3. Pterosaurs from the Lower Cretaceous of Brazil in the Stuttgart Collection

3.1. 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 material in the collection of the Stuttgart museum is obtained from various people. The mandible 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. All bones are from the Cretaceous period, which precludes a designation as Rhamphorhynchoid pterosaurs.

3.2. Abbreviations

<table>
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<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>ad.fos.</td>
<td>adductor fossa</td>
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<td>ang.</td>
<td>angular</td>
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<td>art.</td>
<td>articular</td>
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<td>b.t.</td>
<td>?biceps tubercle</td>
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<td>cap.</td>
<td>humeral head</td>
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<tr>
<td>cond.dors.</td>
<td>dorsal condyle</td>
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<td>cond.vent.</td>
<td>humeral ventral</td>
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<td>cot.dors.</td>
<td>dorsal cotyle</td>
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<td>cot.lat.</td>
<td>lateral cotyle</td>
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<td>d.sag.cr.</td>
<td>dentary sagittal crest</td>
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<td>del.cr.</td>
<td>deltopectoral crest</td>
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<tr>
<td>dent.</td>
<td>dentary</td>
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<td>dent.ra.</td>
<td>dent for radius</td>
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<td>f.t.l.</td>
<td>first tooth left</td>
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<td>pn.for.</td>
<td>pneumatic foramen</td>
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<td>hum.</td>
<td>humerus</td>
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<td>i.cond.gr.</td>
<td>humeral intercondylar groove</td>
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<td>post.tub.</td>
<td>posterior tuberosity</td>
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<td>pre.art.</td>
<td>prearticular</td>
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<tr>
<td>ra.</td>
<td>radius</td>
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<tr>
<td>s.t.l.</td>
<td>second tooth left</td>
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<tr>
<td>scap.cor.</td>
<td>scapulocoracoideum</td>
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<td>su.</td>
<td>surangular</td>
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<tr>
<td>sul.an.med.</td>
<td>sulcus anconaeus medialis</td>
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<td>(Wellnhofer, 1985: 121)</td>
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<td>sup.pr.</td>
<td>supracondylar process</td>
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<td>ul.</td>
<td>ulna</td>
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3.3. Systematic palaeontology, description and comparison

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, northeast 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).
3.3.1. Mandible SMNS 56994 (figures 3.1, 3.2; table 3.1)

Family Anhangueridae Campos & Kellner, 1985b
Genus Criorhynchus (Owen, 1861)\textsuperscript{15}

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 mandible BSP 1987 I 46, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany

Diagnosis *Tropeognathus mesembrinus* according to Wellnhofer (1987: 179): 
"*Tropeognathus* with high, rounded [...] smaller \{than premaxillary sagittal crest\} 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

The mandible (figure 3.1, 3.2; table 3.1) 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 retroarticular process is partially restored whereas the left one is restored completely. The ventral edge of the dentary sagittal crest 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 mandible shows a high degree of co-ossification and the lateral aspects are characterised by the relief of the attachment areas of the different bones of the mandible. The rami are bent slightly into medial direction. The posterior extremities, of which only the right one is preserved partially, is formed by the retroarticular process and expand strongly medially. Seen from posterior, the dorsal part of the retroarticular process shows a lateral cotyle (cot.lat) that occupies the entire lateromedial width without any internal divisions. The medial half of the lateral cotyle is less broad in dorsoventral plane, relative to the lateral part. The surangular (su.) forms strong dorsal boundaries of the lateral cotyle and overhangs especially the medial half. Seen from dorsal, the surangular commences at the mediadorsal 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 articular (art.) is reconstructed. The praearticular (pre.art.) forms the ventral border of the adductor fossa. The medial aspects of the rami are obscured by matrix, but seen from ventral, the posterior parts of the adductor fossa are still visible. The exact course of the praearticular cannot be established. The elongated angular (ang.) 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 dentary (dent.). The dentary extends ventrally, forming a smoothly curved dentary sagittal crest (d.sag.cr.), which continues anteriorly to the anterior aspect of the mandible. The crest, 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 mandible 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 relative to the first pair of teeth. The following teeth, at least up to 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 curved. The alveoli of the ninth up to 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.

Discussion

Few toothed pterosaurs are known from Brazil with dentary sagittal crests. *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 (2003a) published the first *Coloborhynchus* with post–cranial material. Fossils, named as species of *Anhanguera* are described by Campos & Kellner (1985a, b), Kellner & Tomida (2000) and Weltnhofer (1985, 1991b). Toothed species without a dentary sagittal crest are *Brasiliodactylus* (Kellner, 1984), *Cearadactylus* (Leonardi & Borgomanoer, 1985; Dalla Vecchia, 1993). Possibly, *Santanadactylus*, as published by Weltnhofer (1985, 1991b) lacks a crest as well. *Anhanguera* might have had a crest that does not commence at the anterior aspect of the mandible but rather posterior to the anterior aspect and is therefore different (Weltnhofer, 1991b). Recently however, it is suggested that the dentary sagittal crest starts anteriorty as well (see Kellner & Tomida, 2000, figure 66). *Pteranodon* does not have a dentary sagittal crest. Furthermore, *Pteranodon* is edentulous, as are Azharchidae, Tapejaridae and Nyctosauridae. The teeth of Dsungaripteraidae and Pterodaustroidae differ completely from the teeth of the discussed mandible (e.g. Martill et al., 2000; Weltnhofer, 1991a).

The general layouts of the toothed mandible are comparable. A comparison with crested pterosaurs shows that the curvature of the rami is less and the mandible is shorter relative to *Co. spielbergi*. The comparatively long mandible of *Co. robustus* show short rami relative to SMNS 56994. The rami display almost no curving. The powerful teeth of *Co. robustus*, which display a different dentition pattern, clearly distinguish *Coloborhynchus* from the Stuttgart mandible. Furthermore, the mandible of *Coloborhynchus* is anteriorly expanded, in contrast to the straight mandible discussed here. One other species, *Cr. mesembrinus*, has a combination of a dentary sagittal crest, teeth and non–expanding snout as well. The mandible of *Cr. mesembrinus* (BSP 1987 I 46) 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 teeth. The curvature of the rami of *Cr. mesembrinus* is slightly less strong relative to *Co. spielbergi* but still stronger relative to SMNS 56994. The main difference between the two mandibles is the size difference. The compared mandible (BSP 1987 I 46) has an estimated (because the retroarticular process 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 two possibilities. 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\(^9\) seems to support this suggestion but pterosaurs display true allometry (Brower & Veinus, 1981; Wellnhofer, 1970, 1991b). The ratios do not exclude intraspecific variability and are based on individuals only. *Criorhynchus mesembrinus* has a characteristic deep and, towards the symphysis, broad dentary sagittal groove. Because the Stuttgart mandible 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 mandible as possible (*cf.* *Cr. mesembrinus*, classified to the Anhangueridae. This systematic interpretation follows Fastnacht (2001) opposed to the classification as *Tr. mesembrinus* in the clade of Anhangueridae by Kellner & Tomida (2000).

### 3.3.2. Isolated humeri SMNS 55407, 55408, 55409, 55883 (figures 3.3, 3.4; table 3.2)

**Humerus SMNS 55407**

The right humerus with inventory number SMNS 55407 is incomplete (figure 3.3A, 3.4A; table 3.2). 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 deltopectoral crest 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 there are no signs of preparation. 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 brush strokes, are clearly to recognise. Consequently, there is no certainty whether the proximal and distal parts belong to one bone and therefore no further attention is given to the bone.

**Humerus SMNS 55408**

Family, genus, species indet.\(^{20}\)

The left humerus with inventory number SMNS 55408 is incomplete (figures 3.3B, 3.4B; table 3.2). The bone is still embedded in matrix and only the posterior and dorsal aspects are (partially) visible. The deltopectoral crest is still embedded. A large part of the posterior tuberosity (post.tub.) is missing. The specimen is considered isolated despite the fact that remnants of the ulna and remnants of the scapulocoracoid are still articulated. Isolated from the humerus is a small, straight piece of bone, which cannot be identified due
to its fragmentary state. The head 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. The damaged state of the bones results in the lack of diagnostic features.

Humerus SMNS 55409 (figures 3.3C, 3.4C; table 3.2)

Family Anhangueridae Campos & Kellner, 1985b
Genus Coloborhynchus Owen, 1874

Diagnosis *Santanadactylus* according to De Buisonjé (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–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. [...]"

*Coloborhynchus araripensis* (Wellnhofer, 1985)

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


Description

The left humerus with inventory number SMNS 55409 (figure 3.3C, 3.4C; table 3.2) 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 condyles and epicondyles are firmly fused with the humerus.

The humeral head is angled relative to the shaft. Seen from proximal, the head 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 posterior tuberosity from the rest of the head.

Seen from ventral, the ventralmost extension of the strong developed deltopectoral crest extends diagonally distal–proximal and the ventralmost tip is curved in proximal direction. This part of the proces is thicker relative to the, in posterior direction bent, ventral edge, which commences from the head and extends towards the ventralmost, curled
tip. The posteroproximal surface of the ventralmost extension of the deltopectoral crest is distinct concave. The ventral aspect of the humerus expands at the opposite side of the deltopectoral crest, *i.e.* the posteroventral corner. This is caused by the posterior tuberosity. The area between the posterior tuberosity and the deltopectoral crest 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 deltopectoral crest. Proximally, the posterior tuberosity extends in posterior direction. A foramen inserts anterodistally in the attachment area between the process and the shaft.

Despite being partly obscured by matrix, it is good to observe that the supracondylar process (sup.pr.) at the distal half, is strongly developed and 3 mm at its highest point. The process 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 supracondylar process and slightly more posteriorly is another ridge, identified as a muscle scar, which extends towards the ventral condyle (cond.vent.) at the distal aspect. The intercondylar groove (i.cond.gr.) separates the dorsal condyle (cond.dors.) from the ventral one.

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

Seen from dorsal, two broad and shallow grooves flank a raised structure at the distal extremity. The anterior groove is identified as “sulcus anconaeus medialis” (Wellnhofer, 1985: 121), and is, seen from distal, distinct. The opposite, posterior groove extends into the distal aspect, forming a well defined, sharp ridge posterior to the pneumatic foramen (pn.for.) and anterior to the ventral epicondyle. This ridge describes an angle of approximately 90°, with the angle pointed anteroventrally.

Humerus SMNS 55883

Family Ornithocheiridae Seeley, 1870
Genus Santanadactylus De Buisonjé, 1980
*Santanadactylus pricei* Wellnhofer, 1985
*cf. Santanadactylus pricei*

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

Diagnosis *S. pricei* according to Wellnhofer (1985: 132): "Eine Art der Gattung *Santanadactylus*, die kleiner ist als *S. araripensis* und *S. brasilensis*. 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. brasilensis*. Humerus without epiphysis of trochlea, upper edge of the deltopectoral crest bent.")

**Description**

The right humerus with the inventory number SMNS 55883, lacks the distal half (figure 3.3D, 3.4D; table 3.2). 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
The proximal end shows a head at a distinct angle with the shaft. The ventral edge of the deltopectoral crest commences at the head and continues straight into distal direction, after which it forms the convex distalmost outcrop of the process. The ventralmost three quarters of the distal edge of the process is at right angles with the shaft, but the remaining quarter, closest to the shaft, bends concavely towards the shaft.

Discussion

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 (SMNS 55409). Consequently, humerus SMNS 55408 cannot be determined on family, genus or species level.

Humerus SMNS 55409 is not Azhdarchid, because the deltopectoral crest of Azhdarchid humeri is substantially larger and the corpus comparatively more robust (Padian & Smith, 1992). The humerus of *Co. spielbergi* has a deltopectoral crest with a straight ventral edge and the ventralmost tip is not as strongly curved proximally. Furthermore, the head lacks the distinct ridge (Veldmeijer, 2003a). The humerus of *Co. piscator* (Kellner & Tomida, 2000) and *An. santanae* (Wellnhofer, 1985, 1991b), compares well with SMNS 55409. In both cases, the ventral edge of the deltopectoral crest curves in posterior direction, the ventral tip of this process is strongly curved, creating a concave posteroproximal surface; the pneumatic foramen is placed at the same position 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 head 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).26

The broad (in dorsal–ventral plane) head of *S. brasilensis*, as described by De Buisonjé (1980), together with the relatively small posterior tuberosity, the drooping ventral tip of the deltopectoral crest if seen from anterior and the relatively short deltopectoral crest differs with SMNS 55409. The main differences with *S. pricei*, published by Wellnhofer (1985, 1991b), are the stronger ventral edge of the deltopectoral crest and the stronger angle of the head relative to the shaft. Furthermore, the general size of *S. pricei* is smaller. The humerus compares therefore best with *Co. araripensis*, especially because of the shape of the head, deltopectoral crest (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 55409. The deltopectoral crest of Azhdarchid pterosaurs is substantially larger and the shaft comparatively more robust. The general size is larger as well (Padian & Smith, 1992). The deltopectoral crest of the humeri of *Anhanguera*, as presented by Wellnhofer (1991b), has a strong posterior–orientated bending, which apparently lacks with SMNS 55883 but which is also visible in *Co. piscator* (Kellner & Tomida, 2000). The humerus of *Co. spielbergi* has a deltopectoral crest with a straight ventral edge. The humeri of both species are substantially larger as well. According to Wellnhofer (1985), the humerus of *Co.
araripensis has a comparable deltopectoral process, but a ridge pronounces the head. This cannot be ruled out for the Stuttgart humerus. The ventral edge of the deltopectoral crest of S. brasilensis, described by De Buisonjé (1980) is far straighter and the head is clearly separated from the shaft by a ridge. SMNS 55883 most closely resembles the humerus of S. pricei. The measurements of the humeri show less difference in size relative to the humeri of other Brazilian pterosaurs and the shape of the deltopectoral crest is highly comparable. Furthermore, the angle of the head which has no ridge to separate it from the shaft, 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. S. pricei.

The humerus SMNS 55883, as determined to be cf. S. pricei, belongs according to Wellnhofer (1985, 1991b) to the family of Ornithocheiridae, which is in contrast to the designation of Santanadactylus to Criorhynchidae by De Buisonjé (1980). Kellner & Tomida (2000) regard all specimens of S. pricei except the holotype (BSP 1980 I 122) as 'Pterodactyloidea indet.'. Also the New York specimen (Wellnhofer, 1991b), is referred to as 'Pterodactyloidea indet.' The comparison of the Stuttgart humerus shows a close relationship with Anhanguerid humeri. However, the clade Anhangueridae as established by Campos & Kellner (1985b) 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 in detail on the basis of postcranial elements.

3.3.3. Isolated ulnae and radii SMNS 55410, 55411, 55413, 82001 (figures 3.5, 3.6; tables 3.3, 3.4)

Ulna SMNS 55410, ulna and radius SMNS 55411

*Santanadactylus pricei* Wellnhofer, 1985
cf. *Santanadactylus pricei*

Holotype: BSP 1980 I 122, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany. 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 (figures 3.5A, 3.6A; table 3.3) is still embedded in matrix, exposing only the anterior aspect. The bone is badly preserved and substantial parts of the proximal end as well as the distal end are severely damaged or missing. Only a small part remains of the dorsal cotyle. The proximalmost part is missing as well as the area ventral to the dorsal cotyle. An area of about 45 mm of the anterior aspect lacks the outer bone layer.

This ulna is a straight bone with dorsoventrally expanding proximal and distal ends and an elliptical cross-section. The remnants of the severely damaged dorsal cotyle suggest that it is not strongly developed. The shaft is flattened as an imaginary continuation of the dorsal cotyle. The slightly dented area between the proximal view and dorsal cotyle for the reception of the radius, 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 (figures 3.5B, 3.6B; table 3.3) is bad and therefore of no morphological importance. The nodule is broken at two places, both at the distalmost ends of the ulna and radius.

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 ulnar head is severely damaged and the dorsal cotyle is largely obscured. The radius is not articulated anymore but displaced. The bone is extremely badly preserved. The shaft of the ulna is elliptical in cross-section. The proximal aspect is damaged and the dorsal cotyle is obscured for its larger part but the remaining parts suggest that is was stronger developed relative to SMNS 55410. The dent for the reception of the radius 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.

Ulna SMNS 55413

Family Anhangueridae Campos & Kellner, 1985b

Genus Coloborhynchus Owen, 1874

Coloborhynchus spielbergi Veldmeijer, 2003a

cf. Coloborhynchus spielbergi


Diagnosis: The diagnosis of Coloborhynchus spielbergi according to Veldmeijer (2003a) does not include the ulna.

Description

The right ulna with inventory number SMNS 55413 (figures 3.5C, 3.6C; table 3.3) is still embedded as well, only exposing the anterior aspect. This ulna is complete and in good condition, despite the crack distal to the proximal end and proximal to the distal end and the crack in the middle of the nodule. The ulnar head, however, is damaged.

The right ulna SMNS 55413 is a straight bone with dorsoventrally expanding proximal and distal ends and an elliptical cross-section. The dorsal cotyle 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) dent for the reception of the radius. The distal end shows a distally expanding depression, flanked by a low but broad dorsal condyle.
Ulna SMNS 82001

Family, genus, species indet.²⁹

Description

The small fragment of bone with the inventory number SMNS 82001 (figures 3.5D, 3.6D; table 3.3) is still largely embedded and rather damaged, especially the proximal end 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 pneumatic foramen of only few millimeters cross–section, ventral to the damaged and obscured proximal aspect. The ulnar head 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 depression for reception of the radius is small and shallow but the damaged state of the bone prohibits a more detailed evaluation. The shaft is slightly elliptical in cross–section and is, as far as can be determined from the incomplete specimen, slightly bent.

Discussion

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 detailed published ulnae and radii hinder an extensive comparison, except for S. pricei, Co. araripensis, Co. spielbergi and one example of Anhanguera.

The ulna SMNS 55411 is substantially shorter than the ulna of Co. araripensis and An. Santanae: the ratio is 1:1.5 and 1.4 respectively. The difference in length with Co. spielbergi 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 S. pricei and SMNS 55410 and 55411, despite a comparable length (table 3.3). The pneumatic foramen at the dorsal cotyle cannot be attested at the Stuttgart ulnae but cannot be precluded as well. The pneumatic foramen at the proximal border of the depression for the reception of the radius seen in SMNS 55411 is also attested with S. pricei and cannot be precluded for SMNS 55410.

A comparison of the diameters of the shafts of the ulnae and radii, table 3.4, shows that the diameter of the radius of S. 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 given. A proposed classification as cf. S. pricei for SMNS 55411 on basis of biometrical arguments as well as the presence of a pneumatic foramen at the dent for the reception of the radius, the shape of this dent and shape of the shaft is defendable. 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 S. pricei. The resemblance of SMNS 55410 with SMNS 55411 forces to classify this specimen as cf. S. pricei as well. SMNS 55413, however, differs from S. pricei especially from a biometrical point of view. The length of the ulna of the Munich S. 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 S. pricei (AMNH 22552) and SMNS 55413. This is hardly to explain by intraspecific variation. Seen from anterior, Co. araripensis has a pneumatic foramen at the distal end, which lacks with SMNS 55413
and the diameter of the shaft of the Stuttgart ulna is more elliptical contrasting the almost circular cross-section of *Co. araripensis*. The cross-section of the *Anhanguera* ulna is oval in contrast to the elliptical cross-section of SMNS 55413. The ulna of *Co. spielbergi* is more elliptical and compares well with SMNS 55413. The ratio of the length of SMNS 55413 and *Co. 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. On the basis of the, admittedly meagre, morphological resemblance and the above–mentioned biometrical arguments, the specimen is tentatively referred to as *Co. spielbergi*. The problematic position is visualised by the addition 'cf.'

The ulna SMNS 82001 has no visible diagnostic features due to the incomplete preservation and preparation. Few diagnostic features are recognised at ulnae: traditionally, the diagnosticity of the ulna is combined with the radius in terms of diameters of the shaft (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 depression for the reception of the radius and the ulnar head, are severely damaged. On the other hand, the almost circular shaft is seen with ulnae of some pterosaurs, for instance *S. pricei*. Consequently, there is not enough evidence to warrant a more precise classification.

3.3.4. Associated humerus and ulna/radius SMNS 81976

Family, genus, species indet.

Description

A calcareous nodule with the inventory number SMNS 81976 contains a right humerus and the articulated ulna/radius (figures 3.7, 3.8; tables 3.4, 3.5). 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 halfs of the ulna and radius are 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 shafts 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 ends 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° angle approximately. This position is seen with other pterosaurs as well (Wellnhofer, 1985). The ventral edge of the deltopectoral crest has a strong convex course and the humeral head is set at a distinct angle relative to the strikingly slender corpus. The ulna and radius, in articulation with each other and the humerus, are elliptical of cross-section.

Discussion

The length of the humerus is comparable to the humerus of *S. pricei* (BSP 1980 I 43; Wellnhofer, 1985), and the New York specimen of *S. pricei* (the status of *S. pricei* is discussed previously in this chapter).

The shaft of the humerus is very slender relative to its length (ratio 1:10.9), which is,
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compared with the ratios established for other pterosaurs, the largest (cf. Veldmeijer, 2003a). 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 (table 3.5), which is the same as calculated for SMNS 55411 and differs especially with S. pricei (table 3.4). 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 above with 'Isolated humeri') morphological feature, viz. the convexity of the (badly preserved) deltopectoral crest, and the biometrical arguments (see also the discussion above with 'Mandible') are not unambiguous enough in this specimen to warrant a classification more precise than on the level of suborder.

3.3.5. Phalanges of wing finger SMNS 55412, 55415 (figures 3.9, 3.10; table 3.6)

Family, genus, species indet.

Description SMNS 55412

The specimen with inventory number SMNS 55412 is a slab and counter slab (figures 3.9A, 3.10A; table 3.6). 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 proximal end 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 distal end is missing, but the shaft expands slightly in anteroposterior plane towards this end. The shaft has a flattened, oval cross-section, based on the outside observations. Remarkable of this phalanx is its size (table 3.6), even more so taking the not fully-grown status of the bone (grain and cartilage at the proximal end) into account.

Description SMNS 55415 (figures 3.9B, 3.10B; table 3.6)

The specimen with inventory number SMNS 55415 is a calcareous nodule containing a large, well preserved phalanx (figures 3.9B, 3.10B). 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 proximal end and less oval in cross-section at the distal end, based on outside observations, expands in anteroposterior plane towards the proximal end more severely relative to the distal end. 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 distal end is slightly recurved, forming a clear ridge that separates the shaft from the distal aspect. The distal end has two small foramina. The rugosities at the proximal end might be, according to Kellner & Tomida (2000: 68): "the insertion surfaces for interphalangeal ligaments."
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. 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. Compared with the length of the second phalanx of S. pricei (length 325 mm, Wellnhofer, 1985 and 324 mm, Wellnhofer, 1991b) and Art. conandoylei (length of 402 mm, Frey & Martill, 1994) the phalanx is large and more in line with the data given of Co. 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, the extensor tendon process (cf. 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 proximal and distal ends 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 S. pricei (a length of 252 mm and a width of the distal end of 13.5 mm, Wellnhofer, 1991b) and Art. conandoylei (a length of 313 mm, Frey & Martill, 1994). It is more in line with Co. piscator (preserved length of 218 mm and about 17 mm width of distal aspect, Kellner & Tomida, 2000).

The nature of especially the second, third and fourth wing phalanges as well as the lack of detailed published specimens precludes accurate taxonomic designation. The resemblance between the distal end of the present specimen and the distal end published by Della 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; the phalanx published by Dalla Vecchia & Ligabue (ibidem) might be a second rather than a first phalanx.

3.3.6. Partial front extremity SMNS 80437 (figures 3.11, 3.12; table 3.7)

Family, genus, species indet.

Description

The specimen with inventory number SMNS 80437 (figures 3.11, 3.12; table 3.7) is a calcareous nodule, containing five fragments of bone (numbered and referred to as 1, 2, 3, 4 and 5). 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° angle approximately, relative to bones 1–3.

The cross–section of the bone numbered ’1’ is circular to elliptical. The proximal end is not complete and partly obscured by matrix, but the widening of the shaft towards the end (from 7.8 mm to 10.7 mm) as well as the deep articulation socket, which is separated from the shaft by a clear ridge that continues into the shaft as a slight groove, suggests that the bone is the second phalanx of the right fourth wing digit. 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 distal end (from 12.4 mm to 6.2 mm). The large pneumatic foramen at the posteroventral aspect is clearly visible. A shallow groove continues as an extension of the pneumatic foramen.

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 ulnar head entirely and the dorsal cotyle almost completely. The cross-section of the ulna is circular. A pneumatic foramen is situated in the dent for the reception of the radius, close to the edge of the proximal aspect. This depression is not clearly separated from the ulnar head by an elevated concave margin, as seen in SMNS 55413.

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* (Wellnhofer, 1985, 1991b), which is oval and the elliptical cross-section of SMNS 55413 and *Co. spielbergi*. The arrangement of the pneumatic foramen, and especially the lacking separation of the radial depression and the ulnar head differs from SMNS 55413 and is more comparable to *Co. 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.

3.4. Concluding remarks

The description of the material of the Staatliches Museum für Naturkunde Stuttgart proved to be especially important because the second almost complete mandible of *Cr. 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 possible.

The limited diagnostic value of humeri (Kellner & Tomida, 2000; Veldmeijer, 2003a) 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 *S. brasilensis*, 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 deltopectoral crest can be used for classifying on family level. For instance, the deltopectoral crest of the Nyctosaurid humerus is hatchet–shaped (Bennett, 1993) and the deltopectoral crest of Pterodaustrid humerus is positioned at a completely different angle (Wellnhofer, 1978). The use of slight differences in shape of the deltopectoral crest as a diagnostic feature on species level (*e.g.* Wellnhofer, 1985) neglects
intraspecific variability as well as sexual dimorphism. Furthermore, the convexity of the ventral edge of the deltopectoral crest 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 humeral head meets comparable problems, although the distinct ridge at the head is an exclusive feature of *Santanadactylus* and is a distinct diagnostic feature on family level (contra the view that this is due to the age of the animal).  

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.