Sinomacrops bondei, a new anurognathid pterosaur from the Jurassic of China and comments on the group (#53890)

First revision

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Sinomacrops bondei, a new anurognathid pterosaur from the Jurassic of China and comments on the group

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Abstract

Anurognathids are an elusive group of diminutive, potentially arboreal pterosaurs. Even though their monophyly has been well-supported, their intrarelationships have been obscure, and their phylogenetic placement even more. In the present work, we present a new genus and species from the Middle-Late Jurassic Tiaojishan Formation, the third nominal anurognathid species from the Jurassic of China. The new species provides new information concerning morphological diversity for the group. Furthermore, we provide a new phylogenetic analysis incorporating into a single data set characters from diverging phylogenetic proposals. Our

results place them as the sister-group of Darwinoptera + Pterodactyloidea, as basal members of the Monofenestrata.

Introduction

Pterosaurs, a group of archosauromorph reptiles of disputed placement (see Renesto & Binelli 2004, Hone & Benton 2007, Bennett 2013, Ezcurra *et al.* 2020), were the first vertebrates known to conquer active flight, with a fossil record stretching from the Late Triassic to the K/Pg boundary (Wellnhofer 1991, Andres *et al.* 2014, Dalla Vecchia 2014). The Anurognathidae are a very peculiar pterosaur group still poorly understood and rather obscure, characterized by a unique morphology and involved in a complex history of uncertainty about their phylogenetic affinities (Hone 2020). Spanning from the Middle Jurassic (Callovian) to the Early Cretaceous (Aptian), anurognathids are small-sized (up to 900 mm in wingspan) and exhibit short skulls with a diminutive preorbital region, huge orbits and rounded jaws that are wider than long (Bennett 2007, Hone 2020). Due to their short wings with low aspect ratios and their peg-like teeth, these small pterosaurs have been interpreted as aerial insectivores (Bennett 2007, Witton 2008, 2013, Ösi 2011, Habib 2011, Hone 2020), of possible arboreal habits (Ji & Ji 1998, Bennett 2007, Witton 2013, Lü *et al.* 2018, Hone 2020).

The Anurognathidae have been defined as a node-based group, as the least inclusive clade containing *Anurognathus ammoni* and *Batrachognathus volans* (Kellner 2003, Unwin 2003). Recently, it has been redefined as a branch-based group, englobing all species closer to *Anurognathus* than to *Dimorphodon*, *Pterodactylus* or *Scaphognathus* (Hone, 2020). So far, this group comprises six nominal species, and is known by 12 specimens from Germany, Kazakhstan, Mongolia, China and North Korea (with a putative 13th one from the USA). The first described one was *Anurognathus ammoni*, coming from the Tithonian Solnhofen limestones of Bavaria (Döderlein 1923) and being represented by two specimens (Bennett 2007). It was not until the second specimen was described that several aspects of its morphology were clarified, such as the broad wings, the short preorbital region and extensive orbit, the jugal overlying the maxilla, the vertical (or slightly anteriorly inclined) quadrate, the reduced palatal elements, and the short tail lacking filiform processes of the zygapophyses and haemapophyses, convergent with pterodactyloids (Bennett 2007).

The second nominal species was *Batrachognathus volans*, described from an incomplete skeleton including a partial skull from the Oxfordian-Kimmeridgian Karabastau Formation of Kazakhstan (Riabinin 1948). A second specimen of *Batrachognathus volans* (Unwin *et al.* 2000), still awaiting a full description, possesses a long tail, with developed rod-like processes of the haemapophyses and zygapophyses (Costa *et al.* 2013). With this discovery, *Batrachognathus volans* became the first known anurognathid to exhibit a long tail with developed rod-like processes as typical of most non-pterodactyloid pterosaurs (see Costa *et al.* 2013).

The third anurognathid to be described was *Dendrorhynchoides curvidentatus*, the first recovered from a Cretaceous deposit, the early Aptian Jianshangou beds of the Yixian Formation (Ji & Ji 1998). Originally thought of as Barremian, these beds are now viewed as early Aptian in age (see Chang *et al.* 2009).

Jeholopterus ningchengensis, based on an almost complete skeleton with extensive soft tissue preservation coming from the Daohugou beds near Daohugou (Ningcheng County, Inner Mongolia), was later described as another Cretaceous anurognathid (Wang *et al.* 2002), on the basis of the now outdated view of the Daouhugou beds as part of the Yixian Formation (Barremian-Aptian). Subsequently, these beds were reinterpreted as part of the Middle-Late Jurassic Tiaojishan Formation. Presently, these rocks have been once more reinterpreted, and are now considered to belong to the Haifanggou/Jiulongshan Formation (Huang 2015, 2016). The locality that has yielded *Jeholopterus ningchengensis* has been dated as Callovian-Oxfordian (Liu *et al.* 2006, Gao & Shubin 2012). A second specimen from the same locality has been regarded as most likely conspecific with *Jeholopterus ningchengensis*, though a detailed description and a formal taxonomic assessment have not been provided yet (Ji & Yuan 2002, Witton 2013, Yang *et al*. 2019).

Later, a second species for the genus *Dendrorhynchoides*, named *D. mutoudengensis*, was erected based on an almost complete skeleton from the Mutoudeng locality, Tiaojishan Formation (Lü & Hone 2012). Recently, a new genus has been erected to accommodate this species: *Luopterus*, named after the late Prof. Junchang Lü (Hone 2020). Moreover, a second Cretaceous anurognathid was also named recently, *Vesperopterylus lamadongensis*, known from an almost complete holotype from the late Aptian Jiufotang Formation (Lü *et al.* 2018).

Indeterminate specimens include IVPP V16728, which stands out as the second specimen with a long tail and developed rod-like processes, similar to *Batrachognathus volans* (see Costa *et al.* 2013) and unlike all remaining anurognathids. NJU–57003 is another long-tailed specimen from the Mutoudeng locality (Daohugou Beds, Tiaojishan Formation), only preliminarily described (Yang *et al*. 2019). A relatively complete specimen from the Early Cretaceous of North Korea also awaits description (Gao *et al.* 2009), as well as a fragmentary specimen comprised of wing elements from the Middle Jurassic (Aalenian/Bajocian) Bakhar deposits of Central Mongolia (Bakhurina & Unwin 1995). Finally, the poorly-known *Mesadactylus ornithosphyos*, based on the holotype BYU 2024 (a synsacrum) from the Kimmeridgian-Tithonian Morrison Formation of the USA (Jensen & Padian 1989), is a potential anurognathid (see Bennett 2007).

Pterosaur phylogeny is intricated with controversies, but no other group compares to the Anurognathidae when it comes to uncertainty concerning its placement (Young 1964, Unwin 1992, 1995, 2003, Viscardi *et al.* 1999; Kellner 2003, Andres *et al.* 2010, Dalla Vecchia 2014, 2019, Hone 2020). Five cladistic hypotheses based on computed analyses have been presented for the Anurognathidae, wherein they are viewed as: the basalmost pterosaur group (Kellner, 2003); the sister-group of the Novialoidea (Unwin 2003); the sister-group of the Breviquartossa (Dalla Vecchia 2019); scaphognathids, whereby these are the sister-group of the Monofenestrata (Vidovic & Martill 2017); or the sister-group of the Pterodactyloidea (Andres *et al.* 2010, 2014). And even though the monophyly of the Anurognathidae has been strongly corroborated (Kellner 2003, Unwin 2003, Bennett 2007, Andres *et al.* 2010, Dalla Vecchia 2019), its intrarelationships have been poorly explored (Hone, 2020).

This work presents a new fossil coming from the Mutoudeng locality, JZMP-2107500095, representing a new genus and species of long-tailed anurognathid. Despite being crushed to the point of obliterating many details, the specimen is rather complete and provides new information for the group, including the first record of an anurognathid skull exposed in lateral view. In other specimens, the skull is either exposed in internal view, as in the holotype of *Anurognathus ammoni* (Döderlein 1923, Wellnhofer 1975, Bennett 2007), or dorsoventrally crushed, as in all other specimens that preserve a skull (Riabinin 1948, Ji & Ji 1998, Bennett 2007, Gao *et al.* 2009, Lü & Hone 2012, Lü *et al.* 2018).

We further review the phylogenetic relationships of the group (both intra and inter), presenting an analysis including all proposed species and a resulting in a new hypothesis for the placement of the group as basal monofenestratans.

Geological setting

The Tiaojishan Formation takes its name from the Tiaojishan Mountain (Mentougou District, Beijing), and was named by Ye (1920). This and the Haifanggou/Jiulongshan Formation have yielded the famous Yanliao Biota in western Liaoning and adjacent regions (Huang 2015, 2016). This biota is well known for the beautiful preservation and abundancy of insects and vertebrate fossils, such as salamanders, feathered dinosaurs, pterosaurs and mammals (Sullivan *et al.*, 2014). The most important localities that yield the Yanliao Biota are Daohugou in Ningcheng County of southeast Inner Mongolia (Haifanggou Fm.), Linglongta of Jianchang County of western Liaoning Province (Tiaojishan Fm.), and Mutoudeng of Qinglong County of northern Hebei Province (Tiaojishan Fm.; Lü et al. 2013, Huang 2015, 2016). From the Haifanggou Formation at Daohugou (Liu *et al.* 2012), pterosaurs are relatively rare, with *Jeholopterus ningchengensis*, *Pterorhynchus wellnhoferi* and *Daohugoupterus delicatus* (Wang et al. 2002, Czerkas & Ji 2002, Cheng et al. 2015). From the slightly younger Tiaojishan Formation at the Linglongta locality, pterosaurs are abundant in number and in diversity, with wukongopterids, *Jianchangopterus*, *Jianchangnathus* and *Fenghuangopterus*, (Wang *et al.* 2009, 2010; Lü *et al.* 2009, 2011a,b, Lü & Bo 2011, Sullivan *et al.* 2014, Cheng *et al*. 2012, 2017). From the Tiaojishan Formation at Mutoudeng come *Luopterus mutoudengensis*, *Qinglongpterus guoi* and *Changchengopterus pani* (Lü 2009, Lü *et al*. 2012, Lü & Hone 2012). It is from the Mutoudeng locality that comes the new specimen herein described (Fig. 1).

The Tiaojishan Formation is mainly distributed in the Chengde Basin (Maoniujiao-Xiaoguozhangzi-Jiyuqing Area) in northern Hebei Province. The thickness is around 300 m (Zhang & Chen, 2015). It is mainly composed of neutral volcanic rock (Zhang & Chen, 2015). The lithology of the lower member includes dark grey, grey purple trachyandesites, quartz trachyandesites, small trachyandesitic agglomerate, small trachyandesitic ignimbrite (Zhang & Chen, 2015). The lithology of upper member includes dark grey, burgundy trachyandesites, trachyandesitic agglomerate, partially containing grayish purple, grayish green sedimentary tuff, tuffaceous conglomerate and tuffaceous sandstone (Zhang & Chen, 2015).

Zhang *et al.* (2008) analyzed samples of volcanic rock from several typical localities (Luanping Basin, Chengde Basin, Sanshijiazi Basin and Jinlingsi-Yangshan Basin), utilizing LA-ICP-MS Zircon U-Pb. Their result suggest that the lower limit age of the Tiaojishan Formation should be around 165 Ma. Li *et al.* (2019) analyzed samples of volcanic rock from the bottom of the lower section and andesite from the top of the upper section, utilizing LA-ICP-MS Zircon U-Pb. Their result gave an age range of 170–153 Ma for the Formation as a whole, that is, from the Bajocian until the Kimmeridgian. A specific dating for the strata of the Linglongta locality has been provided by Liu *et al.* (2012), in order to provide a constrained age range for Linglongta wukongopterid pterosaurs. The bottom and the top of this locality were dated, resulting in an age range of 161-160 Ma (Liu *et al.*, 2012), falling within the Oxfordian (early Late Jurassic). Specific dating under geochemical approaches still lack for the Mutoudeng locality. However, biostratigraphic studies, based mainly on conchostracans, suggest that the Linglongta and Mutoudeng strata are chronocorrelate (Chu *et al.*, 2016).

Material & Methods

Institutional abbreviations

BMNHC, Beijing Museum of Natural History, Beijing, China; **BYU,** Brigham Young University Museum of Paleontology, Provo, Utah, USA; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **JPM,** JZMP, Jinzhou Museum of Paleontology, Jinzhou; **NJU,** Nanjing University, Nanjing, China.

Computed tomography (CT) scanning

JPM-2012-001 was computed tomography (CT) scanned using a Nikon XTH225ST scanner at the Laboratory of Stratigraphy and Paleontology, Institute of Geology, Chinese Academy of Geological Sciences (IG-CAGS), Beijing, China. The specimen was scanned at 160 kV and 131 μA. The data set includes 2000 image slices (2000 x 2000 pixels) with a slice thickness of 0.121

mm. The data was imported into digital visualization software Avizo (version 9.1) for image processing and visualization.

Phylogenetic Analysis

Concerning terminal taxa, our phylogenetic analysis is focused on non-pterodactyloid pterosaurs, following previous works that also focused on these forms (e.g. Dalla Vecchia 2009–2019, Andres *et al.* 2010; Lü *et al.* 2012). Concerning our character list, we have gathered discrete characters from Vidovic & Martill (2017), Longrich *et al.* (2018) and Dalla Vecchia (2019), all of which further englobe data from previous studies (e.g. Kellner 2003, Unwin 2003, Dalla Vecchia 2009, Lü *et al.* 2009, Wang *et al.* 2012, Naish *et al.* 2013, Andres *et al.* 2014, Britt *et al.* 2018). Following previous works, we did not employ composite coding (Colless 1985). The character list is available in Supplemental File 1 (a nexus format file for the software Mesquite, containing the data matrix) and Supplemental File 2 (a TNT file ready for executing the analysis, that can also be opened as a txt file).

We did not employ the treatment of continuous data as such (for discussions on the subject see Goloboff *et al.* 2006, Bardin *et al.* 2014, Mongiardino-Koch *et al.* 2015, Vidovic 2018). The original discretized quantitative characters from previous analyses (see our character list) were not modified, except for morphometric characters 270 (humerus/femur length, modified from Kellner, 2003) and 368 (tibia/femur length). Discrete states for the morphometric characters 270 and 368 were categorized (discretized) by using the gap-weighting method (Thiele 1993). In order to optimize the phylogenetic signal, following Bardin *et al.* (2014), state number was set at 3. The morphometric dataset subjected to gap-weighting is available as Supplemental Table S1. The resulting categorization is presented in Supplemental Table S1 and the data matrix (Supplemental Files 1, 2).

Following other works, all characters were treated unordered and equally weighted (e.g. Fitzhugh 2006). The analysis was performed using TNT (Goloboff *et al.* 2018) and was divided in two steps. The first search was performed using New Technology Search (using Sectorial Search, Ratchet, Drift and Tree fusing, default parameters), with random seed = 0. Subsequently, using trees from RAM, we performed a Traditional Search swapping (using TBR, collapsing trees after search). The TNT file is available as Supplemental File 2.

Nomenclatural acts

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:15997DEB-0EF7-40F6-80B0-2C40ED47D43B. LSID for the new genus: urn:lsid:zoobank.org:act:C1268C7D-80AA-4854-93E7-0E60220A05BC. LSID for the new species: urn:lsid:zoobank.org:act:048E9ADE-8C3A-47D4-B074-DCEFA40BDE9A. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Results

Systematic Paleontology

Pterosauria Owen, 1842

Novialoidea Kellner, 2003

Breviquartossa Unwin, 2003

Monofenestrata Lü *et al.*, 2009

Anurognathidae Kuhn, 1937

Batrachognathinae Kellner *et al.* 2010

Definition. The most inclusive clade containing *Batrachognathus volans* but not *Anurognathus ammoni* (Kellner *et al.* 2010).

Synapomorphies. Humeral deltopectoral crest reduced (less wide than humeral shaft; and less wide than proximodistally long), humeral deltopectoral crest subrectangular, ulnar crest of humerus rounded, humeral/femoral length ratio over 1.60, tibial/femoral length ratio over 1.70.

Included species. *Batrachognathus volans* and *Sinomacrops bondei* gen. et sp. nov.

Sinomacrops bondei gen. et sp. nov.

Etymology. The generic name is a combination of *Sino*, *macro* and *ops*; which are Ancient Greek for China, large, and eyes/face, respectively. This is in reference to both the large eyes and the broad faces that are typical of anurognathids, and to the Chinese origin of the new species. The specific epithet honors paleontologist Niels Bonde, for his many scientific contributions and being an inspiration for us.

Holotype. JPM-2012-001 (Figs. 2–6).

Locality and horizon. Mutoudeng, Qinglong County of Hebei Province. Daohugou Beds (Callovian-Oxfordian 164-158 Ma) of the Tiaojishan Formation (see Liu *et al.* 2006a, 2006b, Gao & Shubin 2012).

Diagnosis. The new taxon exhibits two autapomorphies: first three maxillary alveoli closely spaced, and tibiotarsus twice as long as the femur.

Description

Generalities. JPM-2012-001 comprises a crushed skeleton (Fig. 2). While the cranium and some cervical vertebrae are exposed in right lateral aspect (Fig. 3), the remaining of the skeleton is exposed in ventral view. The preserved bone tissue exhibits a fragile, brittle condition. In consequence, in many regions of the skeleton, fragments of bone tissue have been lost posterior to collection of the specimen. These lost fragments left clear impressions on the matrix, indicating where they were originally present. Lost fragments include mainly the caudal vertebrae, sternum, distal epiphysis of right humerus, proximal epiphyses of right ulna and radius, parts of the left humerus, and most of the left manus.

Micro computed tomography scan resulted in images with only limited resolution. Nonetheless, the images permitted better visualization of some impressions on the matrix (represented by empty spaces on the slices), helping in the identification of some bone limits and extensions. Such was the case of elements of the left wing (humerus epiphysis, radius and ulna, wing metacarpal and first wing phalanx), as well as the right humerus (Fig. 4). CT images did not provide enough resolution for additional data on other skeletal regions.

Soft tissue. The skeleton includes preservation of soft tissue patches. The dorsal margin of the skull is covered by skin impressions that descends onto the neck region (Fig. 3). An irregular patch of soft tissue lateral to the left tibiotarsus suggests that the brachiopatagium extended posteriorly onto the distal region of the crus. Another large patch of soft tissue is present medial to the right hindlimb, extending from the femoral region until the distal fifth of the tibiotarsus. This implies in an extensive cruropatagium, though participation of the tail in its sustenance is unclear. A brachiopatagium extending distally on the crus is consistent with what is seen in *Jeholopterus ningchengensis* (see Kellner *et al.* 2009) and pterosaurs in general (see Elgin *et al.* 2011). An extensive cruropatagium can also be found in *Sordes pilosus* (Unwin & Bakhurina 1994). Deeper investigation of the soft tissue remains of JPM-2012-001 is beyond the scope of the present contribution and shall be presented elsewhere.

Cranium. The cranium of JPM-2012-001 is exposed in right lateral aspect (Fig. 3). A small pair of bones on the rostral tip of the skull seem to represent an unfused pair of premaxillae. Individually, they comprise basically two processes, one ascending and another one extending posteriorly. This indicates that the fused premaxillae would display a T-shape similar to what is seen in *Batrachognathus volans*. The right premaxilla is exposed laterally, while the left one is slightly displaced and exposed in anteromedial aspect. The dorsal process of the premaxilla seems to have extended for no further than half the height of the skull. It contacts an anterior process of the frontal, which is elongated and thin, as in *Anurognathus ammoni* (see Bennett 2007). The posterior process of the premaxillae participates on the occlusal jaw margin, and presumably contacted the maxillae, though the bones are slightly displaced and not in natural contact.

The maxilla and jugal are fused, with not visible sutures, forming a large bony structure, posterior to the premaxillae. It forms most of the jaw as well as the ventral border of the orbit. The jugo-maxilla structure houses 9 alveoli. The lacrimal process of the jugal is present on the anterior region of this structure. It forms the anteroventral border of the orbit, and the posteroventral margin of the nasoantorbital fenestra. It is incomplete dorsally, but is clearly slender, much higher than long. The nasal and the lacrimal cannot be distinguished.

It appears that both frontals are visible: the right one in lateral aspect, and the left one in medial aspect. They are both positioned on the posterodorsal region of the orbit, and take part in the dorsal margin of the skull itself. Their limits are not clear, but the dorsal margin of the right frontal is convex, as is the dorsal margin of the skull in lateral view. Posterior to the right frontal, two bones are tentatively interpreted as the right parietal and a misplaced right opisthotic.

A large bone bearing 9 alveoli forms most of the right upper jaw margin, and is here interpreted as a jugomaxilla complex, similar to the one reported for *Anurognathus ammoni* where the jugal overlays the maxilla laterally (Bennett 2007). The structure is seen in lateral view, and no sutures can be seen separating jugal from maxilla. The right jugomaxilla seems to be disarticulated from both the quadrate and the premaxilla.

A triangular bone located on the posterior margin of the orbit is tentatively interpreted as the postorbital. If this identification is correct, then the postorbital of *Sinomacrops* is quite different from that of *Anurognathus*, which is very slender (and dorsoventrally elongated). Thus, the postorbital of *Sinomacrops* would be more similar to that of some non-anurognathid pterosaurs such as *Dimorphodon* or rhamphorhynchids (e.g. Padian 1983, Wellnhofer 1991).

Ventral to the jugomaxilla, a rod-like bone is preserved, adjacent to the impression of another similar rod-like bone. These two rod-like bones are interpreted as either members of the hyoid apparatus, or members of the palate, which is composed of rod-like bones and bony processes (pterygoids, palatines, vomer, ectopterygoids) in *Anurognathus ammoni*, *Jeholopterus ningchengensis* and *Batrachognathus volans* (Riabini 1948, Bennett 2007, Yang *et al*. 2019).

A partial sclerotic ring is preserved, displaced from its natural position and located ventral to the posterior region of the skull. Though partially preserved, it is complete enough to allow for an estimation of its diameter. It is estimated as ~7 mm, what is close to the estimated diameter of the orbit (7.5 mm).

Mandible. An hemimandible is exposed beneath the skull (Fig. 3). No alveoli can be observed, suggesting that it is the left hemimandible in ventral view. We infer that this hemimandible is complete because its length equals that of the upper jaw. It is only slightly bowed, as in *Batrachognathus volans*, instead of strongly semicircular as in the jaws of *Dendrorhynchoides*, *Luopterus*, *Jeholopterus*, *Anurognathus* or *Vesperopterylus* (Ji & Ji 1998, Wang *et al.* 2002, Bennett 2007, Lü & Hone 2012, Lü *et al.* 2018, Hone 2020).

Dentition. A single preserved tooth crown is visible, displaced from the jaws and located near the anterodorsal region of the skull (Fig. 3). This tooth is slender and slightly recurved. At least 9 alveoli are present on the right maxilla. The alveoli on the right premaxilla are unclear. The first three maxillary alveoli are closely spaced, with the spacing between them being shorter than their diameter. Posteriorly, the spacing between the subsequent alveoli is subequal to their diameter.

Axial postcranium. Throughout the whole specimen, vertebrae are highly weathered and details of their anatomy cannot be retrieved (Fig. 2). Still, as the skeleton is almost complete, the lengths of each segment can be estimated, with 23 mm for the cervical series; 30 mm for the dorsal series; 1.1 mm for the sacral series; and > 36 mm for the caudal series. The sacral series thus seems to have been elongated, similarly to the condition seen in the possible anurognathid *Mesadactylus* (see Jensen & Padian, 1989). The rib of the first sacral is strongly inclined posteriorly, while the rib of the second sacral is less inclined (Fig. 5). This configuration is very similar to that of *Mesadactylus* (see Jensen & Padian, 1989). At least 9 pairs of ribs anterior to the sacral region can be seen (Fig. 2), all of which are long and slender, and interpreted as dorsal ribs. This is the same number of dorsal ribs seen in *Dendrorhynchoides* (Ji & Ji 1998), *Anurognathus* (Bennett 2007) and *Jeholopterus* (Wang *et al.* 2002). Concerning caudal vertebrae, only three incomplete remains of proximal caudal centra are present, near the sacral region. They are simple, lacking lateral processes.

Forelimb. The scapulae and coracoids of JPM-2012-001 are elongate and slender, as in other anurognathids (e.g. Bennett 2007, Lü *et al.* 2018). Although fragments of the bone tissue have been lost post-collection due to the brittle nature of the fossil, the remaining impression of the right humerus is quite clear upon close inspection. The deltopectoral crest is subrectangular, as can be better seen on the left side (Fig. 2). As in *Batrachognathus volans*, the deltopectoral crest of the humerus in JPM-2012-001 was reduced (less wide than proximodistally long, and less wide than humeral shaft) and rectangular in shape. The shape of the ulnar crest is rounded, but it is proximodistally shorter than the deltopectoral crest, as in other anurognathids (Döderlein 1923, Riabinin 1948, Ji & Ji 1998, Wang *et al.* 2002, Bennett 2007, Lü & Hone 2012, Lü *et al.* 2018, Yang *et al*. 2019). Incomplete preservation prevents the observation of any details of ulna and radius, although their lengths can be assessed due to their clear impressions on both sides. The right wing-finger preserves complete first, second and third wing phalanges (Fig. 2). The distal region of the third wing phalanx underlies the tibia on the matrix, but the distal end can be seen due to damage on the tibia, revealing the phalanx beneath. The distal end of the third wing phalanx seems to be slightly expanded, indicating a probable articular region for a fourth phalanx, which is not preserved. A free digit with a long, slender proximal phalanx and a robust, strongly recurved ungual is preserved.

Hindlimb. Neither femora are fully preserved in terms of bone tissue, though impressions of the lost regions remain on both sides so that their total lengths can be confidently measured (Fig. 2). The right femur is preserved in an approximately natural position relative to the pelvic region, and only part of the proximal region was lost, though an impression remains, showing that it was preserved in articulation with the pelvis. The left femur is displaced, but the proximal region is preserved. The distal region is lost, but an impression also remains. The tibia is quite elongate relative to the femur (Fig. 2), more so than in any other anurognathid (Table 1). On the right crus, tibia and fibula are incompletely ossified, and a gap can be seen between the two (Fig. 2). Despite damage on the proximal region of the right metatarsus, the distal region is well-preserved. It can be clearly seen that the metatarsal IV is shorter than metatarsals II and III (Fig. 5). A single ungual can be identified on the right pes, which is slightly less robust than the manual unguals (Fig. 6).

Ontogeny. Specimen JPM-2012-001 has not reached osteological maturity, as indicated by the incomplete degree of fusion of the skull bones. Scapula and coracoid seem to be fused, although it remains unclear. A fused puboischiadic plate is present, indicating the specimen must have reached at least "ontogenetic stage 4" of Kellner (2015) and is thus considered a subadult.

Phylogenetic analysis results

Our analysis produced 16 most parsimonious trees, with 1109 steps, CI of 0.458 and RI of 0.666. In the strict consensus tree (Fig. 7), the new species is the sister-group of *Batrachognathus volans*. The Anurognathinae were recovered with *Dendrorhynchoides* at the base, plus the newly recognized clade *Luopterus* + (*Jeholopterus* + *(Anurognathus* + *Vesperopterylus*)).

As in the results from Dalla Vecchia (2019), *"Dimorphodon" weintraubi* is placed as the sister-group of a clade containing all other anurognathids. Under the branch-based definition of the Anurognathidae given by Hone (2020), *"D." weintraubi* can be considered as a basal anurognathid. For the first time, the Anurognathidae is recovered as the sister group of Darwinoptera + Pterodactyloidea. The synapomorphies are discussed further below.

Discussion

Comparisons with other anurognathids

As detailed above, JPM-2012-001 exhibits a particular feature regarding its dentition: the first three maxillary alveoli are closely spaced, with the spacing between them being shorter than their diameter; while the spacing between the subsequent alveoli is subequal to their diameter. This pattern is unprecedented for anurognathids. In *Batrachognathus volans*, *Dendrorhynchoides curvidentatus*, *Jeholopterus ningchengensis* and *Anurognathus ammoni*, tooth spacing is constant and larger than tooth diameter (Riabinin 1948, Ji & Ji 1998, Ji & Yuan 2002, Bennett 2007). In *Vesperopterylus lamadongensis*, tooth spacing is also constant, and subequal to (only fractionally larger than) tooth diameter (Lü *et al.* 2018). The pattern of tooth spacing in *Luopterus mutoudengensis* is so far unclear (Lü & Hone 2012, Hone 2020).

Another particular feature is its tibiotarsus/femur length ratio, which is unique within anurognathids (and pterosaurs overall) in that the tibiotarsus is about twice as long as the femur (Table 2, Supplemental Table S1). In *Batrachognathus volans*, this same ratio is 1.75, while it ranges from 1.22 to 1.47 in other anurognathids (Table 2).

Sinomacrops bondei differs from *Batrachognathus volans* in tooth spacing, tibia/femur length ratio, and in exhibiting a relatively larger ulnar crest of the humerus (Riabinin 1948, Hone 2020). The new species differs from *Anurognathus*, *Jeholopterus* and *Vesperopterylus* in tooth spacing, tibia/femur length ratio, humerus deltopectoral crest shape (trapezoidal in the latter three taxa), and in exhibiting an elongate tail, longer than the dorsal series (Hone 2020). The new species also differs from *Luopterus mutoudengensis* and *Dendrorhynchoides curvidentatus* in the morphology of the deltopectoral crest of the humerus, which is relatively larger and triangular in shape in the latter two (Ji & Ji 1998, Hone & Lü 2012, Hone 2020).

Diversity of the Anurognathidae

It has been observed that some aspects of anurognathid morphology did not change from the Middle Jurassic (in the form of *Jeholopterus*) to the Early Cretaceous (in the form of *Dendrorhynchoides*; prior to the description of the even younger *Vesperopterylus*), such as skull shape, palate morphology and dentition (Unwin *et al.* 2000, Bennett 2007). This has led to the conclusion that the anurognathid bauplan was rather conservative (Unwin *et al.* 2000, Bennett 2007). Nonetheless, several features of anurognathid morphology exhibit some variation, what has been relatively poorly explored so far (Hone 2020). Here we argue that anurognathid morphological diversity is higher than previously thought.

Concerning the particular shape of the anurognathid jaw in dorsal/ventral views, we note that there exists some variation. The roundness of the jaws (both upper and lower) is relatively more pronounced in anurognathines, as can be seen particularly in *Anurognathus* (Bennett 2007), *Jeholopterus* (Wang *et al.* 2002, Ji & Yuan 2002), *Vesperopterylus* (Lü *et al.* 2018) and NJU–57003 (Yang *et al*. 2019). In these, the arching of the jaws is abrupt and approximately continuous (Fig. 8), describing a semicircular shape (Fig. 9). In contrast, in *Batrachognathus* and

Sinomacrops, the arching of the jaws is less pronounced and relatively more gradual (Fig. 8), making the jaws rather elliptical instead of semicircular (Fig. 9).

Some variation on tooth morphology is also found within anurognathids. The dentition of *Anurognathus ammoni* is homodont and was referred to as pupiform, given their resemblance to dipteran pupae (Bennett 2007). The only complete tooth preserved in the referred specimen of *Anurognathus ammoni* is short, has a subcylindrical base and tapers to a sharp end, being only slightly recurved (Bennett 2007). This is very similar to the condition seen in *Vesperopterylus lamadongensis*, except that in this taxon the teeth are relatively stouter (see Lü *et al.* 2018). However, the teeth in *Jeholopterus ningchengensis*, NJU–57003, *Dendrorhynchoides curvidentatus* and *Batrachognathus volans* are relatively longer and more recurved. The single tooth visible in the holotype of *Sinomacrops bondei* is superficially similar to these latter taxa. *Luopterus mutoudengensis* is unique within anurognathids, having been described as exhibiting a heterodont dentition comprising slender, sharp teeth anteriorly and relatively more robust, short teeth posteriorly (Lü & Hone 2012). However, recently, Hone (2020) interpreted that the purported robust teeth may in fact be bone shards.

According to Lü & Hone (2012) and Hone (2020), a noticeable amount of variation in anurognathids is also expressed through the shape of the deltopectoral crest of the humerus (Fig. 10), as follows: rounded for *Anurognathus ammoni*, alate for *Jeholopterus ningchengensis*, triangular for *Dendrorhynchoides curvidentatus* and *Luopterus mutoudengensis*, and sub-rectangular (or parallelogram shaped, Hone 2020) for *Batrachognathus*. However, in the holotype of *Anurognathus*, the structure is not rounded, but trapezoidal (Döderlein 1923, Wellnhofer 1991). Despite not clearly depicted as such in the line-drawings, the humeral deltopectoral crest of the second specimen of *Anurognathus* was also explicitly described as trapezoidal (see Bennett 2007), and is probably relatively smaller due to allometric growth. In *Vesperopterylus*, the deltopectoral crest of the humerus is also trapezoidal, very similar in shape to *Anurognathus* (see Lü *et al.* 2018). In the North Korea specimen, the deltopectoral crest of the humerus seems to be trapezoidal as well (Gao *et al.* 2009). Furthermore, even though the “alate” condition seen in *Jeholopterus* is unique to it, it is still very similar to the trapezoidal conditions of *Anurognathus* and *Vesperopterylus*, differing only in being longer and more curved – they are thus all coded as “trapezoidal” in our analysis (see Supplemental Information). Concerning other anurognathids, NJU–57003 is similar to *Dendrorhynchoides* and *Luopterus* in exhibiting a subtriangular deltopectoral crest of the humerus (Yang *et al*. 2019). In the holotype of *Sinomacrops bondei*, the impression of the deltopectoral crest of the humerus reveals it was subrectangular in shape, being similar to that of *Batrachognathus volans*, but different in that it is relatively shorter and that its distal margin is even straighter than in *B. volans* (Fig. 10A–B). *Sinomacrops* and *Batrachognathus* are further unique in exhibiting deltopectoral crests that are reduced in size, being less wide than the humeral shaft, and less wide than proximodistally long (Fig. 10A–B).

Still concerning the proximal region of the humerus, considerable variation can also be found in the shape of the ulnar crest. In *Batrachognathus volans* and *Sinomacrops bondei*, the distal margin of the ulnar crest is rounded (Fig. 10A–B). In *Dendrorhynchoides curvidentatus*, it is slightly more prominent, subtriangular (Fig. 10). In *Jeholopterus*, it is particularly reduced, and is also prominent (Fig. 10D). In *Anurognathus* and *Vesperopterylus*, it is relatively elongated and oriented obliquely to the humeral shaft (Fig. 10E–F).

Another interesting variation seen within anurognathids concerns the length of their caudal series and the morphology of their caudal vertebrae (Lü & Hone 2012, Costa *et al.* 2013, Jiang *et al.* 2014). *Batrachognathus* and the indeterminate specimens IVPP V16728 and NJU–57003 exhibit the typical non-pterodactyloid condition, with long tails (longer than femur length) and caudal vertebrae bearing long filiform processes of the zygapohyses and haemapophyses (Costa *et al.* 2013, Jiang *et al.* 2014, Yang *et al*. 2019). *Luopterus mutoudengensis* exhibits a relatively short caudal series, that is shorter than the dorsal series and equals 0.85 the femur length (Lü & Hone 2012). As for caudal vertebrae morphology, *Luopterus* was reported to bear filiform processes interpreted as haemapophyses (Lü & Hone 2012). Jiang *et al.* (2014) have suggested that *Luopterus mutoudengensis* possessed processes produced by both the zygapophyses and haemapophyses, and we agree this is rather likely. In our matrix, the haemapophyses processes are coded as present and the zygapophyses processes as "?" until a first-hand reassessment of the specimen is provided. In *Jeholopterus* (both specimens), the tail is most likely shorter than the femur, though details of vertebral morphology cannot be assessed (Wang *et al.* 2002, Ji & Yuan 2002, Jiang *et al.* 2014, Yang *et al*. 2019). Finally, *Anurognathus* and *Vesperopterylus* possess quite shortened tails (accounting for under 60% the femur length) and caudal vertebrae without any filiform processes, in a homoplastic condition relative to the Pterodactyloidea (see Jiang *et al.* 2014). In *Sinomacrops bondei*, even though the total extent of the caudal series is uncertain, the preserved impression indicates it was longer than the femur – in fact, longer than the entire hindlimb.

Intrarelationships of the Anurognathidae

Our phylogenetic analysis places *Sinomacrops bondei* alongside *Batrachognathus volans* forming the Batrachognathinae, separately from the clade containing all other Chinese anurognathids plus *Anurognathus ammoni* (the Anurognathinae as herein defined). Five synapomorphies support Batrachognathinae in our analysis: char. 269(2), humeral/femoral length proportion (over 1.6); char. 271(0) the width of the humeral deltopectoral crest (reduced, less wide than proximodistally long), char 272(3), the shape of the deltopectoral crest (subrectangular); char. 280(2), the shape of the ulnar crest of the humerus (rounded); and char. 367(2), the tibia/femur length proportion (over 1.7).

The Anurognathinae would be composed of, according to our results, *Dendrorhynchoides curvidentatus*, *Luopterus mutoudengensis*, *Jeholopterus ningchengensis*, *Anurognathus ammnoni* and *Vesperopterylus lamadongensis*. These taxa share the following synapomorphies: char. 30(2) the semicircular arching of the jaws, distinct from the elliptical one seen in batrachognathines, char. 244(1) caudal series shorter than the dorsal series, char. 275(1) deltopectoral crest subequal to humeral head in size,and char. 310(5) pteroid curved and subparallel-sided (Andres *et al.* 2014).

The non-monophyly of the genus *Dendrorhynchoides* englobing *D. curvidentatus* plus *D. mutoudengensis* (Lü & Hone 2012) is corroborated here, consistently with Wu *et al.* (2017) and Hone (2020). *Luopterus mutoudengensis* is recovered as the sister-group of the *Jeholopterus-Anurognathus-Vesperopterylus* clade, with which it shares char. 378(0), a straight last phalanx of pedal digit V (whereas this phalanx is curved in *Dendrorhynchoides curvidentatus*). The straight condition is a synapomorphy joining these taxa, while the curved condition is plesiomorphic for anurognathids and present at the base of the Novialoidea, as seen in *Campylognathoides*, *Dimorphodon weintraubi*, *Changchengopterus pani* and wukongopterids (Clark *et al.* 1998, Lü 2009, Padian 2008a,b, Wang *et al.* 2009, 2010).

The clade composed of *Jeholopterus ningchengensis*, *Anurognathus ammoni* and *Vesperopterylus lamadongensis* is supported by three synapomorphies: char. 272(1) deltopectoral crest of the humerus trapezoidal and broad, char 241(0) caudal vertebrae lacking filiform zygapophyses, and char. 242(0) caudal vertebrae lacking filiform haemapophyses.. The sister-group relationship between *Anurognathus ammoni* and *Vesperopterylus lamadongensis* is supported by one synapomorphy: char. 271(2), the complete loss of mid-cervical ribs.

Previous analyses had recovered disparate results. The results of Wang *et al.* (2005), derived from the matrix of Kellner (2003), indicated a basal position for *Anurognathus ammoni*, as the sister-group of a trichotomy comprising *Batrachognathus volans*, *Jeholopterus ningchengensis* and *Dendrorhynchoides curvidentatus*, which thus comprised the Batrachognathinae according to this topology. The relationship between *Batrachognathus volans*, *Jeholopterus ningchengensis* and *Dendrorhynchoides curvidentatus* was based on the following synapomorphy: a very large humerus, with a humeral/femoral length proportion over 1.40 (Kellner 2003, Wang *et al.* 2005).

Such ratio (humeral/femoral length proportion) equals 1.2-1.25 for *Anurognathus ammoni*, 1.43 for *Dendrorhynchoides curvidentatus*, 1.52-1.55 for *Jeholopterus ningchengensis*, and 1.93 for *Batrachognathus volans* (Table 2). As such, it can be seen that the value for *Dendrorhynchoides curvidentatus* and *Jeholopterus* are not that large, not quite close to *Batrachognathus* but actually closer to the one found in *Anurognathus*. Furthermore, all anurognathids subsequently described exhibit such ratios under 1.40: *Vesperopterylus lamadongensis* (1.35) and *Luopterus mutoudengensis* (1.28). Thus, all anurognathids exhibit a humeral/femoral length ratio between 1.2 and 1.55, except for *Sinomacrops bondei* (1.77) and *Batrachognathus volans* (1.93). In order to better investigate the informative value of this morphometric character, we categorized it into discrete states by subjecting a comprehensive morphometric dataset for pterosaurs (see Supplemental Table 1) to a mixture model analysis using the software PAST (see Material and Methods). As a result, we found the following categories: humerus/femur length ratio up to 0.6 (state 0), over 0.6 and under 1.6 (state 1), and equal to 1.6 or over (state 2). We found state 2 to correspond to a synapomorphy for the clade *Sinomacrops* + *Batrachognathus*, being exclusive for these two taxa among pterosaurs except for "*Huaxiapterus" corollatus* (Supplemental Table 1).

In the analysis by Wu *et al.* (2017), a polytypic genus *Dendrorhynchoides* (englobing *D. curvidentatus* and *D. mutoudengensis*) was not recovered as monophyletic. *Dendrorhynchoides curvidentatus* fell at the base of the group, while *Luopterus mutoudengensis* fell as the sister-group of *Batrachognathus volans*. In this analysis (Wu *et al.* 2017), the clade comprising all other anurognathids to the exclusion of *D. curvidentatus* was supported by one synapomorphy: a fifth pedal digit phalanx 2 straight, instead of curved as in *D. curvidentatus*. This bone is clearly curved in *D. curvidentatus* (see Ji & Ji 1998) and straight in *Luopterus mutoudengensis*, *Anurognathus ammoni* and *Jeholopterus ningchengensis* (Wang *et al.* 2002, Bennett 2007, Lü & Hone 2012), however, it is unknown in *Batrachognathus volans* (see Riabinin 1948), as well as in *Sinomacrops bondei*, and thus is not informative concerning the position of *Batrachognathus*.

More recently, in the analysis of Longrich *et al.* (2018), also derived from Andres *et al.* (2014), the results recovered *Anurognathus ammoni* as the sister-group of *Jeholopterus ningchengensis*, with *Dendrorhynchoides curvidentatus* as the next successive sister-group, and then *Batrachognathus volans* at the base of the group. *Luopterus mutoudengensis* was not included in that analysis. Such topology is compatible with the one presented here, which differs only by the inclusion of *Luopterus*, *Vesperopterylus* and *Sinomacrops*.

Phylogenetic placement of the Anurognathidae

Previous works. The interrelationships of anurognathids have been even more obscure than their intrarelationships. Anurognathids have been included in tens of computed phylogenetic analyses, although the cladistic hypotheses concerning their placement can be narrowed down to a total of five (Fig. 11).

In the analysis presented by Kellner (2003), the Anurognathidae have been interpreted as the basal-most known pterosaur lineage (Fig. 11A), as the sister-group of a clade containing all other pterosaurs. This result was reproduced by other workers (Bennett 2007, Lü *et al.* 2018). As anurognathids span from the Callovian to the Aptian, this placement would imply in an extensive ghost lineage, as the pterosaur record dates back to the Carnian-Norian (see Kellner 2003). Later versions of this matrix including darwinopterans preserve the same position for the Anurognathidae (e.g. Wang *et al.* 2009). More recent versions of this data set focus solely on eupterodactyloids and do not contain a comprehensive number of non-pterodactyloids (e.g. Wang *et al.* 2012, Holgado *et al.* 2019, Pêgas *et al.* 2019).

The analyses of Unwin (1992, 1995, 2003) recovered anurognathids as the sister-group of the clade *Campylognathoides* + Breviquartossa (=Rhamphorhynchidae + Pterodactyloidea), which is equivalent to the Novialoidea *sensu* Kellner (2003) (Fig. 10B). Recent versions of this matrix, comprehending further non-pterodactyloids (including darwinopterans), preserve the same position for the Anurognathidae (e.g. Codorniu *et al.* 2016). However, it is interesting to observe that Unwin (2003) also discussed the possibility that anurognathids were, in fact, the sister-group of the Pterodactyloidea, although the strict consensus tree ultimately favored their interpretation as the sister-group of the Novialoidea. Unwin (2003) noted that anurognathids shared with pterodactyloids a reduction of the cervical ribs and reduction of the caudal series, and stated that a possible close relationship between them was worthy of further investigation. Possible relationships between anurognathids and pterodactyloids had already been discussed also by Young (1964).

The analyses of Dalla Vecchia (2009, 2014) recovered Anurognathidae as the sister-group of the Pterodactyloidea, with *Rhamphorhynchus* as the next successive sister-group. However, these analyses did not include any member of the Darwinoptera. More recently, the subsequent analyses by Britt *et al.* (2018) and Dalla Vecchia (2019), which are more comprehensive (Fig. 11C) and incorporate darwinopterans, have produced a different result, with Anurognathidae being the sister-group of the Breviquartossa (Rhamphorhynchidae + Monofenestrata), and thus within Novialoidea but outside Breviquartossa. A sister-group relationship between the Anurognathidae and the Breviquartossa was also proposed previously by Viscardi *et al.* (1999).

Under the hypothesis first put forward by Andres *et al.* (2010), the Anurognathidae are monofenestratans and are closer to pterodactyloids than darwinopterans and rhamphorhynchids (Fig. 11D), thus being comprised within the Breviquartossa and the Monofenestrata This proposition thus echoed the suspicion put forward by Unwin (2003) that anurognathids could, perhaps, be closely related to pterodactyloids; as well as the past results from Dalla Vecchia (2009, 2014) that were later modified (Britt *et al.* 2018, Dalla Vecchia 2019).

The most recent hypothesis was put forward by Vidovic & Martill (2017), whose phylogenetic analysis recovered the Anurognathidae as a clade comprised within Scaphognathidae (Fig. 11E). Similar to the proposal of Dalla Vecchia (2014, 2019), this hypothesis also places anurognathids within breviquartossans and outside the Monofenestrata. However, Vidovic & Martill (2017) expressed concerns about this result for anurognathids, noting that "*[t]heir deeply nested placement within Scaphognathidae is likely to be due to a lack of transitional-morphs combined with their paedomorphism*" (Vidovic & Martill 2017, p. 9). They further noted that "*[t]he paedomorphic characters exhibited by anurognathines (e.g. reduced rostrum length, large orbit, deep skull, shorter caudal vertebrae) might be the reason some researchers (e.g. Kellner 2003; Wang et al. 2009) find them as the most basal taxa in Pterosauria*" (Vidovic & Martill 2017, p. 9).

It is worth noticing that anurognathids have also been regarded as possibly related to *Dimorphodon* (Kuhn 1967, Wellnhofer 1978), based mainly on similarities in skull shape (high skull with a convex dorsal margin in lateral view, and a subvertical quadrate). No computed phylogenetic analyses have recovered a close relationship between dimorphodontids and anurognathids, so far.

In summary, among all proposed hypotheses, three of them converge in recognizing a clade that includes Rhamphorhynchidae, Anurognathidae, Darwinoptera and Pterodactyloidea (Andres *et al.* 2010, Vidovic & Martill 2017, Dalla Vecchia 2019), though disagreeing on the relationships between these subgroups. Two hypotheses (Andres *et al.* 2010; Vidovic & Martill 2017) converge in recovering anurognathids as members of the Breviquartossa. Only the phylogenetic analyses of Andres *et al.* (2010) found support for the monofenestratan nature of anurognathids, although Unwin (2003) already expressed some consideration towards this hypothesis.

Present work. Our dataset combines discrete characters coming from previous contributions (Kellner 2003, Unwin 2003, Dalla Vecchia 2009, 2019, Andres *et al.* 2010, 2014, Vidovic & Martill 2017). According to the present results, anurognathids are basal monofenestratans, and thus are also members of the Novialoidea and of the Breviquartossa. As our results have produced a novel topology, this warrants some discussion.

According to our results, anurognathids exhibit the following synapomorphies of the Novialoidea:

Character 192(0). Dentition, variation in crown shape along the upper jaw: absent; and char. 193(0) for the lower jaw (Unwin 2003, char. 19; Dalla Vecchia 2019 char. 37, and char. 38 for the lower jaw). Remarks: the secondary loss of heterodonty (which is present in basal pterosaurs) had already been recovered previously as a synapomorphy of the Novialoidea (Andres *et al.* 2014, Dalla Vecchia 2014, 2019).

Character 340(1). Postacetabular process of the illium length: shorter than preacetabular process (Vidovic & Martill 2017, char. 212). This feature had already been recovered as a synapomorphy of the Novialoidea (Vidovic & Martill 2017). It can be seen in *Dendrorhynchoides* (Ji & Ji 1998), *Jeholopterus* (Wang *et al.* 2002) and *Anurognathus* (Bennett 2007).

Character 380(2). Pedal digit V, phalanx 2, length: shorter than preceding phalanx (Vidovic & Martill 2017, char. 195). This feature is primitive for novialoids as seen in *Campylognathoides* (Padian 2008b), *Sordes* (Unwin & Bakhurina 1994), *Scaphognathus* (Bennett 2014), darwinopterans (Wang *et al* 2010) and pterodactyloids (see Vidovic & Martill 2017). It is present in *Jeholopterus* and *Luopterus* (Wang *et al.* 2002, Hone & Lü 2012), although it is reversed in *Dendrorhynchoides* and *Anurognathus* (Ji & Ji 1998, Bennett 2007).

Anurognathids further share with the Breviquartossa the following synapomorphies:

Character 48 (1). Premaxilla extending to orbit, but no further. This feature had already been recovered as a synapomorphy of the Breviquartossa by Unwin (2003). This feature can be seen in *Anurognathus* (Bennett 2007).

Character 147(1). Mandible, surangular eminence: absent (Unwin 2003, char. 16). Remarks: the secondary loss of this feature had already been considered a synapomorphy of the Breviquartossa (Unwin, 2003). The feature is absent in *Anurognathus ammoni* (Bennett 2007) and cannot be assessed in other species.

Character 179(2). Dentition, distal teeth, spacing relative to successive teeth: more than diameter of teeth (Andres *et al.* 2014). This character had already been recovered as a synapomorphy of the Breviquartossa (anurognathids included) by Andres *et al.* (2014).

Character 284(1). Humerus, shaft, cross-section: tapered (Andres *et al.* 2014). Remarks: this feature, as opposed to a subcircular cross-section of the humeral shaft, has already been recovered as a synapomorphy of the Breviquartossa, anurognathids included (Andres *et al.* 2014).

Character 368(1). Fibula,relative_length: shorter than tibia (Dalla Vecchia 2009 char. 68, modified from Unwin 2003 char. 8). Remarks: this feature has already been recovered as a synapomorphy of the Breviquartossa, including anurognathids, by Dalla Vecchia (2009).

Char. 373(2). Metatarsals, relative length of metatarsal IV: (Unwin 2003, char. 21). This feature has already been recovered as a synapomorphy of the Breviquartossa, and the clade name actually derives from this feature (Unwin 2003). In anurognathids, this feature can be seen in *Vesperopterylus* and *Jeholopterus*, although metatarsal IV is only slightly shorter than the metatarsal III (by, approximately, the width of their diaphyses; Fig. 12). The length difference is thus less conspicuous than in *Rhamphorhynchus* or *Scaphognathus* (Wellnhofer 1975a, 1978), but similar to that seen in *Sordes* (Wellnhofer 1978), *Darwinopterus* (Lü *et al.* 2009), *Pterodactylus antiquus* or *Diopecephalus kochi* (Wellnhofer 1970, 1978). The feature is lost in *Anurognathus*, in which metatarsals I-IV are subequal in length (Bennett 2007).

Character 378(1). Pedal digit V, phalanx 2, shape: curved (Kellner 2003, char. 74). Remarks: primitively, this phalanx is straight, as seen in non-breviquartossans such as *Campylognathoides* (Wellnhofer 1978, Padian 2008b), *Dimorphodon* (Padian 1983), and Triassic forms (Dalla Vecchia 2014). The phalanx is curved in rhamphorhynchids (Wellnhofer 1975, 1978, Lü *et al.* 2012, Hone *et al.* 2012), *Dendrorhynchoides* (Ji & Ji 1998) and *Kunpengopterus* (Wang *et al.* 2010, Cheng *et al.* 2017), and changes to “bent, angled” (state 2 of same character) in some taxa such as *Dorygnathus*, *Scaphognathus* and *Darwinopterus* (Andres *et al.* 2014, Vidovic & Martill 2017, Dalla Vecchia 2019), and reverses to “straight” (state 0) in the *Luopterus- Jeholopterus-*

Anurognathus clade, in which this phalanx is straight (Wang *et al.* 2002, Lü & Hone 2012, Bennett 2007, Andres *et al.* 2014).

Our analysis has also recovered the Digibrevisauria, coined for a clade that comprises the Scaphognathidae and the Monofenestrata, to the exclusion of rhamphorhynchids (Vidovic & Martill 2017). Anurognathids show the following features that were recovered as synapomorphies of the Digibrevisauria: 236(1) proximal caudal vertebrae lack distinct lateral processes; 275(2) humerus deltopectoral crest not as long as the humeral head is wide (seen in *Sinomacrops* and *Batrachognathus*, reversed to state 1 in the clade containing the remaining anurognathids); 313(1) metacarpal IV lacks a *crista metacarpi*; 375(1) phalanges of pedal digit IV unequal in length with the distal phalanx larger than all those preceding it, and 376(1) phalanges 2 and 3 of pedal digit IV are squared or shorter than they are wide (Vidovic & Martill, 2017).

Within digibrevisaurians, anurognathids were recovered as basal monofenestratans. The Monofenestrata have been phylogenetically defined by Andres *et al.* (2014) as a synapomorphy-based clade, defined by the presence of a confluent nasoantorbital fenestra synapomorphic with the one seen in *Pterodactylus antiquus*. In summary, considering the interpretation put forward by Andres *et al.* (2010) that anurognathids possess a nasoantorbital fenestra (corroborated here), this would mean that the clade Anurognathidae + (Darwinoptera + Pterodactyloidea) corresponds to the Monofenestrata. According to our results, thus, anurognathids are basal monofenestratans. The Monofenestrata were recovered based on the following 4 features:

Character 15(1): Confluent nasoantorbital fenestra. Remarks: most workers have coded a confluent nasoantorbital fenestra as absent for anurognathids (Kellner 2003, Unwin 2003, Bennett 2007, Lü *et al.* 2018, Vidovic & Martill 2018), except for Andres *et al.* (2010, 2014) and Dalla Vecchia (2019). Due to the extremely reduced preorbital region and the small absolute size of anurognathids, investigation of their preorbital fenestration is indeed difficult. In most specimens, the situation cannot be confirmed, such as the holotypes of *Jeholopterus ningchengensis*, *Dendrorhynchoides curvidentatus*, *Luopterus mutoudengensis* and *Vesperopterylus lamadongensis*, and also the specimen NJU–57003. The only specimen for which a skull element was tentatively interpreted as an ascending process of the maxilla (and thus a bony bar effectively separating naris and antorbital fenestra, as two distinct openings) is the second specimen of *Anurognathus ammoni* (Bennett 2007). The identification of this process has been reviewed and challenged by Andres *et al.* (2010), who argued that the purported process could not be unequivocally identified as an ascending maxillary process separating the nares from the antorbital fenestra, as it could only be seen on the right side, was a faint impression, and was displaced, so that even its natural orientation cannot be unambiguously assessed. Based on its rough location and shape, we offer a tentative interpretation for it as a palatal element. Andres *et al.* (2010) further noted that there are two previously described anurognathid specimens in which the preorbital region is well preserved and the ascending processes of the maxilla is absent on both sides: the holotype of *Batrachognathus* and CAGS IG 02-81 (see Riabinin 1948, Ji & Yuan 2002, Andres *et al.* 2010, Yang *et al*. 2019, and also Fig. 13). In accordance, in the small preorbital region of *Sinomacrops*, only a single opening is present. We thus favor the interpretation of Andres *et al.* (2010) that a nasoantorbital fenestra is present in anurognathids (Fig. 13).

Character 95(1). Jugal, lacrimal process, subvertical. Remarks: this feature has already been recovered as a synapomorphy of a clade containing Monofenestrata + *Sordes* (Andres *et al.* 2014). In the present analysis, we coded this character as “anteriorly inclined” (state 0) for *Sordes* (as in the dataset from Vidovic & Martill 2017), so that the feature is restricted to the Monofenestrata.

Character 216(1) Atlantoaxis fusion. Remarks: this feature has already been recovered as a synapomorphy of the Monofenestrata, including anurognathids (Andres *et al.* 2014). This feature is present in *Anurognathus* (Wellnhofer 1975a, Bennett 2007).

Character 221(1). Mid-cervical vertebrae, ribs: short. Remarks: as already noticed before (Unwin 2003), the reduction of mid-cervical ribs can be seen in anurognathids and pterodactyloids. Short mid-cervical ribs have been reported for *Jeholopterus* (see Wang *et al.* 2002) and are absent (state 2 of this same character) in *Anurognathus* and *Vesperopterylus* (see Bennett 2007, Lü *et al.* 2018). The mid-cervical ribs are also short (and quite slender) in the Darwinoptera (Wang *et al.* 2009, 2010, Cheng *et al.* 2017).

Finally, Darwinoptera + Pterodactyloidea is supported by the following features that are absent in anurognathids: char 1(1) elongated skull, over four times skull height (Dalla Vecchia 2019, char. 1), char. 112(1), the craniomandibular joint is located under the orbit (and not posterior to it), char. 230(0) first dorsal rib larger than others (Vidovic & Martill 2017, char. 236; homoplastic with *Eudimorphodon*), char. 311(2) pteroid over 2/5 ulnar length (Dalla Vecchia 2019 char. 70), char. 317(0) metacarpal IV posterior crest absent (Vidovic & Martill 2017 char. 164; present in *Dendrorhynchoides*, see Ji & Ji 1998), char. 366(1) femur less than twice the length of metacarpal IV (Kellner 2003 char. 71; homoplastic with Rhamphorhynchini, *Eudimorphodon*, *Fenghuangopterus* and *Sinomacrops*), 370(1) splayed metatarsals (Dalla Vecchia 2009, char.70; homoplastic with rhamphorhynchids, *Sordes* and *Scaphognathus*), and char. 375(3) distal and proximal phalanges of pedal digit IV longer than those between (reversing to state 1, proximal phalanx is the largest, in the Pterodactyloidea).

In summary, these results provide support for the inclusion of the Anurognathidae within the Breviquartossa and, more specifically, within the Monofenestrata (as in Andres *et al.* 2010, 2014), though not closer to pterodactyloids than darwinopterans. In this way, these results represent a new hypothesis for the position of the group, being somewhat intermediate between the results of Andres *et al.* (2010) and of Dalla Vecchia (2009, 2019). Still, as well-put by a reviewer (N. Jagieslka), pterosaur phylogeny is a "*fluid, ever-expanding field*", and as noted by Vidovic & Martill (2017, p.9), studies of anurognathid phylogeny are hampered by their "*aberrant morphology*". Thus, much work will be needed before the phylogenetic position of anurognathids stabilizes (hopefully with the discovery of "transitional-morphs"), although the present results do lend support for their interpretation as monofenestratans.

A remark on "*Dimorphodon*" *weintraubi*

This is a North American Pliensbachian taxon, represented by a partial skeleton still mostly undescribed (Clark *et al.* 1989) and awaiting a detailed description. If "*D.*" *weintraubi* is taken into consideration, it is recovered as the immediate sister-group of the clade containing all other anurognathids (Dalla Vecchia 2009, 2014, 2019, present work). If Anurognathidae is considered as a branch-based clade (*sensu* Hone, 2020; the most inclusive clade containing *Anurognathus* but not *Scaphognathus*, *Dimorphodon* or *Pterodactylus*), then *"D." weintraubi* would be a basal anurognathid. This relationship is supported in our analysis by two synapomorphies: char. 326(0) first wing phalanx under 0.35 total wing digit length, and char. 331(2) wing phalanx 3 shorter than phalanx 1. According to the results by Britt *et al.* (2018) and Dalla Vecchia (2019), they also share a boot-like prepubis. "*D.*" *weintraubi* further exhibits a conspicuously shortened metatarsal IV (Clark *et al.* 1998), typical of the Breviquartossa.

If this relationship and our new results are correct, then "*D.*" *weintraubi* pushes the origin of the Monofenestrata back to the Early Jurassic (Pliensbachian). The Early-Middle Jurassic pterosaur record is rather scanty, and the diversity of monofenestratans during that time might have been higher than previously thought. Such scenario is not that farfetched, given that the sister-group of the Dibigrevisauria, the Rhamphorhynchidae, dates back to the Toarcian. A detailed redescription and reassessment of "*D.*" *weintraubi* is of the uttermost importance.

Conclusions

JZMP-2107500095 represents a new anurognathid, here named *Sinomacrops bondei* (Fig. 14). It is the second anurognathid from the Tiaojishan Formation, and the first anurognathid specimen to exhibit a skull exposed in lateral view. In our new phylogenetic analysis, it is recovered as the sister-group of *Batrachognathus volans*, with which it comprises the Batrachognathinae. All other taxa were recovered as closer to *Anurognathus*. The exclusion of *Luopterus mutoudengensis* from the genus *Dendrorhynchoides* is corroborated. *Vesperopterylus lamadongensis* is recovered as the sister-group of *Anurognathus ammoni*, with *Jeholopterus ningchengensis* as their successive sister-group.

Some previous interpretations of anurognathid morphology and systematics have relied on limited available information. With time and new specimens being discovered, new data have been provided and new interpretations were presented. For this reason, each new specimen is crucial for the understanding of the group. The present information available leads us to interpret anurognathids as basal members of the Monofenestrata, as the sister-group of Darwinoptera + Pterodactyloidea.

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References

Andres, B., Clark, J. M., and Xing, 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** (1), 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., 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.

Bardin, J., Rouget, I., Yacobucci, M. M., & Cecca, F. 2014. Increasing the number of discrete character states for continuous characters generates well-resolved trees that do not reflect phylogeny. *Integrative Zoology*, **9**(4), 531–541.

Bennett, S. C. 2007. A second specimen of the pterosaur *Anurognathus ammoni*. *Paläontologische Zeitschrift*, **81** (4), 376.

Bennett, S. C. 2014. A new specimen of the pterosaur *Scaphognathus crassirostris*, with comments on constraint of cervical vertebrae number in pterosaurs. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, **271** (3), 327-348.

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** (9), 1386–1392.

Clark, J. M., Hopson, J. A., Fastovsky, D. E., and Montellano, M. 1998. Foot posture in a primitive pterosaur. *Nature*, **391** (6670), 886–889.

Codorniú, L., Carabajal, A. P., Pol, D., Unwin, D. M. and Rauhut, O. W. 2016. A Jurassic pterosaur from Patagonia and the origin of the pterodactyloid neurocranium. *PeerJ*, **4**, e2311.

Colless, D.H. 1985. On "character" and related terms. *Systematic Zoology*, **34**, 229-233.

Costa, F. R., Alifanov, V., Dalla Vecchia, F. M., Kellner, A. W. A. 2013. On the presence of an elongated tail in an undescribed specimen of *Batrachognathus volans* (Pterosauria: Anurognathidae: Batrachognathinae). *In* Sayão, J. M., Costa, F. R., Bantim, R. A. M., Kellner, A. W. A. (eds). *Short communications, Rio Ptero 2013 – International Symposium on Pterosaurs*. Rio de Janeiro: Universidade Federal do Rio de Janeiro, Museu Nacional, 54–56.

Chang, S. C., Zhang, H., Renne, P. R., and Fang, Y. 2009. High–precision 40Ar/39Ar age for the Jehol Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **280** (1–2), 94–104.

Cheng, X., Wang, X., Jiang, S., & Kellner, A. W. 2012. A new scaphognathid pterosaur from western Liaoning, China. *Historical Biology*, **24** (1), 101-111.

Cheng X, Wang X, Jiang S, Kellner A W. 2015. Short note on a non-pterodactyloid pterosaur from Upper Jurassic deposits of Inner Mongolia, China. *Historical Biology*, **27** (6), 749-754.

Cheng, X., Jiang, S., Wang, X., and Kellner, A. W. 2017. New anatomical information of the wukongopterid *Kunpengopterus sinensis* Wang et al., 2010 based on a new specimen. *PeerJ*, **5**, e4102.

Chu, Z., He, H., Ramezani, J., Bowring, S. A., Hu, D., Zhang, L., ... & Guo, J. 2016. High-precision U-Pb geochronology of the Jurassic Yanliao Biota from Jianchang (western Liaoning Province, China): Age constraints on the rise of feathered dinosaurs and eutherian mammals. *Geochemistry, Geophysics, Geosystems*, **17** (10), 3983-3992.

Dalla Vecchia, F. M. 1998. New observations on the osteology and taxonomic status of *Preondactylus buffarinii* Wild, 1984 (Reptilia, Pterosauria). *Bollettino della Societá Paleontologica Italiana*, **36**, 355–366.

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

Dalla Vecchia, F. M. 2009. Anatomy and systematics of the pterosaur *Carniadactylus* gen. n. *rosenfeldi* (Dalla Vecchia, 1995). *Rivista Italiana di Paleontologia e stratigrafia*, **115** (2), 159–188.

Dalla Vecchia, F. M. 2014. Triassic pterosaurs. *Geological Society, London, Special Publications*, **379** (1), 119–155.

Dalla Vecchia, F. M. 2018. Comments on Triassic pterosaurs with a commentary on the" ontogenetic stages" of Kellner (2015) and the validity of *Bergamodactylus wildi*. *Rivista Italiana di Paleontologia e Stratigrafia*, **124** (2).

Dalla Vecchia, F. M. 2019. *Seazzadactylus venieri* gen. et sp. nov., a new pterosaur (Diapsida: Pterosauria) from the Upper Triassic (Norian) of northeastern Italy. *PeerJ*, **7**, e7363.

Dalla Vecchia, F. M., Wild, R., Hopf, H., and Reitner, J. 2002. A crested rhamphorhynchoid pterosaur from the Late Triassic of Austria. *Journal of Vertebrate Paleontology*, **22** (1), 196–199.

Döderlein, L. 1923. *Anurognathus ammoni* ein neuer Flugsaurier. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftlichen*, **1923**, 117–164 **Elgin, R. A., Hone, D. W., & Frey, E. 2011.** The extent of the pterosaur flight membrane. *Acta Palaeontologica Polonica*, **56**(1), 99-111.

Fitzhugh, K. 2006. The philosophical basis of character coding for the inference of phylogenetic hypotheses. *Zoologica scripta*, **35**(3), 261-286.

Gao, K. Q., and Shubin, N. H. 2012. Late Jurassic salamandroid from western Liaoning, China. *Proceedings of the National Academy of Sciences*, **109** (15), 5767–5772.

Gao, K. Q., Li, 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. *J Paleontol Soc Korea*, **25** (1), 57–61.

Goloboff, P. A., Farris, J. S., and Nixon, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24** (5), 774–786.

Habib, M. B. 2011. Functional morphology of anurognathid pterosaurs. *In Geological Society of America Abstracts with Programs* **43** (1), 118.

Holgado, B., Pêgas, R. V., Canudo, J. I., Fortuny, J., Rodrigues, T., Company, J., and Kellner, A. W. 2019. On a new crested pterodactyloid from the Early Cretaceous of the Iberian Peninsula and the radiation of the clade Anhangueria. *Scientific reports*, **9** (1), 1–10.

Hone, D. W. 2020. A review of the taxonomy and palaeoecology of the Anurognathidae (Reptilia, Pterosauria). *Acta Geologica Sinica-English Edition*. In press.

Huang D. 2015. Yangliao biota and Yanshan movement (in Chinese). *Acta Palaeontologica Sinica*, **54**, 501–546.

Huang D. 2016. *The Daohugou Biota (in Chinese).* Shanghai: Shanghai Scientific & Technical Publishers. 332 pp.

Huang D. 2019. Jurassic integrative stratigraphy and timescale of China. *Science China Earth Sciences*, **62,** 223–255.

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*, 364–373.

Ji, S. and Ji, Q. 1998. Discovery of a new pterosaur in Western Liaoning, China. *Acta Geologica Sinica* **71**, 115.

Ji, Q., and Yuan, C. X. 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** (2), 221–224.

Jiang, S., Wang, X., Cheng, X., Costa, F. R., Huang, J., and Kellner, A. W. 2014. Short note on an anurognathid pterosaur with a long tail from the Upper Jurassic of China. *Historical Biology*, **27** (6), 718–722.

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

Kellner, A. W., Wang, X., Tischlinger, H., Campos, D. A., Hone, D. W., and Meng, X. 2010. The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane. *Proceedings of the Royal Society B: Biological Sciences*, **277** (1679), 321–329.

Kuhn, O. 1967. *Die fossile Wirbeltierklasse Pterosauria*. Krailing bei München, Oeben.

Li B, Cheng J, Liu M, Yang F, Wu Z, Du J. 2019. Formation age and geochemical characteristics of the Tiaojishan Formation in the Western Liaoning Province (in Chinese). *Geological Review*, **65**, 63-64.

Liu, Y., Liu, Y., and Yang, Z. 2006. U-Pb zircon age for the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. *Chinese Science Bulletin*, **51** (21), 2634-2644

Liu Y, Kuang H, Jiang X, Peng N, Xu H, Sun H. 2012. Timing of the earliest known feathered dinosaurs and transitional pterosaurs older than the Jehol Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **323**, 1–12.

Longrich, N. R., Martill, D. M., and Andres, B. 2018. Late Maastrichtian pterosaurs from North Africa and mass extinction of Pterosauria at the Cretaceous–Paleogene boundary. *PLoS biology*, **16** (3), e2001663.

Lü, J. 2009. A new non-pterodactyloid pterosaur from Qinglong County, Hebei Province of China. *Acta Geologica Sinica-English Edition*, **83** (2), 189-199.

Lü, J., and Bo, X. 2011. A new rhamphorhynchid pterosaur (Pterosauria) from the Middle Jurassic Tiaojishan Formation of western Liaoning, China. *Acta Geologica Sinica-English Edition*, **85** (5), 977-983.

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

Lü, J. C., Fucha, X. H., and Chen, J. M. 2010. A new scaphognathine pterosaur from the Middle Jurassic of western Liaoning, China. *Diqiu Xuebao(Acta Geoscientica Sinica)*, **31** (2), 263-266.

Lü J, Jin X, Gao C, Du T, Ding M, Sheng Y, Wei X. 2013. Dragons of the Skies (recent advances on the study of pterosaurs from China) (in Chinese). *Zhejiang Science & Technology Press*, **127**.

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.

Lü JC, Unwin DM, Jin XS, Liu YQ, and Ji Q. 2009. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. Proceedings of the Royal Society B: Biological Sciences **277**(1680), 383-389.

Lü, J., Unwin, D. M., Zhao, B., Gao, C., & Shen, C. 2012. A new rhamphorhynchid (Pterosauria: Rhamphorhynchidae) from the Middle/Upper Jurassic of Qinglong, Hebei Province, China. *Zootaxa*, **3158**(1), 1-19.

Mongiardino Koch, N., Soto, I. M., & Ramírez, M. J. 2015. Overcoming problems with the use of ratios as continuous characters for phylogenetic analyses. *Zoologica Scripta*, **44**(5), 463-474.

Naish, D., Simpson, M., & Dyke, G. 2013. A new small-bodied azhdarchoid pterosaur from the Lower Cretaceous of England and its implications for pterosaur anatomy, diversity and phylogeny. *PloS one*, **8**(3), e58451.**Padian, K. 1983.** Osteology and functional morphology of *Dimorphodon macronyx* (Buckland) (Pterosauria: Rhamphorhynchoidea) based on new material in the Yale Peabody Museum. *Postilla*, **189**, 1–44.

Padian, K. 2008a. The Toarcian (Early Jurassic) pterosaur *Dorygnathus* Wagner, 1860. *Palaeontology*, **80**, 1–64.

Padian, K. 2008b. The Early Jurassic pterosaur *Campylognathoides* Strand, 1928. *Palaeontology* **80**, 65–107.

Pêgas, R. V., Holgado, B. and Leal, M. E. C. 2019. On *Targaryendraco wiedenrothi* gen. nov. (Pterodactyloidea, Pteranodontoidea, Lanceodontia) and recognition of a new cosmopolitan lineage of Cretaceous toothed pterodactyloids. *Historical Biology*, **2019**, 1–15.

Riabinin, A. N. 1948. Remarks on a flying reptile from the Jurassic of Kara-Tau. [In Russian.] *Akademii Nauk,* *Paleontological Institute, Trudy* **15**, 86–93.

Sullivan C, Wang Y, Hone DWE, Wang YQ, Xu X, Zhang FC. 2014. The vertebrates of the Jurassic Daohugou Biota of northeastern China. *Journal of Vertebrate Paleontology*, **34**(2), 243–280.

Thiele, K. 1993. The Holy Grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics*, **9**, 275–304.

Unwin, D. M., & Bakhurina, N. N. 1994. *Sordes pilosus* and the nature of the pterosaur flight apparatus. *Nature*, **371**(6492), 62-64.

Unwin, D. M., Lü, J., and Bakhurina, N. N. 2000. On the systematic and stratigraphic significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China. *Fossil Record*, **3**(1), 181–206.

Unwin, D. M. 1992. The phylogeny of the Pterosauria. *Journal of Vertebrate Paleontology*, **12**(3), 57A.

Unwin, D. M. 1995. Preliminary results of a phylogenetic analysis of the Pterosauria (Diapsida: Archosauria)', in *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*. China Ocean Press Beijing, China, pp. 69–72.

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

Vidovic, S. U. 2018. Transformation of Quotient Values for their use as Continuous Cladistic Characters. *bioRxiv*, 333781.

Vidovic, S. U. and Martill, D. M. 2017. The taxonomy and phylogeny of *Diopecephalus kochi* (Wagner, 1837) and '*Germanodactylus rhamphastinus*' (Wagner, 1851). *Geological Society, London, Special Publications*, **455**(1), 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 Paleontology*, **19**, 82A.

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**(3), 226–230.

Wang, X., Kellner, A. W., Zhou, Z., and De Almeida Campos, D. 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. *Nature*, **437**(7060), 875–879.

Wang, X., Kellner, A. W., Jiang, S., and Meng, X. 2009. An unusual long–tailed pterosaur with elongated neck from western Liaoning of China. *Anais da Academia Brasileira de Ciências*, **81**(4), 793–812.

Wang, X., Kellner, A. W., Jiang, S., Cheng, X., Meng, X., and Rodrigues, T. 2010. New long–tailed pterosaurs (Wukongopteridae) from western Liaoning, China. *Anais da Academia Brasileira de Ciências*, **82**(4), 1045–1062.

Wang, X., Kellner, A. W., Jiang, S., and Cheng, X. 2012. New toothed flying reptile from Asia: close similarities between early Cretaceous pterosaur faunas from China and Brazil. *Naturwissenschaften*, **99**(4), 249–257.

Wellnhofer, P. 1970. Die Pterodactyloidea (Pterosauria) der OberjuraPlattenkalke Süddeutschlands. *Bayerische Akademie der Wissenschaften, Mathematisch-Wissenschaftlichen Klasse, Abhandlungen* **141**, 1–133.

Wellnhofer, P. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Suddeutschlands. *Palaeontogr. A.*, **148**, 1–33. Wellnhofer, P. 1978. Pterosauria. Handbuch der Palaeoherpetologie, Teil 19. Stuttgart: Gustav Fischer Verlag.

Wellnhofer, P. 1991. *The Illustrated Encyclopaedia of Pterosaurs*. London, Salamander Books.

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

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

Wu, W. H., Zhou, C. F. and Andres, B. 2017. The toothless pterosaur Jidapterus edentus (Pterodactyloidea: Azhdarchoidea) from the Early Cretaceous Jehol Biota and its paleoecological implications. *PloS One*, **12**, e0185486.

Yang, Z., Jiang, B., Mcnamara, M. E., Kearns, S. L., Pittman, M., Kaye, T. G., ... and Benton, M. J. 2019. Pterosaur integumentary structures with complex feather–like branching. *Nature ecology and evolution*, **3**(1), 24–30.

Young, C. C. 1964. On a new pterosaurian from Sinkiang, China. *Vertebrate Palasiatica* **8**, 221–225.

Zhang H, Wang M X, Liu X M. 2008. The upper age limit of Tiaojishan Formation (western Liaoning and northern Hebei area) volcanic rocks by LA-ICP-MS (in Chinese). *Chinese Science Bulletin*, **15**, 1815-1824.

Zhang Y Q, Chen H Y. 2015. Study on the characteristics of Tiaojishan Formation (Middle Jurassic) laminar volcanic structure of Chengde Basin (in Chinese). *Hebei Geology*, **4**, 8-10.

Figures

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Figure 3. *Sinomacrops bondei* tax. nov., skull of JPM-2012-001. A, photograph; and B, schematic drawing. Light grey represents bones; dark grey represents soft tissue. Abbreviations:

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Figure 5. Sacral region of JPM-2012-001. A, photograph; B, schematic drawing. Abbreviations: ac, acetabulum; ca, caudal vertebrae; fe, femur; pip, puboischiadic plate; prap, preacetabular process of the illium; sa, sacral vertebrae; sr, sacral rib. Scale bar equals 10 mm.

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Figure 9. Variation in anurognathid jaw shape. Schematic drawings of anurognathid mandibles in ventral view. A, *Batrachognathus volans* (based on Riabinin 1948). B, *Sinomacrops bondei*. C, *Jeholopterus ningchengensis* (based on Yang *et al.* 2018). D, *Vesperopterylus lamadongensis* (based on Lü *et al.* 2018). Not to scale, adjusted to matching sizes.

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Supplemental Files

Supplemental Table S1. Morphometric dataset. Morphometric values that were subjected to gap-weighting for character coding.

Supplemental File 1. Mesquite file. A nexus-format file for Mesquite, containing the phylogenetic data matrix.

Supplemental File 2. TNT file for the phylogenetic analysis.

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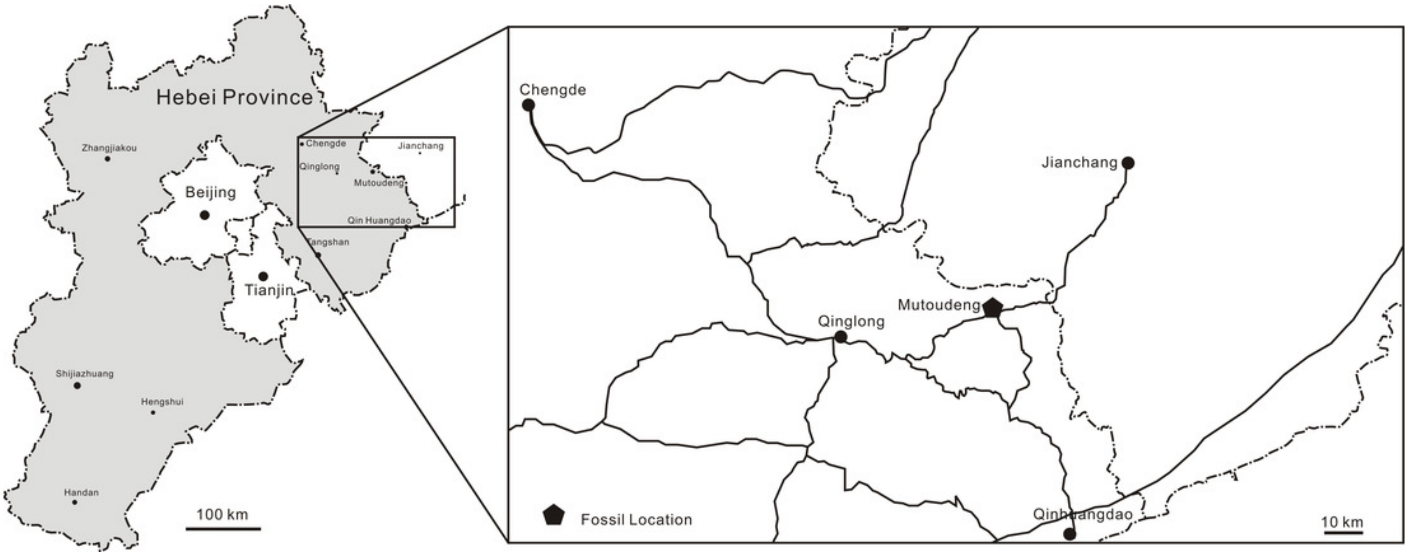

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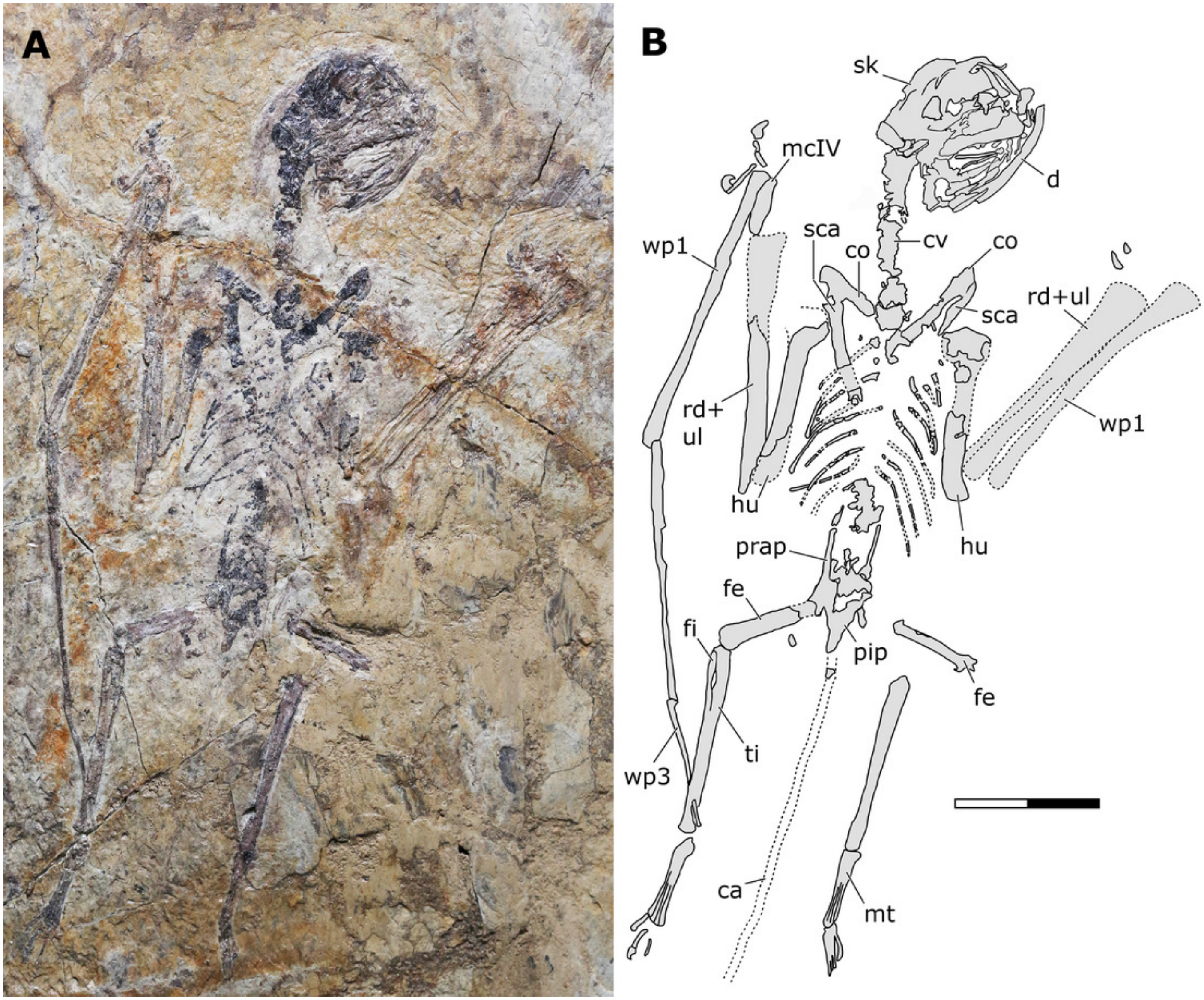

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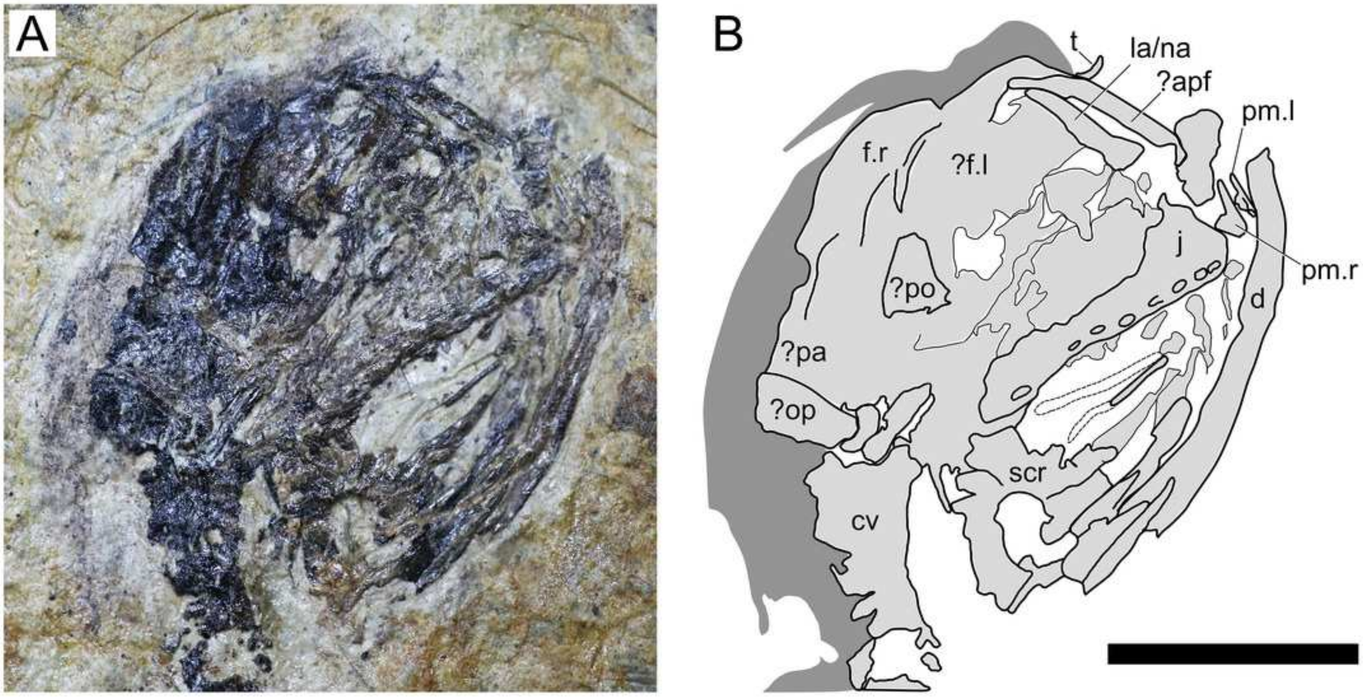

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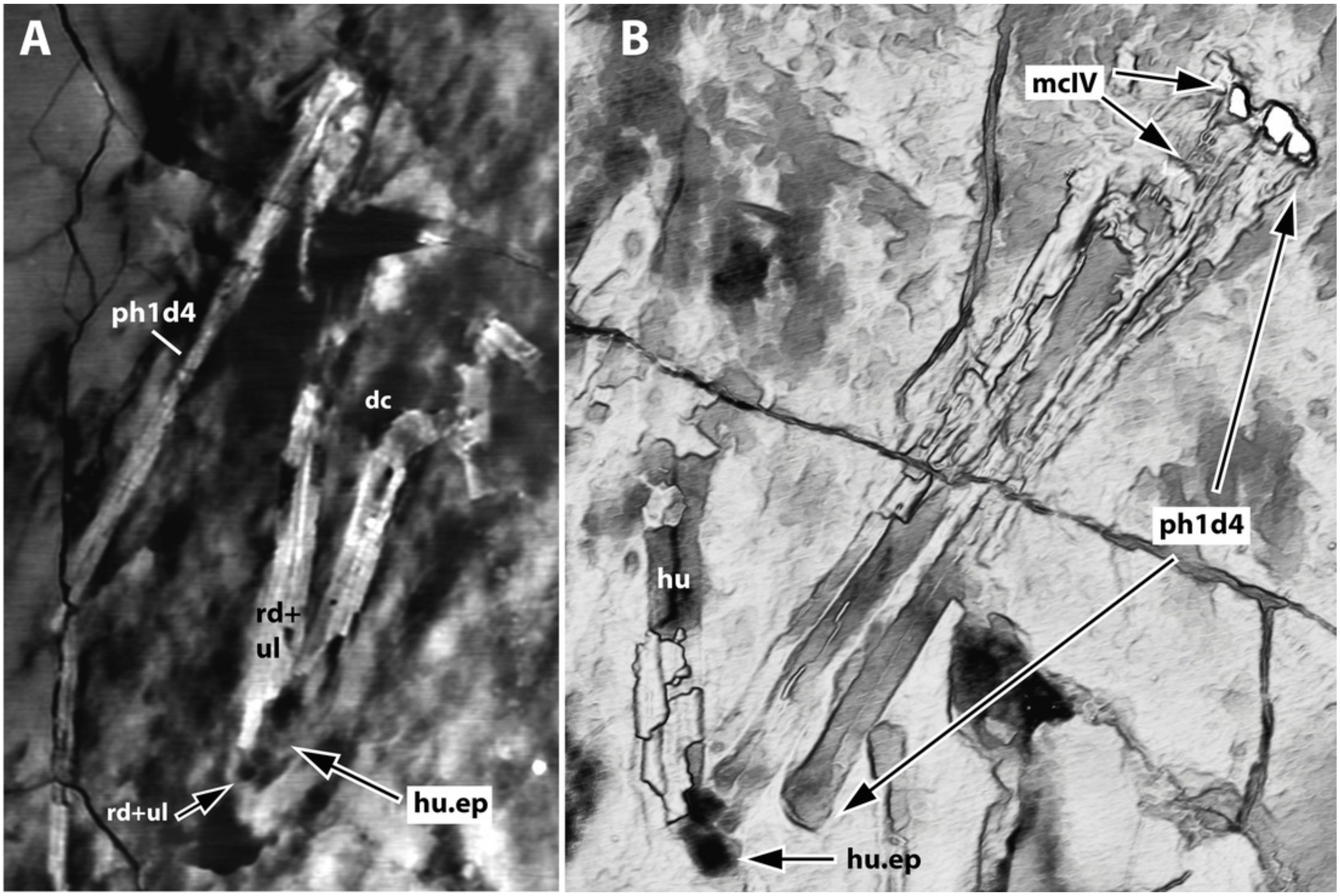

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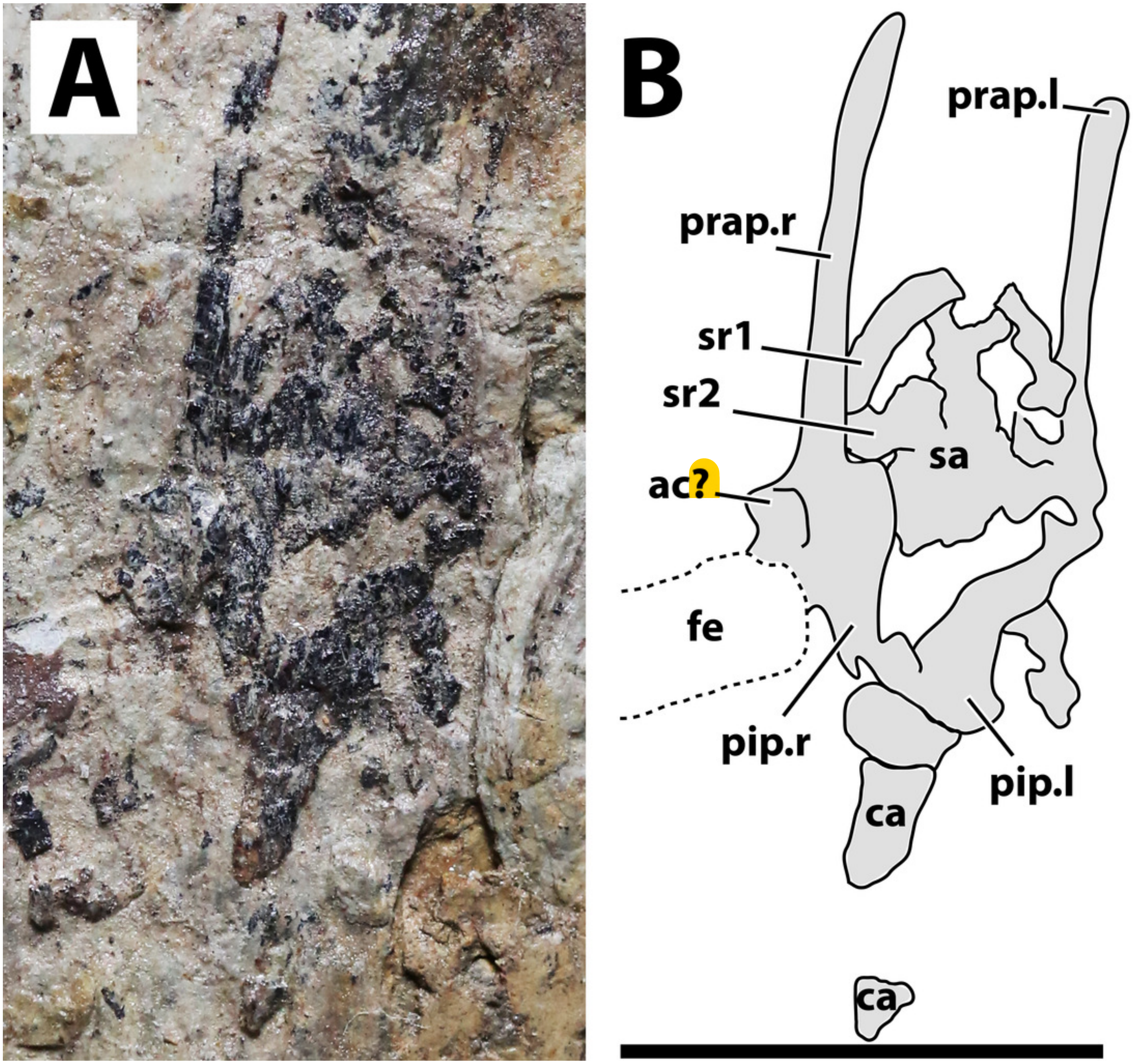

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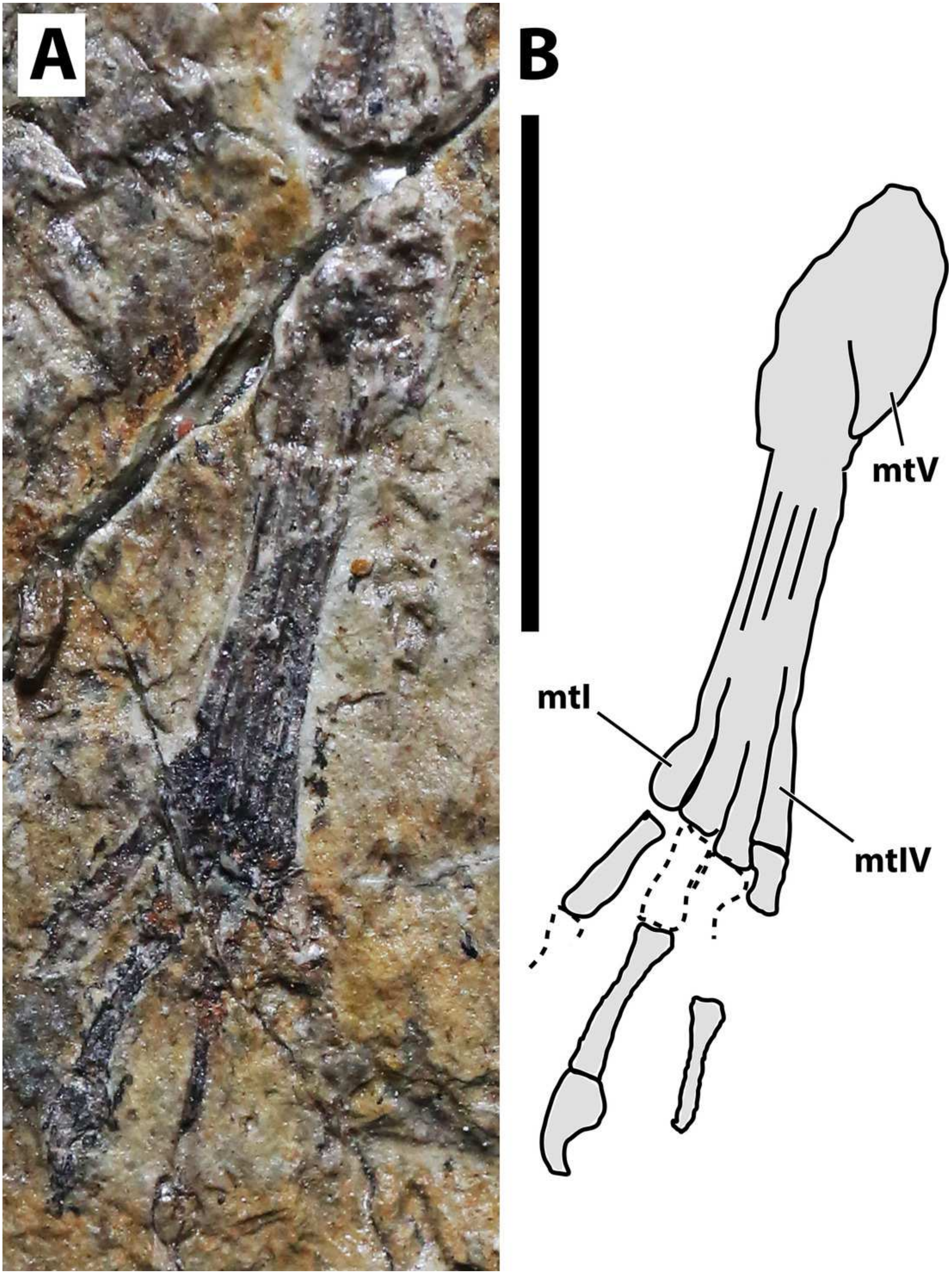
A
B
mtV
mtI
mtIV

Figure 7

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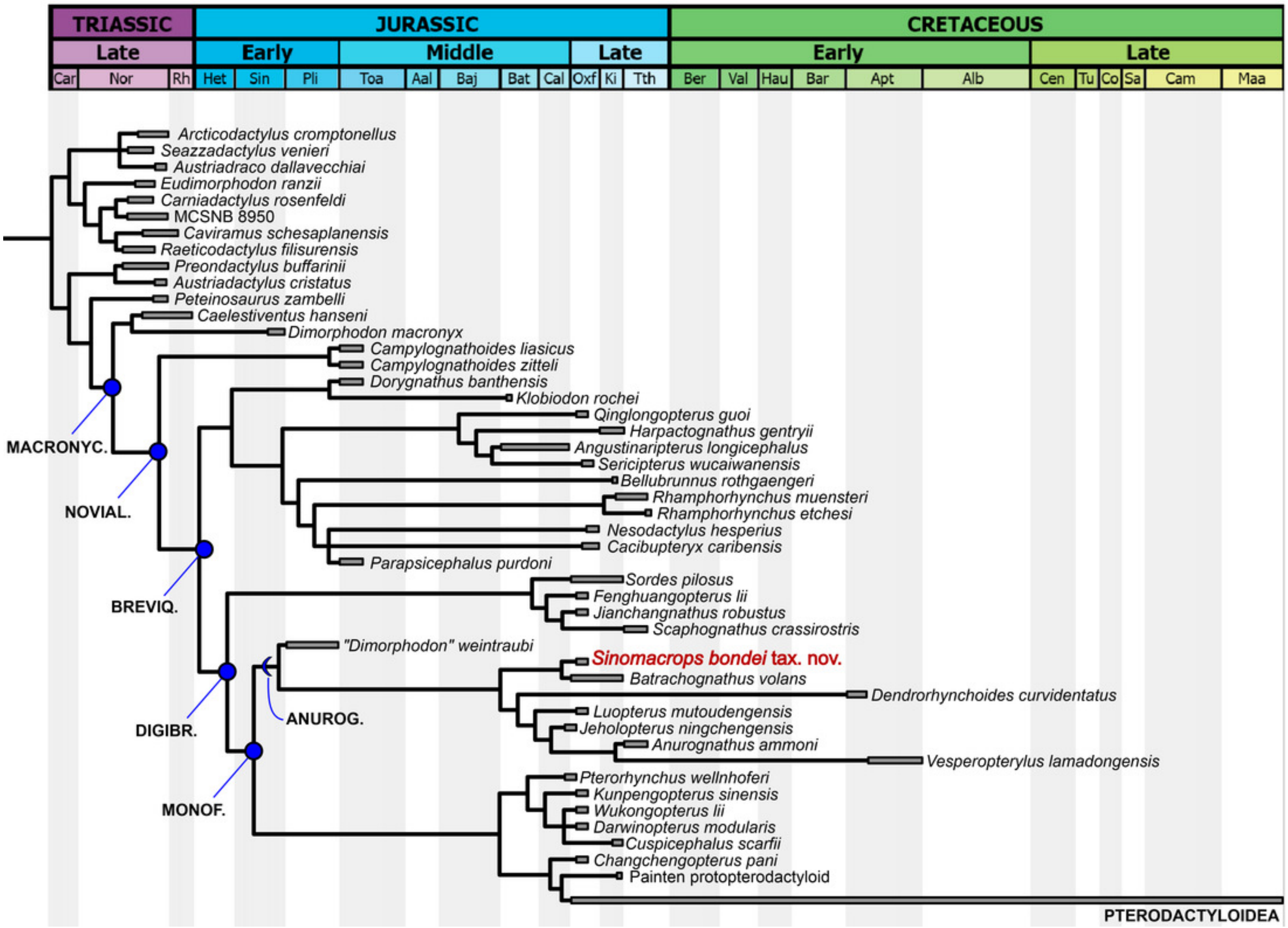

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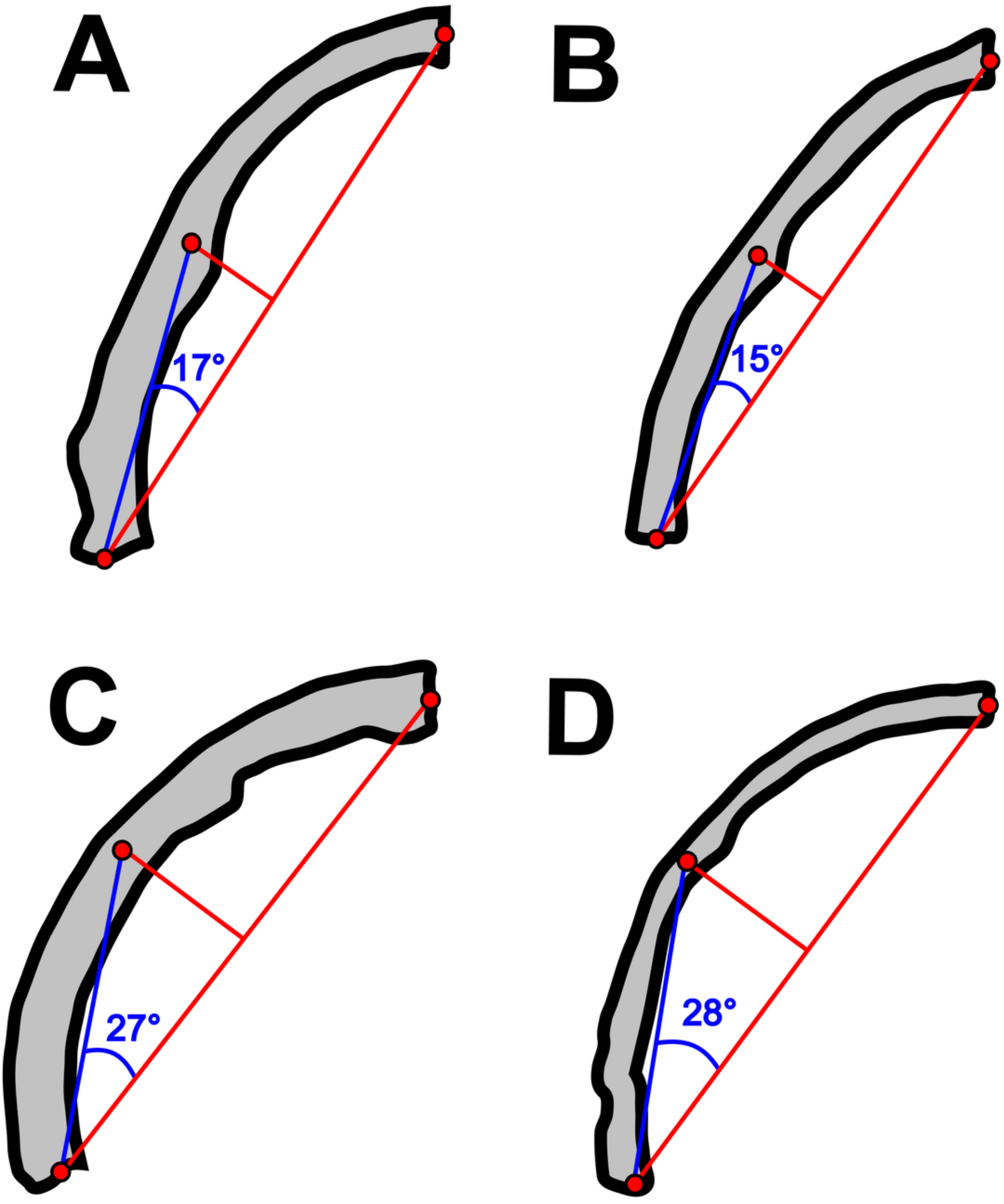
A
17°
B
15°
C
27°
D
28°

Figure 9

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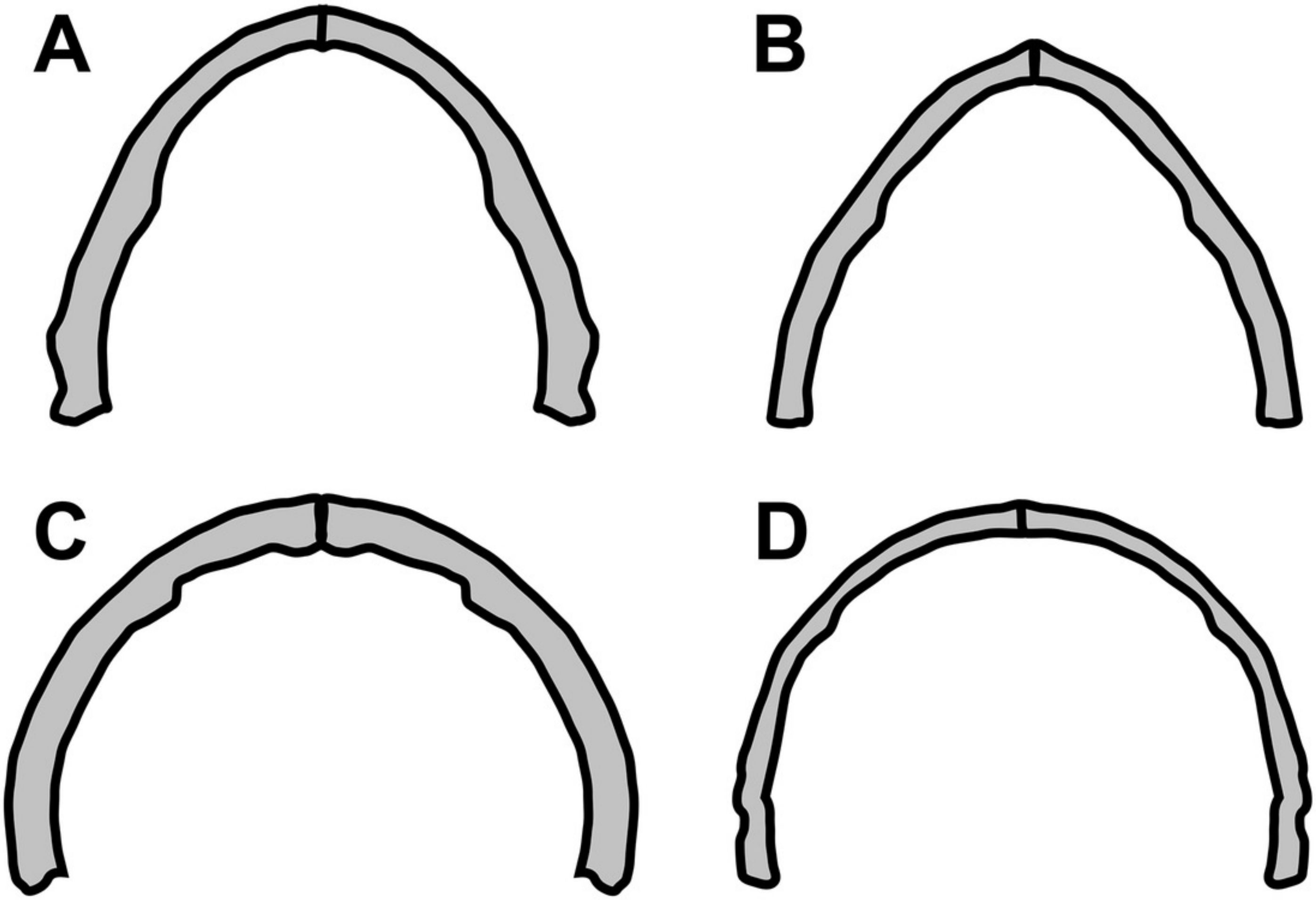

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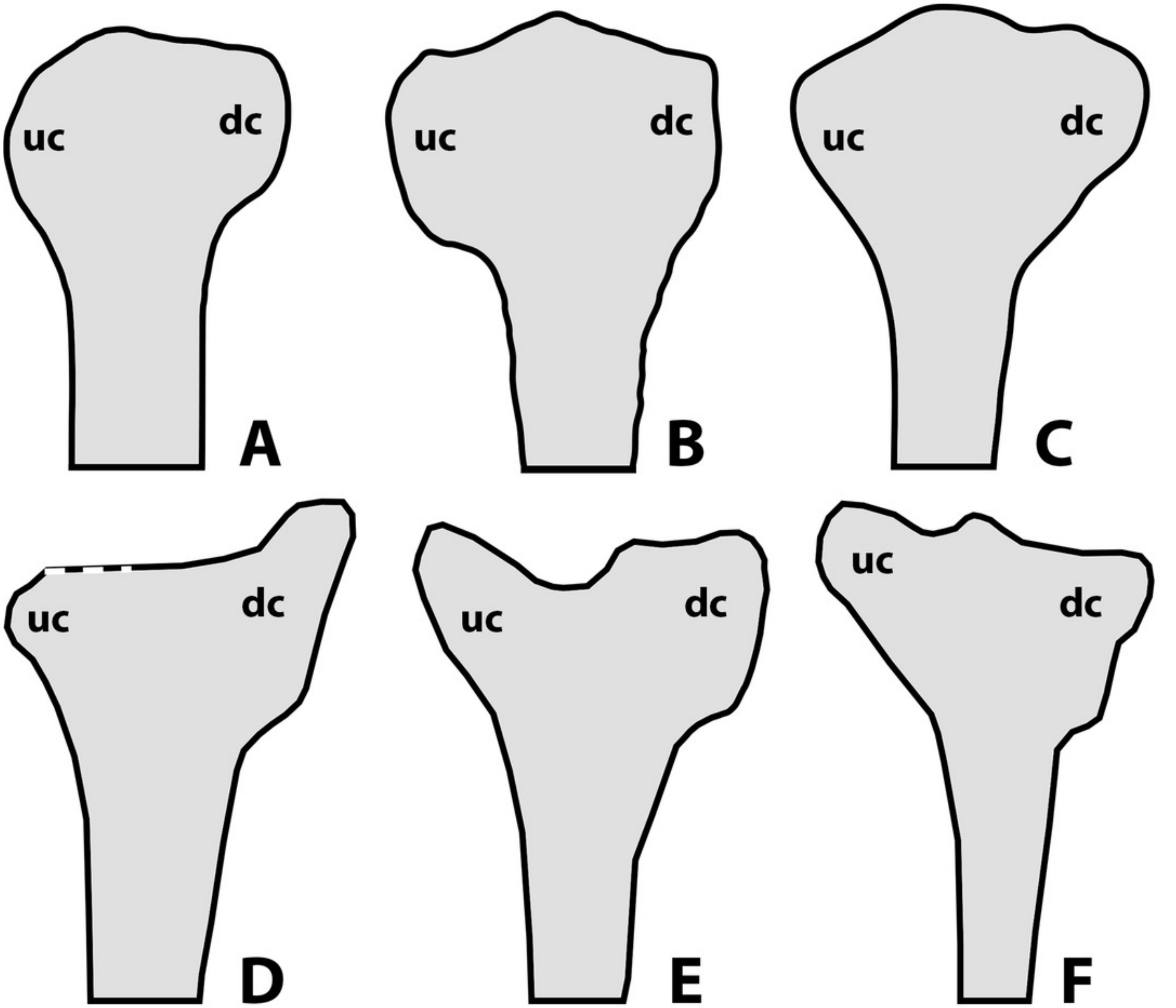
uc
dc
A
uc
dc
B
uc
dc
C
uc
dc
D
uc
dc
E
uc
dc
F

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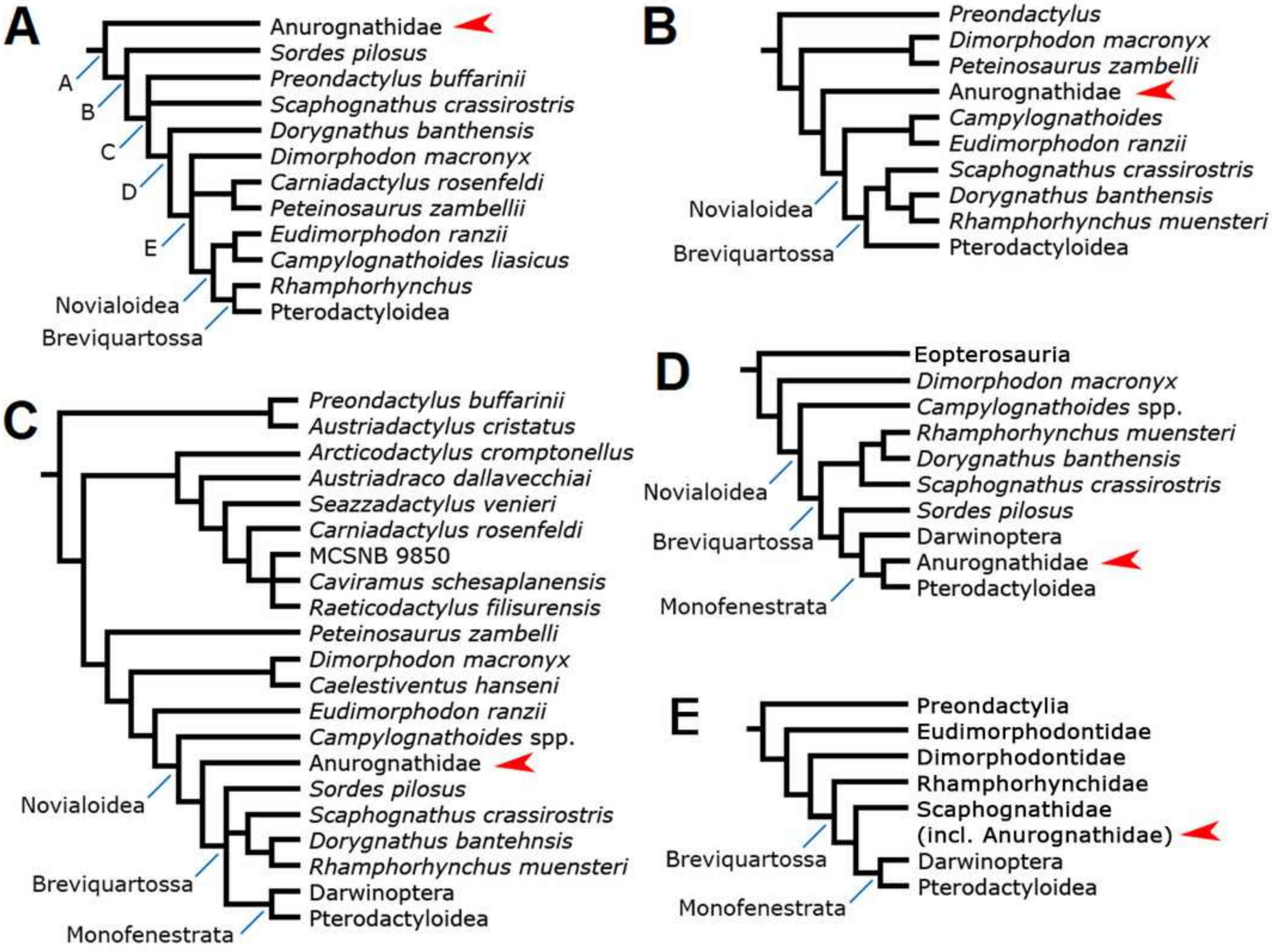

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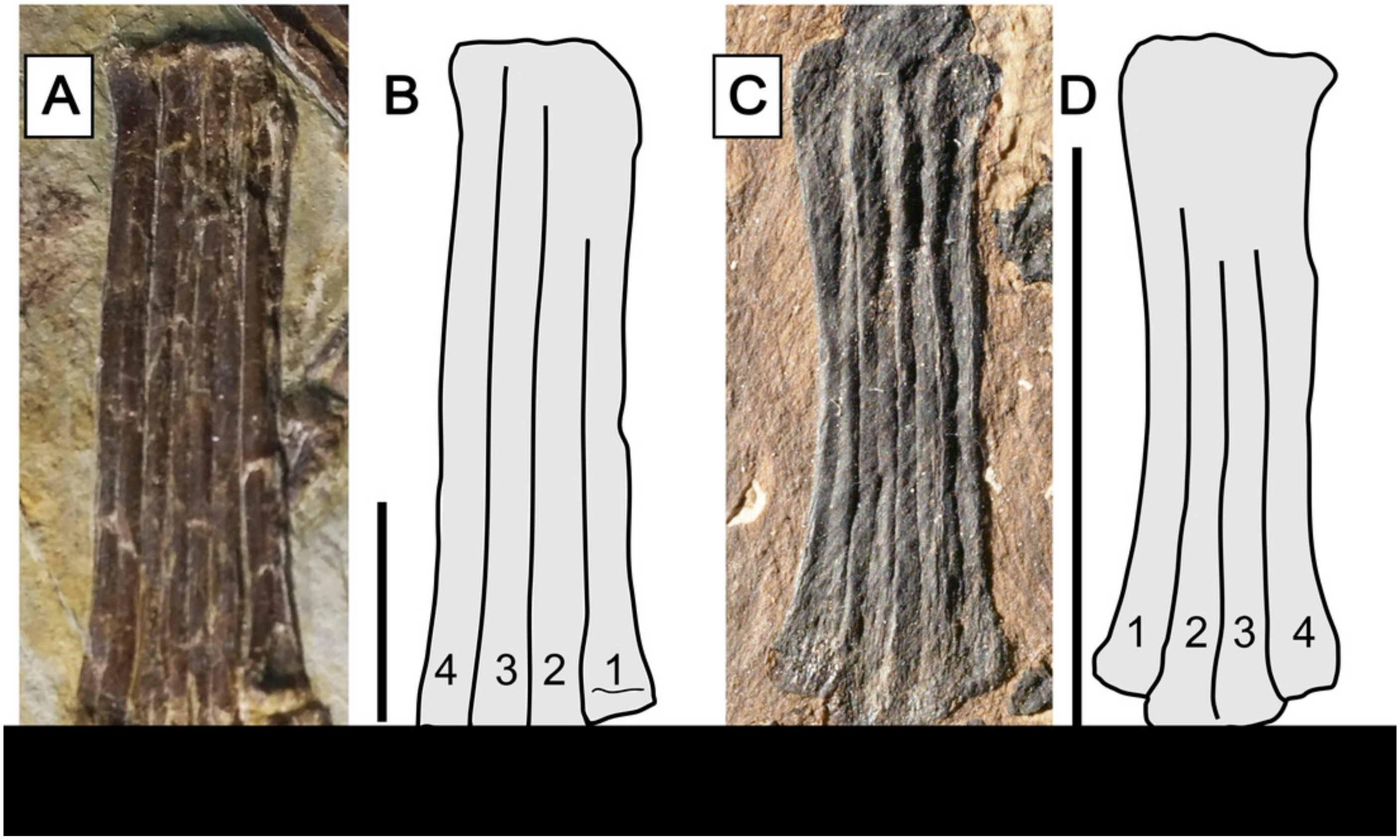

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Figure 13. Nasoantorbital fenestra in *Jeholopterus* CAGS IG 02-81.

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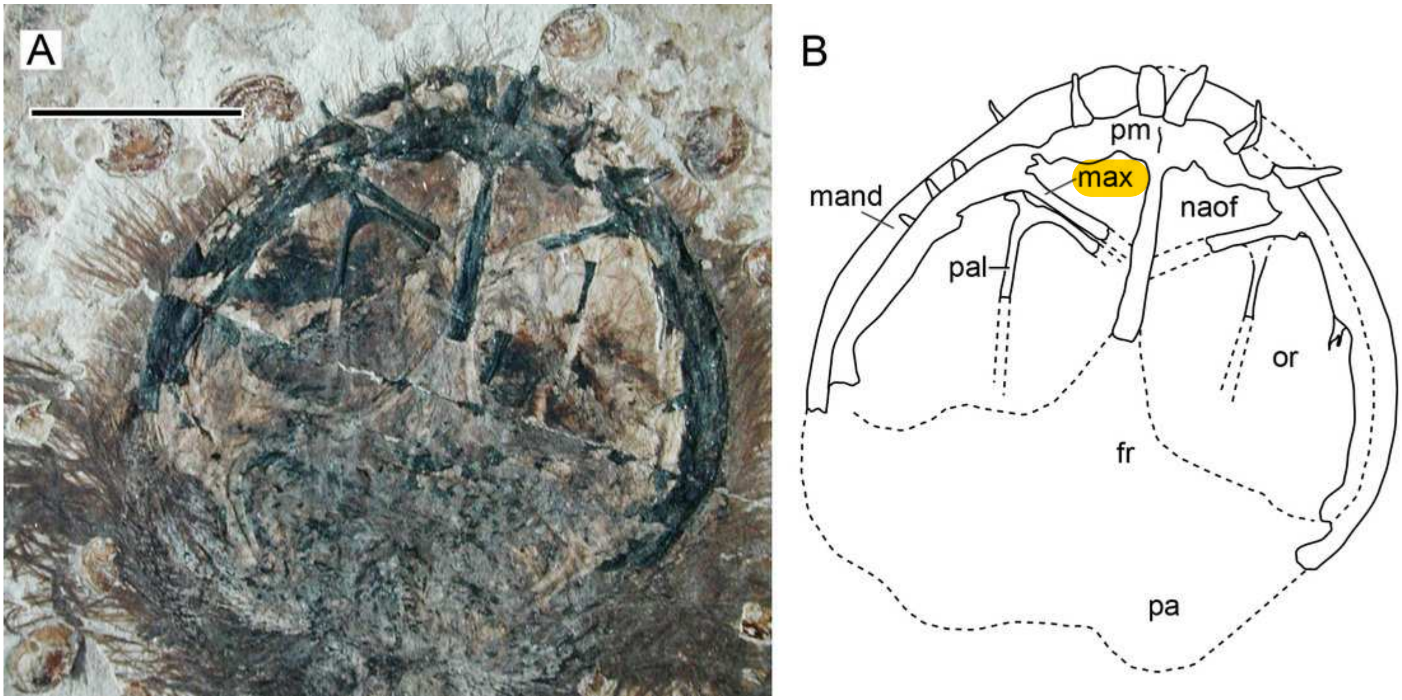

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Paleoart courtesy of Zhao Chuang, reproduced with permission.

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Element	Right	Left
Scapula	~1.95	?
Coracoid	?	~1.37
Humerus	2.36	2.39
Radius/ulna	3.63	3.47
Metacarpal IV	~0.67	-
Wing phalanx 1	4.12	~3.84
Wing phalanx 2	3.60	-
Wing phalanx 3	1.81	-
Femur	1.36	1.31
Tibiotarsus	2.66	2.53*
Metatarsus	~1.1	~1

Table 1. Measurements of JPM-2012-001. Measurements are given in centimeters. Values for long bones correspond to their lengths. Interrogations mean the element is too incomplete for an informative value. Dashes mean the element is not preserved. Asterisk means the element is slightly incomplete.

Table 2(on next page)

Table 2. Comparative table showing skeletal element ratios among anurognathids.

Anurognathidae	**hu/mcIV**	**hu/fe**	**hu/ul**	**hu+ul/fe+ti**	**ul/mcIV**	**ul/fe**	**sc/co**	**ph1d4/ul+mcIV**	**ph1d4/ti**	**ph2d4/ph1d4**	**ph3d4/ph1d4**	**ph3d4/ph2d4**	**ph4d4/ph1d4**	**fe/mcV**	**ti/fe**	**mtIII/ti**	**caS/fe**
Anurognathus ammoni (holotype)	2.91	1.19	0.70	1.16	4.18	1.70	?	1.01	1.49	?	?	?	?	2.45	1.44	0.46	0.50
Anurognathus ammoni (referred)	3.64	1.25	0.70	1.26	5.10	1.76	?	0.95	1.44	0.77	0.44	0.56	?	2.90	1.39	0.42	?
Vesperopterylus lamadongensis	2.75	1.35	0.74	1.34	3.73	1.83	0.97	0.96	1.64	0.81	0.60	0.74	0.12	2.04	1.37	0.47	0.59
Jeholopterus ningchengensis (holotype)	3.26	1.55	0.70	1.67	4.68	2.22	1.96	0.86	1.86	0.88	0.65	0.73	0.17	2.10	1.25	0.44	?
Jeholopterus ningchengensis (CAGS IG 02-81)	3.39	1.52	0.78	1.59	4.03	1.99	1.28	0.88	1.88	0.89	?	?	?	2.02	1.22	0.47	?
Dendrorhynchoides curvidentatus	2.99	1.43	0.78	1.37	3.82	1.82	1.15	0.99	1.66	0.80	?	?	?	2.4	1.37	0.45	?
Luopterus mutoudengensis holotype	2.45	1.28	0.64	1.44	3.81	2.00	1.88	0.94	1.85	0.82	0.50	0.61	0.10	1.91	1.29	0.44	>0.86
NJU–57003	2.60	1.34	0.60	1.42	4.31	2.15	1.27	0.90	1.63	0.86	0.40	0.46	0.10	1.97	1.47	0.45	1.78
IVPP V16728	?	1.43	?	?	?	?	?	?	?	?	?	?	?	?	~1.40	0.38	>1.49
Sinomacrops bondei	3.55	1.77	0.66	1.51	5.29	2.70	1.42	0.97	1.59	0.87	0.44	0.50	?	~2	1.99	0.48	>1.69
Batrachognathus volans	?	1.93	?	?	?	?	?	?	?	?	?	?	?	?	1.75	?	1.47*

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