Comments by S. Christopher Bennett on the manuscript "*Nurhachius luei*, a new istiodactylid pterosaurs (Pterosauria, Pterodactyloidea) from the Early Cretaceous Jiufotang Formation of Chaoyang City, Liaoning Province (China); and comments on the group" by X. Zhou, R. V. Pegas, M. E. C. Leal, and N. Bonde for the journal *PeerJ*.

General Comments for the Editor

I understand this to be a review of a major revision, and it seems to me that the authors have largely followed the suggestions of the previous reviewers. Therefore, I will omit most of the questions from the review formula, only comment where necessary about the revision, and point out a few errors, inconsistencies, etc. that I noticed (see marked up manuscript below). I encourage the authors to follow my suggestions here and in the mark up if they find them useful, and encourage the editor to publish the manuscript with the usual minor revisions.

Numbered Comments for the Authors

The numbered comments below refer to the circled numbers that I have placed in the right margin of the manuscript, and the comments are written as directed to the authors.

• - How is *luei* pronounced? [Cue the Kingsmen's 1963 recording.]

• - In *et al.* citations in the text, it is only necessary to include Wang's initials where Wang L could be confused with Wang M or Wang XL. Oh, and is Wang X different from Wang XL? Wang L is only 2006, Wang M is only 2019, Wang X is only 2018, and Wang XL is neither 2006 nor 2018 nor 2019, so initials are not necessary unless *PeerJ* has a specific policy regarding such cases.

• - Notice that paragraphs were separated by a blank line until the end of the Introduction, and from there on sometimes they are and sometimes they are not. There should be one person in charge of the manuscript who checks everything to ensure consistency throughout. The number of spelling errors, formatting errors, omissions of citations, etc. suggests that no one was in charge or whoever was in charge was not careful. If your writing is sloppy, what are we to think about your scientific content?

1 - No! LPM 00023 is, and will never cease to be, the holotype on *Longchengpterus zhaoi*. It does not matter that *L. zhaoi* has been judged a junior synonym, the name is valid and it should not be put in quotation marks. So the sentence should read: "... its referred specimen (the holotype of *Longchengpterus zhaoi*) come ..."

2 - Dalla Vecchia questioned the significance of the angle. I share his view that there can be individual variation, variation from crushing, etc. I am also concerned that both *N. igna...* specimens are 160°; are you sure one isn't 159.4° and the other 160.9°? Did you have a consistent way of measuring? That said, I see no problem with you viewing the angle of the new specimen as significantly different from that of the old ones until we have a few more specimens

of each species. Note that there is more variation in *Pteranodon* angles than you seem to think there is. If you don't believe me, ask Bennett.

• - The phrase 'result to be' is awkward. Species do not result, they *are*. On the first appearance on line #302, I replaced the phrase with 'are', but one could also use 'were found to be'. Figure out what you want to use, and replace 'result to be' throughout the manuscript and supplemental material.

• - "Subparallel lateral taper" is an oxymoron! Replace or fix.

3 - Again, there is no need for quotation marks for *L. zhaoi*; however, why even mention it? It is a junior synonym, so ignore it, and do not count it as one of the new istiodactylids.

4 - It is my understanding that the zones in the Romualdo that produce concretions represent a small span of time so that it is unlikely that the multiple species of *Anhanguera* represent different points along an anagenetic lineage. There must be another explanation for all the *Anhanguera* species!

• - Line #455: Why is 'sister-group' hyphenated and 'sister taxon' not?.

5 - Paragraphs should normally be two or more sentences.

• - Dalla Vecchia wanted you to code *Longchengpterus zhaoi* separately from *N. igna...* and include it in the cladistic analysis. You replied that you did not want to do so on the grounds that cladistic analyses are normally done on OTU's and not individual specimens. I agree with you and note that you state that you view *L. zhaoi* as a junior synonym on line #43, so it is fine to omit it from the analysis. However, if you found any characters on LPM 00023 that differed from the holotype of *N. igna...*, then things might be different.

• - Dalla Vecchia commented on the character "Slight dorsal deflection of the palate" and stated that the deflection is limited to the "the tip of the snout." You admitted to Dalla Vecchia that that was correct and stated that things were "explained more clearly now." It may be better than it was, but I do not like it at all. You state in the abstract and elsewhere that a 'dorsal deflection of the palate is observed' in the new species. No! Look at Fig. 1. Can you see any of the palate anterior to the NAOF? No! All you can see is max and premax. There may be a little palatine hidden in there between the premaxillae, but you cannot see any. What we can see is that the rostrum anterior to the NAOF curves upward a little, i.e., the median dorsal margin of the paired premaxillae and the ventral jaw margins of the max and premax curve upward a little. One could describe this as dorsal deflection, and indeed in line #166 and 186 you refer to the rostrum and premaxillae being dorsally deflected. However, in lines #319, 321, 372, 375, and 378 you refer to dorsal deflection of the palate. It is true that the upward curvature of the rostrum in BPMC-0204 probably would require the palate to be curved upward as well, but because the premaxillae are also curved upward, it is misleading to refer to the condition as a curvature of the palate without also mentioning the fact that the max and premax also curve, thus acknowledging that it is the entire anterior rostrum. Your reply to Dalla Vecchia stated that "The feature is nonetheless traditionally referred to as a 'dorsal deflection of the palate', as referenced (Rodrigues & Kellner, 2013)." So, Taissa and Alex did a bad job of describing the character state and you don't have the courage to fix their error, is that it? This is science! do it right or don't do it at all. You are already stating in the Suppl. Mat. that the character is modified from Andres & Ji, 2008 and Rodrigues & Kellner, 2013, so correct the wording and prevent further confusion in the future.

Nurhachius luei, a new istiodactylid pterosaur (Pterosauria, Pterodactyloidea) from the Early Cretaceous Jiufotang Formation of Chaoyang City, Liaoning Province (China) and comments on the group

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Abstract

A new istiodactylid pterosaur, *Nurhachius luei* sp. nov., is here reported based on a complete skull with mandible and some cervical vertebrae from the lower part of the Jiufotang Formation of western Liaoning (China). This is the second species of *Nurhachius*, the type-species being *N. ignaciobritoi* from the upper part of the Jiufotang Formation. A revised diagnosis of the genus *Nurhachius* is proposed. In this genus, a slight dorsal deflection of the palate is observed, which is homoplastic with the Anhangueria and *Cimoliopterus*. *Nurhachius luei* sp. nov. shows an unusual

pattern of tooth replacement. The relationships within the Istiodactylidae and with their closest taxa are investigated through a phylogenetic analysis by parsimony.

Introduction

Istiodactylid pterosaurs are characterized by rhombic teeth with lancet-shaped crowns, long skulls with short pre-antorbital portions of the rostrum, and nasoantorbital fenestrae representing over 50 percent of the total skull length and height (Howse et al., 2001; Andres & Ji, 2006; Lü et al., 2013). The group was originally named by Howse et al. (2001) in order to accommodate, then, only *Istiodactylus latidens*. Later, the Istiodactylidae were phylogenetically defined by Andres et al. (2014) as the least inclusive clade containing *Nurhachius* and *Istiodactylus*.

Four pterosaur genera and five species (all represented by a single specimen) have been referred to the Istiodactylidae sensu Andres et al. (2014) in the literature, namely *Istiodactylus latidens*, *I. sinensis*, *Liaoxipterus brachyognathus*, *Nurhachius ignaciobritoi* and *Longchengpterus zhaoi*). However, *Longchengpterus zhaoi* has been considered as a junior synonym of *N. ignaciobritoi* by Lü et al. (2008), a view that is followed here (see Discussion). Therefore, *N. ignaciobritoi* is the only Chinese istiodactylid species to be represented by two specimens so far. *Haopterus gracilis*, *Hongshanopterus lacustris* and *Archaeoistiodactylus linglongtaensis* have been reported in literature as taxa that are close to the Istiodactylidae (Wang XL & Lü, 2001; Wang XL et al., 2008a; Lü & Fucha, 2010). However, the affinity of *Archaeoistiodactylus linglongtaensis* has been questioned by Sullivan et al. (2014).

All istiodactylid pterosaurs are from the Early Cretaceous Jiufotang Formation of northeastern China with the exception of *Istiodactylus latidens*, which is from the Early Cretaceous Vectis Formation of the Isle of Wight, Southern England. Also, the three taxa that are reported as close to istiodactylids come from northeastern China and surrounding areas: *Haopterus gracilis* is from the Early Cretaceous Yixian Formation, *Hongshanopterus lacustris* from the Jiufotang Formation, and *Archaeoistiodactylus linglongtaensis* from the Middle Jurassic Tiaojishan Formation. Apart from the latter, these Chinese pterosaurs belong to the Jehol Biota (see Chang et al., 2003).

By the end of 2016, 23 species of pterosaurs from Jiufotang Formation have been reported (Andres & Ji, 2006; Dong & Lü, 2005; Dong *et al.*, 2003; Jiang *et al.*, 2016; Rodrigues *et al.*, 2015; Li *et al*. 2003; Lü & Ji, 2005; Lü & Yuan, 2005; Lü *et al*., 2006, 2007, 2008, 2016a, 2016b; Wang L *et al*., 2006; Wang XL & Zhou, 2003a, 2003b; Wang XL *et al*., 2005, 2008a, 2008b, 2012, 2014).

In this paper, we describe a second species of *Nurhachius* from the Jiufotang Formation and investigate the phylogenetic relationships of the istiodactylids and purported close taxa.

Geological, paleontological and geochronological information

The Jiufotang Formation is known worldwide for its paleontological richness and the exquisite preservation of its fossils, which include plants, insects, fishes, mammals, birds, non-avian dinosaurs and pterosaurs (Wang XL, 2018; Meng et al., 2011; Wang M and Zhou, 2019; Yao et al., 2019). Fossils occur mainly in the lower part of the formation, known as Boluochi Beds or Boluochi Member (see Chang et al., 2003), which is characterized by the *Jinanichthys* – *Cathayornis* Fauna that includes small feathered dinosaurs like the four-winged *Microraptor* (Xu et al., 2003) and several pterosaurs (Chang et al., 2003; Zhou et al., 2003).

The Jiufotang Formation is 206–2685 m thick according to Chang et al. (2009) and is mainly composed of mudstone, siltstone, shale, sandstone and tuff. A tuff from the basal part of formation (two meters above the boundary between the Yixian and Jiufotang formations) in western Liaoning was dated to 122.1±0.3 Ma by Chang et al. (2009). A basalt in the upper part of the formation in Inner Mongolia was dated to 110.59±0.52 Ma by Eberth et al. (1993), but Chang et al. (2009) objected that the correlation between the Jiufotang Formation in Liaoning and Inner Mongolia is unclear and the age of the uppermost Jiufotang Formation remains unknown. The Aptian Age of the Early Cretaceous ranges ~125-113 Ma according to the International Chronostratigraphic Chart 2018/08. Therefore, the Jiufotang Formation is Aptian in age, but might reach the Albian.

The Jiufotang Formation and the underlying Yixian Formation traditionally constitute the Jehol Group. The Yixian Formation is 225-4000 m thick, varying in thickness and lithology in different areas according to Chang et al. (2009), but only a fraction is made of sedimentary rocks because basalts and lavas represents a substantial part of the section. Chang et al. (2009) dated the basal part of the Yixian Formation in Western Liaoning to 129.7±0.5 and the uppermost part of the underlying Tuchengzi Formation to 139.5±1.0 Ma. The upper part of the Yixian Formation (the Jingangshan Beds) was dated to 126.5 Ma (Chang et al., 2003). Therefore, the Yixian Formation represents an interval of ~7 Ma from early Barremian to early Aptian and the Jiufotang Formation might represents an interval of over 11 Ma from early Aptian to early Albian.

The Jehol Group has yielded the famous Jehol biota. Four fossil-bearing levels with partly different fossil associations have been distinct within the Yixian Formation and only one (corresponding to the Boluochi Beds) in the Jiufotang Formation (Chang et al. 2003).

Both the holotype of *N. ignaciobritoi* and its referred specimen (the former holotype of "*Longchengpterus zhaoi*") come from the upper part of the Jiufotang Formation (see Wu et al., 2018), whereas the new species comes from the Boluochi Beds (lower part of the Jiufotang Formation).

Material & Methods

The holotype and only specimen of the new species consists of a skull with mandible and seven articulated cervical vertebrae. It was previously figured in Lü et al. (2013, figures at pp. 81-82) and reported as an unnamed istiodactylid. The specimen was found near the village of Huanghuatan (Dapingfang town, Chaoyang City, western Liaoning).

For the comparisons we present, the following taxa/specimens were analyzed first-hand (by XZ): *Nurhachius ignaciobritoi* (both specimens, LPM 00023 and IVPP V-13288), *Liaoxipterus brachyognathus* holotype (CAR-0018), *Hongshanopterus lacustris* holotype (IVPP V14582) and *Haopterus gracilis* holotype (IVPP V11726). Data from other taxa was gathered from the literature.

A phylogenetic analysis was performed based on the data matrix by Holgado et al. (2019) modified with the inclusion of characters by Lü et al. (2008), Witton (2012), Andres et al. (2014), and new characters; and the addition of the following taxa: *Archaeoistiodactylus linglongtaensis*, *Kunpengopterus sinensis*, *Liaoxipterus brachyognathus* and *Nurhachius luei* sp. nov. (see SI). The analysis was performed by TNT (Goloboff et al., 2008) using the Traditional Search option, 10000 replicates, random seed = 0 and collapsing trees after search. The character and character states list and the TNT file with the data matrix are available in the SI.

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Results

Systematic Paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger,1901

Istiodactylidae Howse et al., 2001 (sensu Andres et al., 2014)

Nurhachius Wang XL et al., 2005

Type species. *Nurhachius ignaciobritoi* Wang XL *et al.*, 2005

Synonym. *Longchengpterus zhaoi* Wang L *et al.*, 2006

Emended Diagnosis. Istiodactylids that share the following features: slight dorsal deflection of the palate; orbit piriform; craniomandibular joint located under the anterior margin of the orbit; dentary symphysis about one third the length of the mandible; dentary symphysis with gradual taper of the lateral margins; triangular, laterally compressed teeth lacking carinae; crowns with both labial and lingual slight concavities; slight constriction between tooth crown and root.

Nurhachius luei sp. nov.

ZooBank LSID for species. urn:lsid:zoobank.org:act:6F93DC7F-20A7-4CBC-8A38-1D6C802A1906.

Etymology. The specific name honors the late Prof. Junchang Lü, who has made great contributions to the study of Chinese pterosaurs. 'ü' is 'ue' in Latin, so 'lue' means 'lü'.

Holotype. Skull, mandible and seven cervical vertebrae (BPMC-0204). The specimen is permanently deposited and available for researchers at a public repository, the Beipiao Pterosaur Museum of China, Beipiao, Liaoning Province, China (Fig. 1).

Type Locality and Horizon. Huanghuatan village, Dapingfang town, Chaoyang City, Liaoning Province, China (Fig. 2); lower part of the Jiufotang Formation, Early Cretaceous (Aptian).

Differential diagnosis. The new species is diagnosed based on the following features: quadrate inclined at 150°; medial process of the pterygoid broad and plate-like; dorsal median sulcus of the mandibular symphysis extending up to the first pair of mandibular teeth; dorsally directed odontoid (pseudotooth) of the mandibular symphysis, lacking a foramen on the lateral side and with a blunt occlusal surface; ceratobranchial I of the hyoids accounting for 60% of mandibular length; mandibular teeth extending distally beyond the symphysis.

Description

Skull and mandible. The skull is exposed in right lateral view, with some palatal elements that are visible in dorsal view. The mandible is exposed in right dorsolateral view. The skull is 300 mm long from the squamosal to the premaxillary tip (total skull length), and 74 mm high at its greatest height, which is at the level of the occiput. The nasoantorbital fenestra is long, corresponding to 45% of the total skull length (premaxilla to squamosal) and 55% of the length from the craniomandibular joint to the premaxilla. Anterior to the nasoantorbital fenestra, the long axis of the rostrum is slightly deflected dorsally, as in other istiodactylids (Wang XL et al., 2005; Andres & Ji, 2006; Lü et al., 2008; Witton, 2012), as well as *Ikrandraco avatar* and anhanguerians (e.g. Kellner & Tomida, 2000; Wang XL et al., 2014; 2015; Holgado et al., 2019), but unlike boreopterids (Lü & Ji, 2005; Lü, 2010; Jiang et al., 2014). There is a strong palatal keel extending from pre-narial part of the rostrum to the anterior third of the nasoantorbital fenestra. The craniomandibular joint levels with the anterior margin of the orbit, similarly to both specimens of *N. ignaciobritoi* (see Fig. 3; both specimens, LPM 00023 and IVPP V-13288; see Wang XL et al., 2005; Wang L et al., 2006; Lü et al., 2008), *Anhanguera* spp. (see Kellner & Tomida, 2000) and *Linlongopterus jennyae* (see Rodrigues et al., 2015), but unlike *Istiodactylus* spp., in which the joint is located anterior to the orbit (see Andres & Ji, 2006; Witton, 2012), as well as *Ikrandraco avatar* (see Wang XL et al., 2015), *Hamipterus tianshanensis* (see Wang XL et al., 2014) and *Ludodactylus sibbicki* (Frey et al., 2003), where the joint is located under the middle of the orbit. The orbit is piriform, with the ventral being the narrowest part, and without a suborbital vacuity. This is similar to the condition seen in the referred specimen of *N. ignaciobritoi* and unlike the rounded orbit of *Istiodactylus*, which has also a suborbital vacuity (see Andres & Ji, 2006; Lü et al., 2008; Witton, 2012). The infratemporal fenestra is elliptical and much smaller than the orbit. The supratemporal fenestra is poorly preserved.

Premaxilla and Maxilla. The premaxilla is fused with the maxilla and the suture is obliterated, thus the boundary between the two bones cannot be traced. Consequently, the premaxillary and maxillary teeth count is unknown. There is no premaxillary crest, as in all other istiodactylids and *Haopterus gracilis*. The rostral tip of the premaxilla exhibits a slight dorsal deflection (Fig. 4), similarly to what has already been reported for *Cimoliopterus* and anhanguerians (see Rodrigues & Kellner, 2013).

Nasal and Lacrimal. The nasal and lacrimal form the anterodorsal margin of the orbit and the posterodorsal margin of the nasoantorbital fenestra. The anterior end of the nasolacrimal coincides with the highest point of the nasoantorbital fenestra, as in both specimens of *N. ignaciobritoi* and also *Ikrandraco avatar* (Wang XL et al., 2005; Wang L et al., 2006; Andres & Ji, 2006; Lü et al., 2008; Wang XL et al., 2015), but unlike *Istiodactylus latidens* and most anhanguerians (e.g., *Anhanguera, Tropeognathus* and *Hamipterus*), except for *Ludodactylus sibbicki*, in which the highest point is posterior to the anterior end of the nasolacrimal (Campos & Kellner, 1985; Wellnhofer, 1987; Kellner & Tomida, 2000; Wang XL et al., 2014; Frey et al., 2003). A nasal descending process cannot be seen in BPMC-0204, possibly because it is still covered by rock. There are no traces of an orbital process of the lacrimal invading the orbit, but the posterior margin of the lacrimal is slightly damaged and a small process similar to the one seen in the holotype of *N. ignaciobritoi* may had been present and got lost (see Wang XL et al., 2005; Wang L et al., 2006; Andres & Ji, 2006; Lü et al., 2008). The lacrimal contacts the lacrimal process of the jugal at about the mid-height of the posterior margin of the nasoantorbital fenestra. The nasal is bordered dorsally by the premaxilla and by the prefrontal posteroventrally.

Jugal and Quadratojugal. The jugal is partially preserved, missing part of the maxillary process and the base of the lacrimal process. The jugal sends a postorbital process to contact the postorbital, separating the orbit and the infratemporal fenestra. Posteriorly, the jugal contacts the quadratojugal, which forms the anteroventral of the infratemporal fenestra.

Quadrate. Sutures at the lateral surface of the quadrate are unclear. It is unclear whether the articulation with the mandible is helical or not. The mid-region of the quadrate is lost. The dorsal portion of the quadrate contacts the quadratojugal anteriorly and the squamosal dorsally. The quadrate is inclined backwards at an angle of 150°, unlike both specimens of *N. ignaciobritoi* (Fig. 3), in which it slopes at 160° (Wang XL et al., 2005; Wang L et al., 2006).

Prefrontal. The prefrontal is a small bone that forms the anterodorsal margin of the orbit, contacting the nasolacrimal. A suture between these two bones can be seen anteroventrally. The dorsoposterior tip of this bone contacts the frontal.

Frontal. The frontal seems to be fused with the premaxilla and parietal, with no visible sutures. It is unclear whether the posterodorsal extension of the frontal forms a blunt and low frontoparietal crest as in *Anhanguera* (see Kellner & Tomida, 2000) or not.

Parietal and Squamosal. The parietal and squamosal are poorly preserved, especially the latter. The squamosal outline cannot be properly identified. The parietal preserves a shallow depression in its surface that corresponds to the medial wall of the supratemporal fenestra. The dorsal limits of this fossa level with the orbit and extend ventrally to the region of contact between the squamosal and the postorbital.

Postorbital. The postorbital is slender and does not exhibit a triangular shape, oppositely to the triangular condition that is seen in anhanguerids (e.g. Kellner & Tomida, 2000). Instead, it is like a three-pointed star (= concave equilateral hexagon) as in *Haopterus gracilis* (see Wang XL & Lü, 2001); that is, is essentially composed of three connected processes. The anterior region of the postorbital which is formed by the frontal and jugal processes, is arched and forms the posterior margin of the orbit. The squamosal process is shorter than the other processes and separates the supra and infratemporal fenestrae. There is no orbital process of the postorbital invading the orbit, unlike *Istiodactylus* (Andres & Ji, 2006; Witton, 2012).

Palatal elements. Due to crushing, some palatal elements are visible in dorsal view, though few details can be observed. The vomers form a long, slender bony bar that separates the choanae, as in *Hongshanopterus lacustris* (see Wang XL et al., 2008a). Of the pterygoid, only the medial process can be seen. It is large and plate-like as that of *Hongshanopterus lacustris* (see Wang XL et al., 2008a) and, to a lesser extent, the anhanguerids, in which the process is also broad but less medially expanded (e.g., Campos & Kellner, 1985; Frey et al., 2003). This differs from the slender medial processes of the pterygoid of azhdarchoids (e.g., Pinheiro & Schultz, 2012; Kellner, 2013; Pêgas et al., 2018) or those of the referred specimen of *N. ignaciobritoi* (see Wang L et al., 2006; Lü et al., 2008) and *Ikrandraco avatar* (see Wang XL et al., 2015).

Dentary. The dentaries are fused rostrally forming a symphysis that accounts for 36% of total mandibular length, which is 240 mm long. The dorsal surface of the symphysis presents a deep and broad median sulcus that extends anteriorly up to the level of the first pair of teeth (Fig. 5). The rostral tip of the dentary symphysis has an odontoid (pseudotooth), that is located between the first pair of teeth, is smaller than the adjacent tooth crowns and is dorsally directed. The odontoid lacks the neurovascular foramen piercing its surface in the referred specimen of *N. ignaciobritoi* (see Wang L et al., 2006). The odontoid has the same orientation as that of *Istiodactylus latidens* (see Witton, 2012; Martill, 2014) and Lonchodraco giganteus (see Rodrigues & Kellner, 2013, fig. 4E-F), unlike the sub-horizontal odontoids of both specimens of *N. ignaciobritoi* (see Wang XL et al., 2005; Wang L et al., 2006) and *Ikrandraco avatar* (see Wang XL et al., 2015). The symphysis presents 11 tooth positions per side.

Surangular, Articular and Angular. The lateral surface of the posterior region of the right mandibular ramus is composed by the surangular, angular and articular. A suture separates the long anterior process of the surangular from the dentary dorsally. Posteriorly, the surangular becomes deeper and is sutured with the angular. The boundary between the angular and the dentary, however, cannot be distinguished, nor the boundary between the angular and the articular. The articular forms the posterior part of the mandible, including the articular surface for the quadrate and the retroarticular process, which is pointed, dorsoventrally low and distally tapering **Hyoid.** Only the right hyoid can be seen, disarticulated from the left hyoid. Only a small portion of the posterior region is missing. It is a rod-like, elongated bone that is positioned from near the region of separation between the mandibular rami until the retroarticular process.

Hyoid. Only the right ceratobranchial I is exposed along the ventral margin of the right mandibular ramus (Fig. 1). A small portion of the posterior part is missing. The ceratobranchial I is a long rod-like bone extending along the whole length of the mandibular rami.

Dentition. There are 12 tooth positions along the right side of the upper jaw and 11 tooth positions along each side of the lower jaw, with an inferred total count of 46 tooth positions. The first two teeth of the upper jaw (which are presumably premaxillary teeth) are procumbent. The first tooth forms an angle of 130° with the main axis of the rostrum, while the second forms and angle of 123°. The third tooth is also slightly procumbent, forming an angle of 100° with the palatal plane. All subsequent teeth are perpendicular to the main axis of the rostrum. The first two dentary teeth are also slightly procumbent. The last two alveoli of the right maxilla are empty, and the last one is placed just anterior to the level of the rostral end of the nasoantorbital fenestra. All of the crowns are triangular in labiolingual view and labiolingually compressed, as typical of the Istiodactylidae. The base of the crowns is mesiodistally inflated. The lingual surface of the crown is concave with a well-marked basoapical depression and a low transversal convexity at the base, that forms a lingual cingulum. The labial surface is mostly convex with a shallow concavity in the middle of the basal part of the crown. No carinae are present along the mesial and distal cutting margins of the crowns. The same features occur in the crowns of the holotype of *N. ignaciobritoi*. The teeth exhibit a slight constriction between crown and root (Fig. 5). This feature is also shared with *N. ignaciobritoi* (see Wang XL et al., 2005).

The first nine pairs of teeth of the upper jaw are large and subequal in size. Their apicosabal total length of their crowns is about 12 mm and the crown apicobasal length is about 7 mm, and the mesiodistal width of the socket is 4 mm. The smallest crown is 6 mm in apicobasal length and 2 mm in mesiodistal width.

N. luei sp. nov. also presents an interesting pattern of tooth replacement. Two teeth occur in the tenth alveolus of the right dentary: a large functional one and a not yet fully erupted replacement tooth. The replacement tooth was erupting anterolabially to the functional tooth, instead of posterolingually as reported in other pterodactyloid pterosaurs like *Anhanguera* (see Kellner & Tomida, 2000; Fastnatch, 2001) and '*Cearadactylus*' *ligabuei* (see Dalla Vecchia, 1993).

Cervical vertebrae. Seven cervical vertebrae are preserved, including the atlas-axis complex (although the atlas itself cannot be individually visualized). They are articulated, except for the 7th vertebra, which is disarticulated but still contacting the 6th vertebra. The 3rd cervical, with 38.36 mm, is longer than the 4th through 7th cervicals which are of similar length. The neural spine is damaged in most cervicals, except that of the 4th vertebra, which is high and with a peculiar shape (its anterior margin is anteriorly inclined). The apex of the neural spine is gently rounded. The postzygapophyses are posterodorsally oriented. The centrum extends posterior to the postzygapophyses. In the 3rd to the 7th cervicals, a large pneumatic foramen can be seen on the posterior half of the centrum below the neural arch.

Phylogenetic analysis results

The phylogenetic analysis by parsimony produced 51 most parsimonious trees with a minimum length of 360 steps, with minimum consistency index of 0.642 and retention index of 0.862. As supected by Witton (2012), *Hongshanopterus lacustris* and *Haopterus gracilis* result to be closely related to the Istiodactylidae in the strict consensus tree (Fig. 6), but they fall outside them. The Istiodactylidae have been defined by Andres et al. (2014) as the least inclusive clade containing *Istiodactylus latidens* Seeley 1901 and *Nurhachius ignaciobritoi* Wang XL.et al. 2005. In the strict consensus tree (Fig. 6), the Istiodactylidae contain *Nurhachius*, *Liaoxipterus brachyognathus* and *Istiodactylus*. *N. ignaciobritoi* and *N. luei* sp. nov. were recovered as sister taxa. *Istiodactylus latidens* and *I. sinensis* were also recovered as sister taxa and *Liaoxipterus brachyognathus* is the sister taxon of *Istiodactylus*.

Istiodactylus has the following five synapomorphies: presence of a suborbital opening (character 11, state 1); prenarial portion of the rostrum less than 20% the skull length (character 25, state 0); presence of an orbital process in the jugal (character 56, state 1); and sharp carinae in the teeth (character 96, state 1). *Istiodactylus* shares with *Liaoxipterus brachyognathus* the following synapomorphies: subparallel lateral taper of the jaws (character 24, state 1); mandibular symphysis shorter than 33% of the mandible length (character 78, state 1); and rounded outline of the rostral end of the mandible (character 79, state 0).

The genus *Nurhachius* is characterized by the following five synapomorphies: piriform orbit (character 7, state 2); cranio-mandibular articulation under the anterior margin of orbit (character 58, state 2); dorsal deflection of the palate (character 71, state 1); teeth crowns with labial and lingual depressions (character 100, state 1); teeth with a mesiodistal constriction between crown and root (character 101, state 1). The presence of a dorsal deflection of the palate represents a homoplasy with Anhangueria + *Cimoliopterus*.

The Istiodactylidae share the following seven synapomorphies: ventral margin of the nasoantorbital fenestra longer than 40% of skull length (character 4, state 1); orbit reaching high in the skull, with the dorsal margin surpassing the dorsal margin of the nasoantorbital fenestra (character 10, state 1); skull height (exclusive of cranial crests) over 25% of the jaw length (character 23, state 1); lacrimal process of jugal inclined posteriorly (character 54, state 2); helical jaw-joint absent (character 59, state 0); palatal occlusal surface: strong palatal ridge confined to the posterior portion of the palate (character 71, state 3); teeth confined to about the anterior third of the jaws (character 86, state 3).

Hongshanopterus lacustris results to be the sister taxon of the Istiodactylidae. The clade *Hongshanopterus lacustris* + Istiodactylidae presents two synapomorphies: tooth crowns strongly compressed laterally (character 95, state 2); and mesial crowns under twice as long as wide (character 97, state 0).

Haopterus gracilis results as the sister taxon of *Hongshanopterus lacustris* +Istiodactylidae, sharing teeth that are confined to the anterior half of the jaws (character 86, state 2).

The Istiodactylidae, *Hongshanopterus lacustris* and *Haopterus gracilis* share with *Ikrandraco avatar* four synapomorphies: narrow lacrimal process of jugal (character 53, state 1); quadrate inclination relative to the ventral margin of the skull-is 150° or more (character 57, state 3); tooth crowns slightly compressed laterally (character 95, state 2); lingual cingulum present at the base of tooth crown (character 102, state 1). The last two character states are also shared with *Lonchodraco giganteus*.

Bremer support values were 1 for the genus *Istiodactylus*, 3 for *Istiodactylus* + *Liaoxipterus*, 5 for the genus *Nurhachius*, 3 for Istiodactylidae, 3 for *Hongshanopterus* + Istiodactylidae, 1 for *Haopterus* + (*Hongshanopterus* + Istiodactylidae), 1 for *Ikrandraco* + *Lonchodraco* and 2 for the clade that joins all of these taxa.

Discussion

For over a century, *Istiodactylus latidens* has been the only known istiodactylid (Witton, 2012). In the last 15 years, four new istiodactylids have been reported from the Jiufotang Formation of China: *N. ignaciobritoi* (described in 2005); *Istiodactylus sinensis* and "*Longchengpterus zhaoi*" (both described in 2006); and *Liaoxipterus brachyognathus* (originally described in 2005 as a purported ctenochasmatid and later referred to the Istiodactylidae in 2008) (Dong & Lü, 2005;

Wang XL et al., 2005; Wang L et al., 2006; Andres & Ji, 2006; Lü et al., 2008). However, the validity of some of them is debated. According to Lü et al. (2008), the holotypes of "*Longchengpterus zhaoi*" and *N. ignaciobritoi* are indistinguishable, sharing general skull shape and tooth morphology. Therefore, *Longchengpterus zhaoi* was considered a junior synonym of *N. ignaciobritoi* by Lü et al. (2008). Witton (2012) provisionally considered both of them as valid and distinct taxa, coding them separately in his phylogenetic analysis though without discussing it further. They were coded differently as for tooth count and spacing, with *Nurhachius* that was considered to have more numerous and more spaced teeth. However, both specimens exhibit a similar number of upper teeth (13 pairs in the holotype of *N. ignaciobritoi* and 12 pairs in *"L. zhaoi"*) and similar spacing (Wang XL et al., 2005; Lü et al., 2008). Furthermore, the holotypes and only specimens of "*Longchengpterus zhaoi*" and *N. ignaciobritoi* share further features that are unique within istiodactylids (Fig. 3): the high quadrate inclination (160°), the reduced medial process of the pterygoid, the upper dentition ending at the level of the nasoantorbital fenestra, and the sub-horizontal odontoid in the mandibular symphysis. Therefore, we follow Lü et al. (2008) in considering *Longchengpterus zhaoi* as a junior synonym of *N. ignaciobritoi*.

N. luei sp. nov. is an istiodactylid based on the following features: nasoantorbital fenestra longer than 40% of skull length, dentary symphysis less than 33% of mandible length; and triangular, labiolingually compressed tooth crowns. It shares with *N. ignaciobritoi* a piriform orbit, a dorsally deflected palate, a cranio-mandibular articulation positioned under the anterior margin of the orbit (Fig. 3), tooth crowns with labial and lingual depressions, and teeth with mesiodistal constrictions between crown and root (Fig. 5; 6). All these features can be observed in the holotype of *N. ignaciobritoi*, while in the referred specimen the dorsal deflection of the palate cannot be seen as the rostrum tip is missing. Concerning the crown, with both a labial and a lingual depression, we note that this morphology is reflected in the shape of the alveoli in *N. ignaciobritoi*, with concave labial and lingual margins (Fig. 5). The dorsal deflection of the palate can be seen in the rostral tip of the skull of the holotype of *N. ignaciobritoi* (see Fig. 4C-D), although it was not mentioned in the original description (Wang XL et al., 2005), as well as in the holotype of *N. luei*. This character was utilized in a data matrix for the first time by Rodrigues & Kellner (2013), and resulted to be a synapomorphy of Anhangueria + *Cimoliopterus*. According to our phylogenetic analysis (Fig. 7), this feature was independently acquired by *Nurhachius* and Anhangueria + *Cimoliopterus*.

N. luei sp. nov. differs from *N. ignaciobritoi* in the following features: the quadrate is inclined at

150° instead of the 160° of *N. ignaciobritoi*; the medial process of the pterygoid is broad and plate-like, whereas it is reduced in *N. ignaciobritoi* (see Fig. 3); the dorsal median sulcus of the mandibular symphysis extends up to the first pair of teeth, whereas it reaches the sixth pair of teeth in *N. ignaciobritoi* (see Fig. 5); the odontoid (pseudotooth) lacks a lateral foramen, whereas a foramen is present in the referred specimen of *N. ignaciobritoi* (see Martill, 2014, fig. 7C-D); the odontoid has a blunt occlusal surface, whereas the surface is sharp in *N. ignaciobritoi* (Fig. 5); the odontoid is dorsally directed, whereas it is anterodorsally directed in *N. ignaciobritoi* (but see Martill, 2014, p. 57, right column, lines 21-23); and the ceratobranchial I of the hyoid apparatus accounts for 60% of the mandibular length, whereas it accounts for 35% of the mandibular length in *N. ignaciobritoi* (Fig. 5).

Concerning quadrate inclination, we do not regard this variation as intraspecific as the variation does not surpass 3° in the archaeopterodactyloid *Pterodactylus antiquus* (specimens BSPG AS I 739, BSPG 1929 I 18, BMMS 7; see Bennett, 2012; Vidovic & Martill, 2014), 3° in the anhanguerian *Hamipterus tianshanensis* (IVPP V18931.1, holotype, and IVPP V18935.1, paratype; see Wang *et al.*, 2014), 5° in *Aerodactylus scolopaciceps* (BSPG 1883 XVI 1, BSPG 1937 I 18, BSPG AS V 29 a/b; see Vidovic & Martill, 2014), and is less than 6° in *Pteranodon longiceps* (specimens YPM 1177, USNM 13656, KUVP 2212, KUVP 27821) and also in *Pteranodon sternbergi* (specimens FHSM VP 339, YPM 1179, UALVP 24238; see Bennett, 1994; 2001). Quadrate inclination has indeed been regarded as diagnostic before for tapejarids (Kellner, 2013) and *Pteranodon* (Bennett, 1994).

Both specimens of *N. ignaciobritoi* come from the upper part of the Jiufotang Formation (see Wu et al., 2018), while the holotype of *N. luei* comes from the lowermost part of the Jiufotang Formation. This stratigraphic distribution might be suggestive of an anagenetic link between the two species, similarly to the case of *Pteranodon longiceps* (from the upper Niobrara Formation) and *Pteranodon sternbergi* (from the lower Niobrara Formation) according to Bennett (1994), but see taxonomic controversies (Kellner, 2010; 2017; Martin-Silverstone et al., 2017; Acorn et al., 2017). The same has been speculated as a possible explanation for the occurrence of multiple species of *Anhanguera* (Pinheiro & Rodrigues, 2017), *Thalassodromeus* and *Tupuxuara* (Pêgas *et al.*, 2018) in the Romualdo Formation, but these cases still lack stratigraphic control for support.

Wang XL et al. (2008) were unable to differentiate *Liaoxipterus brachyognathus* from "*Longchengpterus zhaoi*", and suggested that "*Longchengpterus zhaoi*" could be a junior synonym of *Liaoxipterus brachyognathus*. However, as observed by Lü et al. (2008), the rostral end of the mandibular symphysis is rounded in *Liaoxipterus brachyognathus* (in dorsal view, as it is in *Istiodactylus latidens*), whereas it is triangular in "*Longchengpterus zhaoi*". Furthermore, as coded by Andres et al. (2014), both jaws show an attenuated taper (in occlusal view) in "*Longchengpterus zhaoi*", while the lateral margins of the lower jaw are sub-parallel in *Liaoxipterus brachyognathus* (Fig. 8A) as in *Istiodactylus latidens*. Furthermore, the mandibular symphysis of *Liaoxipterus brachyognathus* is relatively stouter than that of "*Longchengpterus zhaoi*": their length/width ratios are 0.43 and 0.27, respectively. It is worthy of being noticed that the mandibular symphysis of "*Longchengpterus zhaoi*" is incorrectly drawn in Martill (2014, fig. 7B), as resulting to be much shorter than it is. The actual configuration can be clearly assessed in the description by Lü et al. (2008) and in Fig. 5A. We thus follow Lü et al. (2008) and Witton (2012) in considering *Liaoxipterus brachyognathus* as distinct from "*Longchengpterus zhaoi*", which we consider as a junior synonym of *N. ignaciobritoi*.

Lü et al. (2008) and Witton (2012) noticed that comparisons between *Liaoxipterus brachyognathus* and *Istiodactylus sinensis* is very limited because the former is represented by a mandible exposed in occlusal view, while the latter is a partial skeleton including a mandible exposed in lateral view. However, *Liaoxipterus brachyognathus* differs from *Istiodactylus* in the lack of mesial carinae, according to Lü et al. (2008) and the dataset of Andres et al. (2014). We thus follow these authors in considering *Liaoxipterus brachyognathus* as a valid taxon.

According to our phylogenetic analysis, *Istiodactylus* is monophyletic, comprising *I. latidens* and *I. sinensis*. *Liaoxipterus brachyognathus* is the sister taxon of *Istiodactylus*, and *Nurhachius* is the sister taxon of *Liaoxipterus brachyognathus* + *Istiodactylus*, in agreement with the results of the phylogenetic hypothesis published by Longrich et al. (2018). In our analysis, *N. luei* results to be the sister taxon of *N. ignaciobritoi*, supporting their congeneric status. The relationships within the Istiodactylidae obtained in our analysis are similar to those found by Andres et al. (2014), but *Longchengpterus zhaoi* is not the sister taxon of *N. ignaciobritoi* in the cladogram of figure S2 of Andres et al. (2014).

Haopterus gracilis was first described by Wang XL & Lü (2001) and referred to the Pterodactylidae. However, it resulted to be close to *Istiodactylus latidens* in the 50% majority-rule tree by Lü et al. (2008) and formed a poltomy with *Nurhachius* and *Istiodactylus* in the strict consensus tree by Lü et al. (2009). *Hongshanopterus lacustris*, was described by Wang XL et al.

use commas.

(2008) and interpreted as a primitive istiodactylid. In the strict consensus tree by Witton (2012), the Istiodactylidae include *Nurhachius igniaciobritoi*; *Longchengpterus zhaoi*; *Istiodactylus latidens*; *Istiodactylus sinensis*; and *Liaoxipterus brachyognathus*. *Haopterus gracilis* and *Hongshanopterus lacustris*; form a polytomy with *Pteranodon longiceps*, *Coloborhynchus spielbergi* and the Istiodactylidae (Witton, 2012).

In the phylogenetic analysis of Andres et al. (2014; fig. S2), *Haopterus gracilis* results to be a basal eupterodactyloidean and *Hongshanopterus* a basal ornithocheiromorph. Recently, Holgado et al. (2019) have published a phylogenetic hypothesis in which *Hongshanopterus lacustris* would be the sister-group of the Istiodactylidae (although it is erroneously reported within this clade as the basal member in their fig. 5A), while *Haopterus gracilis* would be closer to anhanguerians than to istiodactylids (see Holgado *et al.*, 2019).

In our analysis, *Haopterus gracilis* and *Hongshanopterus lacustris* are closely related to the Istiodactylidae, as found by Lü et al. (2008) and Wang XL et al. (2008), respectively. *Hongshanopterus lacustris* results to be the sister taxon of the Istiodactylidae, as in the analysis by Holgado et al. (2019). *Hongshanopterus lacustris* shares with the istiodactylids the presence of labiolingually compressed teeth with triangular crowns. *Haopterus gracilis* results to be the sister taxon of *Hongshanopterus lacustris* + Istiodactylidae, a relationship that is supported by the possession of a dentition restricted to the anterior half of the jaws.

Haopterus, *Hongshanopterus* and istiodactylids share also the presence of a lingual cingulum in the tooth crown, a feature that occurs also in *Ikrandraco avatar*. A lingual cingulum can be seen in *Nurhachius luei* and *N. ignaciobritoi* (Fig. 6). The same feature has been previously reported for *Liaoxipterus brachyognathus* (see Lü et al., 2008) and depicted for *Ikrandraco avatar* (see the second figure of Wang XL et al., 2015). In *Haopterus gracilis*, the labiodistal view of the third right upper tooth presents a lingually oriented convexity that also suggests the presence of this feature (Fig. 8).

Ikrandraco avatar shares with istiodactylids also a narrow lacrimal process of the jugal and a quadrate inclined at 150° or over (the inclination of the quadrate is unknown in *Haopterus gracilis* and *Hongshanopterus lacustris*).

Ikrandraco avatar and *Haopterus gracilis* also exhibit a certain degree of labiolingual compression of the teeth, at least in the distal part of the dentition (Wang XL & Lü, 2001; Wang XL et al., 2015), though not to the same degree seen in the istiodactylids and *Hongshanopterus*. The last two

NOT IN REFS.

mandibular alveoli preserved in the holotype of *Lonchodraco giganteus* (the sister taxon of *Ikrandraco avatar* in our analysis) are also labiolingually narrow (see Martill, 2011; Rodrigues & Kellner, 2013).

Furthermore, *Ikrandraco avatar* and *Lonchodraco giganteus* also share with istiodactylids the presence of an odontoid, which is anterodorsally oriented in the former and dorsally oriented in the latter (see Rodrigues & Kellner, 2013; Wang XL et al., 2015).

A close relationship among *Ikrandraco avatar*, *Lonchodraco giganteus* and istiodactylids is found here for the first time. *Ikrandraco avatar* formed a polytomy with the Istiodactylidae, *Cimoliopterus* and the Anhangueria in the phylogenetic analysis by Wang XL et al. (2015) and *Lonchodraco giganteus* is outside the Lanceodontia in the phylogenetic analysis by Longrich et al. (2018).

Archaeoistiodactylus linglongtaensis is based on the sole holotype (JPM04-0008), including fragments of skull and one displaced maxillary tooth, a partial lower jaw in occlusal view with two teeth in place, an almost complete forelimb, a femur and a tibia. It is from the Middle Jurassic (Bathonian-Oxfordian) Tiaojishan Formation. *A. linglongtaensis* was described by Lü & Fucha (2010) who interpreted it as the "ancestor form of the known istiodactylid pterosaur [sic]" (Lü & Fucha, 2010, p. 113). Lü & Fucha (2010) observed that JPM04-0008 and the istiodactylids share teeth with triangular crowns and an odontoid (pseudotooth) on the mandibular symphysis. That odontoid was mistaken for a mid-line, unpaired tooth by Sullivan et al. (2014), but it had been explicitly described as a bony process by Lü & Fucha (2010, p. 116). Lü & Fucha (2010) also observed that the single maxillary tooth is recurved as in *Hongshanopterus lacustris*, and reported the presence of a warped deltopectoral crest in the humerus, which is a diagnostic feature of the Pteranodontoidea (Kellner, 2003). They noted that *A. linglongtaensis* differs from istiodactylids and all other pterodactyloids in the relatively short fourth metacarpal and in the presence of tibia, and second and third phalanges of the wing digit with subequal lengths. If actually a pterodactyloid, it would represent one of the oldest occurrences of the Pterodactyloidea, being coeval or even older than the Callovian-Oxfordian basalmost pterodactyloid *Kryptodrakon progenitor* (see Andres et al., 2014).

Its identification as a pterodactyloid was disputed by Martill & Etches (2013), who affirmed that JPM04-0008 is probably a badly preserved specimen of *Darwinopterus*, though they did not present any evidence to support this statement. According to Sullivan et al. (2014), the short fourth-metacarpal, the long humerus and short first wing phalanx are typical of non-pterodactyloid pterosaurs (see Kellner, 2003; Unwin, 2003; Andres et al., 2010), thus JPM04-0008 is not a pterodactyloid. These features united to the presence of a confluent nasoantorbital fenestra in JPM04-0008, led Sullivan et al. (2014) to interpret *A. linglongtaensis* as a basal monofenestratan. However, *A. linglongtaensis* has never been included in any phylogenetic analysis to test its basal monofenestratan affinity, thus it was included in the analysis performed in this paper. Our results (Fig. 6) confirm the interpretation by Sullivan et al. (2014). *Archaeoistiodactylus linglongtaensis* lacks the following pterodactyloid features: humerus length under 1.5 times metacarpal IV length; ulna under double the length of metacarpal IV; and femur subequal to or shorter than metacarpal IV. The humerus of JPM04-0008 is crushed and the original orientation of the deltopectoral crest cannot be assessed. Differently from pterodactyloids, the deltopectoral crest of JPM04-0008 is confined to the proximal region of the humerus (Wang XL et al., 2009). *A. linglongtaensis* also lacks pneumatic foramina on the centra of the mid-cervical vertebrae, which is a diagnostic feature of the Dsungaripteroidea (the least inclusive clade containing *Nyctosaurus* and *Quetzalcoatlus*, which includes also the Istiodactylidae; Kellner, 2003; Andres et al., 2014). Furthermore, *A. linglongtaensis* exhibits low neural spines, like wukongopterids (see Wang XL et al. 2009; 2010; Lü et al., 2009; 2011; Cheng et al., 2017) and unlike istiodactylids (see Wang L et al., 2006; Lü et al., 2008).

The dentition of *A. linglongtaensis* is indeed reminiscent of that of the Istiodactylidae due to the short triangular aspect of the crowns in labiolingual view. However, this feature is also present in the wukongopterids *Wukongopterus lii*, *Darwinopterus robustodens*, *Darwinopterus linglongtaensis* and *Kunpengopterus sinensis*, though not in *Darwinopterus modularis* (see Wang XL et al. 2009; 2010; Lü et al., 2009; 2011; Cheng et al., 2017). Furthermore, in *A. linglongtaensis* the alveoli are circular (Lü & Fucha, 2010), as in wukongopterids, not labiolingually compressed triangular teeth as in istiodactylids. The presence or absence of an odontoid in the lower jaw cannot be confidently assessed in *Wukongopterus* and *Darwinopterus*, but can be seen in a specimen referred to *Kunpengopterus sinensis* (see Cheng et al., 2017), in convergence with the istiodactylids. Finally, *A. linglongtaensis* shares with *Darwinopterus* and *Kunpengopterus*, but not with *Wukongopterus*, the subequal in length second and third phalanges of the wing digit. Thus, *A. linglongtaensis* may be closely related to *Darwinopterus* or *Kunpengopterus*. In our analysis, *A. linglongtaensis* falls in a polytomy with *Darwinopterus linglongtaensis, D. robustodens* and

Kunpengopterus sinensis (Fig. 6). However, we were unable to access the specimen first-hand and further scrutiny is desirable in order to confirm or deny this affinity.

Conclusions

The new specimen here described represents the second species for the genus *Nurhachius*, previously restricted to its type-species *N. ignaciobritoi*. A slight dorsal deflection of the palate revealed to be a synapomorphy of *N. ignaciobritoi* and *N. luei*. That feature was previously thought to be restricted to the Anhangueria and *Cimoliopterus*. Unlike other pterodactyloids, the holotype of *N. luei* sp. nov. shows an anterolabial tooth replacement. The position of *Hongshanopterus lacustris* and *Haopterus gracilis* as close taxa to the Istiodactylids is supported by the performed phylogenetic analysis. *Ikrandraco avatar* and *Lonchodraco giganteus* resulted to be sister taxa, and closer to istiodactylids than to other lanceodontians. The phylogenetic analysis supports the reinterpretation of *Archaeoistiodactylus linglongtaensis* as a non-pterodactyloid monofenestratan, probably a wukongopterid.

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Figures

Figure 1. *Nurhachius luei* sp. nov., BPMC-0204, holotype, photograph and line drawing. The scale bar in the line drawing equals 50 mm. Abbreviations: alv, alveolus; an, angular; art, articular; ax, axis; ceI, ceratobranchial I; ch, choana; cv, cervical vertebra; d, dentary; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; naof, nasoantorbital fenestra; odp, odontoid process; or, orbit; pa, parietal; pf, prefrontal; pmax, premaxilla; po, postorbital; prid, palatal ridge; pty, pterygoid; q, quadrate; vo, vomer. Isolated numbers indicate tooth positions. Note: the visible region of the pterygoid corresponds to the medial process of the bone. Photo by Xuanyu Zhou. Drawing by Maria Eduarda Leal.

Figure 2. Location of the site where BPMC-0204 was found.

Figure 3. *Nurhachius ignaciobritoi* specimens, photographs and line drawings. (A) LPM 00023, referred specimen (former holotype of *"Longchengpterus zhaoi"*), skull and mandible in right lateral view. (B) IVPP V-13288, holotype, skull (mirrored) and mandible in right lateral view. Scale bars equal 50 mm. Abbreviations: art, articular; ch, choana; d, dentary; f, frontal; ios, interorbital septum; j, jugal; ls, laterosphenoid; m, maxilla; n, nasal; op, opisthotic; or, orbit; pa, parietal; pf, prefrontal; pm, premaxilla; prid, palatal ridge; pty, pterygoid; q, quadrate; san, surangular; sq, squamosal. Photographs by Xuanyu Zhou. Drawings by Rodrigo V. Pêgas.

Figure 4. Close view of the rostral tip of *Nurhachius* species in right lateral view. (A) *Nurhachius luei* sp. nov., holotype and (C) *Nurhachius ignaciobritoi*, IVPP V-13288, holotype, mirrored. (B) and (D), respective schematic drawings of (A) and (C), showing the slight dorsal

deflection of the palate (notice the positions of the first and second alveoli in both specimens). Numbers indicate tooth positions. Scale bars equal 20 mm. Photos by Xuanyu Zhou. Drawings by Rodrigo V. Pêgas.

Figure 5. Close view of the dentary symphysis of *Nurhachius* species. (A) *Nurhachius luei* sp. nov. holotype in dorsolateral view, and (B) line drawing. (C) *Nurhachius ignaciobritoi*, LPM 00023, referred specimen, occlusal view, and (D), line drawing. Abbreviations: mg, median groove; odp, odontoid process. Red arrows indicate the mesiodistal constrictions between crown and root. Photos by Xuanyu Zhou. Drawings by Maria Eduarda Leal and Rodrigo V. Pêgas.

Figure 6. Close view of the dentition in *Nurhachius* species. (A) *Nurhachius ignaciobritoi*, LPM 00023, referred specimen, isolated tooth in lingual view, and (B) line drawing. (C) *Nurhachius luei* sp. nov. holotype, ninth left mandibular tooth in lingual view, and (D) line drawing. Red arrows indicate the mesiodistal constrictions between crown and root. Blue arrows indicate the horizontal elevation at the base of the crown (cingulum). Photos by Xuanyu Zhou. Drawings by Rodrigo V. Pêgas.

Figure 7. *Nurhachius luei* sp. nov. phylogenetic relationships. Strict consensus tree of 51 most parsimonious trees. Tree length is 358, consistency index 0.644 and retention index 0.867. The red rectangle indicates the Istiodactylidae and its two closest taxa.

Figure 8. Other istiodactylids and close taxa. (A) *Liaoxipterus brachyognathus*, CAR-0018, holotype, lower jaw in dorsal view. (B) *Haopterus gracilis*, IVPP V11726, holotype, skull in right lateral view. (C) *Hongshanopterus lacustris*, IVPP V14582, holotype, skull in ventral view. All scale bars equal 50 mm. (A) and (C) by Xuanyu Zhou; (B) by Shunxing Jiang (courtesy of IVPP).

Figure 1

Nurhachius luei sp. nov., BPMC-0204, holotype, photograph and line drawing.

The scale bar in the line drawing equals 50 mm. Abbreviations: alv, alveolus; an, angular; art, articular; ax, axis; ceI, ceratobranchial I; ch, choana; cv, cervical vertebra; d, dentary; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; naof, nasoantorbital fenestra; odp, odontoid process; or, orbit; pa, parietal; pf, prefrontal; pmax, premaxilla; po, postorbital; prid, palatal ridge; pty, pterygoid; q, quadrate; vo, vomer. Isolated numbers indicate tooth positions. Note: the visible region of the pterygoid corresponds to the medial process of the bone. Photo by Xuanyu Zhou. Drawing by Maria Eduarda Leal.

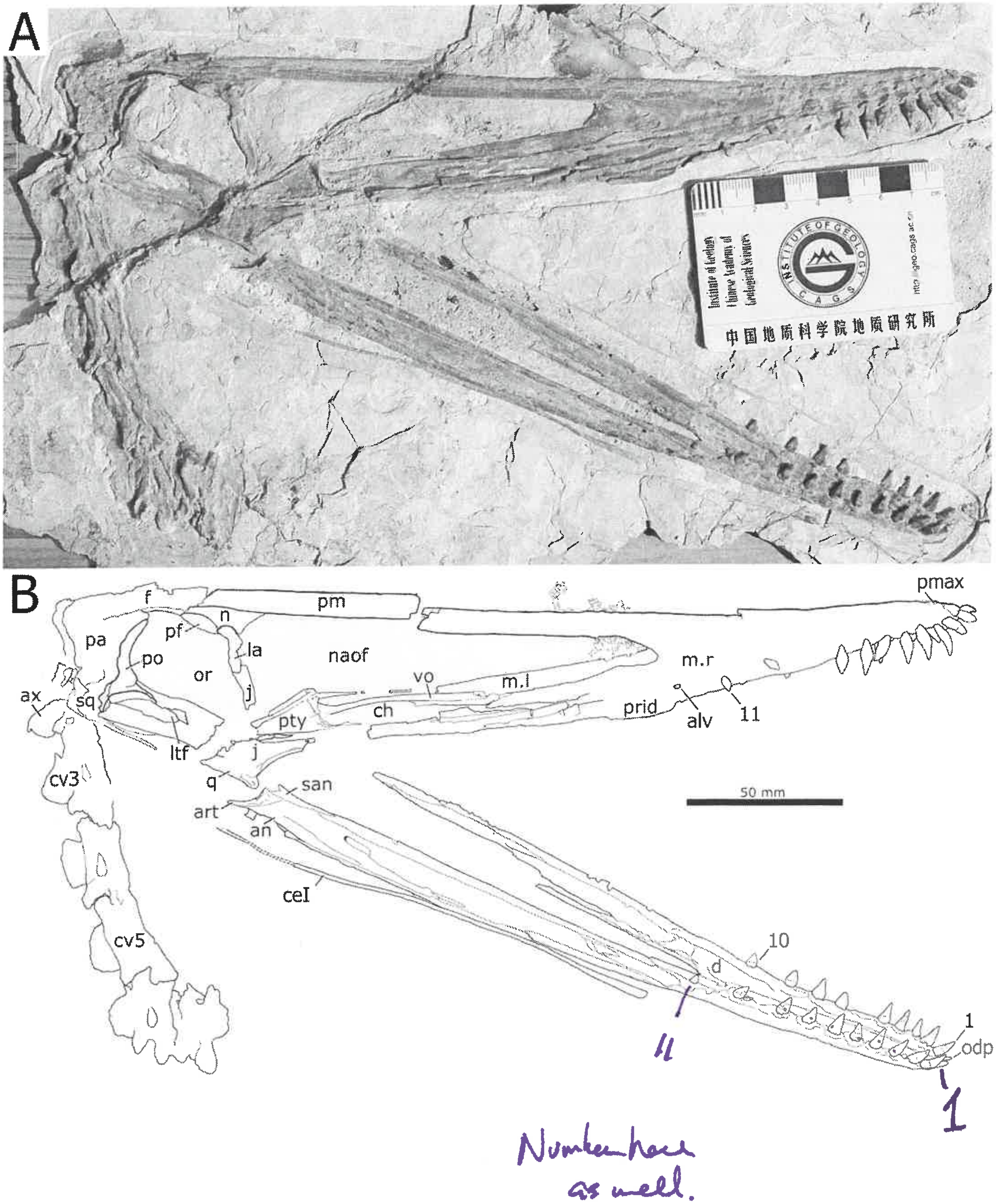
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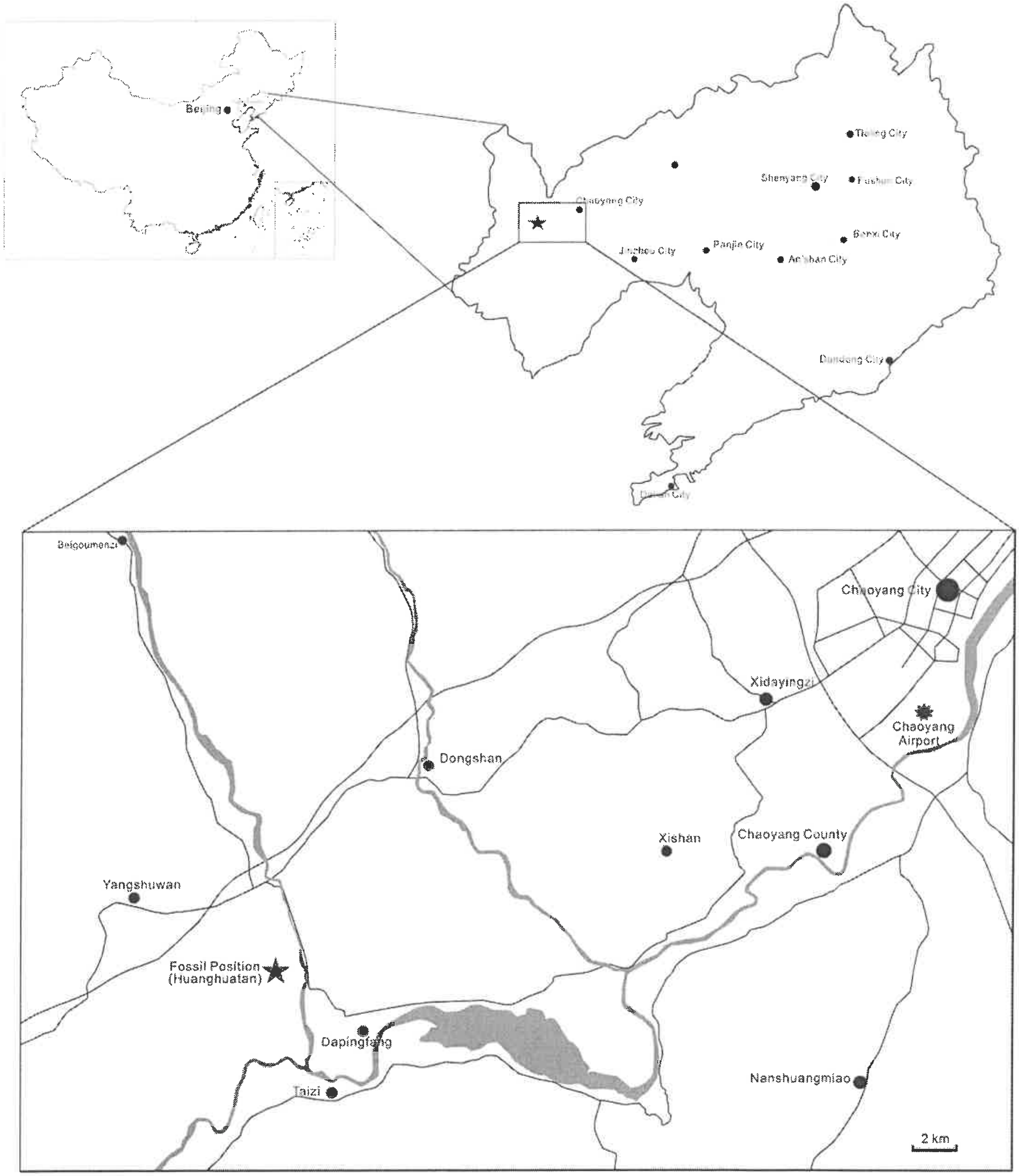
Figure 2

Location of the site where BPMC-0204 was found.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Fossil Position
(Huanghuatan)
Dapingfang
Taizi
Nanshuangmiao
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Figure 3

Nurhachius ignaciobritoi specimens, photographs and line drawings.

(A) LPM 00023, referred specimen (former holotype of "*Longchengpterus zhaoi*"), skull and mandible in right lateral view; and (B) interpretative line drawing. (C) IVPP V-13288, holotype, skull (mirrored) and mandible in right lateral view; and (D) interpretative line drawing . Scale bars equal 50 mm. Abbreviations: art, articular; ch, choana; d, dentary; f, frontal; ios, interorbital septum; j, jugal; ls, laterosphenoid; m, maxilla; n, nasal; op, opisthotic; or, orbit; pa, parietal; pf, prefrontal; pm, premaxilla; prid, palatal ridge; pty, pterygoid; q, quadrate; san, surangular; sq, squamosal. Photographs by Xuanyu Zhou. Drawings by Rodrigo V. Pêgas.

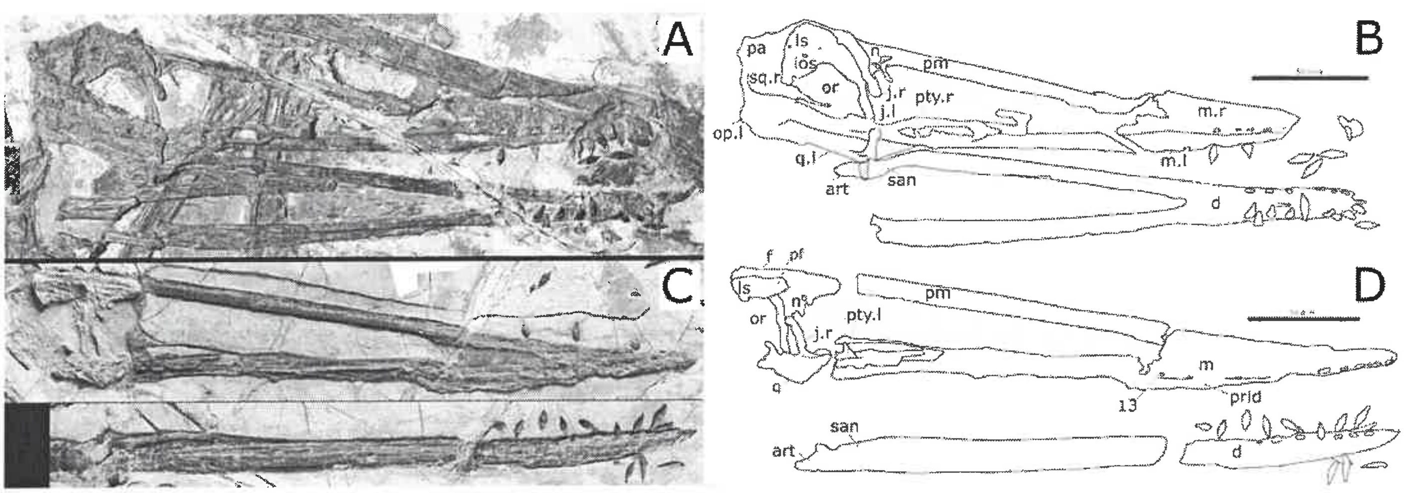

Figure 4

Close view of the rostral tip of *Nurhachius* species in right lateral view.

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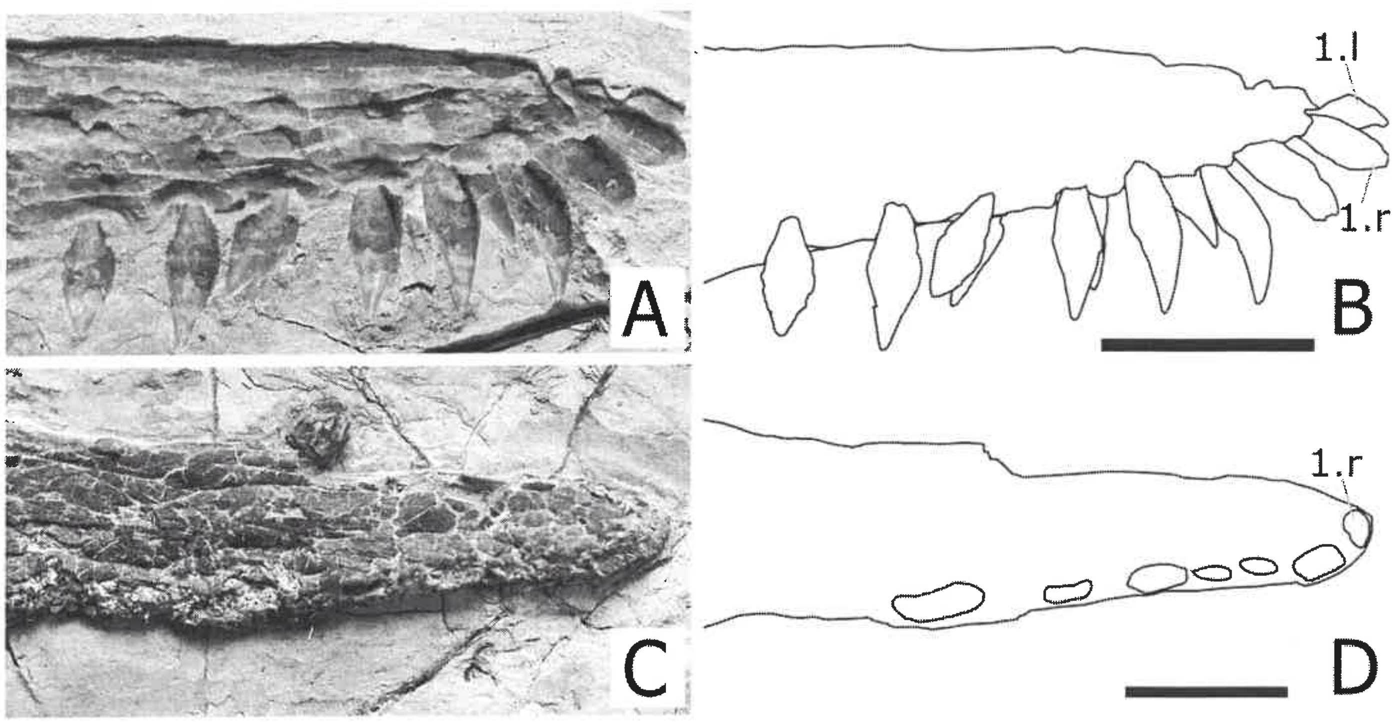

Figure 5

Close view of the dentary symphysis of *Nurhachius* species.

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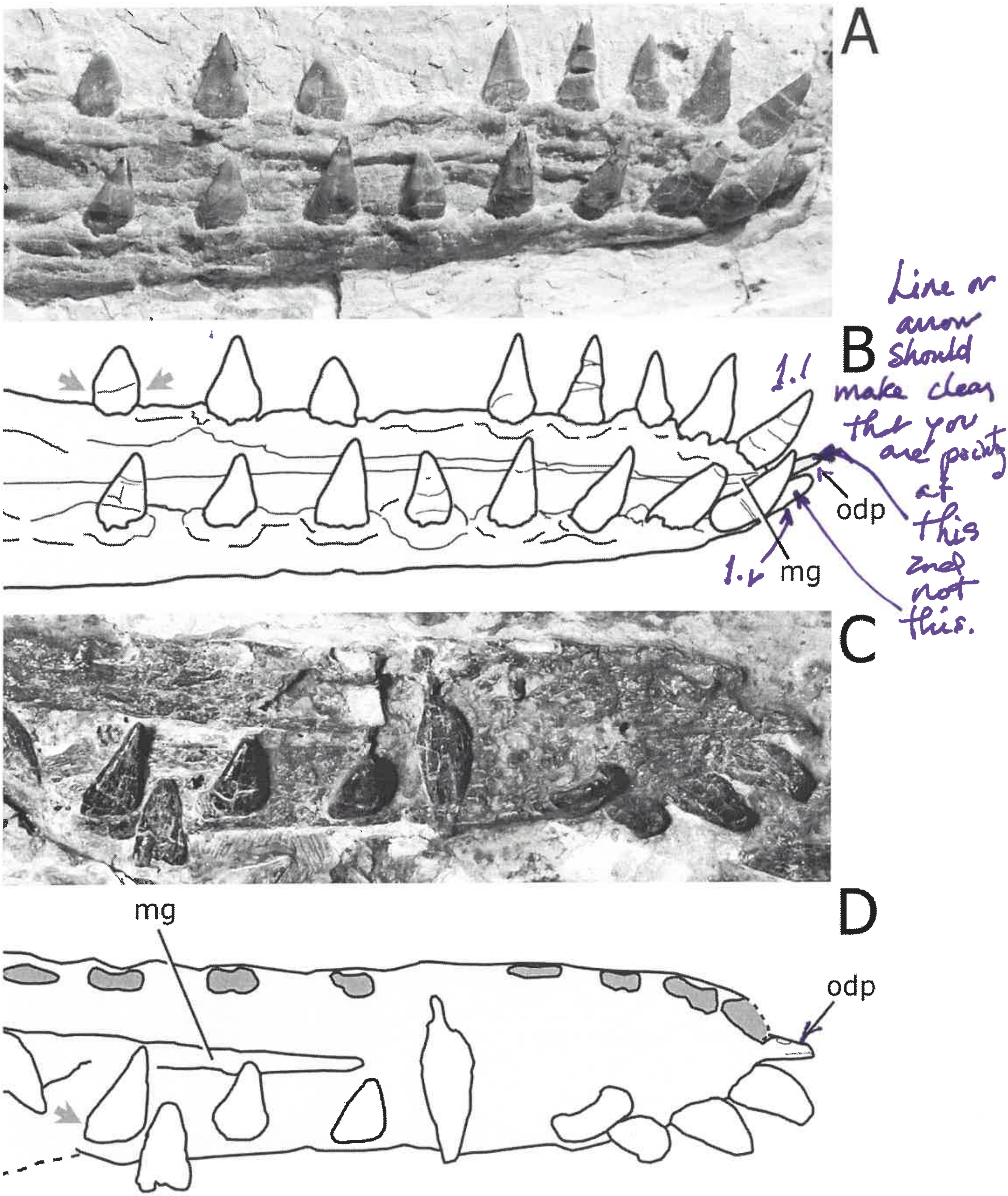
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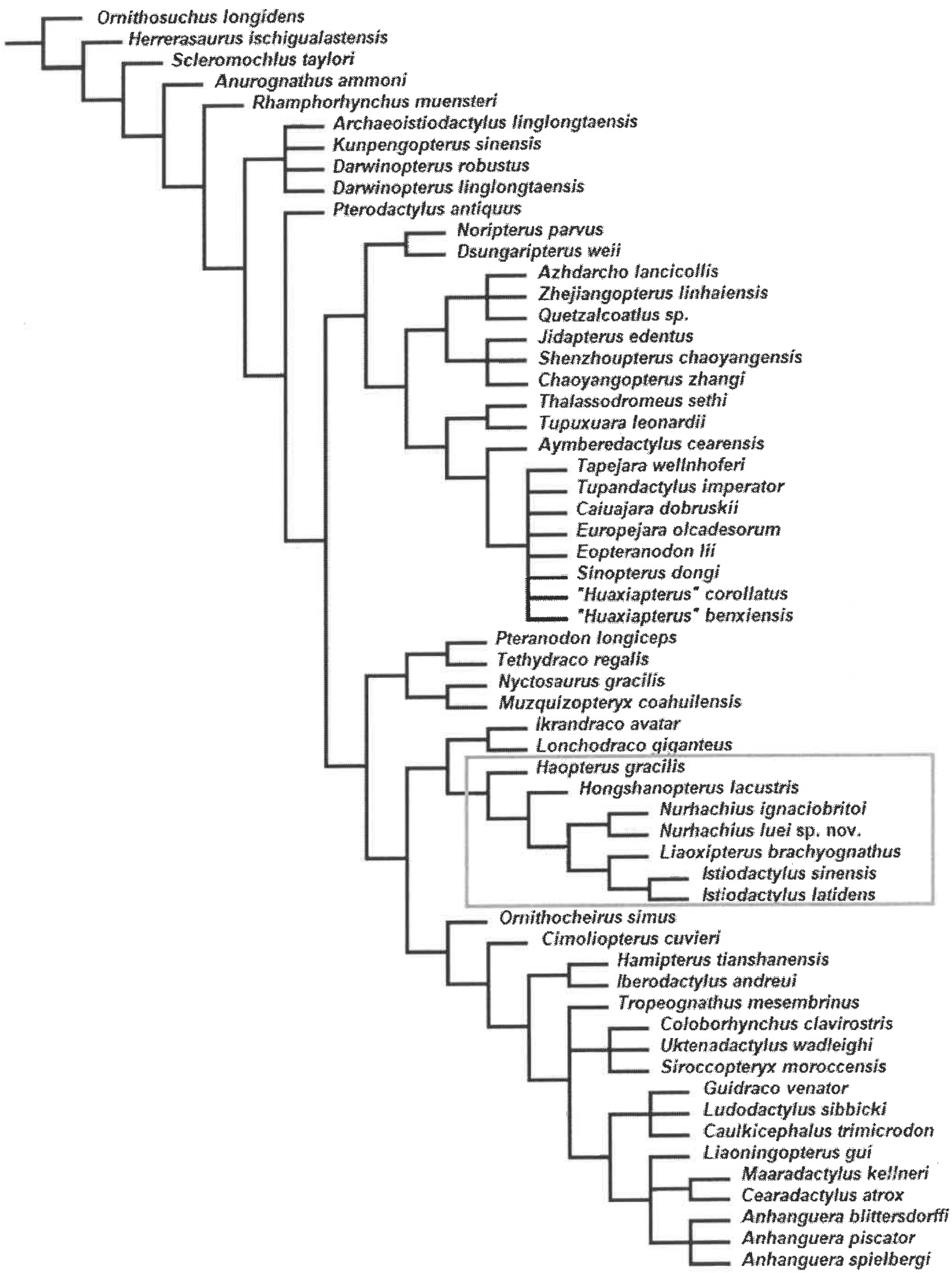
Figure 6

Nurhachius luei sp. nov. phylogenetic relationships.

Strict consensus tree of 51 most parsimonious trees. Tree length is 360, consistency index 0.642 and retention index 0.864. The red rectangle indicates the Istiodactylidae and its two closest taxa.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Rhamphorhynchus muensteri
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Kunpengopterus sinensis
Darwinopterus robustus
Darwinopterus linglongtaensis
Pterodactylus antiquus
Noripterus parvus
Dsungaripterus weii
Azhdarcho lancicollis
Zhejiangopterus linhaiensis
Quetzalcoatlus sp.
Jidapterus edentus
Shenzhoupterus chaoyangensis
Chaoyangopterus zhangi
Thalassodromeus sethi
Tupuxuara leonardii
Aymberedactylus cearensis
Tapejara wellnhoferi
Tupandactylus imperator
Caiuajara dobruskii
Europejara olcadesorum
Eopteranodon lii
Sinopterus dongi
"Huaxiapterus" corollatus
"Huaxiapterus" benxiensis
Pteranodon longiceps
Tethydraco regalis
Nyctosaurus gracilis
Muzquizopteryx coahuilensis
Ikrandraco avatar
Lonchodraco giganteus
Haopterus gracilis
Hongshanopterus lacustris
Nurhachius ignaciobritoi
Nurhachius luei sp. nov.
Liaoxipterus brachyognathus
Istiodactylus sinensis
Istiodactylus latidens
Ornithocheirus simus
Cimoliopterus cuvieri
Hamipterus tianshanensis
Iberodactylus andreui
Tropeognathus mesembrinus
Coloborhynchus clavirostris
Uktenadactylus wadleighi
Siroccopteryx moroccensis
Guidraco venator
Ludodactylus sibbicki
Caulkicephalus trimicrodon
Liaoningopterus gui
Maaradactylus kellneri
Cearadactylus atrox
Anhanguera blittersdorffi
Anhanguera piscator
Anhanguera spielbergi

Figure 7

Close view of the dentition in *Nurhachius* species

(A) *Nurhachius ignaciobritoi*, LPM 00023, referred specimen, isolated tooth in lingual view, and (B) line drawing. (C) *Nurhachius luei* sp. nov. holotype, ninth left mandibular tooth in lingual view, and (D) line drawing. Red arrows indicate the mesiodistal constrictions between crown and root. Blue arrows indicate the horizontal elevation at the base of the crown (cingulum). Photos by Xuanyu Zhou. Drawings by Rodrigo V. Pêgas.

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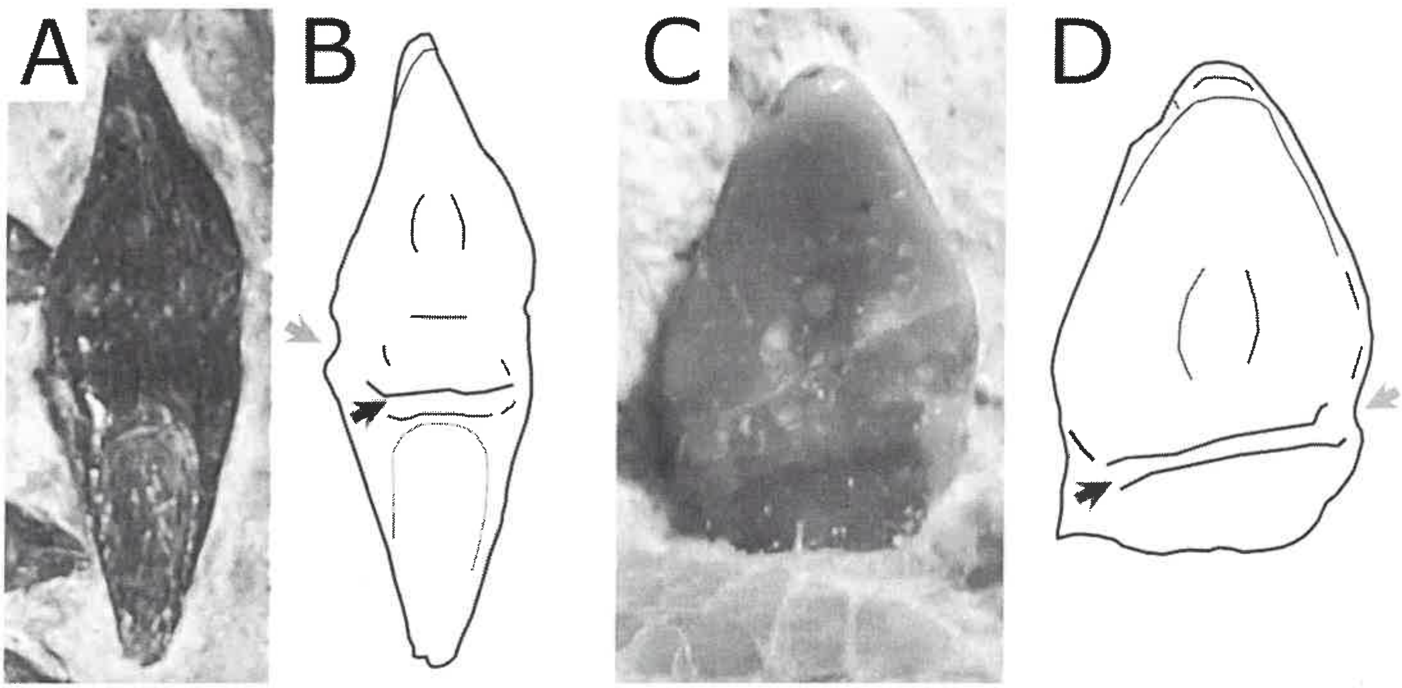

Figure 8

Other istiodactylids and close taxa.

(A) *Liaoxipterus brachyognathus*, CAR-0018, holotype, lower jaw in dorsal view. (B) *Haopterus gracilis*, IVPP V11726, holotype, skull in right lateral view. (C) *Hongshanopterus lacustris*, IVPP V14582, holotype, skull in ventral view. All scale bars equal 50 mm. (A) and (C) by Xuanyu Zhou; (B) by Shunxing Jiang (courtesy of IVPP).