

THE EARLY CRETACEOUS PTERODACTYLOID PTEROSAUR *COLOBORHYNCHUS* FROM NORTH AMERICA

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ABSTRACT. *Coloborhynchus wadleighi*, a new pterosaur from the Paw Paw Formation (upper Albian), Texas, is closely related to an English species *Coloborhynchus clavirostris*. A dentulous partial snout shows unique tooth arrangement and a dorsal medial crest on the anterior portion of the premaxilla. This is the first tooth-bearing pterodactyloid pterosaur known from North America. The genus *Coloborhynchus* is assigned to the family Ornithocheiridae.

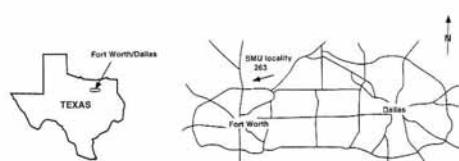
CRETACEOUS pterodactyloid pterosaurs previously recognized in North America are referred to the families Nyctosauridae, Pteranodontidae, and Azhdarchidae (*sensu* Wellnhofer 1991a). The Nyctosauridae and Pteranodontidae are best known in North America from the Niobrara Formation (Coniacian to Campanian) of western Kansas (Marsh 1872, 1876; Miller 1972). The Azhdarchidae are from the Judith River Formation (Campanian) in Alberta, Canada (Currie and Russell 1982), the Two Medicine Formation (Campanian) of Montana (Padian and Smith 1992), and the Javelina Formation (Maastrichtian) of Big Bend National Park, Texas (Lawson 1975).

In the Lower Cretaceous of North America, pterodactyloid pterosaurs are represented by three humeri. *Bennettazhia oregonensis* (Gilmore) is from the Hudspeth Formation (Albian), Oregon (Gilmore 1928; Nesson 1991), and an indeterminate pteranodontid humerus is known from the Mowry Shale of Montana (*sensu* Bennett 1989). The third humerus is an azhdarchid from the Glen Rose Formation (uppermost Aptian to lower Albian), Texas (Murry *et al.* 1991).

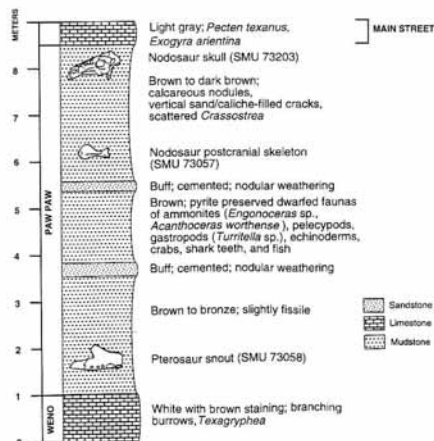
A new pterosaur specimen was discovered in the Paw Paw Formation (upper Albian), Fort Worth, Texas. It is a partial snout preserved in three dimensions. The snout has teeth and a pronounced sagittal crest. The presence of teeth clearly distinguishes the new specimen from toothless forms of North American pterodactyloid pterosaurs previously recognized from cranial remains.

OCCURRENCE

The specimen (SMU 73058, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas) was discovered in 1992 in the Paw Paw Formation, Tarrant County, Texas (Text-fig. 1). The Paw Paw Formation was named by Hill (1894) for exposures of an 18 m thick ferruginous sand and clay sequence found along Paw Paw Creek in northeast Denton and Grayson counties, Texas. Southward from the type locality, it thins and typically comprises more marine facies (Perkins and Albritton 1955). In the Tarrant County area, the formation is a brown to yellow, fossiliferous clay (8 m thick), with scattered sandstone partings. The age of the Paw Paw is between 100 and 97.5 Ma in this area, based on invertebrate faunas (Jacobs *et al.* 1994). Its environment of deposition has been interpreted to be predominantly nearshore marine, including deltaic and estuarine environments (Scott *et al.* 1978).



TEXT-FIG. 1. SMU locality 263 in Tarrant County, Texas, and stratigraphical section of the Paw Paw Formation. Inset shows major highways in Dallas/Forth Worth.



SYSTEMATIC PALAEOLOGY

Order PTEROSAURIA Kaup, 1834

Suborder PTERODACTYLOIDEA Plieninger, 1901

Family ORNITHOCHEIRIDAE Seeley, 1870

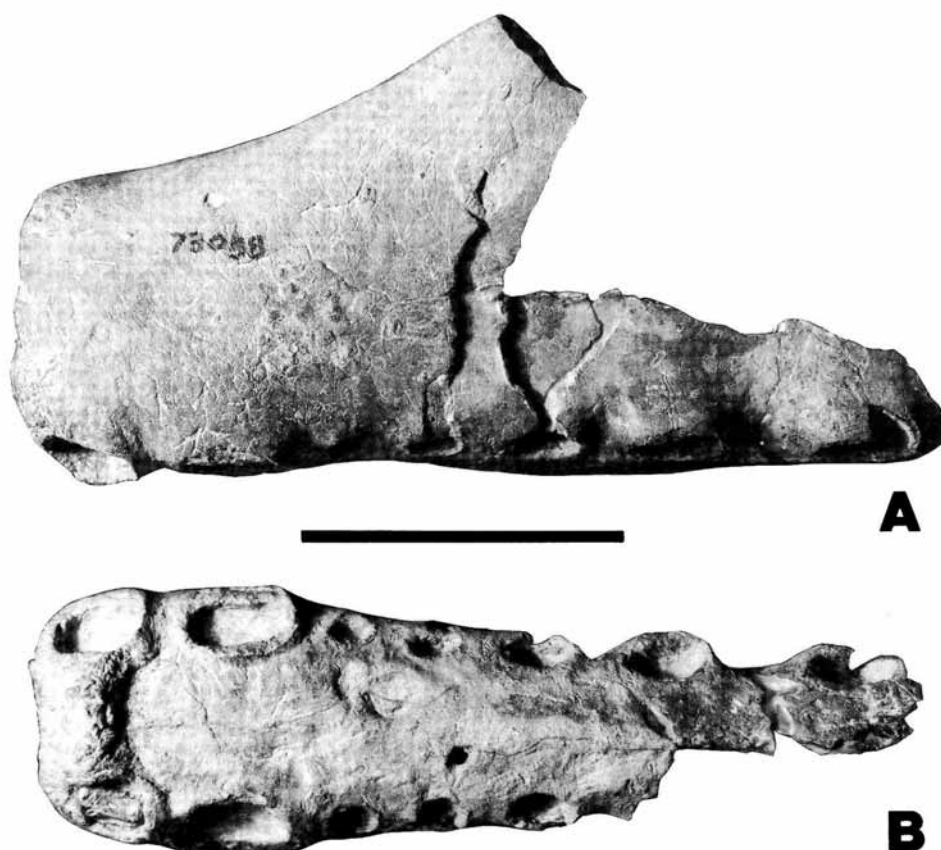
Genus *Coloborhynchus* Owen, 1874

Type species. Coloborhynchus clavirostris Owen, 1874.

Age and distribution. Berriasian to Valanginian of the Hastings Sands, St. Leonard's-on-Sea, UK, and Albian of the Paw Paw Formation, Fort Worth, Texas, USA.

Diagnosis. (Modified after Owen 1874.) The flattened anterior margin of the premaxilla is triangular in shape. A pair of teeth project anteriorly from the blunt anterior margin at a significant elevation above the palate relative to subsequent teeth. A median depression occurs on the anterior margin. The medial crest rises from near the tip of the snout.

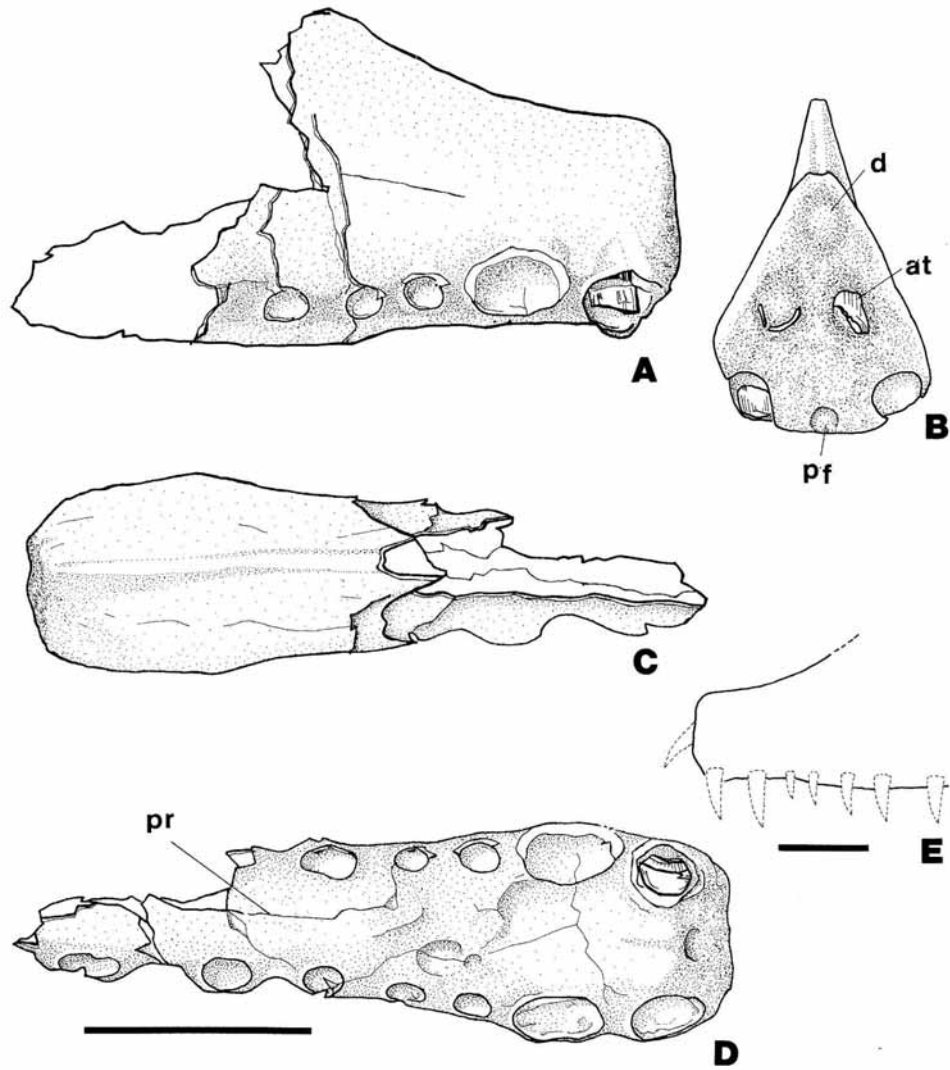
Discussion. The taxonomic history of *Coloborhynchus* is complex. Seeley (1869) grouped numerous fragments of jaws and odd bones of pterosaurs from the Cambridge Greensand into two genera, *Ptenodactylus* and *Ornithocheirus*. His original diagnosis for the genus *Ornithocheirus* was 'no teeth anterior to the palate' (Seeley 1869, p. 16). It included three species, and had for its type *Pterodactylus simus* of Owen. In 1870, Seeley's book *The Ornithosauria* was published, in which he abandoned the genus *Ptenodactylus* and referred all of the species described from the Cambridge Greensand to *Ornithocheirus*, incorrectly interpreting the type of *Pterodactylus simus* to be a lower jaw. He rediagnosed the genus *Ornithocheirus* as 'having teeth prolonged anterior to the muzzle,' and as 'having a palate with a longitudinal ridge' (Seeley 1870, p. 112). However, Owen (1874) did



TEXT-FIG. 2. *Coloborhynchus wadleighi* sp. nov.; SMU 73058, holotype; Tarrant County, Texas; Paw Paw Formation (Albian); partial snout in left lateral (A) and palatal (B) views. Scale bar represents 50 mm.

not consider *Ornithocheirus* to be valid and did not accept Seeley's conclusion that *Pterodactylus simus* belonged to *Ornithocheirus* because it is not a lower jaw. He stated 'I have no evidence, and Mr Seeley has given none, of such departure from the Pterosaurian type of hand as would justify the term *Ornithocheirus* proposed by Mr Seeley for *Pterodactylus sedgwickii* in his 'Ornithosauria' in 1870' (Owen 1874, p. 6). This circumstance led Owen to establish the new generic names, *Coloborhynchus* and *Criorhynchus*, abandoning *Ornithocheirus* in 1874.

Coloborhynchus was named for pterosaurs that have 'the foremost pair of teeth projecting forward in the upper jaw from the truncate surface at a higher level than the alveolar border' (Owen 1874, p. 6). Describing the type species, *Coloborhynchus clavirostris*, a partial snout from the Hastings Sands of the Wealden, Owen (1874) referred two other species to this genus, *Coloborhynchus cuvieri* and *C. sedgwickii*. The former was originally named by Bowerbank as *Pterodactylus cuvieri* for the anterior part of the upper jaw from the Lower Chalk of Kent at the meeting of the Zoological Society, January 14th, 1851, and the latter was described as *Pterodactylus sedgwickii* for the anterior parts of a skull and mandible from the Upper Greensand of Cambridge



TEXT-FIG. 3. *Coloborhynchus wadleighi* sp. nov.; SMU 73058, holotype; Tarrant County, Texas; Paw Paw Formation (Albian). A–D, partial snout in right lateral (A), anterior (B), dorsal (C) and palatal (D) views. E, reconstructed dentition in left lateral view. Abbreviations: at, anterior tooth; d, depression; pf, pneumatic foramen; pr, palatal ridge. Scale bars represent 50 mm.

(Owen 1859). They had been renamed *Ornithocheirus cuvieri* and *O. sedgwickii* according to Seeley's (1870) definition of *Ornithocheirus* prior to their referral to *Coloborhynchus*.

Coloborhynchus clavirostris has a medial crest. Owen (1874) described this character as 'the flattened fore part of premaxillary is broader and of less height in *Coloborhynchus clavirostris* before

the narrow upper surface begins to slope backward to the contour of the cranium' (Owen 1874, p. 7; pl. 1, figs 1–4). However, he did not include this character in the definition of *Coloborhynchus*. Owen believed *Ornithocheirus* (*sensu* Seeley 1870) was invalid and therefore included *Ornithocheirus cuvieri* and *O. sedgwickii* in his new genus *Coloborhynchus* because they shared anteriorly projecting teeth. Neither has a medial crest. To distinguish a blunt-snouted specimen with no anteriorly projecting teeth from *Coloborhynchus*, he also renamed *Pterodactylus simus*, described by himself in 1861, as *Criorhynchus simus*.

In 1881, Seeley naturally regarded *Coloborhynchus* as a synonym of *Ornithocheirus*. Citing *Coloborhynchus cuvieri* and *C. sedgwickii* as examples, he mentioned *Coloborhynchus* as follows: 'I am unable to detect any difference between Prof. Owen's definition of that genus and my previous definition in 1870 of *Ornithocheirus*' (Seeley 1881, p. 16). Therefore, *Coloborhynchus clavirostris*, which has different characters from *C. cuvieri* or *C. sedgwickii*, was implied to belong to *Ornithocheirus* (Seeley 1881).

The systematic position of *Ornithocheirus* became more and more obscure because various incomplete pterosaur bones have been referred to this genus. Hooley (1914) tried to divide the cranial material from the Cambridge Greensand, referred to the genus *Ornithocheirus* by Seeley (1870), into five named groups. Owen's two referred species of *Coloborhynchus* (*C. cuvieri* and *C. sedgwickii*) were referred to Hooley's Group 1 with the generic name *Ornithocheirus*. He knew that *Coloborhynchus clavirostris* could be distinguished from *Ornithocheirus* by its medial crest and put it into his Group 4, *Criorhynchus*. He also made it clear that *Criorhynchus simus*, the type of *Ornithocheirus*, is an upper, not a lower jaw, by the presence of a longitudinal ridge on the palate.

Owen (1874) had some doubts about the validity of *Criorhynchus*. He considered that this genus may represent a specimen of *Coloborhynchus* with shed and unreplaced anterior teeth. However, Hooley (1914) believed that *Coloborhynchus clavirostris* was a synonym of *Criorhynchus simus* in which erosion had worn the tip of the snout to expose the bases of the teeth. Thus, *Coloborhynchus* disappeared with the synonymy of *C. clavirostris* with *Criorhynchus simus*. Wellnhofer (1978, 1987) accepted the synonymy of *Coloborhynchus clavirostris* and *Criorhynchus simus*, and placed the species in the separate family Criorhynchidae.

The new material reported here clearly validates Owen's view that the two genera are distinct. The anterior margin of *Coloborhynchus clavirostris* is duplicated in the Texas specimen and is not water-worn. *Coloborhynchus clavirostris* is not a synonym of *Criorhynchus simus*. Therefore, the species should be resurrected and the genus *Coloborhynchus* is also valid with modification.

Coloborhynchus wadleighi sp. nov.

Text-figures 2–3

Holotype. SMU 73058, Shuler Museum of Paleontology, Southern Methodist University; a partial snout.

Type locality and horizon. Paw Paw Formation (Lower Cretaceous, upper Albian), Tarrant County, Texas, USA (SMU locality 263, exact location on file at SMU).

Diagnosis. Snout with flattened anterior margin from which projects a pair of anteroventrally directed teeth. An oval median depression lies above the anterior teeth. A pneumatic foramen occurs between the second pair of teeth. The second and third pairs of teeth are large and project vertically as shown by the orientation of the tooth sockets. The medial crest has a concave anterior margin beginning at the tip of the snout and rising posteriorly.

Derivation of name. *wadleighi*, in honour of Mr Chris Wadleigh, who found the specimen.

Description. The specimen is a partial snout with a median crest formed at least in part by the premaxillae (Text-fig. 2). Posterior parts of the skull including the nasopreorbital opening are missing. The cortical bone is thin (0.5–0.8 mm) and dark yellowish brown. Delicate buttresses and struts are developed on the internal

surface of the bone. This architecture, along with the thin cortical bone, persuasively shows the lightness of pterosaurian construction for flight. The crest extends from the tip of the snout and is concave as far as preserved. The concave margin of the flange as preserved represents the arc of a circle with a diameter of 240 mm, limited by a chord of 75 mm. The crest decreases in width continuously from the lateral margins of the jaw dorsally to where it forms a thin ridge (Text-fig. 3c). The ridge is approximately 4 mm wide at its narrowest. The midline forms a shallow gutter.

The rugose, flattened anterior margin of *C. wadleighi* is shaped like an acute triangle in anterior view. The corners of the triangle are rounded (Text-fig. 3B). A small pneumatic foramen lies between the second pair of teeth. The alveoli for a pair of anterior teeth are in the middle of the anterior margin, and at a greater elevation above the tooth sockets of the second pair of teeth. The anterior teeth projected anteroventrally. Just above the anterior teeth there is a shallow oval depression. The second pair of teeth occurs at the corners of the base of the anterior triangle. They project ventrally.

In palatal view (Text-figs 2B, 3D), the snout is expanded anteriorly. A broad ridge on the palate projects below the level of the tooth sockets and runs posteriorly from the fourth pair of tooth sockets. Eight oval alveoli are preserved on the left side, six on the right in this specimen. All tooth sockets on the palate face ventrally and their long axes are arranged anteroposteriorly. The tooth arrangement is somewhat peculiar (Text-fig. 3E). The middle three tooth pairs (4th, 5th, and 6th from the anterior) of *C. wadleighi* are approximately half the size of the more anterior and posterior teeth. The third tooth is the largest and the fourth tooth the smallest in this specimen, as estimated from the sizes of the alveoli (Table 1). The base of the second right tooth, oval in cross section, is preserved. The maximum diameter of this tooth is 9.2 mm.

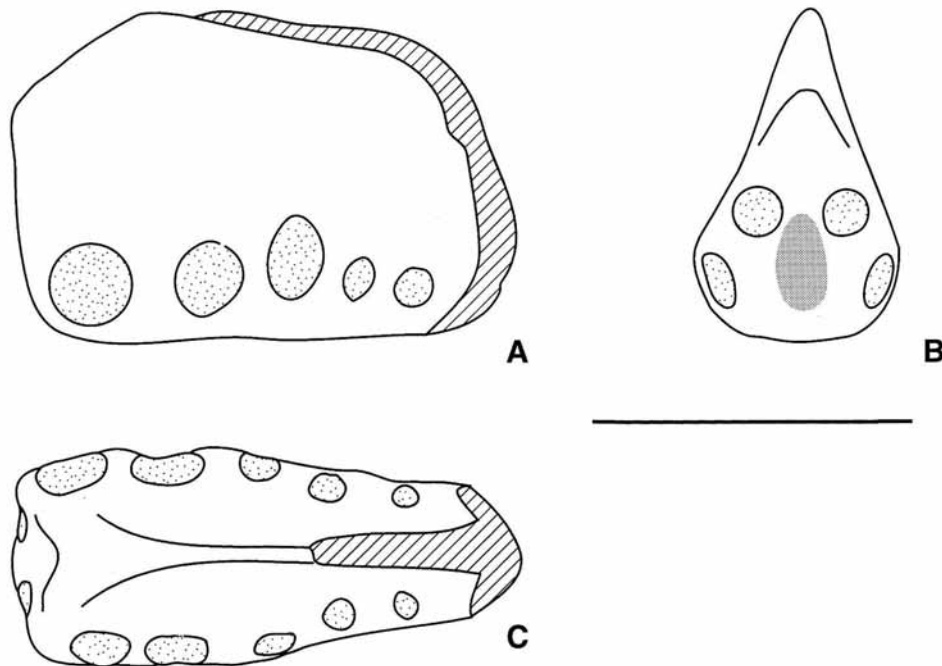
TABLE 1. Measurements in mm of maximal diameters of alveoli (anterior = 1).

	1st	2nd	3rd	4th	5th	6th	7th	8th
Left	13.0	15.0	17.7	7.2	7.9	9.8	13.6	14.3
Right	13.0	13.8	17.6	7.3	7.4	9.7	—	—

Comparisons. *Coloborhynchus wadleighi* can be compared to *C. clavirostris* (Text-fig. 4) in the position of the anterior oval depression, the crest angle, and the size and position of teeth based on sockets. An oval median depression is developed above the anterior teeth in *C. wadleighi*, while it is below the anterior teeth in *C. clavirostris*. The crest angle of *C. wadleighi* begins lower than that of *C. clavirostris* (approximately 15° and 45°, respectively). Both snouts are expanded anteriorly, but the position of tooth sockets is different in each. The palate of *C. wadleighi* is flat and teeth project ventrally. In *C. clavirostris*, the anterior three tooth sockets are ventrolaterally displaced relative to the row of subsequent teeth. The anterior three pairs of teeth are sub-equal and project ventrolaterally (Unwin 1991). In *C. wadleighi*, the first two pairs of palatal teeth are larger than the succeeding teeth.

Coloborhynchus cuvieri and *C. sedgwickii*, which Owen (1874) referred along with the type species, are excluded from *Coloborhynchus* by the absence of a median depression on the anterior margin and a medial crest rising from the snout. They are referred to *Ornithocheirus* (Seeley 1881; Hooley 1914; Wellnhofer 1978).

Discussion. *Coloborhynchus* can be distinguished easily from other dentulous crested-snout pterosaurs, *Anhanguera*, *Criorhynchus*, and *Tropeognathus*. *Anhanguera* is one of the best known pterosaurs from the Santana Formation (Aptian), Araripe Plateau, Brazil. The type species (*A. blittersdorffi*) was described and a separate family, the Anhangueridae, was erected for it by Campos and Kellner (1985). One of its conspicuous features is the 'presence of an enlargement of the distal (anterior) part of the skull, where the premaxillar (*sic*) teeth, the biggest teeth of all, are found' (Campos and Kellner 1985, p. 459). Wellnhofer (1991c) rediagnosed *Anhanguera*, the most remarkable character being the low medial crest anterior to the nasopreorbital opening, but not extending to the tip of the snout. The most distinct difference between *Coloborhynchus* and



TEXT-FIG. 4. *Coloborhynchus clavirostris* Owen; holotype; Wealden Hastings Sands; partial snout in left lateral (A), anterior (B), and palatal (C) views (drawn from Owen 1874); shadow area in B shows oval depression; scale bar represents 50 mm.

Anhanguera is the position of the medial crest. While the crest of *Anhanguera* does not extend to the tip of the snout, in *Coloborhynchus* it begins at the anterior margin of snout. Unlike *Coloborhynchus*, the crest of *Anhanguera* is thin (Campos and Kellner 1985, pl. 2, text-fig. 1), even at the base, which often causes it to be broken off. In contrast, the crest of *Coloborhynchus* decreases in width continuously from the lateral margins of the jaw to the dorsal edge where it forms a thin ridge (Text-fig. 3c). The anterior end of the snout of *Anhanguera* is not blunt but acute. The first and second teeth of *A. santanae* (AMNH 22555, American Museum of Natural History, New York) project anteroventrally (Wellnhofer 1991b, text-fig. 2), while in *Coloborhynchus* the second tooth projects ventrally from palate.

Wellnhofer (1987) assigned *Tropeognathus* from the Santana Formation to the Criorhynchidae (Hooley 1914, Group 4). The family was originally erected on the basis of fragmentary skull material of *Criorhynchus simus* from the Cambridge Greensand, England (Owen 1861). Affinity of the two genera is supported by similar high medial crests at the front end of the skull and the dentition. The laterally compressed anterior snouts without teeth of criorhynchids are clearly distinct from *Coloborhynchus*, which has a blunt triangular anterior end from which prominent anterior teeth project. In addition, the crest of *Coloborhynchus* is concave from the tip of the snout, in contrast to the convex and steep crest of *Criorhynchus* and *Tropeognathus*.

The Ornithocheiridae are based on *Ornithocheirus* (Seeley 1870, = subfamily Ornithocheirae), and are defined by two characters: 'teeth are prolonged anterior to the muzzle, and the palate has a longitudinal ridge'. The snout of *Coloborhynchus* exhibits these characters. Therefore, it is assigned to the family Ornithocheiridae.

The similarity between the Brazilian and the English Early Cretaceous pterosaurs has been suggested using as examples *Tropeognathus* and *Criorhynchus*, or *Araripesaurus* and *Ornithocheirus* (Wellnhofer 1987; Unwin 1988). However, the relationships of North American pterosaurs with English and South American pterosaurs have always been a puzzle. This is due to the very patchy fossil record of Early Cretaceous pterosaurs in North America. Therefore, the discovery of *Coloborhynchus wadleighi* is important because it is the first record that shows affinity with English pterosaurs in the Early Cretaceous. Although the phylogenetic relationships between *Coloborhynchus wadleighi* and other North American pterodactyloid pterosaurs are uncertain, it lived in North America prior to the flourishing of edentulous forms in the Late Cretaceous.

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REFERENCES

- BENNETT, S. C. 1989. A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *Journal of Paleontology*, **63**, 669–677.
- CAMPOS, D. A. and KELLNER, A. W. A. 1985. Panorama of the flying reptiles study in Brazil and South America. *Anais da Academia Brasileira de Ciências*, **57** (4), 453–466.
- CURRIE, P. J. and RUSSELL, D. A. 1982. A giant pterosaur (Reptilia: Archosauria) from the Judith River (Oldman) Formation of Alberta. *Canadian Journal of Earth Science*, **19**, 894–897.
- GILMORE, C. W. 1928. A new pterosaurian reptile from the marine Cretaceous of Oregon. *Proceedings of the United States National Museum*, **73** (24), 1–5.
- HILL, R. T. 1894. Geology of parts of Texas, Indian Territory and Arkansas adjacent to the Red River region. *Bulletin of the Geological Society of America*, **5**, 297–380.
- HOOLEY, R. W. 1914. On the ornithosaurian genus *Ornithocheirus* with a review of the specimens from the Cambridge Greensand in the Sedgwick Museum, Cambridge. *Annals and Magazine of Natural History, Series 8*, **13**, 529–557.
- JACOBS, L. L., WINKLER, D. A., MURRY, P. A. and MAURICE, J. M. 1994. A nodosaurid scuteling from the Texas shore of the Western Interior seaway. 337–346. In CARPENTER, K., HIRSCH, K. F. and HORNER, J. R. (eds.). *Dinosaur eggs and babies*. Cambridge University Press, Cambridge, 372 pp.
- KAUP, J. 1834. *Isis*, 315.
- LAWSON, D. A. 1975. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. *Science*, **187**, 947–948.
- MARSH, O. C. 1872. Discovery of additional remains of Pterosauria. *American Journal of Science*, **3**, 241.
- 1876. Notice of a new sub-order of Pterosauria. *American Journal of Science, Series 3*, **11**, 507–509.
- MILLER, H. W. 1972. The taxonomy of the *Pteranodon* species from Kansas. *Transactions of the Kansas Academy of Science*, **74** (1), 1–19.
- MURRY, P. A., WINKLER, D. A. and JACOBS, L. L. 1991. An azhdarchid pterosaur humerus from the Lower Cretaceous Glen Rose Formation of Texas. *Journal of Paleontology*, **65**, 167–170.
- NESSOV, L. A. 1991. [Giant flying reptiles of the family Azhdarchidae: I. morphology and systematics]. *Vestnik Leningradskogo Universiteta, Seriya 7, Geologiya, Geografiya*, **2**, 14–23. [In Russian with English summary].
- OWEN, R. 1851. Monograph of the fossil Reptilia of the Cretaceous formations. III. *Palaontographical Society Monograph*, **5**, 1–118.
- 1859. Monograph on the fossil Reptilia of the Cretaceous formations. Supplement. I. *Palaontographical Society Monograph*, **11**, 1–19.
- 1861. Monograph on the fossil Reptilia of the Cretaceous formations. Supplement. III. *Palaontographical Society Monograph*, **12**, 1–25.

- 1874. Monograph of the fossil Reptilia of the Mesozoic formations. I. Pterosauria. *Palaeontographical Society Monograph*, **27**, 1–14.
- PADIAN, K. and SMITH, M. 1992. New light on Late Cretaceous pterosaur material from Montana. *Journal of Vertebrate Paleontology*, **12**, 87–92.
- PERKINS, B. F. and ALBRITTON, C. C. 1955. The Washita Group in the valley of the Trinity river, Texas. A Field Guide. *Fondren Science Series*, **5**, 1–27.
- PLIENINGER, F. 1901. Beiträge zur Kenntnis der Flugsaurier. *Palaeontographica*, **48**, 65–90.
- SCOTT, R. W., FEE, D., MAGEE, R. and LAALLI, H. 1978. Epeiric depositional models for the Lower Cretaceous Washita Group. *Report of Investigation, Bureau of Economic Geology, The University of Texas at Austin*, **94**, 1–23.
- SEELEY, H. G. 1869. Index to the fossil remains of Aves, Ornithosauria and Reptilia in the Woodwardian Museum Cambridge. *Proceedings of the Cambridge Philosophical Society*, **3**, 1–169.
- 1870. *The Ornithosauria: an elementary study of the bones of pterodactyles*. Cambridge, 135 pp.
- 1881. On evidence of two ornithosaurians referable to the genus *Ornithocheirus*. *Geological Magazine*, **8**, 13–20.
- UNWIN, D. M. 1988. New pterosaurs from Brazil. *Nature*, **332**, 398–399.
- 1991. The morphology, systematics and evolutionary history of pterosaurs from the Cretaceous Cambridge Greensand of England. Unpublished Ph.D. thesis, University of Reading.
- WELLNHOFFER, P. 1978. *Handbuch der Paläoherpologie, Teil 19: Pterosauria*. Gustav Fischer Verlag, Stuttgart, 82 pp.
- 1987. New crested pterosaurs from the Lower Cretaceous of Brazil. *Mitteilung der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, **27**, 175–186.
- 1991a. *The illustrated encyclopedia of pterosaurs*. Crescent Books, New York, 192 pp.
- 1991b. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica, Abteilung A*, **215**, 43–101.
- 1991c. The Santana Formation pterosaurs. 351–370. In MAISEY, J. G. (ed.). *Santana fossils: an illustrated atlas*. T. F. H. Publications, Neptune City, 459 pp.

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