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Description of two pterosaur (Pterodactyloidea) mandibles from the Lower Cretaceous Santana Formation, Brazil

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Two mandibles of pterodactyloid pterosaurs from the Lower Cretaceous Santana Formation (Romualdo, Albian) of Brazil are described and classified. The edentulous jaw is assigned to *Thalassodromeus*. This anterior part completes the reconstruction of the lower jaw, hitherto based on the holotype lacking this part. The toothed mandible is assigned to *Anhanguera* and is the first complete mandible of this taxon.

Keywords: *Anhanguera*, *Thalassodromeus*, *Coloborhynchus*, Lower Cretaceous, Santana Formation, Romualdo.

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INTRODUCTION

The described specimens both originate from the Romualdo Member (Albian) of the Santana Formation (Aptian-Albian) (Martill *et al.* 1993; see also Beurlen 1971; Kellner & Tomida 2000; Maisey 1991; Pons *et al.* 1990), in Chapada do Araripe in the province of Ceará, Brazil. Here new material of *Thalassodromeus* is described and compared with other edentulous taxa. The toothed jaw is briefly described; the focus is on the discussion of morphological differences relative to other pterosaurs from Brazil. For a broader description of the general layout of these pterosaurs, see Kellner & Tomida (2000), Kellner & Campos (2002),Veldmeijer (2003a), and Wellnhofer (1985, 1991). Dentition patterns (i.e. the graph that visualises the size and position of the teeth) are plotted and discussed only briefly, because a broader study is in progress (Veldmeijer, in press).

The material is housed in the collection Oberli; casts of SAO 251093 are housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany, the Staatliches Museum für Naturkunde, Stuttgart, Germany and Museu Nacional, Rio de Janeiro, Brazil.

Although it is not common to publish material from private collections, the decision to do so is based on the fact that the collection is unconditionally accessible. Furthermore, other scientists (i.e. Wellnhofer & Kellner 1991) have used the collection in their studies, which underlines the quality of the collection and its professional management. Finally, none of the fossils are holotypes. Access to the original specimens can be arranged

through the owner of the collection (St. Gallen, Switzerland, oberliurs@gmx.ch) or the Natural History Museum at St. Gallen (T. Bürgin, Naturmuseum Sankt Gallen, Museumstrasse 32, info@naturmuseumsg.ch).

ABBREVIATIONS

ad.fos.	adductor fossa
ang.	angular
ch.t.	foramen chorda tympani
d.	dentary
d.e.	dorsal cutting edge
d.sag.cr.	dentary sagittal crest
lat.cot.	lateral cotyle
man.sul.	mandibular sulcus
m.fos.	Meckelian fossa
med.cot.	medial cotyle
pat.	pathology
pn.for.	pneumatic foramen
pre.art.	prearticular
ret.pr.	retroarticular process
r.	ramus
ri.	ridge
s.sh.	symphyseal shelf
spl.	splenial
sur.	surangular
sym.cav.	symphyseal cavity
t.b.r.	elevated tooth-bearing rim

SYSTEMATIC PALAEONTOLOGY

Order Pterosauria KAUP, 1834
Suborder Pterodactyloidea PLIENINGER, 1901

Mandible SAO 251093

Figures 1, 2; Table 1

Family Tapejaridae KELLNER, 1989

Genus *Thalassodromeus* KELLNER & CAMPOS, 2002

Type species and specimen *Thalassodromeus sethi* KELLNER & CAMPOS, 2002 - large part of skull and mandible, DGM 1476-M, Museu de Ciências da Terra/Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.

Diagnosis *Thalassodromeus* according to Kellner & Campos (2002: 389) the same as for the species *T. sethi*. "[…] anterior portion of the premaxillae and dentary with sharp dorsal and ventral edges; […]" Between […] information on other parts than the mandible.

Species *Thalassodromeus sethi*

Holotype As for the type specimen.

Etymology note One of the authors (Kellner, pers.com. 2002) explained that the shape of the crest of the pterosaur reminded them of the crown of the god Seth. It is however noteworthy that the crown, representing the solar disk with two tall plumes, is typically worn by the god Amon (later Amon-Ra), or manifestations of him, and not by Seth (for instance Baines & Málek 1981).

Amended diagnosis Anterior part, starting from the anterior border of the mandibular sulcus, bent in dorsal direction.

DESCRIPTION

The specimen represents the symphyseal portion of the anterior mandible, but lacks the tip (approximately 10 mm). Rami are missing; the remaining part of the right one is slightly longer than the left one. The specimen is broken in two parts. The fossil has been completely prepared mechanically except at the tip where some matrix remains to protect the fragile point from breaking. No sutures are discernable.

The symphysis of the edentulous mandible is curved dorsally, starting from the anterior border of the symphyseal shelf (s.sh.). The dorsal aspect of the slender terminal point has a sharp cutting edge (d.e.) whereas the ventral aspect is less sharp, resulting in a tear-drop cross-section. Posteriorly, the dorsal cutting edge terminates at the shelf. The shelf rapidly increases in width posteriorly, diverging with the rami. In dorsal view, two low ridges (ri.) occur left and right of the middle of the shelf, 10 mm ventral to the dorsal edge, with a length

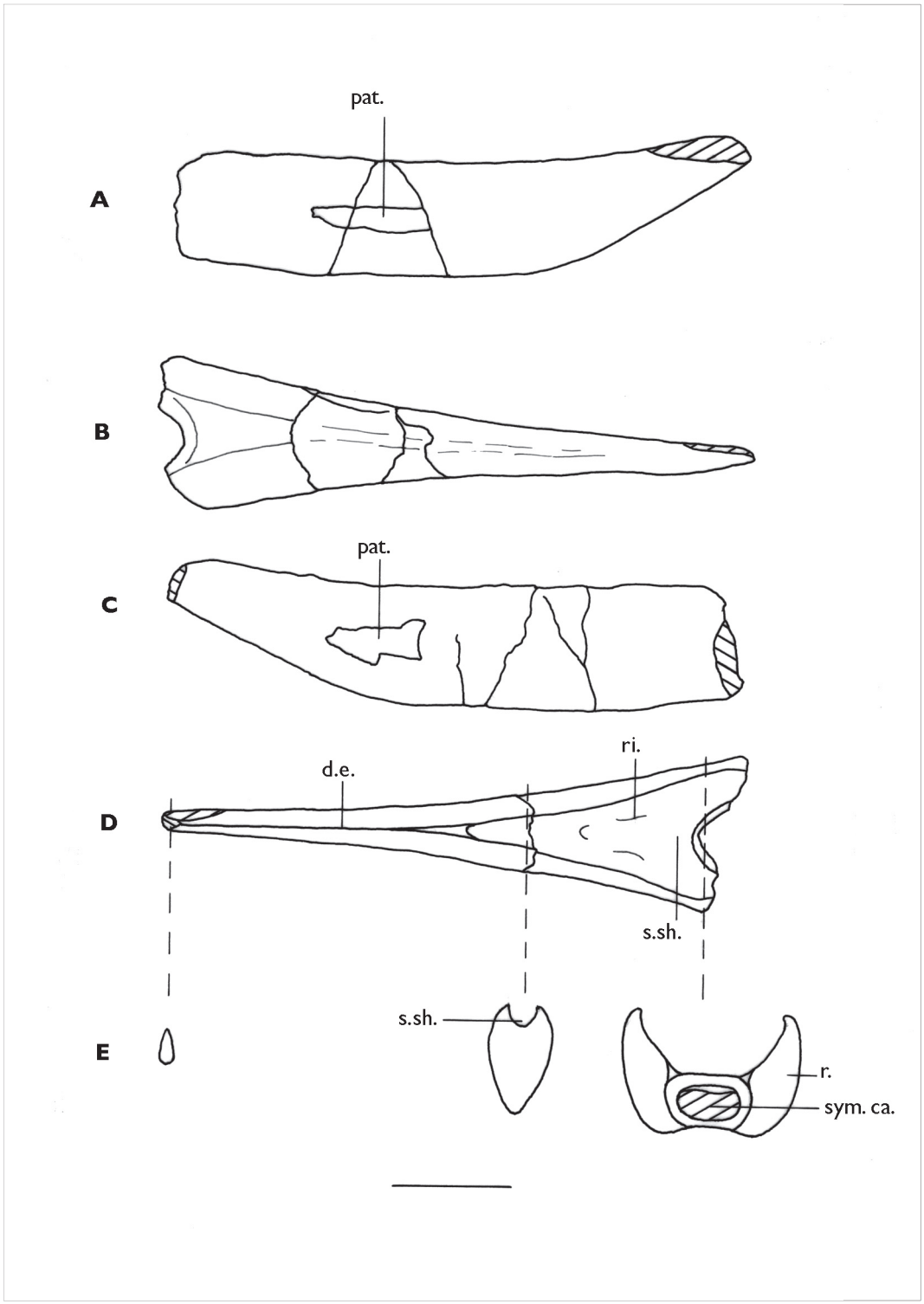

Figure 1 *Thalassodromeus sethi*, mandible SAO 251093 in various aspects. Right lateral (**A**), ventral (**B**), left lateral (**C**) and dorsal (**D**) view. Cross-sections at various points (**E**). Scale bar = 50 mm. [illustration: A.J. Veldmeijer]

Figure 2 *Thalassodromeus sethi*, mandible SAO 251093 in various aspects. Right lateral (**A**), ventral (**B**), left lateral (**C**) and dorsal (**D**) view. Scale bar = 50 mm. [photographs: E. Endenburg, reworked by J.H. van Leeuwen, courtesy Oberli]

of approximately 30 mm. Both are orientated slightly posterodorsally.

The posterior symphysis exposes an anterior cavity (sym.cav.). It appears to extend at least as far as the anterior half of the symphyseal shelf. The mandibular shelf has an oval cross-section with an indented rim. The little part of the rami that is preserved has a slender dorsal edge, which is slightly curved medially. The width of the rami increases posteriorly and ventrally and produces a lingual concavity. In lateral view the rami are convex.

As is common in pterosaurs, the mandible is lightly built with a bone thickness often less than 1.0 mm. A posterior view clearly shows the cross-section of the posterior mandible, including the reinforcement of the hollow bone by means of thin reticulate plates, forming large square-like pneumatized 'cells', which gives the bone optimal strength in combination with extreme weight reduction. The dorsal edges of the rami and the symphyseal shelf are more robust. Transverse bony plates here are more compact, resulting in smaller 'cells'. A clear lateroventral border separates this area from the more lightly constructed central and ventral areas.

Two irregularities are visible at both lateral surfaces. On the left is a small uneven area (pat.), interpreted as pathology. On the right is a comparable irregularity, but longer anteroposteriorly and smaller dorsoventrally. Both protrude slightly; the right one a bit more than the left one. The surrounding surfaces are slightly dented. It is tentatively suggested that these areas may be pathological in origin. Other pathologies are described by Bennett (1989, 2003a), Kellner & Tomida (2000), Mader & Kellner (1999). Reports by Kellner & Tomida (2000) on the left jugal and quadratojugal pathologies in *Coloborhynchus piscator* resemble the ones observed here.

COMPARISON AND DISCUSSION

A detailed comparison of SAO 251093 with other taxa is difficult because only the symphysis is known. Since SAO 251093 lacks teeth and alveoli, comparisons are limited to the edentulous pterosaurs, some of which are yet unknown from Brazil. One toothed exception, *Dsungaripterus,* is considered here because the anterior mandible is edentulous (Young 1964; Martil *et al.* 2000), curved dorsally and it is compressed laterally. The symphysis in *Dsungaripterus* is marked by a weak ridge, that is lacking in SAO 251093. The medial posterior mandibular shelf of *Dsungaripterus* is not present in SAO 251093. Furthermore, anterior teeth erupt in *Dsungaripterus* where no alveoli are present in SAO 251093. Due to the small dimensions of it in SAO 251093, it can not be determined whether this jaw is part of an endentulous, more advanced *Dsungaripterus* and classification as such is therefore ruled out for the time being.

Pteranodon has a mandibular cavity with a triangular section and thus is not consistent with the flattened circular cross-section in SAO 251093. Furthermore, the symphysis is proportionally larger in *Pteranodon*. The dorsal aspect of the mandible can be straight (*P. longiceps*) or dorsally bent (*P. sternbergi*) (Eaton 1910; Bennett 1994, 2001). In *Nyctosaurus* no dorsal curvature can be seen (Bennett 2003b; Williston 1902a,b, 1903). Furthermore, all known nyctosaurs are substantially smaller with a skull length of about 30 cm.

Also the non-Brazilian *Quetzalcoatlus* is an edentulous pterosaur. These azdarchid pterosaurs however are very poorly represented by mandibular remnants. Few mandibles, although not well-preserved, serve for comparison (Kellner & Langston 1996). The elongated symphysis is approximately 60 % of the total length. The cross-section of the dentary is triangular which is not consistent with the cross-section in SAO 251093. The dorsal rim of the anterior part of the symphysis in *Quetzalcoatlus* is almost flat. Ventrally, the joined dentaries form a sharp keel that declines posteriorly. A mandibular cavity is present, but its extent is unknown. No statement regarding the cross-section was made by Kellner & Langston (1996: 230), but they suggest a fur-

ther investigation into the hypothesis that the cavity "[...] might be linked with the presence of a gular sac […]". The transverse section of the rami are laterally convex and medially concave, so no medial decrease in width is observed, as in SAO 251093.

The family Tapejaridae consists of the genera *Tapejara*, *Tupuxuara* and *Thalassodromeus* from Brazil and *Sinopterus* from China. *Tapejara* is an edentulous pterosaur genus, consisting of two species from Brazil, *Tapejara wellnhoferi* KELLNER, 1989 and *Tapejara imperator* CAMPOS & KELLNER, 1997. The mandible in *Ta. wellnhoferi* has a depressed tip, a ventral keel, and a depressed shelf bordered by the raised lateral rims of the dorsal margin. Thus it differs from SAO 251093 which lacks a crest, has a dorsal curvature and lacks the depressed but has a distinct sulcus. No mandible is known of *Ta. imperator*, but the depressed rostral tip suggests a dorsal contour of the mandible similar to that of *Ta. wellnhoferi*. *Sinopterus dongi* WANG & ZHOU, 2000 is similar in gross morphology to *Tapejara* and is, therefore dissimilar to SAO 251093.

Tupuxuara is also an edentulous taxon from Brazil but descriptions of complete mandibles have not been published despite the fact that mandibles are known. However, a nearly complete specimen of *Tu. leonardii* KELLNER & CAMPOS, 1994 in the Iwaki Museum of Coal Mining & Fossils, Japan, and the partial skeleton in the Prefectural Museum of Natural History, Kanagawa, Japan, include mandibles. In general, the mandible is longer and smaller than in *Tapejara*. In dorsal view the anterior third of the symphyseal shelf is flat, with slightly raised rims, contrasting the sharp dorsal cutting edge of SAO 251093. Furthermore, the mandibles in *Tupuxuara* shows no dorsal curvature. The mandible in *Tu. leonardii* has a comparable symphyseal shelf but anteriorly the shelf fades into a flat surface. By comparison, the mandibular shelf in SAO 251093 does not flatten into the rim.

The edentulous pterosaur, recently described as *Thalassodromeus sethi* KELLNER & CAMPOS, 2002, was first published in 1990 (Kellner & Campos 1990). The type specimen includes pieces of the mandible. According to the authors (Kellner & Campos 2002: 391): "A strong concavity formed by the palatine and bordered laterally by the maxillae is present under the anterior half of the nasoantorbital fenestrae. Anterior to this concavity, the palate is convex, forming a short ventral keel that turns into a sharp blade anteriorly. The fused dentaries form a perfect counterpart to the palate, with a developed concavity, followed by a short, deep sulcus (that during occlusion encases the palatal keel, forming a strong interlocking mechanism) and an anterior sharp bony blade. Between both blades there is a gap." Following this preliminary analysis, a complete description is forthcoming in the near future (Kellner, pers.comm. 2002).

It is clear that the mandible SAO 251093 can be regarded as *Thalassodromeus*, having a short and deep shelf posterior to the concave, sharp edged blade. However, the rami in *Th. sethi* are straight and diverge slightly posterolaterally. This contrasts with SAO 251093 in which rami diverge stronger posterolaterally and exhibit a slight but distinct bending in lateral direction. The mediodorsal parts of the rami in *Th. sethi* are more concave relative to the rami in the St. Galler mandible. Here the mediodorsal side of the rami is only slightly concave and slightly extends to the bottom of the shelf. In lateral view the mandible of *Th. sethi* shows a distinct rise, whereas in SAO 251093 its only slightly convex. In ventral view *Thalassodromeus* anteriorly displays a distinct ventrally bulging area. In similar fashion, the anterior tip in SAO 251093 is bent in dorsal direction, starting at the anterior border of the symphyseal shelf. Although the anterior tip in *Th. sethi* is missing, there is no indication of bending at the anterior border of the preserved mandible, contra the reconstruction shown by Kellner & Campos (2002).

So far, only bones were found which show the familiar trabecular system (for instance in anhanguerids) or a plate-like construction as encountered in *Tu. leonardii*. But the bone structure described here differs from these;

Table 1 Measurements of mandible *Thalassodromeus sethi* (SAO 251093) in mm.

Anterior part	
Length	153*
Height anterior part, anteriormost tip	19.4
Height anterior part, halfway length	46.8
Height anterior part, posteriormost end	51.3
Width anterior part, anteriormost tip	7.2
Width anterior part, posteriormost end	31.2
Width mandible at anteriormost end symphyseal shelf	25.1
Width symphyseal shelf at posteriormost end	14.2
Posterior part	
Length posterior part, right side	120*
Length posterior part, left side	107*
Height posterior part, anteriormost end	52.4
Height posterior part, posteriormost end, right side	45.5
Largest width posterior part, anteriormost end	32.7
Width posterior part, anteriormost end, halfway dorsal-ventral	27.6
Smallest width posterior part, anteriormost end	9.3
Width symphyseal shelf at anteriormost end	14.6
Depth symphyseal shelf at posteriormost end	10.5
Width mandibular cavity	29.4
Height mandibular cavity	16.3
Width right ramus, measured at one third height (from dorsal)	1.1**
Width right ramus, measured at floor shelf	16.4**
Total	
Length, as preserved, right side	273*
Length, as preserved, left side	260*

* Including the bending ** Measured medial-lateral

a slightly comparable inner bone structure is mentioned for a ?Pteranodontidae premaxilla (Wellnhofer & Buffetaut 1999). Possibly, the internal structure of the lower part of the mandible (i.e. the 'cells'), is comparable to the situation reported for a Romanian giant pterosaurian skull (Buffetaut *et al.* 2001). The strengthening of the dorsal rims and, to a lesser extent of the sulcus, compares with the strengthening of the tooth-bearing parts in toothed pterosaurs as reported in *Coloborhynchus* (Veldmeijer 2003a). This kind of structure might have served to better withstand the forces exerted on these parts of the mandible during feeding. The question rises whether this might be an evolutionary remnant of a primitively dented maxilla.

In conclusion SAO 251093 is a small fragment relative to the type specimen of *Thalassodromeus*, but the general morphological features compare well with this taxon. The two differ in various small details, which in summary are not significant enough to justify the erection of a new species designation for SAO 251093. The importance of the Swiss specimen lies in the fact that it fills in the grey areas imagined by Kellner & Campos (2002) and thus makes the complete reconstruction of the skull of *Thalassodromeus* possible and expands the diagnosis of the species.

SYSTEMATIC PALAEONTOLOGY

Order Pterosauria KAUP, 1834
Suborder Pterodactyloidea PLIENINGER, 1901

Mandible SAO 200602
Figures 3-5; Table 2

Family Anhangueridae CAMPOS & KELLNER, 1985

Genus *Anhanguera* CAMPOS & KELLNER, 1985

Type species and specimen *Anhanguera blittersdorffi*, skull, MN 4805-V, Museu Nacional, Rio de Janeiro, Brazil.

Remark to diagnosis No diagnostic description was provided for the anterior part of the mandible in the original description of the holotype, due to its absence.

Amended diagnosis Mandible with smooth spoon-shaped expanded anterior part, containing the largest teeth. Presence of mandibular sulcus, which is flanked by raised rims, extending until the anterior expansion.

Anhanguera sp. indet.

DESCRIPTION

The mandible is complete, but broken into three pieces, the two rami and the anterior portion. Remaining matrix protects the teeth from damage but a small area close to the start of the symphysis is prepared. The toothed mandible is long and slender with a ventrally projecting dentary sagittal crest and straight diverging rami. The general anatomical features agree with previous descriptions of toothed pterosaurs (Kellner & Tomida 2000; Veldmeijer 2002, 2003a; Wellnhofer 1985, 1987). Here emphasis is placed on new features. A discussion on the validity of certain characters in other specimens follows.

Dentary

The dorsal margin of the mandible is largely obscured by matrix, but it can be observed that the anterior part of the mandible is slightly expanded. The tooth-bearing rims are raised. The depressed area between the rims has a sulcus (man.sul.), which is flanked by tiny raised ridges. It is uncertain how far the sulcus extends anteriorly and posteriorly. The dorsal margins of the rami are dentaries (d.) that form the dorsal limit of the adductor fossa (ad.fos.). The left and right dentaries join in a symphysis anterior to the Meckelian fossa (m.fos.). A deep dentary sagittal crest (d.sag.cr.) is present, starting 45 mm anterior to the dentary joint. This crest continuously decreases in width ventrally. Fine features include small (< 1 mm) grooves and a few small (< 1 mm) perforations that insert obliquely, with the grooves leading towards them. The ventral tip of the crest is slightly abraded.

Teeth

All anterior teeth are complete except for two on the right (numbers 12 and 13), which are broken at the alveoli. The left side has 14 intact teeth. The right has 15. No alveoli could be distinguished at the left ramus. Three teeth of the right ramus are partially embedded and separated from the rest of the ramus (they are not illustrated). In anterior view the first alveolus is oriented anterodorsally. The alveoli two and three are laterodorsally and anteriorly positioned. Alveolus four is placed laterodorsally and slightly anteriorly. The subsequent alveoli, numbers six to ten, are increasingly laterally oriented but less posteriorly.

The largest alveolar cross-section is the third one. The second is only slightly smaller. In general, the teeth are curved in a medial and posterior direction, although the curvature decreases posteriorly. Teeth one to four are more strongly curved. The teeth cross-section is elliptical with the long axis oriented anteromedially and at right angles to the curvature of the teeth. Right tooth nine has an anterolateral tip facet extending laterally. The polished edges of the facet suggest that the damage is

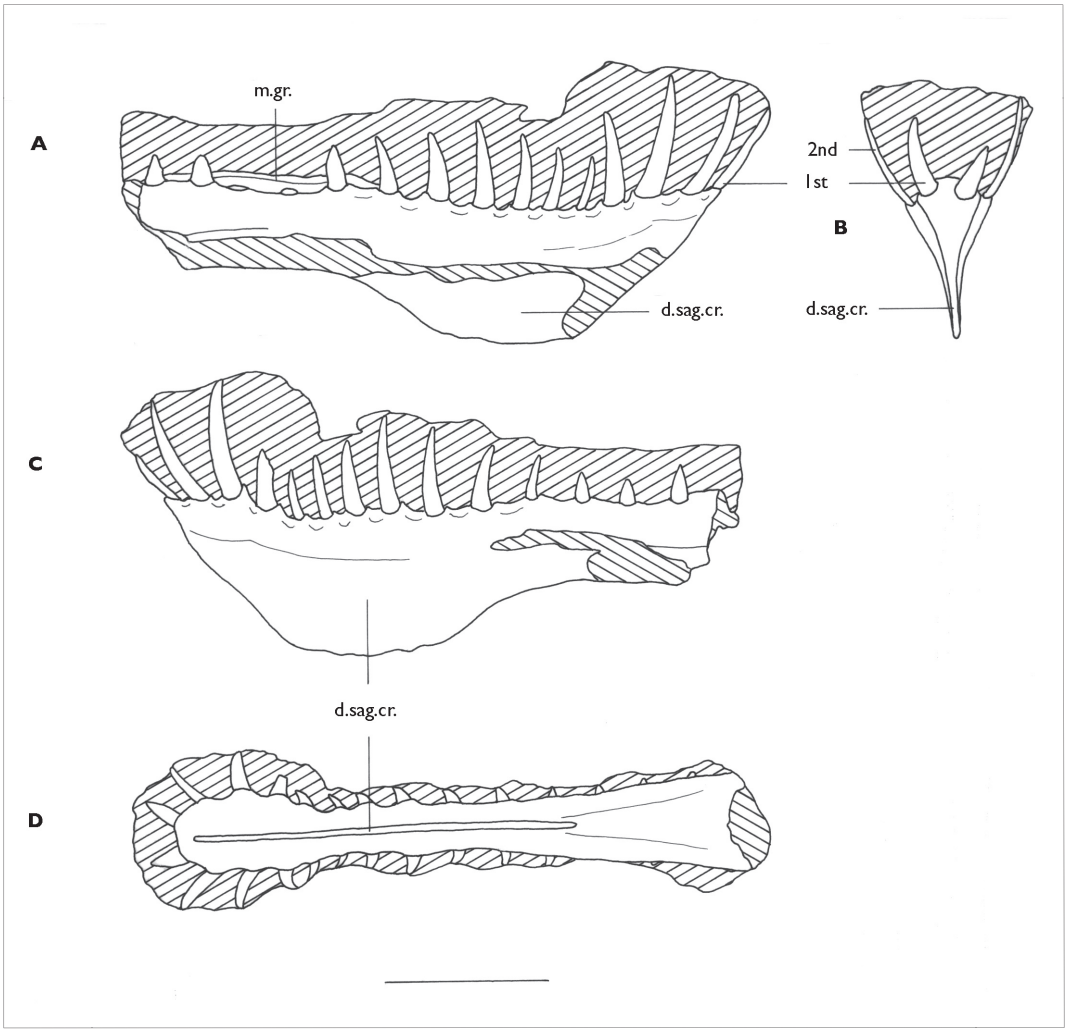

Figure 3 *Anhanguera* sp. indet., mandible SAO 200602 in various aspects. Symphysis in right lateral (**A**), anterior (**B**), left lateral (**C**) and ventral (**D**) view. Scale bar = 50 mm. [illustration: A.J. Veldmeijer]

not post-mortem. Right tooth 10 has a similar but much smaller facet.

Retroarticular process

The posterior quarter and retroarticular process (ret.pr.) of the diverging rami are twisted medially relative to the anterior portions. The articular (art.) however, is orientated slightly more laterally relative to the surangular. The inner portion of the articulation area (med. cot.), anterior and dorsal to the pneumatic foramen (pn.for.), is separated from the outer portion (lat.cot.) by a diagonal ridge (ri.) that is orientated anteromedially and dorsally. This ridge is more prominent relative to another ridge described for the articular (see below). The articular has a small (50 mm) pneumatic foramen at its anteroventral corner, which is separated from the posterior part by a shallow diagonal ridge that extends anterolaterally. The posterior part is twisted more mediodorsally relative to the medial and lateral cotyles. The posteriormost articular is slightly convex. The ventral aspect of the retroarticular process con-

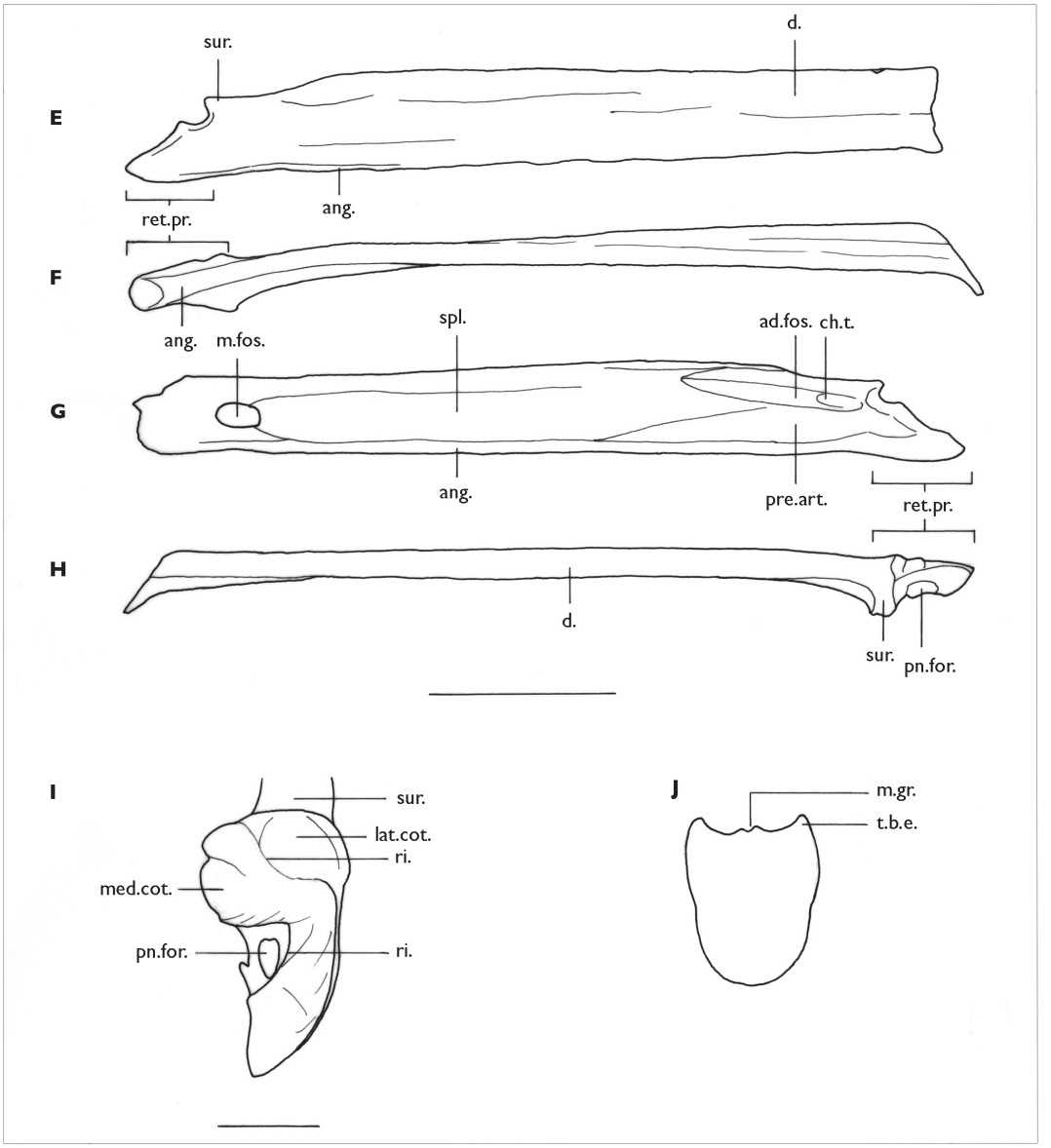

Figure 3 (continued) *Anhanguera* sp. indet., mandible SAO 200602 in various aspects. Right ramus in lateral (**E**), ventral (**F**), medial (**G**) and dorsal (**H**) views; right retroarticular process in posterior view (**I**) and cross section (**J**) of the symphysis. Scale bar = 50 mm. [illustration: A.J. Veldmeijer]

sists only of the articular. Against the lateral expansion of the surangular, the adductor fossa is provided with a foramen for the transmission of the chorda tympani (ch.t.).

Surangular

In dorsal view, the surangular (sur.) overhangs the articulation area dorsally, medially and laterally. The edges of the cotyles (cot.) expand dorsally, laterally and medially. In medial view the surangular forms the dorsal limit of the posterior mandibular opening. The anterior border is not differentiated. Ventrally, the bone does not extend more than a few millimeters.

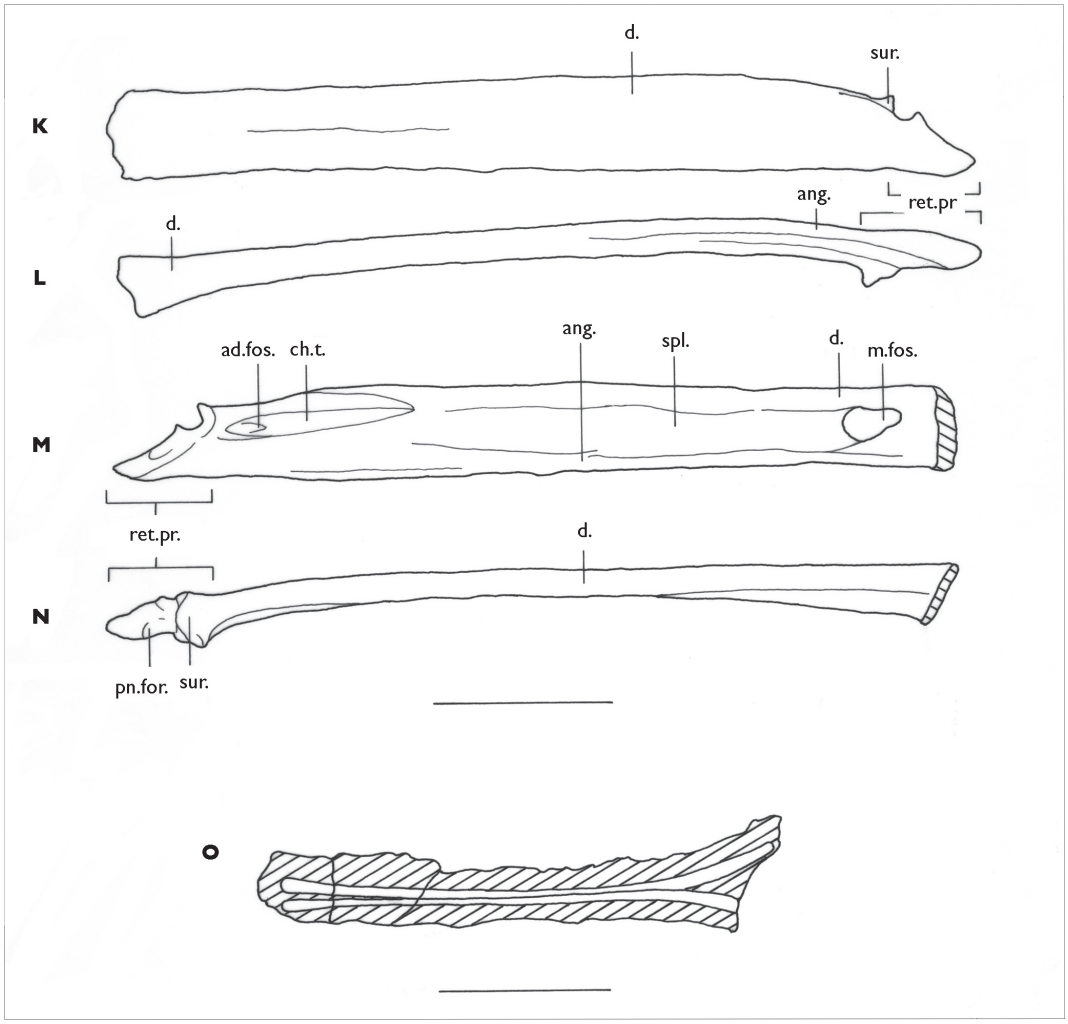

Figure 3 (continued) *Anhanguera* sp. indet., mandible SAO 200602 in various aspects. Left ramus in lateral (**K**), ventral (**L**), medial (**M**) and dorsal (**N**) views; ceratobranchials (**O**). Scale bar = 50 mm. [illustration: A.J. Veldmeijer]

Angular

Ventrally the angular extends posteriorly to the articular. In medial view the bone is slender and extends far anteriorly, forming the ventral border of the mandibular ramus. Possibly, the angular extends even further, but the exact course cannot be determined. In lateral view, the angular can be traced to the posterior part of the rami, displaying a small strip of bone of few mm in height. Though not traceable along the entire length of the ramus, the anterior part reveals a small strip of the angular immediately posterior to the symphysis.

Prearticular

The prearticular (pre.art.) forms the ventral border of the adductor fossa. It is bordered ventrally by the angular (ang.), anterodorsally by the splenial (spl.) and posteriorly by the articular. Consequently, it closes the medial aspect of the retroarticular process.

Splenial

In medial view the splenial covers the majority of each ramus. It forms the posterior border of the Meckelian fossa and extends towards the adductor fossa, forming its anteroventral bor-

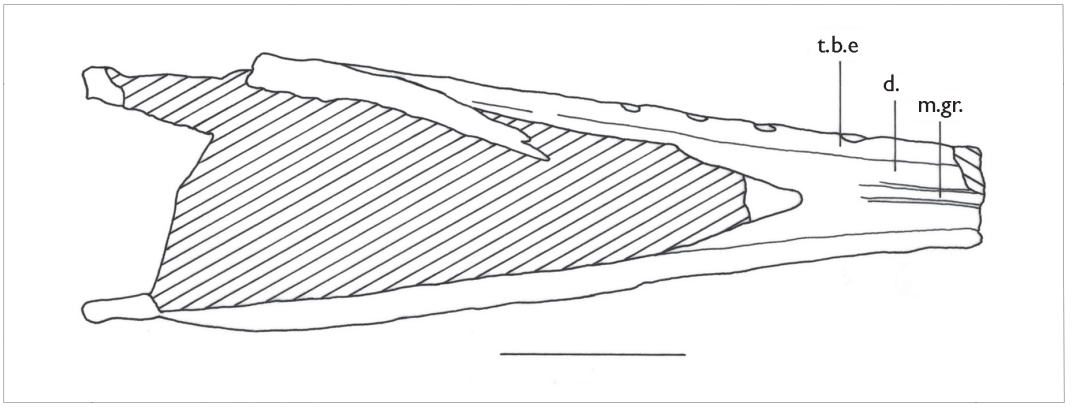

Figure 4 *Anhanguera santanae*, holotype BSP 1982 I 90 in dorsal view. Scale bar = 50 mm. [illustration: E. Endenburg / A.J. Veldmeijer]

der. Ventrally, the splenial is bordered by the angular and posteroventrally by the prearticular. The dorsal border is limited by the dentary.

Hyoid apparatus

Small rod-like bones, separated from the mandible *in situ*, are identified as ceratobranchial I of the hyoid apparatus. The anteriormost ends of the long and slender bones diverge slightly laterally. Consequently, the anterior aspects are not in contact with each other. Anteriorly the rods are blunt and slightly bulbous.

COMPARISON AND DISCUSSION

A comparison of SAO 200602 is limited to the toothed taxa from Brazil. Comparison follows publication date. The validity of the Anhangueridae is controversial (Unwin 2001, Veldmeijer, in press) and beyond the scope of this work. The Cambridge Greensands material is, in general, severely fragmented and often diagnosed on ambiguous characters, so comparative studies would be extremely limited and, in most cases, not worthwhile. The validity of *Criorhynchus* is controversial as well (Fastnacht 2001; Kellner & Tomida 2000; Unwin 2001), nevertheless the most recent diagnosis of *Criorhynchus* (Fastnacht 2001), is used here. At present *Coloborhynchus*, with *Co. clavirostis* Owen, 1874 from the Cambridge Greensands as type specimen, is generally accepted.

The mandible of *Brasileodactylus araripensis* Kellner, 1984 has no sagittal crest (see also Sayão & Kellner 2000, Veldmeijer 2003b, Veldmeijer *et al.* 2005) and is provided with a sagittal sulcus, starting at the anteriormost tip, which has anteriolaterally side-sulcii. *Cearadactylus atrox* Leonardi & Borgomanero, 1985 lacks a sagittal crest (however, the presence cannot be ruled out entirely as explained by Kellner & Tomida 2000), on the condition that the classification of *Cearadactylus? ligabuei* Dalla Vecchia, 1993 is accepted and following Dalla Vecchia's interpretation that the different parts belong to the same individual (but see Kellner & Tomida 2000). Furthermore, the dentary is sloping, containing the largest teeth. Recently, Unwin (2002) concluded in his review of *Cearadactylus* that *Ce. atrox* is a valid species and assigned *Ce.? ligabuei* tentatively to *Anhanguera*.

The main problem in comparing the present mandible with *Anhanguera blittersdorffi* Campos & Kellner, 1985 is the fact that the holotype lacks a mandible. The mandible in the referred specimen (Kellner & Tomida 2000), is substantially smaller in all respects and lacks the retroarticular process. The dorsal aspect however is comparable. The mandible includes a posteriorly recessed and anteriorly narrow medial portion with raised tooth-bearing rims posterior to the spoonshaped anterior.

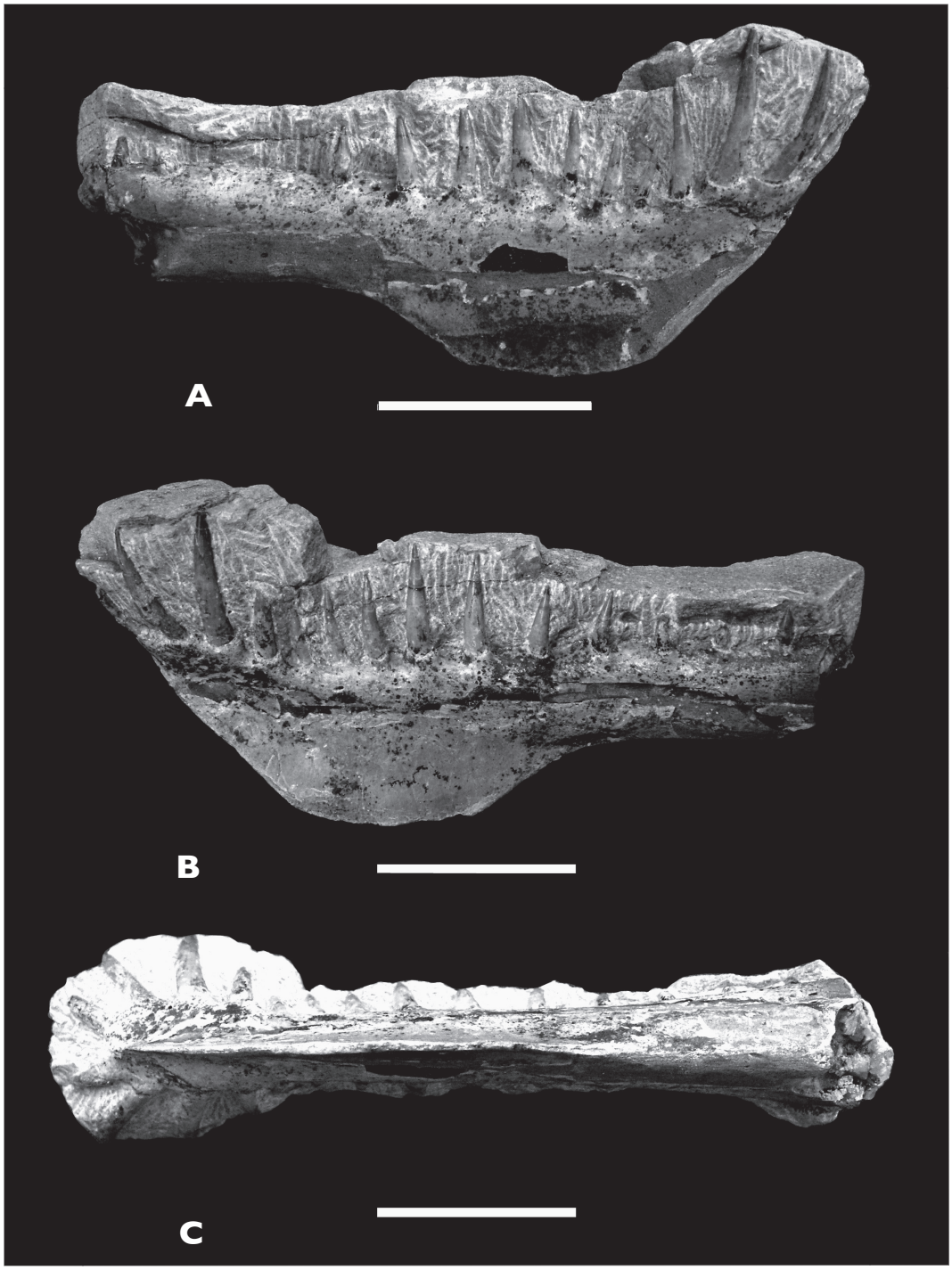

Figure 5 *Anhanguera* sp. indet., mandible SAO 200602 in various aspects. Symphysis in right lateral (**A**), left lateral (**B**) and ventral (**C**) view. Scale bar = 50 mm. [photographs: E. Endenburg, reworked by J.H. van Leeuwen, courtesy Oberli]

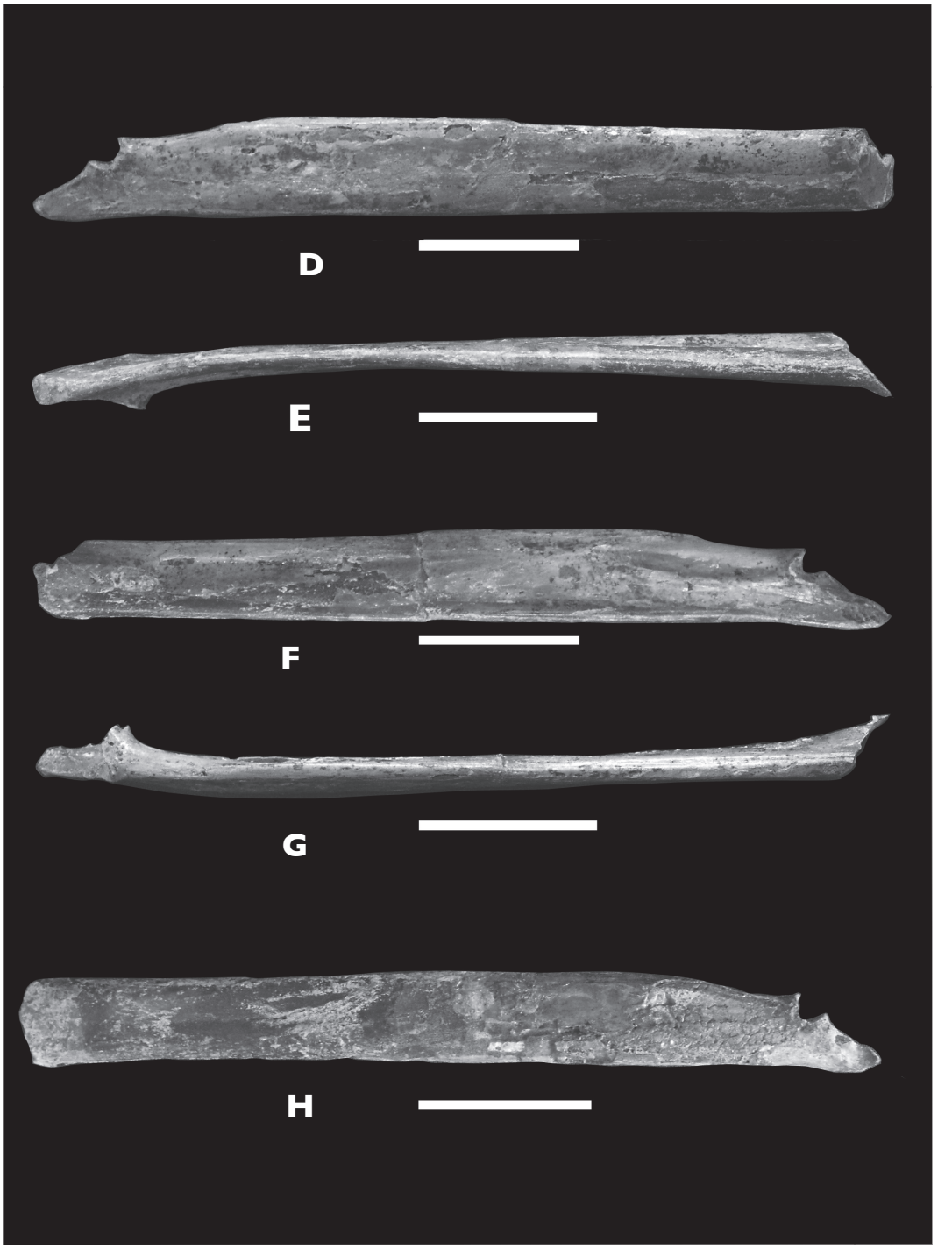

Figure 5 (continued) *Anhanguera* sp. indet., mandible SAO 200602 in various aspects. Right ramus in lateral (**D**), ventral (**E**), medial (**F**) and dorsal (**G**) views; left ramus in lateral (**H**) view. [photographs: E. Endenburg, reworked by J.H. van Leeuwen, courtesy Oberli]

Figure 5 (continued) *Anhanguera* sp. indet., mandible SAO 200602 in various aspects. Left ramus in ventral (**I**), medial (**J**) and dorsal (**K**) views; ceratobranchials (**L**). Scale bar = 50 mm. [photographs: E. Endenburg, reworked by J.H. van Leeuwen, courtesy Oberli]

Table 2 Measurements of mandible *Anhanguera* sp. (SAO 200602) in mm.

Length	403
Length retroarticular process-symphysis	238
Thickness ramus (possible) last alveolus	7.2
Width expanded anterior part between alveolus 2-3 (ventrally)	20.0
Width expanded anterior part between alveolus 3-4 (ventrally)	8.5
Width expanded anterior part between alveolus 4-5 (ventrally)	15.0
Width at symphysis	37*
Width over surangular	12**
Length dentary sagittal crest	115
Maximal height dentary sagittal crest	39.7
Length ceratobranchials, including the bending	144
Width, posterior aspect (one bone)	4.0
Width, halfway (both bones)	4.0
Width, anterior aspect (both bones)	7.0

* Approximate, because the right ramus is not preserved at this point. ** Approximate, because the rami are separated from each other and the symphysis.

Furthermore, a medial sulcus is also found in *A. blittersdorffi* in the depressed area.

Comparison with *Coloborhynchus araripensis* (WELLNHOFER, 1985) is limited to the rami, which are highly comparable. The foramina of that splenial are not observed in SAO 200602. Furthermore, there is no indication of a mandibular sulcus but this might be due to the incompleteness of this specimen.

The holotype of *Anhanguera santanae* (WELLNHOFER, 1985) lacks a complete retroarticular process (Fig. 4). The anterior portion of the holotype is not preserved, thus the presence of a crest is uncertain, but Wellnhofer (1991) and Kellner & Tomida (2000) assume its presence. The lack of the anterior mandible in the holotype and in AMNH 22555 (Wellnhofer 1991) makes it impossible to determine the dentition pattern in these specimens. The inclination of the retroarticular process and the configuration of the posterior part of the symphysis in SAO 200602 is similar to *A. santanae*.

The present mandible differs from the holotype of *Coloborhynchus robustus* (Wellnhofer 1987) in that the anterior expansion in *Coloborhynchus* is distinctly more robust and the symphysis is noticeably longer. Fastnacht (2001) notes the enlarged second and third pair of alveoli relative to the others in another specimen of *Co. robustus* (SMNK 2302 PAL), matching SAO 200602 (see below). The medial sulcus originates between the ninth and tenth alveoli, despite the illustration by Fastnacht (2001) which does not show this. A similar situation is also seen in the referred specimen of *Anhanguera blittersdorffi*. The sulcus in the referred specimen of *A. bittersdorffi* originates at the eighth alveolus, thus not as far anteriorly, and continues posteriorly in ever increasing distinctness and width. The sulcus originates against the symphysis, and becomes clearly visible at the twelfth alveolus in the holotype of *Co. robustus*; the posterior extent of the sulcus cannot be observed in SMNK 2302 PAL because it is not preserved.

The mandible in *Criorhynchus mesembrinus* (WELLNHOFER, 1987) has no anterior expansion (see also Veldmeijer 2002). The teeth show no distinct variation in size, as seen in *Coloborhynchus* or *Anhanguera*, and the dorsal aspect lacks a simple sulcus as described in the present work. Instead, *Cr. mesembrinus* has a deep and posteriorly widening sulcus. The retroarticular process is more sharply inclined medially relative to SAO 200602. Kellner (1996) notes that in anhanguerids the fifth and

sixth pair of alveoli are smaller relative to the third and seventh pair, as in SAO 200602 and *Co. robustus* (BSP 1987 I 47). Fastnacht (2001) notes that in *Coloborhynchus* the second and third pairs of alveoli are the largest, but in the referred specimen of *Coloborhynchus araripensis* the third and fourth alveoli are the biggest. In *Coloborhynchus spielbergi* the ninth alveolus is larger than the second one. In *Coloborhynchus piscator* the second and third alveoli are the biggest (Veldmeijer, *et al*, in press.) and again the ninth is larger than the second. Consequently, separating the dental pattern as done by Fastnacht (2001) and Unwin (2001) from the rest may be premature. At the moment too little is known of the diagnostic status of dentition and this character should be considered with great caution.

Comparison with the mandible in *Coloborhynchus piscator* (Kellner & Tomida 2000) is limited because the mandible is not fully prepared. The difference in size, however, is great. Although not fully ossified, the mandible of this juvenile pterosaur is 533 mm (Kellner & Tomida 2000), thus substantially larger than the present specimen. The rami of the Leiden specimen of *Coloborborchynchus spielbergi* are more strongly bent relative to the present manbible and the symphysis is longer. Furthermore, the Leiden mandible has no clearly discernible sulcus. The mandible is 50 % larger than SAO 200602. This difference is probably not ontogenetic because all these specimens are adults. The second and third pairs of alveoli are the largest in the Leiden specimen.

The mandible cannot be classified in the new genus *Ludodactylus* FREY *et al.*, 2003 because this genus lack a mandibular crest and no expansion is reported.

Comparison of the ceratobranchials is limited. Taking into account the fact that comparison is made with Brazilian pterosaurs only, the only other examples of ceratobranchials reported are those in *Coloborhynchus araripensis* (WELLNHOFER 1985) and *Criorhynchus mesembrinus* (not published) but the ceratobranchials in both of them are less complete than in SAO 200602. The anterior extremity of the ceratobranchials is similarly expanded and the measurements are similar.

In summary, the configuration of SAO 200602 in dorsal view (medial portion recessed relative to the tooth-bearing rims) is also observed in *Brasileodactylus*, *Coloborhynchus*, *Criorhynchus* and *Anhanguera*. The sulcus, however, only occurs in *A. santanae* and *A. blittersdorffi* and thus is an important character separating these otherwise similar taxa. The well-preserved *Coloborhynchus* specimens have either a sulcus extending towards the anterior aspect (i.e. *Co. robustus*) or else a weakly developed sulcus (i.e. *Co. spielbergi*). The sulcus in *Criorhynchus* shows a different morphology. The sulcus in *Brasileodactylus* extends to the anteriormost tip, lacks the associated ridges and has small anteriolaterally extending side sulcii. Consequently, the mandible can be classified to *Anhanguera* sp. The differences between the present mandible and the compared *Coloborhynchus* mandibles are larger than the differences between the present mandible and the compared *Anhanguera* mandibles, but still minor. The relatively small anterior expansion, the sulcus with raised rims and the relatively short symphysis, clearly distinguish the present specimen from the *Coloborhynchus* jaws.

The absence of mandibles in *A. blittersdorffi* and *A. santanae* is sufficient reason to avoid a specific classification. The reconstructed length of the holotype of *A. santanae* as well as the width at the symphysis is comparable to SAO 200602 (in contrast to the slightly shorter and smaller jaw of *A. blittersdorffi*), but this alone is not a strong argument for a classification at species level. The problems distinguishing the various toothed taxa from Brazil are clear (see also Veldmeijer & Signore 2004); the systematics are often based on one specimen only, despite the fact that material is housed in various collections all over the world. The additional description of this seemingly unimportant material can nevertheless add important details to the discussion, as has been demonstrated in this paper.

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REFERENCES

Baines, J. & Málek, J., 1981 - Atlas van het oude Egypte - Elsevier, Amsterdam/Brussel

Bennett, S.C., 1989 - Pathologies of the large pterodactyloid pterosaurs *Ornithocheirus* and *Pteranodon* - Journal of Vertebrate Paleontology 9 (3): 13A

Bennett, S.C., 1993 - The ontogeny of *Pteranodon* and other pterosaurs - Paleobiology 19 (1): 92-106

Bennett, S.C., 1994 - Taxonomy and systematics of the Late Cretaceous pterosaur Pteranodon (Pterosauria, Pterodactyloidea) - Occasional papers of the Natural History Museum 169 (University of Kansas, Lawrence)

Bennett, S.C., 2001 - The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon* - Palaeontographica A, 260: 1-153

Bennett, S.C., 2003a - A survey of pathologies of large pterodactyloid pterosaurs - Palaeontology 46 (1): 185-198

Bennett, S.C., 2003b - New crested specimens of the Late Cretaceous pterosaur Nyctosaurus - Paläontologische Zeitschrift 77 (1): 61-75

Beurlen, K., 1971 - As condições ecológicas e faci ológicas da Formação Santana na Chapada do Araripe (Nordeste do Brasil) - Anais Academia Brasileira de Ciências 43: 411-415.

Buffetaut, E., Grigorescu, D. & Csiki, Z., 2001 - Giant pterosaurs from the Upper Cretaceous of Transylvania (western Romania) - Strata 1 (11): 26-28

Campos, D.A. & Kellner, A.W.A., 1985 - Panorama of the flying reptiles study in Brazil and South America - Anais Academia Brasileira de Ciências 57 (4): 453-466

Campos, D.A. & Kellner, A.W.A., 1997 - Short note on the first occurrence of Tapejaridae in the Crato Member (Aptian), Santana Formation, Araripe Basin, Northeast Brazil - Anais Academia Brasileira de Ciências 69 (1): 83-87

Dalla Vecchia, F.M., 1993 - *Cearadactylus? ligabuei* nov.sp., a new early Cretaceous (Aptian) pterosaur from Chapada do Araripe (Northeastern Brazil) - Bolletino della Società paleontologica Italiana 31 (3): 401-409

Eaton, G.F., 1910 - Osteology of *Pteranodon*. - Memoirs of the Connecticut Academy of Arts and Sciences 2, New Haven

Fastnacht, M., 2001 - First record of *Coloborhynchus* (Pterosauria) from the Santana Formation (Lower Cretaceous) of the Chapada do Araripe of Brazil - Paläontologische Zeitschrift 75 (1): 23-36

Frey, E., Martill, D.M. & Buchy, M.-C., 2003 - A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur - in: Buffetaut, E. & Mazin, J.-M., (2003) - Evolution and palaeobiology of pterosaurs - pp. 55-63, Geological Society, London (Special publications)

Kaup, J., 1834 - Versuch einer Einteilung der Säugetiere in 6 Stämme und der Amphibien in 6 Ordnungen - Isis 315

Kellner, A.W.A., 1984 - Ocorrência de uma mandibula de Pterosauria (*Brasileodactylus araripensis* nov. gen.; nov.sp.) na formação Santana, Cretáceo da chapada do Araripe, Ceará-Brasil - XXXIII Anais Congresso Brasileiro de Geologia, Rio de Janeiro 1984: 578-590

Kellner, A.W.A., 1989 - A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeast Brazil - Anais Academia Brasileira de Ciências 61 (4): 439-446

Kellner, A.W.A., 1996 - Description of new material of Tapejaridae and Anhangueridae (Pterosauria, Pterodactyloidea) and discussion of pterosaur phylogeny - University Microfilms International, Ann Arbor

Kellner, A.W.A. & Campos, D.A., 1988 - Sobre um novo pterosaur com crista sagital de bacia do Araripe, Cretáceo Inferior do Nordeste do Brasil - Anais Academia Brasileira de Ciências 60 (4): 459-469

Kellner, A.W.A. & Campos, D.A., 1990 - Preliminary description of an unusual pterosaur skull of the Lower Cretaceous from the Araripe Basin - Atas I Simposio sobre a Bacia do Araripe e Bacias Interiores do Nordeste, Crato: 401-405

Kellner, A.W.A. & Campos, D.A., 1994 - A new species of *Tupuxuara* (Pterosauria, Tapejaridae) from the Early Cretaceous of Brazil - Anais Academia Brasileira de Ciências 66 (4): 467-473

Kellner, A.W.A. & Campos, D.A., 2002 - The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil - Science 297: 389-392

Kellner, A.W.A. & Langston Jr., W., 1996 - Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park, Texas - Journal of Vertebrate Paleontology 16 (2): 222-231

Kellner, A.W.A. & Tomida, Y., 2000 - Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), Northeastern Brazil - National Science Museum Monographs17, National Science Museum, Tokyo

Leonardi, G. & Borgomanero, G., 1985 - *Cearadactylus atrox* nov. gen., nov. sp., novo pterosauria (Pterodactyloidea) da Chapada do Araripe, Ceará, Brasil - DNPM, Coletânea de Trabalhos Paleontológicos. Série Geologia 27 (2): 75-80

Mader, B.J. & Kellner, A.W.A., 1999 - A new Anhanguerid pterosaur from the Cretaceous of Morocco - Boletim do Museu Nacional 45: 1-11

Maisey, J.G. (ed.), 1991. - Santana fossils: an illustrated atlas - T.F.H. Publications, New Jersey

Martill, D.M., Brito, P.M., Wenz, S. & Wilby, P.R. (eds.), 1993 - Fossils of the Santana and Crato Formations, Brazil - Palaeontological Association Field Guides to Fossils Series 5, London, The Palaeontological Association

Owen, R., 1874 - A monograph on the fossil Reptilia of the Mesozoic Formations. I. Pterosauria - Palaeontographical Society Monograph 27, London: 1-14.

Plieninger, F., 1901 - Beiträge zur Kenntnis der Flugsaurier - Palaeontographica A 48: 65-90

Pons, D., Berthou, P.Y. & Campos, D.A., 1990 - Quelques observation sur la palynologie de l'Aptien Supérieur et de l'Albien du basin d'Araripe (N.E. du Brésil) - Atas do 1. Simposio sobre a Bacia do Araripe e bacias interiores do Nordeste, Crato: 241-252

Sayão, J.M. & Kellner, A.W.A., 2000 - Description of a pterosaur rostrum from the Crato Member, Santana Formation (Aptian-Albian) Northeastern Brazil - Boletim do Museu Nacional 54: 1-8

Unwin, D.M., 2001 - An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England - Mitteilungen Museum für Naturkunde Berlin, Geowissenchaftliche Reihe 4: 189-221

Unwin, D.M., 2002 - On the systematic relationships of *Cearadactylus atrox*, an enigmatic Early Cretaceous pterosaur from the Santana Formation of Brazil - Mitteilungen Museum für Naturkunde Berlin, Geowissenchaftliche Reihe 5: 239-263

Veldmeijer, A.J., 2002 - Pterosaurs from the Lower Cretaceous of Brazil in the Stuttgart Collection - Stuttgart Beiträge zur Naturkunde B 327: 1-27

Veldmeijer, A.J., 2003a - Description of *Coloborhynchus spielbergi* sp.nov. (Pterodactyloidea) from Brazil in the collection of the National Museum of Natural History (Naturalis), Leiden, the Netherlands - Scripta Geologica 125: 35-139

Veldmeijer, A.J., 2003b - Preliminary description of a skull and wing of a Brazilian Cretaceous (Santana Formation; Aptian-Albian) pterosaur (Pterodactyloidea) in the collection of the AMNH - PalArch, series vertebrate palaeontology 0, 0: 1-14

Veldmeijer, A.J., in press (2006) - Toothed pterosaurs

from the Santana Formation (Cretaceous; Aptian-Albian) of northeastern Brazil. A reappraisal on the basis of newly described material - Utrecht University, PhD Thesis

Veldmeijer, A.J. & Signore, M. & H.J.M. Meijer, 2005 - Brasileodactylus, (Pterosauria, Pterodactyloidea, Anhagueridae); an update - Cranium 22(1): 45-54

Veldmeijer, A.J., H.J.M. Meijer & M. Signore, in press (2006) - *Coloborhynchus*. An update - PalArch's journal of vertebrate paleontolgy 3(2): #-#.

Wang, X. & Zhou, Z., 2002 - A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy - Chinese Science Bulletin 47 (20): 1521 (in Chinese)

Wang, X. & Zhou, Z., 2003 - A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy - Chinese Science Bulletin 48 (1): 16-23

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

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

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

Wellnhofer, P., & Buffetaut, E., 1999 - Pterosaur remains from the Cretaceous of Morocco - Paläontologische Zeitschrift 73 (1/2): 133-142

Wellnhofer, P., & Kellner, A.W.A., 1991 - The skull of *Tapejara wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, Northeastern Brazil - Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 31: 89-106

Williston, S.W., 1902a - On the skull of *Nyctodactylus*, an Upper Cretaceous pterodactyl - Journal of Geology 10/5: 520-531

Williston, S.W., 1902b - On the skeleton of *Nyctodactylus*, with restoration - American Journal of Anatomy 1: 297-305

Williston, S.W., 1903 - On the osteology of *Nyctosaurus* (Nyctodactylus), with notes on American pterosaurs - Field Columbian Museum Publication, Geological Series 2: 125-163

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