

***Coloborhynchus* from the Lower Cretaceous Santana Formation, Brazil (Pterosauria, Pterodactyloidea, Anhangueridae); an update**A.J. Veldmeijer¹

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ISSN 1567–2158

11 figures

Abstract

Most of the toothed pterosaurs recovered from the Araripe Basin in Brazil (Santana Formation) have premaxillary sagittal and dentary sagittal crests. Some clear differences (and various less clear features) between the crested taxa have been used to classify the fossils, resulting in much scientific debate. On the other hand, a few potentially important features have been largely neglected so far. The present work presents an update of one of these crested taxa, *Coloborhynchus*, discussing the dentition and other previously unnoticed features in order to evaluate the systematic position of this taxon.

Key-words: Araripe, *Coloborhynchus*, dentary sagittal crest, dentition, premaxillary sagittal crest, pterosaur, Santana Formation

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Institutional abbreviations

BMNH	British Museum of Natural History
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich
IMNH	Iwaki Museum of Coal Mining & Fossils, Iwaki
MN	Museu Nacional, Rio de Janeiro
NSM	National Science Museum, Tokyo
Pz-DBAV-UERJ	Geological Museum University of Rio de Janeiro
RGM	Nationaal Natuurhistorisch Museum (Naturalis), former Rijks Museum voor Geologie en Minerologie, Leiden
SAO	Sammlung Oberli, St. Gallen
SM	Sedgwick Museum, Cambridge
SMNK	Staatliches Museum für Naturkunde, Karlsruhe
SMNS	Staatliches Museum für Naturkunde, Stuttgart

1. Introduction

The pterosaurs from Brazil (Araripe Basin, Santana Formation) have been the topic of much fierce debate ever since the first fossils were published, but especially in the last two decades. The discussion predominantly concerns classification, although topics on functional morphology have been thoroughly discussed more recently. Despite the debates a few characteristics of the pterosaur skeleton (and especially of the skull) have either been overlooked, given only slight attention, or dismissed as insignificant. The present work highlights this data, for example the dental pattern (the size of alveoli and diastemae), and gives an update of the toothed pterodactyloid taxon *Coloborhynchus*. The discussion is limited to the skull, the most diagnostic element of the pterosaur skeleton. Consequently, some taxa from this area will not be mentioned because their fossils do not include cranial parts (*Arthurdactylus conandolei* Frey & Martill, 1994; *Araripedactylus castilhoi* Price, 1971; *Araripedactylus dehmi* Wellnhofer, 1977; *Santanadactylus brasiliensis* De Buissonié, 1980; *Santanadactylus pricei* Wellnhofer, 1985 and *Santanadactylus spixi* Wellnhofer, 1985). Discussion is limited to Brazilian taxa; pterosaurs from the Cambridge Greensands (with the exception of the type specimen of *Coloborhynchus*), are not included.

2. Material and methods

The following specimens are used for comparison:

Skull of *Anhanguera blittersdorffi* MN-4805-V
 Skull and mandible of referred specimen of *Anhanguera blittersdorffi* n. 40 Pz-DBAV-UERJ
 Skull *Anhanguera santanae* AMNH 22555
 Mandible *Anhanguera* sp. AMNH 22573
 Mandible *Anhanguera* sp. SAO 200602
 Anhanguerid skull in the Iwaki Museum, IMNH 1053
 Skull and mandible cf. *Brasileodactylus araripensis* MN-4797-V
 Anterior part mandible *Brasileodactylus araripensis* MN-4804-V
 Anterior part mandible *Brasileodactylus ?araripensis* MN-6517-V
 Skull and mandible *Brasileodactylus* sp. AMNH 24444²
 Partial skull *Brasileodactylus* sp. BSP 1991 I 27
 Anterior part skull *Coloborhynchus clavirostris* BMNH 1822
 Mandible *Coloborhynchus robustus* BSP 1987 I 47
 Skull and mandible *Coloborhynchus piscator* NSM-PV 19892
 Anterior parts skull and mandible *Coloborhynchus robustus* SMNK 2302 PAL
 Skull *Coloborhynchus* sp. MN-4735-V
 Skull *Coloborhynchus* sp. SAO 16494
 Skull and mandible ?*Coloborhynchus* sp. MN-6687-V
 Skull ?*Coloborhynchus* sp. MN-6503-V
 Skull and mandible *Coloborhynchus spielbergi* RGM 401880
 Skull and mandible *Criorhynchus mesembrinus* BSP 1987 I 46
 Mandible cf. *Criorhynchus mesembrinus* SMNS 56994
 Crestless pterosaur in the Kitakyushu museum currently under study³

3. Systematic palaeontology

Order Pterosauria Kaup, 1834
 Suborder Pterodactyloidea Plieninger, 1901
 Family Anhangueridae Campos & Kellner, 1985
 Genus *Coloborhynchus* Owen, 1874

Type species and specimen: *Coloborhynchus clavirostris*, anteriormost part of the cranium, BMNH 1822, British Museum of Natural History, London, Great Britain (figure 1).

² Currently the specimen is under study and temporarily housed in the Natural History Museum Rotterdam, The Netherlands.

³ See Campos & Veldmeijer (2005).



Figure 1. The holotype of *Coloborhynchus clavirostris* (BMNH 1822). Photographs produced by the Natural History Museum Photographic Studio.

The holotype consists of a severely worn anteriormost part of the rostrum, which has been the reason of much debate and various synonymies. As a consequence, the history of *Coloborhynchus* is complex and will not be related here (but see e.g. Hooley, 1914; Wellnhofer, 1978, Unwin, 2001 Veldmeijer, 2006). *Coloborhynchus*'s most characteristic feature is that the two front teeth protrude from the blunt anterior aspect of the rostrum on a more dorsal level relative to the subsequent teeth on the lateral margins (see for overviews and recent participations in the discussion Fastnacht, 2001; Lee, 1994 and Veldmeijer, 2003). The premaxillary sagittal crest, commencing from the anterior view, is broken and inference of the shape of the crest remains dubious, further hindered by the severely eroded state. The palate has a strongly developed ridge, which widens posteriorly.

Diagnosis by Fastnacht (2001: 24), modified after Lee (1994: 756): "Median depression on the anterior margin of the upper jaw. Flattened anterior margin of the premaxilla triangular. Pair of teeth projecting anteriorly from the blunt anterior margin of the upper jaw at a significant elevation above the palate relative to subsequent teeth. Medial crest on the upper jaw rises from the tip of the snout. Upper jaw laterally expanded in a spoon-shape in dorsal view from the second to the fourth pair of alveoli. Lower jaw with medial crest rising from its anterior end. Lower jaw laterally expanded in a spoon-shape from the first to the third pair of alveoli. Second and third pair of alveoli of the upper and lower jaw enlarged relative to other alveoli." Diagnosis of species according to Lee (1994) is the same as for the genus.

3.1. Discussion of diagnosis

A true diagnosis of the genus was never given by Owen; he only gave a description with special attention to the position of the first pair of teeth. The most recent diagnosis was given by Fastnacht (2001: 24), modified

after Lee (1994: 756), cited above. Several problems with this modified diagnosis can be noted. As explained below, the shape of the median depression on the anterior margin of the upper jaw cannot be used as diagnostic feature at the species level because it is found in some species but not in others. Another feature, not included in Fastnacht's diagnosis and only with certainty seen in the Karlsruhe specimen, is the mandibular groove, extending all the way to the anterior margin of the mandible. Mandibular grooves are seen in various other taxa but the true value lies in the different morphology: the groove in *Brasileodactylus* has small side-grooves (Veldmeijer *et al.*, 2005a), in *Criorhynchus* the groove is deep and wide (Wellnhofer, 1987) and in *Anhanguera* the groove is flanked with slightly raised edges (Veldmeijer *et al.*, 2005a). Furthermore, the shape and size of the premaxillary sagittal crest shows an enormous variety and is therefore not to be regarded as diagnostic (Veldmeijer, 2003) as supposed by Kellner & Tomida (2000). The anteroventral projection of the second pair of teeth of the cranium is not unique to *Coloborhynchus* but seen in almost all other toothed taxa from the Araripe Basin. It is important to note that the expansion of the jaws in *Coloborhynchus* is robust ('suarish'), contrasting the smooth ('spoon-shaped') expansion in the other crested taxon *Anhanguera* and the more emphasised expansion in the non-crested *Brasileodactylus*. The jaws in the crested *Criorhynchus* are not expanded. The teeth are, in general, bigger and less numerous than in *Anhanguera* and in size much more comparable to *Criorhynchus*.

3.2. Remarks on dentition

In the type specimen no teeth are preserved, although remnants of the teeth are still visible in some alveoli. Note that some of the alveoli are damaged and thereupon smoothed by what seems to be most likely post-mortem water erosion. The first pair of alveoli are positioned at the anterior aspect, distinctly dorsal to the tooth-bearing border of the cranium; these point anteriorly. The position of the second pair of alveoli is strongly lateral and slightly ventral; they point slightly anteriorly. The positions of the third pair of alveoli is lateroventrally as well, but far more lateral than ventral, close to right angles to the horizontal plane. The subsequent alveoli (at the start of the expansion), numbers four, five and six are lateroventrally oriented but increasingly shifted ventrally. All alveoli are directed slightly anteriorly. The rest of the dentition, based on the few complete skulls, is increasingly ventrally oriented, but the last ones (in *Coloborhynchus piscator*) again have an increasing lateral orientation.

In the mandible, the first pair of alveoli (based on the Munich mandible of *Coloborhynchus robustus*), is positioned at the border of the anterior and dorsal aspect, although for the largest part at the anterior aspect. They stand slightly lateral relative to a true anterior position. The orientation of the alveoli are anterodorsal but the anterior orientation is far less so relative to the dorsal orientation. The orientation of the second to third pairs of alveoli is laterodorsal. These are the alveoli which are positioned at the ventral mandibular expansion. The fourth, although also at the ventral mandibular expansion, is positioned more dorsal relative to the previous ones. The smaller alveoli five and six are positioned laterodorsally but more dorsally relative to the previous alveoli; these are positioned in the laterally indented area posterior to the expansion. All of these alveoli point anterodorsally, but the more posterior ones point less strongly anterodorsally. The subsequent pairs, 7–15, are positioned laterodorsally, but more dorsal than lateral. The last three alveoli have a straight dorsal position.

The front teeth are posteriorly bent. The following two teeth are posterolaterally curved as well; the remaining teeth however, are only slightly bent and more or less straight. The teeth are rounded lingually and flattened labially (for a detailed description see especially Wellnhofer & Buffetaut, 1999). Thus the front of the beak forms a perfect grabbing device with large, interlocking teeth, whereas the teeth more towards the back probably serve, with their orientation and more upright position, to hold and transport the prey towards the throat.

The graph of the measurements of the alveoli (figure 2) shows that the second and third pairs of alveoli are the biggest. The first pair of alveoli, projecting from the anterior aspect, are substantially smaller and of comparable size to the fourth pair of alveoli. The fifth and sixth pairs of alveoli are smallest. The graph of the diastemae (figure 3) shows a clear depression, with the smallest measurement for the diastemae between alveolus four and five.

4. The known specimens

4.1. *Coloborhynchus araripensis* (BSP 1981 I 89, MN 4735–V; SAO 16494; figures 2, 3, 4, 5)

Initially, the Munich specimen (BSP 1982 I 89), consisting of the middle part of the cranium (figure 4) and various post-cranial elements, was described as *Santanadactylus* (Wellnhofer, 1985). Kellner (1990) reclassified it as *An. araripensis*, using another, unpublished and only partially prepared cranium in Museu Nacional (MN 4735–V; Kellner & Tomida, 2000). But the referred specimen and a hitherto unpublished

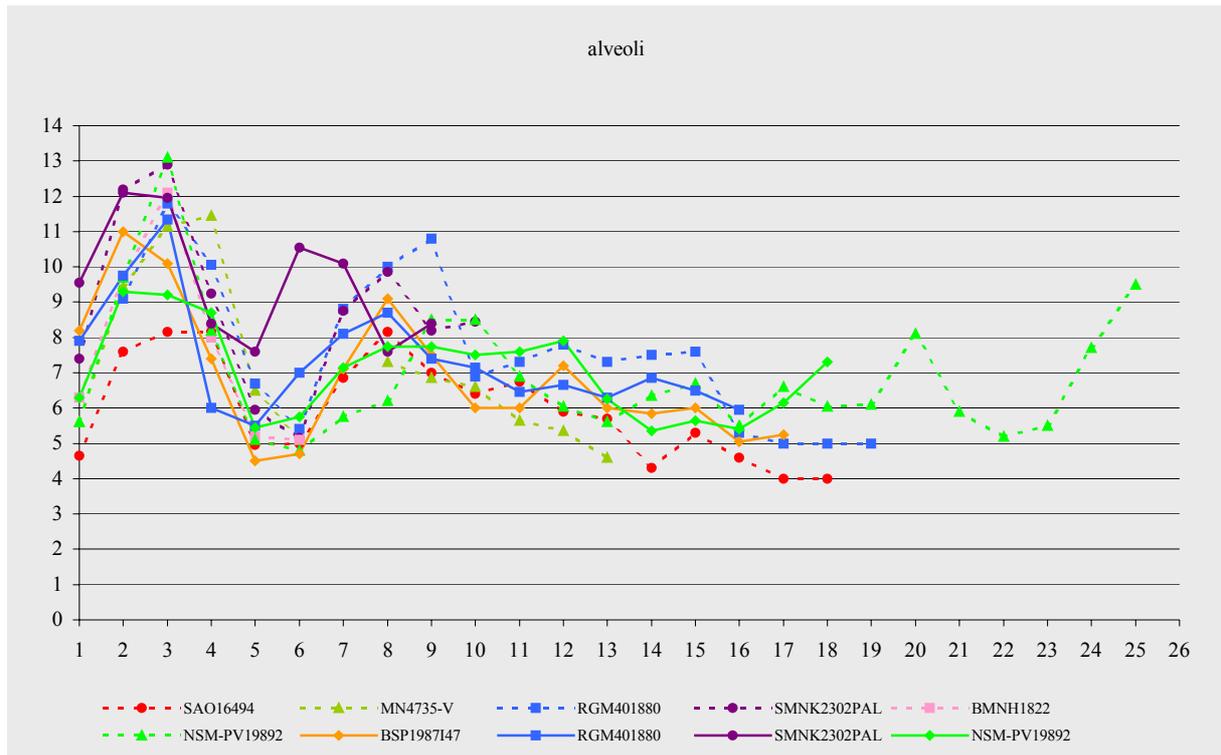


Figure 2. Dentition (alveolar diameter) of the taxon Coloborhynchus. Vertical = the diameter in mm; horizontal = the number of the alveolus, starting anteriorly with 1. The interrupted lines refer to the cranial dentition; the straight lines to the mandibular dentition (see Veldmeijer, 2006 for measurements and isolated graphs).

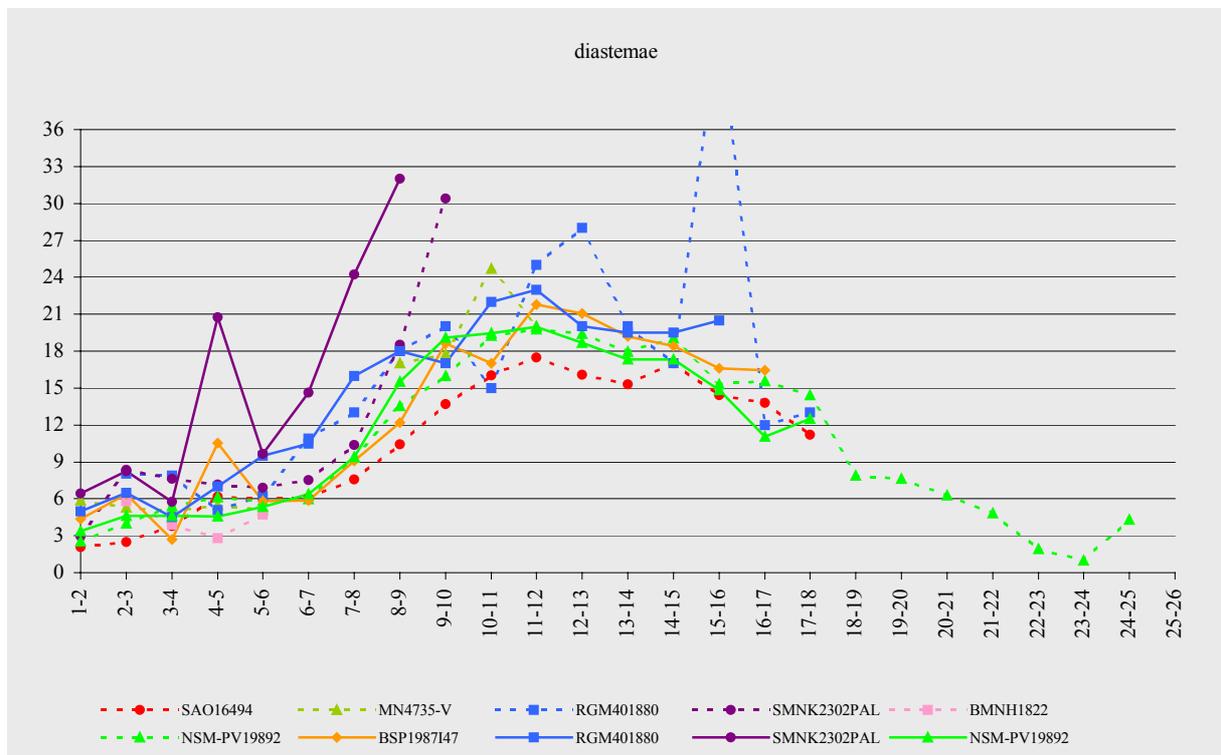


Figure 3. The dentition (diastemae size) of the taxon Coloborhynchus. Vertical the size in mm; horizontal = the number of diastema, starting anteriorly with 1. The interrupted lines refer to the cranial dentition; the straight lines to the mandibular dentition (see Veldmeijer, 2006 for measurements and isolated graphs).



Figure 4. Holotype of *Co. araripensis* (BSP 1982 I 89), right lateral view. Scale bar in cm. Photograph by E. Endenburg/A.J. Veldmeijer. Courtesy of BSP, Munich.

specimen housed in the Collection Oberli, St. Gallen, Switzerland (SAO 16494; figure 5) suggest a reclassification as *Coloborhynchus* because the anterior aspect in the referred specimen is blunt and the first pair of alveoli is situated distinctly more dorsal relative to the subsequent alveoli: a distinct feature of *Coloborhynchus*. *Brasileodactylus* lacks a crest, whereas the premaxillary crest in *Anhanguera* terminates well before the anterior margin. And this in turn contrasts with *Coloborhynchus*, because in this taxon the crest terminates at the anterior margin. Kellner & Tomida (2000) conclude that it is justified to classify *An. araripensis* as a separate species, rather than include them in the already known species, because the holotype as well as the referred specimen have a small process at the pterygoid (arrow in figure 5). Because the St. Galler specimen has exactly such a process too, the fossil is re-classified as *Co. araripensis*.

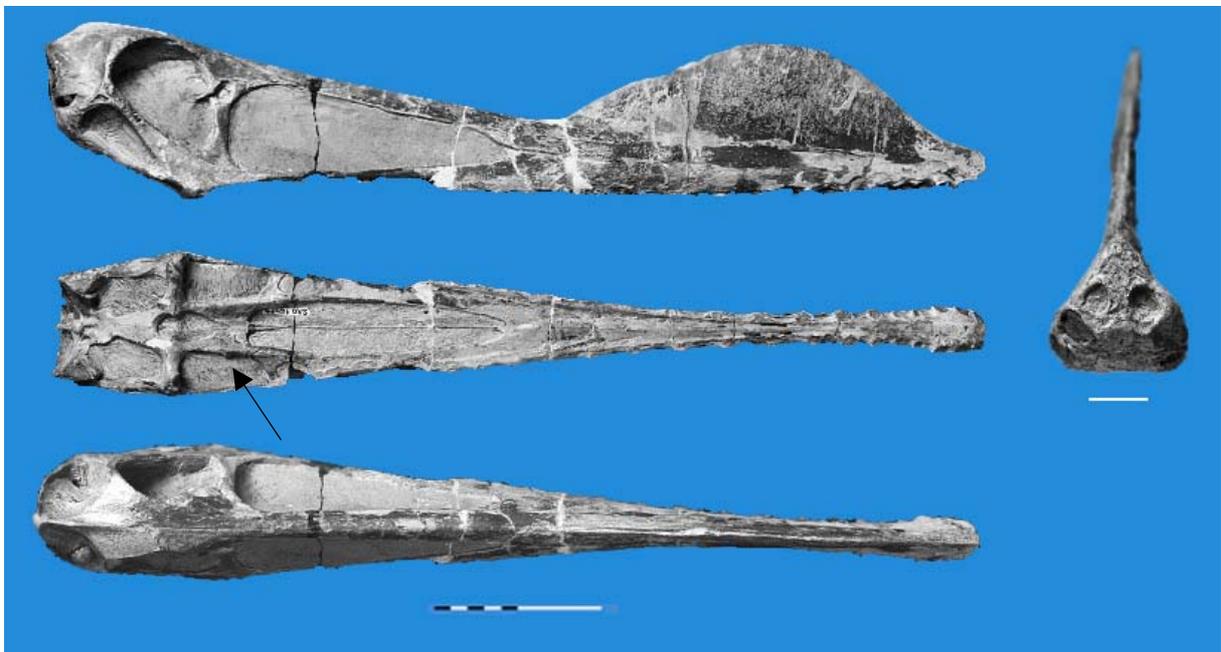


Figure 5. The St. Gallen specimen of *Co. araripensis* (SAO 16494). Scale bars in cm. Photograph by Naturmuseum St. Gallen, reworked by E. Endenburg. Courtesy of U. Oberli, St. Gallen.

The presence of a depression on the anterior aspect, mentioned in the diagnosis of the genus *Coloborhynchus*, is not attested in *Co. araripensis* (SAO 16494; the holotype has no anterior part preserved and

the anterior part in the referred specimen is damaged too much). This feature is not generic for *Coloborhynchus*, but its presence might be specific for certain species or just a feature of fossilisation rather than a morphological feature.

The pattern of alveolar size in the cranium SAO 16494 shows the familiar erratic pattern (figure 2) but in general the size is smaller relative to all other *Coloborhynchus* specimens. Furthermore, there is not a single alveolus much larger than the others, as seen with the other specimens and other *Coloborhynchus* species; instead, the second, third and fourth pairs are about equal in size and comparable in size with number eight. Still, there is a strong decrease in size with alveoli five and six. After the eighth alveolus, size decrease continuously posteriorly.

The graph of MN 4735–V (figure 2) shows a comparable pattern but with one distinct difference: alveolus two, three and four are substantially bigger than the rest and are more in line with the other *Coloborhynchus* graphs (in fact, it is SAO which differs from the others in this respect).

4.2. *Coloborhynchus robustus* (BSP 1987 I 47, SMNK 2302 PAL; figures 2, 3, 6, 7)



Figure 6. The holotype of *Co. robustus* (BSP 1987 I 47), mandible in left lateral view. Scale bar in cm. Photograph by E. Enderburg/A.J. Veldmeijer. Courtesy of BSP, Munich.



Figure 7. The Karlsruhe specimen of *Co. robustus* (SMNK 2302 PAL). Scale bar in cm. Photograph by A.J. Veldmeijer/E. Enderburg. Courtesy of SMN, Karlsruhe.

The holotype, BSP 1987 I 47, housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany, is an isolated mandible (figure 6), which was described by Wellnhofer (1987). Wellnhofer classified it to the new erected genus *Tropeognathus* as *Tropeognathus robustus*, differentiating it

from the other species of *Tropeognathus*, *Tr. mesembrinus* (currently known as *Cr. mesembrinus*). Kellner & Campos (1989) however, classified the mandible to *Anhanguera* because they observed the features mentioned by Wellnhofer (1987) present in *Anhanguera* as well (see also Kellner & Tomida, 2000). Veldmeijer (1998, 2002) however, regarded the specimen as a species of *Coloborhynchus*, supported by Fastnacht (2001), who came to the same conclusion on the basis of the study of the anterior part of the cranium and mandible of another specimen of *Co. robustus* in the collection of the Staatliches Museum für Naturkunde, Karlsruhe (SMNK 2302 PAL; figure 7). The Munich mandible is characterised by a steep and relatively short crest and long narrow symphysis. The anteriormost part is expanded with a flat anterior view. A mandibular sagittal groove, narrow and of equal width (approximately 3 mm), is present but fades in the anterior direction.

Fastnacht (2001) argued that the specimens (both the Munich mandible and the Karlsruhe front parts of cranium and mandible) are different from the other species of *Coloborhynchus* (the type specimen and the American *Co. wadleighi*, Lee, 1994). The jaws have all the characteristics of *Coloborhynchus*, such as the blunt roughly triangular anterior view with the teeth sticking out (the median depression has been discussed above) as well as the robustly expanded anterior part. The premaxillary sagittal crest has a concave anterior edge. The mandible has a small dentary sagittal crest with a distinct, well defined, mandibular sagittal groove (much clearer than in the holotype). Note that this groove has no counterpart on the cranium.

In the Munich mandible, there is a large gap between tooth four and six on the right side, whereas on the left side this gap is filled with alveolus five. This feature has been observed in various other specimens as well, including the Karlsruhe specimen of *Co. robustus*. Fastnacht (2001: 29) suggests that the “the absence of a diastema in BSP 1987 I 47 [the Munich mandible] on the left side, [is] possibly pathological since a diastema is present on the right side” (and thus that the normal situation at the transit of expansion and symphysis is the occurrence of an extra large diastema). But for now, it is not clear whether this is true, or that in contrast, the lack of a tooth (thus the extra large diastema) is pathological. There is, save the fifth and sixth pair of alveoli and some individual small increases in size, a continuous decrease in size in posterior direction (figure 2). The second and third pairs are the biggest alveoli and the fifth pair is the smallest. The seventh and eighth pair of alveoli are larger again, which results in a peak in the graph. The subsequent alveoli decrease in size gradually, with the exception of the twelfth pair.

In the Karlsruhe specimen of *Co. robustus*, the pattern made by the alveoli does not take into account the replacement teeth (replacement teeth are visible posterior to the first functional tooth right, posteromedial to the second right, the third left and the fourth tooth right). The second and third pairs of alveoli of the cranium are the biggest (figure 2). These are followed by a smaller pair, which are followed by the two smallest pairs of alveoli (five and six). Four larger alveoli occur after these latter two, which are of comparable size to the first pair of alveoli. The eighth pair is slightly larger relative to the other three of these four last pairs. The pattern of the mandibular alveoli is highly comparable with one notable exception. Alveolus number six has one of the largest diameters, whereas alveolus six in the cranium is the smallest of all.

4.3. *Coloborhynchus piscator* (NSM–PV 19892; figures 2, 3, 8)



Figure 8. *Co. piscator* (NSM–PV 19892), skull in right lateral view. Scale bar in cm. Photograph by E. Endenburg/A.J. Veldmeijer. Courtesy of NSM, Tokyo.

The most complete and best preserved fossil of a toothed pterosaur from Brazil is the specimen in the National Museum, Tokyo (NSM–PV 19892; figure 8), which initially was described as *An. piscator* (Kellner & Tomida, 2000). However, various features, such as the blunt anterior aspect, the robust expanded jaws and crests have led some scholars (for instance Frey *et al.*, 2003; Unwin, 2001) to classify it, because of the similarities, as *Co. robustus*. Veldmeijer (2003) argued, without going into further detail, that the specimen should be regarded as *Co. piscator*. He came to this conclusion because of the far larger size relative to the other known specimens, even though the Tokyo fossil is certainly not a fully grown animal.

The dentition in *Co. piscator* is complete and well preserved. However, observation is hindered by the fact that the skull has not been prepared completely: the matrix between the jaws remain, obscuring details of the ventral and dorsal aspects. As can be seen in figure 2, the pattern is largely comparable to *Co. robustus* but with few differences. The biggest alveolus is by far the third one. In none of the other specimens is the difference in size so obvious. Furthermore, the smallest alveoli are five and six, after which the size increase, with a peak at alveolus nine and ten; later than seen in the other *Coloborhynchus* fossils (mostly the peak is at number eight) except *Co. spielbergi* (see below). Other less severe peaks in size occur at number 21 and the last ones; but these alveoli are enlarged and contain two teeth.

4.4. *Coloborhynchus spielbergi* (RGM 401 880; figure 2, 3, 9)

The description of the nearly complete skeleton housed in the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands resulted in the fourth known species of *Coloborhynchus* and the first one with post-cranial material (RGM 401 880; figure 9) at that time. Characteristic of course, as with all *Coloborhynchus* species, is the large crest on the anterior part of the cranium and mandible, the two front teeth projecting from the anterior view (here identified with CT scans, because the anterior view is damaged) and the expanded anterior parts of the cranium and mandible. There are some clear differences with the other species, the most important ones being that the anterior expansion of the jaw is less robust and far more spoon-shaped (in this it is more comparable to the morphology in *Anhanguera*), the rami bend strongly medial and the palatal sagittal ridge and corresponding mandibular groove are faint and do not extend onto the anterior aspect of the upper jaw and mandible.

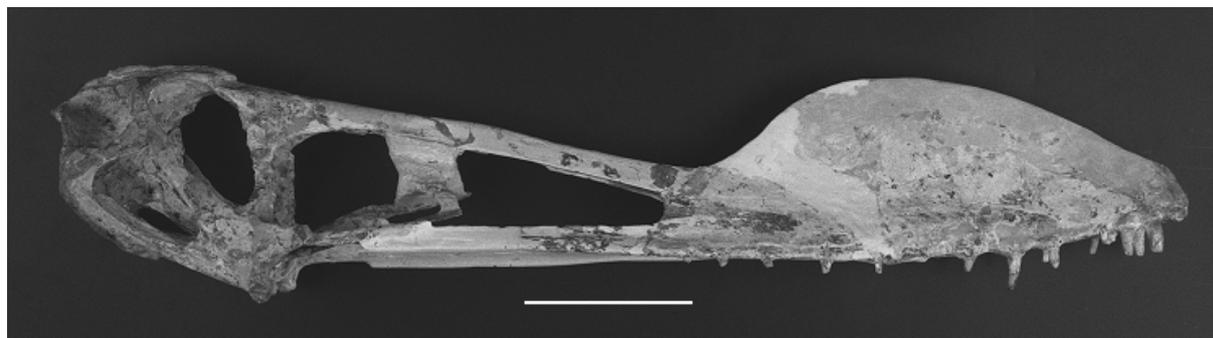


Figure 9. *Co. spielbergi* (RGM 401 880), skull in right lateral view. Scale bar = 10 cm. Photograph by A. 't Hooft. Courtesy of Naturalis, Leiden.

The alveolar pattern of the cranium (figure 2) shows the large second, third and fourth pairs, followed by the far smaller fifth and sixth pairs. The seventh, eighth and ninth pairs again are large, but slightly smaller relative to the first series large alveoli. The alveoli after the ninth pair are of equal size but small relative to the series three to five and seven to nine. On the other hand, these equal the size of pairs five and six. The pattern compares well with *Co. robustus* and less with *Co. piscator*. The alveoli of the mandible shows a slightly comparable pattern but, as also seen in *Co. robustus*, the drop in alveolar size occurs earlier (with numbers four and five). The increase thereafter is also earlier, namely with alveolus eight (number nine of the skull is biggest).

5. Diastemae (figure 3)

The diastemae (figure 3) show a uniform picture, *i.e.* a strong increase in size posteriorly until about halfway the tooth row and a decrease in size in diastemae from that point onwards. There are few exceptions, noted below.

The mandible of *Co. robustus* SMNK 2302 PAL shows a large diastema 4–5 and after a low value for 5–6, which is comparable to the value of diastema 5–6 in the other specimens, the size of diastemae increases far

more rapidly than seen in the others. This rapid increase is also seen for the skull but only with diastema 8–9; previous it is in line with the other graphs.

The value for diastemae 11–12 and 12–13 in the cranium of *Co. spielbergi* are slightly bigger relative to the others; the value for diastema 15–16 is 45 and thus by far the biggest encountered and is probably a result of restoration (Veldmeijer, 2003).

6. Discussion

An update of the taxon *Brasileodactylus* has recently been presented (Veldmeijer *et al.*, 2005b; submitted) and the updates on *Anhanguera* and *Criorhynchus* are forthcoming. The crestless, laterally compressed jaws that strongly decrease in width in anterior direction resulting in a sharp pointed beak of *O. compressirostris* is accepted as the type species for Ornithocheiridae (figure 10, see Kellner & Tomida, 2000), *Coloborhynchus* has to be classified in *Anhangueridae* (see Veldmeijer *et al.*, 2005b; contra Unwin, 2001 who classifies *Coloborhynchus* to the Ornithocheiridae).



Figure 10. Type specimen of *Ornithocheirus* and holotype of *O. compressirostris* (BMNH 39410), photographed in the same way as illustrated in Owen (1851). Photographs produced by the Natural History Museum Photographic Studio.

The acceptance of *O. compressirostris* as the type species for Ornithocheiridae contradicts with Unwin's (2001) vision and diagnosis. It is interesting to note that Unwin assigned the specimen *Criorhynchus simus*, as the type species of Ornithocheiridae (contra Fastnact, 2001). The diagnosis is, according to Unwin (2001: 204)4: "The first three teeth are relatively large, forming a terminal rosette, and show a marked increase in size posteriorly. The fourth tooth pair is much reduced in size and smaller than the first pair of teeth. Proceeding posteriorly, there is a steady decrease in tooth size up to, typically, the ninth pair, which are of similar basal dimensions to the largest teeth in the terminal rosette. Further posteriorly, tooth size decline again. Consequently, in dorsal view, the rostrum has an expanded anterior tip [...]. The expansion of the anterior end of the rostrum is most marked in large species and adult individuals, but may be practically absent in small species and juveniles." Without going into detail too much, as a detailed discussion of his vision is clearly beyond the scope of this work, a few remarks need to be made in light of the systematic palaeontology used here. First, as shown in figure 11, the type specimen is a small piece, in which only four alveoli are preserved, mostly badly damaged. So, the

description of dentition given by Unwin apparently has been based on other material (not on the type specimen), but he does not mention it: the description fits the dentition of Anhangueridae surprisingly well. *Criorhynchus*, on the basis of the Munich specimen of *Cr. mesembrinus*, does not have expanded jaws (in this clearly differs from *Anhanguera*, *Coloborhynchus* and *Brasileodactylus*), no rosette with teeth and does not have a ninth tooth larger than the other ones (this is almost never encountered, see dentition graphs). The non-expanding jaws is a feature that, among others, separates *Criorhynchus* from the others and is seen in other toothed pterosaurs as well, such as *O. compressirostris*. In other words, if a character is used in the diagnosis, as Unwin does, specimens not exhibiting this feature should not be classified to this group. Furthermore, explaining differences by means of ontogeny is extremely difficult as there is no way in the scanty pterosaur fossil record to know in most cases what a juvenile and what an adult is (or better 'not fully-grown' and 'fully-grown'). At present, too little is known to be sure on the ontogenetic status (see also Veldmeijer & Signore, 2004).



Figure 11. Type specimen of *Criorhynchus* and holotype of *Cr. simus* (CAMS B.54428), anterior, left lateral and ventral view of the anterior part of the rostrum. Scale bar = 5 cm. Photograph by E. Endenburg/A.J. Veldmeijer. Courtesy of the SM, Cambridge.

Coloborhynchus clearly differs from *Brasileodactylus* in the fact that the expansion of the jaws is more robust and *Coloborhynchus* has premaxillary and dentary sagittal crests. Furthermore, the morphology of the dentary groove and spoon-shaped part differs. Although *Anhanguera* has a crest as well, it terminates well before the anterior end of the cranium; the expansion of the jaws is far less robust and the morphology of the mandibular groove differs. The dentition patterns support the difference between *Brasileodactylus* and *Coloborhynchus*. The latter show a more erratic pattern, especially in the front part, with larger alveoli. Unfortunately, as most of the *Brasileodactylus* fossils are partial, predominantly front parts of the cranium and mandible, little can be said on the last part of the dentition and comparison with *Coloborhynchus* is therefore impossible. Further support for the separation of *Brasileodactylus* and *Coloborhynchus* has been provided by Veldmeijer *et al.* (in press) who indicated that the dentary crest was an important part of the fishing technique. Since *Brasileodactylus* does not have a dentary sagittal crest, they are forced to other food-gathering methods (the crest's primary reason seems functional rather than sexual display) and thus can be regarded as different animal, likely inhabiting a different niche than *Coloborhynchus*.

Alveolar data presented graphically here also provides further support for the classification of *Coloborhynchus piscator* as a valid taxon (see Veldmeijer, 2003): it is the only species of *Coloborhynchus* with as many as 25 alveoli on one side.

7. Acknowledgements

The following persons are acknowledged for kindly allowing access to the collections under their care or for helping with visiting it (in alphabetical order): T. Bürgin, D.A. Campos, C. Collins, F. Dalla Vecchia, M. Dorling, E. Frey, J. Gamble, A. Keefer, A.W.A. Kellner, G. Mauricio, H. Mayr, A.C. Milner, S. Nabana, M.A. Norell, U. & S. Oberli, Y. Okazaki, M. Oshima, I. Rutzky, Y. Takakuwa, Y. Tomida, J. de Vos, P. Wellnhofer, R. Wild. Unfortunately, material in Berlin remained inaccessible. A. 't Hooft, J.W.F Reumer and J. de Vos are kindly thanked for their help and advice. B.L. Beatty is thanked for upgrading the English as well as his critical remarks.

The study of various collections by AJV (Germany, Rio de Janeiro and New York) has been made possible due to the financial support by the Jan Joost ter Pelkwijkfonds, Stichting Molengraaff Fonds, Mej. A.M Buitendijkfonds and Mr. & Mrs. Endenburg. The study of the material in various collections in Japan was made possibly by the Netherlands Organization for Scientific Research (NWO). Due to the grant of the Egypt Exploration Society for studying archaeological material in Cambridge, AJV was able to study some of the type specimens from the Cambridge Greensands. The Natural History Museum Rotterdam (www.nmr.nl) and the National Museum of Natural History (Naturalis), Leiden (www.naturalis.nl), are thanked for their support; Naturalis is also thanked for financing the costs involved in scanning the skull of *Coloborhynchus spielbergi* in Mainz, Germany.

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Submitted: 1 June 2006

Published: 1 July 2006

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