

A New Chinese Anurognathid Pterosaur and the Evolution of Pterosaurian Tail Lengths

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Abstract: A new anurognathid pterosaur specimen from the Middle Jurassic Tiaojishan Formation of Qinglong, northern Hebei Province is described. The new specimen is referred to *Dendrorhynchoides*, based on the general morphology of the skeleton, but it represents a new species, named here as *Dendrorhynchoides mutoudengensis* sp. nov.. It is characterized by the presence of short, robust and straight teeth, and bearing wing metacarpal approximately 40% of the length of humerus. The new specimen provides further osteological information for anurognathid pterosaurs, especially the presence of a relatively elongate tail.

Keywords Pterosauria, rhamphothynchoids, anurognathid, *Dendrorhynchoides mutoudengensis*, pterodactyloids, tail evolution.

1 Introduction

Pterosaurs are an enigmatic group of flying reptiles that lived in the Mesozoic. Traditionally they have been divided into two well separated groups - the derived pterodactyloids with large heads, long necks, and short tails, and a basal grade of paraphyletic non-pterodactyloids ('rhamphorhynchoids') with short heads and necks and long tails (among other characteristics). While the morphological gap between the two groups has been dramatically reduced by the discovery of the transitional form *Darwinopterus* (Lü et al., 2010; 2011), the anurognathid clade remain an interesting group of non-pterodactyloids notable for the presence of a pterodactyloid-like short tail.

Anurognathid pterosaurs were first recognized with the description of *Anurognathus* from the German Solnhofen beds in 1923 (Döderlein), though this was based on a poorly preserved and fragmentary specimen. Nevertheless, it was clear that anurognathids were unusual, even for pterosaurs, with very short, broad skulls, 'flexed' wings and reduced tails (Wellnhofer, 1975). A suite of characters show that anurognathids are non-pterodactyloid pterosaurs (e.g. see Kellner, 2003; Unwin, 2003), but their short tails provides at least some evidence that they may in fact be closer to the pterodactyloids (Andres et al., 2010) than their

more 'typical' phylogenetic position as very basal taxa.

Only very few anurognathid pterosaurs have been described, though most are from Asia. A second *Anurognathus* specimen was recently described from Germany (Bennett, 2007a) and there is a possible anurognathid sacrum from the US (Bennett, 2007b), but all other definitive material is Asian in origin. *Batrachognathus* is known from two specimens from Kazakhstan (Unwin and Bakhurina, 2000) and there is also a specimen from Mongolia (Bakhurina and Unwin, 1995), and more recently a new specimen from North Korea (Gao et al., 2009). China is especially rich in anurognathids with four specimens having been described (including the material reported here) and at least two more are held in private collections.

The first Chinese anurognathid named was *Dendrorhynchus* (Ji and Ji, 1998), but later the generic name was found to be preoccupied by a parasitic worm named in 1920 by David Keilin and it was renamed as *Dendrorhynchoides* (Ji et al., 1999). Two specimens of *Jeholopterus* (Wang et al., 2002; Ji and Yuan, 2002) followed. All three of these are preserved in dorsal view and are largely complete and articulated and with much soft tissue preserved (e.g. see Kellner et al., 2009). However, *Dendrorhynchoides* has proved especially problematic owing to a fake tail (likely dromaeosaurid in origin) that was inserted into the holotype specimen (Unwin et al., 2000). Thus, despite previous claims that a long-tailed

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anurognathid was known (Ji et al., 1999), so far all specimens are considered to have very short, pterodactyloid-like tails.

A new anurognathid specimen is described here and referred to the genus *Dendrorhynchoides* (Hone and Lü, 2010). It is similar to the holotype, but it provides further osteological and distribution information. Notably a genuinely longer tail than seen in other anurognathids is preserved – the first for this group. The specimen is discovered from the Middle Jurassic Tiaojishan Formation of Qinglong County, northern part of Hebei Province (Fig. 1).

Museum Abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; GLGM, Guilin Geological Museum; JZMP, Jinzhou Paleontological Museum, Liaoning Province; NMNH, National Museum of Ireland, Natural History, Dublin, Ireland; NSM-PV, Division of vertebrate Paleontology, National Science Museum, Tokyo, Japan; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; SOS, Jura Museum (Solnhofen Sammlung), Eichstätt; YH, Yizhou Museum, Yixian, Liaoning Province.

2 Systematic Paleontology

Pterosauria Kaup, 1834

Anurognathidae Kuhn 1937

Dendrorhynchoides (= *Dendrorhynchus*) Ji et Ji, 1998

Dendrorhynchoides Ji et al, 1999

Dendrorhynchoides mutoudengensis sp. nov.

Etymology: The specific name refers to Mutoudeng of Qinglong County, where the type specimen was found.

Type specimen: Almost complete skeleton with skull and jaws (The specimen is originally stored in the Guilin Geological Museum (GLGMV 0002; Hone and Lü, 2010)). The specimen is now stored in the Jinzhou Paleontological Museum, Liaoning Province (JZMP-04-07-3).

Type Locality and Horizon: Mutoudeng, Qinglong County of Hebei Province (Figure 1); Middle Jurassic, Tiaojishan Formation (Bureau of Geology and Mineral Resources of Hebei Province, 1989). This contrasts with the Early Cretaceous (Yixian Formation) date for the holotype of *Dendrorhynchoides*.

Notes: At present, all the Chinese anurognathid pterosaurs are from the Middle Jurassic (two specimens of *Jeholopterus*, *Dendrorhynchoides mutoudengensis* sp. nov. are from the Middle Jurassic deposits, although *Jeholopterus* was regarded from the Early Cretaceous Yixian Formation (Wang et al., 2002), the latter geological studies show that *Jeholopterus*-bearing deposits belong to the Middle Jurassic (Gao and Ren, 2006). Therefore, it is possible that the holotype *Dendrorhynchoides* was also discovered from the Middle Jurassic deposits.

Diagnosis: A new *Dendrorhynchoides* species that differs from other anurognathids in that the skull is smaller and less wide, ratio of length to width approximately 80%; dimorphic teeth where some teeth are short, robust and straight, and longer teeth with slightly curved tips; wing

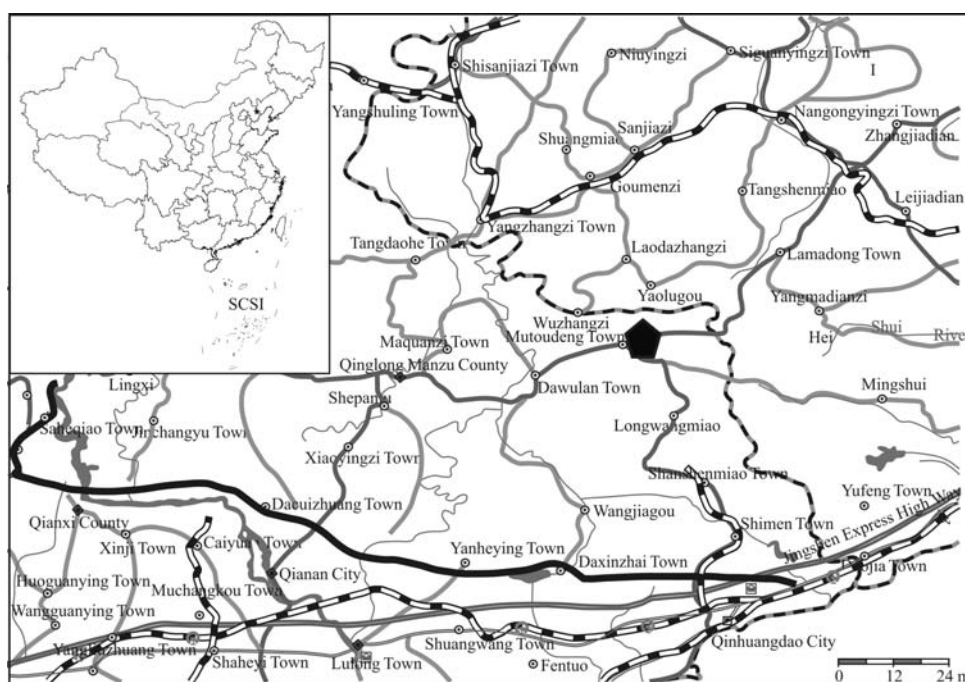


Fig. 1. Map of the fossil locality. The solid pentagon represents the fossil site.

metacarpal approximately 40.7% of the length of humerus.

3 Description

The specimen is largely complete and articulated and is preserved in ventral view (based on the palate being uppermost). The skeleton is not very well preserved (Figs. 2, 3, 4, Table 1). The skull is crushed, and the neck partially disarticulated at least. The postcranial skeleton is preserved mostly as bone, though other elements are left only as impressions in the matrix (except for much of the pre-sacral vertebral column which appears to be missing entirely). Some damage is also present on the posterior part of the skeleton through marks made by a chisel, during discovery and excavation. However, despite this, the impressions are of high quality and details are clearly preserved. Some elements are also separated into a number of small counter-plate pieces. Thus the detailed structures can be observed and accurate measurements can be obtained.

Some soft tissues including pycnofibers on the body (Kellner et al., 2009), and parts of the wings (including actinofibrils) and the uropatagium are also preserved.

Investigations with UV light can reveal much new information in Jehol specimens (e.g. see Kellner et al., 2009; Hone et al., 2010), however, the use of glues, preservatives and other chemicals can mask these tissues. A preliminary investigation by H. Tischlinger revealed no further details in the soft tissues. Although possible, it was therefore decided to leave the specimen untreated and no cast or mould will be made of the specimen until further

investigations have taken place.

The specimen appears to represent a juvenile animal. There is no evidence of the grainy bone texture used by Bennett (2001) to diagnose very young individuals ('hatchlings'), but nor is the animal an adult. Elements that typically fused in adult pterosaurs (e.g. the wrist, sacrum, scapula and coracoid) are here unfused. The new specimen is also somewhat smaller than the holotype of *Dendrorhynchoides* (here a wingspan estimated as 40 cm compared to over 50 cm) also suggesting that it is not an adult, though the holotype of *D. curvidentatus* itself is also unlikely to be an adult individual.

As with other dorso-ventrally preserved anurognathid specimens, the skull is crushed flat and little detail can be reconstructed or identified (Fig. 4). However, most if not all elements are likely preserved as there is only limited disarticulation. Numerous small and splint-like palatal elements (as described by Bennett, 2007a and also seen in other specimens, e.g. *Batrachognathus*) are visible on the surface (suggesting that the specimen is preserved in ventral view) but their exact identities cannot be easily determined. The skull appears to be smaller and may be less wide than in other anurognathids (approximately 20 mm wide vs 16 mm long) but still has the generally short and broad proportions of an anurognathid. The anterior margin of the skull is gently rounded while the posterior margin is straight.

Most teeth are missing, or perhaps more likely covered, given the apparent completeness of the skull. One large tooth is short, and robust. It is blunt, but end is either worn or broken. Some longitudinal striations are visible on the surface enamel and the tooth has a little curvature. Two other teeth are preserved together on what may be a fragment of dentary. These are longer and thinner than the robust tooth and while one is broken, the other is largely intact and distally curves posteriorly. Anurognathids have a homodont dentition and as these latter teeth are more typical of anurognathid teeth and of *D. curvidentatus*. The robust tooth of *Dendrorhynchoides mutoudengensis* indicates that it does not have a homodont dentition, which is different from that of *Dendrorhynchoides curvidentatus*.

The cervical column is disarticulated with three vertebrae lying to the posterior lateral side of the skull. They are short and robust, but little else can be determined. No other evidence of the cervicals is present, either in bones or impressions in the matrix. No information is available on the dorsal vertebrae as there are no bones or impressions present. At least three sacral vertebrae are preserved. They are short and broad overall, but relatively long compared to other anurognathids. These articulate with the tail vertebrae, implying that these are the three most distal sacral vertebrae. Although the cervical vertebrae are displaced, the skull lies in a line with the

Table 1 Measurements of the specimen (JZMP-04-07-3). Widths of the long bones are taken from the midpoint of the shaft except the fibula

Skeletal Element	Length (mm)	Width (mm)
Skull	16	20
Pre-caudal series	58	-
Caudal series	18	-
Coracoid	9	2
Scapula	17	1
Humerus	27	3
Ulna	42	2
Radius	42	2
Metacarpals (1-4)	11	-, -, -, 0.2
Wph1	50	2
Wph2	41	1
Wph3	25	0.6
Wph4	5	0.2
Femur	21	2
Tibia	27	2
Fibula	15	1
Metatarsal I-V	12; 12; 12; 12; 0.3	-
Pedal digit I	2.5; 2.2 (ungual)	-
Pedal digit II	2; 4; 2	-
Pedal digit III	2; 1; 4; 2	-
Pedal digit IV	2; 15; 1; 3; 2	-
Pedal digit V	10; 9	-

Notes: Measurements were taken from the better preserved side in each case. - indicates that these could not easily be measured accurately or were not preserved.



Fig. 2. Photo of specimen (a) and counter-plate pieces (b, c). Scales are in centimeters.

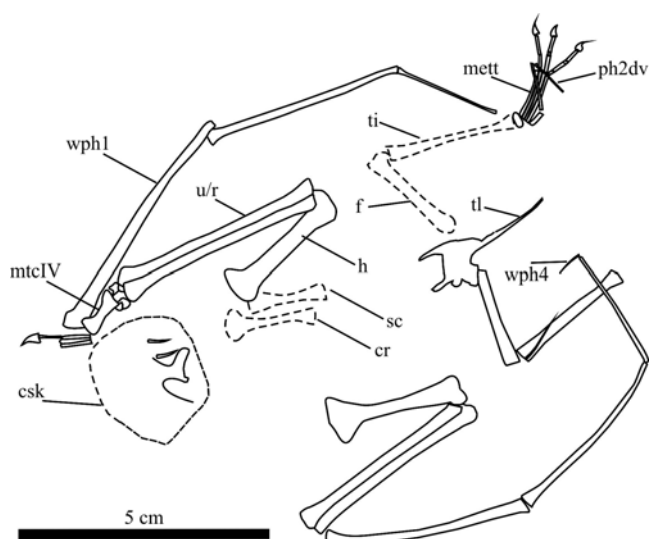


Fig. 3. Line drawing of main specimen with labels.

Abbreviations: cr. coracoid; csk. crushed skull; f. femur; h. humerus; mtcIV. metacarpal IV; met. metatarsals; ph2dv. Phalanx 2 of digit V; u/r. ulna and radius; tl. tail; ti. tibia; wph1, wph4.: wing phalanx 1, wing phalanx 4.

pelvis and between the arms and is likely in a natural position. Thus the length of the pre-caudal vertebral column can be estimated from the base of the skull to the sacral vertebrae at 58 mm in length.

The tail, while short, is much longer than is preserved in other anurognathids and is at least 18 mm long. It is preserved proximally, but distally is left as an impression in the slab and the end is missing, though perhaps just one or two caudal vertebrae are absent given the way in which the tail is tapering at this point. Approximately 15 caudal vertebrae are present – the exact number is difficult to determine owing to the preservation of the elements. The anterior three vertebrae are short and wide and appear as

biconvex articular ends. However, the latter vertebrae are more typically pterosaurian and are twice as long as broad. They lack any obvious zygapophyses etc. Additionally, a number of associated thin rods of bone are present that are interpreted as chevrons. These are approximately the same length as the caudal vertebrae with which they are associated and lie sub-parallel to the tail, though they are not in direct articulation. Given the general articulation of the material, these are unlikely to be dorsal ribs or gastralia, and there is no evidence of contaminating material from other specimens (e.g. fish bones).

Impressions of six dorsal ribs with some bone flakes are on the animal's left hand side and also the impression of at least one gastralia is present.

The scapula is nearly twice the length of the coracoid. The distal end of the scapula is slightly expanded. Both the scapular and coracoid are straight elements.

The proximal end of the humerus is missing, but the impression shows that the deltopectoral crest is small and positioned proximally, and while damaged, appears to be sub-triangular in shape. The medial crest of the proximal humerus is small. The shaft is straight, and distally the two condyles are developed. The humerus is longer than femur and it is the same length with tibia. The wing metacarpal is 40.7% of the length of the humerus.

Both ulna and radius are the straight, and they are only slightly shorter than the first wing phalanx and are subequal to the second wing phalanx in length. The ulna on the right hand side appears to have an unfused epiphysis attached to the end of the bone that makes it is total slightly longer than the radius.

At least four and perhaps as many as five carpal elements can be observed. The distal one is the largest and it is

slightly narrower than the proximal end of the wing metacarpal. The left pteroid is absent, but the articulating carpal element is present. On the right side an impression of the pteroid is present, though perhaps not all of the bone is preserved in this impression. In any case, the pteroid is short, robust and slightly curved and its distal end is blunt. The manual claws are short and robust, and are similar to these of the pedal claw in shape but the manual unguals are larger. The four metacarpals are equal in length, such that metacarpals I-III reaches the distal carpals. The wing metacarpal (the fourth metacarpal) is short and stout.

There are four wing phalanges and they gradually reduce in length along the row, thus the first wing phalanx is the longest and the fourth is the shortest. Phalanx 3 is only half length of the wing phalanx 1. The middle portion of the impression of the second wing phalanx displays a deep longitudinal groove on the posterior surface (or as scars on dorsal surface sensu Bennett, 2008 – i.e. the surface of the wing phalanx into which the wing membrane would attach), as is the case in *Rhamphorhynchus* (Wellnhofer, 1991). From the reflected part we can see that there is also a slight ridge on the ventral side of the phalanx. The forth wing phalanx is disarticulated from the other three in both wings. Its proximal end is slightly narrower than the distal end of third wing phalanx, but its shaft suddenly becomes very thin distally. The shaft is straight. As with other anurognathid specimens (Bennett, 2007a), the wing phalanges do not lie in a straight line with each other, but instead the phalanges are ‘jointed’ in the manner or a normal tetrapod joint.

The pelvis is largely missing and the structure of the remainder is not clear. However, the long anterior ramus of the ilium is preserved on the right side.

Most of the hindlimbs are preserved as impressions only. The femur is straight with a strongly turned femoral head, which is at approximately 90 degrees to the shaft. It is 78% length of the tibia. The fibula is not fused to the tibia and is clearly short, tapering rapidly to a point and being half the

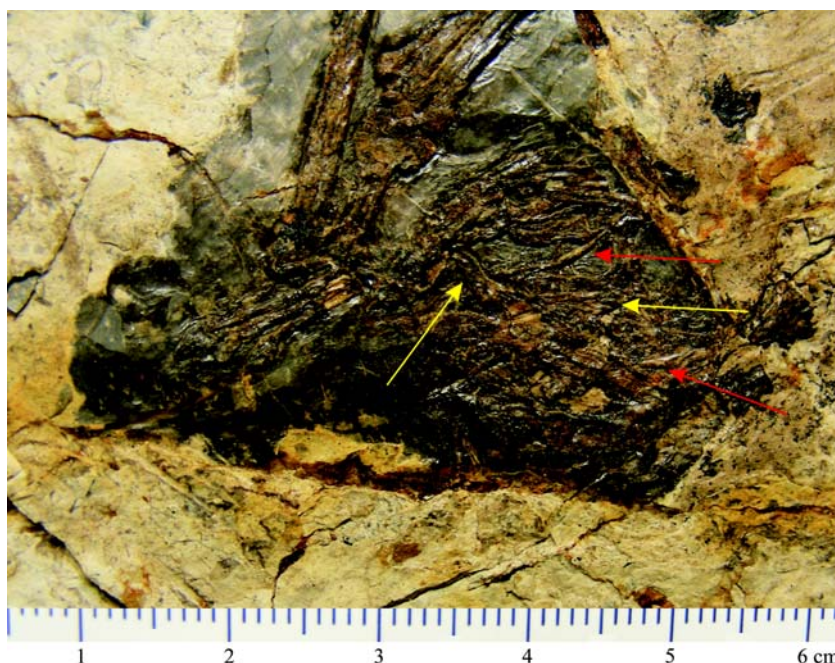


Fig. 4. Close-up of skull. Arrows indicate teeth and palatal elements.



Fig. 5. Close-up of knee counterplate with soft tissues. Scale bar is in millimeter.

length of the tibia.

Metatarsals I-IV (Fig. 5) are the same in length and unusually, so to are digits I-IV (this is also true of *Jeholopterus*, but not *Anurognathus*). The phalangeal formula is 2-3-4-5-2. The pedal unguals are short and robust with very narrow, needle-like distal ends.

Digit V lies across of the other metatarsals as seen in e.g. *Anurognathus* (Bennett, 2007a) and also indicates that the specimen is in ventral view. The second phalanx of digit V is long and straight, not curved as in many other rhamphorhynchoids.

A number of soft tissue elements are preserved on the specimen. The large dark stain on the anterior left side is a crystal or matrix of some kind but other stains on the matrix appear to be soft tissue in origins. Pycnofibers around the right hand shoulder are preserved, though probably as impressions. Traces of the wing membrane and actinobibrils, and traces of the uropatagium are also preserved.

4 Discussion and Conclusions

The new specimen can be referred to Anurognathidae based on a suite of characters (see Bennett, 2007a). The skull is short and broad, palatal elements are reduced to thin splints, the wings are preserved in a ‘flexed’ posture, the manual unguals are large and robust and the tail (while longer than other anurognathids) is short.

Diagnoses of the anurognathid genera have been problematic with numerous characteristics been used to diagnose individual genera instead are present in other taxa. A review of the anurognathids (Hone, submitted MS) suggested that *Dendrorhynchoids curvidentatus* had just two characters that could be used to separate it from other anurognathids. First, the deltopectoral crest of the humerus is sub-triangular in shape, contrasting with the rounded one of *Anurognathus*, the sub-rectangular one of *Batrachognathus* and the alate crest of *Jeholopterus*. The lateral humeral crest is also smaller in *D. curvidentatus* than other anurognathids. Both of these features are seen in the specimen here.

Secondly, the teeth of *D. curvidentatus* are both longer and more recurved than in other anurognathids. However, here in *Dendrorhynchoides mutoudengensis* there is a mixture of short teeth, but also longer curved ones.

The humeral shape of *Dendrorhynchoides mutoudengensis* is a close match for *D. curvidentatus*, and is clearly different to other anurognathids, but the teeth are less close match, hence in part, the erection of a new species.

Dendrorhynchoides mutoudengensis differs from *Dendrorhynchoids curvidentatus* in that there is no straight, short teeth and the ratio of wing metacarpal is smaller (33.5%) in *Dendrorhynchoids curvidentatus* than in *Dendrorhynchoides mutoudengensis* (40.7%), and the length ratio of tibia to ulna (64%) is smaller than that of *Dendrorhynchoids curvidentatus* (75%; see Ji and Ji, 1998).

On tail lengths in pterosaurs

While damaged and somewhat incomplete, this specimen nevertheless adds new information on *Dendrorhynchoides* and anurognathids. Most notably it is clear now that the tail of at least one anurognathid is much greater in length than previously appreciated. Indeed, the variation seen in pterosaurs as a whole is far greater than

the often depicted ‘long tail vs short tail’ dichotomy of pterosaurs. The tail of the specimen presented here is approximately 85% of the length of the femur compared to 50% for *Anurognathus* (based on the so-called ‘new specimen’, Bennett, 2007a), the only other anurognathid with a complete tail preserved (see Table 2). This is still considerably smaller than other rhamphorhynchoids and on a par with, but higher than, many pterodactyloids though the overall range is from under 15% of femur length to more than 1000% of femoral length (see Table 2).

It should be noted that perhaps *Jeholopterus* also has a relatively long tail for an anurognathid. Although there is no trace of bone or even impression on the holotype specimen, there is a distinctive halo of pycnofibers around the area the tail would have occupied. If this was indeed originally in association with the tail (and the rest of the specimen and its soft tissues appear undisturbed) then *Jeholopterus* would have had a tail of similar proportion to that of *Dendrorhynchoides*.

The short tail of the pterodactyloid pterosaurs has long formed at least one important character in diagnosing the clade to the point where some researchers use the terms ‘long-tailed’ and ‘short-tailed’ pterosaurs for the non-pterodactyloids and pterodactyloids respectively, despite the short anurognathid tail. However, we would suggest that the range of variation here can hardly be encompassed by a simple dichotomous character and indeed that further phylogenetic information may be obtained using tail length as a character. The use of such terms should be stopped given that there are non-pterodactyloid pterosaurs with tails shorter than those of pterodactyloids (e.g. *Anurognathus*) and there are also pterodactyloids with tails longer than those of some non-pterodactyloids (e.g. *Anhanguera*, *Pterodaustro*).

It is especially notable that while the tail is not entirely complete, *Darwinopterus* appears to have a tail that is considerably shorter than that of other non-anurognathid ‘rhamphorhynchoids’. This morphology fits with the transitional position that *Darwinopterus* holds between the ‘rhamphorhynchoids’ and pterodactyloids (Lü et al., 2010, 2011) and suggests that perhaps the pterodactyloid reduced tail was incipient in the monofenestratan clade (and is also seen in another monofenestratan - *Wukongopterus* (Wang et al., 2009)).

Also worthy of note is the distribution of the tail length within the pterodactyloids. While the lengths of the tails are fairly conservative, it is clear that a significant reduction has occurred independently in the nyctosaurs and the azhdarchoids, while the ctenochasmatis retain relatively long tails (perhaps suggesting that they are the basalmost pterodactyloid group). This suggests that there was further independent reduction of tail length in more than one

Table 2 Proportional tail lengths of various pterosaurian taxa

Taxon	Tail: Femur % length	Source	Notes
Non-pterodactyls			
<i>Dendrorhynchoides</i>	85	JZMP-04-07-3	Some distalmost caudals may be absent.
<i>Anurognathus</i>	50	Bennett, 2007a	Young juvenile.
<i>Eudimorphodon</i>	839	Wild, 1978 – Figure 5	Distalmost caudals may be missing.
<i>Campyloganthoides</i>	847	Padian, 2008b p74	
<i>Pterorhynchus</i>	1085	Czerkas & Ji, 2002	
<i>Rhamphorhynchus</i>	619	BSPG 1938 I 503	Juvenile specimen.
<i>Rhamphorhynchus</i>	982	BSPG 1889 XI 1	Young juvenile.
<i>Rhamphorhynchus</i>	754	BSPG 1877 X 1	Young juvenile.
<i>Rhamphorhynchus</i>	900	BSPG 1927 I 36	Juvenile specimen.
<i>Rhamphorhynchus</i>	836	SOS 2819	Juvenile specimen.
<i>Rhamphorhynchus</i>	1067	NMINH F 10172	Young juvenile.
<i>Rhamphorhynchus</i>	700	BSPG 1960 I 470a	Young juvenile.
<i>Sordes</i>	770	Wellnhofer, 1978 p40	
<i>Scaphognathus</i>	428	Wellnhofer, 1978 p35	Juvenile specimen.
<i>Dorygnathus</i>	850	Padian, 2008a p21	
<i>Wukongopterus</i>	460	Wang et al., 2009	Anteriormost and distalmost caudals may be missing.
<i>Darwinopterus</i>	535	YH-2000	Distalmost caudals may be missing.
Pterodactyls			
<i>Pterodactylus</i>	87	BSPG AS V 29a	Juvenile specimen.
<i>Pterodactylus</i>	92	BSPG 1969 I 82	Young juvenile.
<i>Pterodactylus</i>	77	BSPG 1937 I 18 a	Some caudals may be missing. Juvenile specimen.
<i>Pterodactylus</i>	52	BSPG 1911 I 31	Juvenile specimen.
<i>Pterodactylus</i>	88	SOS 4592	Juvenile specimen.
<i>Pterodactylus</i>	69	SOS 4008	Juvenile specimen.
? <i>Pterodactylus</i>	67	SOS 4593	Young juvenile.
<i>Germanodactylus</i>	46	BSPG 1892 IV 1	Some caudals may be missing.
<i>Ctenochasmata</i>	40	Wellnhofer, 1978 p45	
<i>Pterodaustro</i>	188	Codorniu, 2005; Codorniu and Chiappe, 2004	Estimate from a composite, MHIN- UNSL- GEO V 241 and V 243.
<i>Pteranodon</i>	84	Bennett, 2001 p58, 102	Estimate from composite, but based on YPM 2489.
<i>Musquizopteryx</i>	31	Frey et al., 2006	
<i>Anhanguera</i>	70	NSM-PV 19892	Distalmost caudals may be missing.
<i>Boreopterus</i>	92	Lü, 2006 p47	
<i>Zhenyuanopterus</i>	76	Lü, 2010	
<i>Zhejiangopterus</i>	14	Cai and Wei, 1994	
Unnamed azhdarchid	42	Elgin pers. comm.	Unnumbered specimen from Karlsruhe (SMNK).
<i>Nemicolopterus</i>	17	Wang et al., 2008	A very young juvenile specimen.

Note: The length of the femur was taken as a proxy for body mass. Some ratios are calculated despite part of the tail being absent provided it was largely complete and so the true value was unlikely to be significantly different.

lineage, even after the initial reduction between monofenestrates and pterodactyls.

The azhdarchoids have remarkably short tails, even by pterodactyl standards and indeed it is possible that some taxa are genuinely tailless. We note that there are a number of otherwise very well preserved azhdarchoids from various lagerstätte deposit that are effectively complete but lack tails. For this to happen regularly implies that tails are easily lost, were poorly ossified, or were genuinely absent. To select between the three possibilities is not possible at present, but we would urge our colleagues to make careful examination of such specimens in the future. Genuine absence can of course only be inferred when other possibilities have been ruled out, and isolated tails would favour the detached option, and faint impressions may be present or elements visible under UV light would show that they are normally present but not preserved. The possibility remains however that some azhdarchoids were genuinely tailless and this should not be discounted in future studies.

Some intraspecific variation is also seen in both rhamphorhynchoids and pterodactyls over multiple specimens of *Rhamphorhynchus* and *Pterodactylus* (see table 2). Especially in the former, tail lengths range from around 600 to over 1000% the length of the femur, but are more conservative (while still relatively varied) in *Pterodactylus* (from around 60-90). This is perhaps not unexpected given the range of variation recorded in tail lengths for a wide variety of taxa including snakes, lizards, mammals and non-avian dinosaurs (Hone, 2012). However, the generally accepted hypothesis that the long tails of rhamphorhynchoids, in conjunction with their tail vanes, acted as steering systems (e.g. see Frey et al., 2003) and thus a greater level of consistency might have been expected. This variation does not appear to be linked to ontogeny however, as there is variation in both younger and older specimens of each taxon.

The phylogenetic position of the anurognathids:

Phylogenetic analyses of non-pterodactyls have

produced numerous and radically different positions for the anurognathids. The results of Kellner (2003), Wang et al., (2005), Lü and Ji (2006) and Bennett (2007a) have them as the most basal of pterosaurs. Unwin (2003a, b) has them in a relatively basal position but with the dimorphodontids and *Preondactylus* below them. Dalla Vecchia (2009) and Andres et al. (2010) produced a heterodox view with the anurognathids as the sister taxon to the pterodactyloids. In all cases though, the absence of the unusual intermediate taxon *Darwinopterus* (which has a pterodactyloid-like head and neck, but with a long, rhamphorhynchoid-like tail) analyses may make these results uncertain. The phylogenetic analysis performed with the description of *Darwinopterus* (Lü et al., 2010) placed anurognathids derived with respect to dimorphodontids, but basal to other non-pterodactyloids (as with Unwin, 2003a, 2003b) though this perhaps merely emphasizes the differences in datasets as well as phylogenetic positioning of various taxa (as seen in Unwin and Lü, 2010).

At the very least the optimisation of the character of tail-length is highly complex with otherwise short-tailed anurognathids lying within the long-tailed non-pterodactyloids. If they are indeed the sister-taxon to the pterodactyloids then this complicates the picture further as this would require a massive convergence of cranial characters to have occurred between *Darwinopterus* and the pterodactyloids or a very rapid evolution of the anurognathids from the ancestral pterodactyloid stock. Pterosaur phylogenies are characterized by having relatively few characters supporting each node on the cladogram and thus large rearrangements of the positions of clades are common based on only small changes of characters, coding or included taxonomic units.

The discovery of *Dendrorhynchoides mutoudengensis* indicates that the heterodont dentition is present in the anurognathids – a character normally associated with only the most basal pterosaurs. The anurognathid pterosaurs show a higher diversity than previous thought. *Dendrorhynchoides mutoudengensis* provides further osteological information for anurognathid pterosaurs, especially the presence of an elongate tail.

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