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A Review of the Taxonomy and Palaeoecology of the Anurognathidae (Reptilia, Pterosauria)

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Abstract: The anurognathids are an enigmatic and distinctive clade of small, non-pterodactyloid pterosaurs with an unusual combination of anatomical traits in the head, neck, wings and tail. They are known from very limited remains and few have been described in detail, and as a result, much of their biology remains uncertain. This is despite their importance as potentially one of the earliest branches of pterosaur evolution or even lying close to the origins of pterodactyloids. This review covers the taxonomy and palaeoecology of the anurognathids, which remain an interesting branch of pterosaurian evolution.

Key words: non-pterodactyloid, palaeobiology, flight, Ornithodira

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1 Introduction

Anurognathids were a distinctive clade of small, early-diverging non-pterodactyloid pterosaurs from the Middle Jurassic to Early Cretaceous of Eurasia (Lü and Hone, 2012; Witton, 2013). They are easily distinguished from other pterosaurs by a large number of diagnostic characters occurring throughout the skeleton but notably include an exceptionally short and broad skull, a wing finger capable of flexion at all joints, small, simple and peg-like teeth, and a short tail (see Fig. 1). Anurognathids have been interpreted as specialised insectivores, catching flying invertebrates on the wing in low light conditions (Bennett, 2007a). They were likely the only clade of non-pterodactyloid pterosaurs to have crossed the Jurassic-Cretaceous boundary (Hone and Benton, 2007). Anurognathids are rare, with less than a dozen specimens reported, and most of these having been discovered only in the last fifteen years (Bennett, 2007a; Gao et al., 2009; Lü and Hone, 2012; Jiang et al., 2015; Lü et al., 2018; Yang et al., 2019).

1.1 History

The first example of an anurognathid was described by Döderlein (1923) who named *Anurognathus ammoni* from the Solnhofen limestone of southern Germany. The holotype, and for many years the only specimen, is poorly preserved with numerous fragmented bones and calcite deposits on the joints making interpretation difficult (see Fig. 2). Nonetheless, it could clearly be identified as a new and unusual small pterosaur with an exceptionally broad and short skull and a short tail. The reduced tail in pterosaurs is an important apomorphy of pterodactyloid pterosaurs, yet despite this, *Anurognathus* was correctly assigned to the 'rhamphorhynchoids' (i.e. non-pterodactyloid pterosaurs) by Döderlein (1923).

The second anurognathid specimen became the holotype of *Batrachognathus* which was discovered in the Jurassic Karatau beds of Kazakhstan in 1933, but only described fifteen years later (Ryabinin, 1948). Although preserved in far better condition than the holotype of *Anurognathus*, the specimen was incomplete, lacking much of the postcranial skeleton. A second specimen of *Batrachognathus* was subsequently discovered, preserved in association with the holotype of the scaphognathine pterosaur *Sordes* which is on the same slab. However, this is yet to be described (see Unwin and Bakhurina, 2000). It was suggested by Ryabinin (1948) that *Batrachognathus* was closely related to *Anurognathus* and should perhaps be included in a new subfamily to represent this, apparently unaware that Nopsca (1928) had already erected the Anurognathinae for *Anurognathus* within the then family ranked Rhamphorhynchoidea.

Due to the relatively poor preservation of *Anurognathus* and the incompleteness and inaccessibility to many scientists of *Batrachognathus* (the specimens were housed in the PIN in Moscow), the anurognathids (such as they were) became a footnote in pterosaur research which itself was largely neglected for the much of the Twentieth Century (Wellnhofer, 2008). They were certainly non-pterodactyloids (Wellnhofer, 1975) and, based on their skull shape, perhaps had affinities with dimorphodontids (Wellnhofer, 1978) while the broad skull, peg-like teeth, and small size led to the assumption that they were aerial insectivores (Wellnhofer, 1975).

Happily, a flurry of discoveries in the 1990s and early 21st century have dramatically increased our knowledge of the anurognathids. Firstly, *Dendrorhynchoides* was discovered in the now famously productive 'Jehol' beds of China (Ji and Ji, 1998) with a second specimen described

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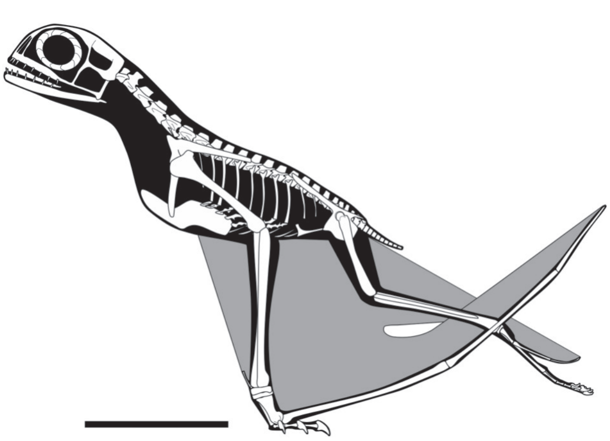

Fig. 1. Line drawing of the skeleton of the anurognathid, *Anurognathus ammoni* based on the new specimen, illustrated here with three wing phalanges (which may not be correct, see text for details). Scale bar is 30 mm. Image by Mark Witton used with permission.

some years later (Lü and Hone, 2012). *Dendrorhynchoides* (Ji and Ji, 1998) was originally named as '*Dendrorhynchus*' but as this name was preoccupied by a ribbon worm, and the pterosaur was given a replacement name by Ji et al. (1999). Initially *Dendrorhynchoides* was described as being most similar to *Rhamphorhynchus* in the proportions of the limbs (Ji et al., 1999), but this hypothesis was rapidly abandoned and *Dendrorhynchoides* was placed within the Anurognathidae with which it shares numerous apomorphies (Unwin et al., 2000). The second specimen of *Dendrorhynchoides* (Hone and Lü, 2010) was diagnosed as a new species *D. mutoudengensis* (Lü and Hone, 2012).

Two specimens of *Jeholopterus* were described in 2002 (Wang et al., 2002; Ji and Yuan, 2002) with each being largely complete and with extensive soft tissue preservation – perhaps the best preserved of all anurognathids (Fig. 3). Both came from the Daohugou beds of what was then considered the Jehol Group in China and thus apparently marked the first record of a non-pterodactyloid in the Cretaceous (though these beds are now considered Jurassic in age – see Sullivan et al., 2014). Dalla Vecchia (2002) noted problems with the diagnosis of Wang et al. (2002) for *Jeholopterus* and suggested that the referral to the Anurognathidae was questionable. However, this is a problem of non-specific characters (e.g. 'body size') being used which could be referred to other taxa (including other anurognathids), rather than an issue of incorrect assignment as made clear both by the large number of apomorphies *Jeholopterus* shares with other anurognathids (see below) and the position recovered in phylogenetic analyses (e.g. see Kellner, 2003).

A largely complete, but poorly preserved, specimen has been described from North Korea (Gao et al., 2009), but little information is currently available about its anatomy or likely affinities, and a fragmentary specimen with a relatively long tail was identified by Jiang et al., (2015). Bennett (2007a) mentioned a possible anurognathid sacrum heralding from the Late Jurassic Morrison Formation of North America, that was originally assigned to *Mesadactylus* (Jensen and Padian, 1989) but this has yet to be described, and the presence of a supraneural plate on this suggests it may belong to a pterodactyloid (Sprague and McLain, 2018). A partial forelimb of a ?juvenile pterosaur from the Middle Jurassic Bakhar Formation of Mongolia has been identified as an anurognathid (Bakhurina and Unwin, 1995). However, as little information is available, it is impossible to comment further on the specimen's morphology or affinities (it has yet to be confirmed that it is indeed an anurognathid) and thus is not considered any further here.

Most recently, *Vesperopterylus* (Lü et al., 2018) has been named and briefly described. This unusual anurognathid had a relatively small skull and apparently also a reversed first toe giving it some grasping ability. Finally, one more anurognathid has appeared in the literature (Yang et al., 2019) which is undescribed but shows some unusual proportions but preserves extensive soft tissues. Thus even among the relatively low morphological diversity of the anurognathids seen to date, there are still novelties being discovered.

These newer specimens are in general nearly complete, mostly articulated and have some preserved soft tissues and add much needed information on these animals. Key among them is the second specimen of *Anurognathus* (Bennett, 2003, 2007a) in Germany [Note: as this specimen lacks a catalogue number, it is referred to as 'the new specimen' throughout following Bennett, 2007a] which is perhaps the best preserved anurognathid known to date (Fig. 2b). Collectively, these specimens have provided important insights into anurognathid anatomy and have greatly advanced our knowledge and understanding of the clade. Other specimens, which likely include new taxa (Hone, pers. obs.), are also in scientific collections and await description.

Historically, the anurognathids have been difficult to place within pterosaur phylogeny. In his original description, Döderlein (1923) correctly identified *Anurognathus* as a 'rhamphorhynchoid' (i.e. non-pterodactyloid) despite the poor condition of the material and the obvious pterodactyloid character of a short tail. A subfamily, Anurognathinae, was erected for the taxon by Nopsca (1928) and this was later elevated to family level status (Kuhn, 1937). Kuhn (1961) later suggested a link between anurognathids and the dimorphodontids and rhamphorhynchines, with Wellnhofer (1978) also suggesting possible ties to the dimorphodontids. Both Wellnhofer (1978) and Kuhn (1961) noted the large skull that is common to both groups. Based on the short tail and tall skull, Young (1964) ascribed *Anurognathus* to the pterodactyloids, despite also noting it might be a descendent of *Dimorphodon*, but this was later reversed by Wellnhofer (1975). Ji and Ji (1998) incorrectly assigned *Dendrorhynchoides* to the Rhamphorhynchinae by due to the putative presence of a long tail (see below) and thus suggested a possible link between this group and the anurognathids (rapidly corrected by Unwin et al., 2000). But it was the application of cladistic analyses to the Pterosauria that produced the first systematic appraisals of anurognathid relationships.

In 2003 two landmark studies were published by

Fig. 2. (a) The holotype of *Anurognathus* (BSPG 1922.1.42), the only anurognathid preserved in lateral view, and (b) the much better preserved 'new' specimen in dorsal view, taken under UV light. Scale bars both 20 mm. The image of the new specimen by Helmut Tischlinger, used with permission.

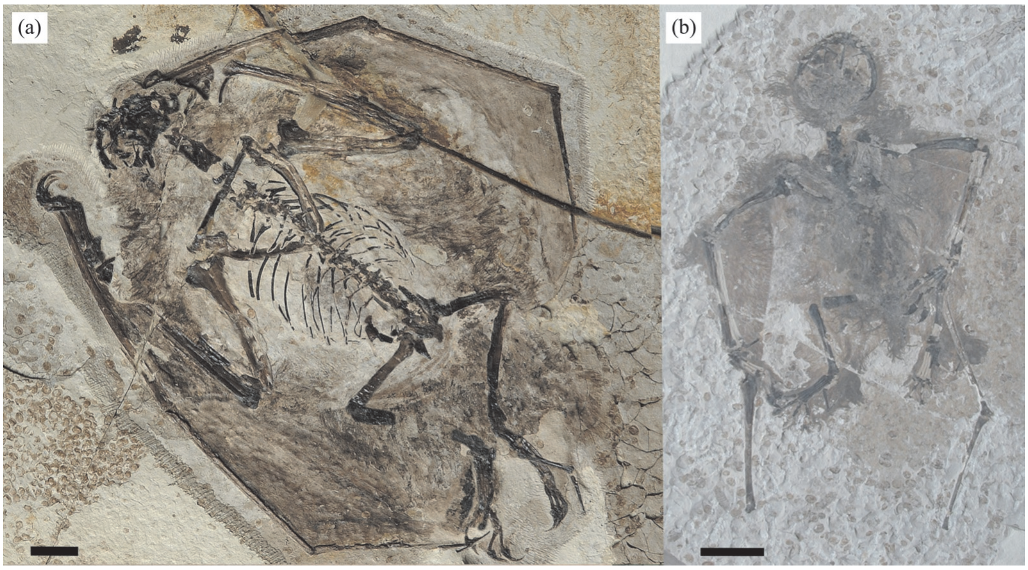

Fig. 3. The two well-preserved anurognathid specimens given as *Jeholopterus*.
(a) the holotype (a digital composite of the plate and counterplate as a single image – IVPP V 12705) and (b) the referred smaller specimen (CGAS IG I 02 81). Scale bars both 20 mm.

Kellner (2003) and Unwin (2003a) evaluating the systematic relationships of the Pterosauria. Despite significant differences between the results of the two works, both were congruent in many ways, and the anurognathids were recovered in similar phylogenetic positions by these authors. In both, the anurognathids are recovered in an early branching position either as the earliest-diverging clade within Pterosauria (Kellner, 2003) or branching off after only *Preondactylus* and the Dimorphodontidae (Unwin, 2003a). Most other analyses (both before and after those of 2003) consistently reflected these positions with anurognathids either as the first branching clade in the pterosaurian tree (Kellner, 1996; Lü and Ji, 2006; Bennett, 2007a; Wang et al., 2008; Lü et al., 2018) or in an early branching position (Unwin, 1995, 2003b; Viscardi et al., 1999; Lü et al., 2010) with only one or two taxa in earlier branching positions. Recently, Vidovic and Martill (2018) recovered the anurognathids as a clade within a Scaphognathinae (and therefore suggested they should be renamed the Anurognathinae) based on the curvature of the skull and teeth, and shape of the pubis, and this hypothesis should not be overlooked. Similarly, Britt et al. (2018) recovered the poorly described *'Dimorphodon' weintraubi* as the sister taxon to the anurognathids and this clade was recovered sister to Breviquartossa within Novialoidea, placing *'D.'*

weintraubi+Anurognathidae in the ‘middle’ topology of Pterosauria.

An alternative relationship was recovered by Unwin (2003a) with the anurognathids retaining an early-diverging position in the tree, but as the sister taxon to the Pterodactyloidea. To recover this relationship required only limited modification of the analysis (though few nodes are well supported in most pterosaur phylogenies). The observation is interesting and important given the previous occasional association of anurognathids with Pterodactyloidea and the uncertainty of several cranial characters in that clade. The analyses of Andres et al. (2010, 2014) recovered the anurognathids as the sister taxon to the pterodactyloids as the most parsimonious result. However, in this analysis the Anurognathidae had several heterodox scorings of character states that differed markedly from previous interpretations of their anatomy. Most notably, Andres et al. (2010) considered anurognathids to have a confluent nasoantorbital fenestra – a feature typical of the Monofenestrata. Although anurognathids do share some features with pterodactyloids (e.g. reduced cervical ribs and a relatively short tail), and have a long ghost lineage, other characters do link them to a more basal position with respect to Pterodactyloidea. More recently the appearance of *Darwinopterus* and kin provides a strong anatomical link between some derived non-ptoerdactyloids like rhamphorhynchines and early-diverging pterodactyloids, which will likely be at the expense of anurognathids. However, this does require significant modification to the current consensus of pterosaur characteristics and this is perhaps a greater reflection of the low numbers of characters available to pterosaurian systematicists than an actual likely relationship between anurognathids and pterodactyloids. Given the long ghost lineage of anurognathids and the low numbers of characters used in pterosaur phylogenetics, this is perhaps more likely to be a case of long branch attraction between anurognathids and pterodactyloids rather than a case of genuine relationships.

1.2 Institutional abbreviations

BMNHC, Beijing Museum of Natural History, Beijing, China

BSPG, Bavarian State Collection for Palaeontology, Munich, Germany

CAGS, Chinese Academy of Geological Sciences, Beijing, China

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

JZMP, Jinzhou Paleontological Museum, Jinzhou, China.

NJU, Nanjing University, Nanjing, China

PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia

SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany

2 The Anurognathidae

2.1 Definition and content

The Anurognathidae is here defined as all taxa more closely related to *Anurognathus* than *Dimorphodon*, *Pterodactylus* or *Scaphognathus*. This contains the taxa *Anurognathus*, *Batrachognathus*, *Dendrorhynchoides*, *Jeholopterus, Luopterus* (gen. nov.), and *Vesperopterylus*. Each exhibits a wide suite of characteristics that are diagnostic for the clade. This clade has been confirmed as monophyletic in numerous cladistic analyses (e.g. Kellner, 2003; Unwin, 2003b; Lü and Ji, 2006; Andres et al., 2010, Lü et al., 2018; Vidovic and Martill, 2018).

2.2 Diagnosis

Skull anteroposteriorly short and broad – the two dimensions being approximately equal or the skull even being broader than long (Kellner, 2003; Unwin, 2003a).

Anterior face of the premaxilla and mandible rounded (Bennett, 2007a).

T-shaped premaxilla (Unwin et al., 2000; Bennett, 2007a).

Narrow process separating the nares (Kellner, 2003).

Palatal bones reduced to thin splints (Bakhurina and Unwin, 1995; Kellner, 2003; Unwin, 2003 a,b; Bennett, 2007a). Cannot be observed in *Jeholopterus*.

Narrow naris and antorbital fenestra (Bennett, 2007a).

Minimal pre-narial rostrum (Bennett, 2007a).

Proximal end of the humeral head in dorsal view nearly symmetrical i.e. the deltopectoral crest and medial crest are similar in size (Unwin et al., 2000).

Pteroid less than 1/5th of the length of the ulna.

Very short and robust wing metacarpal (Witton, 2013; Vidovic and Martill, 2018).

Dorsoventrally tall manual and pedal unguals. Proximal end of ungual is 2-2.5x the height of the distal end of the penultimate phalanx with which it articulates. Cannot be determined in *Dendrorhynchoides*.

Wing phalanx 2 subequal to, or longer than, the ulna (Unwin et al., 2000). Cannot be determined in *Batrachognathus*.

Flexed joints between wing finger phalanges (Bennett, 2007a). The joints between the phalanges of the wing finger were loose and permitted some motion, which post mortem preserves a curved wing outline. Cannot be determined in *Batrachognathus*.

Combined length of the dorsal and sacral vertebrae are subequal to the length of the ulna (Unwin et al., 2000).

2.3 Distribution

Middle Jurassic (?)Aalenian to Early Cretaceous (?) Aptian. This span is complicated by the uncertain ages of various specimens and the horizons from which they may originate. Notably, the holotype of *Dendrorhynchoides* is considered to be from the Yixian Formation and thus Early Cretaceous in age, but its precise stratigraphic horizon has been challenged by Lü and Hone (2012). However, the North Korean specimen was apparently found in beds also containing avialans (Gao et al. 2009), suggesting a true Cretaceous age. Gao et al. (2009) even suggested that the anurognathids might even extend into the Late Cretaceous based on this specimen. The recently described *Vesperopterylus* was recorded as coming from the Albian aged Jiufotang Formation and, if correct, would mark the most recent age of the anurognathids and place them firmly in the Cretaceous. If the putative anurognathid from Mongolia is not an anurognathid, then the earliest record would be from the Upper Jurassic Oxfordian (based on *Batrachognathus* from the Karatau) rather than Aalenian as given here. The long anurognathid ghost lineage (see Unwin, 2003a) suggests much older specimens might one day be recovered.

Anurognathids are currently known from Germany, Kazakhstan, China, North Korea and possibly Mongolia and thus are restricted to Eurasia. Bennett (2007a) suggested that a pterosaur sacrum from the Late Jurassic Morrison of the U.S.A. may belong to an anurognathid (though see below).

2.4 Description

Most anurognathid specimens represent juveniles (see below for details) and thus some of the following descriptions and diagnoses may not represent the condition in adults. All specimens, apart from the badly preserved *Anurognathus* holotype (Fig. 2a), are also preserved in dorsal or ventral view, limiting the available information on some aspects of the anatomy. Only the 'new specimen' of *Anurognathus* (Bennett, 2007a) is both well preserved and has been thoroughly described and illustrated, making comparisons to other taxa difficult.

2.4.1 Cranium

The skull is anteroposteriorly short and laterally broad (Fig. 1) with the two dimensions generally subequal. The anterior margin of the skull is gently rounded to give a semi-circular profile in dorsal view. Size varies widely with some having very large heads (e.g. *Anurognathus*) and others relatively small (e.g. *Jeholopterus*).

T-shaped premaxilla. Frontals subtriangular and tapering anteriorly. Parietals large and rectangular. Vertically positioned postorbital bar. Vertically positioned quadrate. Palatal bones exceptionally thin and splint-like leaving large fenestrae in the palate.

Naris is dorsoventrally tall though anteroposteriorly short and sits at the very anterior margin of the skull. Antorbital fenestra similar in appearance and separated from the naris anteriorly and the orbit posteriorly by only thin splints of bone. Orbit is extremely large and occupies approximately half of the lateral face of the skull. The sclerotic ring is large and fills the orbit. Upper and lower temporal fenestra are sub-rectangular in outline.

The mandible, as with the upper jaw, is broad and rounded, though dorsoventrally short. The jaw joint appears to be a relatively simple hinge and not helical.

2.4.2 Dentition

Teeth evenly and well spaced in both jaws and are present in the premaxilla, maxilla and dentary. There are approximately 36 teeth in total: two or three in each premaxilla and eight in each maxilla and each dentary. All teeth are of generally similar morphology and do not vary significantly in the upper or lower jaws (cf e.g. *Dimorphodon, Rhamphorhynchus*). Teeth are generally short, simple pin-like or peg-like spikes, with some curvature in *Dendrorhynchoides* and greater in *Batrachognathus*.

2.4.3 Axial skeleton

Vertebral count of approximately nine cervicals, eleven dorsals, an unknown number of sacrals (probably three or four) and from eight to ?20 caudals (Fig. 1). Due to poor preservation, counts are uncertain. Cervical vertebrae are large and square in dorsal view. Dorsal neural spines are low, and the transverse processes are short and directed slightly posteriorly. Variation in the lengths of the cervical and dorsal series and the animals may have proportionally long or short necks and long or short torsos. The tail is short (approximately the length of the sacrum) and tapers strongly. Caudal vertebrae are usually small, disc-like and subcircular and there are normally no chevrons (though see Jiang et al., 2015). Tail not fused into a pygostyle-like structure. Cervical ribs reduced or absent. Dorsal ribs long, tapering to a point, and straight or gently curved. Posterior dorsal ribs are slightly shorter than those of the anterior so the body has a somewhat ovate profile (unlike the triangular, posteriorly-tapering torso seen in other pterosaurs). At least eight pairs of long, thin gastralia fused in the midline to form very shallow V-s. Chevrons may be present on the tail, but if so, they are not elongated in the manner of e.g., rhamphorhynchines.

2.4.4 Pectoral and pelvic girdles

Scapula may be longer than coracoid, (*Jeholopterus*) or subequal (*Vesperopterylus*). Both bones long and rod-like. Coracoid is nearly circular in cross-section with expanded distal end contributing to a large glenoid fossa. Scapula and coracoid meet forming a 'V' shape at an angle of approximately 60°. Sternum approximately the length of four dorsal vertebrae, and approximately the same width as the dorsal vertebral column.

Ilium long with the anterior process extending past at least the second (and probably to the fourth) presacral vertebra, but the posterior process is substantially shorter. A prepubis is present, but details are not known (possibly L-shaped). Both pubes and ischia small and plate-like and fused into a strap-like ischiopubis that tapers distally.

2.4.5 Forelimbs

Distal end of humerus curves laterally. Short, simple deltopectoral crest (without a constricted neck as in many other pterosaurs). Large medial crest, close in size to that of the deltopectoral crest lies on opposite margin of the humerus. Large and shallow proximal articular surface. The humerus is highly variable in morphology between specimens and taxa but this does not appear to all be the result of taphonomic distortion or poor preservation given the quality of some specimens.

Ulna and radius both long and straight. Both bones are subequal in width and have only slightly enlarged proximal ends and expanded distal ends. Ulna slightly longer than radius. Two proximal carpals, two distal carpals (in adults, each pair fused into a syncarpal). Short metacarpals (less than 1/3rd humeral length) that are also robust. Wing metacarpal curves posteriorly at the distal end (except *Jeholopterus* where it is straight) and is broad.

Manual phalangeal formula of 2-3-4-4-X. Penultimate phalanges of digits I-III elongate, (more than twice the length of other, more proximal phalanges). Manual unguals long and recurved, and approximately as long as the penultimate phalanx on each respective digit measured along the dorsal edge of the ungual. Dorsoventral height of unguals more than twice that of the preceding phalanx.

Four wing phalanges (this probably includes *Anurognathus* – see below). Dramatic reduction in phalanges of wing-finger along the length, with each phalanx significantly shorter than the preceding one. Second wing phalanx longer than the ulna.

Total wing length approximately five times that of the dorsal vertebral series. Approximate proportions of wing bones as follows (scaled to the length of the humerus): radius / ulna 0.7, metacarpal 0.3, first phalanx 0.6, second phalanx 0.7, third phalanx 1.0, fourth phalanx 0.5.

2.4.6 Hindlimbs

Femur straight. Femoral head offset by approximately 45˚. Femoral length variable but around 70% of the length of the humerus (range 52–81%). Small lesser trochanter. Tibia has similar diameter to that of the femur. Fibula present and separate from the tibia, but slender and only half the length of the tibia. Astragalus and calcaneum present and possibly fused.

Metatarsals I-IV subequal in length and width, appressed together with cylindrical shafts. Metatarsal V more robust than I-IV in some taxa. Pedal phalangeal formula of 2-3-4-5-2. Elongate penultimate pedal phalanges. Pedal unguals large, dorsoventral height of unguals more than twice that of the preceding phalanx (reduced in *Batrachognathus*). Pedal digit five with a long first phalanx and a shorter, curved second phalanx.

3 Taxonomy

The definitions and diagnoses of the anurognathids remain highly problematic. A lack of detailed descriptions for most specimens, coupled with their incomplete and disarticulated remains makes them very difficult to compare with one another. This, coupled with the extreme overall similarities in form, makes it very hard to separate them from one another (see Table 1 for major proportions of the skeleton). For example, of the original diagnosis of *Dendrorhynchoides* by Ji and Ji (1998) only the recurved teeth are actually diagnostic and all other traits are universal for anurognathids (or were linked to the later added tail). Bennett's (2007a) thorough description of the well preserved juvenile *Anurognathus* provided a number of unique traits but several of these are also nondiagnostic in the light of more recent finds. It is currently hard to find more than two or three anatomical traits which might diagnose a single genus for the anurognathids which is a low value even for pterosaurs, and yet still results in some odd assignments. For example, the two specimens of *Jeholopterus* are nearly identical, but one has a skull that is considerably larger than that of the other. Thus, while the current taxonomy is retained here, one could make a credible case for either synonymising many of these putative genera and species, or if such limited traits are considered sufficient to diagnose taxa, elevating current species to genera and naming most of the unnamed specimens as new genera.

Table 1 Major proportions of the skeleton of the known anurognathid specimens as scaled to the lengths of the humerus. Not all values are recorded given the incompleteness of specimens and the difficulties of measuring parts such as the cranium when crushed

Genus	Specimen	Skull length	Cervical length	Dorsal and sacral length	Tail length	Scapula length	Ulna length	Wing MC length	1st wing phx length	2nd wing phx length	3rd wing phx length	4th wing phx	Femur length	Tibia length	Longest metatarsal length
Anurognathus	BSPG 1922.1.42						0.7	2.9	0.55				1.12	0.82	1.78
Anurognathus	New	0.95	0.96	0.5	2.47	1.32	0.7	3.7	0.64	0.78	1.46		1.28	0.92	2.08
Batrachognathus	PIN 52-2	0.92		1.03		1.43								1.1	
Batrachognathus	PIN 2585/4a	1.26													
Dendrorhynchoides	GMV2128					1.39	0.78	2.99	0.62	0.78	0.98			1.04	2.3
Luopterus	JZMP-07-04-3	1.69			1.5	1.59	0.64	2.45	0.54	0.66	1.08	5.4	1.29	1	2.25
Jeholopterus	IVPP V 12705	2.21	1.66	0.65		1.27	0.7	3.26	0.67	0.76	1.03	3.44	1.55	1.24	2.82
Jeholopterus	CAGS-IG-02-81						0.86	2.9	0.71	0.79				1.27	2.65
Vesperopterylus	BMNHC-PH-001311	2.21		1.75	2.3	1.85	0.74	2.75	0.59	0.74	1	4.97	1.26	0.99	2.01
Korean specimen	Unnumbered	1.37	2.29	0.61									1.39		
Long-tailed specimen	IVPP V 16728				0.96								1.43	0.92	2.33
Filament specimen	NJU 57003	1.37		0.65	0.71	1.29	0.59	2.93	0.57	0.65	1.37	5.85	1.24	0.88	2.07

3.1 *Anurognathus* Döderlein, 1923

3.1.1 Distribution and range

Known only from the Solnhofen Formation (Tithonian) of southern Germany.

3.1.2 Diagnosis

Three premaxillary and six maxillary teeth (Bennett, 2007a).

Small, rounded deltopectoral crest (Bennett, 2007a) (see Fig. 4).

Relatively short wing-phalanx 3 (70% of the length of the humerus, compared to over 100% in other anurognathids).

3.1.3 Taxonomy

Anurognathus was named by Döderlein (1923) and remains valid.

3.1.4 *Anurognathus ammoni* Döderlein, 1923

3.1.5 Holotype

BSPG 1922.1.42 a partial specimen that is partly articulated (Fig. 2).

3.1.6 Other material

'New specimen', consisting of a complete and articulated probable juvenile with soft tissues preserved (Bennett, 2007a). Both the plate and counterplate are in separate private collections (Bennett, 2007a), but casts are available in public collections such as SMNS 81928a and b.

3.1.7 Comments

A small anurognathid known from two specimens. Wingspan of approximately 50 cm (Wellnhofer, 1991, p.91) based on the holotype, though this may not be an adult specimen (see below). Despite the poor preservation of the holotype it is clearly anurognathid based on the shape of the skull, enlarged manual claws and the reduced tail. It can be identified by the semi-circular deltopectoral crest on the new specimen, though a more triangular one is visible on the holotype (although it is not especially clear). Bennett (2007a) described this as having a long dorsal series compared to other anurognathids, although it has the shortest proportional length of the combined dorsal and sacral vertebrae of the taxa examined here. He similarly described this as having uniquely straight ribs, but these are similar in form to those of *Dendrorhynchoides*, at least.

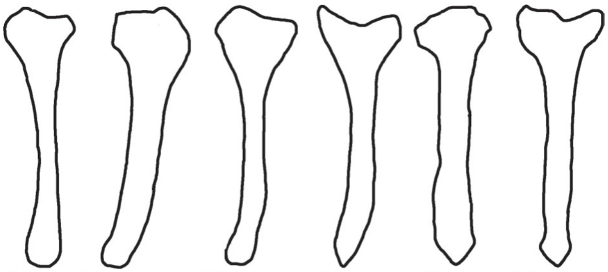

Fig. 4. The left humerus (posterior view) of the anurognathids showing the distinctive variation in deltopectoral crest shape.

(a) *Anurognathus* (b) *Batrachognathus* (d) *Dendrorhynchoides*, (j) *Jeholopterus* (l) *Luopterus* and (v) *Vesperopterylus* (l and v show a reflected right humerus). Drawings are scaled so each is the same size and are respectively traced from Bennett, 2007a; Ryabinin, 1948; Ji and Ji, 1998; Wang et al., 2002; Lü and Hone, 2012; Lü et al., 2018.

There is uncertainty over the number of phalanges in the wing-finger of *Anurognathus*. This cannot be determined in the holotype specimen, but the new specimen appears to have only three phalanges on each wing (Bennett, 2007a). However, on the right wing a 4th phalanx could be hidden behind the right tibia (see Fig. 2b). Based on the extreme reduction of the 4th phalanx in *Jeholopterus*, it is likely that the 4th phalanx was exceptionally small if present at all in *Anurognathus*. On the left wing of the new specimen the distal tip of the 3rd phalanx seems to end with a flattened articular surface (contra Bennett, 2007a) and not a tapered point as might be expected with a distal phalanx, and as found in all other pterosaurs (including *Nyctosaurus* a pterodactyloid with only three wing phalanges – Bennett, 2003). Finally, the third wing-finger phalanx of *Anurognathus* is comparatively short for an anurognathid (70% of the length of the humerus, as opposed to close to 100% in *Jeholopterus*, *Dendrorhynchoides* and *Vesperopterylus*) with the others being of comparable lengths, whereas one might expect the other phalanges to elongate to account for the reduced number as in *Nyctosaurus* (although this is a very distant relative with a very different ecology – Witton, 2013). Given the conservatism of anurognathid anatomy in general, it is therefore considered likely that *Anurognathus* did indeed have four wing-phalanges and that one is hidden and the other either lost, or more likely (given the quality of the preservation and lack of disarticulation on the specimen) concealed within the matrix. An attempt to test this hypothesis is being undertaken with additional preparation work on the new specimen (H. Tischlinger, pers. comm.). A further possibility is that the 4th phalanx was present, but being so small and the specimen representing a young juvenile it was unossified and thus not preserved. This is considered unlikely given the overall ossification of the rest of the skeleton, though distal wing phalanges may be less well ossified than the rest of the wing (Hone et al., 2015). Based on these possibilities, and the conservative nature of anurognathids as a whole, *Anurognathus* is here considered to have had four wing-phalanges, though this must remain uncertain.

The number of phalanges on the 5th toe has also been a source of contention in *Anurognathus*, though this revolved around the holotype and was a result of its poor preservation. Döderlein (1923) considered there to be four phalanges whereas Wiman (1928) counted only two. Wellnhofer (1975) counted four, but this interpretation was questioned, by Padian (1980 p. 87) who also considered there to be only two. The new specimen and the condition seen in other anurognathids confirms that only two phalanges are present on the fifth toe.

Anurognathus is the only anurognathid for which a lateral view of the skull is available (and some other bones are preserved in different orientations to that of other anurognathid specimens) contrasting with the dorsal view available for other fossils and thus provides much important information, despite the relatively poor condition of the material. This shows the shape and extent of the various fenestrae in the skull, most importantly the large orbit and narrow naris (see Fig. 1).

3.2 *Batrachognathus* Ryabinin, 1948

3.2.1 Distribution and range

The Karabastau Formation, Upper Jurassic Oxfordian-Kimmeridgian of Kazakhstan.

3.2.2 Diagnosis

At least 11 teeth in the upper jaw (Unwin and Bakhurina, 2000).

Parallelogram shaped deltopectoral crest (see Fig. 4).

Robust and curved humerus.

3.2.3 Taxonomy

Batrachognathus was named by Ryabinin (1948) and remains valid.

3.2.4 *Batrachognathus volans* Ryabinin, 1948

3.2.5 Holotype

PIN 52-2, a partial specimen of a skull and various postcranial bones (Fig. 5).

3.2.6 Other material

PIN 2585/4a is a crushed and partial specimen including a skull. It lies in association with the holotype of *Sordes pilosus* (Unwin and Bakhurina, 2000) the only known association of two different pterosaur species.

3.2.7 Comments

Typical anurognathid known from two partial specimens. Wingspan of approximately 75 cm (Bakhurina and Unwin, 1995). Based on the disarticulation of both specimens, especially the skull, these may not be adult animals. The holotype preserves a partial skull, partial dorsal vertebral column and one partial forelimb and one partial hindlimb. The second specimen includes preserved integumentary soft tissues.

Fig. 5. The incomplete but well preserved holotype of *Batrachognathus* (PIN 52-2). Scale bar 20 mm.

3.3 *Dendrorhynchoides* Ji and Ji, 1998

3.3.1 Distribution

The holotype is from the Yixian Formation (Lower Cretaceous) of eastern China according to Ji and Ji (1998) but it has been suggested that it may instead herald from the Daohugou beds of the Middle Jurassic (Lü and Hone, 2012) from which many early finds were mistakenly attributed to the Jehol biota that includes the Yixian Formation (Sullivan et al., 2014).

3.3.2 Diagnosis

Teeth relatively long and curved distally.

Subtriangular deltopectoral crest and pointed medial humeral crest (see Fig. 4).

Wing metacarpal 30% of the length of the humerus

3.3.3 Taxonomy

This was originally named as *Dendrorhynchus* (Ji and Ji, 1998) but changed to *Dendrorhynchoides* due to preoccupation (Ji et al., 1999).

3.3.4 *Dendrorhynchoides curvidentatus* (Ji and Ji, 1998)

3.3.5 Holotype

#GMV2128, a near complete specimen with only parts of the feet missing. A tail has been added, probably dromaeosaur in origin (Unwin et al., 2000). Evidence of extensive soft tissue of the wing membranes is preserved.

3.3.6 Comments

The holotype has a wingspan of 48 cm, (measured from Unwin et al., 2000) though this animal may not be an adult based on the unfused scapula and coracoid. The skull may be especially broad but is disarticulated and difficult to measure.

The tail of *Dendrorhynchoides* is controversial. Originally described by Ji and Ji (1998) as being very long and typical of rhamphorhynchines, it was for this reason assigned to this clade. Unwin et al. (2000) suggested that the distal part of the tail did not belong to the fossil and in fact had been inserted from another specimen (probably a dromaeosaurid dinosaur from one of the Liaoning fossil beds) with only the proximal part of the tail being genuine. The proximal caudals of *Dendrorhynchoides* are similar in appearance to those of other anurognathids (Unwin et al., 2000) and thus it was a reasonable conclusion that *Dendrorhynchoides* had a typically short anurognathid tail. However, further examination of the material suggests that while there certainly is a piece of material added to the slab, there are structures distal to this false piece that include genuine bone. Unwin et al. (2000) originally included these in their description as part of the faked section (their fig. 2) but is clearly different and separate from the fabricated piece.

The observed structures consist of a series of irregularities in the matrix and two small pieces of bone. The bones are small and elongate and appear to have suffered some damage. Examination suggests that these are in fact from the otherwise missing right pes of the animal, and indeed their position matches a point where disarticulated bones from that foot might have easily come to rest. The tail therefore is short and more typical of other anurognathids, this is followed by the added part, and then elements of the pes.

As in the new *Anurognathus* specimen (see above) *Dendrorhynchoides* has only three wing phalanges preserved, although four were probably present (Ji and Ji, 1998). However, the distal elements of the forelimb in *Dendrorhynchoides* are somewhat disarticulated and parts of the lower half of the specimen are missing. It is therefore likely that four phalanges were present, but have not been preserved. This is reinforced by the presence of a clear articular surface on the distal end of the right (unbroken) phalanx 3, which suggests that phalanx 4 was present in life.

The exact age of *D. curvidentatus* is uncertain and this species was recovered at a time before it was realised that the 'Jehol Biota' included multiple faunas including those well separated and including the Middle Jurassic and Early Cretaceous (Sullivan et al., 2014). Given that this specimen was also reworked with the addition of the tail, its exact origins are clearly uncertain and it may in fact come from another site.

3.4 *Jeholopterus* Wang et al., 2002

3.4.1 Distribution and range

The Daohugou Formation, Middle Jurassic of northeastern China.

3.4.2 Diagnosis

Small skull (approximately half the length of the cervical series, compared to subequal skull and cervical length in other anurognathids).

Narrow and alate (recurved, triangular) deltopectoral crest that significantly exceeds the height of the proximal articular surface of the humerus (see Fig. 4).

Each manual ungual much longer than preceding phalanx.

Short tibia (80% of the length of the humerus, compared to around 100% in other anurognathids).

3.4.3 Taxonomy

Jeholopterus was named by Wang et al., (2002) and remains valid.

3.4.4 *Jeholopterus ningchengensis* Wang et al., 2002

3.4.5 Holotype

IVPP V 12705, a complete and articulated specimen preserved on a plate and counterplate. Extensive soft tissue is preserved including integument and the wing membranes.

3.4.6 Other material

CAGS-IG-02-81, a near complete and articulated specimen of a juvenile animal with much soft tissue preserved (Ji and Yuan, 2002).

3.4.7 Comments

An anurognathid known from two specimens (one adult – fused scapulocoracoid, pelvis and skull, and one juvenile – various unfused bones). Wingspan at adult of 90 cm (Wang et al., 2002). The neck may be long and the hindlimbs robust, but more complete specimens are required to confirm this. It shares a robust 5th pedal digit with *Vesperopterylus*.

The two specimens of *Jeholopterus* are significantly different in size, with the second specimen having a wingspan less than half that of the holotype. Given that the holotype clearly represents an adult (large size, fused scapulocoracoids, apparently some fused cranial elements, fused extensor tendon process), the obvious conclusion is that the second specimen represents a juvenile individual and the disarticulated and unfused nature of the skull and other bones of the second specimen tends to confirm this. Although incomplete and difficult to measure the skull of the second specimen is clearly proportionally much larger than that of the holotype suggesting either considerable variation in this trait or that this is a distinct, if closely related, taxon. Otherwise they are similar though the holotype does also have a slightly longer ulna and shorter wing metacarpal than the small specimen.

The tail of *Jeholopterus* may be longer than that of *Batrachognathus* or *Anurognathus* based on slight impressions visible on the holotype specimen and the apparent surrounding pycnofibers (Lü and Hone, 2012) to a length approximately the same as the femur.

3.5 *Luopterus* gen nov.

3.5.1 Etymology

'Lu' in honour of the memory of Professor Lü Junchang, pterosaur researcher who contributed a huge amount of work on Chinese pterosaurs and other fossil reptiles, and 'pterus' from the Ancient Greek for 'wing'. Thus it is 'Lü's wing'.

3.5.2 Distribution

The Daohugou beds of the Middle Jurassic (Lü and Hone, 2012).

3.5.3 Diagnosis

Proportionally long tail of simple vertebrae.

Straight, broad-shafted humerus.

Humerus with reduced deltopectoral and medial crests (see Fig. 4).

Very short wing metacarpal, 40% of the length of the humerus.

Long ulna, 155% of the length of the humerus.

3.5.4 Taxonomy

A new genus. Was originally named as a second species of *Dendrorhynchoides* but shows several different features not seen in the holotype or other anurognathids, and so is here separated into its own genus.

3.5.5 *Luopterus mutoutdengensis* (Lü and Hone, 2012) comb. nov.

The holotype is JZMP-07-04-3 (formerly GLGMV 0002), a largely complete and severely crushed juvenile individual (Lü and Hone, 2012). Some parts are present as impression in the matrix or have separated as small counterplates. Extensive patches of soft tissue of the wing membranes are preserved. Diagnosis and distribution as for the genus.

3.5.6 Comments

The specimen is of a small individual (about 40 cm in wingspan) and is poorly preserved, though nearly complete. Providing an interesting counterpoint to the fake long tail on the holotype of *D. curvidentatus*, the holotpye of *L. mutoutdengensis* has an incomplete, but rather long tail for an anurognathid (Hone and Lü, 2010).

This taxon was partially diagnosed by the presence of heterodont teeth with some being large and robust (Lü and Hone 2012) but the nature of the broken skull makes it very hard to differentiate between teeth and skull fragments and it is probable that the larger teeth are shards of bone.

Despite the crushed nature of the specimen, the outline of the humerus is relatively well preserved and does not appear to be distorted (as with other major long bones), and features like the straight shaft and the pointed distal end also appear in other, better preserved, specimens such as *Vespterpterylus*. As such, the morphology is considered to be reflective of the *in vivo* condition.

Note that the current given specimen number for this (JZMP-07-04-3) is the same as that of the holotype of *Boreopterus* (Lü and Ji, 2005). This is clearly an error and needs correcting, and since the anurognathid was given the number second, the ID is presumably correct for the other pterosaur.

3.6 *Vesperopterylus* Lü et al., 2018

3.6.1 Distribution and range

The Jiufotang Formation, Early Cretaceous Aptian of China.

3.6.2 Diagnosis

Scapula and coracoid subequal in length.

Humerus that tapers along the length of the shaft.

Reversed first toes.

3.6.3 Taxonomy

Vesperopterylus was named by Lü et al. (2018) and remains valid. In a preprint version of the paper the name was incorrectly spelled as '*Versperopterylus*' but this was corrected in the published version as this was not the intention of the authors and was changed under section 32.5 of the ICZN.

3.6.4 *Vesperopterylus lamadongensis* Lü et al., 2018

The holotype is BMNHC-PH-001311 (see Fig. 6) a near complete skeleton that is partially disarticulated and lacks several cervical vertebrae and dorsal ribs and the right scapulocoracoid.

3.6.5 Comments

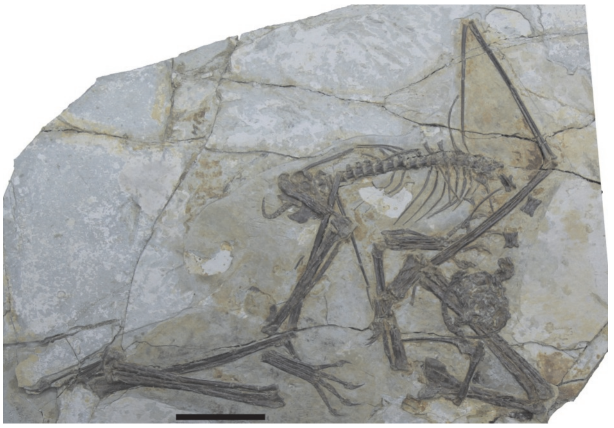

Fig. 6. The near complete and large holotype of *Vesperopterylus (*BMNHC-PH-001311). Scale bar is 50 mm.

Typical anurognathid know from a single, near complete specimen. Wingspan of approximately 1 m (Lü et al., 2018). Based on the fusion of various elements including the scapula and coracoid and the various elements of the pelvis, this is likely an adult or near-adult animal. The holotype preserves a nearly complete and partially articulated skeleton, thought with no apparent soft tissue preservation. It has a robust 5th toe which was previously considered an autapomorphy of *Jeholopterus,* and its head is of intermediate size between the small-headed *Jeholopterus* and the large headed *Anurognathus*. The apparently reversed first toe could be a result of the way the specimen is preserved, but is present on both feet and despite other anurognathids being similarly preserved this is not seen in other specimens.

3.7 Unnamed anurognathid (Bakhurina and Unwin, 1995)

3.7.1 Distribution and range

Known from the Aalenian/Bajocian Bakhar Svita beds of Mongolia (Unwin and Bakhurian, 2000).

3.7.2 Comments

Only a single, partial, undescribed wing of a probable juvenile is known, an unnumbered specimen now with the PIN. This was assigned to the anurognathids based on the morphology of the humerus (Unwin and Bakhurina, 2000) but this has yet to be confirmed.

3.8 Unnamed anurognathid (Gao et al, 2009)

3.8.1 Distribution and range

Known from the Early Cretaceous Sinuiju beds of north western North Korea (Gao et al., 2009). These deposits yield fossils similar to those of the Jehol Biota (Gao et al., 2009).

3.8.2 Comments

A single incomplete specimen was described by Gao et al. (2009) though the paper implies that other specimens might have been recovered. The specimen is poorly preserved and crushed, and with both feet, and parts of the wings, torso and skull missing. The specimen is preserved as a part and counterpart and appears to be an adult based on the fusion of various elements and the relatively large size of the individual (estimated at around 80 cm wingspan by Gao et al., 2009). Gao et al. (2009) suggested a number of features that marked out this specimen from *Jeholopterus*, but these cannot be easily seen or accurately determined given the state of the material and it is possible that this material could be referred to any of the Chinese anurognathid genera with close examination and comparisons. It does have a similarly long torso to *Jeholopterus* but does have a much larger head and shorter neck compared to this and the other east Asian anurognathids, suggesting it is a distinct taxon.

3.9 Unnamed anurognathid (Jiang et al., 2015)

3.9.1 Distribution and range

Recovered from the Middle Jurassic Jiufotang Formation of China (Jiang et al., 2015).

3.9.2 Comments

A single incomplete specimen was described by Jiang et al. (2015). The specimen is not very well preserved and is rather incomplete but had a partial skull, some parts of the wings and a nearly complete set of hindlimbs and, for anurognathids, a relatively long tail with elongate chevrons. The latter trait is not seen in any other anurognathid, including the specimen described below.

3.10 Unnamed anurognathid (Yang et al., 2019).

3.10.1 Distribution and range

Recovered from the Middle to Late Jurassic Yanliao Biota of China (Yang et al., 2019).

3.10.2 Comments

This specimen was illustrated only with an image taken under laser-stimulated fluoresnce and so details are limited. However, it is clearly a small and nearly complete specimen that shows a remarkably long ulna and tail that appears to be longer than even that of the 'long-tailed' specimen described above. Both the tibia and the 3rd wing phalanx are unusual for anurognathids. It preserves extensive soft tissues including numerous pycnofibers.

4 Relationships

Initially the intra-relationships of the anurognathids were not studied by palaeontologists. With a limited number of fossils and, until the description of the new *Anurognathus* specimen (Bennett, 2007a), limited information available for both *Anurognathus* and *Batrachognathus*, little value would be gained from the exercise (and until the discovery of *Dendrorhynchoides*, quite pointless with only two taxa). Numerous more recent analyses have included multiple anurognathid taxa with conflicting results. An unresolved polytomy of all included taxa has been recovered (e.g. Unwin, 2003b), or a near unresolved polytomy such as that of Lü et al. (2018) which found *Vesperopterylus to be the first branching genus with all others in a polytomy. Anurognathus* has often been recovered as the first branching (Kellner, 2003; Lü and Ji, 2006) with the other taxa forming a clade, which Kellner (2003) termed the Asiaticognathidae. Other relationships have also been recovered, however. Andres et al., (2014) recovered *Dendrorhycnhoides* as the first branching genus, followed by *Jeholopterus* and then a sister taxon pairing of *Batrachognathus* and *Anurognathus*. In contrast, Vidovic and Martill (2018) recovered *Anurognathus* as the first branching taxon in the clade followed by *Dendrorhynchoides* and then with *Batrachognathus* as being closest to *Jeholopterus* and Wang et al. (2002) suggested that *Dendrorhyncoides* and *Jeholopterus* were most similar to each other, based on the shape of their skulls.

In short, almost any combination of relationships between these four genera have been recovered in various analyses and even the more recent and comprehensive ones have different greatly in their results. The position of *Anurognathus* as the earliest-diverging member of the clade is typically supported by a single character – the proportional size of the humerus compared to the femur (Kellner, 2003) and thus may yet be reversed or at least countered by any single change elsewhere or addition of additional characters. Bennett (2007a) has noted that the name Asiaticognathidae should be replaced on the grounds that such family level designations should be based on taxon names within that family, but given these uncertainties over relationships it may well not be a valid group in any case. Additional observations here mean that a specimen-level approach in future should be taken. Variations in the apparent shape of the deltopectoral crest and head size and shape within species are not being recorded, and features previously considered unique to some species (e.g. the long tail in *Luopterus*, the robust 5th toe of *Jeholopterus*) are more widely dispersed. This means that a more thorough analysis of the relationships of this group is necessary to understand the distribution of traits and their changes over time, though the varying preservation and ontogenetic status of the various specimens will remain a major issue.

5 Palaeobiology

Among the earliest references to anurognathids is the suggestion that their lifestyle was one of aerial insectivory (including Döderlein, 1923; Böker, 1924), catching flying insects on the wing. Ryabinin (1948) suggested a combination of insects and small fish, but this concept has had little traction in the literature (Wellnhofer, 1991; Unwin, 2006; Bennett, 2007a; Bestwick et al., 2018). Flying insects were both common and diverse throughout the Mesozoic and would have provided a rich source of protein to an animal engaged in a high metabolic activity (powered flight) and with perhaps few competitors (Unwin, 2003), and insectivory is generally well supported and accepted as the primary diet of these animals (Bestwick et al., 2018) (Fig. 7).

The teeth and jaws of anurognathids are well suited to insectivory (Ösi, 2010). The skull is exceptionally broad and the jaws can be opened to produce a very wide gape (Bennett, 2007a; Ösi, 2010) which is analogous to a number of birds that also feed by catching flying insects in the air (e.g. Caprimulgiformes – nightjars and whippoorwhills; see also Bakhurina and Unwin, 1995). Notably, the head varies in size considerably between taxa and this may relate to the diets of different species. In the case of *Jeholopterus*, the juvenile specimen has a much

Fig. 7. Life reconstruction of the anurognathid pterosaur *Jeholopterus*. Image by Mark Witton used with permission, he retains the copyright on this image.

larger head proportionally than the adult one. This may represent unusual intraspecific variation, an unrecognised taxonomic difference with there being two species present here, or even an ontogenetic shift with a large head in the juveniles to capture a specific size of prey which then does not grow as the animal increases in size to maintain a specialisation of prey at this size.

The teeth are typically small, peg-like and well spaced in the jaw and again appear well suited to insectivory being similar to the anterior teeth of at least some insectivorous bats (e.g. *Craseonycteris* – Hill and Smith, 1981) and provide a combination of piercing and holding. It is notable that the teeth of *Dendrorhynchoides* are considerably longer than those of other anurognathids and may represent a primitive condition. However, the damage to the skull of both specimens on this genus means that the orientation of these teeth in the jaws is unknown and the teeth could potentially have been positioned so that they spread out from the jaws to form a prey catching basket in the manner of *Angustinaripterus*.

It has been proposed by Bennett (2007a) that the series of exceptionally small pits seen around the premaxilla of *Anurognathus* may have housed long filaments in the manner of the rictal bristles of whippoorwhills and some other insectivorous avians, and performed an analogous function of increasing the effective gape of the jaws in the manner hypothesized here for *Dendrorhynchoides*. Aside from the clearly visible pits on the premaxilla there is no evidence for the presence of such filaments in the new specimen of *Anurognathus* despite extensive soft tissue preservation. In both specimens of *Jeholopterus* there is excellent soft tissue preservation for the whole body but no evidence for such extended bristles. While there is a clear fringe of hair around the skull of *Jeholopterus* (see Fig. 3) there is no evidence of them being arranged in a specific manner or being stiffened to project from the jaws. *Batrachognathus,* like *Jeholopterus,* has a fringe of fibers around the skull but although previously described as ‘bristles’ (see Unwin, 2005 p 93) these do not have the length or stiffness (they are sinusoidal, and not straight) to act in the manner hypothesized by Bennett. Nor do these filaments match those seen in extant birds, and instead are the same as those seen elsewhere on the body covering of anurognathids and other pterosaurs. Yang et al., (2019) similarly commented that their type III fibers on the face of anurognathids could have had a tactile function, but these are curved and taper and even show branching and thus are unlike the bristles hypothesized for anurognathids or found in extant birds. The hypothesis of rictal bristles therefore lacks support. The bristles in birds are modified contour feathers but lack osteological correlates. Indeed, they are not restricted to insectivorous birds and may have an alternate function of providing sensory data as opposed to prey capture (Lederer, 1972).

Despite examples of exceptional preservation, no stomach contents are known for anurognathids, which perhaps might be expected if their primary diet was insects or other invertebrates. However, in the new *Anurognathus* specimen Bennett (2007a) observed a collection of small “problematic spherical objects” apparently preserved at least partly inside the ribcage of the animal. It was not possible to determine the nature of these spheres or determine if they were truly associated with the skeleton at all (Bennett, 2007a).

Anurognathids are known from terrestrially-based, non-marine deposits (the Yixian and Daohugou, Karatau, Bakhar Formations) and in the case of the Solnhofen Formation lagoons, a locality closely linked to a terrestrial environment (Barthel et al., 1990). This argues against any obvious habitually marine or coastal habitat (and against the occasional hypothesis that they may have taken fish as part of their diet), and their rarity suggest they only infrequently came into contact with water, though they could simply have been rare. Furthermore, the localities from which anurognathids are known also has an extensive and diverse insect fauna preserved (Barthel et al., 1990 [Solnhofen], Zhang and Zhang, 2003 [Yixian], Bakhurina and Unwin, 1995 [Karatau], Rasnitsyn and Quicke, 2002 [Bakhar]). While insects are typically rarely recorded from fossil excavations and this could again simply be because anurognathids are also found in sites of exceptional terrestrial preservation, it does add weight to the argument that they are terrestrially based insectivores.

The orbits and large sclerotic ring of anurognathids are large, even by pterosaurian standards, implying large eyeballs (Bennett, 2007a) and this has been interpreted as evidence for a crepuscular (Bennett, 2007a) lifestyle, though it could also imply a nocturnal habit (Bakhurina, 1988). However, their inferred primary habitat of a terrestrial and forested environment means that even operating during the day, they may have experienced relatively low light conditions and thus it is hard to provide an absolute statement of their likely circadian cycle. In any case, the large anteriorly directed orbits (Bennett, 2007a) are typical of actively predatory animals, and a large eye would also assist in identifying small flying prey (Bennett, 2007a).

Several specimens provide evidence for the wingshape of anurognathids, especially the two specimens of *Jeholopterus*. For their body size, anurognathids had a relatively short wingspan (Bennett, 2007a; contra Wellnhofer, 1991 p.93 who stated that they had 'extremely long wings'), and the chord of the wing was broad (Wang et al., 2002; Bennett, 2007a), terminating at the ankle (Bennett, 2007a) as seen in other pterosaurs (Elgin et al., 2011) resulting in wing planforms with both a low aspect ratio and low wing loading. Such wings are suited to low speed turns and for increased maneuverability and is consistent with the hypothesis of active predation on flying insects as this is similar to the wing planform of insectivorous bats (Bennett, 2007a). Witton (2008) suggested that their wing profiles would have placed them in a similar flight capability to extant flacons and swifts which matches this hypothesis.

Habib (2011) noted that anurognathids had powerfully built wing elements with high loading potential, implying they were powerful fliers and in particular were good at launching, and Yang et al., (2019) suggested that the body covering of anurognathids likely had a thermoregulatory function that might be important for flying animals. The variation seen in the deltopectoral crest both between and even within species may be partially a result of taphonomic distortion and poor preservation, but at least some are well preserved and are much more variable in form than within other pterosaur clades suggesting a variation in musculature and by extensions flight style not seen in other pterosaurs though this yet to be investigated. *Jeholopterus* has some unusual tufts of pycnofibers at the tips of the wings giving it a brush-like effect (Kellner et al., 2009) which could have improved streamlining or been an adaptation similar to that of owls to reduce noise generated by the wings in flight (Witton, 2013).

The varying proportions of the anurognathids must also have had some influence on their flight. Although lightly constructed, the very large heads of some would presumably have shifted the centre of mass forwards on these species. The new specimen of *Anurognathus* has a head around 80% of the length of the humerus and also a relatively long cervical series is slightly longer than the humerus, whereas in contrast the holotype of *Jeholopterus* has a head less than half the length of the humerus and also a relatively short neck of around 60% of the humeral length. In addition, *Jeholopterus* has a relatively long torso and so must have had a centre of mass shifted well to the rear compared to *Anurognathus* resulting in a more swept-back wing position to maintain a more posteriorly positioned centre of lift. Other anurognathids lie between these extremes, but there must have been some variation in the flight profiles of the various species as a result of these differences.

The propatagium of anurognathids appears to be relatively large based on its preservation in the second *Jeholopterus* specimen (Unwin, 2006: see fig. 3) despite the small size of the pteroid in this clade. However, the pteroid is clearly in an unusual position here and appears to have become dislodged - its position is not shared in other anurognathid specimens, nor does the pteroid contact the leading edge of the propatagium as would seem essential for its function (Bennett, 2007b). The propatagium is also very rarely preserved in pterosaurs, even for those which do preserve a brachiopatagium. Furthermore, the tissue also shows evidence of structural fibres that are not known in the propatagium of other pterosaurs which also supports the idea that this is in fact part of the main wing. However, it is also possible that these structures may be part of the integumentary covering of the body that have moved (e.g. as with *Sordes*). Thus, it is here considered more likely that this structure in fact represents a shrunken and disassociated brachiopatagium rather than the propatagium (see also Elgin et al., 2011).

The uropatagium (or cruropatagium) is partially preserved in both the holotype of *Jeholopterus* (Wang et al., 2002 - though this is hard to distinguish from other soft-tissues and is partly missing) and in the second specimen (Ji and Yuan, 2002). This is understandable as despite the often high quality of preserved specimens of anuroganthids, the uropatagium is only very rarely preserved in pterosaurs. The uropatagium in the holotype is attached to the fifth toe of each foot and is an expansive sheet of tissue that largely 'fills' the space between the hindlimbs and is a typical of the non-pterodactyloid configuration (Unwin and Bakhurina, 1994 - although Bennett, 2007a argues for a unique pterodactyloid-style reduced uropatagium). Anurognathids, unlike other non-pterodactyloids, did not possess a tail vane, as none are preserved and these robust structures often survive when other soft tissues do not, and would be of little effect with such a short lever arm on a short tail. Note that even the longer-tailed anurognathid specimens (Lü and Hone, 2012; Jiang et al., 2015) still have tails that are short overall. Bennett (2007a) noted that the reduced tail of anurognathids, compared to other non-pterodactyloids, would reduce stability and, by inference, increase maneuverability. If the tail is integrated into the uropatagium then the variation in tail lengths could have a major effect on the size of the uropatagium and its function in flight. On the other hand, if it is entirely separate then it may have had very little function. The differences in the form of the tail (notably the chevrons seen in the Jiang et al., 2015 specimen) do generally point to this being functionally important. Webbing between the toes is also known in anurognathids, being present on the *Jeholopterus* holotype.

The unusual structure of the anurognathid wing finger has some interesting implications for both flight and on the ground. In those pterosaurs where it can be determined, the normal condition is for the four wing phalanges to be articulated and held in a nearly straight line. In anurognathids however, the finger is always preserved with flexion at the joints between the phalanges. Bennett (2007a) suggested that it may have been possible for the finger to be actively flexed during flight to modify the shape of the wing and thus provide a measure of increased flight control. This is plausible as simple contraction of the muscle layer in the brachiopatagium could contribute to this flexion and certainly the ability to actively change the shape and profile of the wing could indeed greatly benefit the animal in making tight turns while hunting, though at the expense of increased structure stresses in the joints during flight. This idea should be explored further.

The apparent flexibility of joints in the anurognathid wing finger may be primitive for pterosaurs, since clearly all other archosaurs can flex their fourth fingers freely and this would certainly be the condition for pterosaurian ancestors. This supports the idea that anurognathids are an early branching lineage of pterosaurs since all others lack this flexibility in the wing phalanx joints. This flexion may also potentially represent the retention of a paedomorphic condition in anurognathids since of the three pterosaurian embryos known, each has the wing-finger flexed at the joints allowing them to fit into the egg (e.g. see Unwin and Deeming, 2008). However, putative hatchling pterosaurs have extended and straight fingers, suggesting this happened shortly after hatching, possibly as a necessary precursor to flight in other clades that was never established in anurognathids, or was reverted to the paedomorphic condition. Andres et al. (2010) considered this flexion to be a result of disarticulation in anurognathid specimens, but this is not supported given the fact that it occurs in all specimens, even when the rest of the material is well articulated, and disarticulation of the wing phalanges is rare in all other pterosaurs.

The terrestrial ability of anurognathids has had little attention in the literature as this has primarily revolved around the bipedal / quadrupedal debate and issues of arboreality in pterosaurs (e.g. see Unwin, 1996; Witton, 2015). However, the unusual wings and claws of anurognathids, as well as their inferred habitat, is worthy of comment. The compact resting posture noted by Bennett (2007a) would allow anurognathids to conceal themselves in small spaces secure from predation, and this is further increased compared to other pterosaurs by the apparent flexibility of the wing finger. Bennett (2007a) also suggested that anurognathids might have been scansorial or occasionally caught prey on the ground. Certainly the large robust unguals (on both mani and pedes) with enlarged flexor tubercles would have given anurognathids a strong grip and allowed them to grip awkward surfaces, and the elongate penultimate phalanges imply grasping and climbing capabilities (Unwin, 2005 p.294). Combined with their overall small size and light-weight, they would have perhaps been able to climb well on vertical surfaces and to access places that even other pterosaurs could not.

It is also worth adding that even animals with no apparent specialisation towards terrestriality or cursoriality are nonetheless capable of active predation on the ground. The microchiropteran *Mystacina tuberculata* is a good example which hunts extensively on the forest floor for insect prey in addition to hunting on the wing (Jones et al., 2003), and it is possible that anurognathids did not just take prey from the ground, but actively sought it out on foot. It is currently not known if this is even possible and indeed non-pterodactyloids have been considered poor locomotors on the ground since the hindlimbs were intrinsically linked with the uropatagium (Unwin, 2006, though see Witton, 2015), something that may not have affected anurognathids if they had a reduced uropatagium (a suggested by Bennett, 2007a). The manual and pedal unguals of *Batrachognathus* are rather reduced compared to other anurognathids which implies less arboreality in this taxon. By contrast the unguals of *Jeholopterus* for both the manus and pes are exceptionally long and curved and might indicate special affinity for the trees. Work on terrestrially competent bats suggest that future research into indicators of hindlimb strength may help resolve this issue (Swartz et al., 2003), though this has subsequently been challenged (Riskin et al., 2005).

Vesperopterylus was described as having a reversed first toe that allowed it to have a perching-like grip with the foot (Lü et al., 2018), though how this would function in a plantigrade quadrupedal animal is not clear. Notably, the toes of anurognathids generally are divergent and well spread (e.g. see Batrachognathus and the holotype of Anurognathus) in contrast to most other pterosaurs who hold their digits in line with the metatarsals and would potentially allow the foot to grasp in some way. Some early branching pterosaur clades do show some separation of the toes but it appears to be greater in the anurognathids. Both Vesperopterylus and Jeholopterus have an unusually robust fifth toe which suggests a great degree of functionality for this digit in contrast to all other non-pterodactyloid pterosaurs. Recently trackways for non-pterodactyloid pterosaurs have been discovered showing that at least some walked with the fifth toe fully contacting the ground (Mazin and Pouech, 2020) so it is possible that this was an issue of weight bearing in these animals.

Bennett (2007a) concluded that anurognathids may also have been cryptically coloured in order to conceal themselves still further from potential predators when at rest, and this is potentially supported by the discovery of reddish paheomelanosomes in anuroganthids (Yang et al., 2019). This fits with the above model, and also with the fact that anurognathids are one of the very few pterosaurian lineages with no evidence for any form of cranial crest (Hone et al., 2012). Cryptic colouration would be severely disrupted by a large and / or brightly coloured crest, and the animal would have greater difficulty concealing itself. The presence of a crest would have added weight and potential aerodynamic instability to an animal that relies on maneuverability for its survival.

As has been pointed out above, the majority of known anurognathids have evidence of soft tissue preservation associated with their skeletal remains. This may in part be because they are only known from sites of exceptional fossil preservation. However, it still provides useful information on pterosaur integumentary coverings (Ji and Yuan, 2002), and wingshape (Elgin et al., 2011) which are rare in the pterosaurian fossil record. Anurognathids had an extensive integumentary covering with the main fibres on the body being especially long when compared to other pterosaurs where they are preserved, as seen best in

Jeholopterus (Kellner et al., 2009 fig. 3). These appear in clumps suggesting a possible common origin on the skin for each cluster, and taper distally (Wang et al., 2002) and may also be branching (Yang et al., 2019).

The anurognathids were among the smallest pterosaurs (Hone and Benton, 2007). They ranged in wingspan from around 0.50 m to 0.90 m (*Anurognathus* and *Jeholopterus* respectively) at adult. However, it is possible that some, if not most, of the specimens of anurognathids are juveniles or subadults (in terms at least of size, sensu Hone et al., 2016). The new specimen of *Anurognathus* certainly belonged to a young individual (Bennett, 2007a – unfused skull, scapula and coracoid, wrist and pelvis), and despite their obvious fragility, the ease with which the skull bones of both specimens of *Batrachognathus* and *Dendrorhynchoides* have disarticulated suggests that these may also not be adult animals, and the latter also has external bone surface texture common in juvenile pterosaurs (Bennett, 1996). The holotype of *Anurognathus* also has an unfused pelvis (Bennett, 2007a), as are the scapulocoracoids of *Dendrorhynchoides*, implying immaturity. This is perhaps to be expected as in the Solnhofen limestones at least as it is clear that the majority of pterosaur specimens represent non-adult individuals (Bennett, 1995, 1996), and this may be true of other pterosaur localities. This would imply that anurognathids may have been larger at adult size than previously thought (e.g., see Hone and Benton, 2007).

Obviously, the rarity of anurognathids and the potentially long ghost range between their origination and preservation is problematic. As a result, important questions about their origin and evolution are unlikely to be resolved without earlier-diverging representatives being discovered. However, given the scarcity of anurognathids as a whole, these discoveries may be a long time coming. The inferred habitats of anurognathids (arboreal environments away from large bodies of water) make them poor candidates for preservation, and their small size is also a handicap towards recovery. It is quite possible that in terms of numbers of individuals, the anurognathids were common animals (Bennett, 2007a) and are simply drastically underrepresented in the fossil record. It is notable that they are common in the various Jurassic and Cretaceous beds of Liaoning that do generally preserve large numbers of small animals that are generally rare in the Mesozoic (e.g. small dinosaurs, avians). A lack of other obvious competitors for flying insects (other pterosaurs apparently shunned such prey since none share the adaptations seen in anurognathids, birds capable of powered flight did not appear until the Late Jurassic and predatory insects themselves were rare, though present) would imply that anurognathids were numerous and / or diverse with a large amount of prey and potentially little competition in the air.

The pterosaur bauplan tends to be conservative within clades, and this is especially true of the anurognathids, (Unwin et al., 2000). Despite the exceptional preservation and relative completeness of many anurognathid specimens, they are hard to differentiate. In spite of the potential long ghost lineage until their appearance in the Middle to Late Jurassic and the wide geographical separation of the taxa (western Europe to eastern Asia), anurognathid taxa are remarkably similar. This suggests that anurognathids were very highly specialised for their lifestyle to a point where even relatively minor changes to their anatomy were apparently absent, although as noted above, there was some variation in key traits like head size and the morphology of the humerus.

The phylogenetic position of Anurognathidae as a likely very early branching clade raises interesting questions about their history given the long ghost lineage between their inferred point of origin (sometime in the Late Triassic) and their first appearance in the fossil record (Middle to Late Jurassic) (e.g. see Unwin, 2003b). The nature of the anurognathid bauplan seen in the small number of known specimens implies that their morphology was very conservative, yet clearly they are considerably different to other pterosaurian taxa and highly derived in this respect. Obviously, this creates problems with determining both their phylogenetic position, and in a wider context trying to determine the origin of the pterosaurs themselves (Hone and Benton, 2008). However, in some ways they do fit the model of an early pterosaur well – they were small, probably arboreal, insectivorous, and had exceptionally broad wings, and with a low wing loading - all predictable features for an animal that had recently evolved powered flight from almost any archosauromorph lineage (Unwin, 2005 p. 230). They maintain flexion in the joints of the wing finger and have well spread toes which are traits seen in other reptiles but not in other pterosaurs and might point to their ancestry and retention of primitive traits.

Anurognathids therefore remain central to the question of pterosaur origins and pterosaur evolution. Their anatomical bauplan is unique even among pterosaurs and clearly they were highly specialised. The glut of recent finds, many of which are preserved with extensive soft tissues, make them still more significant and promises much from future studies.

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References

Andres, B., Clark, J.M., and Xu, X., 2010. A new rhamphorhynchid pterosaur from the Upper Jurassic of Xinjiang, China, and the phylogenetic relationships of basal pterosaurs. Journal of Vertebrate Paleontology, 30: 163–187.

Andres, B., Clark, J.M., and Xu, X., 2014. The earliest pterodactyloid and the origin of the group. Current Biology, 24: 1011–1016.

Bakhurina, N.N., 1988. On the first rhamphorhynchoid from Asia: Batrachognathus volans Riabinin 1948, from Upper Jurassic beds of Karatau. Abstract of paper in Basic research results of the joint Soviet-Mongolian Palaeontological Expedition, 1969–1988, 17–18. Moscow, Academia Nauk.

Bakhurina, N.N., and Unwin, D.M., 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. Historical Biology, 10: 197–245.

Barthel, K.W., Swinburne, N.H.M., and Conway Morris, S., 1990. Solnhofen: a study in Mesozoic paleontology. Cambridge University Press, 236.

Bennett, S.C., 1995. A statistical study of *Rhamphorhynchus* from the Solnhofen Limestone of Germany – year-classes of a single large species. Journal of Paleontology, 69: 569–580.

Bennett, S.C., 1996. Year-classes of pterosaurs from the Solnhofen Limestone of Germany: taxonomic and systematic implications. Journal of Vertebrate Paleontology, 16: 432–444.

Bennett, S.C., 2003. New crested specimens of the Late Cretaceous pterosaur Nyctosaurus. Paläontologische Zeitschrift, 77: 61–75.

Bennett, S.C., 2007a. A second specimen of the pterosaur Anurognathus ammoni. Paläontologische Zeitschrift, 81: 376–398.

Bennett, S.C., 2007b. Articulation and function of the pteroid bone of pterosaurs. Journal of Vertebrate Paleontology, 27: 881–891.

Bestwick, J., Unwin, D.M., Butler, R.J., Henderson, D.M., and Purnell, M.A., 2018. Pterosaur dietary hypotheses: a review of ideas and approaches. Biological Reviews, 93: 2021–2048.

Böker, H., 1924. On the new pterosaur *Anurognathus ammoni,* Döderlein. Naturwissenschaften, 29: 177–178.

Britt, B.B., Dalla Vecchia, F.M., Chure, D.J., Engelmann, G.F., Whiting, M.F., and Scheetz, R.D., 2018. *Caelestiventus hanseni* gen. et sp. nov. extends the desert-dwelling pterosaur record back 65 million years. Nature Ecology and Evolution, 2: 1386.

Dalla Vecchia, F., 2002. Observations on the non-pterodactyloid pterosaur *Jeholopterus ningchengensis* from the Early Cretaceous of northeastern China. Natura Nascosta, 24: 8–27.

Döderlein, L., 1923. *Anurognathus Ammoni,* ein neuer Flugsaurier. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung*, 1923: 117–164.

Döderlein, L., 1929. Über *Anurognathus Ammoni* Döderlein. Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Abteilung, 1929: 47–63.

Elgin, R.A., Hone, D.W.E., and Frey, E., 2011. The extent of the pterosaur flight membrane. Acta Palaeontologica Polonica, 56: 99–111.

Gao, K.Q., Wei, M., Pak, H., and Pak, I., 2009. Early Cretaceous birds and pterosaurs from the Sinuiju series, and geographic extension of the Jehol Biota into the Korean Peninsula. Journal of the Palaeontological Society of Korea, 25: 57–61.

Habib, M.B., 2011. Functional morphology of anurognathid pterosaurs. Geological Society of America Abstracts with Programs, 43: 118.

Hone, D.W.E., and Benton, M.J., 2007. Cope's Rule in Pterosauria, and differing perceptions of Cope's Rule at different taxonomic levels. Journal of Expermential Biology, 20: 1164–1170.

Hone, D.W.E., and Benton, 2008. Contrasting supertree and total -evidence methods: pterosaur origins. Zitteliana B, 28: 35–60.

Hone, D.W.E., Naish, D., and Cuthill, I.C., 2012. Does mutual sexual selection explain the evolution of head crests in pterosaurs and dinosaurs? Lethaia. 45: 139–156.

Hone, D.W.E., and Lü, J., 2010. A new specimen of *Dendrorhynchoides* (Pterosauria: Anurognathidae) with a long tail and the evolution of the pterosaurian tail. Acta Geoscientica Sinica, 31: 29–30.

Hone, D.W., Farke, A.A. and Wedel, M.J., 2016. Ontogeny and the fossil record: what, if anything, is an adult dinosaur?. Biology Letters, 12: 20150947.

Hone, D.W.E., van Rooijen, M.K. andHabib, M.B., 2015. The wingtips of pterosaurs: anatomy, aeronautical function and ecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology, 440: 431–439.

Hill, J.E., and Smith, S.E., 1981, *Craseonycteris thonglongyai.* Mammalian Species, 160: 1–4.

Jensen, J.A., and Padian, K., 1989 Small Pterosaurs and Dinosaurs from the Uncompahgre Fauna (Brushy Basin Member, Morrison Formation: ?Tithonian), Late Jurassic, Western Colorado. Journal of Paleontology, 63: 364–373.

Ji, S., and Ji, Q., 1998. A new fossil pterosaur (Rhamphorhynchoidea) from Liaoning. Jiangsu Geology, 22: 199–206 (in Chinese).

Ji, S., Ji, Q., and Padian, K., 1999. Biostratigraphy of new pterosaurs from China. Nature, 398: 573–574.

Ji, Q., and Yuan, C., 2002. Discovery of two kinds of protofeathered pterosaurs in the Mesozoic Daohugou Biota in the Ningcheng Region and its stratigraphic and biologic significances. Geological Review, 48: 221–224 (in Chinese).

Jiang, S., Wang, X., Cheng, X., Costa, F.R., Huang, J., and Kellner, A.W., 2015. Short note on an anurognathid pterosaur with a long tail from the Upper Jurassic of China. Historical Biology, 27: 718–722.

Jones, G., Webb, P.I., Sedgeley, J.A., and O'Donnell, C.F.J., 2003. Mysterious *Mystacin*a how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. Journal of Experimental Biology, 206: 4209–4216.

Kellner, A.W. A., 1996. Pterosaur phylogeny. Journal of Vertebrate Paleontology, 16(Suppl. to #3): 45A.

Kellner, A.W.A., 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. Geological Society of London, Special Publication, 217: 105–137.

Kellner, A.W.A., Wang, X., Tischlinger, H., Campos, D.A., Hone, D.W.E., and Meng, X., 2009. The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathidae) and the structure of the pterosaur wing membrane. Proceedings of the Royal Society, Series B, 277: 321–329.

Kuhn, O., 1937. *Die fossilen Reptilien*. Gebrüder Borntraeger, viii + 121 pp.

Kuhn, O., 1961. Pterosauria (Supplementum 1). Fossilium Catalogus I: Animalia. Pars 99, 57–68.

Lederer, R.J., 1972. The role of avian rictal bristles. The Wilson Bulletin, 84: 192–197.

Lü, J-C., and Hone, D.W.E., 2012. A new Chinese anurognathid pterosaur and the evolution of pterosaurian tail lengths. Acta Geologica Sinica (English Edtion), 86(6): 1317–1325.

Lü, J., and Ji, Q., 2005. A new ornithocheirid from the Early Cretaceous of Liaoning Province, China. Acta Geologica Sinica (English Edition), 79(1): 157–163.

Lü, J., and Ji, Q.. 2006. Preliminary results of a phylogenetic analysis of the pterosaurs from Western Liaoning and surrounding areas. Journal of the Paleontological Society of Korea, 22: 239–261.

Lü, J., Unwin, D.M., Jin, X.S., Liu, Y.Q., and Ji, Q., 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *P*roceedings of the Royal Society, Series B, 277: 383–389.

Lü, J., Meng, Q., Wang, B., Liu, D., Shen, C., and Zhang, Y., 2018. Short note on a new anurognathid pterosaur with evidence of perching behaviour from Jianchang of Liaoning Province, China. Geological Society, London, Special Publications, 455: 95–104.

Mazin, J.M., and Pouech, J., 2020. The first non-pterodactyloid pterosaurian trackways and the terrestrial ability of non-pterodactyloid pterosaurs. Geobios.

Nopcsa, F. V., 1928. The genera of reptiles. Palaeobiologica, 1: 163–188.

Ősi, A., 2011. Feeding - related characters in basal pterosaurs: implications for jaw mechanism, dental function and diet. Lethaia, 44: 136–152.

Padian, K., 1980. Studies of the structure, evolution, and flight of pterosaurs (Reptilia: Pterosauria). Unpublished Ph. D. dissertation, Yale University, xiv + 309.

Petronievics, B., 1928. Bemerkungen über *Anurognathus* Döderlein. Anatom. Anzeiger, 65: 214–222.

Rasnitsyn, A. P., and Quicke, D.L.J.. 2002. History of Insects. Kluwer Academic Publishers.

Riskin, D.K., Bertram, J.E.A., and Hermanson J.W., 2005. Testing the hindlimb-strength hypothesis: non-aerial locomotion by Chiroptera in not constrained by the dimensions of the femur or tibia. Journal of Experimental Biology, 208: 1309–1319.

Ryabinin, A.N., 1948. Remarks on a flying reptile from the Jurassic of the Karatau. Transactions of the Palaeontological Institute, 15: 86–93.

Sprague, M., and McLain, M.A., 2018. *Mesadactylus* and the Pterosaur Diversity of Dry Mesa Quarry, Morrison Formation, Colorado. Flugsaurier Los Angeles Abstracts book, 83–85.

Sullivan, C., Wang, Y., Hone, D.W.E., Wang, Y.Q., Xu, X., and Zhang, F., 2014. The vertebrates of the Jurassic Daohugou Biota of Northeastern China. Journal of Vertebrate Paleontology, 34: 243–280

Swartz, S.M., Freeman, P.W., and Stockwell, E.F., 2003. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology. to ecology. In: Kunz, T.H., and Fenton, M.B. (eds.), Ecology of Bats, 257 –300. Chicago: University of Chicago Press.

Unwin, D.M., 1995. Preliminary results of a phylogenetic analysis of the Pterosauria (Diapsida: Archosauria), pp. 69–72. In Sun, A., and Wang, Y. (eds), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota. Short Papers. Beijing: China Ocean Press.

Unwin, D.M., 2003a. On the phylogeny and evolutionary history of pterosaurs. Geological Society of London, Special Publication, 217: 139–190.

Unwin, D.M., 2003b. *Eudimorphodon* and the early history of pterosaurs. In: Renesto, S., ed. Atti del Workshop *Eudimorphodon*: 30th from Discovery. Museo Civico di Scienze Naturali "E. Caffi" di Bergamo, Rivista del Museo Civico di Scienze Naturali "Enrico Caffi", 22: 39–46.

Unwin, D.M., 2005. The Pterosaurs from Deep Time. New York: Pi Press.

Unwin, D.M., and Bakhurian, N.N., 2000. Pterosaurs from Russia, Middle Asia and Mongolia. In: Benton, M.J., Shiskin, M., Unwin, D.M., and Kurochkin, E. (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, 420–433.

Unwin, D.M., and Deeming, D.C., 2008. Pterosaur eggshell structure and its implications for pterosaur reproductive biology. Zitteliana B, 23: 199–207.

Unwin, D.M., Lü, J., and Bakhurina, N.N., 2000. On the systematics and stratigraphic significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China. Mittwilungen Museum für Naturkunde Berlin, Geowissenschaftlichen Reihe, 2: 121–134.

Vidovic, S.U., and Martill, D.M., 2018. The taxonomy and phylogeny of Diopecephalus kochi (Wagner, 1837) and '*Germanodactylus rhamphastinus*' (Wagner, 1851). Geological Society, London, Special Publications, 455: 125–147.

Viscardi, P., Dyke, G.J., Wilkinson, M., and Rayner, J.M.V., 1999. Missing data and the phylogeny of the Pterosauria. Journal of Vertebrate Palaeontology, 19: 83A.

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. Chinese Science Bulletin, 47: 226–232.

Wang, X., Kellner, A.W.A., Zhou Z., and Campos, D.A., 2008. Discovery of a rare arboreal forest-dwelling flying reptile (Pterosauria, Pterodactyloidea) from China. Proceedings of the National Academy of Science, 105: 1983–1987.

Wellnhofer, P., 1975a. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Suddeutschlands. Palaeontographica, *A* 148: 1–33, 148: 132–186, 149: 1–30.

Wellnhofer, P., 1978. Pterosauria. In: Wellnhofer, P. (ed.), Handbuch der Paläoherpetologie, 19: 1–82. Stuttgart: Gustav Fischer Verlag.

Wellnhofer, P., 1991. The Illustrated Encyclopedia of Pterosaurs. London: Salamander Books.

Wellnhofer, P., 2008. A short history of pterosaur research. Zitteliana B, 28: 7–19.

Wilkinson, M.T., Unwin, D.M., and Ellington, C.P., 2006. Lift capability of pterosaur wings and the evolution of gigantism. Proceedings of the Royal Society Series B, 273: 119–126.

Wiman, C., 1928. Einige Beobachtungen an Flugsauriern. Palaeobiologica, 1: 363–370.

Witton, M.P., 2008. A new approach to determining pterosaur body mass and its implications for pterosaur flight. Zitteliana B, 28: 143–158.

Witton, M.P., 2013. Pterosaurs: natural history, evolution, anatomy. Princeton University Press.

Witton, M.P., 2015. Were early pterosaurs inept terrestrial locomotors?. PeerJ, 3: p.e1018.

Yang, Z., Jiang, B., McNamara, M.E., Kearns, S.L., Pittman, M., Kaye, T.G., Orr, P.J., Xu, X., and Benton, M.J., 2019. Pterosaur integumentary structures with complex feather-like branching. Nature Ecology and Evolution, 3: 24.

Young, C.C., 1964. On a new pterosaurian from Sinkiang, China. Vertebrata PalAsiatica, 8: 221–255.

Zhang, J., and Zhang, H., 2003. Insects and spiders. In: Chang, M., Chen, P., Wang, Y., and Wang, Y. (eds.), The Jehol Biota. Shanghai: Shanghai Scientific and Technical Publishers, 59–68.

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