Sinomacrops bondei, a new anurognathid pterosaur from the Jurassic Tiaojishan Formation (China) and a new phylogenetic hypothesis for the group (#53890)

First submission

Guidance from your Editor

Please submit by **6 Nov 2020** for the benefit of the authors (and your $200 publishing discount) .

Structure and Criteria
Please read the 'Structure and Criteria' page for general guidance.

Custom checks
Make sure you include the custom checks shown below, in your review.

Author notes
Have you read the author notes on the guidance page?

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the materials page.

11 Figure file(s)
1 Table file(s)
1 Raw data file(s)

Custom checks

New species checks

- Have you checked our new species policies?
- Do you agree that it is a new species?
- Is it correctly described e.g. meets ICZN standard?

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context. Literature well referenced & relevant.
- Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- Figures are relevant, high quality, well labelled & described.
- Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- Original primary research within Scope of the journal.
- Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- All underlying data have been provided; they are robust, statistically sound, & controlled.
- Speculation is welcome, but should be identified as such.
- Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Sinomacrops bondei, a new anurognathid pterosaur from the Jurassic Tiaojishan Formation (China) and a new phylogenetic hypothesis for the group

Xuefang Wei [Equal first author, 1, 2, 3], **Rodrigo V Pêgas** [Equal first author, 4], **Caizhi Shen** [5], **Yanfang Guo** [5], **Waisum Ma** [6], **Deyu Sun** [7], **Xuanyu Zhou** [Corresp. 8, 9]

[1] Key Laboratory of Stratigraphy and Palaeontology, Ministry of Natural Resource, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China

[2] China University of Geosciences, Beijing, China

[3] Centre of Cores and Samples of Nature Resources, China Geological Survey, Beijing, China

[4] Federal University of ABC, São Bernardo, Brazil

[5] Dalian Natural History Museum, Dalian, Liaoning, China

[6] School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom

[7] Jinzhou Paleontology Museum, Jinzhou, Liaoning, China

[8] Department of Natural History Sciences, Hokkaido University, Sapporo, Japan

[9] Beipiao Pterosaur Museum of China, Beipiao, Liaoning, China

Corresponding Author: Xuanyu Zhou
Email address: xyzhou@elms.hokudai.ac.jp

Anurognathids are an elusive group of diminutive, potentially scansorial/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 this deposit. The new species provides new information concerning morphological diversity for the group, and displays the first anurognathid skull exposed in lateral view. Furthermore, we provide a critical review of the group's phylogeny, incorporating into a single data set characters from diverging phylogenetic proposals. As a result, we obtain a new hypothesis for the placement of the group, somewhat intermediate between other two recent proposals.

Sinomacrops bondei, a new anurognathid pterosaur from the Jurassic Tiaojishan Formation (China) and a new phylogenetic hypothesis for the group

Xuefang Wei[1,2,3], Rodrigo V. Pêgas[4], Caizhi Shen[5], Yanfang Guo[5], Waisum Ma[6], Deyu Sun[7], Xuanyu Zhou[8,9*]

1. Key Laboratory of Stratigraphy and Palaeontology, Ministry of Natural Resource, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China.
2. China University of Geosciences, Beijing, China.
3. Centre of Cores and Samples of Nature Resources, China Geological Survey, Beijing, China.
4. Federal University of ABC, São Bernardo, Brazil.
5. Dalian Natural History Museum, Dalian, Liaoning, China.
6. School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom.
7. Jinzhou Paleontology Museum, Jinzhou, Liaoning, China.
8. Department of Natural History Sciences, Hokkaido University, Sapporo, Japan.
9. Beipiao Pterosaur Museum of China, Beipiao, Liaoning, China.

Corresponding Author:
Xuanyu Zhou
Email address: xyzhou@elms.hokudai.ac.jp

Abstract

Anurognathids are an elusive group of diminutive, potentially scansorial/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 this deposit. The new species provides new information concerning morphological diversity for the group, and displays the first anurognathid skull exposed in lateral view. Furthermore, we provide a critical review of the group's phylogeny, incorporating into a single data set characters from diverging phylogenetic proposals. As a result, we obtain a new

hypothesis for the placement of the group, somewhat intermediate between other two recent proposals.

Introduction

Pterosaurs, a group of archosauromorph reptiles, 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, Witton 2013). 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 its phylogenetic affinities. Spanning from the Middle Jurassic (Callovian) to the Early Cretaceous (Aptian), anurognathids are small-sized (from 400 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, Witton 2013). 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, Habib 2011), of possible arboreal habits (Bennett 2007, Witton 2013, Lü *et al.* 2018).

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). 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 non-pterodactyloid pterosaurs (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, 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). Presently, these beds are interpreted as part of the Tiaojishan Formation and 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, Kellner 2003, Unwin 2003, Andres *et al.* 2010, Dalla Vecchia 2014, 2019). Five cladistic hypotheses have been presented for the phylogenetic position of 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, 2018); 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.

This work presents a new fossil coming from the Mutoudeng locality, JZMP-2107500095, representing a new genus and species of long-tailed anurognathid. Despite crushed to the point of obliterating some 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. We further review the phylogenetic relationships of the group (both intra and inter), presenting an analysis including all proposed species and a new hypothesis for the placement of the group.

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 the abundancy of insects and vertebrate fossils, such as salamanders, feathered dinosaurs, pterosaurs and mammals (Sullivan *et al.*, 2014). The most important localities are Daohugou in Ningcheng County of southeast Inner Mongolia, Linglongta of Jianchang County of western Liaoning Province, and Mutoudeng of Qinglong County of northern Hebei Province (Lü et al. 2013). From the slightly older 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 Tiaojishan Formation at the

Linglongta locality, pterosaurs are abundant in number and in diversity, wukongopterids, *Jianchangopterus*, *Jianchangnathus* and *Fenghuangopterus*, (Wang *et al.* 2009, 2010; Lü *et al.* 2010, 2011a,b, Lü & Bo 2011, Sullivan *et al.* 2014, Cheng *et al*. 2012, 2016, 2017a, 2017b). From the Tiaojishan Formation at Mutoudeng come *Dendrorhynchoides mutoudengensis*, *Qinglongpterus guoi* and *Changchengopterus pani* (Lü 2009, Lü *et al*. 2012, Lü & Hone 2012). It is from the Mutoudeng locality that the new specimen herein described comes (Fig. 1).

The Tiaojishan Formation is mainly distributed in the Chengde Basin (Maoniujiao-Xiaoguozhangzi-Jiyuqing Area) in northern Hebei Province. It is mainly composed of neutral volcanic rock (Zhang & Chen, 2015). The lithology of 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 the bottom of the lower section and andesite at the top of the upper section, utilizing LA-ICP-MS Zircon U-Pb. Their result gave an age range 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 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 Linlongta and Mutoudeng strata are chronocorrelate (Chu *et al.*, 2016).

Material & Methods

Institutional abbreviations

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

We have performed a phylogenetic analysis based on a data matrix modified from Dalla Vecchia (2019), which is focused on non-pterodactyloid relationships (see Supplementary Information for our character list and coding). To this matrix, we have added the herein described species, as well as *Vesperopterylus lamadongensis*, and have split Dalla Vecchia's (2019) OTU "*Dendrorhynchoides* spp." into *Dendrorhynchoides mutoudengensis* and *Luopterus curvidentatus*, coding them separately.

To the character list, we have added some characters from the analyses of Kellner (2003), Unwin (2003) and Andres *et al.* (2014), as can be found in the Supplementary Material. We have further added four new characters: character 7, jaws, lateral margins in dorsal or ventral view, shape (0: straight or slightly concave; 1: convex and elliptical; 2: convex and semicircular); character 37, orbit, size relative to skull length (0: under half of skull length; 1: half of skull length or more); character 81, caudal series, length relative to femur (0: longer than 0.60 femur length; 1: equal to or under 0.60 femur length); and character 115, tibia, length relative to femur (0: equal to or under 1.60 tibia length; 1: over 1.60 tibia length). The TNT file with the complete data matrix is available in the Supplemental Information.

The analysis was performed by TNT (Goloboff *et al.* 2008) using the Traditional Search option with 10000 replicates (memory set at 300 MB, saving 9999 trees), random seed = 0, and collapsing trees after search. All characters were treated unordered and unweighted.

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, 1967

Type genus. *Anurognathus ammoni* Döderlein, 1923.

Definition. The least inclusive clade containing *Anurognathus ammoni* and *Batrachognathus volans* (Kellner 2003).

Synapomorphies. Skull broader than long, broadly arching jaws, skull dorsal margin convex, prenarial rostrum under 20% skull length, nasoantorbital fenestra extends dorsal to premaxillary tooth row, nasoantorbital fenestra higher than long, nasoantorbital fenestra anterior margin bordered by premaxilla only, orbit larger than nasoantorbital fenestra, premaxillary bony bar narrow, jugal anteriorly expanded overlapping maxilla laterally, quadrato-mandibular joint posterior to orbit, quadrate thin and subcylindrical, jugal lacrimal process narrow, palatines reduced to thin bars, unfused dentary symphysis, anterior lateral surface of dentaries pitted, iliac preacetabular process straight (Kellner 2003, Unwin 2003, Andres *et al.* 2010, Dalla Vecchia 2019, this work).

Included species. *Anurognathus ammoni*, *Vesperopterylus lamadongensis*, *Jeholopterus ningchengensis*, *Dendrorhynchoides curvidentatus*, *Luopterus mutoudengensis, Batrachognathus volans* and *Sinomacrops bondei* tax. nov.

Anurognathinae Nopcsa 1928

Definition. The most inclusive clade containing *Anurognathus ammoni* but not *Batrachognathus volans* (new definition).

Synapomorphy. Jaws semicircular in shape, pteroid curved and subparallel-sided.

Included species. *Anurognathus ammoni*, *Vesperopterylus lamadongensis*, *Jeholopterus ningchengensis*, *Dendrorhynchoides curvidentatus*, *Luopterus mutoudengensis*.

Anurognathini new clade name

Definition. The most inclusive clade containing *Anurognathus ammoni* but not *Luopterus mutoudengensis*.

Synapomorphies. Humerus deltopectoral crest trapezoidal, tail/femur length ratio under 0.60, and loss of filiform processes of the caudal zygapophyses and haemapophyses.

Included species. *Anurognathus ammoni*, *Vesperopterylus lamadongensis* and *Jeholopterus ningchengensis*.

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 1.70, tibial/femoral length ratio over 1.60.

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 a relatively long tibia (over 1.80 times femur length).

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 dorsal and caudal vertebrae, sternum, distal epiphysis of right humerus, proximal epiphyses of right ulna and radius, parts of the left humerus, and most of the remaining of the left wing.

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. 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 identified.

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 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 *Dendrorhynchoides curvidentatus*, *Anurognathus ammoni* or *Vesperopterylus lamadongensis* (Ji & Ji 1998, Bennett 2007, Lü *et al.* 2017).

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. This pattern is unprecedented for 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).

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 each segment can be estimated, with 23 mm for the cervical series; 3 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 are less inclined (Fig. 5). This configuration is very similar to that of *Mesadactylus* (see Jensen & Padian, 1989). At least 9 pairs of ribs 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*, *Anurognathus*, *Jeholopterus* (Ji & Ji 1998, Wang *et al.* 2002, Bennett 2007).

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, though 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 is slightly expanded, indicating an articular region for a four 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, though impressions of the lost regions remain on both sides (Fig. 2). The left 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. The right 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).

Phylogenetic analysis results

Our analysis produced 9 most parsimonious trees, with 321 steps, CI of 0.517-0.526 and RI of 0.754-0.764. 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 original results from Dalla Vecchia (2019), *"Dimorphodon" weintraubi* is the sister-group of the Anurognathidae. For the first time, the clade comprising the latter two taxa is recovered as the sister group of Darwinoptera + Pterodactyloidea. The synapomorphies are discussed further below.

Discussion

Diversity of the Anurognathidae

Unwin *et al.* (2000) and Bennett (2007) 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. This led these authors to consider that the anurognathid bauplan was rather conservative (Unwin *et al.* 2000, Bennett 2007). Nonetheless, several features of anurognathid morphology exhibit considerable variation, and here we show 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*, *Jeholopterus*, *Vesperopterylus* and NJU–57003 (Wang *et al.* 2002, Ji & Yuan 2002, Bennett 2007, Lü *et al.* 2018, Yang *et al*. 2019). In these, the arching of the jaws is abrupt and approximately continuous, describing a semicircular shape. In contrast, in *Batrachognathus* and *Sinomacrops*, the arching of the jaws is less pronounced and relatively more gradual, making the jaws rather elliptical instead of semicircular (Fig. 8).

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* 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) speculated that the purported robust teeth may in fact be bone shards, although a close reinspection has not been presented yet.

According to Lü & Hone (2012), a noticeable amount of variation in anurognathids is also expressed through the shape of the deltopectoral crest of the humerus (Fig. 9), as follows: rounded for *Anurognathus ammoni*, alate for *Jeholopterus ningchengensis*, triangular for *Dendrorhynchoides curvidentatus* and *Luopterus mutoudengensis*, and sub-rectangular for *Batrachognathus*. However, in the holotype of *Anurognathus*, the structure is not rounded, but clearly 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. 9A–B). *Sinomacrops* and *Batrachognathus* are further unique in exhibiting deltopectoral crests that are reduced in size, being less wide than humeral shaft, and less wide than proximodistally long (Fig. 9A–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. 9A–B). In *Dendrorhynchoides curvidentatus*, it is slightly more prominent, subtriangular (Fig. 9). In *Jeholopterus*, it is particularly reduced, and is also prominent (Fig. 9D). In *Anurognathus* and *Vesperopterylus*, it is relatively elongated and oriented obliquely to the humeral shaft (Fig. 9E–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 and separately from the clade containing all other Chinese anurognathids plus *Anurognathus ammoni* (the Anurognathinae as herein defined). Five synapomorphies support Batrachognathinae in our analysis: the humeral/femoral length proportion (over 1.7), the width of the humeral deltopectoral crest (reduced, less wide than proximodistally long), the shape of the deltopectoral crest (subrectangular), the shape of the ulnar crest of the humerus (rounded), and the tibia/femur length proportion (over 1.6).

The Anurognathinae are composed, according to our results, of *Dendrorhynchoides curvidentatus*, *Luopterus mutoudenensis*, *Jeholopterus ningchengensis*, *Anurognathus ammnoni* and *Vesperopterylus lamadongensis*. These taxa share the semicircular arching of the jaws, distinct from the elliptical one seen in batrachognathines (new character state), and the pteroid shape, 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 Anurognathini, with which it shares a straight last phalanx of pedal digit V, whereas this phalanx is curved in *Dendrorhynchoides curvidentatus*. The straight condition is a synapomorphy joining *Luopterus* + Anurognathini, 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* (the newly defined Anurognathini) is strongly supported by six synapomorphies: deltopectoral crest of the humerus trapezoidal, caudal series shorter than 0.60 femur length (new character), caudal vertebrae lacking filiform zygapophyses, caudal vertebrae lacking filiform haemapophyses, pedal digit V phalanx 2 straight, and pedal digit V phalanx 2 shorter than phalanx 1 (new character). The sister-group relationship between *Anurognathus*

ammoni and *Vesperopterylus lamadongensis* is supported by one synapomorphy: the loss of mid-cervical ribs. This result is interesting in implying in the temporal coexistence, in the Tiaojishan Formation, of three lineages of anurognathids: batrachognathines, *Luopterus*, and anurognathinins.

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 composed 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* (see Table 1). 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 that 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* (1.80) and *Batrachognathus volans* (1.93). In our analysis, we modified the character from Kellner (2003), now considering a humeral/femoral length over 1.70.

This is the second phylogenetic analysis to include all known anurognathid species. The only other phylogenetic analysis to have ever included all (then-known) anurognathids was the one presented in the work by Wu *et al.* (2017), derived from Andres *et al.* (2014), published prior to the description of *Vesperopterylus lamadongensis*. In this analysis, *Dendrorhynchoides* was not recovered as monophyletic. *Dendrorhynchoides curvidentatus* fell at the base of the group, while *Luopterus mutoudengensis* fell as sister-group of *Batrachognathus volans*. In this analysis, 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 cannot join *Batrachognathus* with the Anurognathini.

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. Five cladistic hypotheses have been put forward in the literature. In the first one, the Anurognathidae have been interpreted as the basal-most known pterosaur lineage (Fig. 10A), as the sister-group of a clade containing all other pterosaurs (Kellner 2003, 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 analysis of Unwin (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).

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. Subsequent analyses by Britt *et al.* (2018) and Dalla Vecchia (2019) are more comprehensive (Fig. 10C), incorporating darwinopterans, and have produced a different result, with Anurognathidae + *Dimorphodon weintraubi* being the sister-group of Rhamphorhynchidae + Monofenestrata (= Darwinoptera + Pterodactyloidea), and thus within Novialoidea but outside Breviquartossa.

The most recent hypothesis was put forward by Vidovic & Martill (2018), whose phylogenetic analysis recovered the Anurognathidae as a clade comprised within a Scaphognathidae (outside Rhamphorhynchidae). Similar to the proposal of Dalla Vecchia (2014, 2019), this hypothesis also places anurognathids within breviquartossans but outside the Monofenestrata.

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. 10D), thus being comprised within the Breviquartossa. Among all proposed hypotheses, these latter two converge in recognizing a clade comprised of Rhamphorhynchidae, Anurognathidae, Darwinoptera and Pterodactyloidea, though disagreeing on the relationships between these four subgroups.

The sections below present a critical discussion of the characters behind the different hypotheses, and coding differences between previous analyses and the present one. For the sake of simplicity, the discussion below will follow the simplified result of our analysis: Rhamphorhynchidae + (Anurognathidae + (Darwinoptera + Pterodactyloidea). We will leave *Dimorphodon weintraubi* and *Changchengopterus pani* momentarily aside. *Dimorphodon weintraubi* is a species from the Pliensbachian of North America, still lacking a detailed and complete description (Clark *et al.* 1998), and does not belong within the genus *Dimorphodon* (see Britt *et al.* 2018, Dalla Vecchia 2019), and thus still requires a redescription and renaming. It was recovered as the sister-group of the Anurognathidae by Britt *et al.* (2018) and Dalla Vecchia (2019). This species and its relationships with the Anurognathidae will be addressed at the end of this section.

Anurognathids as the basalmost pterosaurs?

According to the analysis presented by Kellner (2003), the clade containing all other pterosaurs to the exclusion of anurognathids (node B of Fig. 10A) is supported on the basis of 2 synapomorphies: (1) prenarial rostrum elongated (less than 60% of the skull length); and (2) external naris displaced posterior to premaxillary tooth row. The first feature is indeed absent in anurognathids, due to their derived condition of an extremely shortened skull. However, the second feature is actually present in *Anurognathus ammoni*, *Batrachognathus volans*, *Jeholopterus ningchengensis* (see Riabini 1948, Bennett 2007, Yang *et al*. 2019) and *Sinomacrops bondei*.

Node C of Fig. 10A was supported by two synapomorphies: (1) humerus less than 2.5 times but more than 1.5 times longer than the metacarpal IV (1.50 < hu/mclV < 2.50); and (2) length of ulna between 2 and 4 times the length of metacarpal IV (4 > ul/mclV > 2) (Kellner 2003). Concerning both features, almost all pterosaurs (except for MCSNB 8950 and anurognathids) exhibit them. In our analysis, both are recovered as synapomorphies for the Anurognathidae, and not as simplesiomorphies.

Node D of Fig. 10A was supported by one synapomorphy: femur longer but less than twice the length of metacarpal IV (Kellner 2003). The femur is about twice or longer than metacarpal IV in most anurognathids (though not in *Sinomacrops bondei*). However, in our analysis, a femur about twice or longer than metacarpal IV was recovered as the plesiomorphic condition for the Breviquartossa, as seen in *Sordes* and *Scaphognathus*. A femur longer but less than twice the length of metacarpal IV occurs homoplastically in the Rhamphorhynchini and Pterodactyloidea + Darwinoptera in our analysis.

Node E of Fig. 10A was supported by one synapomorphy: diameter of radius no more than half that of ulna (Kellner 2003). As observed by Kellner (2003), the diameter of the radius and ulna are subequal in the basal pterosaur *Preondactylus buffarini*. The same is true for its sister-group, *Austriadactylus cristatus* (see Dalla Vecchia 2009b). The diameter of the radius is inferior to half that of the ulna in *Dimorphodon*, *Campylognathoides*, *Rhamphorhynchus* and pterodactyloids (see Kellner 2003), and was thus recovered as a synapomorphy of the clade joining them on the analysis presented by Kellner (2003). However, the diameters of ulna and radius are subequal in

Changchengopterus pani and darwinopterans (then unknown in 2003), as well as *Sordes* and *Scaphognathus* (rhamphorhynchids in our analysis). Thus, in our analysis, we recover that subequal diameters form a synapomorphy for the Breviquartossa, reversed in *Rhamphorhynchus* and Pterodactyloidea.

Finally, the clade Novialoidea (thereby named in order to encompass *Campylognathus* and the Breviquartossa) is supported by two synapomorphies: (1) third phalanx of manual digit IV shorter than first (ph3d4); and (2) third phalanx of manual digit 1V shorter than second (ph3d4). Both of these two features were coded as "?" for *Anurognathus ammoni*, *Batrachognathus volans* and *Dendrorhynchoides curvidentatus* in the data matrix of Kellner (2003). However, both features are present in *D. curvidentatus* (see Ji & Qiang 1988, Ji & Ji 1998). Presently, these features are also known to be present in *Anurognathus ammoni*, *Jeholopterus ningchengensis*, *Luopterus mutoudengensis* and *Vesperoptertylus lamadongensis* (Wang *et al.* 2002, Bennett 2007, Lü & Hone 2012, Lü *et al.* 2018).

The features of the next relevant node, that of the Breviquartossa, will be discussed further below. The discussion above justifies why, under the present analysis, anurognathids cannot be viewed as the basalmost pterosaurs.

Anurognathids as the sister-group of Novialoidea*?*

Moving on to the analysis presented by Unwin (2003), the clade containing *Campylognathoides*, rhamphorhynchids and pterodactyloids (equivalent to the Novialoidea) to the exclusion of anurognathids was supported on the basis of six synapomorphies: (1) rostrum low with straight or concave dorsal outline; (2) posterior process of premaxillae interfingers between frontals; (3) external naris low and elongate; (4) nasal process of maxilla inclined backwards; (5) broad maxilla-nasal contact; (6) orbit larger than antorbital fenestra. In order to better organize the discussion on these six features, the comments below are numbered.

Comments:

1. Rostrum low with straight or concave dorsal outline.
   The dorsal outline of the rostrum of anurognathids is indeed convex, as can be seen in *Anurognathus ammoni* (Döderlein 1923, Bennett 2007) and *Sinomacrops bondei*, but it is not convex in most other basal pterosaurs (see Dalla Vecchia 2014, 2019) such as *Austriadactylus*, *Preondactylus*, *Arcticodactylus*, *Carniadactylus*, *Raeticodactylus* and *Eudimorphodon* (*contra* Unwin 2003). Only in dimorphodontids is the outline convex as well (Padian 1983, Britts *et al.* 2018), though this was recovered as a homoplasy relative to anurognathids in our analysis.
2. Posterior process of premaxillae interfingers between frontals.
   A posterior process of premaxillae interfingering between the frontals is present in *Anurognathus*, as reported by Bennett (2007).
3. External naris low and elongate.
   An external naris low and elongate is indeed absent in anurognathids (see Bennett 2007).
4. Nasal process of maxilla inclined backwards – 5. Broad maxilla-nasal contact.
   A nasal process of the maxilla, as well as a contact between maxilla and nasal, are actually absent in anurognathids (see Andres *et al.* 2010 and discussion below). Furthermore, a posteriorly inclined nasal process of the maxilla is widely distributed within basal pterosaurs (and not only novialoids), as seen in *Preondactylus*, *Austriadactylus*, *Arcticodactylus*, *Carniadactylus*, *Seazzadactylus*, *Raeticodactylus*, *Caelestiventus* and *Dimorphodon* (Dalla Vecchia 1998, 2009, 2013, 2018, 2019, Dalla Vecchia *et al.* 2002, Stetcher 2008, Britt *et al.* 2018).

6. Orbit larger than antorbital fenestra.
   An orbit larger than the antorbital fenestra is present in *Campylognathoides* and rhamphorhynchids, thus being a synapomorphy for the node joining them according to Unwin (2003). An individual antorbital fenestra is not present in anurognathids (see further below), but still, the orbit in anurognathids is much larger than the nasoantorbital fenestra as a whole (Bennett 2007), what actually could suggest affinities to the Novialoidea.

Therefore, anurognathids cannot be confidently excluded from the Novialoidea (*contra* Unwin 2003). Still concerning the analysis of Unwin (2003), the Breviquartossa (excluding

anurognathids) shared seven synapomorphies: (1) ventral margin of skull curved downwards posteriorly; (2) loss of "coronoid" eminence on posterior end of mandible; (3) development of bony mandibular symphysis; (4) mandibular symphysis more than 30% the length of the mandible; (5) loss of heterodonty in the mandibular dentition; (6) metacarpals I, II and III of equivalent length; and (7) a short metatarsal IV. However, five of these features actually support the placement of the Anurognathidae within the Breviquartossa. Comments are again numbered below.

Comments:

1. Ventral margin of skull curved downwards posteriorly.
   A ventral margin of the skull curved downwards posteriorly was coded as absent in Anurognathidae by Unwin (2003), and as absent in *Anurognathus* and *Batrachognathus* by Dalla Vecchia (2019), but this feature cannot be assessed in any of the two known specimens of *Anurognathus* (Döderlein 1923, Bennett 2007), nor in the holotype of *Batrachognathus* (see Riabinin 1948). In our analysis, this feature was recoded as "?" for them. In *Sinomacrops*, it can be seen that the feature is present, and was coded as such for this new taxon.
2. Loss of "coronoid" eminence on posterior end of mandible.
   A "coronoid" eminence in the lower jaw was coded as present for the Anurognathidae by Unwin (2003), but is absent in *Anurognathus* (Bennett 2007) and cannot be assessed in other species.
3. Development of bony mandibular symphysis.
   Development of an extended mandibular symphysis is indeed absent in anurognathids, as can be seen in *Sinomacrops*, *Anurognathus*, *Batrachognathus*, *Jeholopterus* and *Vesperopterylus* (Döderlein 1923, Riabinin 1948, Wang *et al.* 2002, Lü *et al.* 2018). In our analysis, the development of an extended mandibular symphysis was once again recovered as a synapomorphy of the Breviquartossa, but its absence was recovered as a reversion for the Anurognathidae. Intuitively, we propose that the secondary loss of the symphysis extension in anurognathids is biologically related to the evolutionary process of shortening of the rostrum, a derived feature of anurognathids.

4. Mandibular symphysis more than 30% the length of the mandible.
   See above (3).
5. Loss of heterodonty in the mandibular dentition.
   The particular heterodonty of basal pterosaurs is actually absent in anurognathids (e.g. Dalla Vecchia 2014, 2019, *contra* Unwin 2003), further corroborating their placement within the Breviquartossa.
6. Metacarpals I, II and III of equivalent length.
   Similarly, metacarpals I-III are of equivalent size in anurognathids, as in other breviquartossans (Ji & Ji 1998, Wang *et al.* 2002, Bennett 2007, Lü *et al.* 2018, Yang *et al*. 2019, *contra* Unwin 2003).
7. Short metatarsal IV.
   Finally, a review of the configuration of the fourth metatarsal in anurognathids further supports their interpretation as breviquartossans. The metatarsals of *Batrachognathus volans*, *Luopterus mutoudengensis* and *Dendrorhynchoides curvidentatus* can hardly be discerned (Riabinin 1948, Ji & Ji 1998, Lü & Hone 2012), and this condition was thus coded as "?" for them in our analysis. However, in *Sinomacrops bondei*, it can be clearly seen that metatarsal IV is distinctively shorter than metatarsals I-III (Fig. 5). In *Vesperopterylus* the metatarsals are very clearly preserved, so that it can be also seen that metatarsals I-III are subequal while metatarsal IV is noticeably shorter (Lü *et al.* 2018). The same is true for *Jeholopterus*, both the holotype (Wang *et al.* 2002) and the referred specimen (Ji & Yuan 2002, Yang *et al*. 2019). Only in *Anurognathus* can it be clearly seen that metatarsal IV is subequal to the other metatarsals (Bennett 2007). In our analysis, this condition for *Anurognathus* represents a reversion.

Therefore, the analysis presented by Unwin (2003) cannot support exclusion of the Anurognathidae from the Breviquartossa.

Anurognathids as non-breviquartossan novialoids?

According to the analysis presented by Dalla Vecchia (2019), anurognathids are novialoids (*contra* Kellner 2003, Unwin 2003), but are excluded from the Breviquartossa (Fig. 10C). Under

the analysis of Dalla Vecchia (2019), the Breviquartossa, to the exclusion of anurognathids, share three synapomorphies: (1) ventral margin of skull curved downwards posteriorly; (2) the development of a dentary symphysis; and (3) metatarsals tightly bounded (instead of spreading as in rhamphorhynchids, darwinopterans and *Pterodactylus*).

The first and second features were already explored (see above). As for the third feature, the ancestral condition for the Breviquartossa was recovered as ambiguous in our analysis. We therefore question a non-breviquartossan nature for anurognathids.

Anurognathids as "scaphognathids"?

In the analysis presented by Vidovic & Martill (2018), the Anurognathidae are comprised within a Scaphognathidae group (Fig. 10E). Note that the Scaphognathidae *sensu* Vidovic & Martill (2018) was recovered outside of the Rhamphorhynchidae, differently from the analysis presented here, as well as from Andres *et al.* (2014) and Dalla Vecchia (2019), which have recovered *Scaphognathus*, or the Scaphognathinae, as comprised within Rhamphorhynchidae. Turning back to the analysis of Vidovic & Martill (2018), their Scaphognathidae was recovered as the sister-group of the Monofenestrata (Fig. 10E).

In their analysis, monofenestratans share the following 7 features to the exclusion of scaphognathids (including anurognathids): (1) greater angle of the quadrate to the occlusal margin of the rostrum (transformed from 130˚ to 139.5˚-150.5˚); (2) the orbit is lower relative to the skull depth; (3) orbit comparatively larger relative to the inferior temporal fenestra length; (4) the center of the orbit lies above the quadrate; (5) a longer, lower nasoantorbital fenestra (6) nasal contacts the antorbital fenestra; and (7) nares and antorbital fenestra is confluent.

Comments:

1. Quadrate angle.
   This angle is low in anurognathids, in which the quadrate is approximately perpendicular relative to the jawline. However, in the present analysis, this is

recovered as apomorphic for anurognathids. It differs not only from monofenestratans, but even from *Scaphognathus* (135°, see Bennett 2014).

2. Orbit relatively lower relative to skull depth (continuous character).
   It is unclear what difference was found between monofenestratans and scaphognathids (including anurognathids) relative to this feature. The ratio between orbit height and skull height is similar across non-pterodactyloid breviquartossans, as the orbit height is 66% of skull height in *Dorygnathus*, 54-68% in *Rhamphorhynchus*, 65% in *Scaphognathus*, ~69% for *Darwinopterus* and 64% for *Kunpengopterus* (Wellnhofer 1975, Padian 1983, 2008a, Bennett 2007, 2014, Lü *et al.* 2009, Wang *et al.* 2010). The codification in their dataset should be revised, as the values in non-monofenestratan breviquartossans and darwinopterans are too similar to distinguish between non-monofenestratans and monofenestratans. The value for *Anurognathus ammoni* is ~71% (Döderlein, 1923) and for *Sinomacrops bondei* is ~75%.
3. Lower nasoantorbital fenestra (continuous character).
   This character is not much informative for anurognathids, since confidently measuring the height/depth of the nasoantorbital fenestra is not feasible in any known anurognathid species due to crushing. Anyway, we do agree that the nasoantorbital fenestra is higher in anurognathids relative to darwinopterans + pterodactyloids, which share longer, lower nasoantorbital fenestra. This feature does set anurognathids apart from darwinopterans + pterodactyloids, what is consistent with the results presented here.
4. Orbit comparatively larger relative to the lower temporal fenestra (LTF) length (continuous character).
   However different this ratio may be between scaphognathids/scaphognathines and monofenestratans according to Vidovic & Martill (2018), the extension of the LFT cannot be confidently estimated in any anurognathid specimen.
5. Center of the orbit lies above the quadrate.
   Throughout non-monofenestratans, the center of the orbit typically lies anterior to the level of the quadrate, as seen in *Scaphognathus* and anurognathids, indeed (Bennett 2007, 2014). However, the same is true for all wukongopterids (Lü *et al.* 2009, Wang *et al.* 2009, 2010). In the dataset presented by Vidovic & Martill (2018),

wukongopterids were miscoded as exhibiting the center of the orbit above the quadrate, what led to the mistaken recovery of this feature as a purported synapomorphy of the Monofenestrata, but should be restricted to pterodactyloids (though not universal).

6. Nasal contacts the "antorbital fenestra".

   The nasal does seem to contact the remnant of the "antorbital fenestra" space in *Anurognathus ammoni* (see Bennett, 2007), as well as in *Sinomacrops bondei*, although this is hard to confirm due to the crushed nature of the available specimens. Thus, this feature cannot be considered as absent in anurognathids, and is possibly present.

7. Nares and antorbital fenestra are confluent.

   Most workers have coded a confluent nasoantorbital fenestra as absent for anurognathids (Kellner 2003, Unwin 2003, Bennett 2007, Lü *et al.* 2018, Vidovi & 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 could be observed and 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). In accordance, in the small preorbital region of *Sinomacrops*, only a single opening is present. We favor the interpretation of Andres *et al.* (2010) that a nasoantorbital fenestra is present in anurognathids.

Furthermore, Vidovic & Martill (2018) proposed five synapomorphies that defined their Scaphognathidae to the inclusion of anurognathids: (1) humerus slenderer than the ancestral condition (continuous character); (2) tooth crowns are recurved; (3) the displacement of tooth curvature is at least one tooth width; (4) the preorbital rostrum lateral margin is convex in dorsal view; and (5) the prepubic boot is spatulate and narrow. We discuss below problems related to features 2–5.

Comments:

2. Tooth crowns, recurved.
   This feature was recovered as a synapomorphy of scaphognathids (including anurognathids) *sensu* Vidovic & Martill (2018). In the dataset presented by these workers, this feature was coded as "?" in *Rhamphorhynchus*, *Dorygnathus*, *Campylognathoides* and *Dimorphodon*. However, this feature is not unknown in these taxa; instead, it is well-reported as present in these forms (Wellnhofer 1975, Padian 1983, 2008a,b). As such, in the present analysis, a posteriorly recurved tooth crown, character 56(0), is plesiomorphic for both anurognathids and scaphognathines.
3. Tooth crown curvature displacement.
   As mentioned by Vidovic & Martill (2018), this character comes from the dataset of Andres *et al.* (2014). Curved tooth crows whose curvature displacement is equivalent to at least the crown diameter had already been recovered as characteristic of the Rhamphorhynchidae by Andres *et al.* (2014), englobing species considered as scaphognathids by Vidovic & Martill (2018). However, this feature is not present in anurognathids, as can be seen from the well-preserved teeth of *Anurognathus*, *Batrachognathus*, *Dendrorhynchoides* and *Jeholopterus* (Riabinin 1948, Ji & Ji 1998, Wang *et al.* 2002, Bennett 2007). Accordingly, in the original dataset of Andres *et al.* (2014), this feature was not coded as present in anurognathids.

4. Preorbital lateral margin convex (in dorsal view).
   In the matrix presented by Vidovic & Martill (2018), this character describes the shape of the preorbital rostrum in dorsal view. It is thus similar to our character 7(1): jaws, lateral margins in dorsal or ventral view, convex and elliptical. In our present analysis, character 7(1) was recovered as a homoplasy between anurognathids and *Scaphognathus*.
5. Prepubis spatulate and narrow.
   This feature was included in the synapomorphy list of the Scaphognathidae *sensu* Vidovic & Martill (2018) in their supplementary text. However, even though this feature was indeed recovered as a synapomorphy for the Scaphognathidae *sensu* Vidovic & Martill (2018), this character state does not join anurognathids and scaphognathids, and is not present in anurognathids. Character 208 of Vidovic & Martill (2018), relative to prepubic "boot" shape, contains three states: rounded/rocker shaped (0); angular, square (1); angular, triangular (2); and spatulate (3). In their dataset, state 3 is entirely restricted to non-anurognathid scaphognathids (and present as well in *Rhamphorhynchus* as a homoplasy). *Jeholopterus* is coded as "0", to which we agree (Wang *et al.* 2002), and not as spatulate. *Jeholopterus* is the only anurognathid species coded for this character, and the configuration is unknown for other anurognathids. This was recovered as a reversion by Vidovic & Martill (2018). In our present analysis, this is recovered as a plesiomorphy for *Jeholopterus*, and not as a reversion. Either way, even according to the dataset of Vidovic & Martill (2018), it is safe to say that anurognathids and scaphognathids do not share a similar prepubic morphology.

Anurognathids as the sister-group of the Pterodactyloidea?

In the analysis presented by Andres *et al.* (2014) and Longrich *et al.* (2018), anurognathids are breviquartossans. More specifically, they are recovered as monofenestratans. Within the Breviquartossa, the Monofenestrata is a synapomorphy-based clade defined by the presence of a confluent nasoantorbital fenestra synapomorphic with that in *Pterodactylus antiquus* (Lü *et al.*

2010, Andres *et al.* 2014). According to the analyses of Andres *et al.* (2010, 2014) and Longrich *et al.* (2018), this clade comprises anurognathids, darwinopterans and pterodactyloids, based on four synapomorphies: (1) confluent nasoantorbital fenestra; (2) atlantoaxis fusion; (3) mid-cervical neural spines low; (4) eight cervical neural spine low. All of these features support placement of the Anurognathidae within the Monofenestrata (*contra* Kellner 2003, Unwin 2003, Dalla Vecchia 2019).

Comments:

1. Confluent nasoantorbital fenestra.
   In our present analysis, this feature is coded as present in *Jeholopterus*, *Batrachognathus* and *Sinomacrops*, as explored in the section above.
2. – 4. Concerning cervical morphology, atlantoaxis fusion was reported for *Anurognathus* (see Bennett 2007) and the neural spines of the cervicals are low in *Vesperopterylus* (see Lü *et al.* 2018).

Therefore, all of the comments above corroborate the monofenestratan nature of anurognathids. Within the Monofenestrata, under the work of Andres *et al.* (2010, 2014) and Longrich *et al.* (2018), three synapomorphies joined the Anurognathidae and the Pterodactyloidea, to the exclusion of darwinopterans: (1) mid-cervical ribs reduced; (2) less than 15 caudal vertebrae; (3) filiform processes of the caudal zygapophyses reduced.

Comments:

1. Mid-cervical ribs are often hard to preserve, but developed ones (though relatively short) have been reported for *Jeholopterus* (see Wang *et al.* 2002) though seem to be absent in *Anurognathus* and *Vesperopterylus* (see Bennett 2007, Lü *et al.* 2018). However, slender mid-cervical ribs are also clearly present in the Darwinoptera (Wang *et al.* 2009, 2010, Cheng *et al.* 2017).
2. – 3. Concerning the last two caudal features, they were coded as "?" for *Batrachognathus* by Andres *et al.* (2010), but later works demonstrated that they are both present in this taxon (Costa *et al.* 2013, Jiang *et al.* 2014), and are coded as such in the present analysis. The same is true for the caudals of *Luopterus*

mutoudengensis and IVPP V16728 (Lü & Hone 2012, Jiang *et al.* 2014). In our analysis, the diminishment of the caudal series and the loss of the filiform processes of the zygapophyses and haemapophyses in *Jeholopterus* + (*Anurognathus* + *Vesperopterylus*) were recovered as homoplastic conditions relative to the Pterodactyloidea.

Due to the comments above, we regard that a clade joining anurognathids and pterodactyloids, to the exclusion of darwinopterans, is questionable.

Anurognathids as basal monofenestratans (new hypothesis)

After taking into account all of the observations above and incorporating them into the dataset of Dalla Vecchia (2019), our final result provides strong support for the inclusion of the Anurognathidae within the Breviquartossa (*contra* Kellner 2003, Unwin 2003, Dalla Vecchia 2019) and, more specifically, within the Monofenestrata (as in Andres *et al.* 2010, 2014), though not closer to pterodactyloids than darwinopterans (*contra* Andres *et al.* 2010, 2014). In this way, our 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).

In our analysis, the Breviquartossa (including anurognathids) is supported by six synapomorphies: (1) skull ventral margin at the articulation with mandible curving down posteriorly; (2) dentary anterior end straight; (3) sternal plate lateral processes on each side of posterior end absent; (4) metacarpals I-III subequal in length; (5) fibula not reaching the tarsus; and (6) metatarsal IV shorter than metatarsals I-III. The Monofenestrata (including anurognathids, darwinopterans and pterodactyloids) are supported by four features: (1) confluent nasoantorbital fenestra present; (2) atlantoaxis fusion; (3) low mid-cervical neural spines; and (4) mid-cervical ribs reduced. Finally, Darwinoptera + Pterodactyloidea is supported by four features that are absent in anurognathids: (1) elongated skull (over four times skull height); (2) maxillary process of the premaxilla bordering ventrally the external naris absent; (3) deltopectoral crest of humerus tongue-like (*sensu* Unwin 2003); and (4) femur longer but less

than twice the length of metacarpal IV (homoplastic with Rhamphorhynchini, *Eudimorphodon* and *Carniadactylus*).

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 Anurognathidae (Dalla Vecchia 2009, 2014, 2019, present work). Their relationship is supported by three synapomorphies: (1) first wing phalanx under 0.35 total wing digit length; (2) wing phalanx 2 shorter than phalanx 1; and (3) a boot-like prepubis (see Dalla Vecchia 2009, 2014, 2019). *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 Monofenestrata, 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. 10). It is the third 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 composes the Batrachognathinae. All other taxa were recovered as closer to *Anurognathus*, composing the Anurognathinae. 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 reinterpret the phylogenetic position of the Anurognathidae lineage, as the sister-group of Darwinoptera + Pterodactyloidea.

Acknowledgements

We thank the Willi Hennig Society for making TNT freely available. We thank Q. Fang and G. Wu (IG-CAGS) for assistance in CT-scanning. Special thanks to C. Zhao for kindly providing his artwork. XW and XZ thank National Natural Science Foundation of China (grant #41688103, #41672019, #41790452), National Key R&D Program of China (2019YFC0605403), China Geological Survey (DD20190397). RVP thanks Maria E. Leal (Aarhus University) for discussions, and FAPESP for a scholarship (#2019/10231-6). XW, CS, WM and XZ thank the late Junchang Lü (IG-CAGS) for his guidance and support. RVP and XZ deeply thank Niels Bonde (Zoological Museum, Copenhagen) for his heartful support and for fostering our productive network.

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.

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.

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., Zheng, X., Wang, X., Zhou, Z., Deng, C., 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

Gao, K., 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., 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. 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. 2015. 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.. 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., 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.

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., Fucha, X., Chen, J. 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, J., Unwin, D. M., Jin, X., Liu, Y., 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.

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.

Stecher, R. 2008. A new Triassic pterosaur from Switzerland (Central Austroalpine, Grisons), *Raeticodactylus filisurensis* gen. et sp. nov. *Swiss Journal of Geosciences*, **101** (1), 185–201.

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

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., Campos, D. A.. 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. *Nature*, **437** (7060), 875–879.

Wang, X., Kellner, A. W., Jiang, S., 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., 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. 1975. Die Rhamphorhynchoidea (Pterosauria) der Oberjura-Plattenkalke Suddeutschlands. *Palaeontogr A.*, **148**, 1–33.

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., Zhou, C., 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., Orr, P. J., Xu, X., Benton, M. J. 2019. Pterosaur integumentary structures with complex feather–like branching. *Nature ecology and evolution*, **3** (1), 24–30.

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

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

Figures

Figure 1. Fossil provenance. Maps indicating Hebei province (China). JPM-2012-001 comes from the Mutoudeng locality.

Figure 2. *Sinomacrops bondei* tax. nov., holotype (JPM-2012-001) overview. A, photograph; and B, schematic drawing. Abbreviations: ca, caudal vertebrae; co, coracoid; cv, cervical vertebrae; d, dentary; fe, femur; fi, fibula; hu, humerus; mcIV, metacarpal IV; pip, puboischiadic plate; prap, preacetabular process of the illium; rd, radius; sca, scapula; sk, skull; ul, ulna; wp, wing phalanx. Scale bar equals 20 mm.

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:

apf, anterior process of the frontal; cv, cervical vertebrae; d, dentary; f, frontal; j, jugal; la, lacrimal; na, nasal; pa, parietal; po, postorbital; pm, premaxilla; op, opisthotic; scr, sclerotic ring. Scale bar equals 10 mm.

Figure 4. Computed-tomography images of the wings of JPM-2012-001. A, right wing; B, left wing. Abbreviations: d, digit; dc, deltopectoral crest; hu.ep, humeral epiphysis; mc, metacarpal; ph, phalanx; rd, radius; ul, ulna.

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.

Figure 6. Right pes of JPM-2012-001. Abbreviations: mt, metatarsal. Scale bar equals 10 mm.

Figure 7. Phylogenetic analysis results. Strict consensus tree showing the phylogenetic relationships of *Sinomacrops bondei* and anurognathids. Dashed line indicates result exclusive to the semi-strict consensus tree.

Figure 8. 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.

Figure 9. Schematic drawings of anurognathid humeri. A, *Batrachognathus volans* (based on Riabinin 1948). B, *Sinomacrops bondei*. C, *Dendrorhynchoides curvidentatus* (based on Ji & Ji 1999). D, *Jeholopterus ningchengensis* (based on Kellner *et al.* 2009). E, *Vesperopterylus lamadongensis* (based on Lü *et al.* 2018). F, *Anurognathus ammoni* based on Wellnhofer (1991). Not to scale, adjusted to matching sizes. Abbreviations: dc, deltopectoral crest; uc, ulnar crest.

Figure 10. Previous phylogenetic hypotheses for the position of the Anurognathidae. Simplified cladograms. A, from Kellner (2003). B, from Unwin (2003). C, from Dalla Vecchia (2019). D, from Andres *et al.* (2010, 2014). E, from Vidovic & Martill (2018). Red arrows indicate the Anurognathidae.

Figure 11. Life reconstruction of *Sinomacrops bondei*. Paleoart courtesy of Zhao Chuang, reproduced with permission.

Figure 1

Fossil provenance.

Maps indicating Hebei province (China). JPM-2012-001 comes from the Mutoudeng locality.

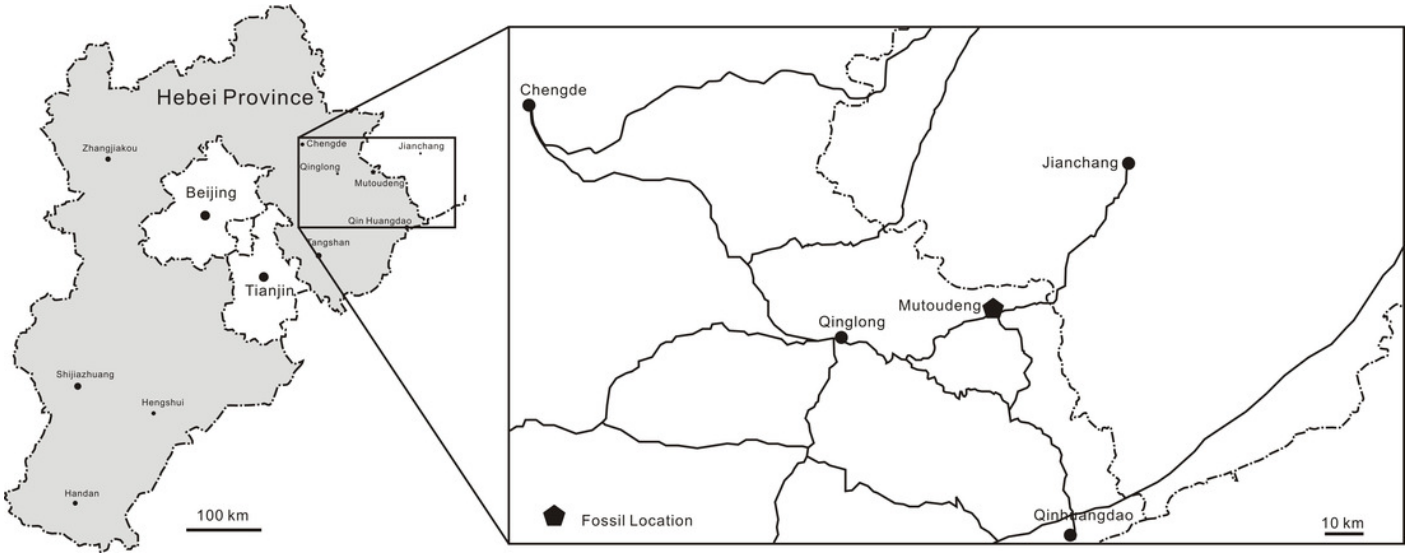

Figure 2

Sinomacrops bondei tax. nov., holotype (JPM-2012-001) overview.

A, photograph; and B, schematic drawing. Abbreviations: ca, caudal vertebrae; co, coracoid; cv, cervical vertebrae; d, dentary; fe, femur; fi, fibula; hu, humerus; mcIV, metacarpal IV; pip, puboischiadic plate; prap, preacetabular process of the illium; rd, radius; sca, scapula; sk, skull; ul, ulna; wp, wing phalanx. Scale bar equals 20 mm.

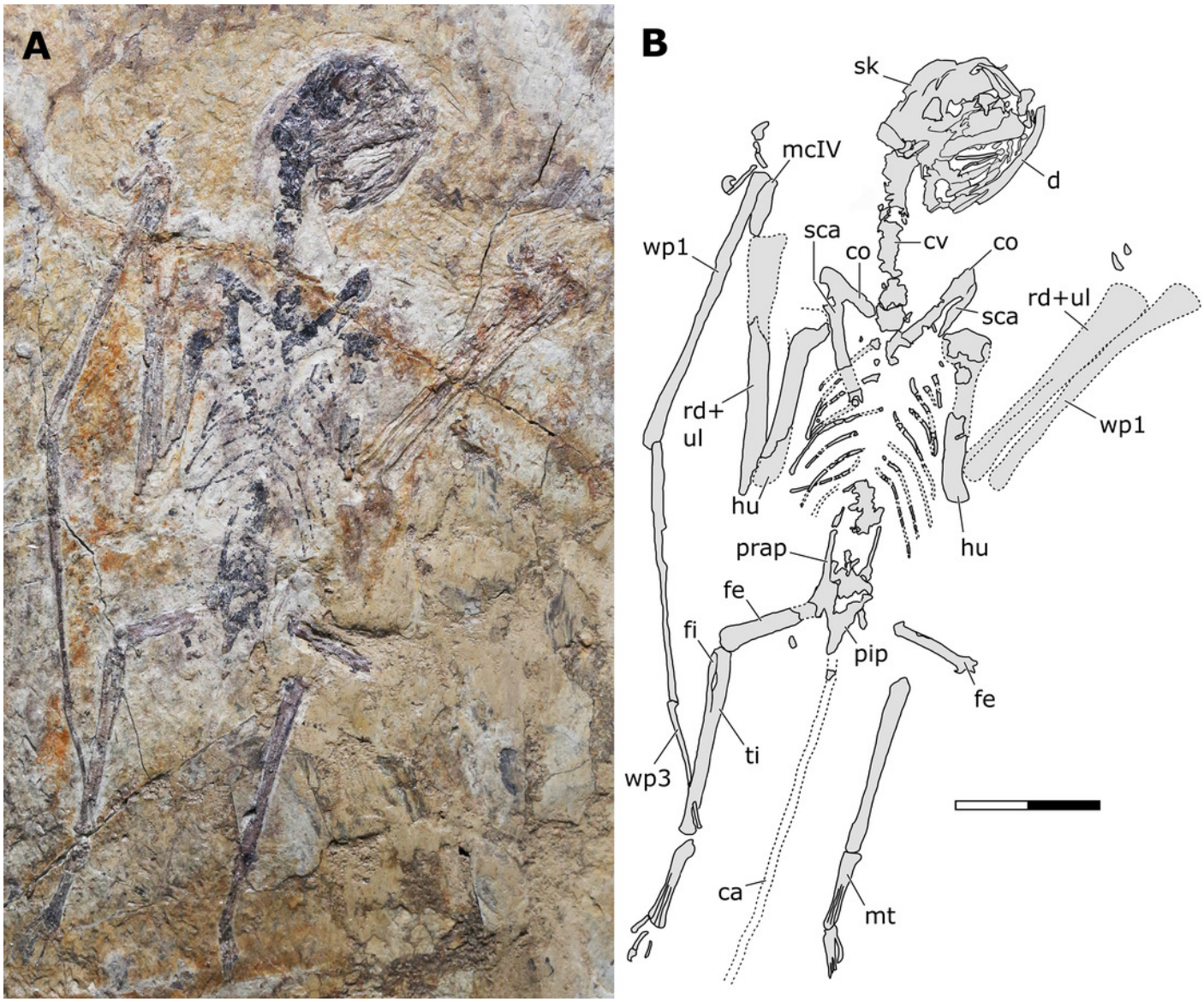

Figure 3

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: apf, anterior process of the frontal; cv, cervical vertebrae; d, dentary; f, frontal; j, jugal; la, lacrimal; na, nasal; pa, parietal; po, postorbital; pm, premaxilla; op, opisthotic; scr, sclerotic ring. Scale bar equals 10 mm.

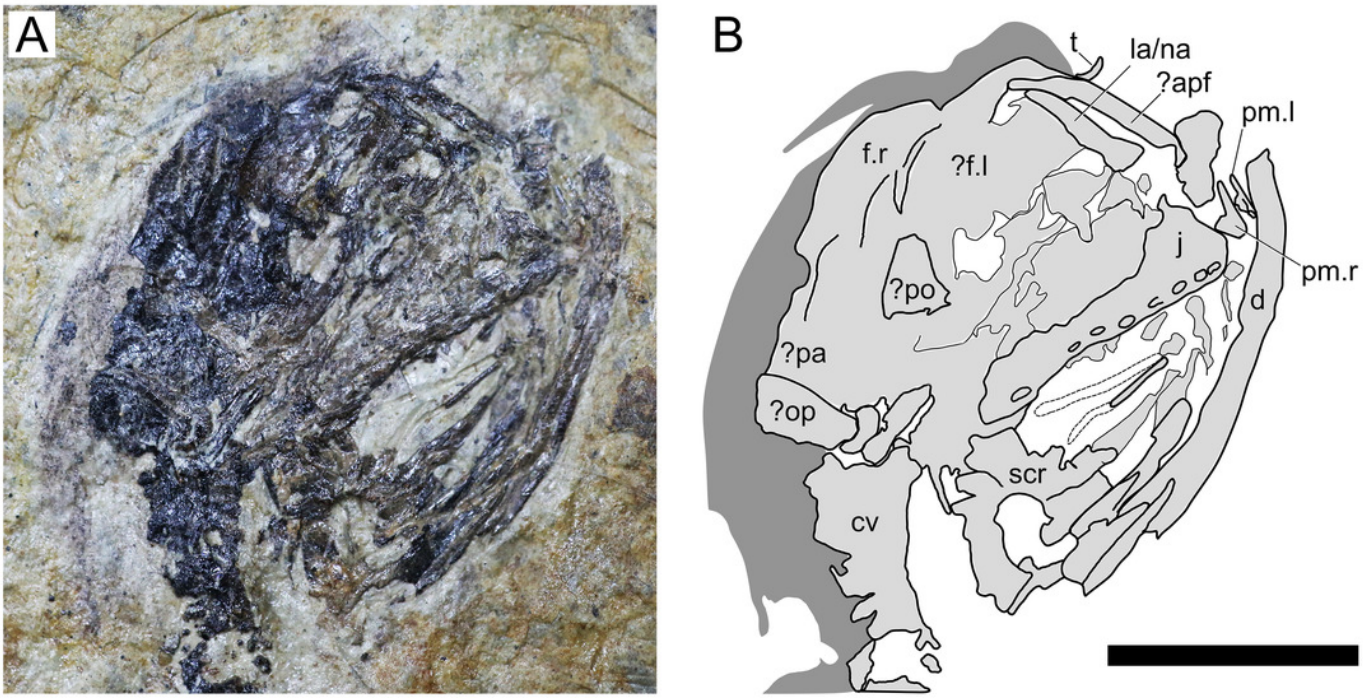

Figure 4

Computed-tomography images of the wings of JPM-2012-001.

A, right wing; B, left wing. Abbreviations: d, digit; dc, deltopectoral crest; hu.ep, humeral epiphysis; mc, metacarpal; ph, phalanx; rd, radius; ul, ulna.

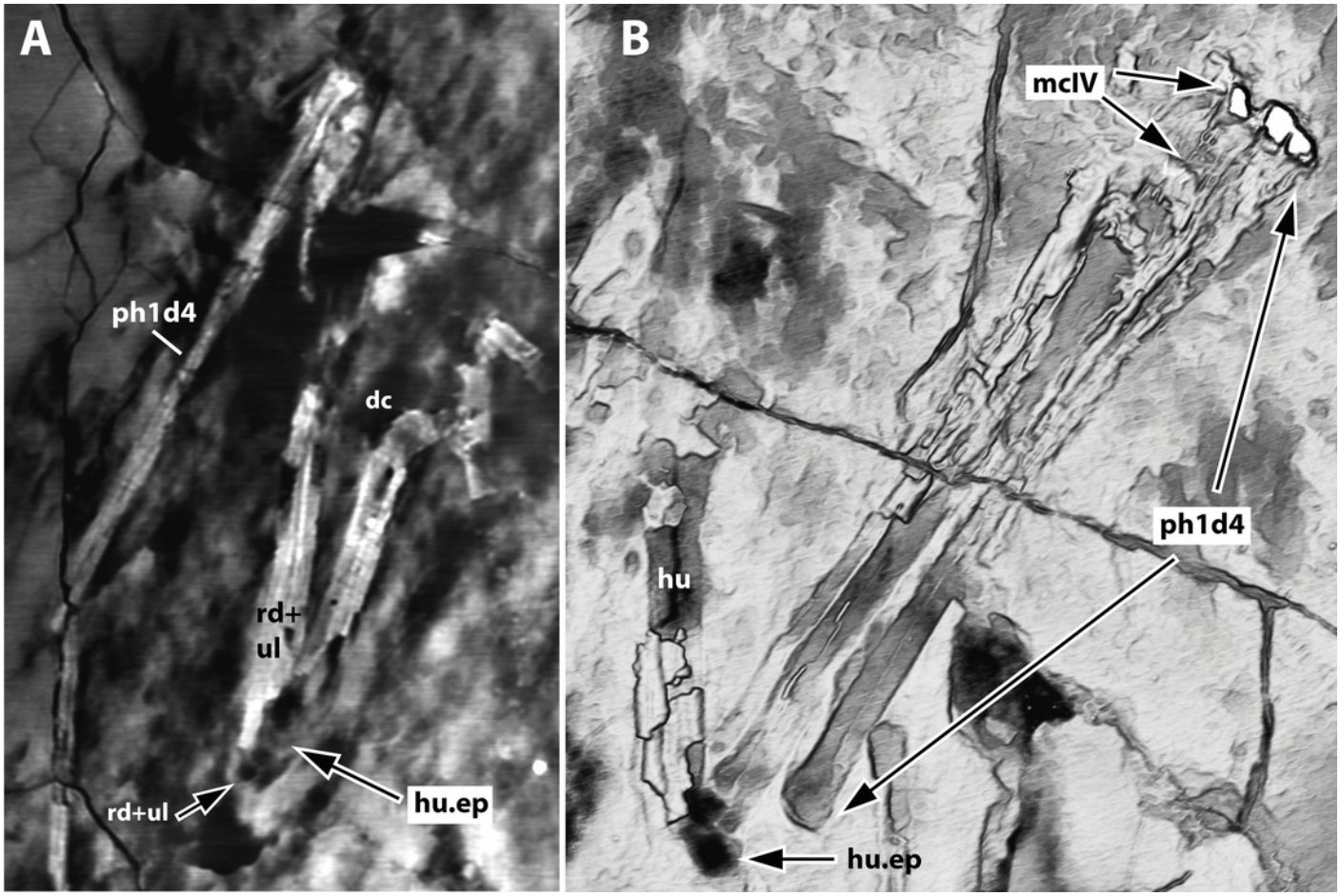

Figure 5

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.

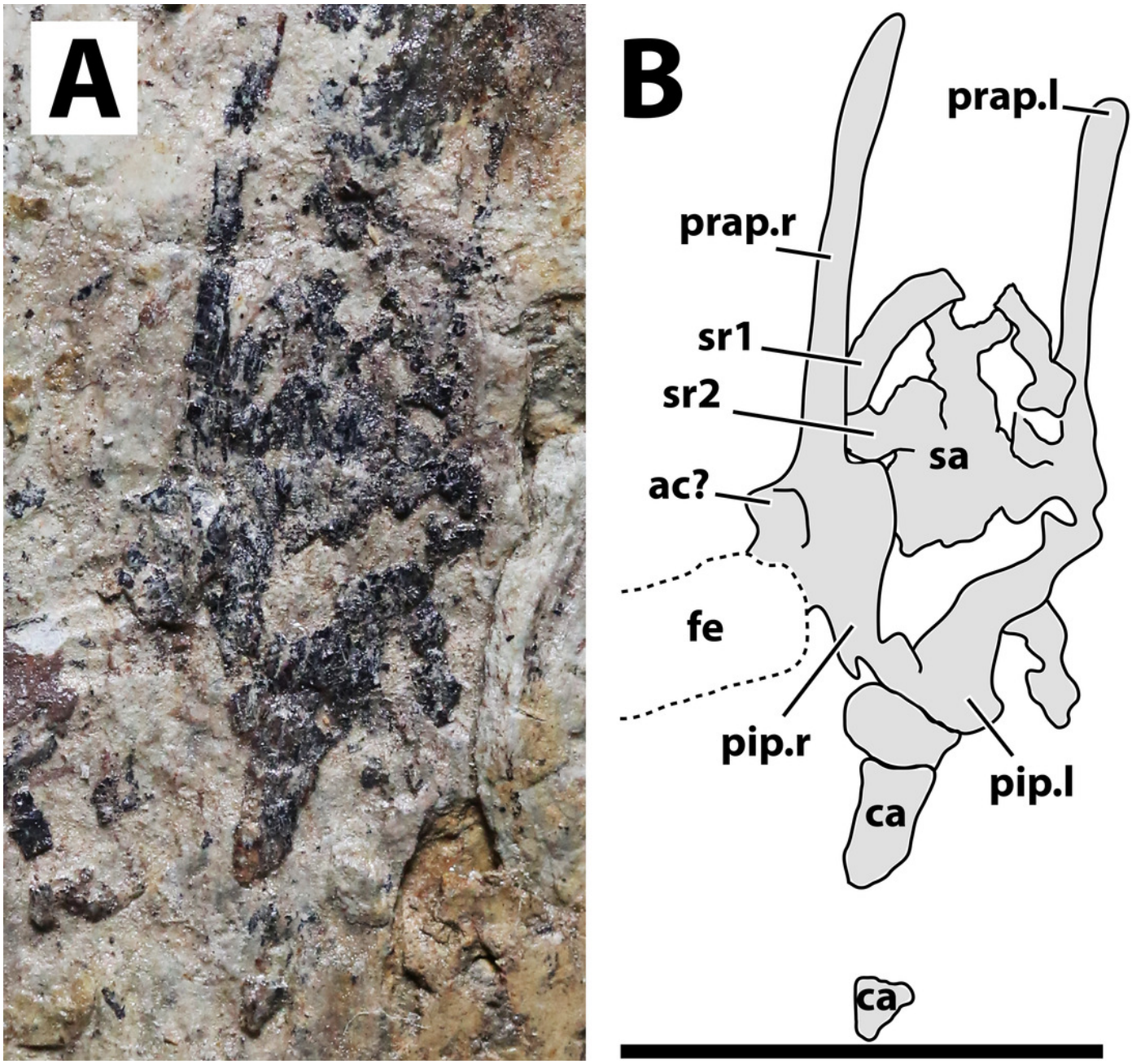

Figure 6

Right pes of JPM-2012-001.

Abbreviations: mt, metatarsal. Scale bar equals 10 mm.

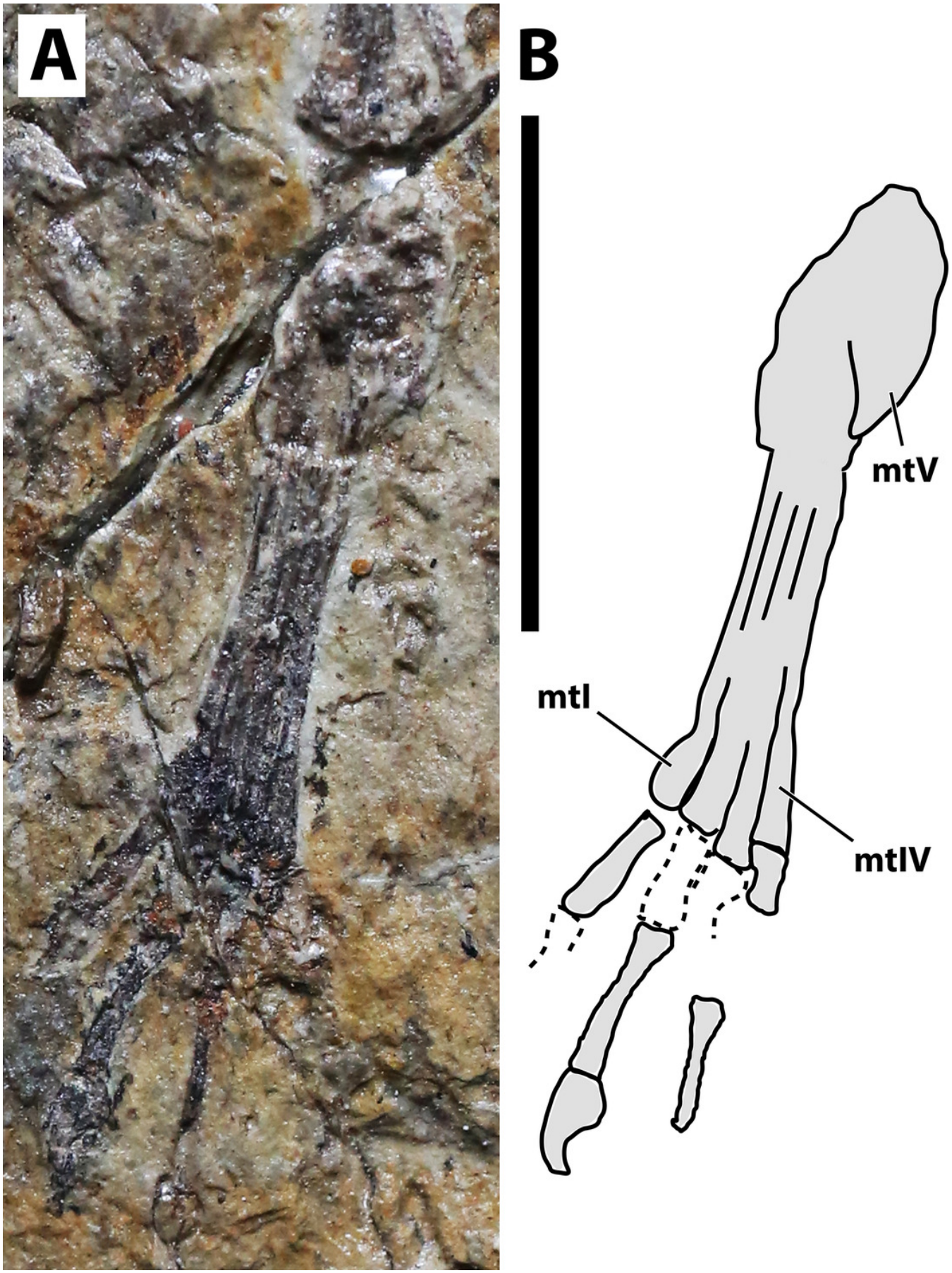
A
B
mtV
mtI
mtIV

Figure 7

Phylogenetic analysis results.

Strict consensus tree showing the phylogenetic relationships of *Sinomacrops bondei* and anurognathids. Dashed line indicates result exclusive to the semi-strict consensus tree.

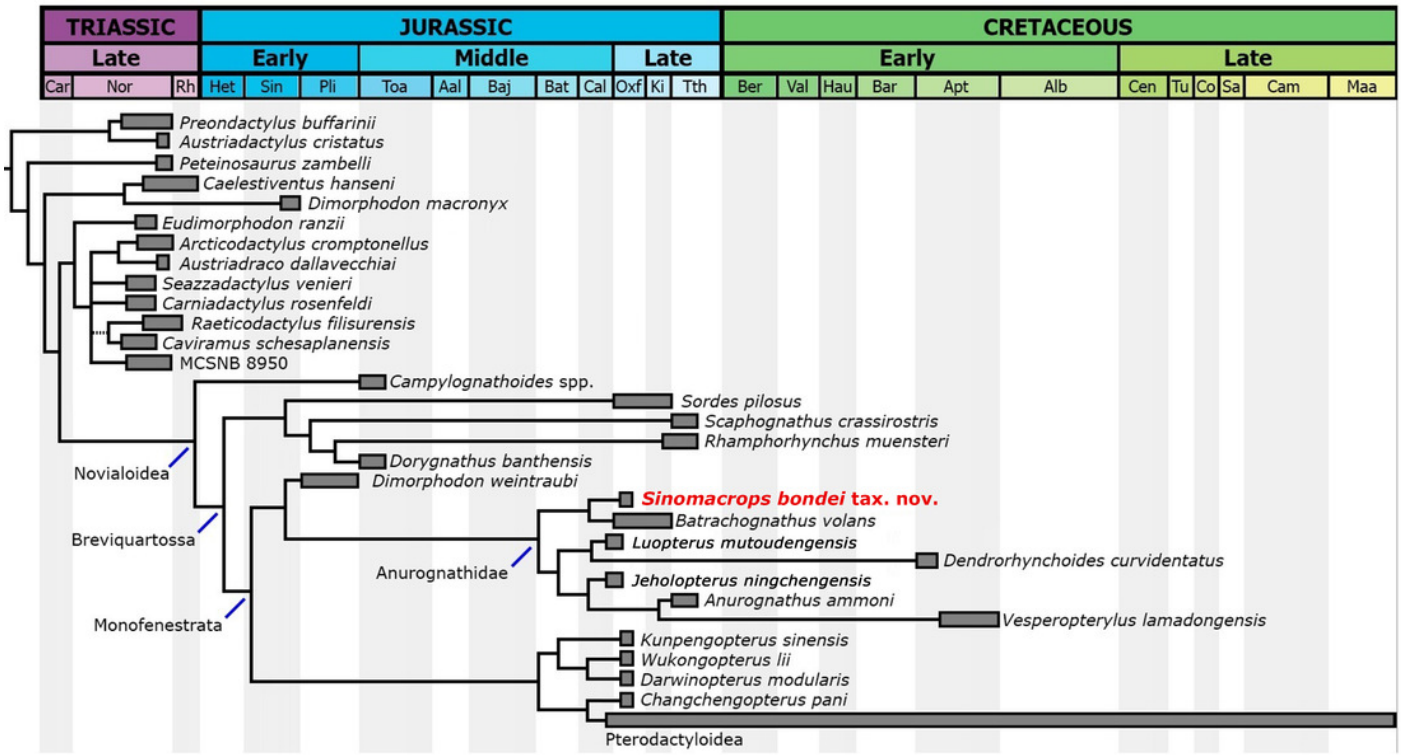

Figure 8

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.

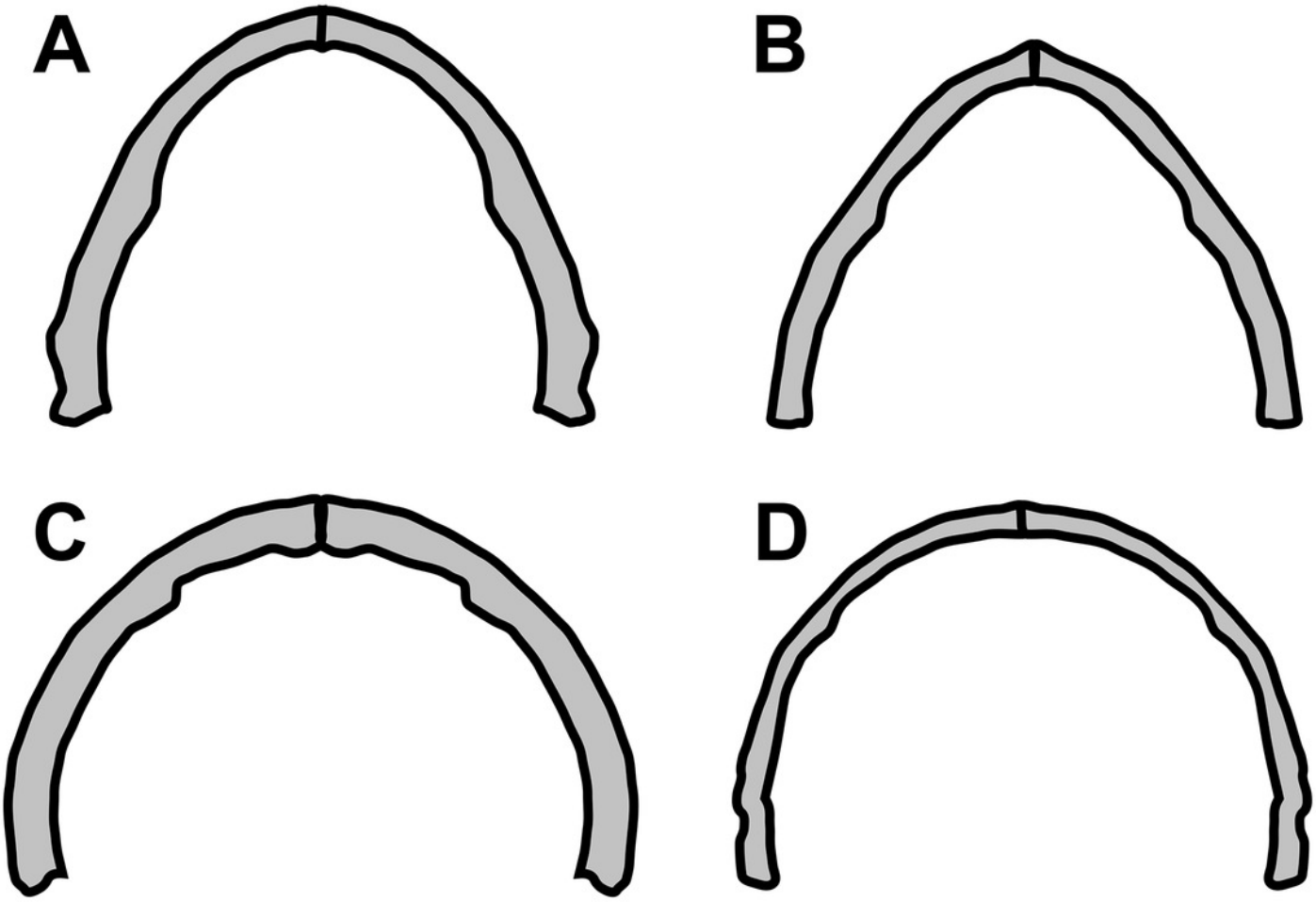

Figure 9

Schematic drawings of anurognathid humeri.

A, *Batrachognathus volans* (based on Riabinin 1948). B, *Sinomacrops bondei*. C, *Dendrorhynchoides curvidentatus* (based on Ji & Ji 1999). D, *Jeholopterus ningchengensis* (based on Kellner *et al.* 2009). E, *Vesperopterylus lamadongensis* (based on Lü *et al.* 2018). F, *Anurognathus ammoni* based on Wellnhofer (1991). Not to scale, adjusted to matching sizes. Abbreviations: dc, deltopectoral crest; uc, ulnar crest.

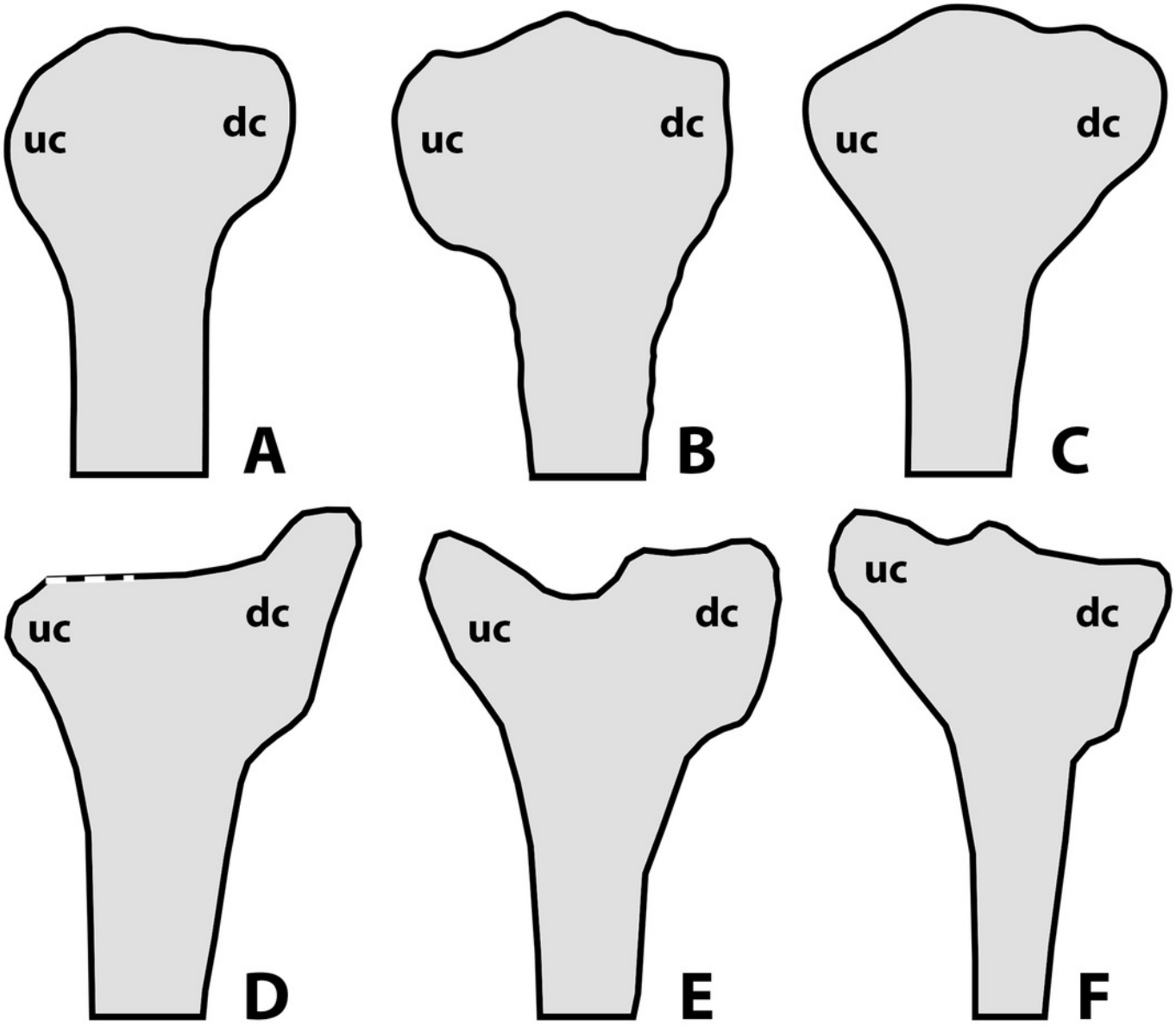
uc
dc
A
uc
dc
B
uc
dc
C
uc
dc
D
uc
dc
E
uc
dc
F

Figure 10

Previous phylogenetic hypotheses for the position of the Anurognathidae.

Simplified cladograms. A, from Kellner (2003). B, from Unwin (2003). C, from Dalla Vecchia (2019). D, from Andres *et al.* (2010, 2014). E, from Vidovic & Martill (2018). Red arrows indicate the Anurognathidae.

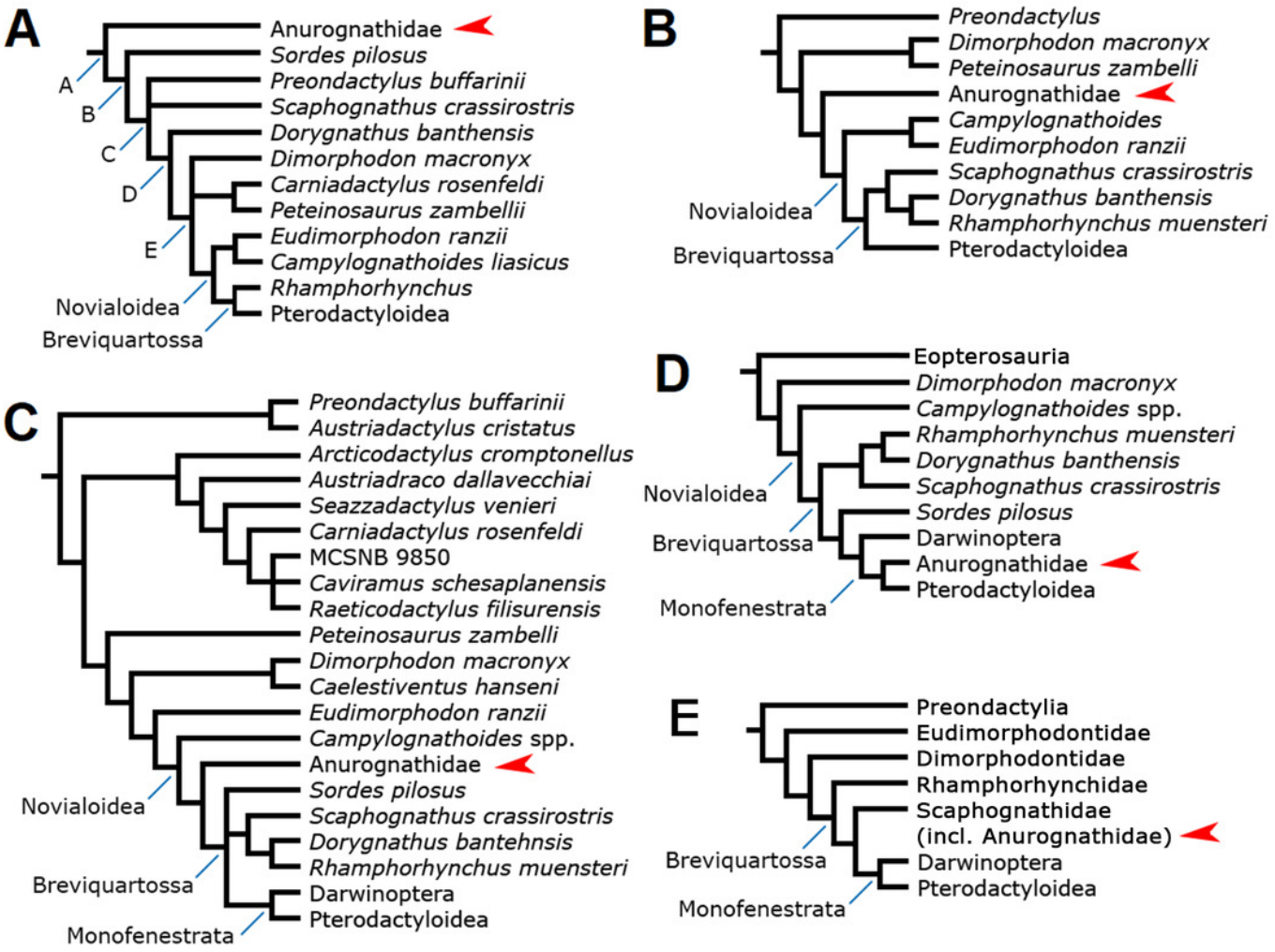

Figure 11

Life reconstruction of *Sinomacrops bondei*.

Paleoart courtesy of Zhao Chuang, reproduced with permission.

Table 1(on next page)

Skeletal proportions in anurognathids.

Abbreviations: caS, caudal series; co, coracoid; fe, femur; hu, humerus; mc, metacarpal; mt, metatarsal; ph, phalanx; rd, radius; sc, scapula; ti, tibia; ul, ulna. *CaS/fe ratio for *Batrachognathus* is based on the referred specimen (Costa *et al*., 2013; Jiang *et al.*, 2014). Measurements from *Sinomacrops bondei* were taken first-hand, data on other species was taken from the literature (Döderlein, 1923; Riabinin, 1948; Ji & Ji, 1998; Wang *et al.*, 2002; Ji & Yuan, 2002; Bennett, 2007; Lü & Hone, 2012; Jiang *et al.*, 2014; Lü *et al.*, 2018; Yang *et al.*, 2019).

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	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
IVPP V16728	?	1.43	?	?	?	?	?	?	?	?	?	?	?	?	~1.40	0.38	>1.49
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
Sinomacrops bondei	2.86	1.76	0.59	1.63	4.84	2.96	1.18	0.86	1.63	0.89	0.45	0.50	?	~1.8	2.12	0.48	>1.69
Batrachognathus volans	?	1.93	?	?	?	?	?	?	?	?	?	?	?	?	1.75	?	1.47*

Table 1. Skeletal proportions in anurognathids. Abbreviations: caS, caudal series; co, coracoid; fe, femur; hu, humerus; mc, metacarpal; mt, metatarsal; ph, phalanx; rd, radius; sc, scapula; ti, tibia; ul, ulna. *CaS/fe ratio for *Batrachognathus* is based on the referred specimen (Costa *et al*., 2013; Jiang *et al.*, 2014). Measurements from *Sinomacrops bondei* were taken first-hand, data on other species was taken from the literature (Döderlein, 1923; Riabinin, 1948; Ji & Ji, 1998; Wang *et al.*, 2002; Ji & Yuan, 2002; Bennett, 2007; Lü & Hone, 2012; Jiang *et al.*, 2014; Lü *et al.*, 2018; Yang *et al.*, 2019).