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Taxonomy of the Lonchodectidae (Pterosauria, Pterodactyloidea)

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ABSTRACT

The pterodactyloid family Lonchodectidae includes three genera, *Lonchodectes* Hooley, 1914, *Lonchodraco* Rodrigues et Kellner, 2013, and *Ikrandraco* Wang et al., 2014, and four species, *Lonchodectes compressirostris* (Owen, 1851), *Lonchodraco giganteus* (Bowerbank, 1846), *Ikrandraco avatar* Wang et al., 2014, and *Ikrandraco machaerorhynchus* (Seeley, 1870) comb. nov. [=*Ornithocheirus microdon* Seeley, 1870 syn. nov.]. The holotype of *Lonchodectes compressirostris* (NHMUK PV 39410) consists of two fragments of the anterior rostrum, not the mandibular and rostrum fragments as was supposed previously. The difference between *Lonchodectes* and *Ikrandraco* is not clear and the taxa could be synonyms. The diagnostic characters for the Lonchodectidae are the presence of the palatal ridge, elevated alveolar margin of the upper and lower jaws, small teeth that are not varying in size, and a prominent mandibular crest (unknown for *Lonchodectes*). The family includes taxa with long and low rostrum and prominent mandibular crest (*Ikrandraco* and, possibly, *Lonchodectes*), or with both premaxillary and mandibular crests (*Lonchodraco*). Various phylogenetic analyses place the Lonchodectidae within the Ornithocheiroidea, frequently as a sister taxon to the Anhangueria. The family is known from the mid-Cretaceous (Albian-Turonian) of England (*Lonchodectes compressirostris*, *Lonchodraco giganteus*, *Ikrandraco machaerorhynchus*), the Lower Cretaceous (Aptian) of China (*Ikrandraco avatar*), and the Late Cretaceous (Cenomanian) of European Russia (*Lonchodraco* (?) sp.). The putative records of the Lonchodectidae from the Lower Cretaceous of England (*Serradraco sagittirostris* (Owen, 1874), BEXHM 2015.18, and *Palaeornis cliftii* Mantell, 1844), Spain (*Prejanopterus curvirostris* Fuentes Vidarte et Meijide Calvo, 2010), and Brazil (*Unwindia trigonus* Martill, 2011) are reviewed. None of them can be attributed to that group.

Key words: Cretaceous, Lonchodectidae, Pterosauria, taxonomy

Таксономия Lonchodectidae (Pterosauria, Pterodactyloidea)

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РЕЗЮМЕ

Семейство птеродактилоидов Lonchodectidae включает три рода, *Lonchodectes* Hooley, 1914, *Lonchodraco* Rodrigues et Kellner, 2013 и *Ikrandraco* Wang et al., 2014, и четыре вида, *Lonchodectes compressirostris* (Owen, 1851), *Lonchodraco giganteus* (Bowerbank, 1846), *Ikrandraco avatar* Wang et al., 2014 и *Ikrandraco machaerorhynchus* (Seeley, 1870) comb. nov. [=*Ornithocheirus microdon* Seeley, 1870 syn. nov.]. Голотип *Lonchodectes compressirostris* (NHMUK PV 39410) состоит из двух фрагментов передней части ростра, а не из фрагментов нижней челюсти и ростра, как предполагалось ранее. Различия между *Lonchodectes* и *Ikrandraco* не ясны и оба таксона могут оказаться синонимами. Диагностичными признаками семейства Lonchodectidae являются присутствие нёбного гребня, приподнятые альвеолярные края верхних и нижних челюстей, маленькие зубы, которые не варьируют по размерам, и выступающий мандибулярный гребень (неизвестен для *Lonchodectes*). Семейство включает таксоны с длинным и низким ростром

и выступающим мандибулярным гребнем (*Ikrandraco* и, возможно, *Lonchodectes*), или с обоими премаксиллярным и мандибулярным гребнями (*Lonchodraco*). По данным разных филогенетических исследований, Lonchodectidae помещаются среди Ornithocheiroidea, часто как сестринский таксон к Anhangueria. Семейство известно из середины мела (альб-турон) Англии (*Lonchodectes compressirostris*, *Lonchodraco giganteus*, *Ikrandraco machaerorhynchus*), раннего мела (апт) Китая (*Ikrandraco avatar*) и позднего мела Европейской России (*Lonchodraco* (?) sp.). Рассмотрены также другие предполагаемые находки Lonchodectidae из раннего мела Англии (*Serradraco sagittirostris* (Owen, 1874), BEXHM 2015.18 и *Palaeornis cliftii* Mantell, 1844), Испании (*Prejanopterus curvirostris* Fuentes Vidarte et Meijide Calvo, 2010) и Бразилии (*Unwindia trigonus* Martill, 2011). Ни одна из этих находок не может быть отнесена к данному семейству.

Ключевые слова: меловой период, Lonchodectidae, Pterosauria, таксономия

INTRODUCTION

The Lonchodectidae are a small family of relatively rare mid-Cretaceous pterosaurs, of which the content, phylogenetic relationships, and even validity are vigorously debated. The first described lonchodectid was *Pterodactylus giganteus* from the Cenomanian-Turonian Chalk Formation of England based on several specimens, including an anterior portion of the skull with mandibles (NHMUK PV 39412) (Bowerbank 1846). Later Bowerbank (1848) described the microscopic structure of some of these bones. Owen in Dixon (1850) proposed a new name, *Pterodactylus conirostris*, for NHMUK PV 39412, which is a rare case of objective synonyms.

Hooley (1914) revised the genus *Ornithocheirus* and referred nine species to his "Group no. 2," for which he proposed the name *Lonchodectes*. He did not indicate the type species for the latter genus and listed the species in alphabetic order. Kuhn (1967) considered *Lonchodectes* a junior synonym of *Ornithocheirus* and designated *Pterodactylus compressirostris* as a type species of both genera, creating taxonomic confusion for further research (Wellnhofer 1978; Wild 1990). In fact, the type species of *Ornithocheirus* is *Pterodactylus simus* Owen, 1861 (Unwin 2001).

Unwin (2001) in his review of the pterosaur fauna of Cambridge Greensand re-established the genus *Lonchodectes* with six valid species (*L. compressirostris*, *L. machaerorhynchus*, *L. microdon*, *L. giganteus*, *L. sagittirostris*, and *L. platystomus*). In this paper, he also established the family Lonchodectidae Unwin, 2001. In a subsequent article, Unwin (2003) questioned the reference of *L. sagittirostris* to *Lonchodectes*. In addition, Unwin (2001, 2003) referred to *Lonchodectes* sp. some postcranial bones from Cambridge Greensand, including elongated cervical vertebra NHMUK R2287c (Unwin 2003: fig. 15f), humerus CAMSM B54.081 (Unwin 2003: fig. 17j), and femur CAMSM B54.262. The humerus and cervical vertebrae were figured and also referred to as *Lonchodectes* or Lonchodectidae in Witton et al. (2009: fig. 5C) and Witton (2013: fig. 21.4).

According to Averianov (2012), the above mentioned postcranial bones belong to the azhdarchoid *Ornithostoma sedgwicki* Seeley, 1891, also known from the edentulous jaw fragments and posterior part of the skull from the Cambridge Greensand.

Rodrigues and Kellner (2013) considered *Lonchodectes compressirostris* a *nomen dubium* mostly because of their misinterpretation of the anterior rostrum fragment of the holotype as a mandibular symphysis. These authors placed *Pterodactylus giganteus* in a new genus *Lonchodraco*, which also included *Ornithocheirus machaerorhynchus* and, questionably, *O. microdon*. For *Lonchodraco*, they proposed the monotypic family Lonchodraconidae Rodrigues et Kellner, 2013.

Rigal et al. (2017) reviewed *Lonchodectes sagittirostris* and referred it to a new genus *Serradraco* Rigal et al., 2017. These authors also described a fragmentary lonchodectid skeleton, which was referred to the genus *Lonchodraco*.

In this paper, I review the taxonomy of the Lonchodectidae, their diagnostic characters, and putative records of lonchodectids.

Institutional abbreviations. BEXHM, Bexhill Museum, Bexhill, United Kingdom; CAMSM, Sedgwick Museum, Cambridge, United Kingdom; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NHMUK, Natural History Museum of United Kingdom, London, United Kingdom; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany.

DIAGNOSTIC CHARACTERS OF LONCHODECTIDAE

Nasoantorbital fenestra. Anterior border of nasoantorbital fenestra located above tooth pairs 13–14 is an apomorphy (autapomorphy?) of *Lonchodraco* according to Rigal et al. (2017). A nasoantorbital fenestra was indicated for the holotype of *L. giganteus* by Owen (1851a: pl. 31, fig. 2). However, Rodrigues and Kellner (2013) considered this opening as a breakage rather than an antorbital fenestra because it is not present on both sides. That interpretation is followed here.

Snout shape. The rounded anterior portion of premaxillae and dentaries is a diagnostic character of *Lonchodraco giganteus* according to Rodrigues and Kellner (2013). In *Lonchodraco* sp. from the Cenomanian Melovatka Formation of Volgograd Region, Russia, the snout is pointed (Averianov and Kurochkin 2010: fig. 1). The snout shape is unknown in other lonchodectid taxa. This character could be an autapomorphy of *L. giganteus*.

Dorsoventrally flattened jaw tips. This is a diagnostic character of the Lonchodectidae, according to Unwin (2001). This character is present in *L. giganteus* (Rodrigues and Kellner 2013). In *L. compressirostris*, the tip of the rostrum likely was transversely compressed rather than dorsoventrally flattened. In *Ikrandraco avatar*, only the tip of the rostrum is dorsoventrally flattened. In *Ikrandraco machaerorhynchus* the tip of rostrum is unknown, but the tip of the mandible is flattened dorsoventrally. The taxonomic value of this character is not clear.

Alveolar margins divergence. Divergent alveolar margins of the anterior end of the upper and lower jaws is a diagnostic character of *Lonchodraco giganteus* (Rodrigues and Kellner 2013). According to these authors, *L. machaerorhynchus* differs from *L. giganteus* by "straight" alveolar margins in dorsal view (Rodrigues and Kellner 2013: 28). "Parallel margins" is a more appropriate term in this case as diverging margins are also straight. This term was used in the original description of *Ornithocheirus machaerorhynchus* by Seeley (1870: 114). The state of this character is unknown for *Ikrandraco avatar*.

Palatal ridge. Longitudinal ridge on the palate was used for diagnosing the genus *Lonchodectes* (Hooley 1914). Unwin (2003: 179) formulated this character in the diagnosis of *Lonchodectes* as "a prominent, sharply ridged, median keel on the occlusal surface of the rostrum." A deep palatal ridge is a diagnostic character of *Lonchodraco*, according to Rodrigues and Kellner (2013). The palatal ridge was indicated for *L. giganteus* (Rodrigues and Kellner 2013: fig. 4D) although it is obscured by matrix. A deep palatal ridge was also cited as an autapomorphy of *Lonchodraco* (?) *microdon* by Rodrigues and Kellner (2013). This species is considered here to be a synonym of *L. machaerorhynchus*. In *Lonchodectes compressirostris*, the palatal ridge is confined to the posterior part of the palate apparently because of the great transverse narrowness of the anterior part of the snout. The palatal ridge is here considered to be a diagnostic character for the Lonchodectidae, while a short posteriorly located palatal ridge is diagnostic for *Lonchodectes compressirostris*.

Palatal surface shape. Palate between the elevation of the alveolar margins and the palatal ridge concave is a diagnostic character of *Lonchodraco* (?) *microdon* according to Rodrigues and Kellner (2013). However, the palatal surface is obscured by matrix in *L. giganteus*. In *Lonchodectes compressirostris*, the palatal surface between the palatal ridge and alveolar margins has a similar concave shape (Owen 1851a: pl. 28, fig. 9). This character does not help to distinguish taxa within the Lonchodectidae.

Premaxillae dorsal margin. Rounded dorsal margin of premaxillae is a diagnostic character of *Lonchodraco* (?) *microdon*, according to Rodrigues and Kellner (2013). This character is redundant because it is correlative with the absence of a premaxillary crest in this taxon.

Premaxillary crest. The premaxillary crest is a diagnostic character of *Lonchodraco giganteus*, according to Rodrigues and Kellner (2013). The absence of a premaxillary crest is a diagnostic character of *Lonchodraco* (?) *microdon*, according to Rodrigues and Kellner (2013). According to Rigal et al. (2017), there is no evidence of a premaxillary crest in *L. giganteus*. In the absence of a definition what constitutes a premaxillary crest it is a matter of opinion to describe the condition seen in *L. giganteus* as a premaxillary crest or tall premaxilla. In contrast with the mandibular crest, the premaxillary crest has no evident transverse constriction in relation to the rest of the premaxilla. The premaxillary crest is also absent in *Lonchodectes* and *Ikrandraco*. Here the premaxillary crest is considered a diagnostic character for the genus *Lonchodraco*.

Odontoid process. Rigal et al. (2017) diagnosed *Lonchodraco* as having a triangular dorsally directed perforate process at the symphysis extending two to three millimeters above the dental border. This structure corresponds to an odontoid process present in some pterodactyloids (Martill 2014; Kellner et al. 2019a; Pêgas et al. 2019). As this character has a wider distribution, it cannot be diagnostic for *Lonchodraco*.

Mandibular groove. A deep, V-shaped median sulcus on the occlusal surface of the mandibular symphysis is a diagnostic feature of *Lonchodectes* according to Unwin (2003). Wide mandibular groove is an autapomorphy of *Lonchodraco machaerorhynchus*, according to Rodrigues and Kellner (2013). A deep mandibular groove is present in *Lonchodraco giganteus*, but its details are obscured by matrix (Rodrigues and Kellner 2013). A distinctly wider mandibular groove is present in the anterior mandible fragment NHMUK R2269 from the Cambridge Greensand, referred to *Lonchodectes microdon* by Unwin (2001: fig. 11F) and not mentioned by Rodrigues and Kellner (2013). The mandible is unknown for *Lonchodectes compressirostris*, but this taxon might not have the mandibular groove because of a strongly transversely narrow snout and short palatal ridge confined to the posterior part of the palate. In *Ikrandraco avatar* the presence of a mandibular groove cannot be established because of the flattened preservation. This character is a possible synapomorphy for the Lonchodectidae.

Mandibular crest. The mandibular crest is a diagnostic character of *Lonchodraco*, according to Rodrigues and Kellner (2013). Short, low, blade-like dentary crest is an autapomorphy of *Lonchodraco giganteus* (Rodrigues and Kellner 2013). Deep dentary crest is an autapomorphy of *Lonchodraco machaerorhynchus* (Rodrigues and Kellner 2013). However, according to my observation, there is no significant difference in the relative dorsoventral depth of the mandibular crest between these two taxa. Rodrigues and Kellner (2013) also noted that *L. giganteus* differs from anhanguerids in that the mandibular crest does not start at the tip of the mandible. Indeed, the dorsoventrally low mandibular crest in *L. giganteus* starts some distance posterior to the anterior margin of the mandible and does not increase in depth for some distance. A similar low mandibular crest in the anterior portion of the mandible is present in *Lonchodraco microdon* (NHMUK R2269). Rodrigues and Kellner (2013) considered *Lonchodectes compressirostris* to lack the mandibular crest based on the erroneous interpretation of the anterior rostrum fragment as a fragment of the mandibular symphysis. A mandibular crest is currently unknown for that taxon. A very prominent mandibular crest is present in *Ikrandraco*. The mandibular crest is presently considered as a diagnostic character for the Lonchodectidae (unknown in *Lonchodectes*).

Ventral margin of mandible posterior to mandibular crest. The ventral margin of mandible posterior to the mandibular crest ascending in lateral view is an autapomorphy of *Lonchodraco machaerorhynchus*, according to Rodrigues and Kellner (2013). See the next character for discussion.

Ventral depression of mandible. Ventral depression located posterior to the mandibular crest is an autapomorphy of *Lonchodraco machaerorhynchus* according to Rodrigues and Kellner (2013). Seeley (1870) considered a peculiar posterior margin of the mandibular crest of the holotype of *Ornithocheirus machaerorhynchus* (CAMSM B54855) as the angular facet, a feature differentiating this taxon from the other pterodactyloids known at that time. In *Pteranodon*, the angular comes close to the mandibular symphysis but contacts the dentary dorsally, not posteriorly (Bennett 2001: fig. 22B). Rodrigues and Kellner (2013) interpreted this margin as the posterior surface of the mandibular crest. They proposed two autapomorphies for this taxon based on this interpretation: ventral depression located posteriorly to the dentary crest and ventral margin of the mandible posterior to the dental crest ascending in lateral view. However, this surface is likely the broken surface, and the mandibular crest was continuing posteriorly. This is supported by the ventral margin of the mandibular crest, which deepens posteriorly and probably attained the maximum depth in the missing posterior part.

Alveolar parapet. Alveoli placed in an elevation in relation to the palate and the dorsal margin of the mandible is a diagnostic character of the Lonchodectidae according to Unwin (2001, 2003), or an autapomorphy of *Lonchodraco*, according to Rodrigues and Kellner (2013). This character is present in *Lonchodectes compressirostris* (contra Rodrigues and Kellner 2013). Here it is considered a diagnostic character of the Lonchodectidae.

Raised margins of alveoli. Unwin (2001) considered dental alveoli with margins that are raised into a low collar so that the teeth appear to be "pedicellate," as a character diagnostic for the Lonchodec-

tidae. Later he formulated this character as "alveoli with margins raised into a low collar" (Unwin 2003: 179). According to Rigal et al. (2017), the teeth set in raised alveoli, separated by a C-shaped depression, is a diagnostic character for *Lonchodraco*, a view, which is followed here.

Size of alveoli. Comparatively small alveoli (up to 4 mm in diameter) in the anterior portions of the upper and lower jaws is a diagnostic character of the Lonchodectidae or *Lonchodraco*, according to Unwin (2001, 2003) and Rodrigues and Kellner (2013), respectively. Small alveoli are present also in *Lonchodectes compressirostris* and *Ikrandraco avatar*. This character is considered here diagnostic for the Lonchodectidae.

Size variation of alveoli. Teeth "uniform in size" was cited in the original diagnosis of *Lonchodectes* (Hooley 1914: 535). "Subequal sized" alveoli are diagnostic for *Lonchodectes*, according to Unwin (2003: 179). Alveoli of the anterior portions of the upper and lower jaws without significant variation in size is a diagnostic character of *Lonchodraco* according to Rodrigues and Kellner (2013). The teeth do not vary in size in *Ikrandraco avatar*. The same condition was likely present in *Lonchodectes compressirostris*, although the tip of the snout is unknown in this taxon. The size variation of alveoli is considered here diagnostic for the Lonchodectidae.

Spacing between alveoli. Spacing between alveoli roughly equivalent to their diameters is a diagnostic character of *Lonchodraco* according to Rodrigues and Kellner (2013). Spacing between alveoli larger than their diameters is an autapomorphy of *Lonchodraco* (?) *microdon* according to Rodrigues and Kellner (2013). The latter character contradicts the generic diagnosis of *Lonchodraco*. In *Ikrandraco avatar* and *I. machaerorhynchus*, the spaces between the alveoli are of variable size, some are similar in length with the alveoli, whereas others are larger. Here this character is considered diagnostic for the genus *Lonchodraco*.

The number of alveoli per 3 cm. Approximately six alveoli per 3 cm of jaw margin is an autapomorphy of *Lonchodraco giganteus*, according to Rodrigues and Kellner (2013). About 4.5 alveoli per 3 cm of jaw margin is an autapomorphy of *Lonchodraco machaerorhynchus* and, at the same time, is a diagnostic character for *Lonchodraco* (?) *microdon*, according to Rodrigues and Kellner (2013). In *Ikrandraco avatar*, the average number of alveoli per 3 cm is 3.8 for dentary. Rigal et al. (2017) considered tooth count per 3 cm a not taxonomically reliable character because it varies ontogenetically. This could be well true, but the size difference between the holotypes of *L. giganteus* and *I. machaerorhynchus* is not significant, and both likely belong to adult individuals. However, the spacing of teeth is markedly different between these two taxa, being denser in *L. giganteus*. Here these characters are considered diagnostic for the genera *Lonchodraco* and *Ikrandraco*.

Tooth shape. "More or less laterally compressed teeth" is a diagnostic feature of the genus *Lonchodectes* according to Hooley (1914: 535). According to Unwin (2003), in *Lonchodectes*, the teeth have constricted bases. Rigal et al. (2017) diagnosed *Lonchodraco* as having short, conical teeth that are gently recurved labially. However, in most of the lonchodectid specimens, the teeth are not preserved, and the diagnostic value of these characters cannot be evaluated.

SYSTEMATICS

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Lonchodectidae Unwin, 2001

Lonchodectidae [nomen nudum]: Unwin et al. 2000: 194.
Lonchodectidae: Unwin 2001: 208; Unwin 2003: 179.
Lonchodraconidae: Rodrigues and Kellner 2013: 23.

Type genus. *Lonchodectes* Hooley, 1914.

Diagnosis. Differs from other pterodactyloid pterosaurs by the combination of the following characters: the palate has a midline ridge; the alveolar margins of upper and lower jaws are elevated in relation to the palatal or dorsal mandibular surface; in the anterior part of the upper and lower jaws, the alveoli are small (up to 4 mm in diameter), without a significant variation in size; mandible with a prominent mandibular crest (unknown for *Lonchodectes*).

Included genera. The type genus, *Lonchodraco* Rodrigues et Kellner, 2013 and *Ikrandraco* Wang et al., 2014.

Comments. Witton et al. (2009) erroneously cited Hooley (1914) as the author of the family Lonchodectidae.

Genus *Lonchodectes* Hooley, 1914

Lonchodectes: Hooley 1914: 535; Kuhn 1967: 46; Unwin 2003: 179.

Type species. *Pterodactylus compressirostris* Owen, 1851 (Kuhn 1967: 46).

Diagnosis. Differs from *Lonchodraco* Rodrigues et Kellner, 2013 by low rostrum lacking the premaxillary crest and considerably constricted transversely, and short palatal ridge, confined to the posterior part of the palate.

Included species. Type species only.

Comments. *Lonchodectes* cannot be currently distinguished from *Ikrandraco* Wang et al., 2014 (see comments to that taxon).

Lonchodectes compressirostris (Owen, 1851)
(Fig. 1)

Pterodactylus compressirostris: Owen 1851a: 95, pl. 27, fig. 5, pl. 28, figs 8–10; Owen 1851b: 32, pl. 5, figs 1–3; Rodrigues and Kellner 2013: 52, fig. 14.
Ornithochirus compressirostris: Seeley 1870: 114; Lydekker 1888: 11; Woodward 1888: 336.
Ornithocheirus compressirostris: Arthaber 1922: 16, fig. 5; Wellnhofer 1978: 56, fig. 4; Milner 2002: 340.
Lonchodectes compressirostris: Hooley 1914: 535; Unwin 2001: tab. 1, fig. 11A, B; Martill 2011: fig. 2.

Holotype. NHMUK PV 39410, partial rostrum in two fragments.

Type locality and horizon. Culand Pits, Burham, Kent, England; Chalk Formation (Cenomanian-Turonian).

Referred specimens. CAMS B54.584, rostrum fragment; Cambridge, Cambridgeshire, England; Cambridge Greensand (Albian).

Diagnosis. As for the genus.

Comments. Two parts of the holotype were considered as parts of a single rostrum in the original description (Owen 1851a, b) and most subsequent publications. Kellner (1990) challenged this view, considering the smaller part as a fragment of dentary symphysis based on the presence of a medial groove. This view was held in Rodrigues and Kellner (2013). However, what Kellner took for the medial groove is a palatal surface between the two narrowing rostral parapets (Fig. 1C). The medial groove on lonchodectid dentaries is separated from the alveolar parapet by flat mandibular surface (Fig. 1C). There is no reason to change the interpretation of NHMUK PV 39410 rostral fragments and no need to renumber the specimens. This taxon might not have the medial groove on the symphysis at all because it has a short palatal ridge placed far behind the supposed symphysis. Following their interpretation of a small part

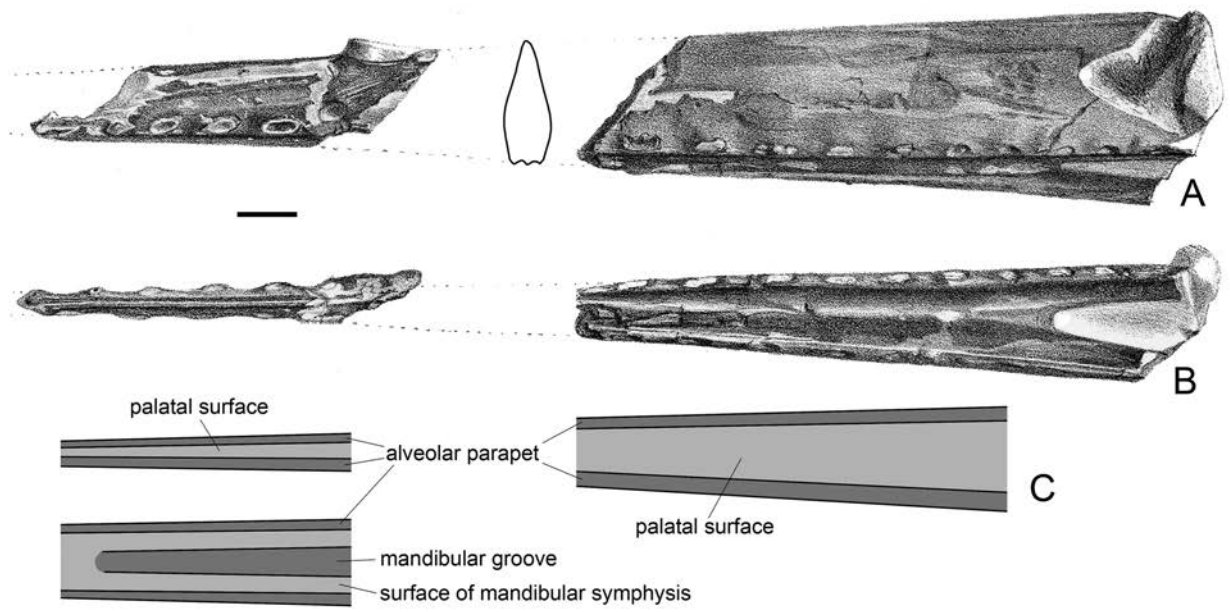

Fig. 1. *Lonchodectes compressirostris* (Owen, 1851), NHMUK PV 39410, holotype, partial rostrum in two pieces, in lateral (A) and ventral (B) views (after Owen, 1851a: pl. 28, figs 7–8). C – scheme explaining the difference between the anterior part of the rostrum and the anterior part of mandibular symphysis with mandibular groove. On the rostrum, the flat palatal surface is between the raised alveolar borders (alveolar parapet). On the mandibular symphysis, the mandibular groove is a depression flanked by the flat surface of the mandibular symphysis. Scale bar = 10 mm.

of NHMUK PV 39410 as a mandibular symphysis, Rodrigues and Kellner (2013) consider *P. compressirostris* to lack the mandibular crest and did not include this taxon in their family Lonchodraconidae.

Owen referred to *Pterodactylus compressirostris* an associated ulna and radius (NHMUK 49004) and two proximal fragments of first wing phalanx (NHMUK 39411 and 49003; Lydekker (1888: 12)) from the type locality (Owen 1851a: pl. 30, figs 4–5, pl. 32, fig. 2). However, as these bones were not directly associated with the holotype and there at least two other pterosaur species in the type locality, these specimens are not included in the hypodigm of *L. compressirostris*.

Lonchodraco Rodrigues et Kellner, 2013

Lonchodraco: Rodrigues and Kellner 2013: 23.

Type species. *Pterodactylus giganteus* Bowerbank, 1846.

Diagnosis. Differs from *Lonchodectes* Hooley, 1914 and *Ikrandraco* Wang et al., 2014 by premaxillary crest present, spacing between alveoli roughly equivalent to their diameters, approximately six alveoli per 3 cm of alveolar margin, and teeth set in raised alveoli separated by a C-shaped depression. Additionally differs from *Ikrandraco avatar* Wang et al., 2014 by anterior end of mandible dorsoventrally flattened, from *I. machaerorhynchus* (Seeley, 1870) by slightly diverging alveolar margins.

Included species. Type species and, tentatively, *Lonchodraco* (?) sp.

Lonchodraco giganteus (Bowerbank, 1846) (Fig. 2)

Pterodactylus giganteus: Bowerbank 1846: 8, pl. 1; Bowerbank 1848: pl. 2, figs 1–3; Owen 1851a: 91, pl. 31, figs 1–9, 12–13; Martill 2010: fig. 11.
Pterodactylus conirostris: Owen in Dixon 1850: 401, pl. 38, figs 4–6.
Ornithochirus (?) *giganteus*: Lydekker 1888: 12.
Ornithocheirus giganteus: Woodward 1888: 336; Wellnhofer 1978: 57, fig. 28; Milner 2002: 339, pl. 65, fig. 2.
Lonchodectes giganteus: Hooley 1914: 538; Unwin 2001: 210; Martill 2011: fig. 3; Witton 2013: fig. 12.2A.
Ornithodesmus (?) *giganteus*: Arthaber 1922: fig. 10.
Ornithocheirus compressirostris: Benton and Spencer 1995: fig. 8.20D.
Lonchodraco giganteus: Rodrigues and Kellner 2013: 24, fig. 4.

Lectotype. NHMUK PV 39412, anterior portions of the rostrum and mandible, incomplete scapulocoracoid, proximal ends of the humerus and ulna, and a partial wing phalanx. The lectotype was designated by Rodrigues and Kellner (2013).

Type locality and horizon. Culand Pits, Burham, Kent, England; Chalk Formation (Cenomanian-Turonian).

Diagnosis. As for the genus.

Lonchodraco (?) sp.

Lonchodectes sp.: Averianov and Kurochkin 2010: fig. 1.

Material. PIN 5028/4, an anterior fragment of mandibular symphysis; Melovatka 3 locality, Volgograd Region, Russia; Melovatka Formation (Cenomanian).

Comments. This specimen resembles *L. giganteus* in having similar tooth spacing (5.6 teeth per 3 mm) and a low mandibular crest at the anterior end of the mandibular symphysis but differs in a pointed anterior end of the mandible (rounded in *L. giganteus*). Also, it lacks the odontoid process, present in *L. giganteus*.

Ikrandraco Wang et al., 2014

Ikrandraco: Wang et al. 2014: 1.

Type species. *Ikrandraco avatar* Wang et al., 2014.

Diagnosis. Differs from *Lonchodraco* Rodrigues et Kellner, 2013 by lack of premaxillary crest and less densely spaced teeth (3.8–4.5 per 3 cm).

Included species. Type species and *I. machaerorhynchus* (Seeley, 1870) comb. nov.

Comments. *Ikrandraco* is included in the Lonchodectidae because it possesses three characters diagnostic for this group: the palate has a midline ridge and small alveoli in the anterior part of the upper and lower jaws (up to 4 mm in diameter), without a significant variation in size. The presence of an elevated alveolar margin of upper and lower jaws cannot be established for *I. avatar* because of its flattened preservation.

Currently, *Ikrandraco* cannot be reliably distinguished from *Lonchodectes* Hooley, 1914. The latter taxon has somewhat more widely spaced teeth (about 3.3 teeth per 3 cm). Another potential difference is a greater transverse flattening of the rostrum in

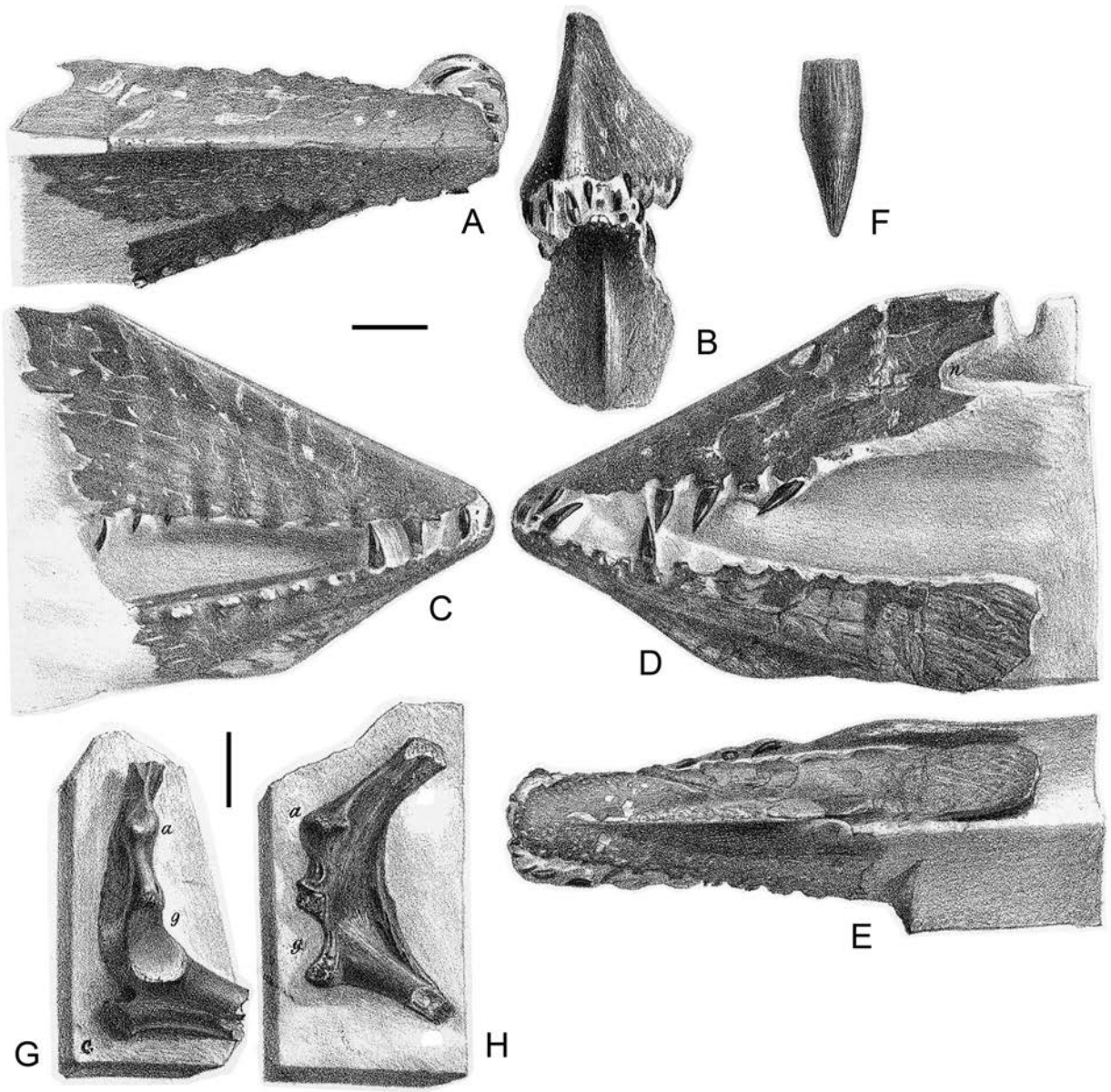

Fig. 2. *Lonchodraco giganteus* (Bowerbank, 1846), NHMUK PV 39412, holotype, anterior portions of the rostrum and mandible, in dorsal (A), anterior (B), right lateral (C), left lateral (D), and ventral (E) views, enlarged view of a tooth (F), and incomplete left scapulocoracoid, in lateral (G) and posterior (H) views (after Owen, 1851a: pl. 31, figs 1–8). Scale bars = 10 mm.

Lonchodectes. This character cannot be evaluated in *Ikrandraco* because of its flattened preservation. For this reason, it cannot be excluded that *Ikrandraco* Wang et al., 2014 is a junior subjective synonym of *Lonchodectes* Hooley, 1914. Both taxa are currently retained as valid because of incomplete knowledge of *Lonchodectes*.

Some characters cited in the original diagnosis of *Ikrandraco* cannot be checked in other lonchodectid taxa (slightly arched dorsal margin of the skull above the nasoantorbital fenestrae; lateral depression on the nasal; strongly inclined quadrate (150°); median hook-like process on the posterior edge of the mandibular crest; two well-developed pneumatic

foramina piercing the lateral surface of the axis; a ventral pneumatic foramen on the proximal portion of the second and third wing phalanges). At least some of these characters could be diagnostic for the Lonchodectidae. A very low skull is likely present also in *Lonchodectes compressirostris* and *Ikrandraco machaerorhynchus*. These two taxa also share with *I. avatar* the lack of the premaxillary crest. A deep mandibular crest is also present in *Lonchodraco giganteus* and *I. machaerorhynchus*.

The humerus of the holotype of *I. avatar* was described as having "a warped deltopectoral crest, with the proximal margin rounded" (Wang et al. 2014: 3). However, the rounded margin of the deltopectoral crest is anterior, not proximal. This crest is undoubtedly not "warped" as in ornithocheirid pterosaurs.

In the original description, *Ikrandraco* was referred to as Pteranodontia incertae sedis (Wang et al. 2014). The phylogenetic analysis performed in that paper does not include any lonchodectid taxon. In the analysis by Zhou et al. (2019), *Ikrandraco avatar* is the sister taxon to *Lonchodraco giganteus*.

Ikrandraco avatar Wang et al., 2014

Ikrandraco avatar: Wang et al. 2014: 2, figs 1–3, 4a, b, S1–4; Jiang et al. 2020: fig. 3H.

Holotype. IVPP V18199, partial skeleton.

Type locality and horizon. Lamadong, Jianchang County, Liaoning Province, China; Jiufotang Formation (Aptian).

Referred specimens. IVPP V18406, partial skeleton; Sihedang, Lingyuan County, Liaoning Province, China; Jiufotang Formation (Aptian). The third specimen of *I. avatar* was announced by Chen et al. (2018).

Diagnosis. Differs from *I. machaerorhynchus* by a relatively deeper mandibular crest and approximately 3.8 alveoli per 3 cm of alveolar margin.

Comments. In the supplementary information to Wang et al. (2014), a specimen number IVPP V18904 was applied to both the holotype and the referred specimen.

Ikrandraco machaerorhynchus (Seeley, 1870) comb. nov.

(Figs 3, 4)

Ptenodactylus machaerorhynchus: Seeley 1869: xvi.
Ptenodactylus oweni: Seeley 1869: xvi.
Ptenodactylus microdon: Seeley 1869: xvi.
Ornithocheirus machaerorhynchus: Seeley 1870: 113, pl. 12, figs 1–2.
Ornithocheirus oweni: Seeley 1870: 115.
Ornithocheirus microdon syn. nov.: Seeley 1870: 116, pl. 12, figs 6–7; Wellnhofer 1978: 58.
Lonchodectes machaerorhynchus: Hooley 1914: 535; Unwin 2001: 195, fig. 12D–E.
Lonchodectes microdon: Hooley 1914: 535; Unwin 2001: 195, fig. 11C–F.
Lonchodectes oweni: Hooley 1914: 535.
Lonchodraco machaerorhynchus: Rodrigues and Kellner 2013: 27, fig. 5.
Lonchodraco (?) *microdon*: Rodrigues and Kellner 2013: 29, fig. 6.

Holotype. CAMSM B54.855, partial mandibular symphysis.

Type locality and horizon. Cambridge, Cambridgeshire, England; Cambridge Greensand (Albian).

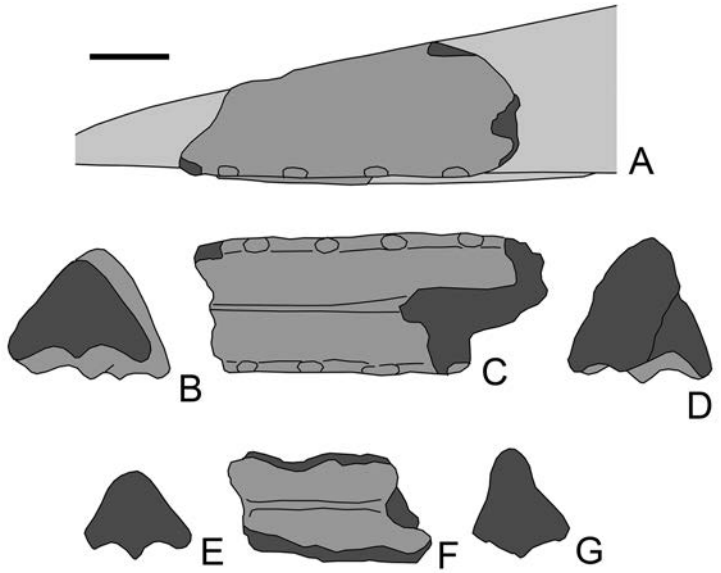

Fig. 3. Rostrum fragments of *Ikrandraco machaerorhynchus* (Seeley, 1870). A–D – CAMSM B54486, holotype of *Ornithocheirus microdon* Seeley, 1870, in lateral (A), anterior (B), ventral (C), and posterior (D) views (images in A and C are flipped horizontally). E, F – CAMSM D54439, holotype of *Ornithocheirus oweni* Seeley, 1870, in anterior (E), ventral (F), and posterior (G) views. Modified from Unwin (2001: fig. 11C, D) and Rodrigues and Kellner (2013: fig. 6D, F, H, J, L). Scale bar = 10 mm.

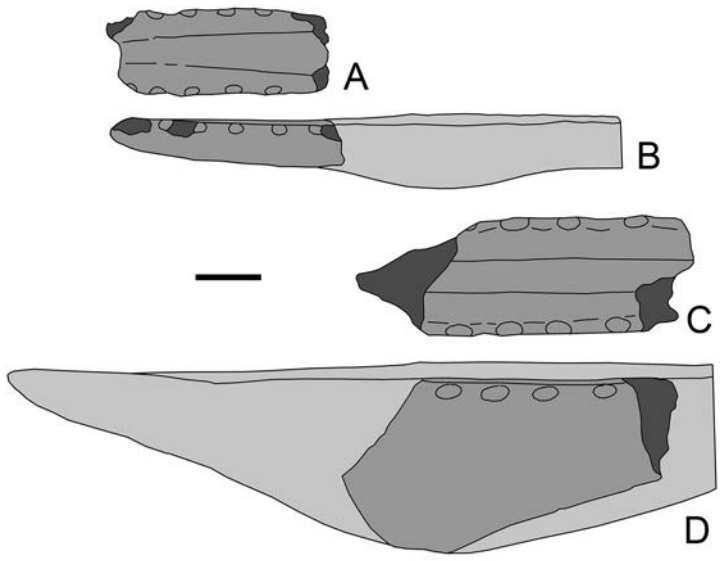

Fig. 4. Mandibular fragments of *Ikrandraco machaerorhynchus* (Seeley, 1870). A, B – NHMUK R2269, an anterior fragment of the mandibular symphysis, in dorsal (A) and lateral (B) views (image in B is flipped horizontally). C, D – CAMSM B54855, holotype, a middle fragment of the mandibular symphysis, in dorsal (C) and lateral (D) views. Modified from Unwin (2001: figs 11E, F, 12D, E). Scale bar = 10 mm.

Referred specimens. CAMSM B54.486, rostrum fragment (holotype of *Ornithocheirus microdon* Seele, 1870); CAMSM B54.439, rostrum fragment (holotype of *Ornithocheirus oweni* Seeley, 1870); NHMUK R2268 and R2269, fragments of the mandibular symphysis; all from the type locality.

Diagnosis. Differs from *I. avatar* by a relatively shallower mandibular crest and approximately 4.5 alveoli per 3 cm of alveolar margin.

Comments. According to Wang et al. (2014), a combination of a low and elongate crestless skull with a lower jaw that has a well developed mandibular crest with a hook-shaped posterior process found in *I. avatar* has no parallel among the known pterosaur species. However, at least two of these features are found in a pterosaur species from Cambridge Greensand: a low crestless skull (*Ornithocheirus microdon*) and a developed mandibular crest (*Ornithocheirus machaerorhynchus*). The presence of a hook-shaped posterior process of dentary cannot be established for the Cambridge Greensand species because of its incompleteness. *Ornithocheirus microdon* is based on rostrum fragment and *O. machaerorhynchus* – on a dentary fragment. These fragments are referred here to a single species, which is referred to as *Ikrandraco* because of a combination of crestless skull and large mandibular crest. *Ornithocheirus machaerorhynchus* was previously reconstructed as having the deepest point of the mandibular crest near the anterior end of the dentary (Unwin 2001: fig. 12D), but there is no evidence for this. Here it is reconstructed as having the deepest point of the mandibular crest at the middle of the mandibular symphysis (Fig. 4D), similar to the condition present in *L. giganteus* and *I. avatar.*

PUTATIVE RECORDS OF LONCHODECTIDAE

***Serradraco sagittirostris* (Owen, 1874).** This taxon is known from a single specimen (NHMUK PV R 1823) from the Upper Tunbridge Wells Sand Formation at St Leonards on Sea, East Sussex, England. The specimen, holotype of *Pterodactylus sagittirostris* Owen, 1874, consists of two fragmentary mandibular rami posterior to the mandibular symphysis (Owen 1874: pl. 2). This taxon was subsequently referred to as *Ornithocheirus* (Seeley 1901; Wellnhofer 1978), *Lonchodectes* (Hooley 1914; Unwin 2001), or its own genus *Serradraco* (Rigal et al. 2017). Rodrigues and Kellner (2013) considered *Pterodactylus sagittirostris* a nomen dubium. As was noted by these authors, it cannot be directly compared with most of the lonchodectid taxa, which are based on jaw tips. The most characteristic feature of this taxon is asymmetric borders of the raised alveoli, which slope gently anteriorly and steeply posteriorly, giving to the alveolar border a peculiar saw-like appearance (Rigal et al. 2017). It should be noted, however, that this particular pattern of alveolar border is confined only to the anterior preserved part of the dentary, in more posterior parts the alveoli are little raised and have symmetric borders. *S. sagittirostris* is also peculiar in having a distinct groove on the external surface of the mandible ventral to the alveolar border, which is connected with branching grooves for blood vessels covering most of the mandibular external surface. None of the lonchodectid taxa has a similar alveolar edge and external mandibular groove. *Serradraco sagittirostris* does not preserve any character considered here to be diagnostic for the Lonchodectidae. The alveoli are raised, but in the Lonchodecti-

dae, they are raised above the surface of the palate or mandibular symphysis that cannot be checked for *S. sagittirostris*. Therefore, this taxon is not included in the Lonchodectidae.

BEXHM 2015.18. It is a fragmentary pterosaur skeleton from the Upper Tunbridge Wells Sand Formation or Lower Weald Clay Formation (upper Valanginian or lower Hauterivian) at Foreshore at Bexhill, East Sussex, England. It includes a jaw fragment with three teeth, six articulated dorsal vertebrae, distal ulna fragment, proximal syncarpal, and fragments of wing phalanges (Rigal et al. 2017). The jaw is likely part of the mandibular ramus posterior to the symphysis. The teeth are small with conical crowns, evenly spaced and located in alveoli with prominent, dorsally raised borders. The dorsal vertebrae are not fused. According to the original description, the anterior-most complete vertebra has an articular facet for the rib that is significantly larger than that of all of the more posterior vertebrae. Rigal et al. (2017) think that the enlarged size of the parapophysis of the anterior-most complete vertebra suggests that it is a free dorsal vertebra. I assume that the authors mean the height of the transverse process rather than the size of the rib articulation facet. The rib articular surfaces (parapophysis and diapophysis) appear to be missing in all vertebrae. The preserved cross-section of the transverse process of the first vertebra is not significantly larger than in other vertebrae. The free vertebrae have a high transverse process but do not have an enlarged parapophyses (articular facet for the rib capitulum). They have a joined articular facet for a single-headed rib, and this facet is distinctly smaller than rib articular facets in anterior dorsals. In free dorsals, the height of the transverse process is more or less uniform. In BEXHM 2015.18, the transverse process of the first complete dorsal vertebra is, however, higher than in other vertebrae. In the two succeeding vertebrae, the height of the transverse process decreases and then slightly increases in the more posterior vertebrae. In *Pteranodon*, the dorsal vertebrae with a similarly high transverse process is the fifth dorsal, which is followed by dorsals with the decreased height of the transverse process (Bennett 2001: fig. 46). The fifth and sixth dorsals are incorporated in the notarium in *Pteranodon*. The lower neural spines of dorsal vertebrae in BEXHM 2015.18 also suggest that they are anterior dorsals, not posterior dorsals, as was assumed by the Rigal et al. (2017). It is either this specimen is immature with unfused notarium, and missing supraneural plate or notarium was shorter in this taxon.

Rigal et al. (2017) identified in BEXHM 2015.18 a distal fragment of the left ulna and right proximal syncarpal. However, the ulna is the right one according to its morphology. It is more likely to find the association of the bones from a wing of the same side, not a mixture of right and left wing elements, especially for the distal ulna and proximal syncarpal that are articulated in life and closely approximated postmortem in BEXHM 2015.18. The exposed flattened surface of the ulna indeed accommodated the radius, but this is the anterior ulna surface, not posterior surface, as indicated in Rigal et al. (2017: fig. 4b). The proximal syncarpal retains a suture between its ulnar and radial parts. This is in line with likely not ossified notarium in BEXHM 2015.18 and suggests a juvenile age for this specimen.

Rigal et al. (2017) also indicated fragments of the second, third, and fourth phalanges of the left wing digit. However, these fragments are poorly preserved and do not preserve any characters that may suggest an attribution to the left or right side wing. As was noted above, all wing elements in BEXHM 2015.18 appear to be from the right side. Also, I cannot follow the attribution of these fragments to the second, third, and fourth phalanges. Some of these fragments could be pieces of the first wing phalanx. The idea that a subtriangular cross-section of the fourth wing phalanx may be a diagnostic character for the Lonchodectidae is unfounded because identification of this piece of bone as a fourth wing phalanx is dubious and attribution of BEXHM 2015.18 to the Lonchodectidae is poorly supported.

BEXHM 2015.18 was referred to the Lonchodectidae because of flattened, simple cone-shaped tooth crowns in alveoli with raised borders (Rigal et al. 2017). The latter character was considered an autapomorphy of the Lonchodectidae by Unwin (2001). Rigal et al. (2017) differentiated BEXHM 2015.18 from *Serradraco sagittirostris* by having vertically directed teeth and raised alveolae with symmetric borders. According to these authors, BEXHM 2015.18 agrees well in these features with *Lonchodraco giganteus* and for this reason this specimen was referred to *Lonchodraco* sp. However, the tooth inclination may vary within the jaw, with more vertical teeth anteriorly. The only known specimen of *S. sagittirostris* (NHMUK R1823) comprises posterior dentary fragments. I cannot confirm that the

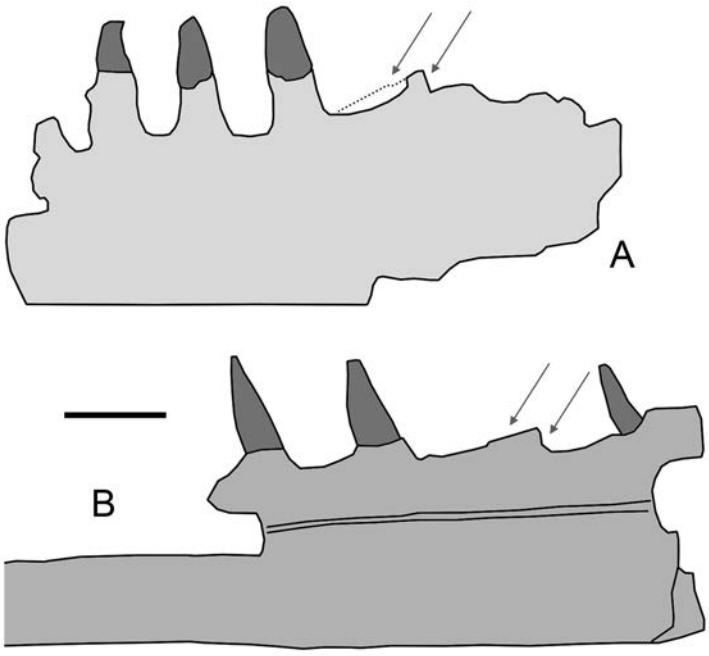

Fig. 5. Dentary fragments BEXHM 2015.18 (A) and NHMUK R1823, holotype of *Serradraco sagittirostris* (Owen, 1874) (B) (after Rigal et al., 2017: figs 5a and 7c). Arrows indicate asymmetric alveolar borders. Scale bar = 10 cm.

teeth in BEXHM 2015.18 have raised alveoli with symmetric borders. This interpretation is based on a poorly preserved part of the jaw with most of the bone is missing. Moreover, the better preserved alveolar margin posterior to the preserved teeth shows the asymmetric alveolar borders, so characteristic for *S. sagittirostris* (Fig. 5). *Serradraco sagittirostris* comes the Upper Tunbridge Wells Sand Formation, from where BEXHM 2015.18 may also come. The latter specimen is more likely belong to *S. sagittirostris* and thus excluded from the Lonchodectidae.

***Palaeornis cliftii* Mantell, 1844.** This species is based on an isolated humerus broken in two parts (NHMUK 2353 and 2353a) from the Hastings Beds Group (probably from the Valanginian Upper Tunbridge Wells Formation) at Cuckfield, West Sussex, England (Witton et al. 2009: figs 3–4). Witton et al. (2009) referred this specimen to the Lonchodectidae indet. based on its similarity with isolated humerus CAMSM B54.081 from Cambridge Greensand, which Unwin (2003) referred to *Lonchodectes* sp. However, there are no grounds for referral of the latter humerus to *Lonchodectes*, and reference of the "*Palaeornis*" humerus to the Lonchodectidae is similarly groundless. The humerus of the lonchodectid *Ikrandraco avatar* (Wang et al. 2014: fig. 3e) has a similar plesiomorphic, not "warped" deltopectoral crest with parallel margins (*contra* the original description). Still, this crest is distinctly shorter than in "*Palaeornis*." The morphology of NHMUK 2353 and 2353a was reviewed by Averianov (2012), who considered it as belonging to a basal azhdarchoid.

The "Moon Goddess." A well preserved pterosaur skeleton from the Aptian Jiufotang Formation of Liaoning Province, China has been attributed to still undescribed lonchodectid taxon, informally known as the "Moon Goddess," or "Chang-e" (Unwin et al. 2008; Witton 2013). Lonchodectids are present in the Jiufotang Formation, as shown by *Ikrandraco avatar*.

***Unwindia trigonus* Martill, 2011.** This taxon is based on a partial rostrum SMNK PAL 6597 from the Albian Romualdo Formation in Santana do Cariri region, Ceará Province, Brazil (Martill 2011). The genus is characterized by reduced dentition with only seven tooth pairs anterior to the nasoantorbital fenestra. The teeth are of similar size, in contrast with the heterodont dentition of ornithocheiroid taxa. Originally, the taxon was referred to the Ctenochasmatoidea (Martill 2011). Witton (2013: 211) cited personal communication from D.M. Unwin that "several features of its jaw and dental morphology are consistent with a lonchodectid identity." Indeed, the long and low rostrum resembles that of *Lonchodectes* and *Ikrandraco*, and the variation of the tooth size is not significant. Nevertheless, the tooth size variation is more pronounced than in lonchodectids: the terminal teeth are somewhat bigger and separated from the lateral teeth by a small tooth. This condition is more reminiscent of the ornithocheiroid dentition. *Unwindia* could represent an ancestral stage in teeth reduction leading to the Lonchodectidae, but cannot be included in that group.

***Prejanopterus curvirostris* Fuentes Vidarte et Meijide Calvo, 2010.** *Prejanopterus* is known from disarticulated cranial and postcranial elements of several individuals from the Aptian Leza Formation at Fuente Amarga, Préjano, La Rioja Province, Spain (Fuentes Vidarte and Meijide Calvo 2010). *Prejanopterus* was originally referred to Pterodactyloidea

incertae sedis, but then assigned to the Pterodactylidae (Pereda Suberbiola et al. 2012). According to Witton (2013), "the long, low nature of its jaw and unusual tooth socket morphology tentatively suggest it might represent a lonchodectid." Similarities with the Lonchodectidae include a low elongated rostrum lacking the premaxillary crest (present in *Lonchodraco* but not in *Lonchodectes* and *Ikrandraco*) and small homodont teeth. However, *Prejanopterus* lacks raised alveolar margins, palatal ridge, and mandibular crest. These characters do not allow the attribution of *Prejanopterus* to the Lonchodectidae.

PHYLOGENETIC POSITION OF LONCHODECTIDAE

Unwin (2003) used the Lonchodectidae as a combined terminal taxon in his phylogenetic analysis. The Lonchodectidae were recovered in a polytomy with *Pterodactylus* Cuvier, 1809 and Ctenochasmatidae Nopcsa, 1928. In this analysis, the terminal taxon Lonchodectidae also included postcranial bones of the azhdarchoid *Ornithostoma*, in particular, the elongated cervical vertebrae. This might be the reason that the Lonchodectidae was found related to the Ctenochasmatidae.

Ornithocheirus (=*Lonchodectes*) *compressirostris* was found as a sister taxon of the Anhangueridae by Kellner (2003). It was united with the Anhangueridae by a discrete palatal ridge, tapering anteriorly. This result is repeated in the analyses based on the same or slightly modified data set (Kellner 2004; Wang et al. 2005, 2008). In these analyses, *O. compressirostris* was scored only for the type skull material.

In the phylogenetic analysis of pterosaurs performed by Andres and Ji (2008), *L. compressirostris* is also a sister taxon of Anhangueridae. In this analysis, *L. compressirostris* was scored for some postcranial characters, which are actually not known for this taxon. This terminal taxon is likely a chimera combining characters of *Lonchodectes* and *Ornithostoma*. In more recent versions of this analysis, *L. compressirostris* is between the Istiodactylidae Howse, Milner et Martill, 2001 and Ornithocheiroidea (Andres and Myers 2013; Bantim et al. 2014), or a sister taxon to the clade Lanceodontia (Istiodactylidae + Anhangueria) (Andres et al. 2014). *Lonchodraco giganteus* was found as a sister taxon to *Ikrandraco avatar* in the analysis by Zhou et al. (2019). These two taxa form a polytomy with the clade Ornithocheirae in the analysis by Kellner et al. (2019b). The mentioned phylogenetic analyses suggest that the Lonchodectidae are part of the ornithocheiroid radiation, likely the sister taxon to the Anhangueria.

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