specimens have yet been reported. It is worth noting that *Jianchangopterus zhaoianus*, first published as a rhamphorhynchid pterosaur, may represent a young wukongopterid (Witton 2013, Wu et al. 2017). The only specimen of *Jianchangopterus* should have been housed at Yizhou Museum (Lü & Bo 2011), but none of the staff knew the whereabouts of this specimen when two of our authors (JS & CX) checked in the museum in 2019. Without observation of the holotype, especially the confluent condition of the nasoantorbital fenestra, it is impossible to confirm whether *Jianchangopterus* is a wukongopterid. Here, we described the first small-sized wukongopterid pterosaur to show some skeletal changes during ontogeny and revised the diagnosis of *Kunpengopterus sinensis*.

SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup 1834

Wukongopteridae Wang et al. 2009

Kunpengopterus Wang et al. 2010

Kunpengopterus sinensis Wang et al. 2010

Holotype: IVPP V 16047, a nearly complete skeleton with complete upper and lower jaws, housed at the Institute of Vertebrate Paleontology

and Paleoanthropology (IVPP), Chinese Academy of Sciences (CAS), Beijing, China.

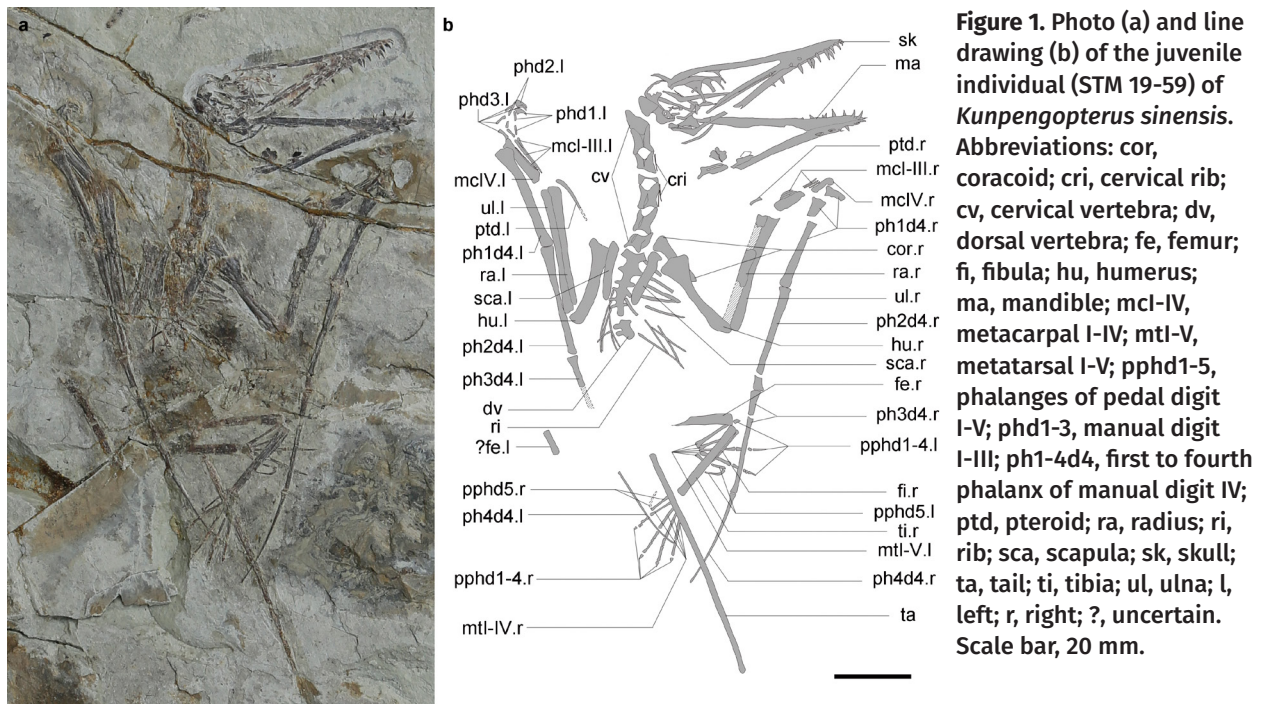
Referred specimens: IVPP V 23674, a nearly complete skeleton including the upper and lower jaws, housed at the IVPP, CAS, Beijing, China (Cheng et al. 2017a); STM 19-59, a small-sized individual with a nearly complete skeleton including the upper and lower jaws, housed at the Tianyu Natural History Museum of Shandong (STM), Pingyi, China (Figures 1-5; Tables I-III).

Horizon and Locality: Linglongta, Jianchang, Liaoning, China. Tiaojishan Formation, Late Jurassic.

Revised 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*; absence of premaxillary crest; nasoantorbital fenestra approximately 40% of the skull length in subadult or adult individuals*; maxillary process of the jugal thin and relatively short in subadult or adult individuals*; lacrimal process of the jugal thick; presence of a soft tissue crest above the frontal; posterodorsal margin of ischium rising dorsally; proximal end of the prepubis very short and wide*; first pedal phalanx of digit V short, less than 70% of metatarsal IV*; curved second pedal phalanx of the fifth toe with an angle between the proximal and distal segments of approximately 145°*; proximal segment of the second pedal phalanx of the fifth toe approximately 30% length of the distal segment, shorter than in other wukongopterids* (Wang et al. 2010, Cheng et al. 2017a).

DESCRIPTION AND COMPARISON

This new material (STM 19-59) consists of a nearly complete skeleton, most of whose elements are closely associated or articulated (Figure 1a). It



was collected from a local farmer, and some elements of the hindlimbs are artificial, which were identified under the microscope and excluded in the line drawing (see Figure 1b); the other elements are natural and should belong to the same individual.

Skull

The skull is nearly complete and articulated, although some elements are quite fragile (Figures 2, 3). The length from the tip of the premaxilla to the end of the squamosal is approximately 53.0 mm, and the rostrum is 23.0 mm, occupying 43.4% of the skull length (Table I), which is larger than in other wukongopterid specimens, such as *Wukongopterus* (27.2%, Wang et al. 2009), *Darwinopterus linglongtaensis* (25.4%, Wang et al. 2010), *D. robustodens* (35.6%, Lü et al. 2011b), and the two specimens of *Kunpengopterus sinensis* (37.9%, Wang et al. 2010 and 36.5%, Cheng et al. 2017a). The nasoantorbital fenestra is incomplete, lacking the posterior border, which is formed by the jugal and lacrimal. Since

the right nasal is preserved in its anatomical position and the distance between the left nasal and lacrimal can be measured, the estimated length of the nasoantorbital fenestra is ~14.5 mm, nearly a quarter of the skull length, much smaller than those in the other two specimens of *K. sinensis* (41.1% and 40.7%, Cheng et al. 2017a), as well as the other non-pterodactyloid monofenestratans (Wang et al. 2010, Lü et al.

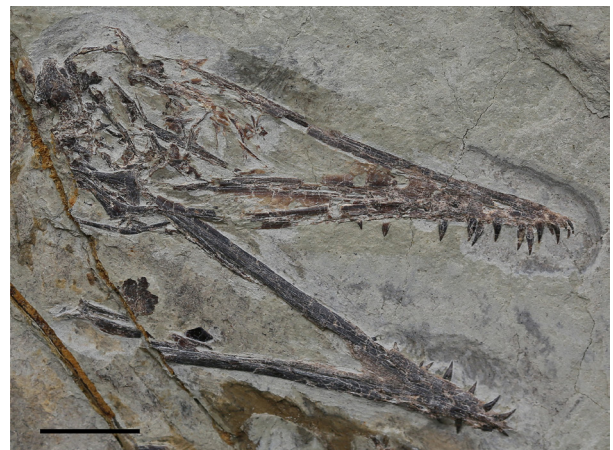


Figure 2. Photo of the upper and lower jaws of the juvenile individual (STM 19-59) of *Kunpengopterus sinensis*. Scale bar, 10 mm.

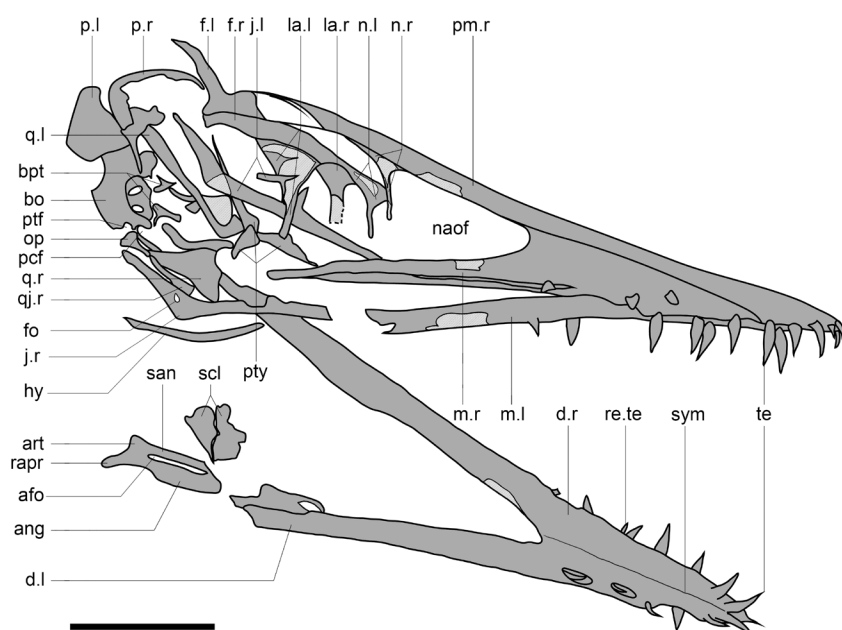


Figure 3. Line drawing of the upper and lower jaws of the juvenile individual (STM 19-59) of *Kunpengopterus sinensis*. Abbreviations: afo, adductor fossa; ang, angular; art, articular; bo, basioccipital; bpt, basipterygoid; d, dentary; f, frontal; fo, foramen; hy, hyoid bone; j, jugal; la, lacrimal; m, maxilla; n, nasal; naof, nasoantorbital fenestra; op, opisthotic; p, parietal; pcf, postcranial fenestra; pm, premaxilla; ptf, posttemporal fenestra; pty, pterygoid; q, quadrate; qj, quadratojugal; rapr, retroarticular process; re.te, replacement tooth; san, surangular; scl, sclerotic ring; sym, symphysis; te, tooth; l, left; r, right; ?, uncertain. Scale bar, 10 mm.

2010, 2011a, b, Tischlinger & Frey 2013, Cheng et al. 2016, Unwin & Deeming 2019). The upper and lower temporal fenestrae and orbits are hard to distinguish.

The premaxilla and maxilla form the lateral side of the anterior part of the skull, and no crest can be observed on the top of the skull. The suture between the premaxilla and maxilla is clear, even at the anterior portion (Figure 4a). The premaxilla is low and elongated, extending at least beyond the lacrimal. The light brown aspect of the maxilla in comparison to a much darker, solid color of the premaxilla seems to be related to different bone thicknesses (thinner in the former). The region of the maxilla forming the anterior margin of the nasoantorbital fenestrae is quite thin and nearly transparent, making it difficult to distinguish the boundary between the maxilla and the matrix.

Both nasals are preserved, and the right one is in its anatomical position (Figure 4d). They are triradial bones, and their dorsal margins connect with the premaxillae. The descending process is thin and elongated, approximately half the height of the nasoantorbital fenestrae. It is

nearly vertical to the ventral margin of the skull, different from the anteroventral inclination in other wukongopterids. A foramen should have lain at the base of the nasal (Cheng et al. 2017a); however, a hole is located at the medial side of the left nasal, which might be an expansion of the nasal foramen, and is not found at the right nasal because of the extensive breakage of this element.

Only the outlines of both lacrimals can be detected (Figure 4d). They are triangular bones bearing no evidence of lacrimal foramina. They form the posterodorsal corners of the nasoantorbital fenestrae and the anterodorsal corners of the orbits. The descending process is thin, and the left one is nearly articulated with the lacrimal process of the jugal.

The right jugal is incomplete; its maxillary and postorbital processes are clear, forming a 140° angle; the lacrimal process is only preserved in the left jugal, broken and twisted (Figure 4d). The distance between the lacrimal and postorbital processes is large, similar to that in the holotype of *K. sinensis* as well as that in *Darwinopterus linglongtaensis* and two

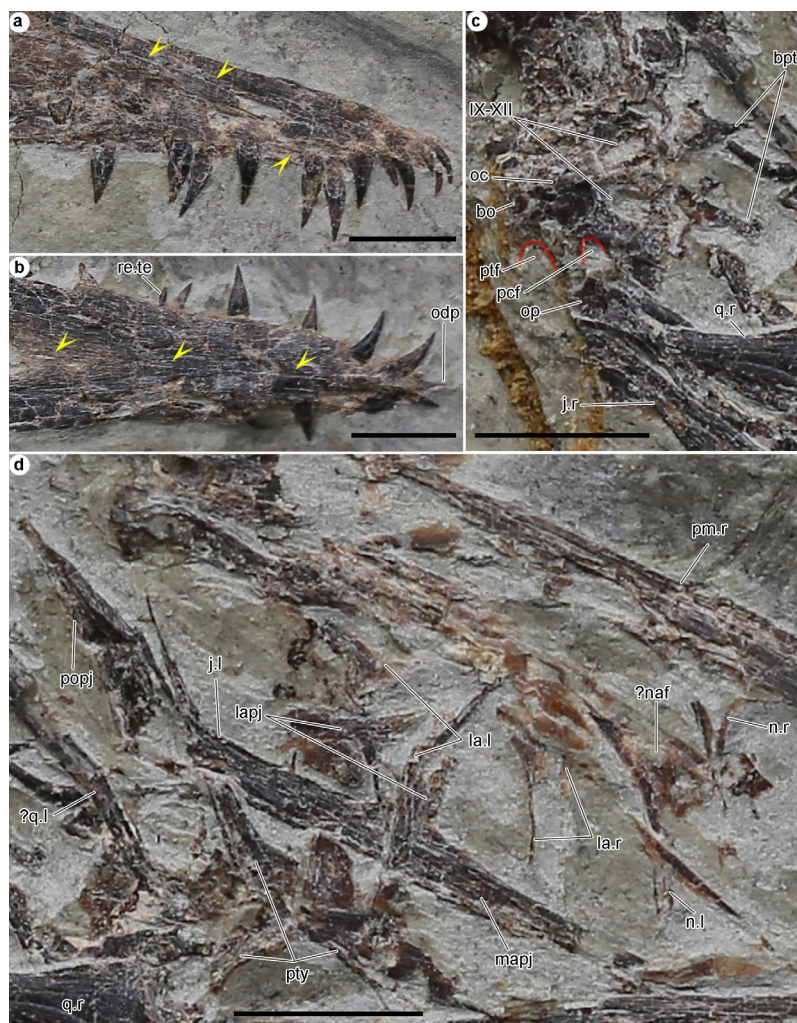


Figure 4. Close-up of the cranial elements of the juvenile individual (STM 19-59). a, anterior portion of the upper jaw, yellow arrows indicating the suture between the maxilla and premaxilla; b, anterior portion of the lower jaw, yellow arrows indicating unfused mandibular symphysis; c, occipital region of the upper jaw, red curves indicating margins of postcranial and posttemporal fenestrae; d, middle region of the upper jaw. Abbreviations: IX-XII, foramina for ninth to twelfth cranial nerves; lapj, lacrimal process of the jugal; mapj, maxillary process of the jugal; naf, nasal foramen; oc, occipital condyle; odp, odontoid process; popj, postorbital process of the jugal; others as in the caption of Figure 3. Scale bars, 4 mm.

unnamed wukongopterid specimens (Wang et al. 2010, Cheng et al. 2017b), indicating the broad ventral margin of the orbit, while these two processes form an acute angular ventral margin of the orbit in *D. modularis* and *D. robustodens* (Lü et al. 2010, 2011b). The preserved length of the maxillary process is 7.5 mm, occupying at least 51.7% of the length of the nasoantorbital fenestrae. There is a small foramen in the medial side of the right jugal.

The anterior portion of the right quadrate is well preserved in ventral view (Figures 2, 3). It is a triangular bone tapering posteriorly. The anteroventral condyle of the quadrate contacts the right articular to form the jaw joint.

The frontal and parietal bones form the posterodorsal roof of the skull (Figures 2, 3). The frontals are severely fragmented, and both parietals are preserved. The left parietal is complete, and it has a smooth surface. The suture between the two parietals is clear.

The occipital region is preserved in posterior view (Figure 4c). The occipital condyle is small, and two foramina are present for the ninth to twelfth cranial nerves. There are two additional incomplete foramina on the right side of the occipital region, which are interpreted as postcranial and posttemporal fenestrae. The bones between them should be the opisthotic and exoccipital, although there is a cracking

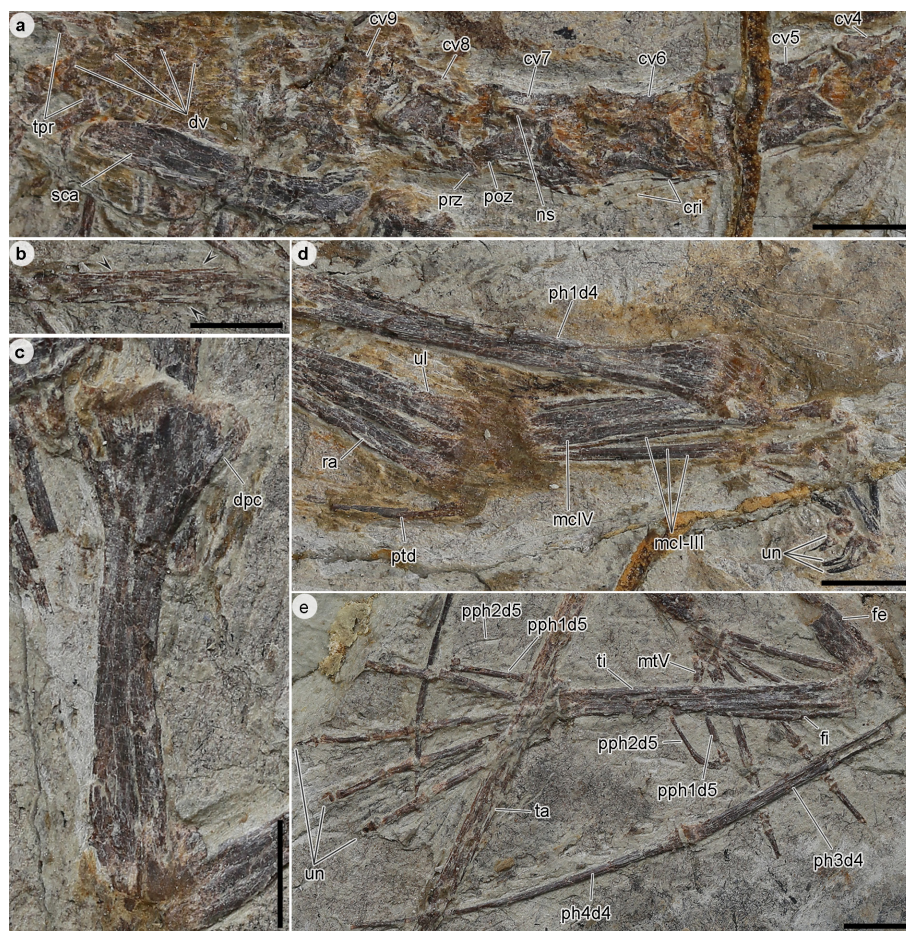


Figure 5. Close-up of the postcranial elements of the juvenile individual (STM 19-59). a, cervical and dorsal vertebrae; b, caudal vertebrae, arrows indicating rod-like zygapophyses and chevrons; c, right humerus; d, part of the left wing, showing the region of unossified carpals and partially ossified epiphyses of the long bones; E, feet. Abbreviation: dpc, deltopectoral crest; ns, neural spine; poz, postzygapophysis; pph1d5/pph2d5, first or second phalanx of pedal digit V; prz, prezygapophysis; tpr, transverse process; un, ungual; others as in the caption of Figure 1. Scale bars, 5 mm.

between this bone and other bones in the occipital region.

There are some other thin and fragmentary elements that are interpreted as bones in the palatal region, such as the pterygoid (Figure 4d). However, new information is unavailable.

There is a slightly curved rod-like bone, which is probably an incomplete ceratobranchial of the hyoid apparatus (Figures 2, 3). Some small subsquared and thin pieces of elements are scattered around the cranial elements, and they might be pieces of ossified sclerotic rings (Figures 2, 3).

Mandible

Most of the mandible is preserved in ventral view and the posterior part of the left ramus is exposed in medial view (Figures 2, 3). The

anterior tip has a pointed and anteriorly directed projection (Figure 4b), which has never been reported in wukongopterids previously (Wang et al. 2009, 2010, Lü et al. 2010, 2011a). The mandibular symphysis has an apparent suture and occupies 34.8% of the length of the lower jaw (Table I), quite larger than in any other wukongopterid specimens, such as the holotype of *K. sinensis* (Wang et al. 2010) and *Darwinopterus* with eggs (Lü et al. 2011a). Two mandibular rami are nearly straight and form a 19.9° angle between the two lateral margins at their anterior portion. On the medial side of the left ramus, it is difficult to distinguish the limits of the articular, angular or surangular, and only the low and elongated adductor fossa is discernible.

Dentition

There are probably twelve teeth per side in the upper jaw, including five pairs of premaxillary teeth (Figures 2-4). The ninth tooth or alveolus is not visible, and it is indicated due to the distance between the anterior and posterior teeth. The other teeth or alveoli are clearly preserved, but the 12th alveolus is not clear due to a small breakage, and it was considered an alveolus based on its distance from the 11th alveolus. Most teeth are conical and similar in size; they are labiolingually curved and vertical to the ventral margin of the skull. The first three pairs are slender and inclined anteriorly. The distances between two successive teeth or alveoli slightly increase posteriorly.

There are at least seven teeth per side in the lower jaw, and the fifth right one has a replacement tooth. The seventh tooth is slightly posterior to the end of the mandibular symphysis, and no further tooth or alveolus can be found beyond it. The teeth in the lower jaw are similar to those in the upper jaw, and the anterior teeth show lateral inclination. This latter feature does not seem to be a result of taphonomy since it would not be possible to have the first four pairs of teeth pointing to nearly opposite directions if the lateral inclination was

not natural. The left fifth and sixth teeth do not present this lateral inclination and can only be observed from the breakages of the mandible, indicating the absence or reduction of lateral inclination. Hence, the lateral inclination is present in the teeth of the lower jaw, at least the anterior ones, and the degrees vary along the tooth row, probably the same condition as the teeth in the upper jaw. Compared with the referred *K. sinensis* specimen, the new material has four fewer teeth per side in the upper and lower jaws (Cheng et al. 2017a).

Vertebrae

In this specimen, the cervical, dorsal, and caudal vertebrae are preserved in their original position; no sacral vertebra can be found (Figure 5a, b). The third to sixth cervical vertebrae are exposed in dorsal view, and the seventh to ninth cervical vertebrae are twisted and exposed in laterodorsal view (Figure 5a). Except for the incomplete third cervical, the neural spines bear low ridges. The fifth to eighth cervicals bear ribs, which are very thin and nearly the same length as each vertebral centrum, contrary to the reduction in the cervical ribs extensively found in wukongopterid pterosaurs, such as in *Wukongopterus* (Wang et al. 2009),

Table I. Measurements of cranial elements in *Kunpengopterus sinensis* (STM 19-59) (in mm).

	Length	Height (width)
Skull	52.95 ^a (pr-sq)	-
Rostrum	22.95	5.87
Nasoantorbital fenestra	14.50 ^a	8.38 ^a
Mandible	46.80	19.28 (maximum width); 6.50 (width at posterior end of symphysis)
Mandibular symphysis	16.29	-

^aEstimated length.

Darwinopterus (Wang et al. 2010, Lü et al. 2010, 2011b), and even in the holotype of *K. sinensis* (Wang et al. 2010, Cheng et al. 2017a). The mid-cervicals are slightly elongated, and the ratio of the length between the zygapophyses and the mid-part width is in the range of 1.5-1.9 (Table II). Seven dorsal vertebrae are preserved in dorsal view, not forming a notarium (Figure 5a). Their length is 22.76 mm. The transverse processes of some of the dorsal vertebrae are preserved, and some connect with ribs. Twenty-six caudal vertebrae are preserved, and both the anterior- and posterior-most parts of the tail are missing. The caudal vertebrae are extremely elongated, bearing rod-like zygapophyses and chevrons (Figure 5b), which is common in long-tailed non-pterodactyloid pterosaurs (Wang et al. 2009, 2010, Lü et al. 2010). The total length of the preserved tail is 63.47 mm, and the width is approximately 1.5 mm.

Pectoral girdle and fore limbs

The scapula and coracoid are not fused. Each scapula is elongated and without constriction in the shaft (Figure 5a). Each coracoid is overlapped by a humerus, and only the length of the right coracoid can be detected, which is slightly longer than that of the scapula (Table

III), differing from the much longer scapular bones in other wukongopterid specimens (Wang et al. 2009, 2010, Lü et al. 2010, 2011b, Cheng et al. 2016, 2017a, b). The right humerus is exposed in dorsal view (Figure 5c), and the left humerus is exposed in the anterodorsal view. The humerus is ventrally curved, without constriction in the mid-shaft. The deltopectoral crest is placed proximally and slightly expanded. The right crest is complete and has a 7.27 mm length along the shaft, occupying 29.5% of the humerus length, which is quite larger than the percentage in larger-sized wukongopterids (Lü et al. 2010, 2011b, Cheng et al. 2017a). No foramina can be observed on the dorsal side of the humeri. The left and right ulnae, left radius, and the mid-part of the right radius are preserved. The articulations are unclear, probably due to partial ossification. The diameters of the radius and ulna are similar in the mid-part of the shaft. The carpals are not ossified. The left metacarpals are complete, although the articulations are also unclear (Figure 5d). Metacarpals I-III have the same length as the fourth metacarpal, which is common in non-pterodactyloids (Kellner 2003, Unwin 2003, Wang et al. 2017a). The left pteroid is nearly complete, missing the most proximal portion. The preserved part is straight and tapers distally, with a pointed end; the expansion is only seen in one specimen (IVPP V 17959) of wukongopterid (Cheng et al. 2016). The wing phalanges shorten distally (Table III), which is different from the condition found in other wukongopterid specimens (Wang et al. 2009, 2010, Lü et al. 2010, 2011b, Cheng et al. 2016, 2017a, b). Neither extensor tendon process of the first wing phalanx is ossified. The fourth wing phalanx is nearly straight, without an expanded distal end. The left manual digits I-III are preserved in a poor condition, but the unguals are quite large, more than two times the size of the pedal unguals (Figure 5d, e).

Table II. Measurements of cervical vertebrae in *Kunpengopterus sinensis* (STM 19-59) (in mm).

	Length (prz-poz)	Width in the middle
Cervical 4	6.00	3.81
Cervical 5	7.85	4.26
Cervical 6	6.96	3.88
Cervical 7	6.37	3.37
Cervical 8	4.65	-
Cervical 9	4.02	-

Table III. Measurements of postcranial elements in *Kunpengopterus sinensis* (STM 19-59) (in mm).

	Left	Right
scapula	15.38	15.39
coracoid	-	15.71
humerus	22.87 ^b	24.61
radius/ulna	34.53	32.41
metacarpal IV	15.34	15.23 ^a
pteroideum	13.64	-
first phalanx of manual digit IV	30.38	28.89 ^a
second phalanx of manual digit IV	28.91	28.50
third phalanx of manual digit IV	-	27.64
fourth phalanx of manual digit IV	-	26.82
tibia	-	23.15
fibula	-	9.66
metatarsal II	9.93 ^a	-
metatarsal III	9.40	-
metatarsal IV	8.75	8.55 ^a
metatarsal V	1.69 ^a	-
first phalanx of pedal digit V	-	6.08
second phalanx of pedal digit V	1.77/4.13/5.74	-

^aEstimated length.^bPreserved length.

Hindlimbs

The right fibula is 41.7% the length of the tibia and is unfused with the tibia (Figure 5e). No tarsals can be detected. Both feet are well preserved, although some parts overlap with other bones (Figure 5e). Metatarsal II is the longest of all five (Table III). There are two phalanges of the fifth toe. The first one is 69.5% the length of metatarsal

IV (Table III), slightly larger than that in other individuals of *K. sinensis*, but still much smaller than that in the other known wukongopterid specimens (Cheng et al. 2016, 2017a). The second one is strongly curved. It has two segments: the proximal segment is short, and it forms a ~142° angle with the other.

DISCUSSION

This new material is a long-tailed pterosaur with short metacarpal IV and elongated fifth pedal digits, excluding the possibility of it being a pterodactyloid. Meanwhile, the naris and antorbital fenestrae confluent to the nasoantorbital fenestrae indicates a member of the Monofenestrata. The new material also shares some autapomorphies with *Kunpengopterus sinensis*, such as the short first pedal phalanx of digit V, less than 70% of metatarsal IV; the curved second pedal phalanx of the fifth toe with an angle between the proximal and distal segments of approximately 145°; and the proximal segment of the second pedal phalanx of the fifth toe approximately 30% the length of the distal segment (Cheng et al. 2017a). Hence, the new material can be assigned to *K. sinensis*.

The new material is the smallest individual of wukongopterids, with a wingspan of 0.4 m, approximately half the size of the subadult individual of *K. sinensis* (Cheng et al. 2017a). As described above, many cranial elements are unfused, such as the premaxilla-maxilla, parietal-frontal, opposite parietals, and opposite dentaries, indicating at least a juvenile individual (Bennett 1993, Kellner & Tomida 2000) or OS2 in Kellner's ontogenetic sequence (Kellner 2015). Many grooves are parallel to the long axis on the surface of the cranial and postcranial elements, and the partial ossification present in the epiphyses of some of the long bones is

evidence for the juvenile stage (Bennett 1993, Tumarkin-Deratzian et al. 2006, Kellner 2015). In this specimen, some small postcranial elements, such as the carpals, tarsals and extensor tendon processes of the first wing phalanges, are absent. Based on the almost articulated condition, these small elements were possibly unossified when this creature died, which occurs in hatchlings (Kellner 2015). Therefore, the new material is probably a late hatchling or an early juvenile. Compared with two large-sized *K. sinensis* specimens, early juveniles show some interesting varieties, shedding some new light on the ontogeny of wukongopterids, at least those of *K. sinensis*.

Comparing the craniums of this new early juvenile specimen (STM 19-59) and that of the subadult individual IVPP V 23674 (Figure 6), the rostrum/skull length ratio changed from 43.4% to 36.5%; the nasoantorbital fenestrae are elongated from 27.4% to 40.7% the length of the skull; and the maxillary process of the jugal shortened from 50.7% to 25% the length of the nasoantorbital fenestrae. These changes indicate that the growth during the ontogeny of *K. sinensis* occurred mainly in the mid part of the skull (yellow regions in Figure 6),

especially at the posterior part of the maxilla and premaxilla, which hence makes the nasoantorbital fenestrae extend over a broader region of the skull. The latter two of the three characteristics listed above are diagnostic for *K. sinensis* (Cheng et al. 2017a), which changed considerably during ontogeny and should only be diagnostic when the individual is subadult or adult. Regarding the mandible, the symphysis dropped from 34.8% to 26.0% of the whole length (Figure 6), which points to a lower growth rate in the anterior part of the mandible (blue regions in Figure 6), a consistent condition with that of the anterior part of the skull. It is worth noting that this ratio increased from the embryonic state to the large-sized individuals in *Hamipterus* (Wang et al. 2017b), contrary to that of *K. sinensis*. Considering the quite different symphysis/mandible length ratios (26% vs 43-45%) in the large-sized individuals, it could represent the diversity among different taxa, with *K. sinensis* and *Hamipterus* varying in the growth mechanism. Therefore, the anterior regions (green and blue regions in Figure 6) of the upper and lower jaws have a lower growth rate than that of the mid regions (yellow and purple regions in Figure 6). Comparing the teeth

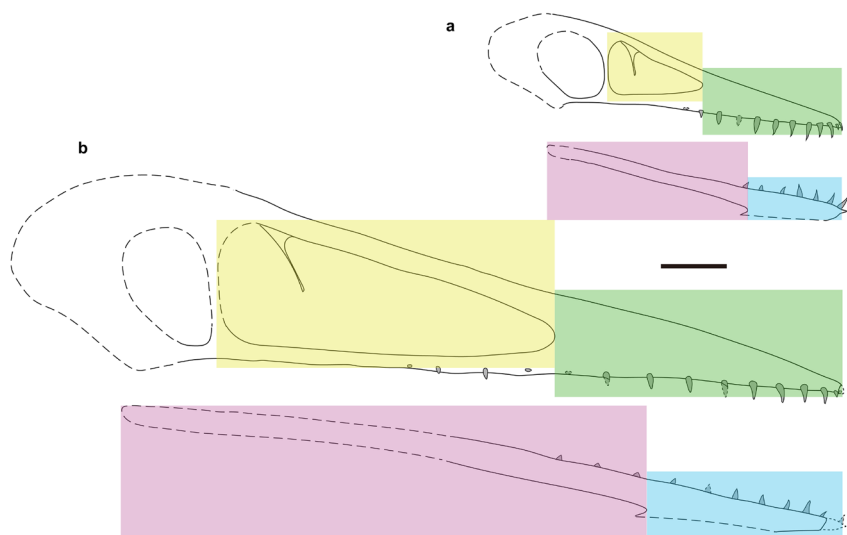


Figure 6. Comparison of the upper and lower jaws between the juvenile and subadult individuals. a, reconstruction based on the juvenile specimen (STM 19-59); b, reconstruction based on the subadult specimen (IVPP V 23674, Cheng et al. 2017a). The yellow, green, purple, and blue regions indicate approximate areas of the nasoantorbital fenestrae, rostrums, mandibular rami, and mandibular symphyses, respectively. Scale bar, 10 mm.

between the two specimens, not only the shape but also the size of the teeth are quite similar (Figure 6), indicating that the teeth may have similar functions at different ontogenetic stages. The upper and lower jaws in the subadult *K. sinensis* have at least 15 and 11 teeth per side, respectively (Cheng et al. 2017b), while the new, small specimen has at least 12 and 7. One more tooth was added in the rostral and mandibular symphyseal regions. The distances between successive teeth in the upper jaw increased during ontogeny, and the more posterior the teeth, the larger the distance was, while these distances in the lower jaw changed slightly. This phenomenon indicates a higher growth rate in the anterior part of the rostrum than in the posterior part and the symphyseal region. We infer that the addition of teeth may occur at the posterior part of the tooth row because the elongation of the maxillae and mandibular rami provides enough space for more teeth.

The number of vertebrae in the juvenile is nearly consistent with that in the subadult individual. However, the length of each single vertebra became quite elongated during ontogeny as well as the condition of *Pterodaustro* (Codorníu 2007). The cervical length/width ratio increased, but the cervical ribs did not elongate as much as the cervical centrums. The tail in the subadult individual is 3.3 times as long as that of the new specimen, while other elements such as skull, mandible, humerus, wing phalanges, and other long bones, are 1.7-2.4 times as large, which indicates the highest growth rate of caudal vertebrae.

The appendicular skeleton in the new specimen resembles that of a large-sized skeleton. The exception is that the wing phalanges decreased distally in length, which is unique among wukongopterids. The longest wing phalanx is the third one in the other two *K. sinensis* specimens, and the shortest is the

fourth one and the first one in the holotype and the other specimen. However, the ratios of each of the two wing phalanges vary slightly, which may be caused by individual differences. The foot presents some diagnostic characteristics of *K. sinensis*, such as the length of the first pedal phalanx of digit V and the angle and length ratio between the two segments of the second phalanx of pedal digit V. These were found to be stable during ontogeny, which can be used as diagnoses not only in adult or subadult specimens but also in juveniles.

CONCLUSIONS

Based on unossified small elements, unfused cranial and postcranial elements, and grooves on the bone surface, this small specimen described here (0.4 m wingspan) is thought to be at least an early juvenile or even a late hatchling. Compared to the subadult *Kunpengopterus sinensis* specimens, the mid-part of its upper and lower jaws had a higher growth rate than the anterior part, and that the growth rates were similar in most postcranial elements, except for a higher rate in caudal vertebrae. Finally, by revising the previous diagnosis of *K. sinensis* we have found that two characteristics, nasoantorbital fenestra approximately 40% of the skull length and a thin and relatively short maxillary process of the jugal should be diagnostic in subadult or adult specimens. We also found that the pedal features are stable during ontogeny and can be diagnostic in juvenile, subadult or adult specimens.

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