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David W. E. Hone & Eric Buffetaut (Guest Editors)

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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CONTENTS/INHALT

Dedication 3

Peter Wellnhofer
A short history of pterosaur research 7

Kevin Padian
Were pterosaur ancestors bipedal or quadrupedal?:
Morphometric, functional, and phylogenetic considerations 21

David W. E. Hone & Michael J. Benton
Contrasting supertree and total-evidence methods: the origin of the pterosaurs 35

Paul M. Barrett, Richard J. Butler, Nicholas P. Edwards & Andrew R. Milner
Pterosaur distribution in time and space: an atlas 61

Lorna Steel
The palaeohistology of pterosaur bone: an overview 109

S. Christopher Bennett
Morphological evolution of the wing of pterosaurs: myology and function 127

Mark P. Witton
A new approach to determining pterosaur body mass and its implications for pterosaur flight 143

Michael B. Habib
Comparative evidence for quadrupedal launch in pterosaurs 159

Ross A. Elgin, Carlos A. Grau, Colin Palmer, David W. E. Hone, Douglas Greenwell & Michael J. Benton
Aerodynamic characters of the cranial crest in *Pteranodon* 167

David M. Martill & Mark P. Witton
Catastrophic failure in a pterosaur skull from the Cretaceous Santana Formation of Brazil 175

Martin Lockley, Jerald D. Harris & Laura Mitchell
A global overview of pterosaur ichnology: tracksite distribution in space and time 185

David M. Unwin & D. Charles Deeming
Pterosaur eggshell structure and its implications for pterosaur reproductive biology 199

David M. Martill, Mark P. Witton & Andrew Gale
Possible azhdarchoid pterosaur remains from the Coniacian (Late Cretaceous) of England 209

Taissa Rodrigues & Alexander W. A. Kellner
Review of the pterodactyloid pterosaur *Coloborhynchus* 219

Junchang Lü, Li Xu & Qiang Ji
Restudy of *Liaoxipterus* (Istiodactylidea: Pterosauria), with comments on the Chinese istiodactylid pterosaurs 229

David M. Martill
First pterosaur remains from the Exu Formation (Cretaceous) of the Araripe Basin, Brazil 243

Eric Buffetaut
Late Cretaceous pterosaurs from France: a review 249

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer; design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

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Review of the pterodactyloid pterosaur *Coloborhynchus*

By
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Abstract

The genus *Coloborhynchus* (Pterosauria, Pterodactyloidea), previously thought to be present in Cretaceous strata of England, Brazil and the United States of America is reviewed. Despite the fragmentary nature of the type material, it shows several distinctive features leading us to restrict *Coloborhynchus* to the type species, *Coloborhynchus clavirostris* Owen, 1874 from the Hastings Beds Group (East Sussex). "*Coloborhynchus*" *wadleighi* Lee, 1994 of the Paw Paw Formation (Texas) lacks the diagnostic features of the English material and is therefore relocated to a new genus (*Uktenadactylus wadleighi* comb. nov.). The occurrence of *Coloborhynchus* in the Santana Formation of Brazil was not corroborated.

Key words: Pterosauria, Anhangueridae, *Coloborhynchus*, taxonomy

Resumo

O gênero *Coloborhynchus*, que antes se acreditava estar presente em depósitos cretáceos da Inglaterra, Brasil e Estados Unidos, é revisto. Apesar da natureza fragmentária de seu material tipo, ele possui várias características distintivas, o que nos levou a restringir *Coloborhynchus* à sua espécie-tipo, *Coloborhynchus clavirostris* Owen, 1874 do Grupo Hastings Beds (East Sussex). "*Coloborhynchus*" *wadleighi* Lee, 1994 da Formação Paw Paw (Texas) não apresenta as características diagnósticas do material inglês e, deste modo, é realocada a um novo gênero (*Uktenadactylus wadleighi* comb. nov.). A ocorrência de *Coloborhynchus* na Formação Santana, Brasil, não foi corroborada.

Palavras chave: Pterosauria, Anhangueridae, *Coloborhynchus*, taxonomia

Zusammenfassung

Die Gattung *Coloborhynchus* (Pterosauria, Pterodactyloidea), die in den kretazischen Schichten von England, Brasilien und Vereinigten Staaten registriert wurde, wird hier neu bewerted. Obwohl der Holotyp der Art *Coloborhynchus clavirostris* Owen, 1874 von den Hastings Beds Group (East Sussex) sehr unvollständig ist, kann man einige unterscheidende Merkmale erkennen so dass wir die Gattung *Coloborhynchus* auf die Typspecies begrenzen können. "*Coloborhynchus*" *wadleighi* Lee, 1994 von der Paw Paw Formation (Texas) besitzt nicht die diagnostischen Merkmale des englisches Material un wird deshalb einer neuen Gattung zugestellt (*Uktenadactylus wadleighi* comb. nov.). Das Vorkommen von *Coloborhynchus* in der Santana Formation wurde nicht bestätigt.

Schlüsselwörter: Pterosauria, Anhangueridae, *Coloborhynchus*, Taxonomie

1. Introduction

The Aptian-Albian (Pons et al. 1990; Maisey 1991; Martill 2007 and references therein) Santana Formation of the Araripe Basin has yielded some of the best preserved pterosaur material in the world. Divided into the Crato, Ipubi and Romualdo Members (Beurlen 1971), pterosaurs have been first collected in the calcareous nodules of the Romualdo Member (e.g., Price 1971; Wellnhofer 1985, 1991b; Campos & Kellner 1985; Kellner & Tomida 2000) but later were also found in the laminated calcareous limestone of the Crato Member (e.g., Frey & Martill 1994; Campos & Kellner 1997; Frey et al. 2003; Sayão & Kellner 2006).

Since the first descriptions, pterosaur specimens from the Araripe Basin have been compared to those from the Cambridge Greensand of eastern England. Several species, for instance, were referred to the Ornithocheiridae or "Criorhynchidae" at the time of their descriptions, such as *Araripesaurus castilhoi*,

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Santanadactylus brasilensis (first classified in the "Criorhynchidae" by Buisonjé 1980, and then in the Ornithocheiridae by Wellnhofer 1985), *Brasileodactylus araripensis*, *Anhanguera araripensis*, *Santanadactylus pricei*, "*Santanadactylus*" *spixi* (now regarded as a possible tapejarid, Kellner 1995, 2004), *Anhanguera santanae*, *Tropeognathus mesembrinus*, *Anhanguera robustus*, *Arthurdactylus conandoylei* and *Ludodactylus sibbicki* (Price 1971; Kellner 1984; Wellnhofer 1985, 1987; Frey & Martill 1994; Frey et al. 2003). All those species, despite being referred to groups known from the Cambridge Greensand, were classified in new genera.

Kellner & Tomida (2000) have made a broad review of the Santana Formation pterosaur fauna, with the exception of the Tapejaridae. In their work, no species were classified in the Ornithocheiridae; *Anhanguera blittersdorffi*, *Anhanguera araripensis*, *Anhanguera santanae*, *Anhanguera robustus*, *Anhanguera piscator* and *Tropeognathus mesembrinus* were referred to the Anhangueridae. However, since then some species of *Anhanguera* have been relocated to *Coloborhynchus* (Fastnacht 2001; Unwin 2001; Frey et al. 2003; Veldmeijer 2003). The latter was first recorded in the Cretaceous of the Wealden Supergroup (Owen 1874) and then supposedly in Albian deposits of Texas, USA (Lee 1994).

As has been pointed out numerous times in the literature, pterosaur specimens from the Cambridge Greensand consist of fragments of bones, the systematic assignment of which is controversial (e.g., Hooley 1914; Wellnhofer 1978; Kellner 1990, 2006; Unwin 2001). This unit comprises marine deposits formed in the Cenomanian and all pterosaur material known so far consists of disarticulated, abraded and usually incomplete elements. It is likely that the fossils were exhumed and reworked from Albian deposits (Wellnhofer 1991a; Unwin 2001).

Here we review all species referred to *Coloborhynchus* and discuss the evidence used to establish the presence of this genus in the Santana Formation. A more extensive discussion of the issues regarding the Anhangueridae, Ornithocheiridae and "Criorhynchidae" will be presented elsewhere (Rodrigues & Kellner *in prep.*).

Institutional abbreviations:

AMNH: American Museum of Natural History, New York, The United States

MN: Museu Nacional / Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

BMNH: The Natural History Museum, London, England

LINHM: Long Island Natural History Museum, New York, The United States

SMNK: Staatliches Museum für Naturkunde, Karlsruhe, Germany

SMU: Southern Methodist University, Dallas, The United States

UERJ: Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

2. Systematic Paleontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Anhangueridae Campos & Kellner, 1985

Genus: *Coloborhynchus* Owen, 1874
Type species: *Coloborhynchus clavirostris* Owen, 1874

Type locality and horizon: Wealden Supergroup (Cretaceous), Hastings Beds Group, St.-Leonards-on-Sea, East Sussex, England.

Diagnosis: the same as for the type species.

Coloborhynchus clavirostris Owen, 1874
(Figs 1.1, 2.1, 3.1)

Holotype: anterior portion of the upper jaw, consisting of premaxillae and possibly part of the maxillae (BMNH R 1822, cast MN 7058-V).

Revised diagnosis: anhanguerid pterosaur with an oval depression beneath the first pair of dental alveoli; second, third and fourth pairs of premaxillary alveoli located laterally; fifth and sixth premaxillary alveoli located more medially than the preceding alveoli on the base of the palatal ridge; anterior part of the palatal ridge bordered by two shallow longitudinally elongated depressions.

Genus: *Uktenadactylus* gen. nov.
Type species: *Uktenadactylus wadleighi* (Lee, 1994) comb. nov.

Etymology: *Uktena*, from the native American Cherokee mythology, is a great deadly snake with horns on its head and a bright blazing crest; *dactylus*, from the Greek language, means finger.

Type locality and horizon: Paw Paw Formation (Albian, Lower Cretaceous), Tarrant County, Texas, USA.

Diagnosis: the same as for the type species.

Uktenadactylus wadleighi (Lee, 1994) comb. nov.
= *Coloborhynchus wadleighi* Lee, 1994
(Figs 1.2,3, 2.2,3, 3.2)

Holotype: anterior portion of the upper jaw, consisting of premaxillae and possibly part of the maxillae (SMU 73058, cast MN 7052-V).

Revised diagnosis: anhanguerid pterosaur with an oval depression above the first pair of alveoli and presence of a ventral medial depression between the second pair of upper alveoli.

3. Taxonomic history of *Coloborhynchus clavirostris*

The genus *Coloborhynchus* was described by R. Owen, in

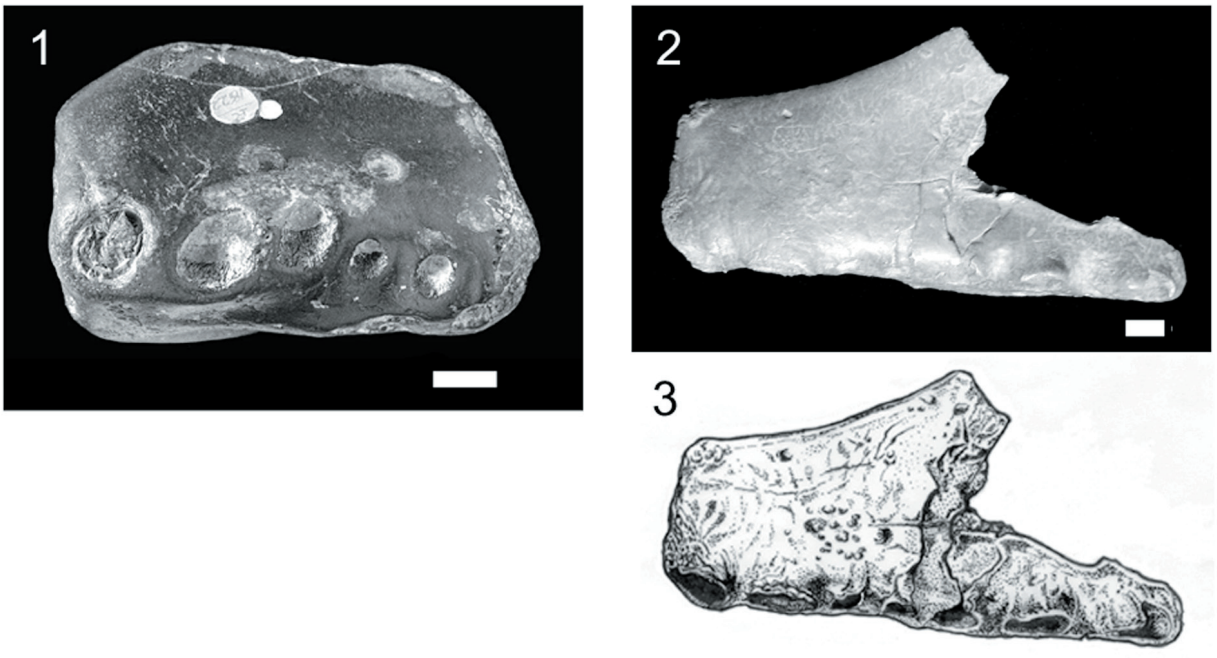

Figure 1: Left lateral view of **1**, holotype of *Coloborhynchus clavirostris* (BMNH R 1822; Cretaceous Wealden Supergroup, Hastings Beds Group, St.-Leonards-on-Sea, East Sussex, England); **2**, cast of the holotype and **3**, drawing of *Uktenadactylus wadleighi* (cast MN 7052-V; Albian, Lower Cretaceous Paw Paw Formation, Tarrant County, Texas, USA). Scale bar = 10 mm. *Coloborhynchus clavirostris* photo courtesy of The Natural History Museum.

1874, and diagnosed by the following combination of characters: anterior end of the upper jaw truncated with the foremost pair of dental alveoli of the upper jaw projecting forward and positioned at a higher level than the alveolar border (Owen 1874: 6). He referred to this genus the species "*Ornithocheirus*" *cuvieri* (Bowerbank, 1851) and "*Ornithocheirus*" *sedgwickii* (Owen, 1859), species that, in their original descriptions, had been referred to *Pterodactylus* (Bowerbank 1851; Owen 1859) and later referred to *Ornithocheirus* by Seeley (1870). Owen also added a new species, *Coloborhynchus clavirostris*, based on the anterior fragment of the upper jaw, mostly formed by the premaxillae (no suture between premaxilla and maxilla is visible). No type species was originally designated for this genus.

While reviewing part of the Cambridge Greensand pterosaur fauna, Hooley (1914: 537–538) argued that the unusual position of the first pair of dental alveoli of *Coloborhynchus clavirostris* resulted from a heavy abrasion of the tip of the premaxilla. Therefore he regarded *Coloborhynchus clavirostris* as a junior synonym of "*Criorhynchus*" *simus*. Hooley (1914) further disregarded the assignment of "*Ornithocheirus*" *cuvieri* and "*Ornithocheirus*" *sedgwickii* to the genus *Coloborhynchus.*

Kuhn (1967) regarded *Coloborhynchus clavirostris* as the type species of the genus (which can be considered a valid subsequent designation) but agreed with Hooley (1914) that this taxon was synonymous with "*Criorhynchus*" *simus*. This was followed by later workers (e.g., Wellnhofer 1978).

While describing a new pterosaur specimen from the Paw Paw Formation of the United States, Lee (1994) re-validated the genus *Coloborhynchus* (with the type species *C. clavirostris*), regarding it distinct from "*Criorhynchus*" *simus.* This was subsequently accepted by other workers (e.g., Kellner & Tomida 2000; Fastnacht 2001; Unwin 2001; Veldmeijer 2003).

Examination of the holotype of *Coloborhynchus clavirostris* (BMNH R 1822; cast MN 7058-V) shows that the anterior margin is flattened, with a relatively deep (ca. 2.5 mm) medial depression beneath the first pair of alveoli. Only the first six pairs of tooth sockets are preserved. As pointed out previously (e.g., Owen 1874), the first pair faces anteriorly and is positioned higher than the second one. The second, third and fourth pairs of alveoli have a lateral orientation, thus forming a high alveolar row (Fig. 1). It is not clear if those are the result of weathering or a true anatomical feature. The two subsequent pairs of alveoli face ventrally. In ventral view, a quadrangular anterior expansion can be observed. The palatal ridge does not reach the tip of the snout, starting at the level of the second alveoli, bordered by two shallow, longitudinally elongated depressions. Posteriorly, this ridge becomes more prominent. The fifth and sixth alveoli are closer to the midline than the others and there is no depressed area showing a clear limit between the palatal ridge and the alveolar row, contrary to the condition observed in other toothed taxa (e.g., *Anhanguera*, *Tropeognathus*). *Coloborhynchus clavirostris* also differs in this respect from *Uktenadactylus wadleighi*: in the latter taxon, this region is broader although not showing a marked depressed area.

The premaxillary crest of *Coloborhynchus clavirostris*, which begins at the tip of the rostrum, is robust but thins from base to top. In lateral view, the anterior-most margin of the

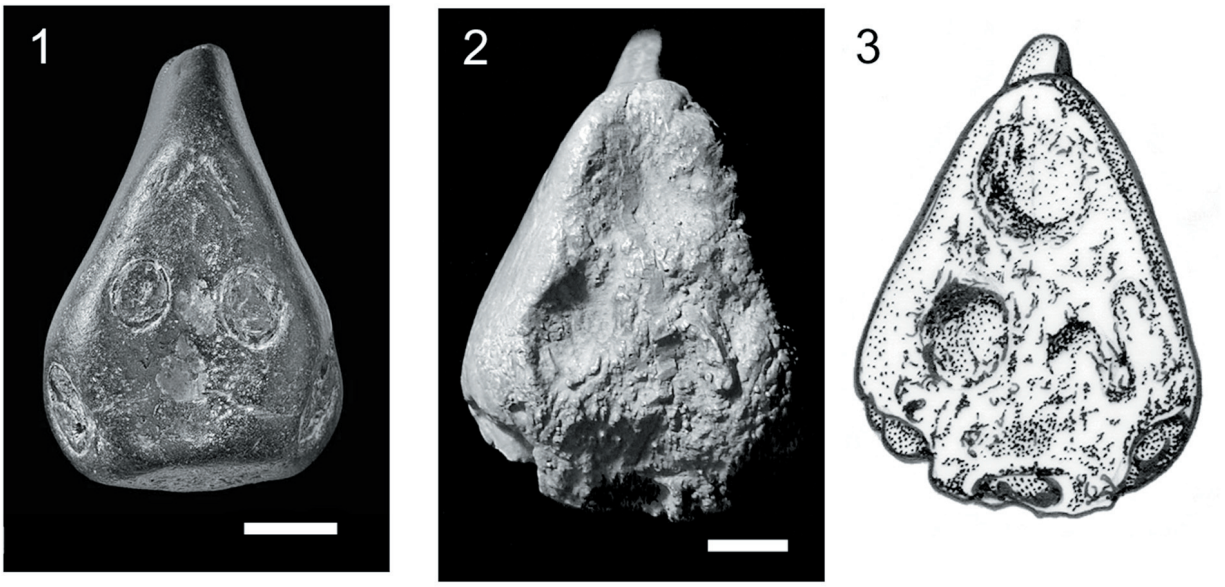

Figure 2: Anterior view of **1**, holotype of *Coloborhynchus clavirostris* (BMNH R 1822; Cretaceous Wealden Supergroup, Hastings Beds Group, St.-Leonards-on-Sea, East Sussex, England); **2**, cast of the holotype and **3**, drawing of *Uktenadactylus wadleighi* (cast MN 7052-V; Albian, Lower Cretaceous Paw Paw Formation, Tarrant County, Texas, USA). Scale bar = 10 mm. *Coloborhynchus clavirostris* photo courtesy of The Natural History Museum.

crest is straight. To our knowledge, the combination of those features has not been reported in any pterodactyloid before. According to Naish (personal communication 2007), a second specimen of *Coloborhynchus clavirostris* shows all the main features of this taxon.

With the description of the species *Uktenadactylus wadleighi* (originally regarded as *Coloborhynchus*), Lee (1994: 756) modified the diagnosis of the genus *Coloborhynchus*, as made by Owen (1874), pointing out the following characters:

1. Flattened and triangular anterior margin of the premaxilla;

2. One pair of teeth projecting anteriorly and located above the subsequent teeth;

3. Presence of an anterior median depression;

4. Premaxillary crest beginning near the tip of the skull.

Regarding character 1, both *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi* have a flattened anterior margin of the skull, a character which suggests that these taxa are closely related. This feature is not present in *Anhanguera*, such as *Anhanguera blittersdorffi* (Campos & Kellner 1985; Lee 1994: 761). The holotype of *Anhanguera spielbergi* does not have the tip of the rostrum preserved and therefore its shape cannot be observed accurately. In MN 4735-V, referred to *Anhanguera araripensis* (Kellner & Tomida 2000), the anterior portion of the snout is slightly rounded, thus differing from *Coloborhynchus clavirostris*. In *Anhanguera piscator*, there is a flattened margin just above the first pair of teeth, but not to the extent observed in *Coloborhynchus clavirostris*. An approximately triangular anterior margin is also absent in *Anhanguera*, being present in both *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi*.

The placement of the first pair of alveoli in a higher level than the second one (character 2) is common in most toothed pterosaurs from the Santana Formation, including the species of *Anhanguera*, *Tropeognathus mesembrinus* and *Ludodactylus sibbicki* (pers. observation). This feature is also present in species from the Cambridge Greensand, such as "*Ornithocheirus*" *sedgwickii* (Owen 1859) and "*Ornithocheirus*" *cuvieri* (Bowerbank 1851), in *Caulkicephalus trimicrodon* from the Isle of Wight (Steel et al. 2005), and *Siroccopteryx moroccensis* from Morocco (Mader & Kellner 1999). Since this feature is present in several genera, we conclude that the position of the first pair of alveoli at a higher level than the others is more widespread in the group (the unnamed clade at node 25 in Kellner 2003), rather than diagnostic for a single genus.

An anteriorly located depression (character 3) is present in both *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi*. However, it is located in different places relative to the position of the first pair of teeth (it is ventral to them on the former and dorsal to them on the later) and therefore does not appear to be homologous but rather different in these taxa.

Coloborhynchus clavirostris has a crest that begins at the tip of the rostrum (character 4 of Lee 1994). A crest in such a position is also present in *Tropeognathus mesembrinus*, where the shape of this structure is convex, differing from the straight anterior margin as preserved on *Coloborhynchus clavirostris*. The crest begins more posteriorly in *Siroccopteryx moroccensis*, *Uktenadactylus wadleighi* (*contra* Lee 1994) and *Anhanguera* (*Anhanguera blittersdorffi*, *Anhanguera piscator* and MN 4735-V) (Lee 1994; Mader & Kellner 1999).

An additional character that Lee (1994) described but did not include in the proposed diagnosis for *Coloborhynchus*

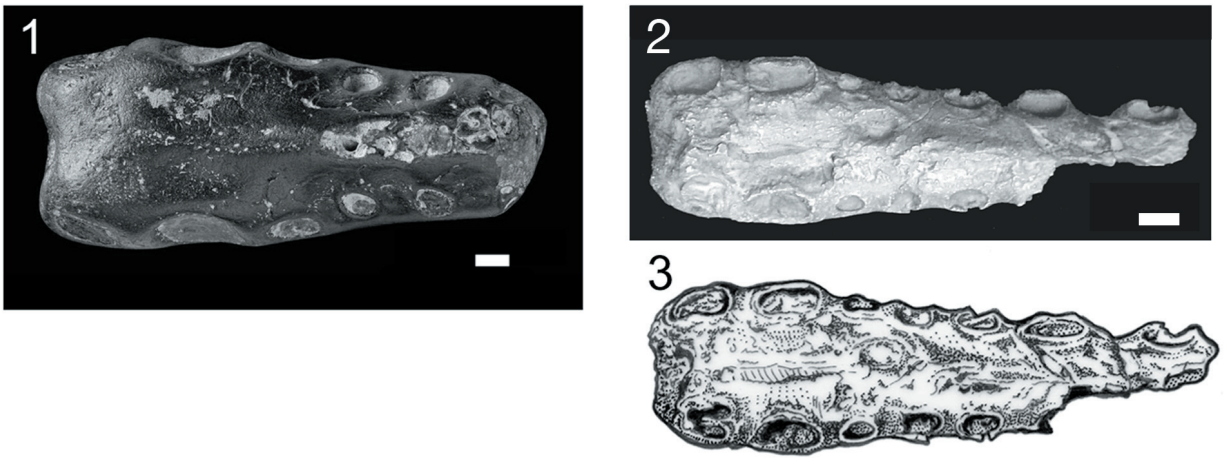

Figure 3: Ventral view of **1**, holotype of *Coloborhynchus clavirostris* (BMNH R 1822; Cretaceous Wealden Supergroup, Hastings Beds Group, St.-Leonards-on-Sea, East Sussex, England); **2**, cast of the holotype of *Uktenadactylus wadleighi* (cast MN 7052-V; Albian, Lower Cretaceous Paw Paw Formation, Tarrant County, Texas, USA). Scale bar = 10 mm. *Coloborhynchus clavirostris* photo courtesy of The Natural History Museum.

regards the thickness of the premaxillary crest. In *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi*, it gets thinner gradually from base to top. Meanwhile, in all species of *Anhanguera* and in *Tropeognathus mesembrinus* (*contra* Wellnhofer 1987) it is very thin, even at the base.

Fastnacht (2001: 24) added the following characters to the generic diagnosis proposed by Lee (1994):

1. Skull with a lateral spoon-shaped expansion from the second to the fourth pairs of alveoli;

2. Mandibular crest beginning anteriorly;

3. Mandible with a lateral spoon-shaped expansion from the first to the third pairs of alveoli;

4. Second and third pairs of upper and lower alveoli relatively larger than the others.

The presence of an anterior expansion of the premaxilla (character 1) is observed in several pterosaur species from the Araripe Basin (and in some from the Cambridge Greensand) regarded as belonging to different genera (e.g., Wellnhofer 1991b; Kellner & Tomida 2000; Fastnacht 2001). Furthermore, this feature has been considered diagnostic for the Anhangueridae by Campos & Kellner (1985) and Kellner & Tomida (2000) (or the Ornithocheiridae, Bakhurina & Unwin 1995) and is present in *Anhanguera*, *Coloborhynchus* and *Tropeognathus*. Fastnacht (2001: 24) pointed out that the posterior limit of this expansion in *Coloborhynchus* is the fourth alveolus, but our examination of *Coloborhynchus clavirostris* (the type species of this genus) showed that the expansion goes up to the fifth alveolus. Although it is not easy to establish the limits of this expansion, *Uktenadactylus wadleighi*, *Anhanguera piscator* and *Anhanguera araripensis* (referred specimen MN 4735-V) also show the posterior end of this expansion up to the fifth alveolus. Therefore we do not regard this feature as diagnostic at a generic level.

The supposed diagnostic features found in the lower jaw (characters 2 and 3) are problematic since the holotype of *Coloborhynchus clavirostris* lacks the mandible and we regard this genus as restricted to the type species (see above). Furthermore, regarding character 2, it is worthy of note that all anhanguerid mandibles bear dentary crests that begin at the tip of the jaw (e.g., *Anhanguera robustus*, *Anhanguera piscator*, *Anhanguera spielbergi* and *Tropeognathus mesembrinus*), indicating that it is widely distributed within this group. The same is true for the distal expansion of the mandible (character 3), that can also be found in *Brasileodactylus araripensis* (Kellner 1984; Kellner & Tomida 2000).

Second and third pairs of alveoli significantly larger than the subsequent ones (character 4 of Fastnacht 2001) is a feature present in the upper jaw of both *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi*. There is some variation in these sizes among the species of *Anhanguera* of the Santana Formation. In *Anhanguera blittersdorffi* (holotype), the second and third alveoli appear to be the largest ones while in Pz-DBAV-UERJ 40 (Kellner & Tomida 2000; Rodrigues & Kellner *in prep.*), AMNH 22555 (referred to *Anhanguera santanae* by Wellnhofer 1991b, mistakenly regarded as the holotype of the species by Fastnacht 2001: 31) and *Anhanguera spielbergi* (Veldmeijer 2003), the largest ones are the third and fourth. Furthermore, this size pattern of the anterior teeth can be also observed in *Caulkicephalus trimicrodon* (second and third are the largest, Steel et al. 2005). On neither of those species, however, are the size differences as much as those observed in *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi*.

Unwin (2001: 205–206), while reviewing the Cambridge Greensand pterosaur species, although not providing a diagnosis for *Coloborhynchus*, pointed out some characters for the genus:

1. Anterodorsal margin of the premaxillary crest concave in lateral view;

2. Second and third upper pairs of alveoli directed forwards and outwards.

Coloborhynchus clavirostris does not possess a concave premaxillary crest (character 1). The alveoli of this species

are indeed directed laterally (character 2), but this is not the condition observed in *Uktenadactylus wadleighi.*

The last researcher to comment on *Coloborhynchus* was Veldmeijer (2003), who also cited some characters as diagnostic of this genus:

1. Maxillae slightly raised in relation to the palate;
2. Presence of a robust distal expansion.

It is not quite clear what is meant by the first feature (character 1). There is no visible suture between the premaxilla and the maxilla in the holotype of *Coloborhynchus clavirostris*, which is also the case in most anhanguerids (e.g., *Anhanguera*, *Uktenadactylus wadleighi*). The alveolar row is placed more laterally (and higher in the skull) in *Coloborhynchus clavirostris* while the palatal ridge is deeper and is visible in lateral view. In *Uktenadactylus wadleighi*, the alveolar row lies ventrally and only a small part of the palatal ridge can be observed in the preserved posterior region.

Both *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi* have a robust quadrangular expansion (Veldmeijer 2003: 45, 96) (character 2). Species of *Anhanguera* have a slight distal expansion (Veldmeijer 2003), and in *Tropeognathus* it is even more discrete, but still present (Kellner & Tomida 2000 and personal observation, *contra* Wellnhofer 1987; Fastnacht 2001).

Based on the observations above, *Coloborhynchus clavirostris* and *Uktenadactylus wadleighi* display features that are regarded as synapomorphies of the Anhangueridae (e.g., Campos & Kellner 1985; Kellner 2003; Wang et al. 2005) such as the laterally expanded anterior end of the upper jaw, the presence of a premaxillary sagittal crest, and the comparatively large premaxillary teeth. They share some characters that appear not to be present in other anhanguerids such as the large second and third pairs of upper alveoli, which are larger relative to the remaining alveoli than in other anhanguerids. They further share some features with *Siroccopteryx moroccensis* (LINHM 016), such as the thickness of the premaxillary crest, the anteriorly-flattened rostrum and the quadrangular anterior expansion of the premaxillae, suggesting that those three taxa are more closely related to one another than to other anhanguerids. They also display features widespread within anhanguerids such as the first pair of teeth projecting anteriorly and located above the subsequent teeth.

Notwithstanding those similarities, each of those taxa presents unique characters. *Coloborhynchus clavirostris* possesses an oval depression ventral to the first pair of alveoli. This species further shows the second, third and fourth pairs of alveoli oriented laterally to a degree not reported in any other anhanguerid. Besides those features, *Coloborhynchus clavirostris* has some alveoli (the fifth and sixth) located on the base of the palatal ridge and very close to the midline of the upper jaw. Lastly, there are two shallow longitudinally elongated depressions bordering the anterior part of the palatal ridge.

Uktenadactylus wadleighi lacks the above mentioned features. This species also shows an oval depression dorsal to the first pair of alveoli that, due to its position, is not regarded as homologous with the more ventrally located depression observed in *Coloborhynchus clavirostris*. Furthermore, *Uktenadactylus wadleighi* displays an unusual ventral medial depression between the second pair of alveoli, a feature regarded by Lee (1994) as a pneumatic foramen.

Although both specimens are quite incomplete, they surprisingly show many distinct anatomical features, among them the position of the premaxillary crest. They further were found in deposits of distinct geographical regions and different age. Therefore we restrict the genus *Coloborhynchus* to the type species (*Coloborhynchus clavirostris*) and erect a new genus for the Paw Paw specimen, *Uktenadactylus wadleighi* gen. nov.

4. Other species referred to *Coloborhynchus*

Fastnacht (2001) described a specimen from the Romualdo Member (SMNK PAL 2302), comprising the anterior portions of an associated skull and mandible, and referred it to *Coloborhynchus* based essentially on Lee's diagnosis (Fastnacht 2001: 27). He regarded this material as representing a previously described species which he relocated to this genus (*Coloborhynchus robustus*).

Although Fastnacht (2001) did not explicitly discuss each feature shared by SMNK PAL 2302 and *Coloborhynchus clavirostris*, he provided a comparative table showing several anatomical characteristics and some other pterosaur species. Since a detailed analysis of those features and species is beyond the scope of this paper, we will restrain our discussion below to the comparisons between SMNK PAL 2302 and *Coloborhynchus clavirostris*.

Four features common to SMNK PAL 2302 and *Coloborhynchus clavirostris* (and *Uktenadactylus wadleighi*, which he regarded as *Coloborhynchus*) were cited by Fastnacht (2001): "heterodonty", anterior expansion of the upper jaw, shape (size?) of the first three pairs of alveoli, and the orientation of the first pair of alveoli. The size pattern of the anterior teeth ("heterodonty") is present in other anhanguerids (Kellner & Tomida 2000) and not exclusive to SMNK PAL 2302 and *Coloborhynchus clavirostris*. As pointed out previously, the expansion of the upper jaw varies and there is no particular detail of this region that could be regarded as exclusive to SMNK PAL 2302 and *Coloborhynchus clavirostris*. On the contrary, *Coloborhynchus clavirostris* has a quadrangular expansion while SMNK PAL 2302 has a more rounded expansion more similar to *Anhanguera* (e.g., *Anhanguera blittersdorffi*). Fastnacht (2001) pointed out a particular difference in size of the diameter of the first alveolus relative to the second and third. However, this feature has to be measured in a larger sample, including more species before its significance can be properly assessed. Our measurements of *Coloborhynchus clavirostris* indicate larger differences from the first to the second and third pairs than indicated by Fastnacht (2001). The last feature listed is the position of the first pair of alveoli, which, however, is more widespread among anhanguerids and related taxa and not exclusive to the genus *Coloborhynchus* (see discussion above).

There are several differences between SMNK PAL 2302 and *Coloborhynchus clavirostris*, some of which have been pointed out by Fastnacht (2001: 32). One of the main differences is the height of the rostrum, which in SMNK PAL 2302 is wider than high, while the reverse is observed in *Coloborhynchus clavirostris* (Fastnacht 2001). The premaxillary crest of the

latter has a thick base while in SMNK PAL 2302 (and in *Anhanguera*) the base is very thin.

Based on the comparisons above, we could not find clear unique features that allow the assignment of SMNK PAL 2302 to *Coloborhynchus*. The configuration of the crest and the comparatively low anterior end of the premaxillae suggest that SMNK PAL 2302 represents a species of *Anhanguera*. The assignment of this specimen to a particular species will be addressed elsewhere (Rodrigues & Kellner, *in prep.*).

Fastnacht (2001) has referred *Anhanguera robustus*, which is based on a lower jaw, to *Coloborhynchus* (known only from upper jaws) only due to the assignment of SMNK PAL 2302 to that genus. Since we restrict the genus to the type species (*Coloborhynchus clavirostris*), there is no reason to refer *Anhanguera robustus* to *Coloborhynchus*, as both lack comparable elements. We follow Kellner & Campos (1988) and Kellner & Tomida (2000) in classifying this species in the genus *Anhanguera*.

Unwin (2002) referred *Anhanguera piscator* to *Coloborhynchus*, as a synonym of *Anhanguera robustus*, using the terminology *Coloborhynchus robustus*. *Anhanguera piscator* presents a rounded anterior expansion of the premaxillae and a thin rounded premaxillary crest that does not begin at the tip of the rostrum (Kellner & Tomida 2000), differing in those aspects from *Coloborhynchus clavirostris*. It also does not present the laterally oriented teeth observed in *Coloborhynchus clavirostris*. We therefore regard *Anhanguera piscator* not referable to the genus *Coloborhynchus*. Its validity as a different species from *Anhanguera robustus* will be discussed elsewhere (Rodrigues & Kellner, *in prep.*).

Veldmeijer (2003) described a pterosaur taxon from the Romualdo Member, naming it "*Coloborhynchus*" *spielbergi*. This assignment was based on the flat anterior surface of the rostrum and the "raised maxillae", both of which, as discussed above, are problematic. According to the original description, the anterior part of the skull is not very well preserved and the first pair of alveoli was only observed using CT-scanning (Veldmeijer 2003: 43, 50–51). Therefore it is not certain how "flat" this anterior portion of the skull is. Nevertheless, although these features might distinguish this species from others, it is widespread within anhanguerids and closely related taxa (see discussion above) and is not unique to *Coloborhynchus*. It is not clear what Veldmeijer (2003) means by "raised maxillae". In any case, the alveolar margin in the type species

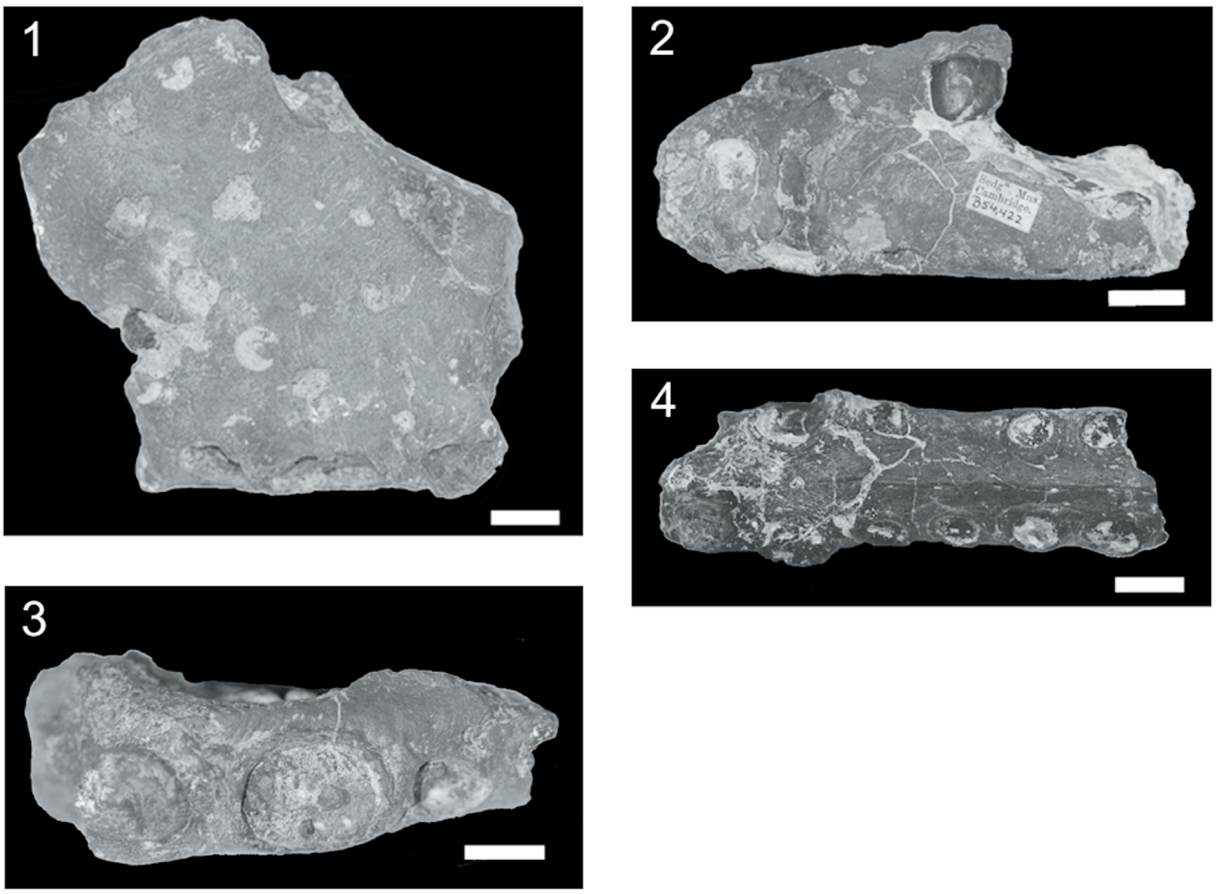

Figure 4: 1, Right lateral view of the holotype of "*Ornithocheirus*" *capito*; **2**, left lateral view of the holotype of "*Ornithocheirus*" *sedgwickii*; **3**, ventral view of the holotype of "*Ornithocheirus*" *capito* (CAMSM B 54625; Cenomanian, Cambridge Greensand, Cambridge, England.); **4**, ventral view of the holotype of "*Ornithocheirus*" *sedgwickii* (CAMSM B 54422; Cenomanian, Cambridge Greensand, Cambridge, England). Scale bar = 10 mm.

of *Coloborhynchus* is positioned higher with respect to the ventral margin, exposing the palate in lateral view, which is not the case in "*Coloborhynchus*" *spielbergi*. This species has a premaxillary crest that is very thin, and a slight, rather than quadrangular, distal expansion of the skull (*contra* Veldmeijer 2003), more similar to the condition reported in *Anhanguera*. Kellner (2006) relocated this species in the genus *Anhanguera*, a decision which will be discussed elsewhere (Rodrigues & Kellner, *in prep.*).

Veldmeijer (2003) further referred *Anhanguera robustus* and *Anhanguera piscator* to *Coloborhynchus* (see above) and also included *Anhanguera araripensis* in this genus. Concerning *Anhanguera araripensis*, its holotype lacks elements comparable with the holotype of *Coloborhynchus clavirostris* and its classification in *Coloborhynchus* was based on MN 4735-V (Veldmeijer 2003: 99), referred to *Anhanguera araripensis* by Kellner & Tomida (2000). The premaxillary crest of MN 4735-V, despite being affected by diagenetic processes, is thin from base to top, differing from *Coloborhynchus clavirostris*. MN 4735-V has a rounded, rather than quadrangular, distal expansion of the skull and does not have much larger second and third pairs of alveoli in relation to subsequent ones, as seen in *Coloborhynchus clavirostris*. It also lacks the diagnostic characters of the latter (see above) and is therefore excluded from this genus.

Unwin (2001: 206) referred *Siroccopteryx moroccensis* from the Albian/Cenomanian of Morocco to the genus *Coloborhynchus*, based on the supposed resemblance of this taxon with *Uktenadactylus wadleighi* (then considered in the genus *Coloborhynchus*, Lee 1994), which was followed by Frey et al. (2003). However, no features supporting this relationship were presented by these authors. As pointed out by Mader & Kellner (1999), *Siroccopteryx moroccensis* differs from *Uktenadactylus wadleighi* in its straight anterior-most margin of the premaxillary crest and the anterior portion of the rostrum, which is narrower than in *Uktenadactylus*, among other differences. *Siroccopteryx moroccensis* still differs from *Coloborhynchus clavirostris* by the location and angle of the crest, and lacks the unique features of *Coloborhynchus clavirostris* (see diagnosis above). We consider *Siroccopteryx moroccensis* a valid taxon, a view that has also been supported by Fastnacht (2001).

Unwin (2001) referred two species from the Cambridge Greensand, "*Ornithocheirus*" *capito* and "*Ornithocheirus*" *sedgwickii* to *Coloborhynchus*. "*Ornithocheirus*" *capito* is represented by a fragmentary anterior portion of the right side of an upper jaw that includes three alveoli (CAMSM B 54625) (Fig. 4.1,3). There is a large sagittal crest but its anterior or dorsal margin is not complete. In the most anterior alveolus there is the base of a tooth showing strong striations. Other than that, there is not much that one can get from this specimen and its classification in *Coloborhynchus* (or any genus) is open to debate.

The holotype of "*Ornithocheirus*" *sedgwickii* comprises two fragments, one of the anterior part of the mandible (CAMSM B 54421) and the other of the skull (CAMSM B 54422) (Fig. 4.1,4), both without crests (Wellnhofer 1978; Unwin 2001). None of the diagnostic features of *Coloborhynchus clavirostris* can be observed. Therefore we do not regard this species as referable to *Coloborhynchus*. If it represents *Ornithocheirus*, as thought by other authors (e.g., Hooley 1914; Wellnhofer 1978; Lee 1994), it is beyond the scope of this paper and will be addressed elsewhere.

5. Final remarks

Working with fragmentary material is a difficult task. It is even more challenging to compare and refer more complete specimens to fragmentary type material. Several authors have approached the taxonomy of the Cambridge Greensand pterosaurs (e.g., Seeley 1870; Owen 1874; Hooley 1914; Kellner 1990; Fastnacht 2001; Unwin 2001) in order to identify characters that could help sort them out into more inclusive groups (i.e., genera, families). As pointed out recently by Fastnacht (2001), *Coloborhynchus clavirostris* has several features that distinguish this taxon from other pterosaurs, which he regards as variation within the same species. However, those differences seem remarkable in such a small fragmentary specimen, and therefore we consider it of taxonomic value. Those characters seem to be replicated in an unpublished specimen referable to *Coloborhynchus clavirostris* (Naish, personal communication 2007). Therefore we restrict the genus *Coloborhynchus* to the type species (*C. clavirostris*).

The species "*Coloborhynchus*" *wadleighi* also possesses unique features (an oval depression dorsal to the first pair of alveoli and a ventral medial depression between the second pair of upper alveoli), besides a particular combination of characters, that distinguish it from all other pterosaurs. Accordingly, we regard it as a representative of a new genus, *Uktenadactylus* gen. nov.

The phylogenetic relationships of the Anhangueridae and related taxa (e.g., Ornithocheiridae, Lonchodectidae) are currently the subject of extensive work (Rodrigues, *in prep.*). We expect that a cladistic analysis of those species may help further untangle the group's taxonomy and systematics.

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6. References

Bakhurina, N. N. & Unwin, D. M. (1995): A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. – Historical Biology, **10:** 1–47.

Beurlen, K. (1971): As condições ecológicas e faciológicas da Formação Santana na Chapada do Araripe (nordeste do Brasil). – Anais da Academia Brasileira de Ciências (supl.), **43:** 411–415.

Bowerbank, J. S. (1851): On the pterodactyles from the Chalk Formation. – Proceedings of the Zoological Society of London: 14–20.

Buisonjé, P. H. (1980): *Santanadactylus brasilensis* nov. gen., nov. sp., a long-necked, large pterosaurier from the Aptian of Brazil. I. – Palaeontology Proceedings, B **83:** 145–157.

Campos, D. A. & Kellner, A. W. A. (1985): Panorama of the flying reptiles study in Brazil and South America. – Anais da Academia Brasileira de Ciências, **57:** 453–466.

Campos, D. A. & Kellner, A. W. A. (1997): Short note on the first occurence of Tapejaridae in the Crato Member (Aptian), Santana Formation, Araripe Basin, northeast Brazil. – Anais da Academia Brasileira de Ciências, **69:** 83–87.

Fastnacht, M. (2001): First record of *Coloborhynchus* (Pterosauria) from the Santana Formation (Lower Cretaceous) of the Chapada do Araripe, Brazil. – Paläontologische Zeitschrift, **75:** 23–36.

Frey, E. & Martill, D. M. (1994): A new pterosaur from the Crato Fomation (Lower Cretaceous, Aptian) of Brazil. – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **194:** 379–412.

Frey, E., Martill, D. M. & Buchy, M. C. (2003): A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur. – In: E. Buffetaut & J.-M. Mazin (Eds.), Evolution and Palaeobiology of Pterosaurs. – London, Geological Society Special Publications, **217:** 55–63.

Hooley, R. W. (1914): On the ornithosaurian genus *Ornithocheirus* with a review of the specimens from Cambridge Greensand in the Sedgwick Museum, Cambridge. – Annals and Magazine of Natural History, **8:** 529–557.

Kellner, A. W. A. (1984): Ocorrência de uma mandíbula de Pterosauria (*Brasileodactylus araripensis*, nov. gen.; nov. sp) na Formação Santana, Cretáceo da Chapada do Araripe, Ceará – Brasil. – In: Anais do XXXIII Congresso Brasileiro de Geologia; Rio de Janeiro (Sociedade Brasileira de Geologia), 578–590.

Kellner, A. W. A. (1990): Os répteis voadores do Cretáceo brasileiro. – Anuário do Instituto de Geociências, UFRJ / CCMN: 86–106.

Kellner, A. W. A. (1995): The relationships of the Tapejaridae (Pterodactyloidea) with comments on pterosaur phylogeny. – In: A. Sun & Y. Wang (Eds), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota; Beijing (China Ocean Press), 73–77.

Kellner, A. W. A. (2003): Pterosaur phylogeny and comments on the evolutionary history of the group. – In: E. Buffetaut & J.-M. Mazin (Eds.), Evolution and Palaeobiology of Pterosaurs. – London, Geological Society Special Publications, **217:** 105–137.

Kellner, A. W. A. (2004): New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. – Ameghiniana, **41:** 521–534.

Kellner, A. W. A. (2006): Pterossauros – os Senhores do Céu do Brasil. Relato inédito da aventura de importantes descobertas da paleontologia; Rio de Janeiro (Vieira & Lent), 176 pp.

Kellner, A. W. A. & Campos, D. A. (1988): Sobre um novo pterossauro com crista sagital da Bacia do Araripe, Cretáceo Inferior do nordeste do Brasil. – Anais da Academia Brasileira de Ciências, **60:** 459–469.

Kellner, A. W. A. & Tomida, Y. (2000): Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), northeastern Brazil. – National Science Museum Monographs no. 17; Tokyo, 135 pp.

Kuhn, O. (1967): Die fossile Wirbeltierklasse Pterosauria; Krailling bei München (Oeben), 52 pp.

Lee, Y. N. (1994): The Early Cretaceous pterodactyloid pterosaur *Coloborhynchus* from North America. – Palaeontology, **37:** 755–763.

Mader, B. J. & Kellner, A. W. A. (1999): A new anhanguerid pterosaur from the Cretaceous of Morocco. – Boletim do Museu Nacional, nova série Geologia, **45:** 1–11.

Maisey, J. G. [Ed.] (1991): Santana Fossils: An Illustrated Atlas; Neptune (T. F. C. Publications), 459 pp.

Martill, D. M. (2007): The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of north-east Brazil: a historical review and an appraisal of the biochronostratigraphic utility of its palaeobiota. – Cretaceous Research, **28:** 895–920.

Owen, R. (1859): Monograph on the fossil Reptilia of the Cretaceous Formations, Supplement no 1. – Monographs of the Paleontographical Society: 1–19.

Owen, R. (1874): Monograph on the fossil Reptilia of the Mesozoic Formations, Part I, Pterosauria; London (The Palaeontolographical Society), 14 p.

Pons, D., Berthou, P. Y. & Campos, D. A. (1990): Quelques observations sur la palynologie de l'Aptien Supérieur et de l'Albien du bassin d'Araripe (N. E. Du Brésil) – In: D. A. Campos, M. S. S. Viana, P. M. Brito & G. Beurlen (Eds.), Atas do 1º Simpósio sobre a bacia do Araripe e bacias interiores do Nordeste, Crato, 241–252.

Price, L. I. (1971): A presença de Pterosauria no Cretáceo inferior da Chapada do Araripe, Brasil. – Anais da Academia Brasileira de Ciências (supl.) **43:** 451–461.

Sayão, J. M. & Kellner, A. W. A. 2006. Novo esqueleto parcial de pterossauro (Pterodactyloidea, Tapejaridae) do Membro Crato (Aptiano), Formação Santana, Bacia do Araripe, nordeste do Brasil. – Estudos Geológicos, **16:** 16–40.

Seeley, H. G. (1870): The Ornithosauria: An Elementary Study of the Bones of Pterodactyles, made from fossil remains found in the Cambridge Upper Greensand, and arranged in the Woodwardian Museum of the University of Cambridge; Cambridge (Deighton, Bell and Co.), 135 pp.

Steel, L., Martill, D. M., Unwin, D. M. & Winch, J. D. (2005): A new pterodactyloid pterosaur from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, England. – Cretaceous Research, **26:** 686–698.

Unwin, D. M. (2001): An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of eastern England. – Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **4:** 189–221.

Unwin, D. M. (2002): On the systematic relationships of *Cearadactylus atrox*, an enigmatic Early Cretaceous pterosaur from the Santana Formation of Brazil. – Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **5:** 239–263.

Veldmeijer, A. J. (2003): Description of *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian (Lower Cretaceous) of Brazil. – Scripta Geologica, **125:** 35–139.

Wang, X., Kellner, A. W. A., Zhou, Z. & Campos, D. A. (2005): Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. – Nature, **437:** 875–879.

Wellnhofer, P. (1978): Pterosauria. Handbuch der Paläoherpetologie, Teil 19; Stuttgart and New York (Gustav Fischer), 82 pp.

Wellnhofer, P. (1985): Neue Pterosaurier aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. – Palaeontographica, Abteilung A, **187:** 105–182.

Wellnhofer, P. (1987): New crested pterosaurs from the Lower Cretaceous of Brazil. – Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **27:** 175–186.

Wellnhofer, P. (1991a): The Illustrated Encyclopedia of Pterosaurs;

London (Salamander Books Ltd.), 192 pp.

WELLNHOFER, P. (1991b): Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. – Palaeontographica, Abteilung A, **215:** 43–101.

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