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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Comentario [F1]: It should be in Portuguese to be consistent with the affiliation n. 4.

Comentario [F2]: In the first page of the PDF of the manuscript, there is a further affiliation: 6 Fur Museum (Museum Saling), Fur, Denmark. Did you forget it here?

The acronym SNM is not explained. All acronyms in the text must be explained.

Abstract: ~~We present~~ 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 ~~at Chaoyang city,~~ of western Liaoning (China). ~~The specimen preserves some three-dimensional structure, especially regarding the dentition~~. ~~In this paper, we also comment on~~ 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.

Comentario [F3]: This part is not adequately explained in the text.

Comentario [F4]: ventral surface of the tip of the snout? It is not the whole palate to deflect dorsally.

The relationships within the ~~in-group and stem-gr~~oup Istiodactylidae and with their closest taxa are investigated though a phylogenetic analysis by parsimony. *Archaeoistiodactylus linglongtaensis* results to be a non-pterodactyloid monofenestratan. ~~, including a new definition of the genus *Nurhachius* which was previously limited to its type-species, *Nurhachius ignaciobritoi* from the upper~~ part of the ~~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~~ the ~~Anhanguería and *Cimoliopterus*~~.

Keywords: Pterosauria, Pterodactyloidea, Istiodactylidae, Jiufotang Formation, Cretaceous, Systematics~~, Taxonomy~~, ~~Three-dimensional Preservation~~

Introduction

Istiodactylid pterosaurs are characterized by ~~the~~ rhombic teeth ~~and~~ with lancet-shaped ~~teeth~~ crowns, long skulls with short pre-antorbital portions of the rostrum~~,~~ and nasoantorbital fenestrae ~~constituting~~ representing over 50 percent of the total 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 (~~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. ~~and 3 genera and species of proposed stem-group istiodactylids (*Haopterus gracilis, Hongshanopterus lacustris, Archaeoistiodactylus linglongtaensis*) have been reported (Lü *et al.*, 2013).~~ *Haopterus gracilis*, *Hongshanopterus lacustris* and *Archaeoistiodactylus linglongtaensis* have been reported in literature as taxa that are close to the Istiodactylidae (REPORT A VALID CITATION/S). However, the affinity of *Archaeoistiodactylus linglongtaensis* has been questioned by Sullivan et al. (2014).

~~However, *Longchengpterus zhaoi* has been interpreted by Lü *et al.* (2008) as a junior~~

Comentario [F5]: 'Lancet-shaped' is referred to the crown only, while the whole tooth is rhombic.
it is not very clear which shape should correspond to the term 'lancet-shaped'.
The 'root' giving the rhombic shape to these teeth is never mentioned elsewhere in this manuscript.

Comentario [F6]: The rostrum is the part of the skull in front of the eyes by definition. Istiodactylidae have a short pre-nasoantorbital portion of the skull.

Comentario [F7]: You use the term "stem-group istiodactylids" throughout the text. This term is incorrect for at least two reasons: FIRST: The terms "stem" and "crown" should be used only for supraspecific taxa that have living species. I know that these terms are often incorrectly used otherwise, but see: Jefferies, R.P.S. (1979). The origin of chordates – a methodological essay. In M.R. House (ed.). The origin of major invertebrate groups. London ; New York: Academic Press for The Systematics Association. pp. 443–447. Pterosaurs are totally extinct, thus "stem" and "crown" cannot be used for them. ... [1]

Comentario [F8]: Is this a reliable source? It is a book that is difficult to find. I do not have a copy, thus I cannot judge.
However, it is not possible that this source considers *Longchengpterus zhaoi* as an istiodactyl when the same authore had established that it is not five years before (2008)!

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 Early Cretaceous Jiufotang Formation of northeastern China to the with the exception of *Istiodactylus latidens*, (which is from the Early Cretaceous Vectis Formation of the Wealden on Isle of Wight, Southern England). Also the three taxa that are reported as close to the 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 (Middle Jurassic). Apart from the latter, these Chinese pterosaurs are all from belong to the Jehol Biota (see Chang et al., 2003). Still, the stem-istiodactylid nature of *Archaeoistiodactylus linglongtaensis* has been questioned by Sullivan et al. (2014).

By the end of 2016, 20 species of pterosaurs have been reported from the Jiufotang Formation (Li et al., 2003; Wang X.L. & Zhou, 2003a, 2003b; Andres & Ji, 2006; Dong & Lü, 2005; Dong et al., 2005; Lü & Ji, 2005; Rodrigues et al., 2015; Lü & Yuan, 2005; Wang X.L. et al., 2005, 2008a, 2008b, 2012, 2014; Lü et al., 2006, 2007, 2008; Wang L. et al., 2006; Jiang et al., 2016).

Comentario [F9]: Not in the reference list.

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 a second species of istiodactylid pterosaur *Nurhachius* from the Jiufotang Formation and investigate the phylogenetic relationships of the istiodactylids and purported close taxa. 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.

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 X., 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 X. 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.

Comentario [F10]: This is a more recent source than those mentioned by the authors.

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).

N. ignaciobritoi was found in the upper part of the Jiufotang Formation (REPORT REFERENCES TO SUPPORT THIS STATEMENT, this is fundamental), whereas the new species is from the Boluochi Beds.

~~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~~

Comentario [F11]: REPORT REFERENCES TO SUPPORT THIS STATEMENT, this is fundamental

Comentario [F12]: This is an old and partly obsolete reference. The International Chronostratigraphic Chart of ICS (IUGS) is updated twice per year.
see www.stratigraphy.org

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.

Comentario [F13]: This part has nothing to do with this paper.

Comentario [F14]: No, this is not necessarily the case. It depends upon the local sedimentation rates and the presence or not of hiatuses within the sections. In fact, both formations have dramatically different thicknesses in different localities.

Material and 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 or Huanghuatian? (Dapingfang, Chaoyang County, western Liaoning). You must report here which specimens you studied personally and which other were coded or described only based on the literature.

A phylogenetic analysis we was performed here is based on a the data matrix modified from by Holgado et al. (2019) modified, with the inclusion of characters by Lü et al. (2008), Witton (2012) and Andres et al. (2014), as well as and the addition of the following taxa: *Archaeoistiodactylus linglongtaensis*, *Kunpengopterus sinensis*, *Liaoxipterus brachyognathus* and *Nurhachius luei* sp. nov. (see Supplementary Material SI). The analysis was conducted on performed by TNT (Goloboff et al., 2008) using the Traditional Search option, 10000 replications replicates, random seed = 0 and

Comentario [F15]: It is reported this way below.

Comentario [F16]: You must report here which specimens you studied personally and which other were coded or described only based on the literature.

collapsing trees after search. ~~A text file with our~~ The character and character states list and the TNT file with ~~our~~ the data matrix are available in the SI ~~as Supplementary Material~~.

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:03EF173E-4AB5-4C74-B80C-A6AAFA65E61C. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Results

Systematic Paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger,1901

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

Nurhachius Wang X.L et al., 2005

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

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

(Figs. 1 and 5A-B)

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*.

Comentario [F17]: All authors must be reported *per extenso*.

Comentario [F18]: All authors must be reported *per extenso*.

Comentario [F19]: Labial and mesial???

Comentario [F20]: A diagnosis and the description of a node in a phylogenetic analysis are two things that are conceptually different. Rewrite the diagnosis listing the combination of characters that is diagnostic of *Nurhachius*. This means a combination of features that are all shared by *N. igniaciobritoi* and *N. luei* and that does not occur in any other istiodactylid.
See attached note for further comments.

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~~ for his fundamental contributions to the study of Chinese pterosaurs.

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

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

Diagnosis. The new species ~~can be~~ is diagnosed based on the following combination of features: quadrate inclined at 150°; medial process of the pterygoid ~~expanded,~~ broad and plate-like; dorsal median sulcus of the mandibular symphysis extending ~~until~~ up to the first pair of ~~dentary~~ mandibular teeth; dorsally directed odontoid (pseudotooth) of the mandibular symphysis ~~process~~ lacking a foramen~~ina~~ on the lateral side,~~; odontoid process~~ and with a smooth occlusal surface ~~;~~ ~~odontoid process vertical~~; ~~hyoid~~ ceratobranchial I of the hyoids 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~~ mandibular teeth extending distally beyond the ~~dentary~~ symphysis.

Description

Skull and mandible ~~generalities~~. The skull is exposed in right lateral view, with some palatal elements that are visible in dorsal view. ~~and~~ The mandible ~~lying~~ is exposed in ~~an oblique~~ right dorsolateral view. ~~It~~ 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 ~~elongated~~, corresponding to 45% of the total skull length ~~(premaxilla to squamosal)~~ and 55% of the total jaw length (craniomandibular joint to premaxilla). Anterior to ~~it~~ the nasoantorbital fenestra, the rostrum ~~exhibits a slight dorsal inclination of its long axis~~ is slightly deflected dorsally, ~~similarly to~~ as in other istiodactylids (Wang X.L. et al., 2005; Andres & Ji, 2006; Lü et

Comentario [F21]: FIRST: where is this Museum? If it is in the town of Beipiao, you must write: Beipiao Pterosaur Museum, Beipiao, Liaoning Province, China. SECOND: is this museum a public repository? Most journals do not accept papers about fossils that are deposited in private collections, mainly if they are holotypes.

Comentario [F22]: This is the name that is reported elsewhere in this manuscript.

Comentario [F23]: This should essentially be a differential diagnosis: a list of features distinguishing *N. luei* from *L. ignaciobritoi*. Is it? Why do you define it "a combination of features"?

Comentario [F24]: blunt?

Comentario [F25]: Actually, this does not appear to be a diagnostic feature in the Discussion section.

Comentario [F26]: This is not discussed as a diagnostic feature in the Discussion section. How many upper and lower jaw teeth does *N. igniaciobritoi* have? Can this difference be due to ontogenetic or other intraspecific kind of variability?

Comentario [F27]: The meaning of "jaw" (it should be upper jaw, anyway) is ambiguous here. You could write only: craniomandibular joint to rostral tip of the premaxilla lenght. However, you can also omit it.

al., 2008; Witton, 2012), as well as *Ikrandraco avatar* and the anhanguerians (e.g. Kellner & Tomida, 2000; Wang X.L. et al., 2014; 2015; Holgado et al., 2016), but unlike the boreopterids (Lü & Ji, 2005; Lü, 2010; Jiang et al., 2014). ~~The palate exhibits~~ There is a strong palatal keel extending from pre-narial part of the rostrum ~~until~~ to the anterior ~~region~~ third? of the nasoantorbital fenestra. The craniomandibular joint levels with the anterior margin of the orbit, similarly to both specimens of *N.~~urhachius~~ ignaciobritoi* ~~(both specimens: its holotype plus former holotype of "*Longchengpterus zhaoi*")~~, *Anhanguera* spp. and *Linlongopterus jennyae*, but unlike *Istiodactylus* spp., in which ~~it~~ the joint 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 X.L. 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 ventral being the narrowest part ~~thinnest region being the ventral region~~, and without ~~any~~ a suborbital vacuity. This is similar to the condition seen in the referred specimen of *N.~~urhachius~~ ignaciobritoi* ~~(as seen in second specimen)~~ and ~~different from~~ unlike the rounded orbit of *Istiodactylus*, ~~with~~ which has also a suborbital vacuity (see Andres & Ji, 2006; Lü et al., 2008; Witton, 2012). The infratemporal fenestra is elliptical and ~~shorter~~ much smaller 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 premaxilla is fused with the maxilla and the suture is obliterated, thus the boundary between the two bones cannot be traced. Consequently, the premaxillary teeth count is unknown. ~~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 gracilis*.

Nasal and Lacrimal. The nasal and lacrimal are fused, ~~forming~~ originating a nasolacrimal that forms the ~~upper anterior~~ anterodorsal margin of the orbit and the posterodorsal margin of the nasoantorbital fenestra. The anterior ~~limit~~ end of the nasolacrimal coincides with the highest point of the nasoantorbital fenestra, as in both specimens of *N.~~urhachius~~ ignaciobritoi* ~~(both specimens)~~ and also *Ikrandraco avatar* (Wang X.L. et al., 2005; Wang L. et al., 2006; Andres & Ji, 2006; Lü et al., 2008; Wang

Comentario [F28]: This is not in the reference list. Do you mean 2019?

Comentario [F29]: I cannot see this in figure 1. Please draw better this feature and indicate with arrows where the keel begins and where it ends.

Comentario [F30]: Report the each reference after the corresponding taxon.

Comentario [F31]: Actually, this is not the description of the pmx. It is the description of the posterodorsal (frontal) process of the pmx.

Comentario [F32]: Which ones? All of them?

Comentario [F33]: If they are fused, why do you draw a boundary line between them in Fig. 1? There is something wrong here.

X.L. et al., 2015), but ~~differently from~~ unlike *Istiodactylus latidens* and most anhanguerians ~~such as~~ (e.g., *Anhanguera*, *Tropeognathus* and *Hamipterus*), except for *Ludodactylus sibbicki*, in which the highest point is posterior to the anterior ~~limit~~ end of the nasolacrimal (~~Kellner & Campos~~ Campos & Kellner, 1985; Wellnhofer, 1987; Kellner & Tomida, 2000; Wang X.L. et al., 2014; Frey et al., 2003). A nasal descending process cannot be seen in ~~the new specimen~~ BPMC-0204, possibly because it is still covered by rock ~~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~~ lacrimal is slightly damaged and a small process similar to the one seen in the holotype of *N.~~urhachius~~ ignaciobritoi* ~~(holotype)~~ ~~could~~ may had been ~~possibly~~ 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. ~~and~~ The ~~nasolacrimal~~ nasal is bordered dorsally by the premaxilla~~. Posteriorly, it~~ and ~~contacts~~ by the prefrontal posteroventrally.

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~~ sends a postorbital process to contact~~ing~~ the ~~squamosal~~ postorbital, 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~~ contacts laterally a small portion of the ~~incompletely preserved~~ incomplete quadrate ~~on the lateral surface of the skull~~, ventral to the quadratojugal~~,~~ as in the holotype of *N.~~urhachius~~ ignaciobritoi* ~~(holotype)~~, *Istiodactylus sinensis* and *Ikrandraco avatar* (Wang X.L. et al., 2005, 2015; 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 X.L. et al., 2014) and pteranodontians (Bennett, 2001; Frey et al., 2006).

Quadrate. ~~The quadrate is incompletely preserved~~. The ventral ~~region~~ portion of the ~~bone~~ quadrate ~~is present,~~ contacts~~ing~~ the jugal ventral to the quadratojugal. It is unclear ~~if~~ whether the articulation with the ~~lower jaw~~ mandible is helical or not. The mid-region of the quadrate is lost.~~,~~ ~~and~~ The dorsal portion of the quadrate ~~can be seen contacting~~ contacts the quadratojugal anteriorly and the squamosal dorsally. The quadrate is ~~posteriorly~~ inclined backward at an angle of 150°, unlike both specimens of *N.~~urhachius~~ ignaciobritoi* ~~(both specimens)~~, in which ~~is inclines~~ it slopes at 160°

Comentario [F34]: Do you have seen the specimen personally? You should be able to understand if it is covered by rock or not.

Comentario [F35]: If so, you must draw this contact in Fig. 1.

Comentario [F36]: It is not drawn in Fig. 1. I cannot check mistakes in this description because the authors give no detailed images of the jugal–quadratojugal–quadrate complex.

Comentario [F37]: Do you mean the margin of the ventroanterior end of the fenestra? Without a drawing, this is unclear.

Comentario [F38]: ????

Comentario [F39]: All these bones must be drawn in Fig. 1. It would be also useful the addition of a detail figure and drawing of this region.

Comentario [F40]: redundant

Comentario [F41]: Draw it in Fig.1! As it is described here, this seems to be impossible!

(Wang X. et al., 2006; Wang L. et al., 2006).

Prefrontal. The prefrontal is a small bone that ~~takes part in the~~ forms 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~~ with the premaxilla and parietal, with no visible sutures. However, there is a round suture between the frontal and postorbital ~~can be seen~~. It is unclear ~~if~~ 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 ~~badly~~ poorly preserved, especially the latter. ~~for which its limits~~ The squamosal outline cannot be properly identified. The parietal preserves a shallow depression in its surface ~~a fossa~~ that corresponds to ~~accounts for~~ the medial wall of the supratemporal fenestra~~,~~. ~~which~~ The dorsal limits of this fossa level with the orbit and extend ventrally ~~until being limited by~~ to the region of contact between the squamosal and the 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~~ it is like a three-pointed star as in *Haopterus gracilis* (see Wang X.L. & Lü, 2001) and *Istiodacylus sinensis* (see ~~Wang & Lü, 2001;~~ Andres & Ji, 2006). The anterior region of the postorbital ~~bone~~, ~~including~~ which is formed by the frontal and jugal processes, is arched ~~very~~ ~~curved, concave and slender (anteroposteriorly compressed), with a round anterior margin taking part in the border~~ and forms the posterior margin of the orbit. ~~Posteriorly,~~ The squamosal process is shorter than the other processes~~—of the postorbital~~ and 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~~ few details can be ~~extracted~~ observed. A long, slender vomer ~~can be seen separating~~ separates the ~~two~~ choanae, as in *Hongshanopterus lacustris* (see Wang et al., 2008). The medial process of the right pterygoid ~~can be seen.~~ ~~It~~ is exposed and ~~is~~ appears to be large and plate-like~~, well-developed and expanded, similar to the condition seen in~~ as that of *Hongshanopterus lacustris* (see Wang et al., 2008) and, to a lesser extent, the anhanguerids (e.g., Campos & Kellner, 1985; Frey et

Comentario [F42]: Not in the reference list.

Comentario [F43]: posteroventrally, according to Fig. 1.

Comentario [F44]: This is not what I see in Fig. 1. Which interpretation is the correct one?

Comentario [F45]: What is a "round suture"?

Comentario [F46]: In the Fig. 1, you wrote PA (parietal) there. That suture appears to be with the parietal.

Comentario [F47]: You could mark its position in Fig. 1, anyway.

Comentario [F48]: The postorbital is not slender. It is the frontal r ... [2]

Comentario [F49]: This is not clear. Explain better.

Comentario [F50]: This is really an obscure comparison. Explain be ... [3]

Comentario [F51]: The postorbital is fused with the neighbor bone ... [4]

Comentario [F52]: This is unclear in Fig. 1.

Comentario [F53]: There are two paired vomers in the reptile skull.

Comentario [F54]: What does this mean? That *Hongshanopterus* h ... [5]

Comentario [F55]: WHICH WANG? WHICH PAPER?

Comentario [F56]: Mark this process in Fig. 1.

Comentario [F57]: You should first describe what is preserved or ... [6]

Comentario [F58]: WHICH ONE?

Comentario [F59]: What does this mean? Less plate-like? Less ... [7]

al., 2003), but ~~differently from~~ unlike the slender ~~condition seen in~~ medial processes of the pterygoid of the azhdarchoids (e.g.,, Pinheiro & Schultz, 2012; Kellner, 2013; Pêgas et al., 2018) or ~~in~~ those of the referred specimen of *N.~~urhachius~~ ignaciobritoi* (~~referred specimen,~~ see Wang L. et al., 2006; Lü et al., 2008) and *Ikrandraco avatar* (see Wang X.L. et al., 2015). A small portion of the medial process of the ectopterygoid ~~can be seen~~ contacts~~ing~~ the medial process of the pterygoid, separating the subtemporal and postapalatinal fenestrae, as ~~can be seen~~ in *Hongshanopterus lacustris* (see Wang et al., 2008) and *N.~~urhachius~~ ignaciobritoi* (Fig. 4).

Dentary. The ~~two~~ dentaries are fused ~~anteriorly~~ rostrally forming a symphysis that accounts for 36% of total mandibular length. ~~On~~ The dorsal surface of the ~~dentary~~ symphysis~~,~~ presents a deep and broad ~~dentary~~ median sulcus ~~can be seen, extending~~ that extends ~~anteriorly~~ rostrally ~~until~~ up to the level of the first pair of alveoli. The ~~anterior~~ rostral tip of the ~~dentary~~ symphysis ~~exhibits~~ has an odontoid (pseudotooth) ~~process~~, that is located ~~in~~ between the first pair of teeth, ~~that~~ is smaller than the adjacent tooth crowns and is dorsally directed ~~curved~~. The odontoid ~~process~~ lacks ~~any~~ the neurovascular foramen~~ina~~ piercing its surface~~, unlike~~ in the referred specimen of *N.~~urhachius~~ ignaciobritoi* (see Wang L. et al., 2006). ~~It is vertically oriented,~~ The odontoid has the same orientation as ~~the one seen in~~ that of *Istiodactylus latidens* (see Martill, 2014) and *Lonchodraco giganteus* (~~Witton, 2012;~~ see Rodrigues & Kellner, 2013, fig. 4E-F; ~~Martill, 2014~~), ~~and~~ unlike the sub-horizontal odontoids ~~seen in~~ of both specimens of *N.~~urhachius~~ ignaciobritoi* (see Wang X. et al., 2006; Wang L. et al., 2006)~~,~~ and ~~also in~~ *Ikrandraco avatar* (see Wang X.L. et al., 2015). The symphysis ~~houses 11 pairs of alveoli~~ presents 11 tooth positions per side~~, with~~ and two further pairs of alveoli ~~being present~~ occur on the ~~separated~~ mandibular rami ~~as well~~.

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 ~~long~~ suture ~~can be seen delineating~~ separates the long anterior process of the surangular from the ~~, dorsal to the~~ dentary dorsally. Posteriorly, ~~this bone~~ the surangular becomes deeper and ~~contacts~~ is sutured with the angular~~, where another suture can be seen~~. The ~~limit~~ boundary between the angular and the dentary, however, cannot be distinguished ~~observed~~, nor the boundary between the angular and the articular. The articular forms the posterior ~~region~~ part of the mandible, including the ~~articulation~~ articular surface for the quadrate and the retroarticular process, which is pointed, dorsoventrally low and distally tapering ~~and elongated~~.

Comentario [F60]: Mark it in Fig. 1.

Comentario [F61]: Where do you see them?

Comentario [F62]: WHICH ONE?

Comentario [F63]: I do not see these fenestrae in Fig. 4. I just see approximate drawings where only a few structures are identified by abbreviations.

Comentario [F64]: You must first report this length. Please, report it where you give an overall description of the skull and mandible.

Comentario [F65]: Do you mean the first pair of teeth (tooth 1)? Otherwise, I totally misunderstood what you are talking about.

Comentario [F66]: I do not see in Fig. 1. You should indicate it in the figure. You should also add a photograph of this structure, which appears to have a taxonomical value.

Comentario [F67]: Can you see the whole surface of this structure, in a way to establish that there are not foramina?

Comentario [F68]: What you report as "sub-horizontal odontoids" is usually described as the pointed rostral end of the mandible in basal pterosaurs.

Comentario [F69]: Not in the reference list.

Comentario [F70]: Only two? Are you sure?

Hyoid. Only the right ~~hyoid~~ ceratobranchial I is exposed along the ventral margin of the right mandibular ramus (Fig. 1) ~~can be seen~~, ~~disarticulated from the left hyoid~~. ~~Only~~ A small portion of the posterior ~~region~~ part is missing. ~~It~~ The ceratobranchial I is a long rod-like~~,~~ ~~elongated~~ bone ~~that is positioned from near the region of separation between~~ extending along the whole length of the mandibular rami ~~until the retroarticular process~~.

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

~~In the upper jaw,~~ The first two teeth of the upper jaw (which are much probably premaxillary teeth) are ~~particularly~~ procumbent. The first ~~teeth~~ tooth 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 of the right maxilla are empty, and the last one is placed ~~only~~ ~~slightly~~ just ~~anterior~~ rostral to the level of the rostral end of the nasoantorbital fenestra. All of the ~~teeth~~ crowns are triangular in labiolingual view and ~~laterally~~ labiolingually compressed, as typical of the Istiodactylidae. The~~y present a crown~~ base of the crowns is mesiodistally inflated. The lingual surface of the crown is concave with a well-marked longitudinal depression and a ~~slight~~ low transversal convexity at the base~~, forming~~ that forms a lingual cingulum. The labial surface is mostly convex with a ~~slight~~ shallow concavity ~~on~~ in the ~~center~~ middle of the basal part of the crown ~~base~~. No carinae are present along the mesial and distal cutting margins of the crowns. The same ~~configuration can be found~~ features occur in ~~on~~ the crowns of the holotype of *N.~~urhachius~~ ignaciobritoi*.

The first nine pairs of teeth ~~in~~ of 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.

N.~~urhachius~~ luei sp. nov. also ~~exhibits~~ presents an interesting pattern of ~~teeth~~ tooth ~~reposition~~ replacement. Two teeth occur in the tenth alveol~~u~~s of the right dentary~~, two teeth are present~~: a large~~, well-developed~~ functional one~~,~~ and a not yet fully erupted ~~reposition~~ replacement tooth ~~still growing~~. The ~~reposition~~ replacement tooth ~~is~~ was erupting ~~anterolaterally~~ anterolabially to the functional tooth ~~larger one~~, instead of

Comentario [F71]: The hyoid is an apparatus. See Romer (1976), p. 420. The single preserved elements are the cornua or ceratobranchials. Usually, the ossified one is the first ceratobranchial in living reptiles.

Comentario [F72]: The print of the missing part is visible in the Fig. 1 (photo). You must indicate this part with dashed lines in the drawing.

Comentario [F73]: However, you can see only the right one, thus you cannot know the count along the left one.

Comentario [F74]: Or the main axis of the skull? The palatal plane should be deflected there, according to your description.

Comentario [F75]: Do you mean basoapical?

Comentario [F76]: You must add photos where these features are clearly shown. I cannot evaluate whether this structure is a cingulum or not.

Comentario [F77]: If the crowns are labiolingually flattened and the cutting margins are sharp, there is no need of carinae.

Comentario [F78]: I do not understand. Explain it better.

Comentario [F79]: What are you talking about? Do you mean that the smallest crown is 6 mm basoapically high and 2 mm mesiodistally long?

Comentario [F80]: What does it mean? That the crowns are sharply pointed? That the cutting margins are sharp?

~~posteromedially~~ posterolingually~~,~~ as reported ~~before for~~ in other pterodactyloid pterosaurs like ~~such as in~~ *Anhanguera* (~~e.g.~~ see Kellner & Tomida, 2000; Fastnatch, 2001) and '*Cearadactylus*' *ligabuei* (see Dalla Vecchia, 1993).

Cervical vertebrae. ~~There are~~ Seven cervical vertebrae are preserved, including the fused atlas-axis complex ~~atlantoaxis which is fused~~. They are ~~preserved in articulation~~ articulated, except for the ~~seventh~~ 7th vertebra, which is disarticulated but still contacting the 6th vertebra. The ~~third~~ 3rd, ~~fourth~~4th and ~~fifth~~5th cervicals are of similar length~~,~~; they are longer than the ~~subsequent ones~~ 6th and 7th vertebrae (which are x and y mm long, respectively) and of the atlas-axis complex ~~atlantoaxis~~ (z mm). The neural spine is damaged in most cervicals, except ~~for the~~ that of the 4th vertebra, ~~fourth in which is configuration can be assessed. In this vertebra, the~~ which is high ~~neural spine is high and exhibits~~ and with a peculiar shape~~, with~~ (~~the~~ its anterior margin ~~being~~ is anteriorly inclined). The ~~dorsal margin~~ apex of the neural spine 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~~ centrum extends posteriorl~~y~~ ~~than~~ 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 ~~, a large pneumatic foramen can be seen in cervicals 3 through 7~~.

Comentario [F81]: Report this length.

Comentario [F82]: Add measurements.

Comentario [F83]: Show it with dashed lines in Fig. 1.

Comentario [F84]: The plesiomorphic condition for all tetrapods.

Phylogenetic analysis results

~~Our~~ The phylogenetic analysis by parsimony produced 51 ~~minimum-length~~ most parsimonious trees ~~with~~ 358 steps long, with consistency index of 0.644 and retention index of 0.867. ~~Under the topology of our strict consensus tree (Fig. 3),~~ As ~~suspected~~ suggested by Witton (2012), *Hongshanopterus lacustris* and *Haopterus gracilis* ~~are~~ result to be closely related to the Istiodactylidae in the strict consensus tree (Fig. 3), but they fall outside ~~of it~~ them. ~~As phylogenetically~~ The Istiodactylidae have been defined by Andres et al. (2014), ~~the Istiodactylidae refers to~~ as the least inclusive clade ~~comprising~~ containing ~~*Nurhachius* and~~ *Istiodactylus latidens* Seeley 1901 and *Nurhachius ignaciobritoi* Wang X.L. et al. 2005. In the ~~present analysis~~ strict consensus tree (Fig. 3), ~~such clade~~ the Istiodactylidae ~~includes~~ contain both *Nurhachius* species ~~(with the type and the new species)~~, *Liaoxipterus brachyognathus* and ~~the genus~~ both *Istiodactylus* species. ~~The species~~ *N.~~urhachius~~ ignaciobritoi* and *N. luei* sp. nov. ~~were recovered as~~ are ~~sister-taxa~~ sister taxa; ~~corroborating~~ this supports their congeneric status. *Istiodactylus latidens* and *I.~~stiodactylus~~ sinensis* are also sister taxa

Comentario [F85]: This could also mean that the holotype of *N. luei* belongs to the same species as *N. ignaciobritoi*.

~~formed sister-groups, with~~ and *Liaoxipterus brachyognathus* ~~as a sister-group to~~ is the sister taxon of *Istiodactylus*.

~~The genus~~ *Istiodactylus* ~~was recovered based on~~ has the following ~~5~~ five synapomorphies: ~~character 11(1),~~ presence of a suborbital opening (character 11, state 1) ~~: present~~; ~~25(0),~~ ~~length of~~ short prenarial portion of the rostrum less than 20% ~~relative to~~ the skull length (character 25, state 0) ~~: reduced, under 20%~~; ~~56(1), jugal, posterior process,~~ presence of an orbital process in the jugal (character 56, state 1) ~~: present~~; and ~~96(1), teeth,~~ sharp carinae in the teeth~~: present~~ (character 96, state 1). ~~This genus~~ *Istiodactylus* shares with *Liaoxipterus brachyognathus* the following synapomorphies ~~characters~~: ~~24(1),~~ ~~jaws, lateral taper:~~ subparallel lateral taper of the jaws (character 24, state 1); ~~77(1)~~ ~~mandibular rostral end, extension of the contact surface of opposing dentaries:~~ mandibular symphysis shorter than 33% of the mandible length (character 77, state 1); ~~78(0),~~ rounded ~~mandibular~~ outline of the rostral end of the mandible, ~~shape: rounded~~ (character 78, state 0).

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

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

Hongshanopterus lacustris ~~was recovered as~~ results to be the sister taxon ~~-group~~ of the Istiodactylidae. The clade *Hongshanopterus lacustris* + Istiodactylidae ~~based on~~

Comentario [F86]: It is the palatal surface of the tip of the snout more that the palate.

presents two synapomorphies: ~~character 95(1), teeth~~, laterally compressed and triangular tooth crowns (character 95, state 1)~~: present;~~ and ~~97(0), teeth,~~ anterior teeth ~~positions, relative elongations:~~ under twice as wide (character 97, state 0).

Comentario [F87]: Mesial. The terminology used in the formulation of the characters and character states is sometimes inappropriate.

Comentario [F88]: less than twice longer than wide? It is the CROWN, anyway, not the whole tooth or the "tooth position", which is a theoretical concept.

Haopterus gracilis ~~was recovered as the next successive-sister group~~ is the sister taxon of *Hongshanopterus lacustris* +Istiodactylidae, sharing ~~based on character 86(2),~~ teeth~~,~~ ~~position and presence:~~ that are confined to the anterior half of the jaws (character 86, state 2).

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

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~~ In the last 15 years, ~~a profusion of~~ four new istiodactylids have been reported from the Jiufotang Formation of China: ~~,~~ ~~with~~ *N.~~urhachius~~ 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 XL. et al., 2005; Wang L. et al., 2006; Andres & Ji, 2006; Lü et al., 2008). ~~With a total of 6~~ six ~~proposed species of istiodactylids coming from the Jiufotang Formation, their taxonomy has been entangled with a series of proposed synonymies~~. However, the validity of some of them is debated. According to Lü et al. (2008), the holotypes of ~~considered that "~~*Longchengpterus zhaoi*~~"~~ and *N. ignaciobritoi* ~~were~~ are indistinguishable, sharing general skull shape and tooth morphology. Therefore, *Longchengpterus zhaoi* must be considered a junior synonym of *N. ignaciobritoi* for Lü et al. (2008) ~~and synonymized them~~. ~~Subsequently,~~ Witton (2012) ~~provisionally~~ considered both of them as valid and distinct taxa, ~~mentioning that these taxa had been coded differently in~~ coding them separately in his phylogenetic analysis though without discussing it further. ~~In the data matrix of Witton (2012), it can be seen that~~ They were coded differently ~~in~~ as for tooth

Comentario [F89]: I count four species above. Which are the other two? Why you do not mention them above?

count and spacing, with *Nurhachius* ~~exhibiting~~ that was considered to have more ~~numerous~~ and more spaced teeth. However, both specimens 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 and only specimens of ~~"~~*Longchengpterus zhaoi*~~"~~ and *N.~~urhachius~~ ignaciobritoi* ~~further~~ share further ~~several traits~~ features 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 sub-horizontal odontoid (pseudotooth) ~~process~~ in the mandibular symphysis. ~~In this way~~ Therefore, we follow Lü et al. (2008) in considering ~~these two taxa as synonyms~~ *Longchengpterus zhaoi* as a junior synonym of *N. ignaciobritoi*.

N.~~urhachius~~ luei sp. nov. ~~can be clearly identified as~~ is an istiodactylid based on the following combination of features: ~~external naris and antorbital~~ nasoantorbital fenestra longer than 40% of skull length, dentary symphysis ~~shorter~~ less than 33% of mandible length; and triangular, ~~laterally~~ labiolingually compressed ~~teeth~~ tooth crowns. ~~Among istiodactylids, as mentioned above,~~ It shares with *N. 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~~ observed in the holotype of *N.~~urhachius~~ 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~~ The slight dorsal deflection of the palate~~, which~~ can be seen in the holotype of *N.~~urhachius~~ ignaciobritoi* (see Fig. 5C-D), ~~despite not having been~~ although it was not mentioned in the original description (Wang X.L. 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~~ and resulted to be a synapomorphy of Anhangueria + *Cimoliopterus*. ~~In this way, in the present~~ According to our phylogenetic analysis (Fig. 3), this feature ~~represents a homoplasy between~~ was independently acquired by *Nurhachius* and Anhangueria + *Cimoliopterus*.

~~The two species of the genus *Nurhachius* differ in that~~ *N. luei* sp. nov. differs from *N. igniaciobritoi* ~~exhibits the~~ in following features: the quadrate is inclined at 150° instead of the 160° of *N. igniaciobritoi*; the medial process of the pterygoid ~~expanded,~~ is broad and plate-like, whereas it is reduced in *N. igniaciobritoi* add references to support this

Comentario [F90]: In this figure, it is impossible to count the teeth positions. Please, number them in the figure.

Comentario [F91]: How is the quadrate inclination in other pterodactyloids? Which is the variability of the quadrate inclination within a pterodactyloid species that is represented by an adequate sample (e.g., *Pteranodon* and *Pterodactylus*)?

Comentario [F92]: Where do you see it in Fig. 4? Please, draw it and indicate it in the figure.

Comentario [F93]: I do not see this feature in Fig. 4. Please, indicate the tooth positions in the figure.

Comentario [F94]: This cannot be seen in figure 4. You must add a further figure showing details in the dentition of all these specimens. I mean a figure with the photos of the single teeth with their features. As it is reported here, the constriction between crown and root is unique of *N. igniaciobritoi*. Is it?

Comentario [F95]: This is not a combination of features, it is a past-and-copy from the description of the node *N. luei* + *N. igniaciobritoi*

Comentario [F96]: This should described in a different way. See below.

Comentario [F97]: of the ventral surface of the tip of the snout? The whole palate is not deflected.

statement; the dentary dorsal median sulcus of the mandibular symphysis extends until up to the first pair of dentary teeth, whereas it reaches the sixth pair of teeth in *N. igniaciobritoi* add references to support this statement or add a clear figure of the detail; the odontoid process (pseudotooth) lacksing a lateral foramen, whereas the foramen is present in the referred specimen of *N. igniaciobritoi* (see Martill, 2014, fig. 7C-D); the odontoid process with has a smooth occlusal surface, whereas the surface is sharp add references to support this statement in *N. igniaciobritoi*; the odontoid process is vertical dorsally directed, whereas it is slightly anterodorsally directed in *N. igniaciobritoi* (but see Martill, 2014, p. 57, right column, lines 21-23); the ceratobranchial I of the hyoid apparatus accounts for 60% of the mandibular length, whereas it accounts for 60% of the mandibular length in *N. igniaciobritoi*; and dentary the mandibular teeth extending distally beyond the dentary symphysis, whereas they are confined to the symphysis in *N. igniaciobritoi* (Fig. 4). You do not include and discuss here the tooth count, which is considered as a diagnostic feature of the new species in the diagnosis.

~~*N. urhachius igniaciobritoi*, 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 *N. urhachius igniaciobritoi* 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 distribution might be suggestive of an anagenetic link between the two species them, similarly to what was proposed by Bennett (1994) for the case of *Pteranodon longiceps* (from the upper Niobrara Formation) and *Pteranodon sternbergi* (from the lower Niobrara Formation) according to Bennett (1994),; but see discussion on the taxonomy of the *Pteranodon*-complex (Kellner, 2010; 2017; Martin-Silverstone et al., 2017; Acorn et al., 2017 for an alternative interpretation).

Concerning other istiodactylids, Wang et al. (2008) were unable to differentiate *Liaoxipterus brachyognathus* from "*Longchengpterus zhaoi*", both from the Jiufotang Formation, and suggested that *Longchengpterus zhaoi* they could thus represent is a younger synonyms of *Liaoxipterus brachyognathus* (the former having priority). However, as observed by Lü et al. (2008), the anterior terminus rostral end of the dentary mandibular symphysis is rounded in *Liaoxipterus brachyognathus* (as it is in

Comentario [F98]: Do you mean that it reaches the tip of the symphysis? You must indicate this sulcus, its beginning and its end in Fig. 1. It would be better to add a figure showing this sulcus in the two species for comparison.

Comentario [F99]: Martill (2014, fig. 7C-D) erroneously reports it as "foramina" (Latin, plural= piercings, natural holes), while it is just a single foramen (Latin, singular = piercing, natural hole).

Comentario [F100]: Blunt?

Comentario [F101]: This means that the *N. luei* and *N. igniaciobritoi* share the same feature. Why do you have reported this here?

Comentario [F102]: You still have to prove it.

Comentario [F103]: Do you have a source for this information?

Comentario [F104]: WHICH ONE?

Comentario [F105]: redundant

Comentario [F106]: In dorsal or lateral view?

Istiodactylus latidens), ~~whilst~~ whereas it is triangular in ~~"~~*Longchengpterus zhaoi*~~"~~. Furthermore, as coded by Andres et al. (2014), jaws show an attenuated taper in ~~"~~*Longchengpterus zhaoi*~~"~~ ~~exhibits~~ an ~~attenuated taper of the jaws~~, while ~~in~~ ~~*Liaoxipterus brachyognathus*~~ the lateral margins of the jaw are sub-parallel in *Liaoxipterus brachyognathus* (Fig. 6A)~~,~~ as in *Istiodactylus latidens*. ~~We further note that~~ Furthermore, the ~~dentary~~ mandibular symphysis of *Liaoxipterus brachyognathus* is relatively ~~shorter~~ stouter than that of ~~"~~*Longchengpterus zhaoi*~~"~~: their length/width ratios are~~, respectively,~~ 0.43 and 0.27, respectively. It ~~should be~~ worthy of being noticed that~~, in the seventh figure by Martill (2014)~~ the ~~dentary~~ mandibular symphysis of ~~"~~*Longchengpterus zhaoi*~~"~~ is incorrectly ~~illustrated~~ drawn in Martill (2014, fig. 7B), ~~depicted~~ as resulting to be much shorter than it is, with the ~~dentary~~ median dorsal sulcus of the mandibular symphysis 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. 4A. ~~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 a younger synonym~~ous~~ ~~with~~ of *N.~~urhachius~~ ignaciobritoi* ~~following Lü *et al.* (2008) as expressed above~~.

Lü et al. (2008) and Witton (2012) noticed that comparison~~s~~ between *Liaoxipterus brachyognathus* and *Istiodactylus sinensis* ~~were~~ is very limited ~~since~~ because the former is represented by a ~~partial~~ mandible exposed in occlusal view, while the latter is a ~~partially complete~~ partial 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 , 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.

~~As expressed above in the Results section,~~ According to our phylogenetic analysis, *Istiodactylus* ~~was recovered as~~ is monophyletic, ~~group~~ comprising *I. latidens* and *I. sinensis*. ~~forming a sister-group to~~ *Liaoxipterus brachyognathus* is the sister taxon of *Istiodactylus*, ~~followed by~~ and *Nurhachius* is the sister taxon of *Liaoxipterus brachyognathus* + *Istiodactylus*, ~~corroborating previous~~ in agreement with the results of the phylogenetic hypothesis published by Longrich et al. (2018). In our analysis, ~~inclusion of the newly reported species~~ *N.~~urhachius~~ luei* result~~sed in its recovery as~~ to be the sister taxon ~~-group~~ of *N.~~urhachius~~ ignaciobritoi*, supporting their congeneric status. ~~In this way,~~ The ~~internal~~ relationships ~~found herein for~~ within the Istiodactylidae

Comentario [F107]: Upper? Lower? Both of them? In which view?

Comentario [F108]: Do you mean "mandibular rami in occlusal view" here? Only the mandible in occlusal view is figured in Fig. 6A.

Comentario [F109]: To show that it is comparatively shorter you have to use the ratio total mandibular length/symphysis length. Here you show only that it is stouter.

Comentario [F110]: I do not understand. Do you mean that the sulcus is filled with rock and appears as the gap between the mandibular rami?

Comentario [F111]: Actually, Fig. 4A (your Fig. 4B) is not clear enough to support your statement and Fig. 4B (your Fig. 4C is just your interpretation).

Comentario [F112]: In which teeth? Mandibular? Maxillary? Premaxillary? All teeth?

obtained in our analysis are in accordance are similar to with those found by Andres et al. (2014), with the addition of the new species but *Longchengpterus zhaoi* is not the sister taxon of *N. ignaciobritoi* in the cladogram of figure S2 of Andres et al. (2014).

Haopterus gracilis, from the Yixian Formation, was first described by Wang X.L. & Lü (2001) and referred interpreted as a member of to the Pterodactylidae. However, subsequently, it resulted to be close to *Istiodactylus latidens* in the 50% majority-rule tree by Lü et al. (2008) and formed a politomy with *Nurhachius* and *Istiodactylus* in the strict consensus tree by Lü et al. (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. In the strict consensus tree by Witton (2012), recovered a clade joining the Istiodactylidae include *Nurhachius igniaciobritoi*; *Longchengpterus zhaoi*; *Istiodactylus latidens*; *Istiodactylus sinensis*; and *Liaoxipterus brachyognathus*. *Istiodactylus*, *Liaoxipterus*, *Longchengpterus* and *Nurhachius* to the exclusion of *Haopterus gracilis* and *Hongshanopterus lacustris*, and restricted the family to the former four taxa. *Haopterus* and *Hongshanopterus* were recovered as indeterminate pteranodontoids, in form a polytomy with *Pteranodon longiceps*, + *Coloborhynchus spielbergi* + and the Istiodactylidae (Witton, 2012).

Subsequently, In the phylogenetic analysis of Andres et al. (2014; fig. S2), *Haopterus gracilis* was recovered as results to be a basal lophocratian eupterodactyloidean 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 have published a phylogenetic analysis hypothesis in which *Hongshanopterus lacustris* appeared as is the sister-group of the Istiodactylidae (although it is erroneously reported within this clade as the basal member in fig. 5A), while and *Haopterus gracilis* was recovered as is 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 Holgado et al. (2019). 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.*

Comentario [F113]: Redundant. You have already said it above,

Comentario [F114]: Redundant

Comentario [F115]: WHICH ONE?

Comentario [F116]: Redundant. You have already said it above.

Comentario [F117]: This is not the case. *Haopterus* is the taxon that follows the Istiodactylidae along the tree at the base of Lanceodontia.

~~(2014)~~. ~~We present a topology with further resolution that corroborates the interpretations of~~ In our analysis, *Haopterus gracilis* and *Hongshanopterus lacustris* ~~as~~ are closely related to the Istiodactylidae, as ~~defended~~ found by Lü et al. (2008) and Wang et al. (2008), respectively. ~~Under our new topology,~~ *Hongshanopterus lacustris* results to be ~~is again recovered as~~ the sister taxon ~~-group~~ of the Istiodactylidae~~,~~ as in the analysis by Holgado et al. (2019). *Hongshanopterus lacustris* shares with the istiodactylids the presence of ~~triangular~~, ~~laterally~~ labiolingually compressed teeth with triangular crowns ~~in the rostrum~~. *Haopterus gracilis* results to be ~~is recovered as~~ the sister taxon ~~-group~~ of ~~the~~ *Hongshanopterus lacustris* + Istiodactylidae ~~+ *Hongshanopterus*~~, a relationship that is supported by the possession of a dentition restricted to the anterior half of the jaws. These taxa ~~further~~ share also the presence of a lingual cingulum in the tooth crown, ~~which~~ a feature that ~~is~~ occurs also ~~shared with~~ in *Ikrandraco avatar* and *Lonchodraco giganteus*. *Ikrandraco avatar* ~~also~~ shares with the istiodactylids also a narrow lacrimal process of the jugal and ~~of~~ a quadrate inclined at 150° or over (the inclination of the quadrate is unknown in *Haopterus gracilis* and *Hongshanopterus lacustris*). ~~It must be further noted that at least~~ *Haopterus gracilis* and *Ikrandraco avatar* exhibit~~, at least on the posterior dentition,~~ a certain degree of ~~lateral~~ labiolingual compression of the teeth, at least in the distal part of the dentition (Lü & Wang, 2001; Wang X.L. et al., 2015), though not to the same degree seen in the istiodactylids ~~or~~ and *Hongshanopterus*. ~~The same seems to be true for~~ The last two mandibular alveoli preserved in the holotype of *Lonchodraco giganteus* (the sister taxon of *Ikrandraco avatar* in our analysis) also seem to be labiolingually narrow (see Rodrigues & Kellner, 2013), but the posterior ~~region~~ part of the jaws ~~are~~ is not preserved in that specimen, ~~and~~ thus ~~further~~ complete jaws ~~material would be needed~~ are necessary to confirm the presence of labiolingually flattened crowns in *Lonchodraco giganteus* ~~this feature for this taxon~~. ~~We highlight that~~ A close relationship ~~between~~ among *Ikrandraco avatar*, *Lonchodraco giganteus* and the istiodactylids is ~~proposed~~ found 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 avatar* ~~has been recovered in~~ forms a polytomy ~~involving~~ with the Istiodactylidae, *Cimoliopterus* and the Anhangueria ~~(~~ in the phylogenetic analysis by Wang X.L. et al. (2015) and *Lonchodraco giganteus* is outside ~~of~~ the Lanceodontia in the phylogenetic analysis by ~~(~~Longrich et al.~~,~~ (2018).

Archaeoistiodactylus linglongtaensis is ~~a taxon~~ based on ~~a single, holotypic specimen~~

Comentario [F118]: Redundant. You have already said this above.

Comentario [F119]: WHICH ONE?

Comentario [F120]: WHICH TAXA? Write it EXPLICITLY

Comentario [F121]: Not in the reference list. Is it Wang X.L. & Lü (2001)?

the sole holotype (JPM04-0008), ~~comprising~~ including fragments of skull ~~bones~~ and one displaced maxillary tooth, a partial lower jaw in ~~dorsal~~ occlusal view with two teeth in place, an almost complete forelimb ~~wing lacking scapulocoracoid~~, a femur and a tibia. It ~~comes~~ is from the Middle Jurassic (Bathonian-Oxfordian) Tiaojishan Formation ~~(Bathonian-Oxfordian, Middle Jurassic)~~.~~, having been described by Lü & Fucha (2010)~~. *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). ~~These authors interpreted it as the most primitive stem-istiodactylid.~~ Lü & Fucha (2010) ~~noted~~ observed that ~~the specimen~~ JPM04-0008 and the istiodactylids shared ~~with~~ ~~istiodactylids~~ teeth with triangular crowns~~, as well as~~ and an odontoid ~~process~~ (pseudotooth) on the ~~lower jaw~~ mandibular symphysis. ~~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~~ it had been explicitly described as a bony process by Lü & Fucha (2010, p. 116). ~~They further noted~~ Lü & Fucha (2010) also observed that the single ~~preserved~~ maxillary tooth is recurved~~,~~ as in *Hongshanopterus lacustris* ~~(see Lü & Fucha, 2010)~~, and ~~also~~ reported ~~on~~ the presence of a warped deltopectoral crest in the humerus, which is a diagnostic feature of the Pteranodontoidea (Kellner, 2003). ~~Still,~~ They noted that ~~the new taxon~~ *A. linglongtaensis* differs~~-ed~~ from the istiodactylids and all other pterodactyloids in ~~exhibiting a~~ the relatively short fourth metacarpal and in the presence of ~~subequal~~ tibia~~,~~ and second and third phalanges of the wing digit with subequal lengths. If ~~indeed a stem-istiodactylid, this taxon~~ actually a pterodactyloid, it would represent one of the oldest occurrences of the Pterodactyloidea, ~~possibly~~ being coeval or even older than the Callovian-Oxfordian basalmost pterodactyloid *Kryptodrakon progenitor* (see Andres et al., 2014).

~~Subsequently, this~~ Its identification as a pterodactyloid was disputed by Martill & Etches (2013), who affirmed~~, though without presenting any justifications,~~ that JPM04-0008 ~~the specimen was~~ is probably a badly preserved specimen of *Darwinopterus*, though ~~without presenting~~ they did not present any evidence ~~justifications,~~ to support this statement. ~~Later,~~ According to Sullivan et al. (2014), ~~considered that~~ 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 ~~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). These features This, allied united to the presence of a confluent nasoantorbital fenestra in JPM04-0008, led Sullivan et al. (2014) to interpret *A.rchaeoistiodactylus linglongtaensis* 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).

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. The results (Fig. 3) of our phylogenetic analysis corroborate confirm the interpretation of by 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* JPM04-0008 is crushed and the original orientation of the deltopectoral crest cannot be assessed. but it can be seen that it Differently from pterodactyloids, the deltopectoral crest of JPM04-0008 is confined to the proximal region of the humerus, differently from pterodactyloids (e.g. Wang et al., 2009). *A.rchaeoistiodactylus linglongtaensis* also lacks pneumatic foramina on the centraum 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* *Archaeoistiodactylus* exhibits low neural spines, similarly to like wukongopterids (see Wang X.L. et al. 2009; 2010; Lü et al., 2009; 2011; Cheng et al., 2017) and differently from unlike istiodactylids (see Wang L. et al., 2006; Lü et al., 2008). For these reasons, *Archaeoistiodactylus* can be placed outside of the Pterodactyloidea.

The dentition of *A. linglongtaensis* *Archaeoistiodactylus* is indeed reminiscent of that of the Istiodactylidae due to the triangular aspect of the crowns in lateral labiolingual view (Lü & Fucha, 2010). but However, this feature is also present in the

Comentario [F122]: Not in the references

Comentario [F123]: Not in the references.

Comentario [F124]: Only triangular or also labiolingually flattened? Most of the pterosaur teeth are triangular in labiolingual view.

wukongopterids Wukongopterus lii, Darwinopterus robustodens, Darwinopterus linglongtaensis and Kunpengopterus sinensis, though not in Darwinopterus modularis (see Wang X.L. et al. 2009; 2010; Lü et al., 2009; 2011; Cheng et al., 2017). Furthermore, in *A. linglongtaensis* ~~*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~~ presence or absence of an odontoid ~~process~~ in the lower jaw cannot be confidently assessed in *Wukongopterus* ~~or~~ and *Darwinopterus*, but can be seen in a specimen referred to *Kunpengopterus sinensis* (see Cheng et al., 2017), in convergence with the istiodactylids. Finally, ~~we further notice that~~ ~~*Archaeoistiodactylus*~~ *A. linglongtaensis* shares with *Darwinopterus* and *Kunpengopterus*, ~~(~~but not with *Wukongopterus*~~)~~, the subequal in length second and third phalanges of the wing digit. ~~In this way~~ Thus, ~~we regard~~ *A.* ~~*rchaeoistiodactylus*~~ *linglongtaensis* ~~to represent~~ may ~~a wukongopterid~~ be closely related to *Darwinopterus* or *Kunpengopterus*. In our analysis, *A. linglongtaensis* falls in a politomy with *Darwinopterus linglongtaensis, D. robustodens* and *Kunpengopterus sinensis* (Fig. 3). 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 deny this affinity ~~not~~, ~~these~~ ~~interpretations~~.

Conclusions

The new specimen here ~~we~~ described ~~here~~ represents ~~a~~ the second species for the genus *Nurhachius*, previously restricted to its type-species *N.*~~*urhachius*~~ *ignaciobritoi* ~~(=*Longchenpterus zhaoi*)~~. ~~Of particular note is the presence of~~ A slight dorsal deflection of the palate~~,~~ ~~as~~ revealed to be a synapomorphy of *N. ignaciobritoi* and *N. luei* ~~the genus,~~ That feature was previously thought to be restricted to the Anhangueria and *Cimoliopterus*. Unlike other pterodactyloids, the holotype of *N.*~~*urhachius*~~ *luei* sp. nov. ~~also~~ shows ~~a novel feature for pterosaurs, which is the growing of reposition tooth in an anterolateral position relative to the older tooth~~ an anterolabial tooth replacement. The new species ~~shows that~~ increases the morphological diversity ~~within~~ of the istiodactylids ~~is higher than previously thought~~. ~~Furthermore, we corroborate here~~ The position of *Hongshanopterus lacustris* and *Haopterus gracilis* as ~~stem-istiodactylids~~ close taxa to the Istiodactylids is supported by the performed phylogenetic analysis.~~,~~ ~~further proposing that~~ *Ikrandraco avatar* and *Lonchodraco giganteus* ~~are probably~~ are sister taxa and are ~~more related~~ closer to them than to other lanceodontians. ~~We also~~

Comentario [F125]: Thus, you must add a figure showing this feature in all the cited taxa. Crown shape is considered a fundamental feature of the istiodactylids, but it appears not to be unique.

Comentario [F126]: Not in the references.

Comentario [F127]: This is senseless. Above you say that this taxon has triangular teeth, thus you know the shape of the crowns. In facts, three teeth are preserved.

Comentario [F128]: palatal side of the tip of the snout

Comentario [F129]: It is not clear to me how it does it. Please, explain better this concept.

Comentario [F130]: WHO?

~~corroborate the recent~~ The phylogenetic analysis support the reinterpretation of *Archaeoistiodactylus linglongtaensis* as a non-pterodactyloid monofenestratan, ~~and more specifically as~~ probably a wukongopterid.

Institutional abbreviations

XXX zzzzzzz zzzzzz, xxxx, yyyyyyyy

YYY zzzzzzz zzzzzz, xxxx, yyyyyyyy

Acknowledgements

We thank Shu'an Ji (IG-CAGS, Institute of Geology, Chinese Academy of Geological Sciences) and Xuefang Wei (IG-CAGS) for assisting us in the whole process. XZ was funded by the National Natural Science Foundation of China (grant no. 41672019, 41688103). RVP thanks Kamila Bandeira, Lucy Souza and Natan Brilhante (Museu Nacional/UFRJ) for technical help with image softwares. Thanks to Cunyu Liu (Beipiao Pterosaur Museum of China), Dongyu Hu (Shenyang Normal University), Xiaolin Wang (IVPP, Institute of Vertebrate Paleontology and Paleoanthropology), and Shunxing Jiang (IVPP) for access to specimens under their care.

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Figures

Comentario [F145]: These captions do not follow the rules given by PeerJ. Read the instructions for the authors.

Figure 1. *Nurhachius luei* sp. nov., BPMC-0204, holotype, photograph and line drawing. ~~of the holotype of *Nurhachius luei* sp. nov. Photo by Xuanyu Zhou. Drawing by Maria Eduarda Leal.~~ The scale bar in the 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. Photo by Xuanyu Zhou. Drawing by Maria Eduarda Leal.

Figure 2. ~~Map showing~~ **Location of** ~~origin of~~ the ~~material herein described~~ **the site where BPMC-0204 was found.**

Figure 3. *Nurhachius luei* sp. nov., BPMC-0204, holotype, phylogenetic relationships. Strict consensus tree of 51 most parsimonious trees. ~~from our phylogenetic analysis~~ Tree length is 358, consistency index 0.644 and retention index 0.867. The red rectangle indicates the Istiodactylidae and its two closest taxa ~~stem-group~~.

Figure 4. ***Nurhachius ignaciobritoi*** **specimens, photographs and line drawings**. A) *Nurhachius luei* sp. nov. holotype, skull and mandible in right lateral view. (A) *Nurhachius ignaciobritoi* LPM 00023, referred specimen (former holotype of "*Longchengpterus zhaoi*"), skull and mandible in right lateral view. (B) *Nurhachius ignaciobritoi* IVPP V-13288, holotype, skull (mirrored) and mandible in right lateral view. Scale bars equal 50 mm. Photographs by Xuanyu Zhou. Drawings by Rodrigo V. Pêgas.

Figure 5. Close view of the rostral tip of *Nurhachius* species in right lateral view. of (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). Scale bars equal 20 mm. Photos by Xuanyu Zhou. Drawings by Rodrigo V. Pêgas.

Comentario [F146]: See comment in the text.

Figure 6. Other istiodactylids and close taxa. (A) *Liaoxipterus brachyognathus*, CAR-0018, holotype, lower jaw in dorsal view. Anterior is to the right. (B) *Haopterus gracilis*, IVPP V11726, holotype, skull of the holotype in right lateral view. (C) *Hongshanopterus lacustris*, IVPP V14582, holotype, skull in ventral view. Anterior is to the left. All scale bars equal 50 mm. Photos by Xuanyu Zhou. THE FIGURE LACKS THE LETTERS!!!!!

Página 2: [1] Comentario [F7]	Fabio	25/05/2019 15:51:00

You use the term "stem-group istiodactylids" throughout the text. This term is incorrect for at least two reasons:
FIRST: The terms "stem" and "crown" should be used only for supraspecific taxa that have living species. I know that these terms are often incorrectly used otherwise, but see: Jefferies, R.P.S. (1979). The origin of chordates – a methodological essay. In M.R. House (ed.). The origin of major invertebrate groups. London ; New York: Academic Press for The Systematics Association. pp. 443–447.
Pterosaurs are totally extinct, thus "stem" and "crown" cannot be used for them.
SECOND: Even if the use of the term "stem" were correct, *Haopterus gracilis*, *Hongshanopterus lacustris* and *Archaeoistiodactylus linglongtaensis* would not be "stem-group istiodactylids" but the stem-taxa of the clade *Archaeoistiodactylus linglongtaensis* + *Haopterus gracilis* + *Hongshanopterus lacustris* + Istiodactlylidae. Anyway, that would be a purported clade, because *Archaeoistiodactylus linglongtaensis* was shown to be even outside the Pterodactyloidea.

It is better to mention here *Haopterus gracilis*, *Hongshanopterus lacustris* and *Archaeoistiodactylus linglongtaensis* as "taxa reported as close to the Istiodactylidae".

As it is reported below in the text, Istiodactylidae are defined by Andres et al. (2014) as "the least inclusive clade containing *Istiodactylus latidens* Seeley and *Nurhachius ignaciobritoi*. It should be specified at the beginning of the paper.

Página 11: [2] Comentario [F48]	Fabio	23/05/2019 13:53:00

The postorbital is not slender. It is the frontal ramus of the postorbital to be slender in Fig. 1.

Página 11: [3] Comentario [F50]	Fabio	23/05/2019 14:36:00

This is really an obscure comparison. Explain better. Describe the bone.

Página 11: [4] Comentario [F51]	Fabio	23/05/2019 14:42:00

The postorbital is fused with the neighbor bones without sutures in the only specimen of this taxon. Therefore, you cannot see its shape.

Página 11: [5] Comentario [F54]	Fabio	25/05/2019 16:28:00

What does this mean? That *Hongshanopterus* has a single long vomer? or that its vomer separates the choanae?

Página 11: [6] Comentario [F57]	Fabio	23/05/2019 15:07:00

You should first describe what is preserved or exposed of the pterygoid.

Página 11: [7] Comentario [F59]	Fabio	23/05/2019 15:04:00

What does this mean? Less plate-like? Less developed and expanded (= large)?