A new istiodactylid pterosaur from the Early Cretaceous Jiufotang Formation of Chaoyang City, Liaoning Province; and comments on the group (#37231)

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A new istiodactylid pterosaur from the Early Cretaceous Jiufotang Formation of Chaoyang City, Liaoning Province; and comments on the group

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We present a new istiodactylid pterosaur, *Nurhachius luei* sp. nov., based on a complete skull and some cervical vertebrae from the lower Jiufotang Formation at Chaoyang city, western Liaoning. The specimen preserves some three-dimensional structure, especially regarding the dentition. In this paper, we also comment on the in-group and stem-group Istiodactylidae, including a new definition of the genus *Nurhachius* which was previously limited to its type-species, *Nurhachius ignaciobritoi* from the upper Jiufotang Formation. The new species we described adds to the current knowledge on istiodactylid diversity, including some features previously not reported for the group such as the presence of a dorsal deflection of the palate in *Nurhachius*, in homoplasy with Anhangueria and *Cimoliopterus*.

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Abstract: We present a new istiodactylid pterosaur, *Nurhachius luei* sp. nov., based on a complete skull and some cervical vertebrae from the lower Jiufotang Formation at Chaoyang city, western Liaoning. The specimen preserves some three-dimensional structure, especially regarding the dentition. In this paper, we also comment on the in-group and stem-group Istiodactylidae, including a new definition of the genus *Nurhachius* which was previously limited to its type-species, *Nurhachius ignaciobritoi* from the upper Jiufotang Formation. The new species we described adds to the current knowledge on istiodactylid diversity, including some features previously not reported for the group such as the presence of a dorsal deflection of the palate in *Nurhachius*, in homoplasy with Anhangueria and *Cimoliopterus*.

Keywords: Istiodactylidae, Jiufotang Formation, Systematics, Taxonomy, Three-dimensional Preservation

Introduction

Istiodactylid pterosaurs are characterized by the rhombic and lancet-shaped teeth, long skull with short rostrum, and nasoantorbital fenestra constituting over 50 percent skull length and height (Howse et al., 2001; Andres & Ji, 2006; Lü, et al., 2013). At present, 4 genera and 5 species of istiodactylid pterosaurs (*Istiodactylus latidens*, *I. sinensis Liaoxipterus brachyognathus*, *Nurhachius ignaciobritoi*, *Longchengpterus zhaoi*) and 3 genera and species of proposed stem-group istiodactylids (*Haopterus gracilis*, *Hongshanopterus lacustris*, *Archaeoistiodactylus linglongtaensis*) have been reported (Lü *et al*., 2013). However, *Longchengpterus zhaoi* has been interpreted by Lü *et al.* (2008) as a junior synonym of *Nurhachius ignaciobritoi*, a view that is followed here. In this way, *Nurhachius ignaciobritoi* would be the only Chinese istiodactylid species represented by two specimens so far. All istiodactylid pterosaurs are from the Jiufotang Formation of northeastern China to the exception of *Istiodactylus latidens* (from the Vectis Formation of the Wealden on Isle of Wight, Southern England). Proposed stem-group istiodactylids come from Northeastern China and surrounding area: *Haopterus gracilis* from the Yixian Formation, *Hongshanopterus lacustris* from Jiufotang Formation, and *Archaeoistiodactylus linglongtaensis* from Tiaojishan Formation (Middle Jurassic). Apart from the latter, these Chinese pterosaurs are all from the Jehol Biotas (see Chang *et al*. 2003). Still, the stem-istiodactylid nature of *Archaeoistiodactylus linglongtaensis* has been questioned by Sullivan *et al.* (2014).

The Jiufotang Formation is known worldwide for its large quantity of fossils, some showing very good preservation. A lot of plants, insects, fishes, mammals, birds, non-avian dinosaurs and pterosaurs was discovered in Jiufotang Formation (Wang X, 2018; Meng et al.,2011; Wang M and Zhou, 2019; Yao et al.,2019), mainly from the lower part, Boluochi Beds (see Chang et al. 2003). By the end of 2016, 20 species of pterosaurs from Jiufotang Formation have been reported (Andres & Ji, 2006; Dong & Lü, 2005; Dong et al., 2005; Jiang et al.,2016; Rodrigues et al., 2015; Li et

al.,2003; Lü & Ji, 2005a; Lü & Yuan, 2005; Lü et al., 2006b, 2007, 2008a; Wang L et al., 2006; Wang X L & Zhou, 2003a, 2003b; Wang X L et al., 2005, 2008a, 2008b, 2012, 2014b). In this paper we describe another species of istiodactylid pterosaur from the Jiufotang Formation. The material consists of the three-dimensional skull and some cervical vertebrae (fig. pp. 81-82 in Lü *et al*. 2013, where it is called an unnamed istiodactylid) from the basal part of Jiufotang Fm. collected in Huanghuatan village, Dapingfang town, Chaoyang city, western Liaoning province.

The age of the Jiufotang Fm is now considered Aptian (according to Gradstein *et al*. 2004 being 112 – 125 Ma old) as the basalts overlying the formation in Inner Mongolia (or rather intruding according to He *et al*. 2004) have been dated ca. 110 Ma (according to Chang et al. [2003 - that is Early Albian]). The lower part of Jiufotang Fm., called Beluochi Bed (or Member), is very rich in fossils, especially birds, fishes and insects, and is often characterized as *Jinanichthys – Cathayornis* fauna, that also comprises small feathered dinosaurs like the four-winged *Microraptor* (Xu *et al*. 2003) and several pterosaurs (Chang *et al*., 2003; Zhou *et al*., 2003). This part has been dated ca 120 Ma by He *et al*. (2004), that is Early Aptian. And Wang *et al*. (2001) dated the lowermost part of Yixian Fm. as 128.4 Ma, implying that Yixian Fm. with four fossil rich levels covers about 8-9 Ma., from E. Barremian to E. Aptian, and its thickness according to Chang *et al*. (2003) is 800 – 1400 m. But of this only 2-300 m are sediments with ashlayers, as basalts and lavas cover as much as 550 – 1200 m. The Jiufotang Fm. according to Chang *et al*. (2003, fig 12) is 800 – 1200 m thick, but comprises no basalts nor lavas, only sandstones, shales and tuffs like the sediments of Yixian Fm.

Jinanicthys (Zhang et al. 1994 for *Lycoptera longicephalus*) in Jiufotang Fm. has replaced another small osteoglossomorph (bony tongue) teleostean fish, *Lycoptera,* that is extremely common with many species in the Yixian Fm. below, and in northern Asia generally (Chang & Jin 1996 on China, Zhang & Jin 2003 on Asia). These two formations traditionally constitute the Jehol Group with the famous Jehol biotas., that occur also in four rich levels from basis to top in Yixian Fm. (Chang et al. 2003).The Jehol biotas are often characterized as *Eoestheria-Ephemopteris (*now *Epicharmeropsis)-Lycoptera* assemblages (Chang et al. 2003), and the most famous birds in these faunas are species of *Confuciusornis*, the early bird with beak and without teeth (see also Hou, 1995). The most common dinosaur is the small, primitive ceratopsian *Psittacosaurus* (Xu & Wang 1998 - and also its nests with many babies), and also the bird *Jeholornis*. Reviews also by Wang

et al. (2000) and Zhou et al. (2003).

More recently the Dabeigou Fm. of Hebei Provins with ages 131 and 134 Ma has been suggested as the basal formation in the Jehol Group with the lowermost Jehol Biota (He *et al.*, 2006), so that the Jehol Group and biotas would then cover at least Hauterivian, Barremian and some of Aptian, about 15-20 Ma or more in the middle part of Early Cretaceous. Meaning there are developing ecosystems (Zhou *et al.*, 2003), but no such thing as a general "Jehol fauna" with a characteristic diversity, but a sequence of rich and quite different biotas, only two of which are very rich in pterosaurs (in the early part of both formations – see Chang et al. 2003 and Unwin et al. 2000).

It is important to note, if the above is correct, that the sediments of Jiufotang Fm. are much thicker than those of Yixian Fm, that covers about 9 Ma. So Jiufotang Fm. may cover well over 10 Ma. And the new species reported herein is from the basal part, while the type species of the genus is from upper part of Jiufotang Fm. 10 Ma or more apart.

The new species we describe here allows us to report on new features within the Istiodactylidae, increasing current knowledge on their morphological diversity and providing new information on interspecific relationships of the group.

Material and Methods

The phylogenetic analysis we perform here is based on a data matrix modified from Holgado *et al.* (2019), with the inclusion of characters by Lü *et al.* (2008), Witton (2012) and Andres *et al.* (2014), as well as of the following taxa: *Archaeoistiodactylus linglongtaensis*, *Kunpengopterus sinensis*, *Liaoxipterus brachyognathus* and *Nurhachius luei* sp. nov. (see Supplementary Material). The analysis was conducted on TNT (Goloboff *et al.*, 2008) using Traditional Search, 10000 replications, random seed = 0 and collapsing trees after search. A text file with our character list and a TNT file with our data matrix are available as Supplementary Material.

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Results

Systematic Paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger,1901

Istiodactylidae Howse *et al*., 2001

Nurhachius Wang *et al*., 2005

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

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

Emended Diagnosis. Istiodactylids that share the following combination of features: (synapomorphies marked with an asterisk): slight dorsal deflection of the palate present*; orbit piriform*; craniomandibular joint located under the anterior margin of the orbit*; lower temporal fenestra slit-like; 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; anteriormost teeth relatively longer than others; crowns with both labial and mesial slight concavities*.

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 pterosaurs.

Holotype. Skull and some cervical vertebrae preserved (BPMC-0204). The specimen is permanently deposited and available for researchers at the Beipiao Pterosaur Museum of China (Fig. 1).

Type Locality and Horizon. Huanghuatian Village, Dapingfang Town, Chaoyang City, Liaoning Province (Fig. 2); lower part of the Jiufotang Formation.

Diagnosis. The new species can be diagnosed based on the following combination of features: quadrate inclined at 150°; medial process of the pterygoid expanded, plate-like; dentary sulcus extending until the first pair of dentary teeth; odontoid process lacking foramina; odontoid process with a smooth occlusal surface; odontoid process vertical; hyoid accounting for 60% of mandibular length; 12 tooth positions in each side of the upper jaw; 11 tooth positions in each side of the lower jaw; dentary teeth extending beyond the dentary symphysis.

Description

Skull generalities. The skull is exposed in right lateral view, with some palatal elements visible in dorsal view and the mandible lying in an oblique dorsolateral view. It is 300 mm long from the squamosal to the premaxillary tip, and 74 mm high at its greatest height, which is at the level of the occiput. The nasoantorbital fenestra is elongated, corresponding to 45% of total skull length (premaxilla to squamosal) and 55% of total jaw length (craniomandibular joint to premaxilla). Anterior to it, the rostrum exhibits a slight dorsal inclination of its long axis, similarly to other istiodactylids (Wang *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 *et al.*, 2014; 2015; Holgado *et al.*, 2016) but unlike boreopterids (Lü & Ji, 2005; Lü, 2010; Jiang *et al.*, 2014). The palate exhibits a strong palatal keel extending from prenarial rostrum until the anterior region of the nasoantorbital fenestra. The craniomandibular joint levels with the anterior margin of the orbit, similarly to *Nurhachius ignaciobritoi* (both specimens: its holotype plus former holotype of "*Longchengpterus zhaoi*"), *Anhanguera* spp. and *Linlongopterus jennyae* but unlike *Istiodactylus*

in which it is located anterior to the orbit, as well as *Ikrandraco avatar*, *Hamipterus tianshanensis* and *Ludodactylus sibbicki* where the joint is located under the middle of the orbit (Kellner & Tomida, 2000; Frey *et al.*, 2003; Wang *et al.*, 2005; 2014; 2015; Andres & Ji, 2006; Lü *et al.*, 2008; Witton, 2012; Rodrigues *et al.*, 2015; Holgado *et al.*, 2019). The orbit is piriform, with the thinnest region being the ventral region, without any suborbital vacuity. This is similar to the condition seen in *Nurhachius ignaciobritoi* (as seen in second specimen) and different from the rounded orbit of *Istiodactylus* with a suborbital vacuity (see Andres & Ji, 2006; Lü *et al.*, 2008; Witton, 2012). The infratemporal fenestra is elliptical and shorter than the orbit. The supratemporal fenestra is poorly preserved.

Premaxilla and Maxilla. The premaxilla is a long, slender bone that forms almost the entire dorsal margin of the skull, overlying the maxilla and the nasoantorbital fenestra. The maxilla is a long, narrow bone has been lateral. The premaxilla and maxilla are fused to such a degree that the suture between the two is not discernable. It is not known how much each constitutes the tooth row. There is no premaxillary crest, as in other istiodactylids and *Haopterus*.

Nasal and Lacrimal. The nasal and lacrimal are fused, forming a nasolacrimal that forms the upper anterior margin of the orbit and the posterodorsal margin of the nasoantorbital fenestra. The anterior limit of the nasolacrimal coincides with the highest point of the nasoantorbital fenestra, as in *Nurhachius ignaciobritoi* (both specimens) and also *Ikrandraco* (Wang X. *et al.*, 2005; Wang L. *et al.*, 2006; Andres & Ji, 2006; Lü *et al.*, 2008; Wang *et al.*, 2015), but differently from *Istiodactylus latidens* and most anhanguerians such as *Anhanguera*, *Tropeognathus* and *Hamipterus*, except for *Ludodactylus*, in which the highest point is posterior to the anterior limit of the nasolacrimal (Kellner & Campos, 1985; Wellnhofer, 1987; Kellner & Tomida, 2000; Wang *et al.*, 2014; Frey *et al.*, 2003). A nasal descending process cannot be seen in the new specimen, being possibly obliterated by matrix. There are no traces of an orbital process of the lacrimal invading the orbit, but the posterior margin of the bone is slightly damaged and a small process similar to the one seen in *Nurhachius ignaciobritoi* (holotype) could have been possibly present and lost (see Wang X. *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, and the nasolacrimal is bordered dorsally by the premaxilla. Posteriorly, it contacts the prefrontal.

Jugal and Quadratojugal. The jugal is only partially preserved, missing part of the maxillary process and the base of the lacrimal process. The jugal also forms a postorbital process contacting the squamosal, separating the orbit and the infratemporal fenestra. Posteriorly, the jugal contacts the quadratojugal, which forms the ventral margin of the infratemporal fenestra. Posteroventrally, the jugal can also be seen contacting a small portion of the incompletely preserved quadrate on the lateral surface of the skull, ventral to the quadratojugal, as in *Nurhachius ignaciobritoi* (holotype), *Istiodactylus sinensis* and *Ikrandraco avatar* (Wang *et al.*, 2005; Andres & Ji, 2006; Wang *et al*, 2015). In contrast, the quadratojugal separates the quadrate from the jugal in the lateral skull surface in other forms such as anhanguerians (e.g. Kellner & Tomida, 2000; Frey *et al.*, 2003; Wang *et al.*, 2014) and pteranodontians (Bennett, 2001; Frey *et al.*, 2006).

Quadrate. The quadrate is incompletely preserved. The ventral region of the bone is present, contacting the jugal ventral to the quadratojugal. It is unclear if the articulation with the lower jaw is helical or not. The mid-region of the quadrate is lost, and the dorsal portion can be seen contacting the quadratojugal anteriorly and the squamosal dorsally. The quadrate is posteriorly inclined at an angle of 150°, unlike *Nurhachius ignaciobritoi* (both specimens) in which is inclines at 160° (Wang X. *et al.*, 2006; Wang L. *et al.*, 2006).

Prefrontal. The prefrontal is a small bone that takes part in the anterodorsal margin of the orbit, contacting the nasolacrimal anteriorly. A suture between these two bones can be seen anteroventrally, but the dorsal and posterior limits of the bone cannot be identified.

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

Parietal and Squamosal. The parietal and squamosal are badly preserved, especially the latter for which its limits cannot be properly identified. The parietal preserves in its surface a fossa that accounts for the medial wall of the supratemporal fenestra, which dorsal limits level with the orbit and extend ventrally until being limited by the region of contact between squamosal and postorbital.

Postorbital. The postorbital in the new specimen is very slender and does not exhibit the same

regular triangular shape that is seen in anhanguerids (e.g. Kellner & Tomida, 2000), instead being more of a three-pointed star as in *Haopterus gracilis* and *Istiodacylus sinensis* (Wang & Lü, 2001; Andres & Ji, 2006). The anterior region of the bone, including the frontal and jugal processes, is very curved, concave and slender (anteroposteriorly compressed), with a round anterior margin taking part in the border of the orbit. Posteriorly, the squamosal process of the postorbital separates the supra and infratemporal fenestrae, being shorter than the other processes. There is no orbital process of the postorbital invading the orbit, unlike *Istiodactylus* (Andres & Ji, 2006; Witton, 2012).

Palatal elements. Due to taphonomical crushing, some palatal elements are visible in dorsal view, though not much details can be extracted. A long, slender vomer can be seen separating the two choanae, as in *Hongshanopterus* (see Wang *et al*., 2008). The medial process of the right pterygoid can be seen. It is plate-like, well-developed and expanded, similar to the condition seen in *Hongshanopterus* (see Wang *et al*., 2008) and, to a lesser extent, anhanguerids (e.g. Campos & Kellner, 1985; Frey *et al.*, 2003), but differently from the slender condition seen in azhdarchoids (e.g. Pinheiro & Schultz, 2012; Kellner, 2013; Pêgas *et al.*, 2018) or in *Nurhachius ignaciobritoi* (referred specimen, see Wang *et al.*, 2006; Lü *et al.*, 2008) and *Ikrandraco avatar* (see Wang *et al.*, 2015). A small portion of the medial process of the ectopterygoid can be seen contacting the medial process of the pterygoid, separating the subtemporal and postapalatinal fenestra, as can be seen in *Hongshanopterus* see Wang *et al.*, 2008) and *Nurhachius ignaciobritoi* (Fig. 4).

Dentary. The two dentaries fuse anteriorly forming a symphysis that accounts for 36% of total mandibular length. On the dorsal surface of the dentary symphysis, a deep and broad dentary sulcus can be seen, extending anteriorly until the level of the first pair of alveoli. The anterior tip of the dentary symphysis exhibits an odontoid process, located in between the first pair of teeth, that is smaller than the teeth and dorsally curved. The odontoid process lacks any neurovascular foramina piercing its surface, unlike the referred specimen of *Nurhachius ignaciobritoi* (Wang *et al.*, 2006). It is vertically oriented, as the one seen in *Istiodactylus latidens* and *Lonchodraco giganteus* (Witton, 2012; Rodrigues & Kellner, 2013; Martill, 2014) and unlike the subhorizontal odontoids seen in both specimens of *Nurhachius ignaciobritoi* (Wang X. *et al.*, 2006; Wang L. *et al.*, 2006), and also in *Ikrandraco avatar* (see Wang *et al.*, 2015). The symphysis houses 11 pairs of alveoli, with two pairs of alveoli being present on the separated mandibular rami as well.

Surangular, Articular and Angular. The lateral surface of the posterior region of the mandibular rami is composed by the surangular, angular and articular. A long suture can be seen delineating the anterior process of the surangular, dorsal to the dentary. Posteriorly, this bone becomes deeper and contacts the angular, where another suture can be seen. The limit between angular and dentary, however, cannot be observed, nor between the angular and articular. The articular forms the posterior region of the mandible, including the articulation surface for the quadrate and the retroarticular process which is pointed and elongated.

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.

Dentition. The dentition comprises 12 tooth positions on each side of the upper jaw and 11 tooth positions on each side of the lower jaw, with the total teeth number being 46.

In the upper jaw, the first two teeth are particularly procumbent. The first teeth forms an angle of 130° with the palatal plane, 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 palatal plane. The first two dentary teeth are also slightly procumbent. The last two right upper alveoli are empty, and the last one is only slightly anterior to the level of the nasoantorbital fenestra. All of the teeth crowns are triangular and laterally compressed, as typical of the Istiodactylidae. They present a crown base mesiodistally inflated. The lingual surface of the crown is concave with a well-marked longitudinal depression and a slight transversal convexity at the base, forming a lingual cingulum. The labial surface is mostly convex with a slight concavity on the center of the crown base. No carinae are present. The same configuration can be found on the crowns of the holotype of *Nurhachius ignaciobritoi*.

The first nine pairs of teeth in the upper jaw are large and subequal in size, the length being about 1.2 cm, the teeth crown equals 0.7 cm, and the width of the socket is 0.4 cm. The minimum teeth measurement is 0.6 cm in length and 0.2 cm in width. All teeth are sharp.

Nurhachius luei sp. nov. also exhibits an interesting pattern of teeth reposition. In the tenth alveolous of the right dentary, two teeth are present: a large, well-developed one, and a reposition tooth still growing. The reposition tooth is erupting anterolaterally to the larger one, instead of

posteromedially, as reported before for pterosaurs such as in *Anhanguera* (e.g. Kellner & Tomida, 2000; Fastnatch, 2001).

Cervical vertebrae. There are seven cervical vertebrae preserved, including the atlantoaxis which is fused. They are preserved in articulation, except for the seventh which is disarticulated. The third, fourth and fifth cervicals are of similar length, longer than the subsequent ones and the atlantoaxis. The neural spine is damaged in most cervicals, except for the fourth in which is configuration can be assessed. In this vertebra, the neural spine is high and exhibits a peculiar shape, with the anterior margin being anterior inclined. The dorsal margin is gently rounded. In all preserved cervicals, the postzygapophyses are posterodorsally oriented, positioned dorsal to the level of the prezygapophyses. The posterior cotyles extend further posteriorly than the postzygapophyses. Under the neural arch, on the posterior half of the centrum, a large pneumatic foramen can be seen in cervicals 3 through 7.

Phylogenetic analysis results

Our analysis produced 51 minimum-length trees with 358 steps, consistency index of 0.644 and retention index of 0.867. Under the topology of our strict consensus tree (Fig. 3), as suspected by Witton (2012), *Hongshanopterus* and *Haopterus* are closely related to the Istiodactylidae but fall outside of it. As phylogenetically defined by Andres *et al.* (2014), the Istiodactylidae refers to the least inclusive clade comprising *Nurhachius* and *Istiodactylus*.

In the present analysis, such clade includes *Nurhachius* (with the type and the new species), *Liaoxipterus brachyognathus* and the genus *Istiodactylus*. The species *Nurhachius ignaciobritoi* and *N. luei* sp. nov. were recovered as sister-taxa, corroborating their congeneric status. *Istiodactylus latidens* and *Istiodactylus sinensis* also formed sister-groups, with *Liaoxipterus* as a sister-group to *Istiodactylus*.

The genus *Istiodactylus* was recovered based on the following 5 synapomorphies: character 11(1), suborbital opening: present; 25(0), length of prenarial rostrum relative to the skull length: reduced, under 20%; 56(1), jugal, posterior process, orbital process: present; and 96(1), teeth, sharp carinae: present. This genus shares with *Liaoxipterus brachyognathus* characters: 24(1), jaws, lateral taper: subparallel; 77(1) mandibular rostral end, extension of the contact surface of opposing dentaries:

shorter than 33% of mandible length; 78(0), mandibular rostral end, shape: rounded.

The genus *Nurhachius* is characterized by the following 3 synapomorphies: character 7(2), orbit, shape: piriform; 58(2), cranio-mandibular articulation, position relative to orbit: under anterior margin of orbit; and 102(1), palate, dorsal deflection: present. This character was recovered as a homoplasy with Anhangueria + *Cimoliopterus*.

The Istiodactylidae, or *Nurhachius* + (*Liaoxipterus* + *Istiodactylus*), share the following 8 synapomorphies: 4(1), external naris and antorbital fenestra (or nasoantorbital fenestra), ventral margin length relative the skull length: longer than 40% of skull length; 10(1), orbit, position: reaching high in the skull, with the dorsal margin surpassing the dorsal margin of the nasoantorbital fenestra; 23(1), skull, height, exclusive of cranial crests: over 25% of jaw length; 54(2) jugal, lacrimal process, inclination: inclined posteriorly; 59(0), helical jaw-joint, absent; 71(3), palatal occlusal surface: strong palatal ridge confined to posterior portion of the palate; 86(3): teeth, position and presence: confined to about the anterior third of the jaws.

Hongshanopterus was recovered as the sister-group of the Istiodactylidae based on character 95(1), teeth, laterally compressed and triangular: present; and 97(0), teeth, anterior positions, relative elongations: under twice as wide.

Haopterus gracilis was recovered as the next successive-sister group based on character 86(2), teeth, position and presence: confined to anterior half of the jaws.

All of these forms (Istiodactylidae, *Hongshanopterus* and *Haopterus*) are united with *Ikrandraco* based on characters 53(1), jugal, lacrimal process, width: narrow; 57(3), quadrate, inclination relative to ventral margin of skull: 150° or above; and 99(1), teeth, crown base, lingual cingulum: present. The last character is also present in *Lonchodraco*.

Discussion

For over a century, *Istiodactylus latidens* has been the only known istiodactylid (Seeley, 1901; Witton, 2012). In the present century, in just a few years, a profusion of new istiodactylids have been reported from the Jiufotang Formation, with *Nurhachius 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 (see Dong & Lü, 2005; Wang X. *et al.*, 2005; Wang L. *et al.*, 2006; Andres & Ji, 2006; Lü *et al.*, 2008). With a total of 6 proposed species of istiodactylids coming from the Jiufotang Formation, their taxonomy has been entangled with a series of proposed synonymies.

Lü *et al.* (2008) considered that "*Longchengpterus zhaoi*" and *Nurhachius ignaciobritoi* were indistinguishable, sharing general skull shape and tooth morphology, and synonymized them. Subsequently, Witton (2012) provisionally considered them as valid and distinct, mentioning that these taxa had been coded differently in his analysis though without discussing it further. In the data matrix of Witton (2012), it can be seen that they were coded differently in tooth count and spacing, with *Nurhachius* exhibiting more numerous and spaced teeth. However, both exhibit a similar number of teeth (13 pairs in the holotype of *N. ignaciobritoi* and 12 pairs in *"L. zhaoi*") and similar spacing (Fig. 4). Furthermore, we notice here that the holotypes of "*Longchengpterus zhaoi*" and *Nurhachius ignaciobritoi* further share several traits that are unique within istiodactylids (Fig. 4): the particularly high quadrate inclination (160°), the reduced medial process of the pterygoid, the upper dentition extension (ending at the level of the nasoantorbital fenestra), the slight constriction between tooth crown and root, and the subhorizontal odontoid process. In this way, we follow Lü *et al.* (2008) in considering these two taxa as synonyms.

Nurhachius luei sp. nov. can be clearly identified as an istiodactylid based on the following combination of features: external naris and antorbital fenestra longer than 40% of skull length, dentary symphysis shorter than 33% of mandible length; and triangular, laterally compressed teeth. Among istiodactylids, as mentioned above, it shares with *Nurhachius ignaciobritoi* the following features: a piriform orbit; a dorsally deflected palate; and a cranio-mandibular articulation positioned under the anterior margin of the orbit (Fig. 4). It must be noticed that all these features can be assessed in the holotype of *Nurhachius ignaciobritoi*, while only the first and third can be seen in the referred specimen (the former holotype of *"Longchengpterus zhaoi*"). Of particular note is the presence of a slight dorsal deflection of the palate, which can be seen in the holotype of *Nurhachius ignaciobritoi* (see Fig. 5), despite not having been mentioned in the original description (Wang *et al.*, 2005), as well as in the holotype of the new species *N. luei*. This character was utilized in a data matrix for the first time by Rodrigues & Kellner (2013), who proposed it as

a synapomorphy of Anhangueria + *Cimoliopterus*. In this way, in the present analysis, this feature represents a homoplasy between *Nurhachius* and Anhangueria + *Cimoliopterus*.

The two species of the genus *Nurhachius* differ in that *N. luei* sp. nov. exhibits the following features: quadrate inclined at 150°; medial process of the pterygoid expanded, plate-like; dentary sulcus extending until the first pair of dentary teeth; odontoid process lacking foramina; odontoid process with a smooth occlusal surface; odontoid process vertical; hyoid accounting for 60% of mandibular length; and dentary teeth extending beyond the dentary symphysis. *Nurhachius ignaciobritoi*, on the other hand, exhibits: quadrate inclined at 160°; medial process of the pterygoid reduced; dentary sulcus extending until the sixth pair of dentary teeth; odontoid process bearing foramina; odontoid process with a sharp occlusal surface; odontoid process subhorizontal; hyoid accounting for 60% of mandibular length; and dentary teeth confined to the dentary symphysis (Fig. 4).

We note that both specimens of *Nurhachius ignaciobritoi* come from the upper part of the Jiufotang Formation, while the holotype of the newly described species, *N. luei*, comes from the lowermost part of the Jiufotang Formation. This stratigraphic segregation might be suggestive of an anagenetic link between them, similarly to what was proposed by Bennett (1994) for *Pteranodon longiceps* (from the upper Niobrara Formation) and *Pteranodon sternbergi* (from the lower Niobrara Formation), see discussion on the taxonomy of the *Pteranodon*-complex (Kellner, 2010; 2017; Martin-Silverstone *et al.*, 2017; Acorn *et al.*, 2017).

Concerning other istiodactylids, Wang *et al.* (2008) were unable to differentiate *Liaoxipterus brachyognathus* from "*Longchengpterus zhaoi*", both from the Jiufotang Formation, and suggested that they could thus represent synonyms (the former having priority). However, as observed by Lü *et al.* (2008), the anterior terminus of the dentary symphysis is rounded in *Liaoxipterus brachyognathus* (as is in *Istiodactylus latidens*) whilst it is triangular in "*Longchengpterus zhaoi*". Furthermore, as coded by Andres *et al.* (2014), "*Longchengpterus zhaoi*" exhibits an attenuated taper of the jaws, while in *Liaoxipterus brachyognathus* the lateral margins of the jaw are subparallel (Fig. 6), as in *Istiodactylus latidens*. We further note that the dentary symphysis of *Liaoxipterus brachyognathus* is relatively shorter than that of "*Longchengpterus zhaoi*": their length/width ratios are, respectively, 0.43 and 0.27. It should be noticed that, in the seventh figure by Martill (2014) the dentary symphysis of "*Longchengpterus zhaoi*" is incorrectly illustrated,

depicted as much shorter, with the dentary sulcus having been mistaken for the separation of the mandibular rami. The actual configuration can be clearly assessed in the description by Lü *et al.* (2008) and in Fig. 4. In this way, we follow Lü *et al.* (2008) and Witton (2012) in considering *Liaoxipterus brachyognathus* as distinct from "*Longchengpterus zhaoi*", which we consider as synonymous with *Nurhachius ignaciobritoi* following Lü *et al.* (2008) as expressed above.

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

As expressed above in the Results section, *Istiodactylus* was recovered as monophyletic group comprising *I. latidens* and *I. sinensis*, forming a sister-group to *Liaoxipterus*, followed by *Nurhachius*, corroborating previous results by Longrich *et al.* (2018). In our analysis, inclusion of the newly reported species *Nurhachius luei* resulted in its recovery as the sister-group of *Nurhachius ignaciobritoi*, supporting their congeneric status. In this way, the internal relationships found herein for the Istiodactylidae are in accordance with those found by Andres *et al.* (2014), with the addition of the new species.

Haopterus gracilis, from the Yixian Formation, was first described by Wang & Lü (2001) and interpreted as a member of the Pterodactylidae. However, subsequently, Lü *et al.* (2008; 2009) recognized its pterodactyloid nature and reinterpreted it as related to istiodactylids based on the similarities in tooth morphology. *Hongshanopterus lacustris*, from the Jiufotang Formation, was described by Wang *et al.* (2008) and interpreted as a primitive istiodactylid. Witton (2012) recovered a clade joining *Istiodactylus*, *Liaoxipterus*, *Longchengpterus* and *Nurhachius* to the exclusion of *Haopterus* and *Hongshanopterus*, and restricted the family to the former four taxa. *Haopterus* and *Hongshanopterus* were recovered as indeterminate pteranodontoids, in a polytomy with *Pteranodon* + *Coloborhynchus* + Istiodactylidae (Witton, 2012).

Subsequently, in the phylogenetic analysis of Andres *et al.* (2014), *Haopterus gracilis* was recovered as a basal lophocratian and *Hongshanopterus* as a basal ornithocheiromorph, though the placement of these taxa have not been the focus of their work nor been discussed. The

Istiodactylidae was phylogenetically defined by Andres *et al.* (2014) as the least inclusive clade containing *Istiodactylus* and *Nurhachius*. More recently, Holgado *et al.* (2019), also not focusing nor discussing these taxa, have nonetheless presented a phylogenetic analysis in which *Hongshanopterus* appeared as the sister-group of the Istiodactylidae and *Haopterus* was recovered as a basal ornithocheiraean. In turn, *Archaeoistiodactylus linglongtaensis*, described by Lü & Fucha (2010) and interpreted as the basal-most stem-istiodactylid, has never been included in any phylogenetic analysis so far, which is done here for the first time.

Our present analysis is based on that of Holgado *et al*. (2019), with the inclusion of characters (see Supplementary Material) based on Lü *et al.* (2008), Witton (2012) and Andres *et al.* (2014). We present a topology with further resolution that corroborates the interpretations of *Haopterus* and *Hongshanopterus* as closely related to the Istiodactylidae, as defended by Lü *et al.* (2008) and Wang *et al.* (2008), respectively. Under our new topology, *Hongshanopterus* is again recovered as the sister-group of the Istiodactylidae, as in the analysis by Holgado *et al*. (2019), *Hongshanopterus lacustris* shares with istiodactylids the presence of triangular, laterally compressed teeth in the rostrum. *Haopterus* is recovered as the sister-group of the Istiodactylidae + *Hongshanopterus*, supported by a dentition restricted to the anterior half of the jaws. These taxa further share the presence of a lingual cingulum, which is also shared with *Ikrandraco avatar* and *Lonchodraco giganteus*. *Ikrandraco avatar* also shares with istiodactylids a narrow lacrimal process of the jugal and of a quadrate inclined at 150° or over (unknown in *Haopterus* and *Hongshanopterus*). It must be further noted that at least *Haopterus* and *Ikrandraco* exhibit, at least on the posterior dentition, a certain degree of lateral compression of the teeth (Lü & Wang, 2001; Wang *et al.*, 2015), though not to the same degree seen in istiodactylids or *Hongshanopterus*. The same seems to be true for the last two mandibular alveoli preserved in the holotype of *Lonchodraco giganteus* (see Rodrigues & Kellner, 2013), but the posterior region of the jaws are not preserved and further material would be needed to confirm this feature for this taxon. We highlight that a close relationship between *Ikrandraco*, *Lonchodraco* and istiodactylids is proposed here for the first time, and that further data on the osteology of these forms are needed in order to corroborate this or not. In previous phylogenetic analyses, *Ikrandraco* has been recovered in a polytomy involving Istiodactylidae, *Cimoliopterus* and Anhangueria (Wang *et al.*, 2015) and *Lonchodraco* outside of the Lanceodontia (Longrich *et al.*, 2018).

Archaeoistiodactylus linglongtaensis is a taxon based on a single, holotypic specimen comprising fragments of skull bones and one displaced maxillary tooth, a partial lower jaw in dorsal view with two teeth in place, an almost complete wing lacking scapulocoracoid, a femur and a tibia. It comes from the Tiaojishan Formation (Bathonian-Oxfordian, Middle Jurassic), having been described by Lü & Fucha (2010). These authors interpreted it as the most primitive stem-istiodactylid. Lü & Fucha (2010) noted that the specimen shared with istiodactylids teeth with triangular crowns, as well as an odontoid process on the lower jaw. It should be noticed that this odontoid process was mistaken for a mid-line, unpaired tooth by Sullivan *et al.* (2014), but that it was explicitly described as a bony process by Lü & Fucha (2010). They further noted that the single preserved maxillary tooth is recurved, as in *Hongshanopterus* (see Lü & Fucha, 2010), and also reported on a warped deltopectoral crest, which is diagnostic of the Pteranodontoidea (Kellner, 2003). Still, they noted that the new taxon differed from istiodactylids in exhibiting a relatively short fourth metacarpal and subequal tibia, second and third phalanges of the wing digit. If indeed a stem-istiodactylid, this taxon would represent one of the oldest occurrences of the Pterodactyloidea, possibly older than the Callovian-Oxfordian basalmost pterodactyloid *Kryptodrakon progenitor* (see Andres *et al.*, 2014).

Subsequently, this identification was disputed by Martill & Etches (2013), who affirmed, though without presenting any justifications, that the specimen was probably a badly preserved specimen of *Darwinopterus*. Later, Sullivan *et al.* (2014) considered that the short fourth-metacarpal could be indicative of a non-pterodactyloid nature, as well as the long humerus and short first wing phalanx, all of which are typical of non-pterodactyloid pterosaurs (Kellner, 2003; Unwin, 2003; Andres *et al.*, 2010). This, allied to the presence of a confluent nasoantorbital fenestra, led Sullivan *et al*. (2014) to interpret *Archaeoistiodactylus* as a basal monofenestratan. Basal monofenestratans comprise the Darwinoptera, which encompass, from the Tiaojishan Formation or Daohugou Beds, the wukongopterids *Wukongopterus*, *Darwinopterus* and *Kunpengopterus* (see Wang *et al.*, 2009; 2010; Lü *et al.*, 2009; 2011), the non-wukongopterid darwinopteran *Pterorhynchus* (Czerkas & Ji, 2002; Andres *et al.*, 2014), and possibly also *Changchengopterus* (Wang *et al*., 2010; but see Andres *et al.*, 2014); and the possible wukongopterid *Cuspicephalus scarfi* from the Brittish Kimmeridge Clay Formation (Martill & Etches, 2013).

The results of our phylogenetic analysis corroborate the interpretation of Sullivan *et al.* (2014). An

istiodactylid nature for *Archaeoistiodactylus linglongtaensis* is not supported due to the lack of 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 *Archaeoistiodactylus* is crushed and the original orientation of the deltopectoral crest cannot be assessed, but it can be seen that it is confined to the proximal region of the humerus, differently from pterodactyloids (e.g. Wang *et al.*, 2009). *Archaeoistiodactylus linglongtaensis* also lacks pneumatic foramina on the centrum of the mid-cervical vertebrae, which is a diagnostic feature of the Dsungaripteroidea (the least inclusive clade containing *Nyctosaurus* and *Quetzalcoatlus*, which includes the Istiodactylidae; Kellner, 2003; Andres *et al.*, 2014). Furthermore, *Archaeoistiodactylus* exhibits low neural spines, similarly to wukongopterids (see Wang *et al.* 2009; 2010; Lü *et al.*, 2009; 2011; Cheng *et al.*, 2017) and differently from istiodactylids (see Wang *et al.*, 2006; Lü *et al.*, 2008). For these reasons, *Archaeoistiodactylus* can be placed outside of the Pterodactyloidea.

The dentition of *Archaeoistiodactylus* is indeed reminiscent of the Istiodactylidae due to the triangular aspect in lateral view (Lü & Fucha, 2010), but this feature is also present in the wukongopterids *Wukongopterus lii*, *Darwinopterus robustodens*, *Darwinopterus linglongtaensis* and *Kunpengopterus sinensis*, though not in *Darwinopterus modularis* (see Wang *et al.* 2009; 2010; Lü *et al.*, 2009; 2011; Cheng *et al.*, 2017). Furthermore, in *Archaeoistiodactylus* the alveoli are circular (Lü & Fucha, 2010), implying in the presence of conical teeth (as in wukongopterids), and not labiolingually compressed triangular teeth (as in istiodactylids). The presence/absence of an odontoid process in the lower jaw cannot be confidently assessed in *Wukongopterus* or *Darwinopterus*, but can be seen in a specimen referred to *Kunpengopterus sinensis* (see Cheng *et al.*, 2017), in convergence with istiodactylids. Finally, we further notice that *Archaeoistiodactylus* shares with *Darwinopterus* and *Kunpengopterus* (but not *Wukongopterus*) the subequal second and third phalanges of the wing digit. In this way, we regard *Archaeoistiodactylus linglongtaensis* to represent a wukongopterid closely related to *Darwinopterus* or *Kunpengopterus*. However, it must be noted that we were unable to access the specimen first-hand and further scrutiny is desirable in order to confirm, or not, these interpretations.

Conclusions

527 The new specimen we describe here represents a second species for the genus *Nurhachius*,
528 previously restricted to its type-species *Nurhachius ignaciobritoi* (=*Longchenpterus zhaoi*). Of
529 particular note is the presence of a slight dorsal deflection of the palate, as a synapomorphy of the
530 genus, previously thought to be restricted to Anhangueria and *Cimoliopterus*. The holotype of
531 *Nurhachius luei* sp. nov. also show a novel feature for pterosaurs, which is the growing of
532 reposition tooth in an anterolateral position relative to the older tooth. The new species shows that
533 the morphological diversity within istiodactylids is higher than previously thought. Furthermore,
534 we corroborate here the position of *Hongshanopterus* and *Haopterus* as stem-istiodactylids, further
535 proposing that *Ikrandraco* and *Lonchodraco* are probably more related to them than to other
536 lanceodontians. We also corroborate the recent reinterpretation of *Archaeoistiodactylus*
537 *linglongtaensis* as a non-pterodactyloid monofenestratan, and more specifically as a
538 wukongopterid.

539

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749

750 **Figures**

751 **Figure 1.** Photograph and line drawing of holotype of *Nurhachius luei* sp. nov. Photo by Xuanyu
752 Zhou. Drawing by Maria Eduarda Leal. Scale bar in line drawing equals 50 mm. Abbreviations:
753 an, angular; art, articular; ax, axis; ch, choana; cv, cervical vertebra; d, dentary; f, frontal; hy, hyoid;
754 j, jugal; la, lacrimal; m, maxilla; n, nasal; naof, nasoantorbital fenestra; or, orbit; pa, parietal; pf,
755 prefrontal; po, postorbital; prid, palatal ridge; pty, pterygoid; q, quadrate; vo, vomer.

756 **Figure 2.** Map showing location of origin of the material herein described.

757 **Figure 3.** Strict consensus tree from our phylogenetic analysis. Red rectangle indicates the
758 Istiodactylidae and its stem-group.

759 **Figure 4.** Photographs and line drawings. A) *Nurhachius luei* sp. nov. holotype, skull and mandible
760 in right lateral view. B) *Nurhachius ignaciobritoi* referred specimen (holotype of
761 "*Longchengpterus zhaoi*"), skull and mandible in right lateral view. C) *Nurhachius ignaciobritoi*
762 holotype, skull (mirrored) and mandible in right lateral view. Photographs by Xuanyu Zhou.
763 Drawings by Rodrigo V. Pêgas.

764 **Figure 5.** Close view of the rostral tip in right lateral view of A) *Nurhachius luei* sp. nov. holotype
765 and B) *Nurhachius ignaciobritoi* holotype, mirrored. C) and D), respective schematic drawings,
766 showing the slight dorsal deflection of the palate (notice positions of first and second alveoli in
767 both specimens). Scale bars equal 20 mm. Photos by Xuanyu Zhou. Drawings by Rodrigo V.
768 Pêgas.

769 **Figure 6.** A) *Liaoxipterus brachyognathus*, holotypic lower jaw in dorsal view. Anterior is to the
770 right. B) *Haopterus gracilis*, skull of the holotype in right lateral view. C) *Hongshanopterus*
771 *lacustris*, holotypic skull in ventral view. Anterior is to the left. All scale bars equal 50 mm. Photos

772 by Xuanyu Zhou.

Figure 1(on next page)

Photograph and line drawing of holotype of *Nurhachius luei* sp. nov.

Photo by Xuanyu Zhou. Scale bar in line drawing equals 50 mm. Abbreviations: an, angular; art, articular; ax, axis; ch, choana; cv, cervical vertebra; d, dentary; f, frontal; hy, hyoid; j, jugal; la, lacrimal; m, maxilla; n, nasal; naof, nasoantorbital fenestra; or, orbit; pa, parietal; pf, prefrontal; po, postorbital; prid, palatal ridge; pty, pterygoid; q, quadrate; vo, vomer.


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Institute of Geology Chinese Academy of Geological Sciences
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中国地质科学院地质研究所

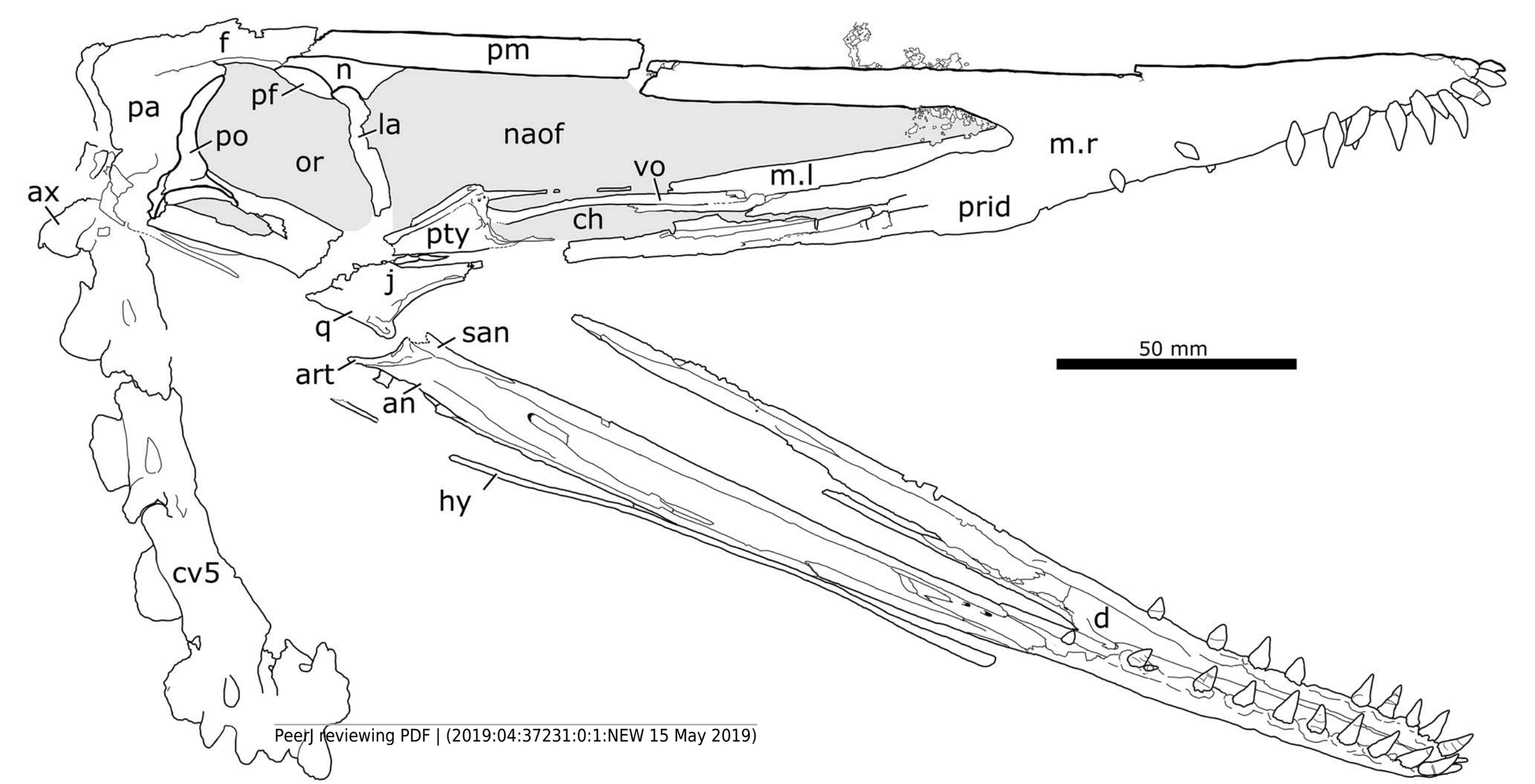
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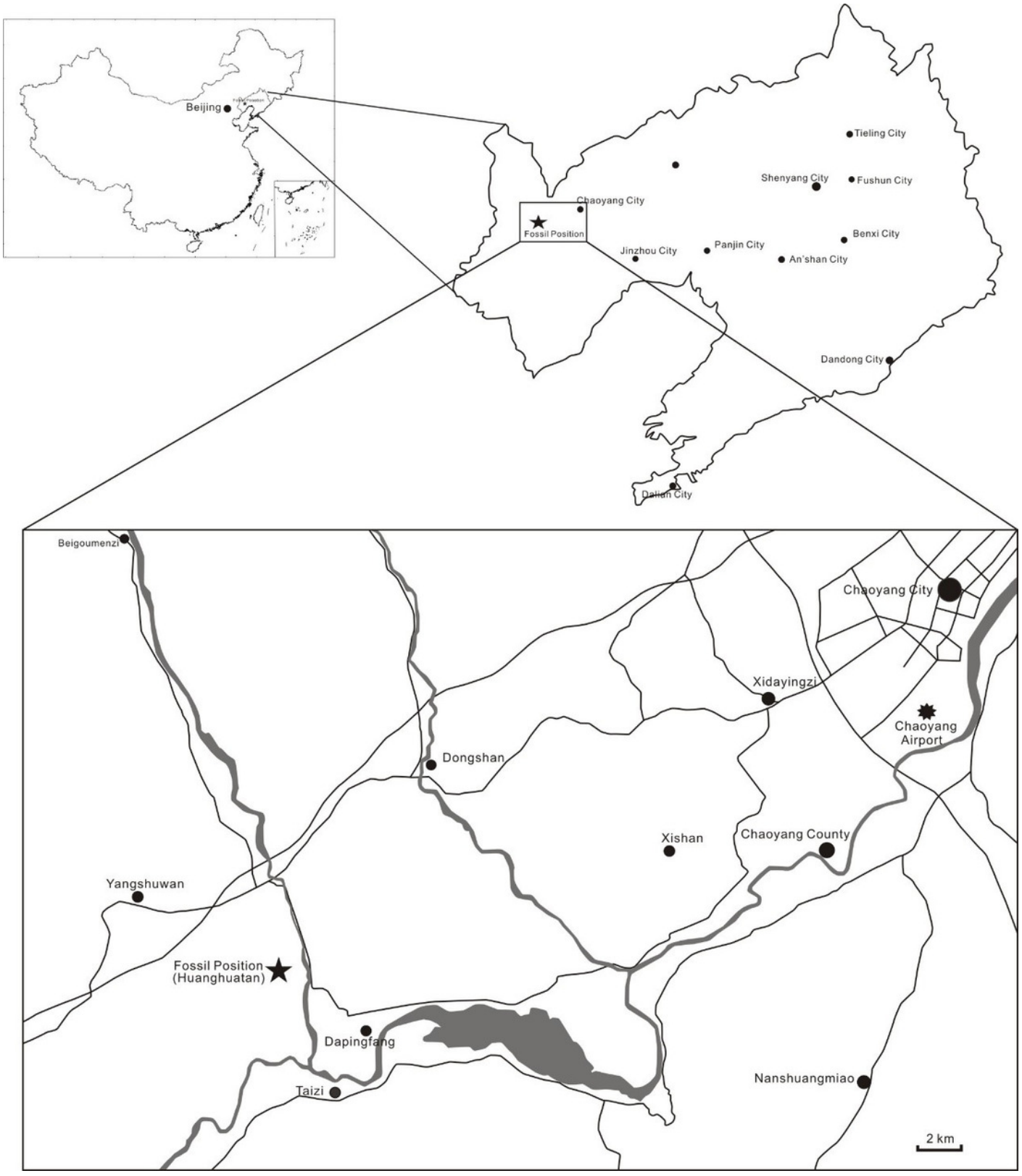
Figure 2

Map showing location of origin of the material herein described.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Chaoyang City
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Fossil Position (Huanghuatan)
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Figure 3(on next page)

Strict consensus tree from our phylogenetic analysis.

Red rectangle indicates the Istiodactylidae and its stem-group.

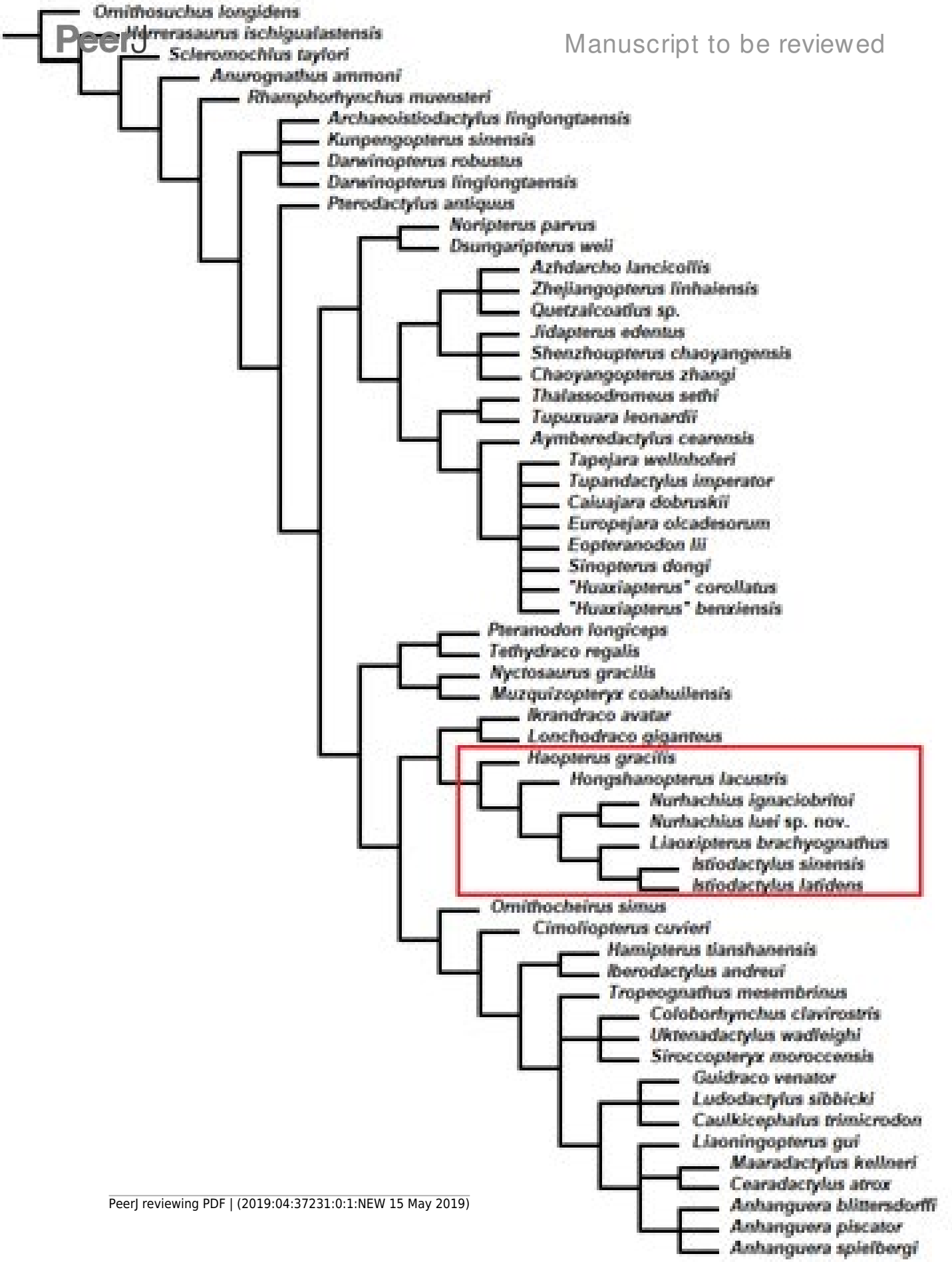
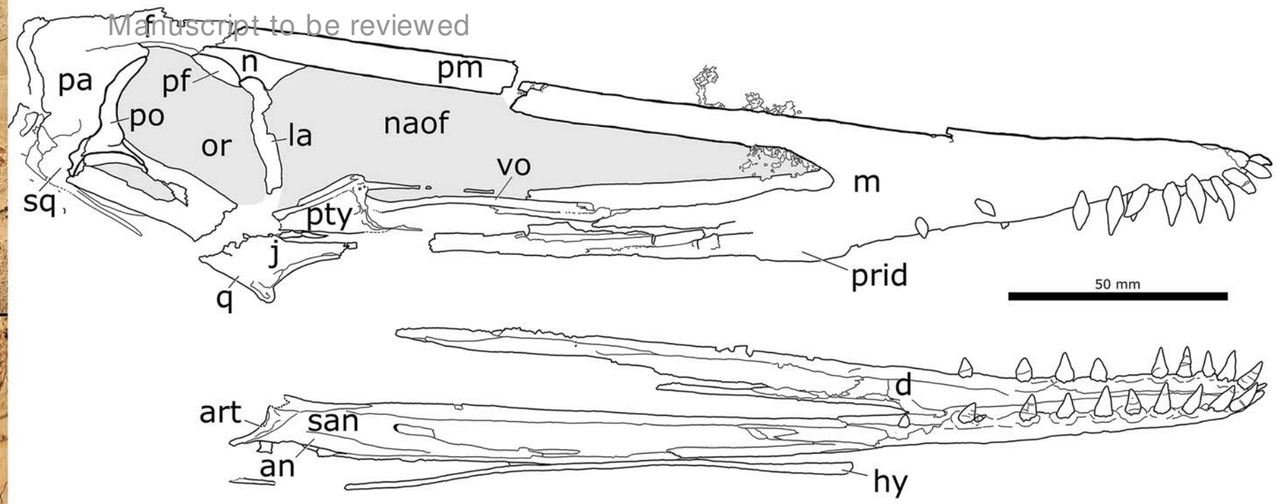
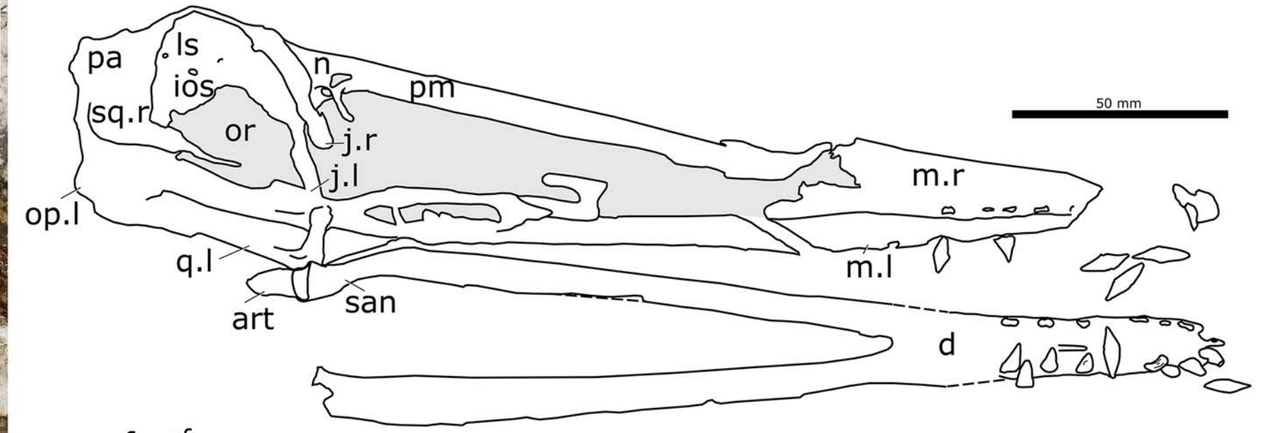


Figure 4(on next page)

Photographs and line drawings.

A) *Nurhachius luei* sp. nov. holotype, skull and mandible in right lateral view. B) *Nurhachius ignaciobritoi* referred specimen (holotype of *"Longchengpterus zhaoi*"), skull and mandible in right lateral view. C) *Nurhachius ignaciobritoi* holotype, skull (mirrored) and mandible in right lateral view. Photographs by Xuanyu Zhou.





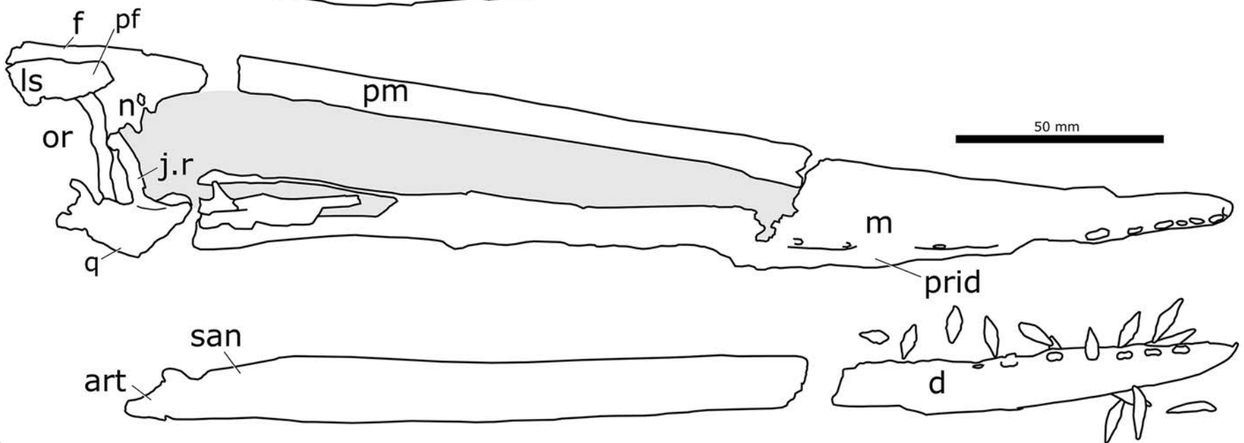
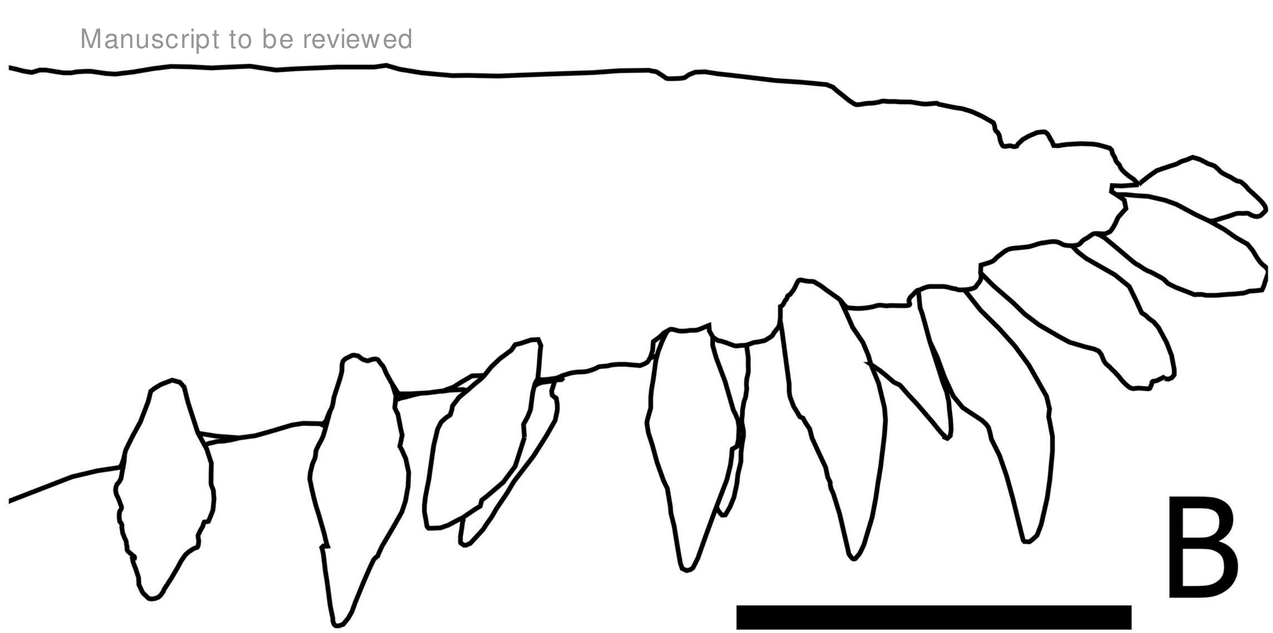


Figure 5(on next page)

Close view of the rostral tip in right lateral view of

A) *Nurhachius luei* sp. nov. holotype and B) *Nurhachius ignaciobritoi* holotype, mirrored. C) and D), respective schematic drawings, showing the slight dorsal deflection of the palate (notice positions of first and second alveoli in both specimens). Scale bars equal 20 mm. Photos by Xuanyu Zhou.



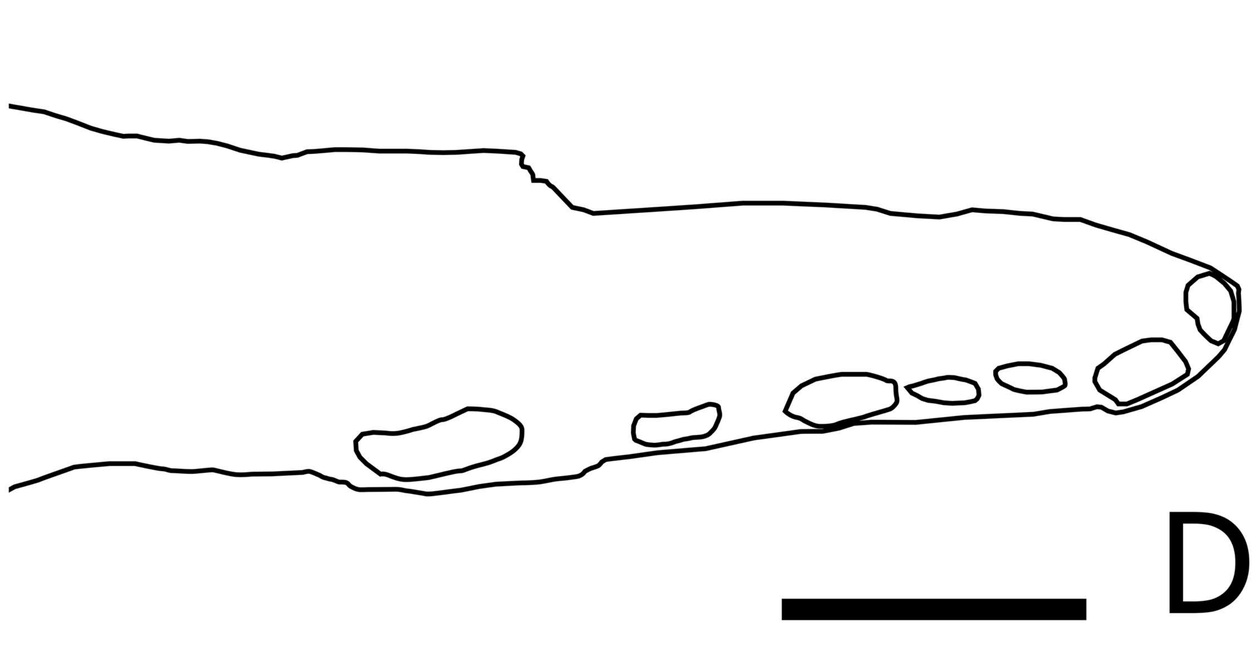


Figure 6(on next page)

Photographs of

A) *Liaoxipterus brachyognathus*, holotypic lower jaw in dorsal view. Anterior is to the right. B) *Haopterus gracilis*, skull of the holotype in right lateral view. C) *Hongshanopterus lacustris*, holotypic skull in ventral view. Anterior is to the left. All scale bars equal 50 mm. Photos by Xuanyu Zhou.