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ORNITHOSTOMA SEDGWICKI – VALID TAXON OF AZHDARCHOID PTEROSAURS

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ABSTRACT

Ornithostoma sedgwicki Seeley, 1891 from the Lower Cretaceous (Albian) Cambridge Greensand of England is represented by edentulous jaw fragments, posterior skull fragment with the supraoccipital crest, and by several postcranial bones attributed previously to *Lonchodectes. Ornithostoma* is referred to the Azhdarchoidea based on a combination of derived characters (teeth absent, middle cervicals moderately elongated, pneumatic foramen on anterior side of humerus, large pneumatic foramen on posterior side of femur at greater trochanter) and plesiomorphic characters (deltopectoral crest not warped, femoral neck to shaft angle less than 145°). The structure of the supraoccipital crest and humerus resembles those in *Tapejara*, but *Ornithostoma* differs from that taxon by a strong median ridge on the occiput presumably associated with a more elongated rostrum. At least three taxa of basal azhdarchoids were present in the British Lower Cretaceous.

Key words: Azhdarchoidea, *Lonchodectes*, Early Cretaceous, *Ornithostoma*, Pterosauria

ORNITHOSTOMA SEDGWICKI – ВАЛИДНЫЙ ТАКСОН АЖДАРХОИДНЫХ ПТЕРОЗАВРОВ

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РЕЗЮМЕ

Ornithostoma sedgwicki Seeley, 1891 из нижнемелового (альб) кембриджского зеленого песчаника Англии представлен фрагментами беззубых челюстей, фрагментом задней части черепа с затылочным гребнем, и некоторыми костями посткраниального скелета, которые раньше относили к *Lonchodectes. Ornithostoma* относится к Azhdarchoidea на основании комбинации продвинутых признаков (отсутствие зубов, умеренно удлиненные среднешейные позвонки, отверстие пневматизации на передней стороне плечевой кости, крупное отверстие пневматизации на задней стороне бедренной кости у большого трохантера) и плезиоморфных признаков (дельтопекторальный гребень не загнут, угол между шейкой и телом бедренной кости меньше 145°). Строение затылочного гребня и плечевой кости сходно с таковыми у *Tapejara*, но *Ornithostoma* отличается от последнего таксона мощным медиальным гребнем на затылке, предположительно связанным с более удлиненной ростральной частью черепа. В нижнем мелу Великобритании существовало, по крайней мере, три таксона базальных аждархоидов.

Ключевые слова: Azhdarchoidea, *Lonchodectes*, ранний мел, *Ornithostoma*, Pterosauria

INTRODUCTION

The first well known toothless pterosaur was *Pteranodon* Marsh, 1876 from the Late Cretaceous of North America. The first discovered specimen of this pterosaur was a wing metacarpal bone described as *Pterodactylus oweni* Marsh, 1871 and its toothless nature was not apparent until discovery of a more complete cranial material, upon which a new genus, “pterodactyl lacking teeth” (meaning of the word *Pteranodon*) was established in 1876 (see Witton 2010 for the history of discoveries). Seven years earlier, Seeley in the catalogue of fossils from the Sedgwick Museum in Cambridge mentioned three jaw fragments from the phosphorite mines within the Albian Cambridge Greensand near Cambridge, England, numbers 1–3 from cabinet J, tablet 16 (Seeley 1869: xvi). He identified these specimens as "?premaxillary bones" and referred them to *Ornithocheirus simus* (Owen, 1861), establishing a new genus *Ornithocheirus* (Seeley 1869: xvi, 6). In the footnote on page xvi he diagnosed the new genus as having "no teeth anterior to the palate". Surprisingly enough, Seeley referred to plate 2 in Owen (1861), where the only figured jaw fragment is toothed. On this and the next pages he provisionally established two additional species of *Ornithocheirus*, which were described later as *Ornithocheirus carteri* Seeley, 1870 and *Ornithocheirus platyrhinus* Seeley, 1870. Both are synonyms of *O. simus* according to Unwin (2001). Formally *Pterodactylus simus* Owen, 1861 should be considered as a type species for *Ornithocheirus* Seeley, 1869, the genus of toothed pterosaurs (Unwin 2001), but Seeley's original intention evidently was to establish *Ornithocheirus* for the toothless pterosaur. Later Seeley changed his mind and used this name for the species of toothed pterosaurs (Seeley 1870). This incongruence was noted and discussed by Hooley (1914). In a subsequent publication Seeley (1871: 35) introduced a new provisional generic name, *Ornithostoma* (meaning "bird mouth"), for these three edentulous jaw fragments. Of these fragments, only one, CAMSM B.54485, was figured by Owen (1859: pl.4, figs 4, 5; see also Unwin 2001: fig. 13), who identified it as the proximal end of wing-finger metacarpal. In 1891 Seeley clearly indicated the latter specimen as the type of *Ornithostoma* and proposed the species epithet for this taxon, *O. sedgwicki* (Seeley 1891: 442). He also concluded that *Ornithostoma* Seeley, 1871 is a senior subjective synonym of *Pteranodon* Marsh, 1876, a conclusion accepted by some previous pterosaur researchers (Williston 1895, 1896, 1897; Bogolubov 1914; Hooley 1914). However, the available date of publication of *Ornithostoma* is 1891 because in 1871 it was proposed as a provisional name without naming the second part of the binomen (ICZN articles 11.5 and 11.9). The two other edentulous jaw fragments from the Cambridge Greensand were found in collection in 1986 (Unwin 2001: 212), but were never figured or described.

An important step towards understanding of *Ornithostoma* was made by Hooley in his revision of the Cambridge Greensand pterosaurs (Hooley 1914). A most notable achievement was identification of CAMSM B.54406 as a posterior skull fragment with the base of the supraoccipital crest (Hooley 1914: pl. 22, figs 1–3). This specimen was identified previously as "orbito-ethmo-sphenoid" bone (Seeley 1870: 85–86, pl. 11, figs 7–9).

Two bones identified by Seeley as a sacral vertebra and a pelvis fragment (Seeley 1870: pl. 8, fig. 3, pl. 10, figs 8, 9), Hooley considered to be parts of the notarium and were referred to *Ornithostoma* (assuming it is a synonym of *Pteranodon*). However, Seeley's identifications were correct; the pelvis fragment was mistaken by Hooley for the supraneural plate of the notarium, confusing the acetabulum with the scapular facet.

Peculiar elongated vertebrae from Cambridge Greensand were initially considered to be caudals (e.g., Owen 1860: pl. 10, figs 35–37; Seeley 1870: pl.10, figs 13–17). Later Seeley (1875) admitted that these vertebrae are cervicals. Hooley (1914: 541) confirmed this identification and concluded that "the absence of transverse processes and their amphiplatyan nature bring them close to *Ornithostoma* (*Pteranodon*)." But transverse processes are absent (actually extremely reduced and fused with rudimentary cervical ribs) in all Pterodactyloidea (Unwin 2003). These vertebrae are typically procoelous, not "amphiplatyan." Padian (1986: 289) considered these vertebrae as "*Azhdarcho*-like cervicals." Their similarity with the azhdarchid cervicals also has been noted by Howse (1986: 320).

Hooley (1914) referred to *Ornithostoma* a scapulocoracoid fragment from Cambridge Greensand figured by Owen (1859: pl. 3, fig. 1) because of a large pneumatic foramen between the scapula and coracoid on the posterior side behind the glenoid. Indeed such a foramen is characteristic for *Pteranodon* (Bennett 2001: fig. 65A), but is also found in ornithocheirids (Wellnhofer 1991: fig. 16d). Hooley (1914) also referred to *Ornithostoma* proximal and distal ends of humeri and ulnae classified in his group B, and proximal ends of femora attributed to group 1.

The revision made by Hooley was challenged by Unwin (2001). Although synonymy of *Ornithostoma* and *Pteranodon* was no longer upheld, Unwin supported referral of *Ornithostoma* to the Pteranodontidae albeit with reservation. He restricted this taxon to the three edentulous jaw fragments, including the holotype CAMSM B.54485, and considered that the posterior skull fragment CAMSM B.54406 might be also belong to this species. According to Unwin (2001), there is no evidence to support referral of any postcranial bones to *Ornithostoma* proposed by Hooley (1914). The elongated cervical vertebrae, attributed to *Ornithostoma* by Hooley (1914), and humerus fragments of group C, not attributed to any known taxon by Hooley, Unwin (2001) referred to the Lonchodectidae. Based on this he concluded that lonchodectids "are certainly not ornithocheiroids" (Unwin 2001: 208). No rationale was given for these attributions, however. In a single phylogenetic analysis employing *Lonchodectes* this taxon was recovered as a sister taxon to "Anhangueridae" (=Ornithocheiridae) (Andres and Ji 2008) within the group equal to the Ornithocheiroidea of Unwin (2003).

In this report I argue for a new interpretation of *Ornithostoma sedgwicki* as an azhdarchoid pterosaur. I refer to this taxon the holotype rostrum fragment (CAMSM B.54485), posterior skull fragment (CAMSM B.54406), elongated cervicals and proximal humerus fragment of Group C of Hooley (1914) which were referred to *Lonchodectes* by Unwin (2001, 2003), and the femur of group 2 (CAMSM B.54262), not attributed to any particular taxon by Hooley (1914) and attributed to *Lonchodectes* sp. by Unwin (2003).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, United Kingdom; BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CAMSM, Sedgwick Museum, Cambridge, United Kingdom; DNPM MCT, Departamento Nacional da Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro, Brazil; GIUA, Geological Institute, University of Amsterdam, Amsterdam, Netherlands; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; USNM, United States National Museum, Washington, DC, USA.

SYSTEMATICS

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Azhdarchoidea Nessov, 1984
Ornithostoma sedgwicki Seeley, 1891

Ornithostoma sedgwicki: Seeley 1891: 442.
Ornithostoma seeleyi: Lydekker 1904: 59.

Holotype. CAMSM B.54485, rostrum fragment (fused premaxillae and maxillae).

Type locality and horizon. A phosphorite mine near Cambridge, England, United Kingdom; Cambridge Greensand, Lower Cretaceous (Albian).

Diagnosis. Referred to the Azhdarchoidea by the combination of the following characters: teeth absent; middle cervicals moderately elongated; lateral pneumatic foramen on middle cervicals reduced or absent; pneumatic foramen on ventral side of humerus near the base of humeral neck; deltopectoral crest of humerus elongated and rounded on distal end, not warped, with parallel sides; angle of femoral neck to shaft less than 145°; a large pneumatic foramen on posterior side of femur between neck and greater trochanter. Differs from the Azhdarchidae by less elongated middle cervicals, with neural arch not confluent with centrum in middle and neural spine not reduced; lateral pneumatic foramen variably present on postaxial cervicals; deltopectoral crest of humerus proximally placed. Differs from *Tupandactylus* by frontal not fused with premaxillary crest. Differs from *Tapejara* by a strong median ridge on the occiput presumably associated with a longer rostrum and supraoccipital crest starting above the orbit. Differs from both *Tupandactylus* and *Tapejara* by more elongated middle cervicals. Differs from *Tupuxuara* by much lower cranial crest above orbit and less elongated middle cervicals.

Referred specimens. Various phosphorite mines around Cambridge, Cambridge Greensand: CAMSM B.54406, posterior skull fragment; CAMSM B.54394 and B.54493, cervical vertebrae; CAMSM B.54081, right humerus; BMNH 35413, proximal fragment of right humerus; CAMSM B.54262, proximal part of right femur.

Comments. The known specimens of *Ornithostoma sedgwicki* show considerable similarity with recently described taxa from the Yixian (Barremian) and Jiufotang (Aptian) formations of Liaoning Province, China classified currently within the azhdarchoid family "Chaoyangopteridae" (Dong et al. 2003; Wang and Zhou 2003; Lü and Ji 2005; Lü and Zhang 2005; Lü et al. 2006, 2008; Zhou 2010). This similarity includes relatively long rostrum, presence of a supraoccipital crest at least in some "chaoyangopterids" (*Eopteranodon*), moderately elongated middle cervicals, and plesiomorphic structure of the humerus. Detailed comparison is limited by incompleteness of the Cambridge Greensand specimens and the state of preservation of the Liaoning specimens. Also the taxonomy of the Chinese taxa is quite confusing and some taxa need a revision. According to Lü et al. (2008: 892) "members of Chaoyangopteridae are distinguished from all other pterosaurs by an unusually slender premaxillary bar bounding the nasoantorbital opening and extension of the nasoantorbital opening posterior to the jaw joint." However, both these characters can be observed only on a single specimen, the holotype of "*Shenzhoupterus chaoyangensis*" from the Jiufotang Formation (Lü et al. 2008: fig. 1). The holotype is a juvenile specimen and this taxon is most likely a junior subjective synonym of *Chaoyangopterus zhangi* Wang et Zhou, 2003 from the same formation. The second of the mentioned characters is likely a preservation artifact caused by filling of the nasoantorbital fenestra by mixture of crushed cranial, and possibly some postcranial, bones. The monophyly of the "Chaoyangopteridae" and validity of some currently recognized taxa referred to this group remain to be demonstrated.

Distribution. Western Europe; Early Cretaceous (Albian).

DESCRIPTION AND COMPARISON

Rostrum fragment

The holotype CAMSM B.54485 (Fig. 1) is a small fragment of an edentulous rostrum. It is roughly triangular in cross section with convex lateral sides and concave ventral occlusal side. The dorsal margin is rounded. In lateral profile the ventral margin is sligthly convex. The dorsal margin is inclined to the ventral margin at 12°. If the angle of dorsal and ventral margin convergence is consistent and the rostrum tapered in a sharp point, the rostrum tip would be located anteriorly at a distance about twice greater than the length of the preserved fragment. It is likely that the tip of the rostrum was straight or slightly bent upwards. Near the broken posterior end of the fragment there is a base of a more abrupt elevation suggesting presence of a premaxillary crest on the posterior part of the rostrum. The rostrum is also widening laterally in the most posterior part of the fragment, where its width about 1.5 times greater than the width at the anterior end of the fragment.

Unwin (2001: 212) noted that the rostrum is elongate. He thought that "the rounded, triangular cross-section of the rostrum [...], which also has low, rounded marginal ridges [...] clearly distinguish *Ornithostoma* from azhdarchids wherein the rostra have concave lateral surfaces and lack marginal ridges on the jaws (Wellnhofer and Buffetaut 1999: fig. 4)." However, the specimen with concave lateral sides to which Unwin is referring, BSP 1996.I.36, is not a rostrum but a mandibular symphysis of a recently described azhdarchid *Alanqa saharica* (Ibrahim et al. 2010).

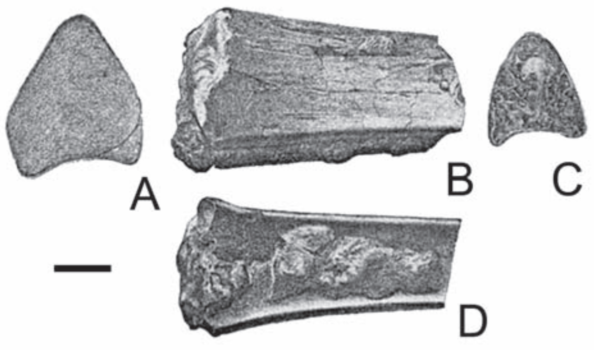

Fig. 1. CAMSM B.54485, holotype, rostrum fragment of *Ornithostoma sedgwicki*, in posterior (A), lateral (B), anterior (C), and ventral (D) views. Reproduced from Owen (1859: pl. 4, figs 4, 5). Scale bar = 1 cm.

According to Bennett (1994: 17) "*Ornithostoma* is quite distinct from *Pteranodon*." "The jaws of *Pteranodon* have marginal ridges that extend 3–4 mm above the floor of roof of the mouth and that are composed of dense bone. The jaw of *Ornithostoma* lacks such ridges; instead, the jaw margins are rounded [...]." Actually CAMSM B.54485 is very similar to the rostrum fragments of *Azhdarcho lancicollis* from the Turonian of Uzbekistan (Averianov 2010). The only sufficient difference is that no known fragment of *Azhdarcho* rostrum has such abrupt lateral widening at the posterior end as in *Ornithostoma*.

Skull fragment

The posterior skull fragment CAMSM B.54406 preserves the dorsal roof of the orbit, the occiput and the base of the supraoccipital crest (Figs 2, 3). The term "supraoccipital crest" is used here, following Hooley (1914), in the meaning "crest above the occiput." The bone sutures are obliterated. The small posterior part of the crest may be formed by the supraoccipital while the larger part was formed by the frontal (anteriorly) and parietal (posteriorly). The space on the ventral side, between the occiput and

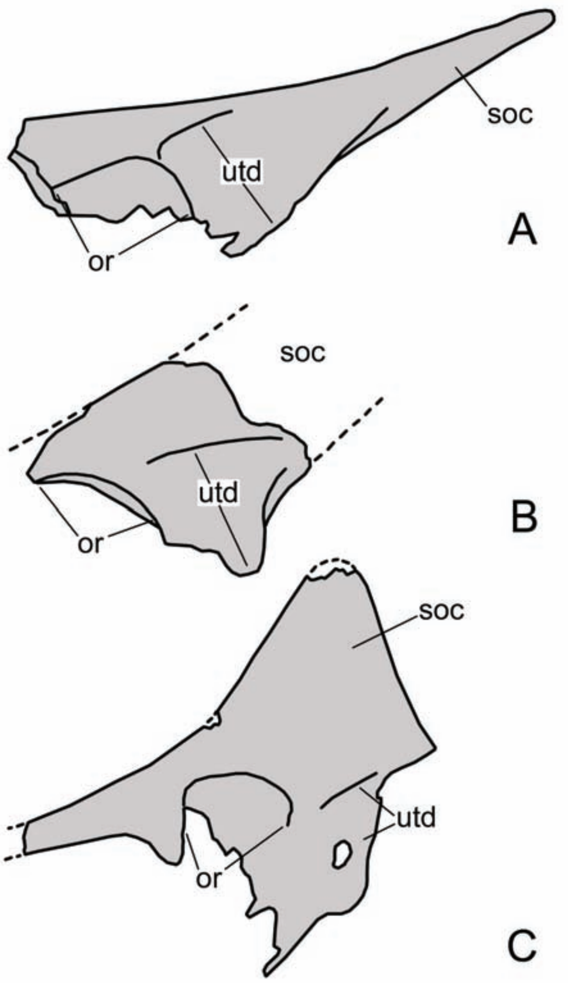

Fig. 2. Posterior skull of *Tapejara wellnhoferi*, SMNK PAL 1137 (A, modified from Eck et al. 2011: fig. 2), *Ornithostoma sedgwicki* (B, CAMSM B 54.406), and *Pteranodon* sp., USNM 13868 (C, modified from Bennett 2001: fig. 11; jugal has been removed), in lateral view.

Abbreviations: or – orbit; soc – supraoccipital crest; utd – upper temporal depression. Not to scale.

the orbital roof, where there should be a depression for the cerebral hemispheres, is poorly preserved and filled by phosphorite. Only the posterior half of the orbital roof is preserved. Hooley (1914: pl. 22, fig. 1) oriented CAMSM B.54406 with the posterior orbital roof facing almost anteriorly and the anterior margin of the supraoccipital crest almost horizontal. Comparison with the posterior skull region in *Tapejara* and *Pteranodon* suggests, however, that this fragment was oriented more vertically, with the orbital roof facing anteroventrally (Fig. 2). The construction of the posterior skull region in *Ornithostoma* is somewhat intermediate between *Tapejara* and *Pteranodon* (Fig. 2). The supraoccipital crest starts above the orbit, as in *Pteranodon*, while in *Tapejara* it is more posterior. The upper temporal depression, delimited dorsally by a prominent ridge between the orbital margin and the occiput, is about twice smaller than in *Tapejara*, but distinctly larger than in *Pteranodon*. In *Tapejara* this depression extends well into the supraoccipital crest. In *Ornithostoma* and *Pteranodon* it does not extend onto supraoccipital crest. The crest of CAMSM B.54406 is rhomboidal in cross section, with the dorsal part of the rhombus about three times greater than the ventral part (Hooley 1914: pl. 22, fig. 3). The lateral angles of the rhombus are made by the ridges delimiting the dorsal margin of the upper temporal depression.

In posterior view CAMSM B.54406 is roughly triangular in shape, tapering dorsally into presumably long supraoccipital crest (Fig. 3D). The relatively small foramen magnum is flanked dorsolaterally by posttemporal fenestrae. In some immature specimens of pterodactyloids (e.g. Fig. 3C; Kellner and Tomida 2000: fig. 9; Bennett 2001: fig. 16) dorsal to the posttemporal fenestra there is a large pneumatic foramen. There is no such foramen in CAMSM B.54406. There is a prominent median ridge between the foramen magnum and the dorsal end of the fragment; its thickness increases gradually towards the dorsal end. A weak median ridge is present in immature specimens of *Pteranodon* and *Anhanguera* (Kellner and Tomida 2000: fig. 9; Bennett 2001: 26). A strong ridge is present in the presumed azhdarchid *Hatzegopteryx* (Buffetaut et al. 2003). The phylogenetic significance of this character is not clear; the ridge development is likely correlated with the ontogenetic age of the animal and its rostrum length (the longer rostrum would required more powerful neck musculature). It is notably lacking in the short-faced *Tapejara* (Fig. 3A–C). The strong median ridge on the occiput of *Ornithostoma* may indicate its mature individual age and a relatively long rostrum. The proportions of the holotype rostrum fragment also argue for an elongated rostrum.

Cervical vertebrae

The cervical vertebrae are elongated (length to middle width ratio is 2.7–2.8; Owen 1860: pl. 10, figs 35–37; Seeley 1870: pl.10, figs 13–17). The elonga-

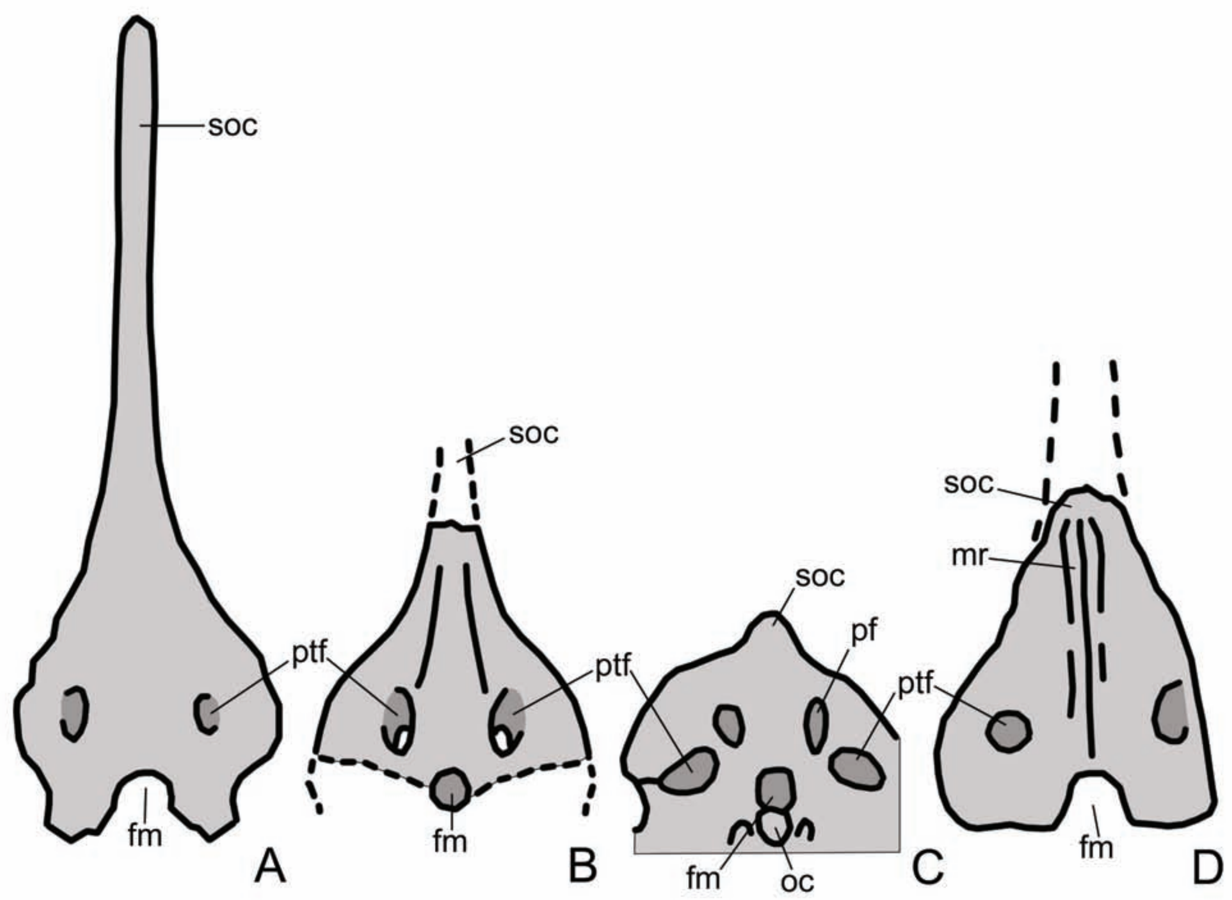

Fig. 3. Occiput of *Tapejara wellnhoferi*, SMNK PAL 1137 (A, modified from Eck et al. 2011: fig. 2), AMNH 2440 (B, modified from Wellnhofer and Kellner 1991: fig. 3b), DNPM MCT 1500–R (C, modified from Kellner 1996: fig. 8) and *Ornithostoma sedgwicki* (D, CAMSM B.54.406), in posteroventral view.

Abbreviations: fm – foramen magnum; mr – median ridge; oc – occipital condyle; pf – pneumatic foramen; ptf – posttemporal fenestra; soc – supraoccipital crest. Not to scale

tion of middle cervicals was independently developed in the Azhdarchoidea and Ctenochasmatoidea (Andres and Ji 2008). *Ornithostoma* shows only the initial stage of the elongation of middle cervicals. In the stem azhdarchid *Tupuxuara* the length to middle width ratio is 3.2 (GIUA 4895, "paratype" of *Santanadactylus brasilensis*; Buisonje 1980: fig. 5, pl. 2). Otherwise the structure of the cervicals of *Ornithostoma* is close to those of *Tupuxuara*. The neural spine is not preserved in any specimen, but apparently was blade-like. There is a pair of pneumatic foramina lateral to the neural canal. In CAMSM B.54493 there is an additional pair of smaller pneumatic foramina ventral to the larger foramina on the posterior side. The anterior side of this specimen is obscured by phosphorite. On some specimens there is a small slit-like pneumatic foramen on the lateral side of the centrum, while other specimens seem to be lacking such a foramen. This foramen is present in the Ornithocheiroidea and *Tupuxuara*. Its absence on postaxial cervical vertebrae is a likely synapomorphy for the Azhdarchidae (Andres and Ji 2008).

Humerus

The humerus CAMSM B.54081 is well preserved and complete; there is a suture between the shaft and distal epiphysis suggesting that the individual was juvenile (Seeley 1870; pl. 4, figs 1, 2; Unwin 2003: fig. 17j; Witton et al. 2009: fig.5C). This specimen was chosen as the "type" of group C of the proximal humerus ends by Hooley (1914). A similar but less complete specimen from the Cambridge Greensand (BMNH 35413) was figured by Owen (1861: pl. 3, fig. 5). The articular surface of the humeral head is crescentic in proximal view and slightly concave. The deltopectoral crest is of primitive morphology, proximally placed, relatively long and straight, with approximately parallel proximal and distal sides. The shaft is slender and straight. On the anterior side, between the bases of the deltopectoral crest and the humeral head, there is a large pneumatic foramen, as in *Azhdarcho* and other azhdarchoids (Averianov 2010). Structurally this specimen is very close to the humerus from the Barremian Wessex Formation of Isle of Wight, England, recently described as "the first record of azhdarchoid pterosaurs in the British Lower Cretaceous" (Witton et al. 2009: 676, figs 6, 7). Actually the first such record was reported 140 years earlier (Seeley 1869), and reference of some specimens from Cambridge Greensand to Azhdarchidae was suggested by previous researchers (Padian 1986; Nesov 1991). The Wessex humerus differs by larger size, more prominent ulnar condyle, relatively longer and curved deltopectoral crest, which is positioned sligthly more distal to the humeral head compared with the Cambridge Greensand specimen. All these characters, however, are likely correlated with the greater ontogenetic age of the Wessex specimen. CAMSM B.54081 is also very similar with the humerus of *Azhdarcho*; in the latter taxon the articulation surface of the humeral head is more concave and the deltopectoral crest placed slightly more distally on the shaft (Averianov 2010).

Femur

CAMSM B.54262 is a well preserved proximal part of the femur (Seeley 1870: pl. 8, figs 7–9). Seeley (1870) referred this specimen to an unknown genus, different from *Ornithocheirus*. Hooley (1914: 556) attributed this specimen to the femur group 2, of which the taxonomic attribution "must remain an open question." Unwin (2003) attributed this specimen to *Lonchodectes* sp. without explanation. CAMSM B.54262 differs from the femora of ornithocheirids known from the Cambridge Greensand by a smaller angle between the neck and the shaft (137°). According to Andres and Ji (2008) this angle of 145° or greater is a synapomorphy of the Pteranodontidae + Ornithocheiridae. Another notable difference is a large pneumatic foramen on the posterior side between the bases of the femoral neck and the greater trochanter. Seeley (1870) interpreted this hole as a pit for the external obturator muscle. A smaller pneumatic foramen in this position is present in *Pteranodon* and *Tapejara* (Bennett 2001: fig. 107B; Eck et al. 2011), but a large slit-like pneumatic foramen is characteristic for the Azhdarchidae (Averianov 2007, 2010). Actually CAMSM B.54262 is almost identical to the femur of *Azhdarcho* (Averianov 2010: fig. 34A–E). Nesov (1991: 19) previously suggested that this specimen might belong to an azhdarchid.

DISCUSSION

The new interpretation of *Ornithostoma sedgwicki* proposed herein combines cranial materials previously referred to that taxon (Seeley 1891; Hooley 1914; Unwin 2001) with the postcranial materials from the Cambridge Greensand, attributed by Unwin (2001, 2003) to *Lonchodectes*. The later attribution had a strong impact on interpretation of *Lonchodectes* as a non-ornithocheiroid pterodactyloid related to azhdarchoids (Unwin 2001, 2003; Witton et al. 2009), because these postcranial elements (cervicals, humerus, and femur) bear certain azhdarchoid characters. However, the known cranial remains of *Lonchodectes*, exclusively consisting of toothed jaw fragments, do not show any specific resemblance with azhdarchoid pterosaurs (Unwin 2001; Martill 2011). It is more parsimonious to combine the cranial remains from the Cambridge Greensand, including the toothless holotype of *O. sedgwicki* and the skull fragment CAMSM B.54406 with *Tapejara*-like supraoccipital crest, with the postcranial elements from the same stratigraphic unit bearing certain azhdarchoid characters (moderately elongated middle cervicals, humerus with straight deltopectoral crest and pneumatic foramen on ventral side, and femur with low neck to shaft angle and large pneumatic foramen at the greater trochanter). The postcranial elements of *Lonchodectes* might be present in the collection from the Cambridge Greensand but currently cannot be differentiated from the postcranial bones of other ornithocheiroids. *Lonchodectes* is likely a member of the Ornithocheiroidea (Andres and Ji 2008), but possibly deserves separation into a distinct family because of its peculiar dentition (Unwin 2001, 2003).

Unwin's interpretation of *Lonchodectes* influenced attribution of BMNH 2353, the humerus from the Valanginian Hastings Beds Group of Tilgate Forest locality in West Sussex, England, which is the holotype of *Palaeornis cliftii* Mantell, 1844, to the Lonchodectidae (Witton et al. 2009; these authors erroneously cited Hooley 1914 as the author of the family Lonchodectidae). Witton et al. (2009: 681) discussed azhdarchoid characters of BMNH 2353 and referred it to the Lonchodectidae because the proximal margins of the deltopectoral and ulnar crests are "confluent" and because of an "atypically expanded lateral condyle." The formulation of the first character is not correct: in CAMSM B.54081, referred to *Lonchodectes* by Unwin (2001, 2003) and Witton et al. (2009) and to *Ornithostoma* here, the deltopectoral and ulnar crests are not confluent, they are separated by the humeral head, but their proximal margins are located at the same level. This is not true for BMNH 2353, where the deltopectoral crest is distinctly placed more distally on the shaft, as in azhdarchids (Averianov 2010), with its proximal margin distal to the proximal margin of the ulnar crest. The lateral expansion of the distal humerus end is also found in other azhdarchoid specimens, like USNM 11925, the holotype of "*Bennettazhia*" *oregonensis* from the Albian Hudspeth Formation of Oregon, USA (Gilmore 1928). BMNH 2353, in spite of its relatively small size, is likely a mature specimen as suggested by accentuated muscle scars on the deltopectoral crest. Generally it is very similar to USNM 11925 and may belong to a closely related taxon of basal azhdarchoids. Because of the more distal position of the deltopectoral crest this taxon is more derived than *Ornithostoma*, which has a more *Tapejara*-like humerus.

Witton et al. (2009: figs 6, 7) described another humerus from the Barremian Wessex Formation of Isle of Wight, England. It is about 1.5 times larger than BMNH 2353 and differs by minor details from the latter. The Wessex specimen also has a more distally placed deltopectoral crest and belongs to an azhdarchoid more derived than *Ornithostoma*. Thus in the Early Cretaceous on the territory of modern England there possibly were at least three azhdarchoid taxa, living in different time intervals (Valanginian, Barremian, and Albian).

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