Preliminary description of a skull and wing of a Brazilian Cretaceous (Santana Formation; Aptian-Albian) pterosaur (Pterodactyloidea) in the collection of the AMNH

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12 figures, 4 tables

Abstract

The skull and wing of a pterodactyloid pterosaur from the Brazilian Lower Cretaceous (Albian) in the collection of the American Museum of Natural History, New York, USA displays the general anatomical features characteristic for these pterosaurs and is shortly described. The largely embedded skeletal remains are tentatively assigned to *Brasileodactylus*. More precise classification, other than genus, proved not possible.

Contents

Abbreviations

1st ph.	1st phalanx wing finger (digit 4)	nas.	nasal
2nd ph.	2nd phalanx wing finger (digit 4)	nas.fen.	nasoantorbital fenestra
4th met.	4th metacarpal	or.	orbit
den.	dentary	par.	parietal
dig. 1-3	digit 1-3	pr.fr.	prefrontal
dist.car.	distal carpal	pr.max.	premaxilla
e.t.p.	extensor tendon process	prox.car.	proximal carpal
fr.	frontal	ra.	radius
fr.cr.	frontoparietal crest	scap.cor.	scapulocoracoid
j.	jugal	s.n.art.	supraneural plate articulation
l.t.f.	lower temporal fenestra	sq.	squamosal
max.	maxilla	ul.	ulna
met.	metacarpal		

1. Introduction

The collection of the American Museum of Natural History, New York, includes numerous remains of pterodactyloid pterosaurs. Apart from the pterosaur fossils that originate from North America (mainly *Pteranodon*), there are some specimens from Brazil. Herein, I discuss a Brazilian pterosaur, AMNH 24444, that was donated to the museum by Dr. Herbert Axelrod.

The main area in Brazil for finding pterosaurs is Chapada do Araripe in the province of Ceará, Piaui and Pernambuco, from which AMNH 24444 originates. The fossil is embedded in a calcareous nodule, which is typical for the Romualdo Member (Albian) of the Santana Formation (Aptian-Albian) (Martill *et al*., 1993; see also Beurlen, 1971; Kellner & Tomida, 2000; Maisey, 1991; Pons *et al*., 1990). The fossils from the Crato Formation (Aptian) are usually compacted and preserved in laminated limestone (Frey & Martill, 1994).

The present paper focuses, after a short general morphological description, on the discussion of morphological differences relative to other pterosaurs from Brazil. Measurements are included to complete the presented text; they are not used for comparison because of the preliminary character of this paper. There is no detailed description; comparable general layouts of the pterosaur skeleton are described extensively elsewhere (especially Kellner & Tomida, 2000; Veldmeijer, 2003; Wellnhofer 1985, 1991). The dentition pattern (i.e. the graph that visualizes the size and position of the teeth) is discussed only in passing, because a separate study on dentition patterns in Brazilian pterosaurs is in progress (Veldmeijer, unpubl.).

2. Preservation

The specimen consists of one concretion (figure 1), broken into 5 fragments, in which the skull, mandible and partial left wing (consisting of the left scapulocoracoid, ulna and radius, proximal and distal carpals, 3rd and 4th metacarpals, first phalanx of the wing finger and the proximal part of the second phalanx, and traces of the first three fingers) are still embedded. It is assumed that the fragments belong to one individual. In general, the preservation of the bones is good, despite the fractures mentioned before. One small bone is isolated, although it is uncertain whether it came from this concretion or not and will not be discussed further.

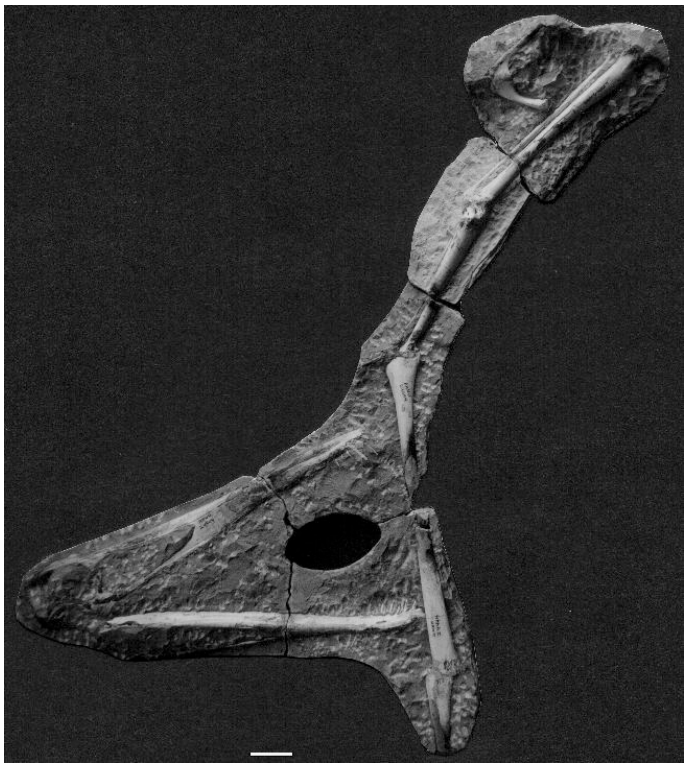


Figure 1. Skull and partial left wing, Brasileodactylus sp. *(AMNH 24444). Scale bar = 50 mm. Photograph by A.J. Veldmeijer.*

The skull is broken at approximately the anterior one third of its total length. The right lateral side is exposed together with the dorsal aspect of the back of the skull. The left lateral aspect of the back of the skull and the dorsal aspect anterior to the orbit are still partly embedded, as well as the posterior and posteroventral aspects. The orbit and nasoantorbital fenestra of the exposed right aspect are completely filled with matrix. The

first six teeth are partially preserved. A small area at the skull, anterior to the nasoantorbital fenestra and extending slightly anterior to the crack that divides the skull in two parts, lacks the outermost bone layer.

The mandible is displaced relative to the skull and its right lateroventral aspect is exposed. The anterior part of the snout is slightly worn; the distal half of the first wing phalanx obscures the anteriormost tip.

The retroarticular processes are not complete, although this feature is admittedly rarely preserved in pterosaur fossils. At a few places, the outer bone layer is missing.

Only the entire anterior aspect and small areas of the medial aspect of the left scapulocoracoid are exposed. The bone lacks the most proximal part of the coracoid; the biceps tubercle is also incomplete. The sternal articulation is severely damaged.

The ulna and radius are embedded in close association with the scapulocoracoid. The bones are broken at approximately two thirds of the length from a proximal point of view and display their dorsal surfaces. The bones lack some parts of the outer bone layer, and the proximal articular surfaces are not completely intact and exposed. The radius is slightly displaced relative to the ulna, but both bones are still in articulation with the carpus.

The dorsal aspect of the articulated carpus is exposed. The carpalia are in good condition, although slightly worn.

The fourth metacarpal is broken at slightly over half of its length, but is still in articulation with the ulna and first phalanx of the wing finger. The exposed dorsal aspect is well preserved, but, as with the carpus, slightly worn. The much smaller third metacarpal is preserved as well, but slightly displaced relative to the fourth metacarpal. The first three fingers are little more than traces in the matrix. The first phalanx of the wing finger is broken approximately halfway, where it lacks a small piece. This results in a preserved length which is probably close to its original length. Traces of the extensor tendon process are visible. In the middle, the outer bone layer lacks partially. The first phalanx is positioned in front of the skull and mandible, and its dorsal aspect is exposed. Only the proximal part of the second phalanx of the wing finger is preserved, still articulated with the first phalanx.

3. Systematic palaeontology

Order Pterosauria Kaup, 1834
Suborder Pterodactyloidea Plieninger, 1901
Family Anhangueridae Campos & Kellner, 1985
Genus *Brasileodactylus* Kellner, 1984

Type species and specimen: *Brasileodactylus araripensis* Kellner, 1984, anterior part mandible, MN 4804-V, Museu Nacional, Rio de Janeiro, Brazil.

Diagnosis: *Brasileodactylus* as diagnosed by Kellner, 1984 (580): "Pterosaurier mit Unterkiefer gebildet aus einer länglichen am Ende abgerundeten Symphyse, leicht nach oben gebogen, triangulärem Querschnitt, Schmälerung ab dem proximalen Teil, wobei ene Verbreiterung an dem distalen Bereich ab der dritten Alveole existiert, die eine flache Oberfläche bildet. Vorhandensein einer medialen Furche an der Dorsalseite der Symphyse, sehr ausgeprägt ab dem Beginn des Unterkiefers (distaler Teil), die sich in proximaler Richtung verbreitet. Alveolen mit eliptischer und rundlicher Form, Zahnabstände vergrössern sich in proximaler Richtung. Bezahnung bis an die Unterkieferspitze, Zähne schmal und spitz, nach vorne stehend." For an English translation see Kellner & Tomida (2000: 102).

Remarks: Kellner & Tomida (2000: 103) evaluated *Brasileodactylus* and came to the conclusion that the following apomorphies defined the genus; "rostral end expand from the 3rd alveoli, forming a flat surface […] medial groove on the dorsal part of the symphysis, starting on the rostral tip and widening caudally." They regarded the degree of expansion as an apomorph. Kellner (1984) regarded *Brasileodactylus* as an Ornithocheirid.

Brasileodactylus sp.

3.1. Description: the cranial parts

Skull

The elongated skull clearly shows the sutures between bone. The posterior slightly concave and anterior slightly convex premaxilla forms the dorsal edge of the anterior part of the skull until the orbit (figure 2). However, anteriorly, the course cannot be established exactly because the suture disappears in the vicinity of the fourth tooth. Possibly, the suture of the premaxilla and maxilla ends between tooth 4 and 5, resulting in four

premaxillary teeth. An additional support comes from the fact that the following, thus maxillary, teeth are substantially smaller. There are no traces of crests and the anterior aspect is pointed rather than blunt (figures 5 and 6). It is not certain whether the jaws expand anteriorly. The premaxillae extend far posterior and end in a point between the eye sockets. Here it is wedged between the nasals and prefrontals and end between the frontals (figures 3 and 4). A sharply defined suture as seen between the premaxilla, nasal and frontal that cannot be observed between the prefrontal and frontal but instead, a slightly dented, rather vague line marks the separation. Seen from posteriorly, approximately 10 mm posterior to the premaxilla, a well-developed frontoparietal crest begins. Unfortunately, the exact extension of this crest cannot be determined because the posterior and dorsal limits are incomplete. The maxillar process of the jugal extends into a point anteriorly. The anteriormost extension is unclear, but it extends farther anteriorly relative to the nasopreorbital fenestra.

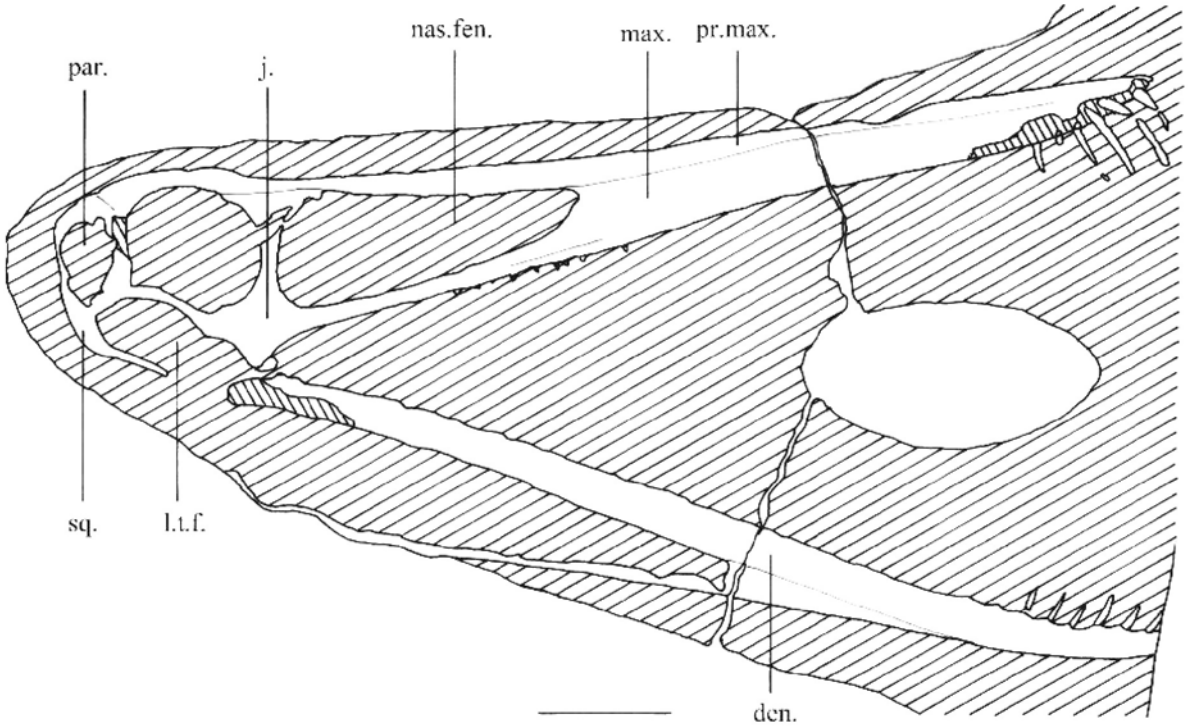


Figure 2. Skull and mandible of Brasileodactylus sp. *(AMNH 24444). The skull is seen from right lateral; the mandible from right lateroventral. Scale bar = 50 mm. Drawing by A.J. Veldmeijer.*

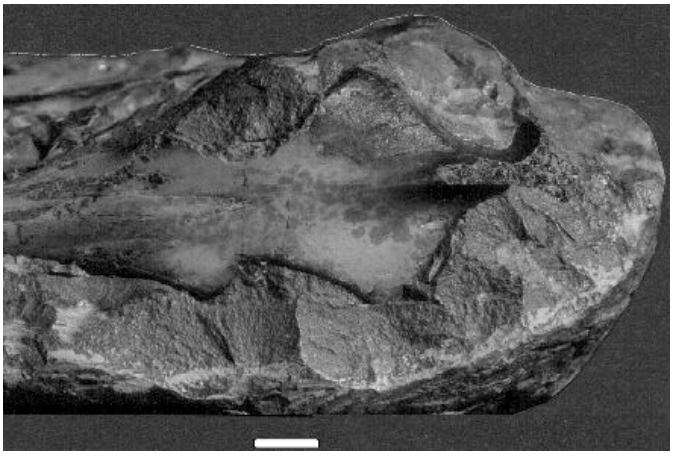
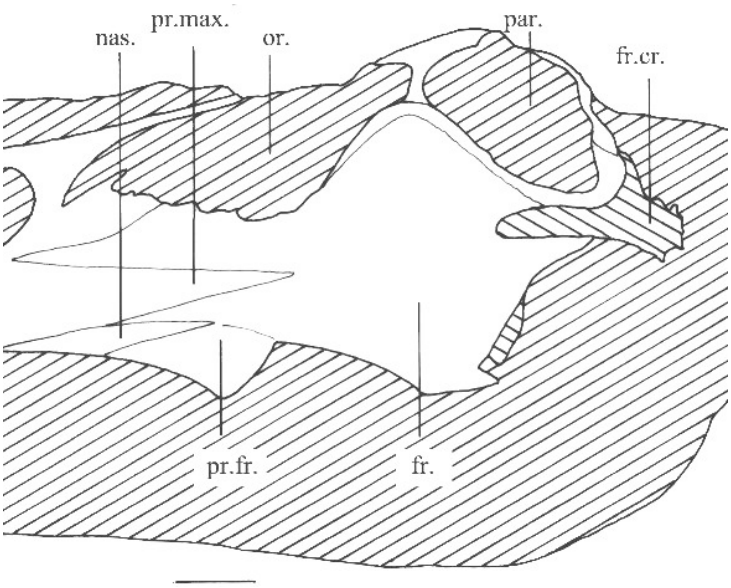


Figure 3 (above) and 4 (p. 5, top). Back of skull in dorsal aspect, Brasileodactylus sp. *(AMNH 24444). Scale bar = 50 mm. Photograph and drawing by A.J. Veldmeijer.*


nas.
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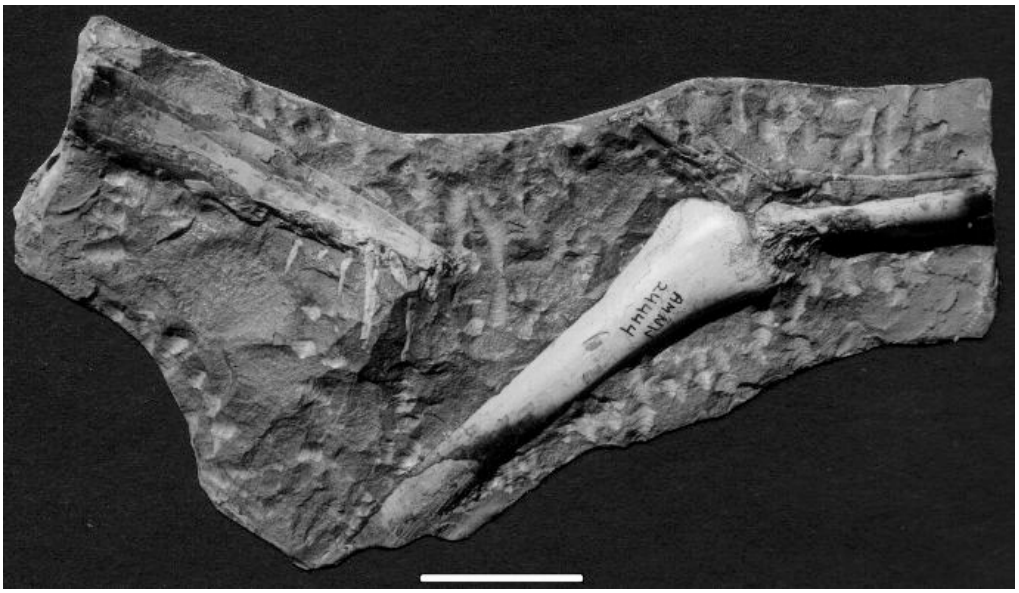


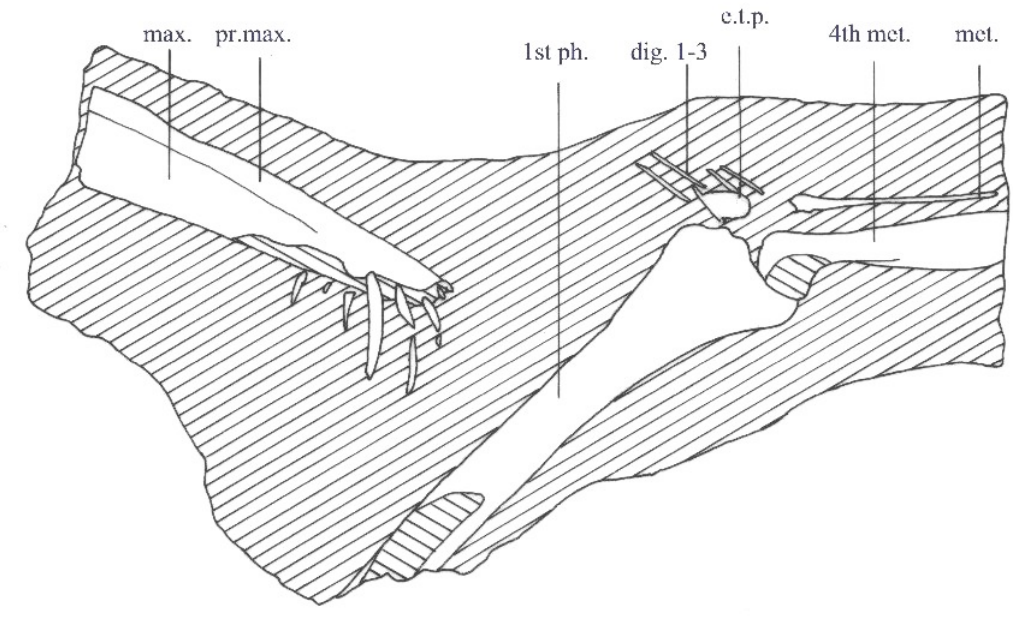

max.
pr.max.
1st ph.
dig. 1-3
e.t.p.
4th met.
met.

Figure 5 (p. 5, middle) and 6 (p. 5, bottom). Anterior part of the skull (right lateral aspect), proximal part of the first phalanx of the left wing finger, the distal part of the left metacarpus and remnants of the three fingers left, Brasileodactylus sp. *(AMNH 24444). Scale bar = 50 mm. Photograph and drawing by A.J. Veldmeijer.*

The first six of at least 26 teeth (not all visible from a lateral aspect), are somewhat unclear due to damage. The first tooth, positioned at the anterior margin and orientated, according to the direction of the alveolus, anteroventrally, is missing. The second and third teeth are large and thin relative to the following teeth and orientated anteroventrally. The exact curvature cannot be established because of the unprepared state of the fossil, but the teeth show at least a curvature in posterior direction. The following teeth are smaller and subsequently decrease in size posteriorly. These teeth are maxillary teeth. They are orientated ventrally. The most posterior teeth are slightly curved posteromedially.

Table 1. Measurements of the skull of Brasileodactylus sp. *(AMNH 24444) in mm.*

Length	429
Right orbit (width x length)	40 x 50*
Height at quadrate	74*
Length nasoantorbital fenestra	116
Height nasoantorbital fenestra	41

*Approximate.

Mandible

The dorsal aspect of the mandible is largely obscured by matrix (figure 2). Consequently, only the first six teeth are visible. The anterior aspect is obscured as well (figures 7 and 8) and it is therefore not certain whether the first visible tooth is the second or third one. The visible teeth are placed in the slender, non-crested, anterior part of the dentary. Only a full preparation can reveal whether the anterior part of the mandible is expanded or not.

The ventral aspect of the mandible extends straight from posterior to anterior, but runs dorsally from the seventh visible tooth. From this point it extends dorsally to form a pointed snout. The degree of co-ossification of the mandible is high relative to the skull.

Only six teeth can be seen, orientated anterodorsally and curved in a posterior direction. It cannot be seen whether or not they are curved medially as well, as is mostly seen in comparable pterosaurs. The teeth are placed dorsally and only slightly laterally. However, the incomplete preparation prohibits a more detailed description.

Table 2. Measurements of the mandible of Brasileodactylus sp. *(AMNH 24444) in mm.*

Length	362*
Length retroarticular process-symphysis (posterior)	193*
Thickness ramus at last alveolus	3.5
Maximal width of symphysis (ventral)	18.7
Maximal width rami (lateral)	48.5
Minimal width symphyseal part (halfway anterior aspect)	11

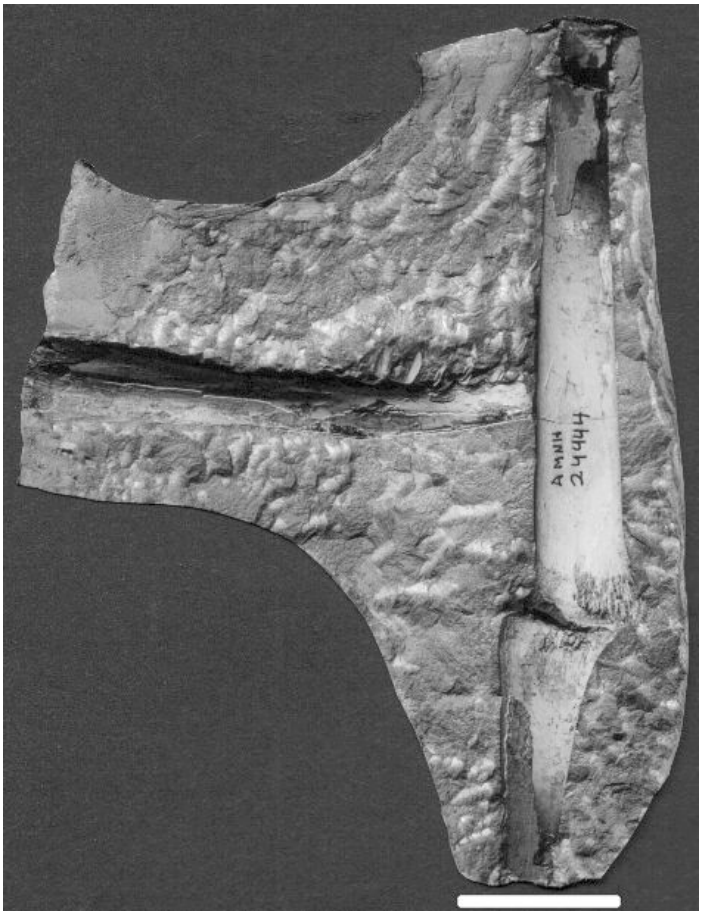
*Approximate.

3.2. Description: post-cranial parts

The largely unprepared state of the ulna, radius, metacarpus and carpus (figures 9-12) does not allow detailed morphological description. Furthermore, the general layout of these bones is directly comparable to previously published material and the diagnostic value is limited, especially if the extremities of the bones are obscured.

Figure 7 (p. 7, top) and 8 (p. 7, bottom). Anterior part of the mandible (right lateral aspect), distal part of the first phalanx of the left wing finger and distal part of the second phalanx of the left wing finger, Brasileodactylus sp. *(AMNH 24444). Scale bar = 50 mm. Photograph and drawing by A.J. Veldmeijer.*

Figure 9 (p. 8, top) and 10 (p. 8, bottom). Left ulna/radius, carpus and metacarpus, Brasileodactylus sp. *(AMNH 24444). Scale bar = 50 mm. Photograph and drawing by A.J. Veldmeijer.*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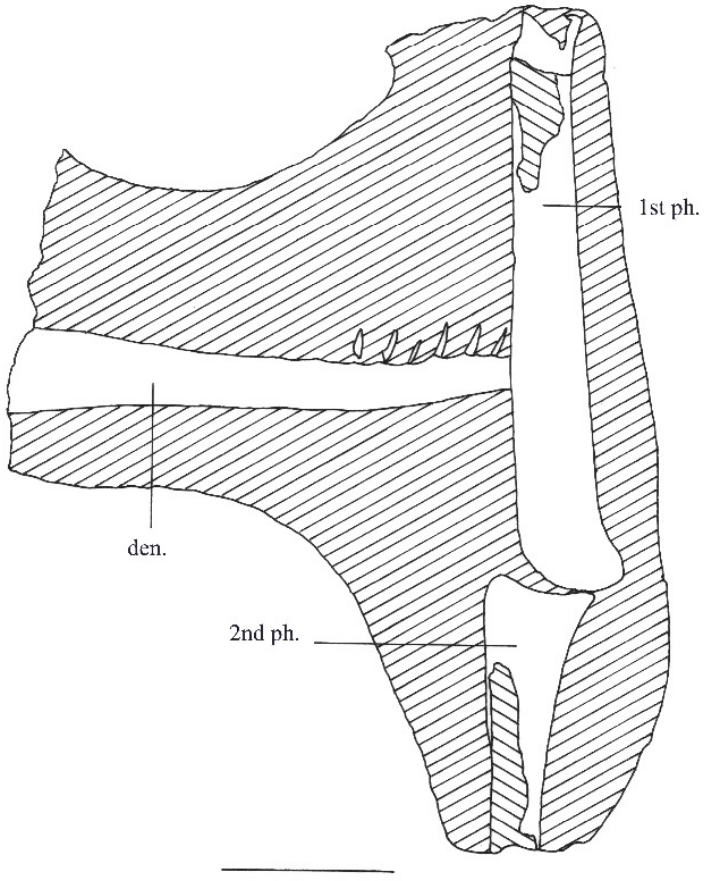
1st ph.
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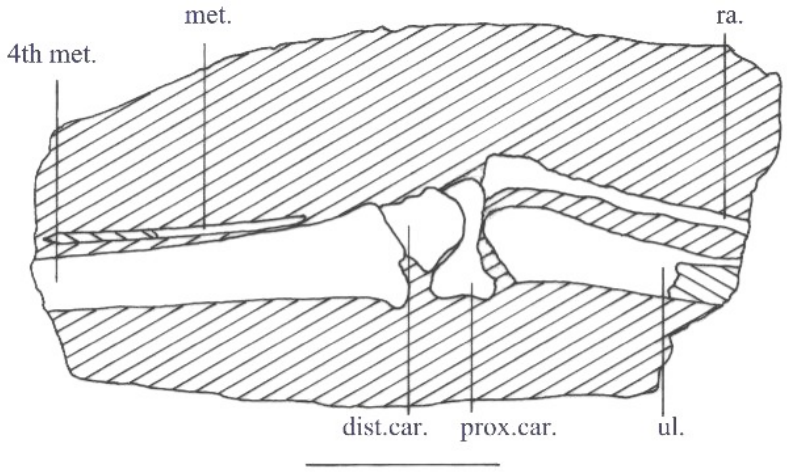
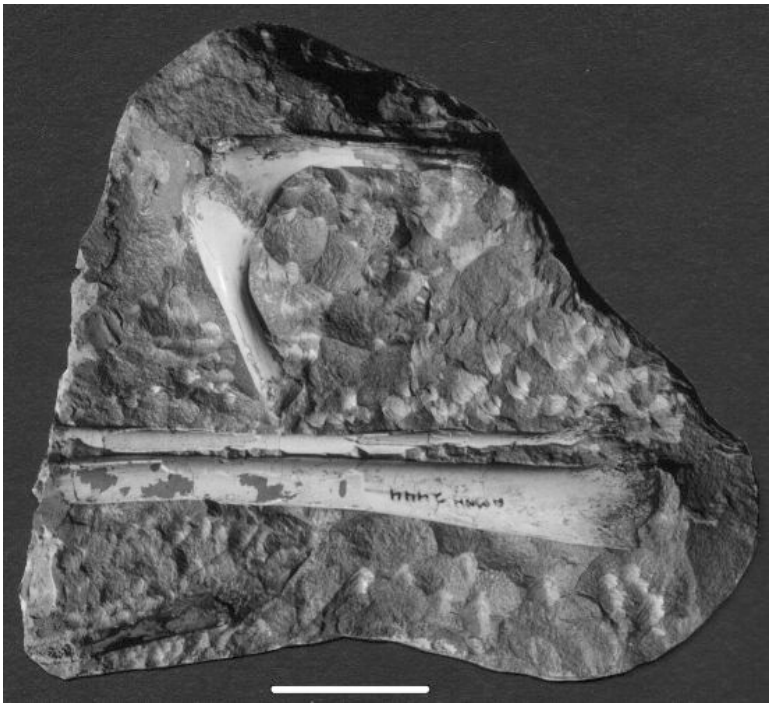


The scapula and coracoid are co-ossified into a scapulocoracoid (figures 11 and 12) on which the suture is indicated by a swollen line. The scapulocoracoid is commonly encountered in Cretaceous pterosaurs and has a limited diagnostic value at species level.



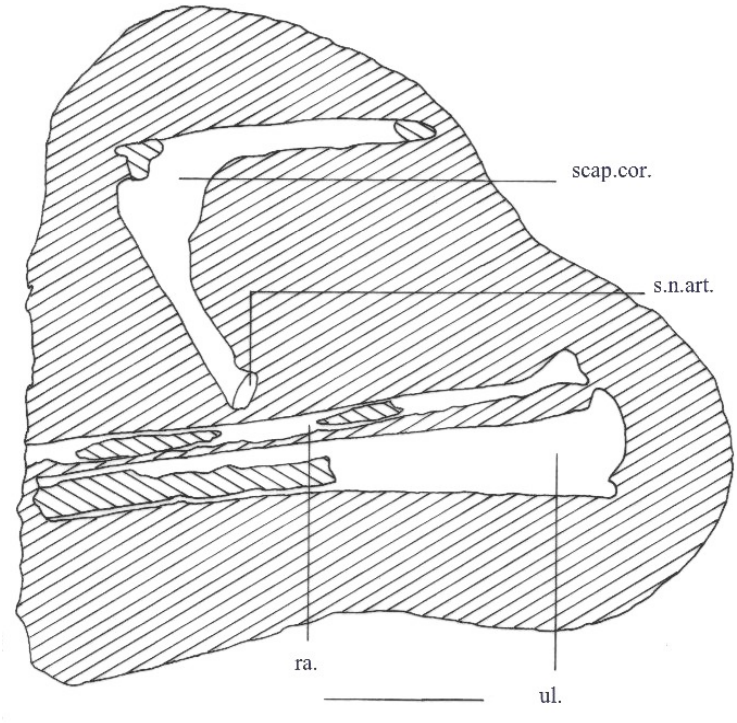


Figure 11 (p. 8, bottom) and 12 (above). Left scapulocoracoid and distal parts of the ulna/radius, Brasileodactylus sp. *(AMNH 24444). Scale bar = 50 mm. Photograph and drawing by A.J. Veldmeijer.*

The metacarpal of the wing finger (figures 5, 6, 9 and 10) is by far the strongest of the metacarpus and is elliptical in cross section, though far less so relative to the first phalanx.

The most remarkable feature of the first phalanx of the wing finger is the elliptical rather than triangular, cross-section of the shaft. The extensor tendon process process is comparatively high, as far as can be observed at this process (it is badly preserved and only a trace is visible).

Table 3. Measurements of the post-cranial bones of Brasileodactylus sp. *(AMNH 24444) in mm.*

Scapulocoracoid	
Length (lateral)	185*
Length scapula	85*
Length coracoid (as preserved)	90*
Width supraneural plate articulation (s.n.art.)	13.0
Smallest diameter scapular shaft	8.0
Width distal end	15*
Smallest diameter coracoid shaft	7.9
Ulna and radius	
Length ulna	246 (66 + 180)
Maximal width of proximal articular surface ulna	31.1
Smallest diameter ulna	14.8 x 19.5
Length radius	238 (70 + 168)
Maximal width of proximal articular surface radius	11.6*
Smallest diameter radius	6.9 x 10.5
Metacarpus	
Length 4th	171 (75 + 96)
Maximal width 4th	2.3*
Diameter distal articular surface 4th	11.7 x 18.1
Smallest diameter shaft 4th	11.1 x 12.3
Thickness 3rd	2.6
Phalanges wing finger	

Length 1st	355 (180 + 175)
Smallest diameter 1st	10.7 x 17.3
Maximal width proximal articular surface 1st	42.3
Maximal width distal articular surface 1st	33*
Length 2nd (as preserved)	86
Width proximal articular surface 2nd	31.2
Diameter shaft	9.6* x 16.4

*Approximate.

4. Comparison and discussion

The classification of the specimen is seriously hindered by the incomplete preparation. The classification proposed here is based on the cranial parts only, because of the limited value of post-cranial bones (worsened by the incomplete preparation) and has to be regarded as preliminary.

The presence of teeth in AMNH 24444 rules out the classification as member of the edentulous family Tapejaridae. Comparison with *Araripesaurus*, *Santanadactylus* and *Arthurdactylus* is hindered by the lack of cranial material in these genera.

Comparable taxa from Brazil are *"Criorhynchus"*, *Coloborhynchus*, *Brasileodactylus*, *Anhanguera* and *Cearadactylus.* Table 4 lists the features visible in the New York fossil; various important features are not listed because these cannot be observed in AMNH 24444. These features are the presence or absence of a dentary sagittal groove and its configuration; the divergence of the rami and the morphology of the retroarticular process. Other supposedly diagnostic features are left out; the depression at the anterior aspect in *Coloborhynchus* (Fastnacht, 2001) is not diagnostic (Veldmeijer, in review) and not only the second pair of alveoli project anteroventrally, although these are often the most distinct, but also the first and second pairs.

The absence of sagittal crests, premaxillary and dentary excludes an assignment to *Anhanguera*, *Coloborhynchus* or *"Criorhynchus."* Further differences between AMNH 24444 and *Anhanguera* are seen in the anterior expansion (absent(?) in the former, but present in the latter) and the dentition pattern (flat and erratic, respectively; table 4). *Anhanguera* and AMNH 24444 have in common the straight extending tip of the snout, the dorsoventrally compressed anterior end, the anterior positioned first pair of teeth which are not distinct dorsally placed relative to the following teeth and the weak frontoparietal crest.

Besides the lack of the crests, AMNH 24444 differs from *Coloborhynchus* in that the jaws of the latter are distinctly expanded anteriorly with an upwards bending tip of the snout, the anterior aspect of the skull is blunt with the first pair of teeth distinct more dorsal than the rest and the dentition patterns are far more erratic. However, the two share the presence of the first pair of teeth at the anterior aspect and the weak frontoparietal crest.

Other differences with *"Criorhynchus"* (table 4) are the slightly upwards-bent snout with the blunt anterior aspect without projecting teeth (in the holotype; BSP 1987 I 46 has teeth at the anterior aspect), the less erratic dentition pattern (compared to *Anhanguera* and *Coloborhynchus*), which is nevertheless more erratic relative to AMNH 24444 and the strong developed frontal crest in *"Criorhynchus."* On the other hand, neither of the two has expanded jaws and the first pair of teeth is not situated distinctly dorsal relative to the remaining teeth (in *"Criorhynchus"* only, BSP 1987 I 46).

Comparison with *Brasileodactylus* reveals a high degree of resemblance (table 4). However, it is not certain to what extent the skull is expanded anteriorly, because the only known specimen including a part of the skull is not entirely prepared (Sayão & Kellner, 2000). The presence of a frontoparietal crest cannot be ascertained either due to the preservation of only the anterior part of the skull. The slight anterior expansion of the mandible in *Brasileodactylus* seems to exclude the classification of AMNH 24444 to this genus, but as stated above, a slight expansion cannot be entirely ruled out.

The presence of a crest (table 4) cannot be excluded in *Cearadactylus atrox*, as explained by Kellner & Tomida, 2000). *Cearadactylus? ligabuei* has no crest, but the status of this specimen is disputed (Kellner & Tomida, 2000). Differences between AMNH 24444 and *Cearadactylus* are the bending of the snout, as seen in *C.? ligabuei* (but not in the type specimen, *C. atrox*). The dentition pattern is not known in *Cearadactylus* and none of the specimens is preserved completely enough to show a frontoparietal crest. There is a slight anterior expansion (but for the meaning of this see above). Another difference between *C. atrox* and AMNH 24444 is seen in the shape of the rostrum, which results in a gap between upper and lower jaws when closed (Leonardi & Borgomanero, 1985). However, Kellner & Tomida (2000) pointed out that this can only be observed after complete preparation and they suggested that the gap is far less pronounced as originally proposed. Comparable features are the straight upper jaw (except for *C.? ligabuei*, in which the jaw is slightly bent), the dorsoventrally compressed jaws (again, not entirely excluded for *C. atrox*) and the presence of an anterior pair of teeth that are positioned at the same level as the following ones.

Table 4. Characters of *Brasileodactylus sp.* (AMNH 24444), compared with Cretaceous toothed taxa from Brazil (Romualdo Member [Albian] of the Santana Formation). Classification follows Veldmeijer, 2003. Summary of descriptions (not to regard as a list of synonymy) used to compile the table: *Anhanguera blittersdorffi** Campos & Kellner, 1985; *Anhanguera santanae** (Wellnhofer, 1985), Wellnhofer, 1991; *Coloborhynchus robustus** (Wellnhofer, 1987), Fastnacht, 2001; *Coloborhynchus spielbergi** Veldmeijer, 2003; *Coloborhynchus araripensis** (Wellnhofer, 1985), Veldmeijer, in review; *Coloborhynchus piscator* (Kellner & Tomida, 2000); *"Criorhynchus" mesembrinus** (Wellnhofer, 1987), Veldmeijer, 2002; *Brasileodactylus araripensis** Kellner, 1984; Sayão & Kellner, 2000; *Cearadactylus atrox* Leonardi & Borgomanero, 1985; *Cearadactylus? ligabuei* Dalla Vecchia, 1993.

Type specimen (except AMNH 24444) → Feature ↓	AMNH 24444*	*Anhanguera** Campos & Kellner, 1985	*Coloborhynchus** Owen, 1874	*Criorhynchus* (Owen, 1861) See remark	*Brasileodactylus** Kellner, 1984	*Cearadactylus* Leonardi & Borgomanero, 1985
Skull						
premaxillary sagittal crest	no	yes, not starting at anterior aspect	yes, starting at anterior aspect	yes, starting at anterior aspect	no	no?
anterior expansion	no (based on the mandible)	yes, slight	yes, robust	no	?	yes, slight
tip bent upwards	no	no in *A. blittersdorffi*) yes in *A. santanae*)	yes	yes	no	no (type specimen)
anterior aspect	dorso-ventrally compressed	dorsoventrally compressed	blunt	blunt	dorsoventrally compressed	dorso-ventrally compressed
1st pair of teeth anterior	yes	yes	yes	no in holotype); anteroventral in BSP 1987 I 46	yes	yes
1st pair of teeth distinct dorsal relative to subsequent teeth	no	no	yes	no	no	no
dentition pattern	flat	erratic	erratic	medium	flat	?
frontoparietal crest	weak	weak	weak	strong	?	?
Mandible						
dentary sagittal crest	no	yes	yes	yes	no	no
anterior expansion	no	yes, slight	yes, robust	no	yes, slight	yes, slight
dentition pattern	flat	erratic	erratic	medium	flat	?

Remark: Specimens marked with * are studied first hand. "*Criorhynchus"* is put between marks as explained in Veldmeijer, 2003. It should not go without saying that BSP 1987 I 46, re-classified by Fastnacht (2001) as *Criorhynchus mesembrinus,* has the first pair of teeth situated at the anterior aspect, contrasting the situation in the type specimen.

On the basis of the above comparisons it is suggested that AMNH 24444 is closest to *Brasileodactylus* and should be classified herein. Until preparation is completed it remains uncertain whether the mandible has the

characteristic dentary sagittal groove that extends to the anterior aspect and if the teeth are situated at the anterior mandibular aspect.

5. Acknowledgments

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