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Pterosaurs from the Lower Cretaceous of Brazil in the Stuttgart Collection

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With 6 figures, 1 plate and 7 tables

Abstract

Bones of pterosaurs from the Cretaceous (Albian) of Brazil kept in the collection of the State Museum of Natural History in Stuttgart, Germany, are described and classified. One complete mandibula is assigned to *Criorhynchus*, three humeri and two ulnae are assigned to *Santanadactylus* and one ulna is assigned to *Coloborhynchus*. It proved not possible to determine various other bones more precisely than suborder or family. Few notes on the diagnostic status of post-cranial material in general and humeri in particular are presented.

Zusammenfassung

Knochen von Flugsauriern aus der Kreide (Alb) von Brasilien, die sich in der Sammlung des Staatlichen Museums für Naturkunde in Stuttgart befinden, werden beschrieben und bestimmt. Ein vollständiger Unterkiefer wird zu *Criorhynchus* gestellt, drei Humeri und zwei Ulnae werden *Santanadactylus* zugewiesen, und eine Ulna wird zu *Coloborhynchus* gestellt. Es erwies sich als nicht möglich, verschiedene andere Knochen genauer zu bestimmen als auf dem Unterordnungs- oder Familien-Niveau. Einige Bemerkungen über die diagnostische Bedeutung von postcranialem Material im allgemeinen und von Humeri im besonderen werden angeführt.

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1. Introduction

The Staatliches Museum für Naturkunde Stuttgart possesses various specimens of pterosaurs, Rhamphorhynchoids as well as Pterodactyloids, from Germany (URLICHS et al., 1994; ZIEGLER, 1992). Besides these ‘native’ pterosaur fossils, the collection incorporates pterosaur remains from the Santana Formation, Brazil.

The Santana Formation in Brazil was already known for its good quality of fossil fishes (see for instance MAISEY, 1991) for a long time before the first pterosaur remains were described as late as the early '70 of the previous century (PRICE, 1971). Since then, the recovery and study of Santana pterosaurs has taken an enormous flight and the Formation proved to be one of the most prolific sites of pterosaurs in the world. Today, numerous species are described from various genera and families (for an overview see VELDMEIJER, 2002).

The geology of the formation is given no attention. Ample attention is given to this topic elsewhere (for instance DE BUISSONJÉ, 1980; KELLNER & TOMIDA, 2000; MAISEY, 1991; MARTILL et al., 1993; WELLNHOFER, 1977, 1985; WELLNHOFER et al., 1983).

The material in the collection of the Stuttgart museum is obtained from various people. The mandibula with the inventory number SMNS 56994 is obtained from C. NOVAES FERREIRA, Sao Paulo, Brazil (7–11–1990) by the Stiftung Stadt Stuttgart. The small nodule with the remnants of various arm bones, SMNS 80437, is a gift of W. LUDWIG, Stuttgart (23–7–1996) and the humerus and radius with the inventory number SMNS 81976 is obtained from U. SEEHUBER (28–5–2001). The other bones are obtained in one transaction from a merchant in fossils, K.H. FRICKHINGER, but it is uncertain whether the bones belonged to one individual. Consequently, the bones are described separately.

The objective of the present work is to present a description and classification of the Brazilian pterosaur material in the collection. Additional photographs can be found at www.PalArch.nl. All bones are from the Cretaceous period, which precludes a designation as Rhamphorhynchoid pterosaurians.

Abbreviations

cap.hum.	caput humeri	os art.	os articulare
cond.dors.ul.	condylus dorsalis ulnae	os dent.	os dentale
cond.dors.hum.	condylus dorsalis humeri	os pre.art.	os prearticulare
cond.vent.hum.	condylus ventralis humeri	os sup.ang.	os supraangulare
cot.lat.	cotylus lateralis	pr.cot.dors.	processus cotylaris dorsalis
cr.man.	crista mandibularis	pr.lat.	processus lateralis
dep.ra.	depressio radialis	pr.med.	processus medialis
ext.prox.	extremitas proximalis	ra.	radius
for.pn.	foramen pneumaticum	scap.cor.	scapulocoracoideum
fos.ad.can.man.	fossa aditus canalis mandibulae	s.t.l.	second tooth left
f.t.l.	first tooth left	sul.an.med.	sulcus anconaeus medialis (Wellnhofer, 1985: 121)
hum.	humerus	tub.sup.vent.	tuberculum supracondylare ventrale
in.in.cond.	incisura intercondylaris humeri	tub.sup.dors.	tuberculum supracondylare dorsale
in.ra.	incisura radialis	ul.	ulna
ole.	olecranon-like tubercle		
os ang.	os angulare		

2. Systematic Palaeontology

Order Pterosauria KAUP, 1834

Suborder Pterodactyloidea PLIENINGER, 1901

The described bones are assigned to the suborder Pterodactyloidea. All described and mentioned Brazilian material is from the region of Chapada do Araripe, north-east Brazil, largely situated in the Province of Ceará; its horizon is the Santana Formation in the sense of the former Romualdo Member (Lower Cretaceous, Albian; see MARTILL et al., 1993).

2.1. Mandibula SMNS 56994

Fig. 1, Pl. 1, Tab. 1

Family Ornithocheiridae SEELEY, 1870

Genus *Criorhynchus* OWEN, 1874

Diagnosis. – *Criorhynchus* according to FASTNACHT (2001: 34). – “[...] Lower jaw with mandibular crest on the symphysis. [...] lower jaw not expanded anteriorly”.

Criorhynchus mesembrinus (WELLNHOFER, 1987)
cf. *Criorhynchus mesembrinus* (WELLNHOFER, 1987)

Holotype: Cranium and mandibula BSP 1987 I 46, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.

Diagnosis. – *Tropeognathus mesembrinus* according to WELLNHOFER (1987: 179): “*Tropeognathus* with high, rounded [...] smaller {than crista praemaxillaris} mandibular crest on the symphysis. [...] Deep groove on the mandibular symphysis. [...] lower jaws are not expanded anteriorly. Dentition with [...] 11 {sic} mandibular teeth in each side.”

Remark: between [] not in original.

Description SMNS 56994

The mandibula is partially prepared from its calcareous matrix, exposing the lateral, anterior and ventral aspects completely and the dorsal aspect partially (only the dorsal aspects of the rami are exposed). The medial aspects of the rami are not visible due to the matrix still in place between them. The right processus retroarticularis is partially restored whereas the left one is restored completely. The ventral edge of the crista mandibularis lacks small pieces. The teeth of the anterior part are well-preserved although some lack the buccal half. The smaller teeth more posterior (numbered 9–12) are missing, except tooth number 10 at the left side, which is still embedded in matrix.

The mandibula shows a high degree of co-ossification and the lateral aspects are characterized by the relief of the attachment areas of the different bones of the mandibula. The rami are bent slightly into medial direction. The posterior extremities, of which only the right one is preserved partially, is formed by the processus retroarticularis and expand strongly medially. Seen from posterior, the dorsal part of the processus retroarticularis shows a cotylus lateralis that occupies the entire lateromedial width without any internal divisions. The medial half of the cotylus later-

alis is less broad in dorsoventral plane, relative to the lateral part. The os supraangulare forms strong dorsal boundaries of the cotylus lateralis and overhangs especially the medial half. Seen from dorsal, the os supraangulare commences at the mediodorsal aspect of the rami, at approximately 35 mm from the proximalmost border, and expands rapidly laterally, occupying the complete dorsal width of the rami at the posteriormost part.

The os articulare is not preserved but the os praearticulare forms the ventral border of the fossa aditus canalis mandibulae. The medial aspects of the rami are obscured by matrix, but seen from ventral, the posterior parts of the fossa aditus canalis mandibulae are still visible. The exact course of the os praearticulare cannot be established. The elongated os angulare commences at the reconstructed parts at the posterior aspects, the exact posterior border cannot be established, and continues, at the right side, to slightly posterior to the tenth tooth. No suture can be traced anterior to this point. A shallow groove can be traced until slightly anterior to the tenth tooth, followed by a piece of suture of the os dentale. The os dentale extends ventrally, forming a smoothly curved crista mandibularis, which continues anteriorly to the anterior aspect of the mandibula. The crista, which commences anterior to the symphysis, decreases in width continuously in ventral direction. Seen from lateral, a shale-like pattern is to discern ventral to the first up to and including the fourth tooth at the right side. Seen from dorsal, the mandibula continues in anterior direction without an increase in width. The measurements of the width vary from 21.0 mm (at the second pair of teeth) to 22.3 mm (at the third pair of teeth). The anterior aspect displays a shallow but distinct depression, venteromedial to the first pair of teeth.

The first pair of teeth is curved posterolingually and point anterodorsally. The second pair of teeth is curved posterolingually as well and the teeth point also anterodorsally, although less strongly anteriorly as the first pair of teeth. The following teeth, at least up to and including the eighth pair of teeth, display a comparable curving although less severe. They point dorsally rather than anterodorsally. The following teeth are not preserved, except the tenth tooth left. This tooth is substantially smaller and does not display curving. The alveoli of the ninth up to and including the twelfth pair of teeth are elliptical and positioned with their long axis anteroposteriorly. The alveoli are positioned at the dorsal aspect of the rami. In contrast, the alveoli of the first eight pair of teeth, which are also elliptical of shape, are placed slightly lateromedially except for the first pair of alveoli, which is placed anterodorsally. The teeth show a continuous decrease in size, based on the measurements of the alveoli, with a continuous increase in diastema size.

Tab. 1. Measurements of the mandibula, SMNS 56994 (in mm).

Length, as preserved	385
Length, reconstructed	400
Height at last alveolus	23.3
Width at symphysis	34.0
Largest width of rami	98.4
Depth crista, as preserved	35
Length crista	118
Width at 2 nd pair of teeth	21.0
Width at 3 rd pair of teeth	22.3
Width at 4 th pair of teeth	21.8
Width at 5 th pair of teeth	21.7

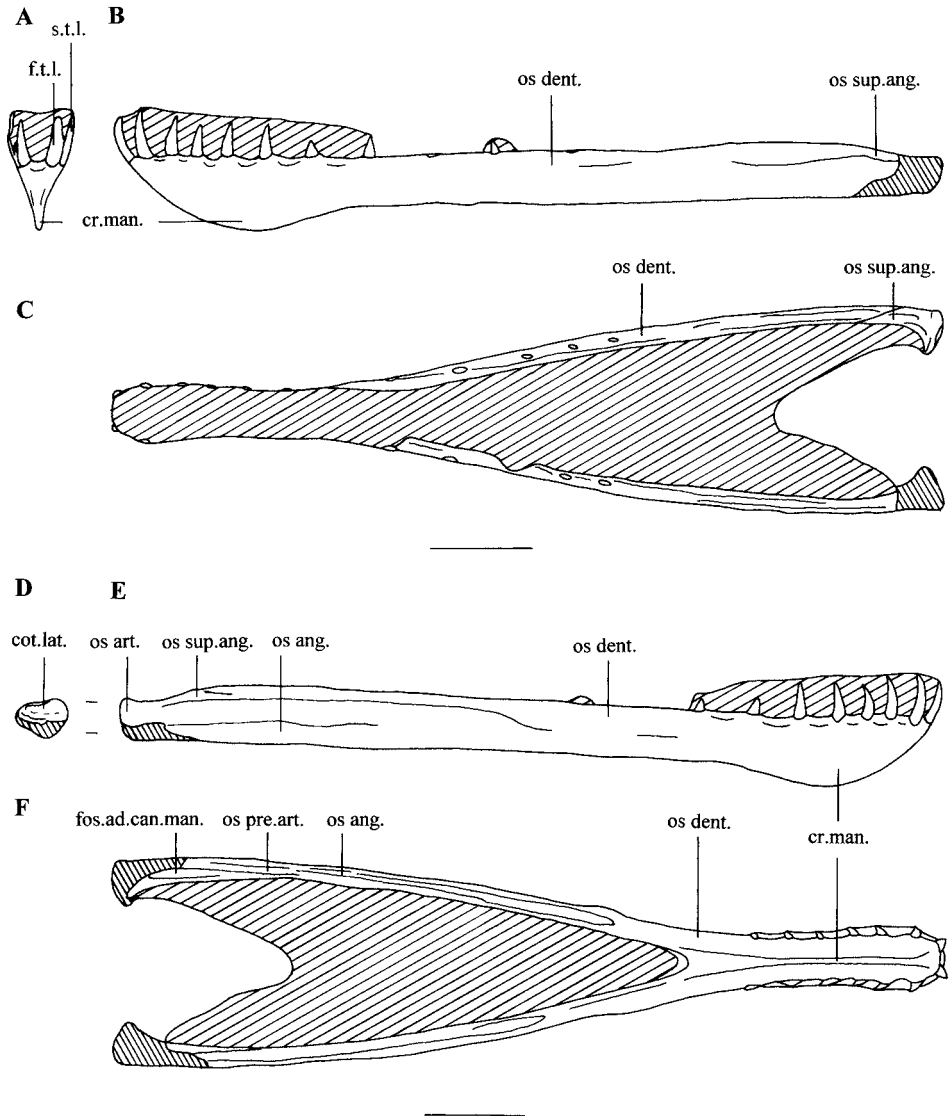


Fig. 1. Mandibula of cf. *Criorhynchus mesembrinus* (SMNS 56994) in various aspects. A: anterior; B: left lateral; C: dorsal; D: posterior (right side); E: right lateral; F: ventral. Scale bars = 50 mm. Drawings by A. J. Veldmeijer/E. Eendenburg.

Discussion

Few toothed pterosaurs are known from Brazil with cristae on the mandibula. *Criorhynchus mesembrinus* is published by WELLNHOFER (1987) and renamed by FASTNACHT (2001). *Coloborhynchus robustus* is also described by WELLNHOFER (1987) and renamed by VELDMEIJER (1998, see also FASTNACHT 2001). VELDMEIJER (in press) published the first *Coloborhynchus* with post-cranial material. Fossils, named as species of *Anhanguera* are described by CAMPOS & KELLNER (1985),

KELLNER & TOMIDA (2000) and WELLNHOFER (1985, 1991b). Toothed species without a crista mandibularis are *Brasileodactylus*, described by KELLNER (1984), *Cearadactylus*, published by LEONARDI & BORGOMANERO (1985) and DALLA VECCHIA (1993). Possibly, *Santanadactylus*, as published by WELLNHOFER (1985, 1991b) lacks a crista as well. *Anhanguera* might have had a crista that does not commence at the anterior aspect of the mandibula but rather posterior to the anterior aspect and is therefore different (WELLNHOFER, 1991b). Recently however, it is suggested that the crista mandibularis starts anteriorly as well (see KELLNER & TOMIDA, 2000, fig. 66). Pteranodontidae do not have cristae on the mandibula. Furthermore, Pteranodontidae are edentulous, as are the Azhdarchidae, Tapejaridae and Nyctosauridae. The teeth of Dsungaripteridae and Pterodaustriidae differ completely from the teeth of the discussed mandibula (MARTILL et al., 2000; WELLNHOFER, 1991a).

The general layouts of the toothed mandibulae are comparable. A comparison with crested pterosaurs shows that the curvature of the rami is less and the mandibula is shorter relative to *Coloborhynchus spielbergi* as published by VELDMEIJER (in press). The comparatively long mandibula of *Coloborhynchus robustus* show short rami relative to the present described mandibula (see also VELDMEIJER, 2002). The rami display almost no curving. The powerful teeth of *Coloborhynchus robustus*, which display a different dentition pattern, clearly distinguish *Coloborhynchus* from the Stuttgart mandibula. Furthermore, the mandibula of *Coloborhynchus* is spoon-shaped, in contrast to the straight mandibula described in the present work. One other species, *Criorhynchus mesembrinus*, has a combination of a crista mandibularis, teeth and non-expanding snout as well. The mandibula of *Criorhynchus mesembrinus* is pointed more sharply anteriorly, relative to SMNS 56994, but this is due to the lack of a small part of the left side. Both specimens have the same number of teeth (12) and a comparable dentition pattern. Note that WELLNHOFER mentions in his diagnosis erroneously 11 mandibular teeth. The curvature of the rami of *Criorhynchus mesembrinus* is slightly less strong relative to *Coloborhynchus spielbergi* but still stronger relative to SMNS 56994. The main difference between the two mandibulae is the large size difference. The compared mandibula has an estimated (because the processus retroarticularis is missing) length of 540 mm (WELLNHOFER, 1987). The length of the Stuttgart specimen is estimated at 400 mm. This means that the Munich specimen is 35 % larger than the Stuttgart specimen. Although this seems too large a difference to be explained by sexual dimorphism or intraspecific variability, there is too little known at present on these topics to exclude either of the two. On the other hand, the lack of identifiable sutures of the Munich specimen suggests a more mature animal than the Stuttgart pterosaur, which might explain the size difference. The difference in ratios (VELDMEIJER, in press) seems to support this suggestion because pterosaurs display true allometry (BROWER & VEINUS, 1981; WELLNHOFER, 1970; 1991a) but the ratios do not exclude intraspecific variability and are based on individuals only. *Criorhynchus mesembrinus* has a characteristic deep and, towards the symphysis, broad sulcus mandibularis. Because the Stuttgart mandibula is not completely freed from its matrix it is proposed, until the remaining matrix is removed and the dorsal aspect is visible, to refer to the mandibula as possible (cf.) *Criorhynchus mesembrinus*, classified to the Ornithocheiridae as explained by FASTNACHT (2001). This systematic interpretation follows FASTNACHT opposed to the classification as *Tropeognathus mesembrinus* in the clade of Anhangueridae by KELLNER & TOMIDA (2000).

2.2. Isolated humeri SMNS 55407, 55408, 55409, 55883
Fig. 2, Tab. 2

Humerus SMNS 55407

Fig. 2A

The right humerus with inventory number SMNS 55407 is incomplete (Fig. 2A). The bone is reconstructed but the transition between the reconstructed parts and bone is hard to distinguish. The reconstruction starts at least 30 mm distal to the processus lateralis and extends at least up to 60 mm proximal to the distal aspect. The reconstructions are recognised on the basis of differences of colour and texture. Furthermore, the matrix surrounding the bones might not be the original matrix. The surface is very smooth and no signs of preparation are to distinguish. The reverse of the 'nodule' has a far darker yellow colour in contrast with the colour of the matrix of the other bones, and strikes, characteristic for paintbrushes, are clearly to recognise. Consequently, there is no certainty whether the extremitas proximalis and the extremitas distalis belongs to one bone and the humerus is therefore not discussed in the present work.

Humerus SMNS 55408

Fig. 2B

Family Ornithocheiridae SEELEY, 1870/Anhangueridae CAMPOS & KELLNER, 1985

Genus, species indet.

Description SMNS 55408

The left humerus with inventory number SMNS 55408 is incomplete (Fig. 2B). The bone is still embedded in matrix and only the posterior and dorsal aspects are (partially) visible. The processus lateralis is still embedded. A large part of the processus medialis is missing. The specimen is considered isolated despite the fact that remnants of the ulna and remnants of the scapulocoracoideum are still articulated with the extremitas distalis and the extremitas proximalis respectively. Isolated from the humerus is a small, straight piece of bone, which cannot be identified due to its fragmentary state.

The caput humeri of SMNS 55408 describes a distinct angle compared to the corpus, not unlike SMNS 55883. A further description of the isolated left humerus SMNS 55408 is limited to the measurements (Tab. 2). The damaged state of the bones results in the lack of diagnostic features. The length of the humerus, as preserved, is 138 mm. The diameter of the corpus is approximately 17 mm.

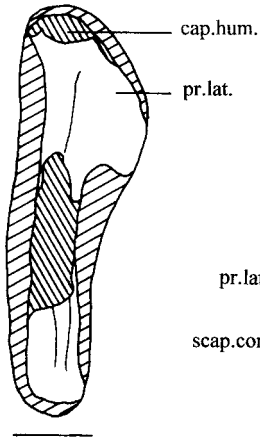
Humerus SMNS 55409

Family Ornithocheiridae SEELEY, 1870

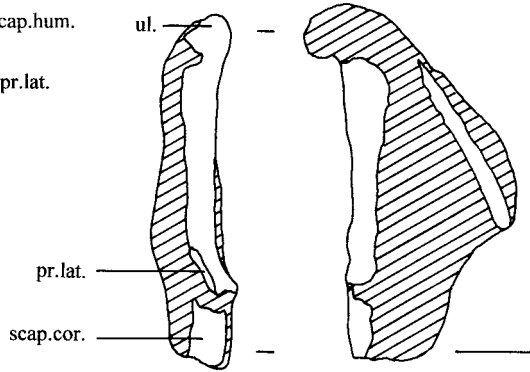
Genus *Santanadactylus* DE BUISSONJÉ, 1980

Diagnosis. – *Santanadactylus* according to DE BUISSONJÉ (1980: 149). – “[...] Humerus with a broad, crescent-shaped proximal articular surface, divided along an oblique line into two areas with slightly different convexity. From the proximal articular surface a gradually broadening deltopectoral radial crest is extending distally along the shaft. A rather low ulnar crest starts at the opposite side of the crescent-

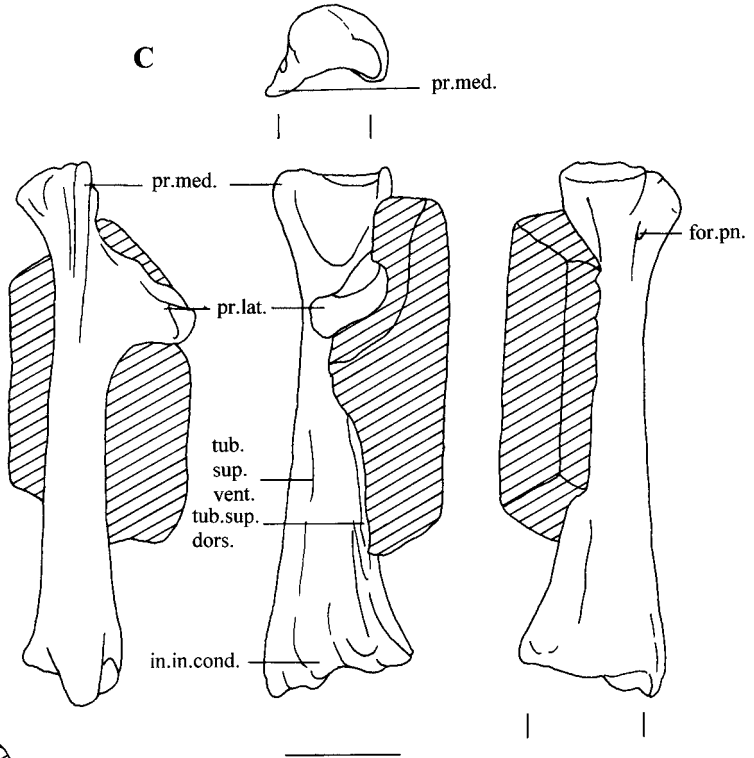
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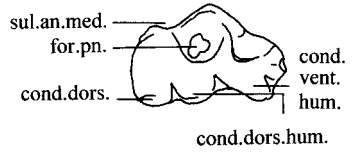
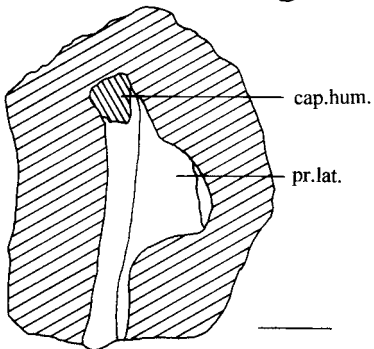
B



C



D



shaped proximal surface and extends distally over almost the same length as the radial crest. In the proximal part of its palmar side the humerus is slightly concave lengthwise and deeply concave perpendicular to the shaft. More distally palmar the shaft becomes convex in both directions and becomes nearly circular in cross section where the distal part of the radial crest meets the shaft. The humerus possesses a wide foramen pneumaticum, two-fifth down the ulnar crest on the convex, anconal side. [...]”

Santanadactylus araripensis WELLNHOFER, 1985

Fig. 2C

Holotype: BSP 1982 I 89, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. Largely complete skeleton.

Diagnosis. – *Santanadactylus araripensis*, according to WELLNHOFER (1985: 110): “[...] Oberrand des Processus lateralis des Humerus mit Knick. [...]” (Translation: “Upper edge of the humeral processus lateralis with bend.”)

Description SMNS 55409

The left humerus with inventory number SMNS 55409 (Fig. 2C) is the best-preserved humerus in the collection and completely intact. Only superficial damage occurs on the posterior and dorsal aspects. On the other hand, still matrix is attached at the anterior and, to a lesser extend, ventral and dorsal aspects. The humerus is a strong bone with, in anterior and posterior direction expanding, proximal and distal extremities. All condylae and epicondylae are firmly fused with the humerus.

The caput humeri is angled relative to the corpus. Seen from proximal, the caput is kidney-shaped and divided in a slightly convex dorsal part and a concave ventral part. The transition between the two areas is marked by a kink. The anterior aspect is entirely and the dorsal and ventral aspects partially confined by a characteristic sharp ridge, which is more pronounced anteriorly than dorsally. A distinct but shallow ridge, relative to the afore mentioned one, separates the processus medialis from the rest of the caput.

Seen from ventral, the ventralmost extension of the strong developed processus lateralis extends diagonally distal-proximal and the most ventral tip is curved in proximal direction. This part of the processus is thicker relative to the, in posterior direction bended, ventral edge of the processes, which commences from the caput and extends towards the ventralmost, curled tip. The posteroproximal surface of the ventralmost extension of the processus lateralis is distinct concave. The ventral aspect of the humerus expands at the opposite side of the processus lateralis, i.e. the posteroventral corner. This is caused by the processus medialis. The area between the processus medialis and processus lateralis is concave and limited by the slight, but distinct ridge of the recessed ventral border of the proximal aspect. Distally, the area fades towards the posteroproximal surface of the processus lateralis. Despite

Fig. 2. Isolated humeri.

A: SMNS 55407; B: SMNS 55408; C: *Santanadactylus araripensis* (SMNS 55409) in proximal (top), posterior (left), ventral (middle), dorsal (right) and distal (bottom) views; D: cf. *Santanadactylus pricei* (SMNS 55883).

Scale bars = 50 mm. Drawings by A. J. Veldmeijer/E. Endenburg.

being partly obscured by matrix, it is good to observe that the, at the distal half situated, tuberculum supracondylare dorsale is strongly developed and 3 mm at its highest point. The tuberculum extends towards the distal aspect but the sharp ridge changes into a shallow bulging ridge more distally. It forms a separation between the flat area anteriorly and the shallow recess posteriorly. Opposite to the tuberculum supracondylare dorsale and slightly more posteriorly is another ridge visible, identified as tuberculum supracondylare ventrale, which extends towards the condylus ventralis at the distal aspect. The incisura intercondylaris separates the condylus dorsalis from the condylus ventralis.

Seen from distal, the condylus dorsalis is more pronounced and bulbous relative to the condylus ventralis and extends farther onto the ventral aspect. A shallow but broad groove separates the dorsal condyl from the ventral one. The condylus ventralis is mainly situated at the distal aspect. The large foramen pneumaticum is clover-shaped.

Seen from dorsal, two broad and shallow sulci flank a raised structure at the distal extremity. The anterior sulcus is identified as sulcus anconaeus medialis (Wellnhofer, 1985: 121), and is, seen from distal, distinct. The opposite, posterior sulcus extends into the distal aspect, forming a well defined, sharp ridge posterior to the foramen pneumaticum and anterior to the epicondylus ventralis. This ridge describes an angle of approximately 90 degree, with the angle pointed anteroventrally. Proximally, the processus medialis extends in posterior direction. A foramen inserts anterodistally in the attachment area between the processus and the corpus.

Humerus SMNS 55883

Family Ornithocheiridae SEELEY, 1870

Genus *Santanadactylus* DE BUISONJÉ, 1980

Santanadactylus pricei WELLNHOFER, 1985

cf. *Santanadactylus pricei*

Fig. 2D

Holotype: BSP 1980 I 122, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. Left front extremities.

Diagnosis. – *Santanadactylus pricei* according to WELLNHOFER (1985: 132): “Eine Art der Gattung *Santanadactylus*, die kleiner ist als *S. araripensis* und *S. brasiliensis*. Am Humerus keine Trochlea-Epiphyse, Processus lateralis mit geknicktem Oberrand. [...]”.

(Translation: “A species of the genus *Santanadactylus* which is smaller than *S. araripensis* and *S. brasiliensis*. Humerus without epiphysis of trochlea, upper edge of the processus lateralis bent.”)

Description SMNS 55883

The right humerus with the inventory number SMNS 55883, lacks the distal half (Fig. 2D). The humerus is embedded with its posterior aspect, showing only the anterior aspect. The ventral and dorsal aspects are obscured by matrix as well. The anterior edge of the caput humeri is incomplete and the ventralmost edge of the processus lateralis is either obscured by matrix or missing.

The proximal end shows a caput humeri at a distinct angle with the corpus. The ventral edge of the processus lateralis commences at the caput and continues straight into distal direction, after which it forms the convex distalmost outcrop of the processus. The ventralmost three quarters of the distal edge of the processus is at right angles with the corpus, but the remaining quarter, closest to the corpus humeri, bends concavely towards the corpus. The length is 154 mm as preserved. The diameter of the corpus, distal to the processus lateralis, is 23.5 mm and the height of the processus lateralis 56.9 mm (Tab. 2).

Tab. 2. Measurements of isolated humeri (in mm).

SMNS 55408:	
Length, as preserved	138
Diameter corpus	approximately 17
SMNS 55409:	
Length	243
Width corpus, dorsal-ventral plane	28.4
Width corpus, anterior-posterior plane	42.9
Width proximal aspect, dorsal-ventral plane	37.3
Width proximal aspect, anterior-posterior plane	56.6
Width distal aspect, dorsal-ventral plane	43.3
Width distal aspect, anterior-posterior plane	67.7
SMNS 55883:	
Length, as preserved	154
Width corpus, dorsal-ventral plane (beginning processus lateralis)	23.5
Width corpus: maximum height processus lateralis, as preserved	56.9

Discussion

Several (parts of) humeri of Brazilian pterosaurs are published (for instance DE BUISSONJÉ, 1980; KELLNER & TOMIDA, 2000; FREY & MARTILL, 1994; VELDMEIJER, 2002; WELLNHOFER, 1985, 1991b).

The uncertain diagnostic value of the humeri (see below) is, in the present work, further reduced by the incompleteness as well as the largely unprepared state of all but one humerus (55409). Consequently, humerus SMNS 55408 cannot be determined on genus or species level and only a tentative determination of family can be presented.

Humerus SMNS 55409 is not Azhdarchid, because the processus lateralis of Azhdarchid humeri is substantially larger and the corpus comparatively more robust (PADIAN & SMITH, 1992). The humerus of *Coloborhynchus spielbergi* has a processus lateralis with a straight ventral edge and the ventralmost tip is not as strongly curved proximally. Furthermore, the caput lacks the distinct ridge (VELDMEIJER, in press). The humeri of *Anhanguera piscator*, described by KELLNER & TOMIDA (2000), and *Anhanguera santanae*, published by WELLNHOFER (1985, 1991b), compares well with SMNS 55409. In both cases, the ventral edge of the processus lateralis is bent in posterior direction, the ventral tip of this processus is strongly curved, creating a concave posteroproximal surface; the foramen pneumaticum is placed at the same place and inserts in a comparable way. The ventral edge, however, is more concave with *Anhanguera*. The comparison of SMNS 55409 with *Santanadactylus* reveals a high degree of resemblance, comparable to the resemblance between the humerus of SMNS 55409 and *Anhanguera*. The caput of *Santanadactylus* has a distinct ridge at

the proximal surface and since this lacks with *Anhanguera*, SMNS 55409 can be assigned to *Santanadactylus*. This ridge is the most important characteristic of the *Santanadactylus* humerus and forces a determination as *Santanadactylus* (see also DE BUISONJÉ, 1980; WELLNHOFER, 1991b).

The broad (in dorsal-ventral plane) caput of *Santanadactylus brasiliensis*, as described by DE BUISONJÉ (1980), together with the relatively small processus medialis, the drooping ventral tip of the processus lateralis if seen from anterior and the relatively short processus lateralis differs with SMNS 55409. The main differences with *Santanadactylus pricei*, published by WELLNHOFER (1985, 1991 b), are the stronger ventral edge of the processus lateralis and the stronger angle of the caput relative to the corpus. Furthermore, the general size of *Santanadactylus pricei* is smaller. The humerus compares therefore best with *Santanadactylus araripensis*, as described by WELLNHOFER (1985), especially because of the shape of the caput, processus lateralis (seen from proximal) and the comparable layout of the various views of the distal extremity. Additional support is the fact that the sulcus anconaeus medialis, seen from distal, is as strongly developed as with SMNS 55409 and the comparable measurements.

Humerus SMNS 55883 has also more points of contact for comparison than SMNS 55408. The processus lateralis of Azhdarchid pterosaurs is substantially larger and the corpus comparatively more robust. The general size is larger as well (PADIAN & SMITH, 1992). The processus lateralis of the humeri of *Anhanguera*, as presented by WELLNHOFER (1991b) and KELLNER & TOMIDA (2000), has a strong posterior-orientated bending, which apparently lacks with SMNS 55883. The humerus of *Coloborhynchus spielbergi* has a processus lateralis with a straight ventral edge. The humeri of both species are substantially larger as well.

According to WELLNHOFER (1985), the humerus of *Santanadactylus araripensis* has a comparable processus lateralis, but a ridge pronounces the caput. This cannot be ruled out for the Stuttgart humerus. The ventral edge of the processus lateralis of *Santanadactylus brasiliensis*, described by DE BUISONJÉ (1980) is far straighter and the caput is clearly separated from the corpus by a ridge. SMNS 55883 most closely resembles the humerus of *Santanadactylus pricei*. The measurements of the humeri show less difference in size relative to the humeri of other Brazilian pterosaurs and the shape of the processus lateralis is highly comparable. Furthermore, the angle of the caput which has no ridge to separate it from the corpus, is comparable. Taking the limited diagnostic value of the above used characters to distinguish humeri into account together with the condition of SMNS 55883, the humerus is tentatively classified as cf. *Santanadactylus pricei*.

The humerus SMNS 55883, as determined to be cf. *Santanadactylus pricei*, belongs according to WELLNHOFER (1985, 1991a) to the family of Ornithocheiridae, which is in contrast to the designation of *Santanadactylus* to Criorhynchidae by DE BUISONJE (1980). KELLNER & TOMIDA (2000) regard all specimens of *Santanadactylus pricei* except the holotype (BSP 1980 I 122) as 'Pterodactyloidea indet.'. Also the New York specimen (WELLNHOFER, 1991b), erroneously referred to as AMNH 22555 by the authors (ibidem: 106) whereas it should be AMNH 22552, is referred to as 'Pterodactyloidea indet.' However, classification as Ornithocheiridae is defendable, as explained by Wellnhofer (1985, 1991a). Furthermore, KELLNER & TOMIDA (2000: 104) reclassify *Santanadactylus araripensis* as *Anhanguera araripensis*, because "the preserved dorsal portion of the praemaxilla becomes gradually sharper

toward the preserved rostral part of the skull, suggesting the presence of a sagittal crest, rostral to the nasoantorbital fenestra". This is not followed here, for reasons discussed elsewhere (VELDMEIJER, in press).

The comparison of the Stuttgart humerus shows a close relationship with Anhanguerid humeri (see VELDMEIJER, in press; WELLNHOFER, 1991b). However, the clade Anhangueridae as established by CAMPOS & KELLNER (1985) is considered invalid by UNWIN (2001), whereas WELLNHOFER (1991b) accepts the clade. It is beyond the scope of the present work to evaluate the validity of the different clades, but in any case it is clear that the animals assigned to either Ornithocheiridae or Anhangueridae display a very close relationship.

2.3. Isolated ulnae and radii SMNS 55410, 55411, 55413, 82001

Fig.3, Tabs. 3, 4

Ulna SMNS 55410, ulna and radius SMNS 55411

Santanadactylus pricei WELLNHOFER, 1985
cf. *Santanadactylus pricei*

Figs. 3A, B

Holotype: BSP 1980 I 122, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. Left front extremities.

Diagnosis. – *Santanadactylus pricei*, according to WELLNHOFER (1985: 132): “[...] Radius nur halb so stark wie die Ulna. [...]”.

(Translation: “Radius merely half as wide as ulna.”)

Description SMNS 55410

The right ulna with the inventory number SMNS 55410 (Fig. 3A) is still embedded in matrix, exposing only the anterior aspect. The bone is badly preserved and substantial parts of the extremitas proximalis as well as the extremitas distalis are severely damaged or missing. The olecranon lacks almost entirely whereas only a small part remains of the processus cotylaris dorsalis. The proximalmost part is missing as well as the area ventral to the processus cotylaris dorsalis. An area of about 45 mm of the anterior aspect lacks the outer bone layer.

This ulna is a straight bone with dorsoventrally expanding extremitas proximalis and distalis and an elliptical cross section. The remnants of the severely damaged processus cotylaris dorsalis suggest that the processus is less strongly developed as for instance with *Coloborhynchus spielbergi*. The corpus is flattened as an imaginary continuation of the processus cotylaris dorsalis. The slightly dented area between the olecranon and processus cotylaris dorsalis, the incisura radialis, is short, approximately 20 mm, and there is no trace of a pneumatic foramen at the proximalmost border. This might be due to the fact that the proximal part of the ulna lacks.

Description SMNS 55411

The preservation of SMNS 55411 (Fig. 3B) is bad. Only the proximal parts of this left ulna is preserved and still largely embedded. A substantial part of the anterior aspect and small parts of the dorsal aspects are visible. The olecranon is severely damaged and the processus cotylaris dorsalis is largely obscured. The radius is not articulated anymore but displaced. The bone is extremely badly preserved and therefore

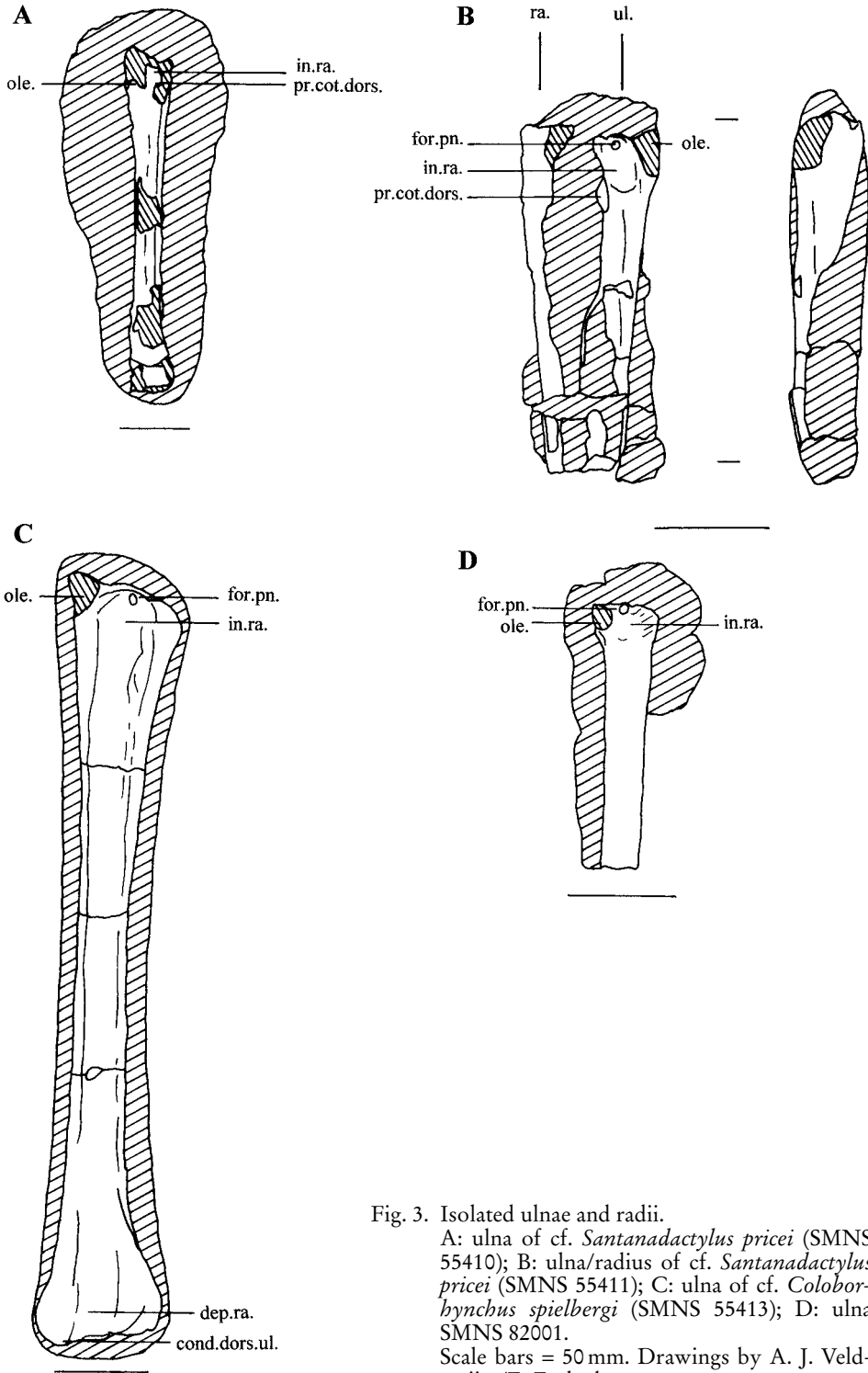


Fig. 3. Isolated ulnae and radii.
 A: ulna of cf. *Santanadactylus pricei* (SMNS 55410); B: ulna/radius of cf. *Santanadactylus pricei* (SMNS 55411); C: ulna of cf. *Coloborhynchus spielbergi* (SMNS 55413); D: ulna SMNS 82001.
 Scale bars = 50 mm. Drawings by A. J. Veldmeijer/E. Eendenburg.

of no morphological importance. The nodule is broken at two places, both at the distalmost ends of the ulna and radius.

SMNS 55411 is partly embedded in matrix, exposing a large part of its anterior aspect as well as the proximal part of its dorsal aspect. The elliptical cross section is therefore visible. The olecranon is damaged and the processus cotylaris dorsalis is obscured for its larger part. The remaining part of the processus suggests a stronger developed processus relative to SMNS 55410. The incisura radialis is deeper relative to SMNS 55410 and longer as well. Seen from anterior, a circular pneumatic foramen is situated at the proximalmost border. Seen from anterodorsal, the ulna is flattened indicated by a clear ridge.

The displaced radius of SMNS 55411 has a substantial smaller diameter relative to the ulna. The bone is too damaged to give a morphological description.

Ulna SMNS 55413

Family Ornithocheiridae SEELEY, 1870/Anhangueridae CAMPOS & KELLNER, 1985

Genus *Coloborhynchus* OWEN, 1874

Coloborhynchus spielbergi VELDMEIJER, in press

cf. *Coloborhynchus spielbergi*

Fig. 3C

Holotype: RGM 401880, National Museum of Natural History, Leiden, The Netherlands. Nearly complete skeleton.

Diagnosis. – The diagnosis of *Coloborhynchus spielbergi* according to VELDMEIJER (in press) does not include the ulna.

Description SMNS 55413

The right ulna with inventory number SMNS 55413 (Fig. 3C) is still embedded as well, only exposing the anterior aspect. This ulna is complete and in good condition, despite the crack distal to the extremitas proximalis and proximal to the extremitas distalis and the crack in the middle of the nodule. The olecranon, however, is damaged.

The right ulna SMNS 55413 is a straight bone with dorsoventrally expanding extremitas proximalis and distalis and an elliptical cross section. The processus cotylaris dorsalis is damaged but from the remnants it is clear that it was strongly developed and stronger relative to the previous discussed ulnae. Seen from anterior, a slightly elongated, circular pneumatic foramen inserts at the proximalmost border of the long (in proximal-distal plane) incisura radialis. The incisura is separated from the olecranon and proximal aspect by an elevated concave margin. The extremitas distalis shows a distally expanding depressio radialis, flanked by a low but broad cotylus dorsalis ulnae.

Ulna SMNS 82001

Family Ornithocheiridae SEELEY, 1870/Anhangueridae CAMPOS & KELLNER, 1985

Genus, species indet.

Fig. 3D

Description SMNS 82001

The small fragment of bone with the inventory number SMNS 82001 (Fig. 3D) is still largely embedded and rather damaged, especially the olecranon of which the outer bone layer is lost. The anterior aspect is entirely freed from matrix and the dorsal, ventral and proximal aspects only partially. Two small pieces of bone flaked from the, in this work illustrated, fragment. The bone is identified as a right ulna.

The proximal area shows a small, circular foramen pneumaticum of only few millimeters cross section, ventral to the damaged and obscured proximal aspect. The olecranon, dorsal to the foramen, is damaged. Again ventral and proximal to the foramen is a small, but distinct bulb situated, which is separated from the foramen by a depression. The incisura radialis is small and shallow but the damaged state of the bone prohibits a more detailed evaluation. The corpus is slightly elliptical in cross section and is, as far as can be determined from the incomplete specimen, slightly bent.

Tab. 3. Measurements of ulnae and radius (in mm).

SMNS 55410 ulna:	
Length, as preserved	255
Diameter corpus (anterior)	19.7
Width extremitas proximalis, as preserved	33
Width extremitas distalis, as preserved	33
SMNS 55411 ulna:	
Length, as preserved	approximately 150
Width extremitas proximalis, as preserved	approximately 27x28
Diameter corpus	19
SMNS 55411 radius:	
Length, as preserved	approximately 150
Width extremitas proximalis, as preserved	approximately 27x11
Diameter corpus	8.3
SMNS 55413 ulna:	
Length	395
Diameter corpus (anterior)	27
Width extremitas proximalis	approximately 66
Width extremitas distalis	69
SMNS 82001 ulna:	
Length, as preserved	117
Width extremitas proximalis	approximately 29
Diameter corpus	12x18

Discussion

Few lower arm bones of Brazilian pterosaurs are published (for instance FREY & MARTILL, 1994; KELLNER & TOMIDA, 2000; VELDMEIJER, in press; WELLNHOFER, 1985). The fact that the proximal and distal aspects are obscured, limits a classification because the morphology of ulnae and radii are, in general, highly comparable. Furthermore, the lack of published ulnae and radii hinder an extensive comparison,

except for species of *Santanadactylus* (*pricei* and *araripensis*), *Coloborhynchus spielbergi* and one example of *Anhanguera*.

The ulna SMNS 55411 is substantially shorter than the ulna of *Santanadactylus araripensis* and *Anhanguera santanae*, described by WELLNHOFER (1985; 1991b); the ratio is 1:1.5 and 1.4 respectively. The difference in length with *Coloborhynchus spielbergi*, published by VELDMEIJER (2002) is even larger and is in the ratio of 1:1.6. Tentatively, it can be assumed that the differences in ratio are too large to be explained by intraspecific variety. There are few differences with the ulna of *Santanadactylus pricei* and SMNS 55410 and 55411, despite a comparable length (Tab. 3). The pneumatic foramen at the processus cotylaris dorsalis cannot be attested at the Stuttgart ulnae but cannot be precluded as well. The pneumatic foramen at the proximal border of the incisura radialis of SMNS 55411 is also attested at the ulnae of *Santanadactylus pricei* and cannot be precluded for SMNS 55410.

A comparison of the diameters of the corpora of the ulnae and radii, Tab. 4, shows that the diameter of the radius of *Santanadactylus pricei* measures about 50 % of the diameter of the ulna, whereas this is 43 % for SMNS 55411. Although the difference is substantial, it is suggested not to assign the ulna and radius to a new taxon, for which no strong evidence can be attested. A proposed classification as cf. *Santanadactylus pricei* for 55411 on basis of biometrical arguments as well as the presence of a pneumatic foramen at the incisura radialis, the shape of the incisura and shape of the corpus is defensible. The classification 'cf.' is added to show the awareness of the differences of ratios of the diameter of the ulna and radius of SMNS 55411 relative to *Santanadactylus pricei*. The resemblance of SMNS 55410 with SMNS 55411 classifies this specimen as cf. *Santanadactylus pricei* as well. SMNS 55413, however, differs from *Santanadactylus pricei* especially from a biometrical point of view. The length of the ulna of the Munich *Santanadactylus pricei* (BSP 1980 I 122) and the Stuttgart ulna are in the ratio of 1:1.8 whereas this ratio is 1:2.4 for the New York *Santanadactylus pricei* (AMNH 22552) and SMNS 55413. This is hardly to explain by intraspecific variation. Seen from anterior, *Santanadactylus araripensis* has a pneumatic foramen at the extremitas distalis (WELLNHOFER, 1985), which lacks with SMNS 55413 and the diameter of the corpus of the Stuttgart ulna is more elliptical contrasting the almost circular cross section of *Santanadactylus araripensis*. The cross section of the *Anhanguera* ulna is oval in contrast to the elliptical cross section of SMNS 55413. The ulna of *Coloborhynchus spielbergi* is more elliptical and compares well with SMNS 55413. The ratio of the length of SMNS 55413 and *Coloborhynchus spielbergi* are in the ratio of 1:1.04. The general morphological resemblance between the ulna and the compared specimen leaves no doubt on the close relationship between the different specimens. However, because the validity of the clade Anhangueridae is questioned (as pointed out above) there is no choice but to refer to the family as Ornithocheiridae/Anhangueridae. On the basis of the, admittedly meagre, morphological resemblance and the above-mentioned biometrical arguments, the specimen is tentatively referred to as *Coloborhynchus spielbergi*. The problematic position is visualized by the addition 'cf.'

The ulna SMNS 82001 has no visible diagnostic features due to the incomplete preservation and preparation. Few diagnostic features are recognized at ulnae: traditionally, the diagnosticity of the ulna is combined with the radius in terms of diameters of the corpus (see above). No ratio can be obtained for the ulna and radius, because the radius is not preserved. Other possible diagnostic features, i.e. the incisura

radialis and the olecranon are severely damaged. On the other hand, the almost circular corpus is seen with ulnae of some pterosaurs, for instance *Santanadactylus pricei*. Consequently, there is not enough evidence to warrant a more precise classification, other than family.

Tab. 4. Ratios of the diameter of ulna/radius.

	Diameter ulna	Diameter radius	Ratio radius:ulna
<i>Santanadactylus pricei</i> *	7.5	13.5	1:1.8
<i>Santanadactylus pricei</i> **	16.3	8.5	1:1.9
SMNS 55411	8.3	19	1:2.3
<i>Coloborhynchus spielbergi</i> ***	11.0	28.5	1:2.6

* BSP 1980 I 122 (Measurements from WELLNHOFER, 1985: 134)

** AMNH 22552

*** For comparative reasons a large ulna and radius (410 and 401 mm respectively)

2.4. Associated humerus and ulna/radius SMNS 81976

Fig. 4, Tabs. 4, 5

Order Pterosauria KAUP, 1834

Suborder Pterodactyloidea PLIENINGER, 1901

Family, genus, species indet.

Fig. 4

Description SMNS 81976

A calcareous nodule with the inventory number SMNS 81976 contains a right humerus and the articulated ulna/radius (Fig. 4). The humerus is embedded in the matrix with its anterior aspect and the ulna/radius are embedded with their dorsal aspects. The complete humerus is sectioned lengthwise. The proximal half of the ulna and the proximal half of the radius is sectioned lengthwise as well, except for the proximalmost part of approximately 40 mm length. The inner side of the bone shows the typical pterosaurian construction; the corpora of the bones are hollow with thin walls (often less than 1 mm thick) and transverse, with each other interconnecting internal struts that "can be regarded as materialized lines of force" (WELLNHOFER, 1991a: 149) providing maximum lightness combined with optimal strength (see also CARTER et al., 1992). The extremities are composed of spongy bone tissue. It is not known whether the struts are more numerous in the humerus relative to the ulna/radius as observed by WELLNHOFER (1985, 1991b) because most of the struts are not preserved.

The humerus and ulna/radius are in contact at a 90-degree angle approximately. This position is seen with other pterosaurs as well (WELLNHOFER, 1985).

The ventral edge of the processus lateralis has a strong convex course and the caput humeri is set at a distinct angle relative to the strikingly slender corpus. The length of the humerus is 182 mm and the diameter of the corpus is 16.7 mm (Tab. 5). The ulna and radius, in articulation with each other and the humerus, are elliptical of cross section.

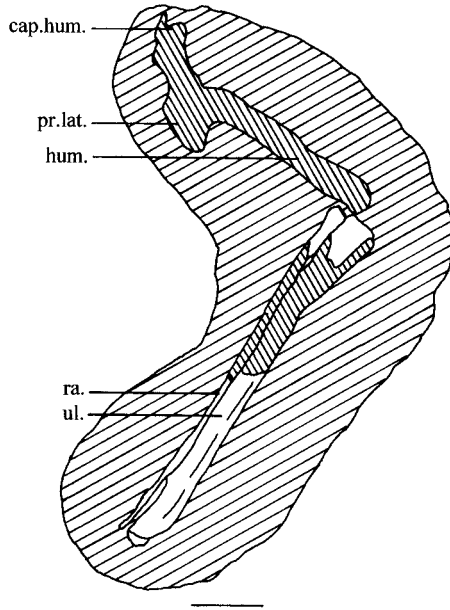


Fig. 4. Associated humerus and ulna/radius (SMNS 81976).
Scale bar = 50 mm. Drawing by A. J. Veldmeijer/E. Eendenburg.

Tab. 5. Measurements of humerus and ulna/radius, SMNS 81976 (in mm).

	Length	Diameter	Ratios	
Humerus	182	16.7	Diameters radius:ulna	1: 2.3
Ulna	260	11.7	Diameter:length humerus	1:10.9
Radius	260*	5*	Lengths humerus:ulna	1: 1.4

* approximately

Discussion

The length of the humerus is comparable to the humerus of *Santanadactylus pricei*, paratype BSP 1980 I 43, published by WELLNHOFER (1985), and the New York specimen of *Santanadactylus pricei*. The status of *Santanadactylus pricei* and its paratypes are discussed previously in the present work.

The corpus of the humerus is very slender relative to its length (ratio 1:10.9), which is, compared with the ratios established for other pterosaurs, the largest (cf. VELDMEIJER, in press). The bone, however, is sectioned lengthwise but not exactly in the middle. In contrast, the sectioning occurred more anteriorly. The measured diameter, therefore, is smaller than the real diameter. The diameters of radius and ulna are in the ratio of 1:2.3 (Tab. 5), which is the same as calculated for SMNS 55411 and differs especially with *Santanadactylus pricei* (Tab. 4). The ratio of the length of the humerus and length of the ulna are about the same in all calculated material (varying from 1:1.4 to 1:1.6).

The one possibly diagnostic (discussed with ‘Isolated humeri’) morphological feature, viz. the convexity of the (badly preserved) processus lateralis, and the biometrical arguments (see also the discussion with ‘Mandibula’) are not unambiguous enough in this specimen to warrant a classification more precise than on the level of suborder.

2.5. Phalanges of wing finger SMNS 55412, 55415

Fig. 5, Tab. 6

Order Pterosauria KAUP, 1834

Suborder Pterodactyloidea PLIENINGER, 1901

Family, genus, species indet.

Description SMNS 55412

The specimen with inventory number SMNS 55412 is a slab and counter slab (Fig. 5A). The phalanx is in good condition despite the breakage at three points and the lack of the distalmost part. Few ostracods are visible in the calcareous matrix.

The ventral and dorsal aspects of this left phalanx are visible. The phalanx is bent into posterior direction. Seen from ventral, the extremitas proximalis is expanded posteriorly and inclined anteriorly. The proximal aspect is strongly concave for the reception of the convex distal aspect of the previous wing phalanx. The wing was bent in posterior direction, due to the bending of this phalanx (and of the other phalanges as well), which is a general characteristic of the pterosaur wing. The extremitas distalis is missing, but the corpus expands slightly in anteroposterior plane towards this extremitas. The corpus has a flattened, oval cross section, based on the outside observations. Remarkable of this phalanx is its size (Tab. 6), even more so taking the not fully-grown status of the bone (grain and cartilage at the extremitas proximalis) into account.

Description SMNS 55415

The specimen with inventory number SMNS 55415 is a calcareous nodule containing a large, well-preserved phalanx (Fig. 5B). The phalanx is complete and displays almost no damage.

The ventral aspect of the left phalanx with inventory number SMNS 55415 is freed from its calcareous matrix. The phalanx is long and slender without bending. The corpus, strongly oval in cross section at the extremitas proximalis and less oval in cross section at the extremitas distalis, based on outside observations, expands in anteroposterior plane towards the extremitas proximalis more severely relative to the extremitas distalis. Seen from ventral, the proximal aspect has a convex area that overhangs the ventral aspect slightly. Due to the matrix, it remains uncertain whether the remaining part of the proximal aspect is concave or convex. The extremitas distalis is slightly recurved, forming a clear ridge that separates the corpus from the distal aspect.

The extremitas distalis has two small foramina. The rugosities at the extremitas proximalis might be, according to KELLNER & TOMIDA (2000: 68): “the insertion surfaces for interphalangeal ligaments.”

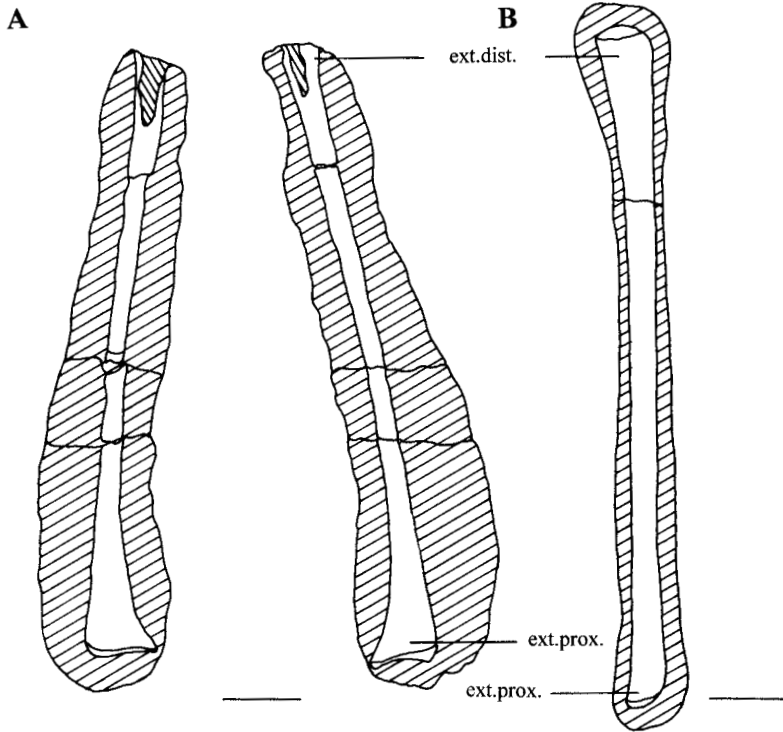


Fig. 5. Phalanges of wing finger.

A: SMNS 55412 (obverse and reverse); B: SMNS 55415 .

Scale bars = 50 mm. Drawings by A. J. Veldmeijer/E. Eendenburg.

Tab. 6. Measurements of phalanges (in mm).

SMNS 55412:	
Length, as preserved	40
Width corpus (anterior-posterior)	approximately 13.6
Width extremitas proximalis	approximately 41.6
Width extremitas distalis (end matrix)	approximately 22.4
SMNS 55415:	
Length	446
Width corpus (anterior-posterior)	18.1
Width extremitas proximalis	41.2
Width extremitas distalis (end matrix)	29.3

Discussion

Compared with the few published phalanges (FREY & MARTILL, 1994; WELLNHOFER, 1985, 1991b) SMNS 55412 is regarded as a second phalanx. This is primarily based on the bending. The shape of the proximal articular aspect excludes a determination as first phalanx (cf. for instance KELLNER & TOMIDA, 2000; WELLNHOFER, 1977, 1985, 1991b) and the bending seems to be too severe for a third phalanx. Furthermore, the proximal aspect is too concave for a third phalanx. The size suggests a large animal since the not fully grown bone measures 440 mm. Com-

pared with the length of the second phalanx of *Santanadactylus pricei* (length 325 mm, WELLNHOFER, 1985 and 324 mm, WELLNHOFER, 1991b) and *Arthurdactylus conandoylei* (length of 402 mm, FREY & MARTILL, 1994) the phalanx is large and more in line with the data given of *Anhanguera piscator* (preserved length of 355 mm, with a maximal width of the proximal aspect of 51 mm, KELLNER & TOMIDA, 2000). But again, the remark must be made that there is no insight in the probably large (DALLA VECCHIA & LIGABUE, 1993) intraspecific variability.

Phalanx SMNS 55415 is not a first phalanx because the proximal aspect of a first phalanx (cf. for instance KELLNER & TOMIDA, 2000; WELLNHOFER, 1977, 1985, 1991b) serves for the articulation with the metacarpal and differs clearly from the proximal aspects of the following wing phalanges. The straightness of the phalanx and the slight differences between the extremitas proximalis and extremitas distalis suggests that the phalanx is a third phalanx. If this is true, the size of this animal is large compared with the measurements of the third phalanges of *Santanadactylus pricei* (a length of 252 mm and a width of the extremitas distalis of 13.5 mm, WELLNHOFER, 1991b) and *Arthurdactylus conandoylei* (a length of 313 mm, FREY & MARTILL, 1994). It is more in line with *Anhanguera piscator* (preserved length of 218 mm and about 17 mm width of distal aspect, KELLNER & TOMIDA, 2000).

The nature of especially the second up to and including the last wing phalanges as well as the lack of detailed published specimens precludes accurate taxonomic designation. The resemblance between the extremitas distalis of the present specimen and the extremitas distalis published by DALLA VECCHIA & LIGABUE (1993), which they interpret as the first phalanx of the wing finger, is apparent despite the slightly more intense curving of the distal aspect, seen from dorsal. However, the incomplete preparation of SMNS 55415 prohibits a firm conclusion, but the phalanx published by DALLA VECCHIA & LIGABUE (1993) might be a second phalanx rather than a first one.

2.6. Partial front extremity SMNS 80437

Fig. 6, Tab. 7

Order Pterosauria KAUP, 1834

Suborder Pterodactyloidea PLIENINGER, 1901

Family, genus, species indet.

Description SMNS 80437

The specimen with inventory number SMNS 80437 is a calcareous nodule, containing five fragments of bone (numbered and referred to as 1, 2, 3, 4 and 5; Fig. 6). The bones are incomplete and prepared only partially. Bones 1–3 lie parallel to each other and run over bones 4 and 5, which are positioned at an 80-degree angle approximately, relative to bones 1–3.

The cross section of the bone numbered '1' is circular to elliptical. The extremitas proximalis is not complete and partly obscured by matrix, but the widening of the corpus towards the extremitas (from 7.8 mm to 10.7 mm) as well as the deep articulation socket, which is separated from the corpus by a clear ridge that continues into the corpus as a slight sulcus, suggests that the bone is the second phalanx of the right wing digit (IV). The close association with bone '2' provides additional support, because this bone is certainly the first phalanx of the right wing digit. This first phalanx tapers towards the extremitas distalis (from 12.4 mm to 6.2 mm). The large foramen pneumaticum at the posteroventral aspect is clearly visible. A shallow

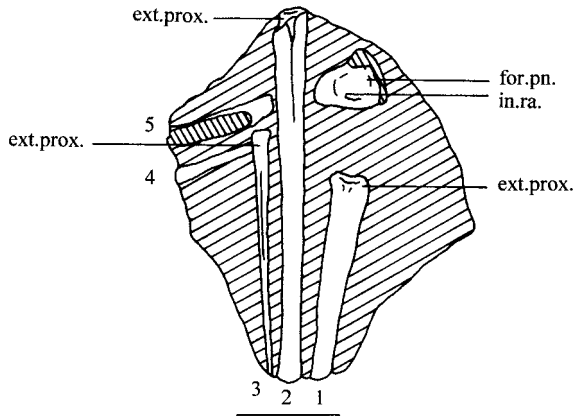


Fig. 6. Partial front extremity (SMNS 80437).
Scale bar = 50 mm. Drawing by A. J. Veldmeijer/E. Endenburg.

groove continues as an extension of the foramen pneumaticum. Remnants of the processus tendinosus extensoris are visible.

The bone referred to as '3' is a slightly tapering bone with a largest diameter of 10.7 mm. A shallow groove runs longitudinally. The bone is tentatively identified as the fourth phalanx of the wing digit, on the basis of the small size relative to the previously described ones, and its association with the first and second phalanx.

Bone '4' has a flattened circular cross section. It does not display any morphological features and is indeterminable.

The largest bone beneath the wing digit, numbered '5', can be identified as the right ulna. It lacks the olecranon entirely and the processus cotylaris dorsalis almost completely. The cross section of the ulna is circular. A foramen pneumaticum is situated in the incisura radialis, close to the edge of the proximal aspect. The incisura is not separated from the olecranon and proximal aspect by a distinct elevated concave margin, as seen with SMNS 55413.

Tab. 7. Measurements of front extremities (in mm).

	Length, as preserved	Diameter
Ulna	92.1	9.5
Radius	35.0	6.8
First ph. IV digit	approximately 158	5.5x124/6.2x9.5*
Second ph. IV digit	86.8	7.8/10.7*
Fourth ph. IV digit	104.6	2.2/7.3*

*Respectively proximal and distal measurements

Discussion

A discussion on ulnae is presented previously. The ulna of SMNS 80437 differs from the known ulnae by its circular cross section. The circular cross section contrasts sharply with the cross section of the ulna of *Anhanguera* as published by WELLNHOFER (1985, 1991b), which is oval and the elliptical cross section of SMNS 55413 and *Coloborhynchus spielbergi*. The arrangement of the foramen pneu-

maticum, and especially its lacking separation from the olecranon and proximal aspect differs from SMNS 55413 and is more comparable to *Coloborhynchus spielbergi*. It cannot be ruled out that the mentioned differences are due to the bad preservation and the partial covering by matrix. A classification is therefore not possible.

A discussion on the phalanges is presented previously. The present phalanges have no visible diagnostic features in order to compare it with other material in such way as to being able to classify them. The lack of information results partly from the fragmentary state and partly from the fact that the bones are embedded for the larger part.

3. Concluding remarks

The description of the material of the Staatliches Museum für Naturkunde Stuttgart proved to be especially important because the second almost complete mandibula of *Criorhynchus mesembrinus* is presented. The additional description of material, post-cranial as well as cranial, of new or existing species helps gaining insight in the diversity of the Santana pterosaurs. Furthermore, the constant adding of data to the fossil record renders comparative anatomy more easy and reliable and more precise diagnoses are possible.

The limited diagnostic value of humeri (KELLNER & TOMIDA, 2000; VELDMEIJER, in press) is partly due to the lack of ‘rules’ how to regard differences, which was, among others, the reason in the present work for uncertainty with some classifications. On the other hand, a seemingly detailed diagnosis of *Santanadactylus brasiliensis*, as quoted above, is of no use because most of the features have no diagnostic value (see also KELLNER & TOMIDA, 2000). At present, the general outline and position of the processus lateralis can be used for classifying on family level. For instance, the processus lateralis of the Nyctosaurid humerus is hatchet-shaped (BENNETT, 1993) and the processus lateralis of Pterodaustriid humerus is positioned at a completely different angle (WELLNHOFER, 1978). The use of slight differences in shape of the processus lateralis as a diagnostic feature on species level (for instance WELLNHOFER, 1985) neglects intraspecific variability as well as sexual dimorphism. Furthermore, the convexity of the ventral edge of the processus lateralis is seen in species of *Anhanguera* as well as *Santanadactylus* (among others the reason of the problems of Anhangueridae versus Ornithocheiridae). On the other hand, FREY & MARTILL (1994) mention problems with the classification of distinct different humeri of *Ornithocheirus* and *Santanadactylus* to the same family (Ornithocheiridae). The use of the shape of the caput humeri meets comparable problems, although the distinct crista at the caput is an exclusive feature of *Santanadactylus* and is a distinct diagnostic feature on family level.

Comparable problems of the ones discussed with humeri occur with all post-cranial (and even cranial) material. It might be useful therefore, to re-evaluate all material and establish diagnoses that also reckons with intraspecific variability and sexual dimorphism.

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Plate 1

Mandibula cf. *Criorhynchus mesembrinus* (SMNS 56994) in various aspects.

A: anterior; B: left lateral; C: ventral.

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