

# Description of *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian (Lower Cretaceous) of Brazil.

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Veldmeijer, A.J. *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian (Lower Cretaceous) of Brazil. *Scripta Geologica* 125: 35-139, 22 figs., 16 pls; Leiden, May 2003.

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A new species of pterosaur, *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea), from the Romualdo Member (Albian) of the Santana Formation is described. The type consists of the skull, mandible and many of the post-cranial bones. The specimen displays a high degree of co-ossification indicating that the animal was an adult and likely quite old when it died. The wingspan is reconstructed at nearly 6 m. Among the characteristic features are a large anteriorly positioned premaxillary sagittal crest and a smaller, also anteriorly positioned dentary sagittal crest, a flat anterior aspect of the skull from which two teeth project and a ventrally fused pelvis. Comments on Brazilian pterosaurs are made in connection with the classification of the Leiden specimen.

Keywords — Pterosaur, *Coloborhynchus*, Santana Formation, Lower Cretaceous, Brazil.

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## Introduction

The objective of the present work is the description and classification of a Brazilian Cretaceous pterosaur (Santana Formation of the Chapada do Araripe; Wellnhofer, 1985, p. 108) in the collection of the Nationaal Natuurhistorisch Museum, Leiden (RGM), the Netherlands. Because general anatomical features of this specimen agree with earlier descriptions (Campos & Kellner, 1985b; Fastnacht, 2001; Kellner, 1996a; Kellner & Tomida, 2000; Veldmeijer, 2002; Wellnhofer, 1985, 1991b), emphasis is placed on the presentation of new information. Consequently, previously described features not considered in the present text may still be indicated in the figures (marked \* in the list of abbreviations). Extra attention is given to parts with higher diagnostic value.

The comparison focuses on the differences rather than similarities with toothed taxa from the Cretaceous of Brazil, excluding non-Brazilian pterosaurs such as Dsungaripterids (Martill *et al.*, 2000) and edentulous pterosaurs such as Tapejarids (Wellnhofer & Kellner, 1991). The one exception is the type species *Coloborhynchus clavirostris* Owen, 1874, from England. Although *Criorhynchus* originated from England as well, Fastnacht (2001) considered the material too fragmented, and consequently no clear distinction could be made between the British *Cr. simus* and the Brazilian *Cr. mesembrinus*. Therefore, the comparison will be focussed on *Cr. mesembrinus*. The problems with the England Greensand material is well known (Kellner & Tomida, 2000; Lee, 1994; Unwin, 2001; Wellnhofer, 1978). However, *Criorhynchus* is not unambiguously accepted and Unwin (2001) regarded it as a synonym of *Ornithocheirus*.

The type locality is uncertain. For the geological setting of the Araripe Basin, the reader is referred to Beurlen (1971), de Buissonjé (1980); Kellner & Tomida (2000); Martill & Wilby (1993); Maisey (1991); Pons *et al.*, (1990); Wellnhofer (1977, 1985) and Wellnhofer *et al.*, (1983). Fossils in nodules are typical for the Romualdo Member of the Santana Formation (Martill, pers. com.).

Campos & Kellner (1985b) related that references to flying reptiles from Brazil were made as early as the nineteenth century. Research was scarce during the following 80 years until Price's description (1971) of the remains of *Araripesaurus castilhoi*. Wellnhofer (1977) published the description of a phalanx of a wing finger of a pterosaur from the Santana Formation and named it *Araripedactylus dehmi*. Since then, much material has been on the pterosaurs from Brazil.

The plateau of the Araripe Basin is famous for its well-preserved fossils and is at present the most important area for pterosaurs globally. Some of this material is severely compacted (Frey & Martill, 1994; Sayão & Kellner, 2000) and preserved on a laminated limestone comparable to that of Solnhofen. However, many pterosaur fossils from Brazil are preserved as three-dimensional parts of skeletons (de Buissonjé, 1980; Campos & Kellner, 1985a, b, 1997; Dalla Vecchia, 1993; Dalla Vecchia & Ligabue, 1993; Fastnacht, 2001; Kellner, 1984, 1995a, 1996a; Kellner & Campos, 1989, 1994; Kellner & Hasegawa, 1993; Leonardi & Borgomanero, 1985, 1987; Martill & Frey, 1999; Price, 1971; Veldmeijer, 2002; Wellnhofer, 1977, 1985, 1987, 1991b; Wellnhofer & Kellner, 1991; Wellnhofer *et al.*, 1983), or almost complete skeletons (Kellner & Tomida, 2000; Wellnhofer, 1985, 1991b). Apart from descriptions palaeobiological studies of Brazilian pterosaurs include those of Bennett (1990, functional morphology; 1992, sexual dimorphism; 1993, ontogeny), Campos *et al.*, (1984, soft tissue), Frey & Martill (1998, ontogeny), Kellner (1994a, soft tissue; 1994b, paleoecology; 1995b, 1996b, phylogeny; 1996c, soft tissue), Kellner & Tomida (1996, phylogeny), Martill & Frey (1998, diversity), Martill & Unwin (1989, soft tissue) and Wellnhofer (1988, functional morphology).

The Leiden specimen is one of few near complete skeletons from Brazil that are prepared in three dimensions. Furthermore, as already pointed out (Veldmeijer, 1998), the specimen is classified in a genus (*Coloborhynchus*) that was unknown from the record of Brazil until recently.

### Material

The fossil was obtained by the RGM. The specimen was still in the matrix of calcareous nodules when offered to the museum (Pl. 1). In order to determine the com-

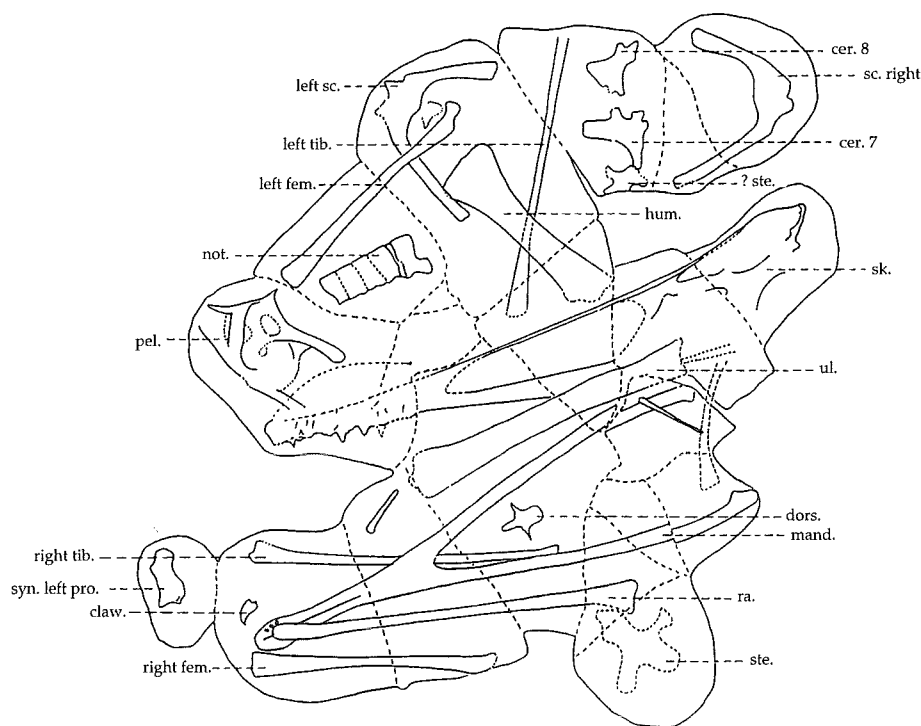


Fig. 1. Drawing of the skeleton as embedded in the nodules (see Pl. 1). Not to scale. (Redrawn after working-drawing de Buissonjé).

pleteness of the specimen, X-rays were made by Dr Ph.J. Hoedemaker in cooperation with the Academisch Ziekenhuis Leiden in January 1993. Dr P.H. de Buissonjé (1993) made an internal report in which he gave a provisional evaluation of the fossil on the basis of these X-rays (fig. 1) as well as external observations of the nodules. The specimen was taken to Leonhardt & Partner, a German institute of palaeontological preparation, in early 1993. The process of preparation was documented photographically and the fossil was prepared in three dimensions, despite the recommendations of de Buissonjé (1993) to perform the preparation in half relief, mechanically.

There were a total of 11 nodules, which had horizontal measurements of 85 by 90 cm (de Buissonjé, 1993). The X-ray photographs did not reveal exactly which part of the skeleton is on top of the other. Due to the lack of information regarding the type locality and original excavation, there is no information on the stratigraphy and it is uncertain which side faced down.

#### Description of nodules

The following description uses the drawing of the X-ray as the reference orientation (fig. 1). Abbreviations are summarised below. The mandible was disconnected from the skull (sk.) but the two were embedded closely together and the articulation areas were still very closely associated. The skull lies on its lateral side, whereas the

mandible is orientated in a ventral aspect. The cervical vertebrae (cer.), easily recognizable by their size and shape show their left lateral sides with their anterior orientated towards the skull. Their position in the nodules, allowing some distortion, was natural. The notarium (not.) was dislocated relative to the eighth cervical vertebra and the scapulocoracoids (sc.). Only two of the free dorsal vertebrae (dors.) were not visible on the X-rays. One is visible between the rami of the mandible and another close to the left radius (fig. 1). The difference in size on the drawing and X-ray was due to the distance of the specific nodules to the X-ray machine. As the nodules were not level, thicker parts were closer to the machinery and appear larger. The lateroventral aspect of the pelvis (pel.) shows on top and the right lateral aspect is directed towards the right femur (fem.)(fig. 1). This right femur was easily recognised due to the incomplete head. The position of both femora was changed over 180° relative to the pelvis. Both tibiae (tib.) were severely dislocated in comparison with the femora. The left scapulocoracoid (fig. 1) is left of the cervical vertebrae; reorientated the bone to the right was the right scapulocoracoid. They were still in their original positions although reorientated onto an anterior aspect. The left humerus (hum.) was still close to the left scapulocoracoid. The sternum (ste.) was possibly situated beneath the cervical vertebrae, based on the small piece of bone visible, which in that case would have been the cristospine. De Buissonjé (1993) suspected that the bone that lay close to the mandible (man.) and the left radius (ra.) was the sternum but it was too thin to be shown clearly on the X-rays. The left ulna (ul.) was still in the neighbourhood of the humerus but at the other side of the skull. It was positioned in such a way that there was a sharp bend between the humerus and ulna. The left ulna was totally disconnected from the radius. The left proximal syncarpal (syn.) was embedded at the end of the left ulna and was more or less in its natural position. One of the claws was situated at some distance of this syncarpal.

#### Description of the preservation after preparation

In general, the state of preservation is typical of fossils from this region. The skeleton is over 60% complete (Table 1) and some parts of the skeleton, notably the pelvis and sternum, are unique in their state of preservation. No uncrushed and/or incomplete or three-dimensionally prepared and complete pelvises from Brazil have been published apart from the study of Kellner & Tomida (2000). Two-dimensional, crushed and/or incomplete pelvises were discussed by Frey & Martill (1994, they used another pelvis for comparison); Wellnhofer (1988, 1991b) and Bennett (1990). The present sternum is one of the first nearly complete specimens to be described from Brazil. Small portions are missing from the one published by Kellner & Tomida (2000).

The skull was embedded in four nodules and has suffered a great deal from the fossilisation process. Parts of the skull, especially on the left side, have been restored. The left maxilla has been restored from three quarters of the premaxillary sagittal crest until the end of the quadrate. A small piece of the right maxilla has been restored. The palate is incompletely preserved, but pieces of the pterygoid have survived, although dislocated slightly dorsally. The right frontal has been compressed slightly in a ventral direction, whereas the left side was not. No serious displacement of the right lacrimal has occurred and this side has also a complete jugal. The left jugal is less well preserved, with only the dorsal part of the lacrimal process and the dorsalmost

part of the postorbital process surviving. The maxillar process of the right jugal is broken behind the centrum and is attached to the medial aspect of this part of the bone, posterior to the break. The left as well as the right pterygoid are incomplete and dislocated. Little remains of the palatine. The left quadrate has been restored entirely. The right quadrate is preserved; the restoration of the left element, seen from a ventral position, continues into the right element. Consequently, the medial margin of the condyloid process cannot be determined. The restoration obscures the fusion between the quadrate and the basisphenoid. The lamella, seen from a medial position, is not complete at the medial (inner) side of the quadrate. The right prootic is still in place, whereas the left one is lost. The mandible has been prepared from one concretion, which was broken into six fragments. It is largely uncrushed although some restoration work was necessary. The left retroarticular process and the right surangular have been partially restored. Most of the teeth are still visible although some have been broken just above the alveolus. A cross section has been made of the part of the mandible between the seventh and ninth tooth. The seventh tooth on the right side has been sectioned lengthwise due to this cross section. The cross section allows the study of the interior of both the tooth and mandible. The mandible has been remodelled at the point where the cross section has been made. The left articular has been partly restored, but the right one is original. The transverse ridge at the retroarticular process of the left articular has been restored almost completely, but the right one is only partly restored. The surangular has been restored on both sides; the left one is almost complete, apart for a small fragment medially. Half of the right surangular has been restored in its medial aspect and both restorations continue dorsally. The sutures of the angular are not observed at the right lateral aspect of the mandible. Parts of the sutures on the left lateral aspect are identified.

The seventh cervical vertebra is in good condition despite some minor restorations. The features of the eighth cervical vertebra are distinguished although the preservation is inferior to the seventh. The capitulum and tuberculum of the rib still articulate with the vertebra and the sutures are visible. The postzygapophysis is either missing (left side) or has been restored (right side).

The notarium is well preserved, although not complete. The distal parts of the transverse processes consist of a light brown homogeneous matrix, which is possibly the same as reported for other pterosaurs of the Santana Formation (Wellnhofer *et al.*, 1983). A chemical, rather than mechanical, preparation would probably have revealed more of the features of the notarium (*cf.* Wellnhofer *et al.*, 1983). The space between the centra of the coalesced notarial vertebrae has not been freed from matrix entirely. A large part of the caudal aspect of the notarium is lacking but has been restored.

All dorsal vertebrae display some damage. Most of them lack the tips of their transverse processes and some display incompleteness of the anterior cotyle and/or posterior condyle.

The sternum is only slightly malformed. The right side of the plate has an almost horizontally extending lateral side, whereas it should be extending smoothly like the left side. The right coracoid facet is incomplete. The dorsal aspect is still partially covered with matrix, which was probably done to avoid damage to the thin and fragile plate.

Both scapulocoracoids are in good condition. The left part of the shoulder girdle is

prepared out of one nodule and the right part out of two. Consequently, the right scapulocoracoid has a fracture on the proximal part near to the articular surface of the coracoid with the sternum, which has been partly reconstructed. The anterior aspect of the left scapulocoracoid, opposite the glenoid fossa, is damaged.

The left humerus, the only one preserved, as with the other bones of the front extremities, has been preserved almost completely. It was embedded in two nodules. The dorsal aspect displays crushing of the distal part. Smaller fractures occur at the rim of the incomplete deltopectoral crest.

The left radius is complete except for some minor restorations. The left ulna is prepared out of two nodules and badly fragmented. It is restored in several places. The bone wall is broken in many pieces and glued with epoxy resin. Furthermore, a part of the anterior aspect is crushed; the area towards the proximal aspect is damaged. A crack starts in the middle of the bone and extends distally. It has a length of 70 mm. The worst damage occurs where the distal articular surface has been restored almost entirely. This restoration continues onto the posterior aspect for one quarter of the length of the bone. Minor restorations occur on the proximal articulation area.

The left proximal syncarpal is completely preserved and in excellent condition without any reconstruction. Three claws are preserved of which one is complete. The other two lack their tips. The smallest claw has been restored partly on one side.

The pelvis was embedded in one big nodule, together with the anterior part of the skull. The bone is exceptionally well preserved. One small part of the right anterior blade of the illium and the caudal part of the synsacrum are missing. The left side is complete.

Both femora are prepared out of two different pieces of concretion. The femoral head of the right femur has been reconstructed partially, but the distal end is almost complete save some minor damage. The femoral head of the left femur is complete, but the distal end has been reconstructed.

Both tibiae are preserved, but have suffered severely from the fossilisation process. Many small restorations have been made of which the partial restoration of the proximal articular surface of the left tibia is the largest. Other parts, like the distal articular surface of the right tibia, are incomplete, but have not been reconstructed. The situation with the distal articular surface of the left tibia is comparable though more intact.

### Abbreviations

#### Institutions

AMNH	American Museum of Natural History, New York, USA.
BMNH	The Natural History Museum, London, England.
BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany.
CB	Borgomanero collection, Italy.
CCSRL	Centro Studi e Ricerche Ligabue, Venice, Italy.
LINHM	Long Island Natural History Museum, Long Island, USA.
MN	Museu Nacional, Rio de Janeiro, Brazil.
RGM	National Natuurhistorisch Museum, Leiden, The Netherlands.
SAO	Sammlung Oberli, St. Gallen, Switzerland (includes one specimen on exhibition in the Natural Museum, St. Gallen).

SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany.
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany.
UvA	Geological Institute of the University of Amsterdam, The Netherlands.

## Figures

a.	articular	in.pt.vac.	interpterygoid vacuity
ac.	acetabulum	in.sep.	interorbital septum
ad.fos.	adductor fossa	is.	ischium
ang.	angular	is.fen.	ischiopubic fenestra
*art.f.f.	articular facet fibula	j.	jugal
b.il.	anterior blade of the ilium	l.t.f.	lower temporal fenestra
b.o.	basioccipital	lac.	lacrimal
b.sph.	basisphenoid	lac.fos.	lacrimal fossa
b.t.	biceps tubercle	lam.	lamella
c.	centrum	lat.cond.	lateral condyle
c.f.	coracoid facet	lat.cot.	lateral cotyle
c.s.	cristospine	lat.ep.	lateral epicondyle
cap.	capitulum	mand.	mandible
cap.cot.	capitular cotyle	max.	maxilla
cer.	cervical vertebra	mec.fos.	Meckelian fossa
ch.	choanae	med.cond.	medial condyle
co.	cotyle	med.cot.	medial cotyle
cr.q.op.	cranioquadrate opening	med.ep.	medial epicondyle
*d.a.s.	distal articulation surface	n.	neck
del.cr.	deltpectoral crest	n.c.	neural canal
den.	dentary	n.s.	neural spine
den.sag.cr.	dentary sagittal crest	*nas.	nasal
den.sag.gr.	dentary sagittal groove	nas.fen.	nasoantorbital fenestra
dep.	depression	not.	notarium
dors.	dorsal vertebra	*o.cond.	occipital condyle
dt.	dentine	o.f.	obturator foramen
duc.lac.	ductus lacrimalis	o.sag.ri.	occipital sagittal ridge
en.	enamel	op.	opisthotic
ex.o.	exoccipital	or.	orbit
fem.	femur	*ov.fos.	oval fossa
for.	foramen	pal.	palatine
for.mag.	foramen magnum	pal.sag.r.	palatinal sagittal ridge
fr.	frontal	par.	parietal
f.t.	fourth trochanter	par.cr.	parietal crest
g.t.	greater trochanter	pat.sul.	patellar sulcus
h.	head	pel.	pelvis
hum.	humerus	pl.	plate
in.sul.	intercondylar sulcus	po.ac.il.	postacetabular process of the illium
in.fos.	intertrochanteric fossa	po.fr.	postfrontal
in.os.mem.	interosseus membrane	po.or.	postorbital
in.pr.for.	interprocessal foramina	p.t.f.	posttemporal fenestra

po.z.	postzygapophysis	v.for.	vagus foramen
pop.fos.	popliteal fossa	sc.art	scapular articulation
post.tub.	posterior tuberosity	sk.	skull
pr.max.	premaxilla	spl.	splenic
*pr.pub.art.	prepubic articulation	sq.	squamosal
pr.sag.cr.	premaxillary sagittal crest	st.	stop in wrist
pr.a.	prearticular	ste.	sternum
*pr.fr.	prefrontal	sul.	sulcus
pr.z.	prezygapophysis	sup.n.p.	supraneural plate
*pro.	prootic	sup.o.	supraoccipital
pt.	pterygoid	sup.pr.	supracondylar process
pub.	pubis	sur.	surangular
pulp.	pulp cavity	sut.	suture
q.	quadrate	syn.	syncarpal
q.j.	quadratojugal	sym.	symphysis
r.	ridge	t.p.	transverse process
ra.	radius	tib.	tibia
rib.	rib articulation	tr.	trochlea
s.p.	sacral process	tr.cot.	trochlear cotyle
s.t.f.	subtemporal fenestra	ul.	ulna
sc.	scapula		

### Systematic palaeontology

Order Pterosauria Kaup, 1834

Superfamily Pterodactyloidea Plieninger, 1901

Family Ornithocheiridae Seeley, 1870 or

Family Anhangueridae Campos & Kellner, 1985b

Genus *Coloborhynchus* Owen, 1874

*Type species* — *Coloborhynchus clavirostris* Owen, 1874.

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

*Coloborhynchus spielbergi* sp. nov.

*Etymology* — *spielbergi*, in honour of Steven Spielberg, the director of the three Jurassic Park movies in which dinosaurs and pterosaurs were animated.

*Holotype* — RGM 401 880, consisting of skull, mandible, seventh and eighth cervi-



cal, notarium, left and right scapulocoracoid, sternum, left humerus, left ulna, left radius, left proximal syncarpal, a third phalanx, three claws, seven dorsals, five pieces of rib, pelvis, both femora and tibiae and fragments of ceratobranchialia.

*Locus typicus* — Unknown. Chapada do Araripe (northeast Brazil).

*Stratum typicum* — Typical calcareous nodule of the Romualdo Member (Albian), Santana Formation (Aptian-Albian) of the Araripe Basin.

*Diagnosis* — Ill-defined, almost absent (lowest and shallowest of all *Coloborhynchus* species) palatal ridge and corresponding mandibular groove; mandibular groove not extending onto spoon-shaped expansion; slight, almost absent, venterolaterally extending tooth-bearing maxillae; large premaxillary sagittal crest, in ratio length-total length skull, which extends dorsally from the anterior aspect until the anterior border of the nasoantorbital fenestra; strongly medial bended rami; sternum with rounded triangular posterior plate of which the length is as long as the width.

## Description and comparison

### Cranial skeleton (Figs. 2-5; Pls. 2, 3; Tables 2-7)

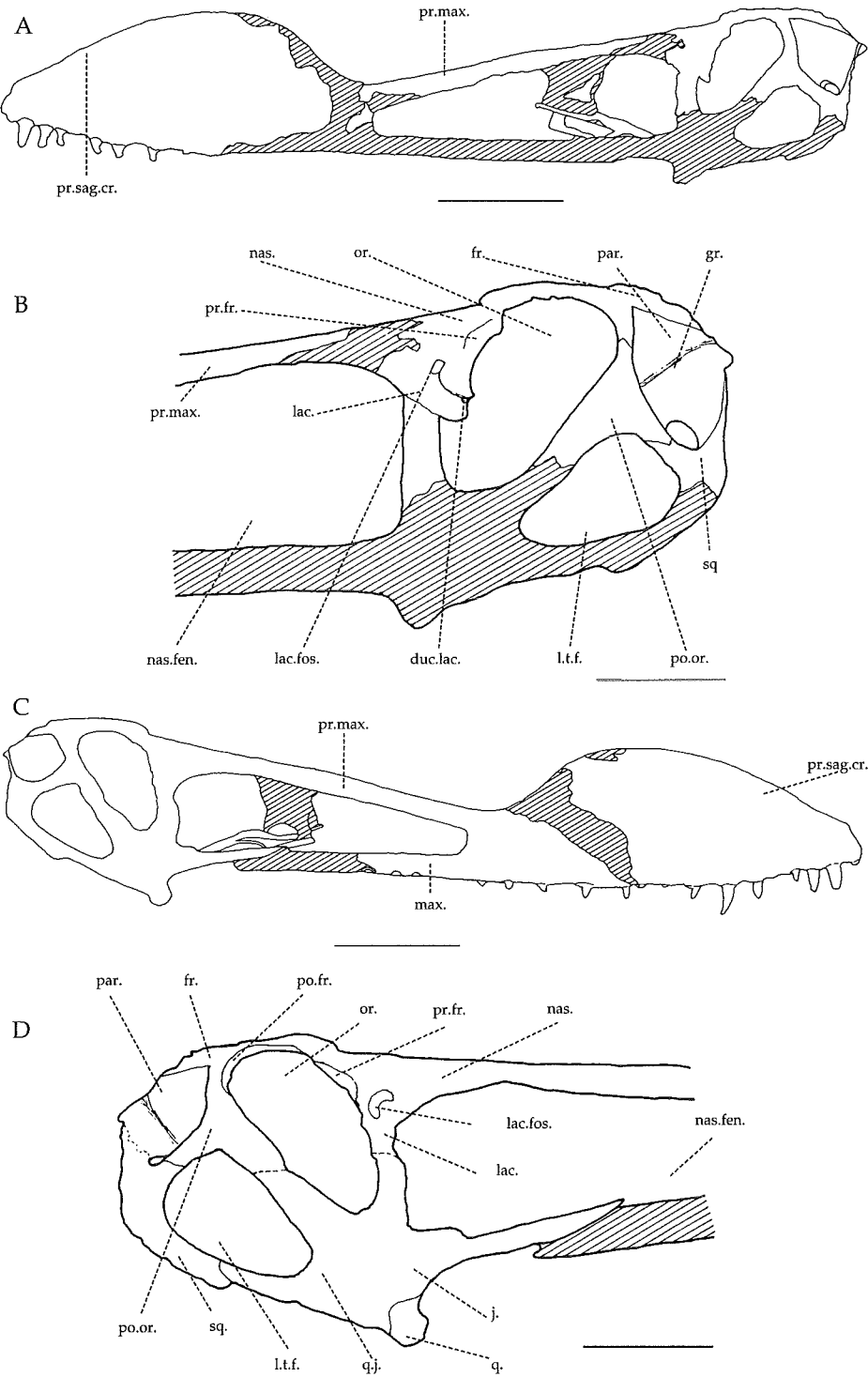
#### Skull

The skull is elongated and slender (figs. 2, 3; Pl. 2; Table 2-4). It is lightly built with many openings, which is a characteristic of pterosaurs. The nasoantorbital fenestra is the biggest. The skull has a large premaxillary sagittal crest in front of the nasoantorbital fenestra. Anteriorly, the skull expands, resulting in a spoon-shaped, expanded anterior part. The anterior aspect is flat and contains two alveoli, which are situated stronger dorsally relative to the subsequent alveoli. The skull has 18 alveoli on each side, which are increasingly wider spaced in a posterior direction. Because both maxillae are incomplete, it is not clear whether this is the original number or not. The skull displays a very high degree of co-ossification and can therefore be regarded as an adult, perhaps even an older animal as suggested by various post-cranial bones (see below).

#### Premaxilla (pr.max.)

The dorsally thin and ventrally widening premaxillary sagittal crest (pr.sag.cr.) extends dorsally, after its start at the anterior aspect (figs. 2A, C, E, I; Pl. 2A-G). It continues with a strong convex dorsal margin to the nasoantorbital fenestra (nas.fen.) where it ends immediately anterior to this fenestra. The anteriormost edge of the dorsal margin is slightly concave. The crest is asymmetrical because the anterior half is less steep relative to the posterior half. The posterior margin of the crest does not extend laterally. The anterior edges extend laterally towards the base and form a triangular anterior aspect. A network of small grooves, mainly less than 1 mm wide, is visible at the crest (Pl. 2G). The grooves occur only on the crest. A patchy brown-yellow colouring is visible in the grooves and in their proximity. A few small holes with diameters of 1 mm or less insert obliquely into the crest.

*Comparison* — *Coloborhynchus clavirostris* Owen, 1874 (fig. 3A) has a depression in the anterior aspect, ventral to the teeth. The anterior aspect in *Co. spielbergi* is only partially complete; it is uncertain whether the aspect has a depression and, if so, where it



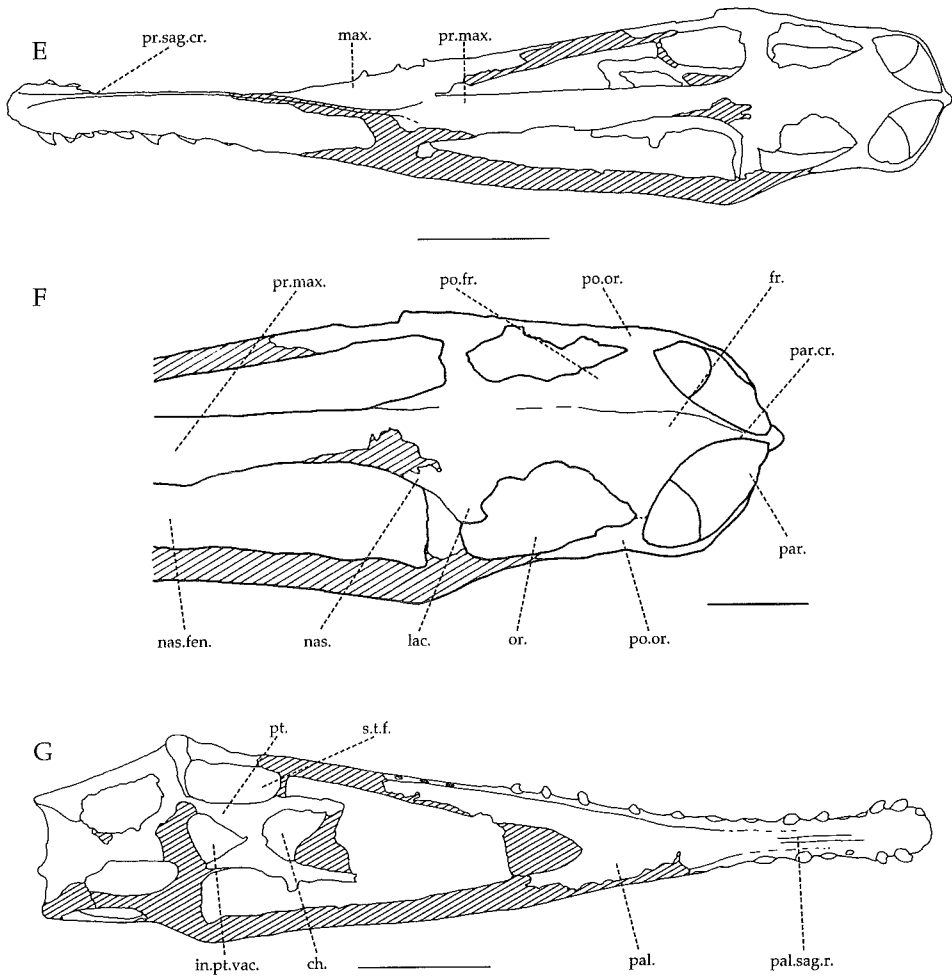
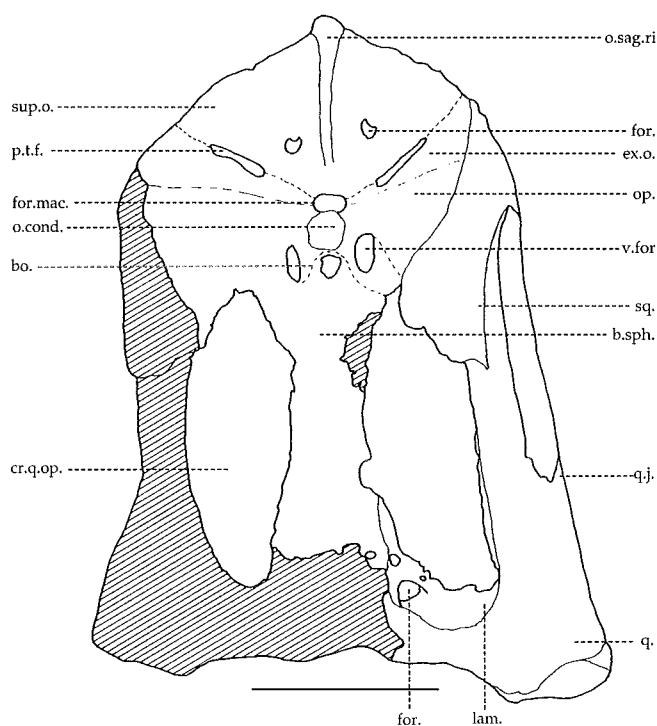


Fig. 2. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the skull in various aspects (with details separately). A: skull, left lateral (scale = 100 mm); B: back of skull, left lateral (scale bar = 50 mm); C: skull, right lateral (scale bar = 100 mm); D: back of skull, right lateral (scale bar = 50 mm); E: skull, dorsal (scale bar = 100 mm); F: back of skull, dorsal (scale bar = 50 mm); G: skull, ventral (scale bar = 100 mm); H: base of skull (scale bar = 50 mm); I: skull, anterior (scale bar = 20 mm); J: inner temporal and otic region, oblique anterolateral view (scale bar = 20 mm). Drawings by the author.

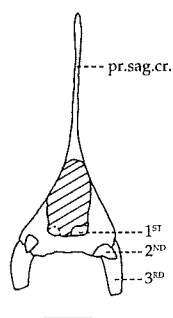
is placed. The palatinal ridge in *Co. clavirostris* is more strongly developed and the anterior spoon-shaped expansion is more robust and square, instead of the rounded expansion in *Co. spielbergi*. The premaxillary sagittal crest is robuster at its base.

Comparison with the holotype of *Brasileodactylus araripensis* Kellner, 1984, is not possible because it is only the anterior part of the mandible, but another specimen (MN 4797-V; fig. 3B), includes the anterior part of the skull (Sayão & Kellner, 2000) and demonstrates that the main difference is the complete absence of a sagittal crest. Furthermore, the snout is not blunt.

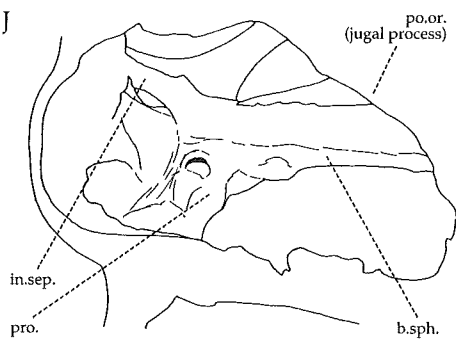
H



I



J



Comparison with *Cearadactylus atrox* Leonardi & Borgomanero, 1985 (fig. 3C), is hindered by the incomplete preparation of the type specimen of this species. However, the premaxilla in *Ce. atrox* as well as in *Cearadactylus? ligabuei* Dalla Vecchia, 1993 (fig. 3D), lacks a sagittal crest. Neither of the two specimens have a flat anterior aspect. This latter also has a wide gap between rostrum and mandible.

In *Anhanguera blittersdorffi* Campos & Kellner, 1985b (MN 4805-V; fig. 3E), the premaxillary crest does not start at the anteriormost aspect, but more posteriorly and ends almost at the anterior border of the nasoantorbital fenestra (Table 4). However, the crest does not extend as far posteriorly in the referred specimen, n. 40 Pz-DBAV-

UERJ; Kellner & Tomida, 2000). Lee (1994) and Fastnacht (2001) remarked that the crest in *An. blittersdorffi* (MN 4805-V) is thin, even at its base. However, Lee must have concluded this on the basis of the published drawings of the skull and was misled by the way the crest was drawn, because two thin lines mark the dorsal extension of the crest and not the base (Campos & Kellner, 1985b). The construction is the same as with other, comparable crests, *viz.* continuously increasing in width ventrally. Anteriorly, the jaw is expanded, but in *Co. spielbergi* this expansion is markedly robust. The anterior aspect of *An. blittersdorffi* is not blunt and the first pair of alveoli are not positioned dorsally relative to the subsequent alveoli.

The holotype of *Coloborhynchus araripensis* (Wellnhofer, 1985) (BSP 1982 I 89; fig. 3F) lacks the anterior part and braincase. However, another specimen of this taxon (SAO 16494; fig. 3G) (Veldmeijer, in review) shows that the premaxillary crest starts at the anterior aspect and initially extends concave, after which it continues convex towards the nasoantorbital fenestra. It ends more posteriorly to this fenestra and is nearly as large as in *Co. spielbergi*. The ratio between the height and length of the crest is largest in a referred specimen of *Co. araripensis*, MN 4735-V (not illustrated; Kellner & Tomida, 2000), but it is large in SAO 16494 and "*Criorhynchus*" *mesembrinus* (BSP 1987 I 46; fig. 3J) relative to the skull length (Table 4). The anterior tip is bent slightly upwards in *Co. araripensis* (SAO 16494), but not in the referred specimen (MN 4735-V). The crest of this latter specimen forms the highest point of the skull.

The premaxilla in the holotype of *Anhanguera santanae* (Wellnhofer, 1985) (BSP 1982 I 90; fig. 3H) is concave and extends steeply in a posterior direction, contrasting with the straight, more horizontal shapes in *Co. spielbergi* and *An. santanae* (AMNH 22555; fig. 3I). However, the holotype of *An. santanae* (BSP 1982 I 90) might not have had a crest (see below); but if there was one it did not extend until close to the anterior limit of the nasoantorbital fenestra, contrasting with both *Co. spielbergi* and *An. santanae* (AMNH 22555). The premaxillary crest in the latter specimen is comparable to that of *An. blittersdorffi* (MN 4805-V) and differs in few respects from *Co. spielbergi*. First, the crest does not start at the anterior aspect and secondly, the crest is substantially smaller, also relative to *An. blittersdorffi* (MN 4805-V) (Table 4), which might be due to the non-adult' stage of growth. The anterior expansion is less relative to *Co. spielbergi* and the anterior aspect is not blunt, but rather flattened dorsoventrally. There is not a pair of more dorsally situated alveoli. The tip of the jaw is turned upwards more severely.

Comparison with the type specimen of "*Criorhynchus*" (or "*Ornithocheirus*") is seriously hindered by that the fragment being the small anteriormost part of the upper jaw. "*Criorhynchus*" *mesembrinus* (Wellnhofer, 1987) (BSP 1987 I 46) has a large premaxillary crest which is symmetrical in the sagittal plane. Compared with *Co. spielbergi*, the crest is smaller in length (relative to skull length), but higher (relative to the crests length; Table 4). The jaw, only slightly bent upwards, has an elongated triangular, flat anterior aspect with a small, shallow, medial depression slightly dorsal to the front teeth. These teeth are not placed substantially more dorsal relative to the subsequent teeth, as seen in *Co. spielbergi*. The anterior part is not expanded.

The holotype of *Coloborhynchus robustus* (Wellnhofer, 1987) (BSP 1987 I 47) lacks a skull but the anterodorsal aspect of the premaxillary crest in another specimen, *Co. robustus* (SMNK 2302 PAL; fig. 3K), starts concave and extends, more dorsally, convex against the almost convex anterodorsal border as in *Co. spielbergi*. The base suggests a

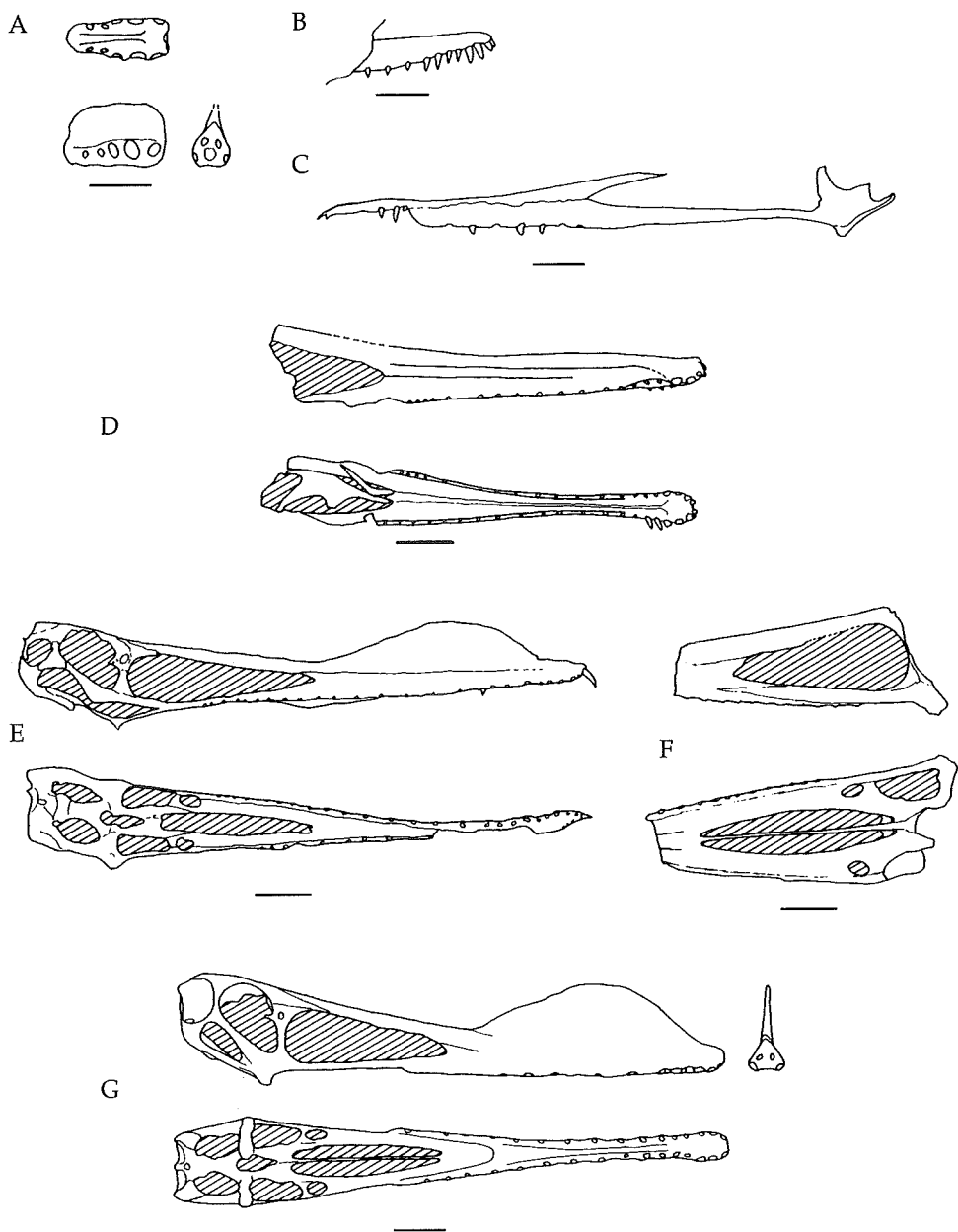
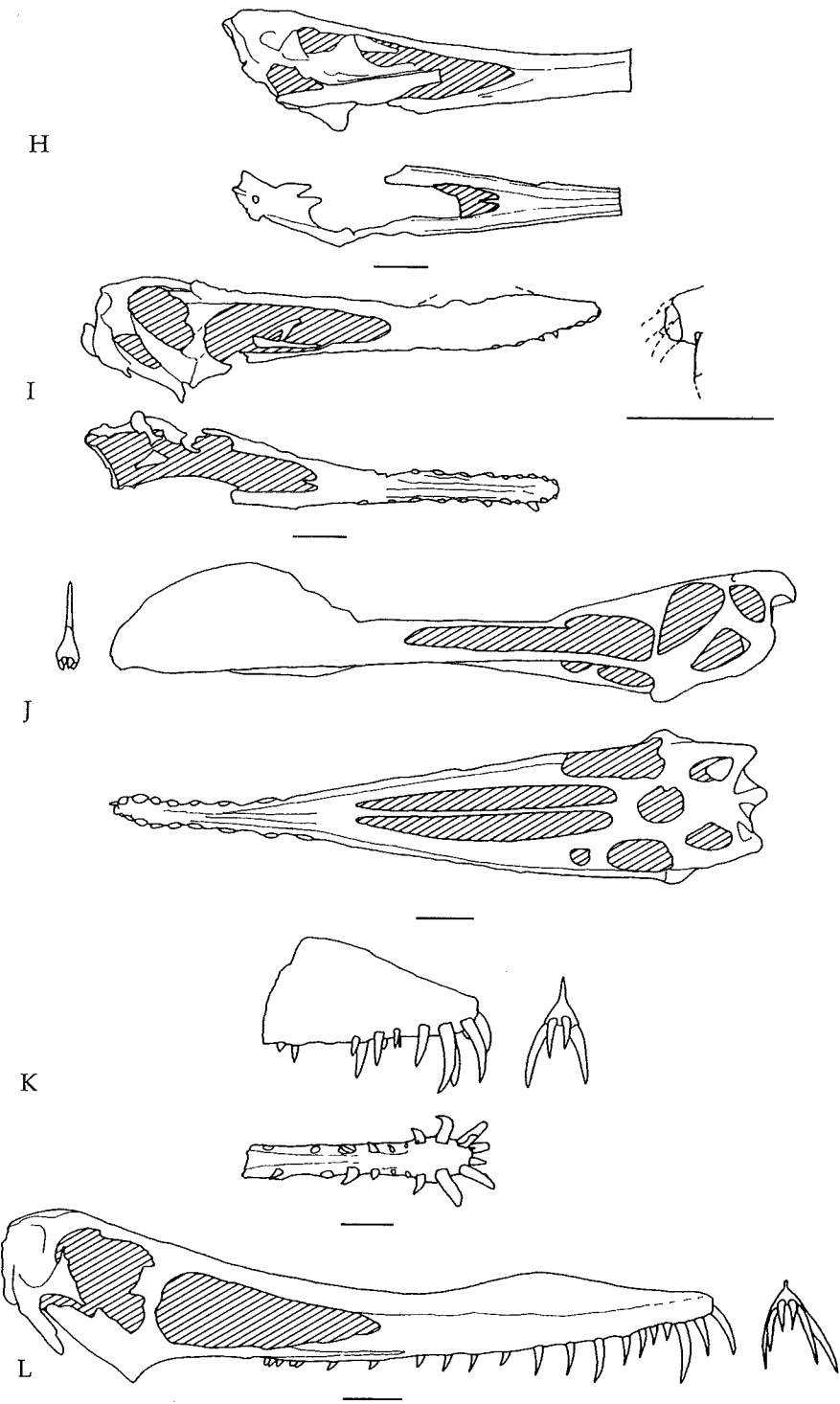


Fig. 3. Skulls of compared pterosaurs in various aspects. A: *Co. clavirostris*; B: *B. cf. araripensis* (MN 4797-V); C: *Ce. atrox* (after Leonardi & Borgomanero, 1985, p. 77); D: *Ce.? ligabuei* (after Dalla Vecchia, 1993, p. 404); E: *An. blittersdorffi* (MN 4805-V); F: *Co. araripensis* (BSP 1982 I 89); G: *Co. araripensis* (SAO 16494); H: *An. santanae* (BSP 1982 I 90); I: *An. santanae* (AMNH 22555: reconstruction after Wellnhofer, 1991b, p. 48); J: "*Cr.*" *mesembrinus* (BSP 1987 I 46); K: *Co. robustus* (SMNK 2302 PAL); L: *Co. piscator* (reconstructed, after Kellner & Tomida, 2000, p. 10, 23). Scale bar = 50 mm (note the different scale of the reconstruction in fig. 3I). Drawings by E. Endenburg and the author.



more robust crest. Furthermore, the triangular anterior aspect in *Co. robustus* (SMNK 2302 PAL) is flat and almost completely filled with the first pair of alveoli, leaving little space dorsal to the teeth. A depression is situated dorsal to these alveoli. The morphology of the anterior aspect in *Co. spielbergi* is unclear due to its damaged state. The spoon-shaped expansion of the skull starts at the fourth alveolar pair in *Co. spielbergi* and at the fifth in *Co. robustus* (SMNK 2302 PAL), and is robuster in the latter. The preserved anterior part is more elongate, corresponding with the more elongated symphysis of the mandible.

The crest in *Coloborhynchus piscator* (Kellner & Tomida, 2000) (fig. 3L) starts well before the anterior border of the nasoantorbital fenestra. The anterodorsal border is strongly concave and extends slightly dorsally. This condition is seen in the referred specimen of *An. blittersdorffi* (n. 40 Pz-DBAV-UERJ) and also *An. santanae* (AMNH 22555). *Coloborhynchus piscator* is a juvenile and the crest is likely not fully grown yet; immaturity may also explain the relatively small length and height (Table 4). The anterior aspect is flat, but smaller relative to *Co. spielbergi*, *Co. araripensis* and *Co. robustus*.

#### *Maxilla* (max.)

The lateroventral border of the skull is straight, but the anterior portion is bent slightly upwards, starting approximately at the posterior beginning of the spoon-shaped expansion (figs. 2C, E, G; Pl. 2B, C, D). Seen in ventral view, the maxilla extends far posteriorly, but the exact posterior course cannot be determined. It continues at least medially and ventrally to the maxillar process of the jugal. The lateral tooth-bearing parts of the maxilla are slightly ventrally raised relative to the palatine (pal.). This is not seen within the tooth-bearing part of the premaxilla; however, the suture is not visible, so the boundary between these two bones cannot be determined. From a lateral perspective, the maxilla forms the anterior and ventral edges of the nasoantorbital fenestra and meets the premaxilla dorsally.

A small fragment of bone 71 mm long is separated from the skull. The fragment is broken into two connected pieces, though displaced. Only the lateral bone wall is preserved. One tooth remains, which is broken at the alveolar border.

*Comparison* — The inclined ventral border of the anterior part of the maxilla distinguishes *Ce. atrox* (fig. 3C) from *Co. spielbergi*. The alveolar margin of the maxilla in *Ce. ligabuei* (fig. 3D) is also recessed, although it starts more posteriorly (at the fifth alveolus) relative to *Ce. atrox* and is shorter, ending at the eighth.

Ventrally, the tooth-bearing maxilla in *An. blittersdorffi* (fig. 3E) protrudes relative to the palatine, which is also seen in *Ce. araripensis* (figs. 3F, G). However, the maxilla in *An. santanae* (fig. 3H, I), protrudes less relative to *An. blittersdorffi* and *Co. araripensis*, but still more than in *Co. spielbergi*. Furthermore, *An. blittersdorffi* has a more distinct palatal ridge.

Alveoli 5-7 are positioned in a concavity in *Co. robustus* (SMNK 2302 PAL; fig. 3K). These concavities are best visible from ventrally and are clearly less prominent than in *Cearadactylus*. Such concavities are absent in *Co. spielbergi*.

#### *Dentition*

The alveoli are orientated lateroventrally except for the anteriormost pair, which is orientated anteriorly (figs. 2G, I; Pl. 2D, E, F; Table 3). The presence of the front alveoli



has been proven using CT-scan (Pl. 2F; the arrow points to the alveoli). The first seven pairs of alveoli are positioned lateroventrally and the teeth are pointing slightly anteriorly. They have a posteromedial curvature. Alveoli 13-15 of the right side are positioned lateroventrally and the teeth have a posteromedial curvature. There is some doubt as to the precise orientation of some teeth, especially for those posterior to tooth eight on the left side, due to poor preservation. On the right side 18 alveoli are present. Due to the reconstruction of the maxilla posterior to tooth 18 on the right side, it is unclear whether there were more teeth or not; only the anterior nine teeth survived on the left side. The size of the first alveolus is uncertain, but the third is probably the largest. The second and fourth alveoli are smaller than the third one. Two smaller alveoli of comparable size follow the fourth tooth. The description is based on the measurements taken at the right side, except for the measurements of the fifth and sixth alveoli, which are based on the measurements taken at the left side. Alveolus 7 and 8 are larger than the two foregoing alveoli, but smaller than the third. Alveolus 9 on the left side is large and comparable to alveolus 2. Alveoli 10-15 are of similar size and the average size is one third of the third alveolus. The last three alveoli (16-18) are the smallest. The diastemae pattern shows a continuous increase in width posteriorly and is slightly more erratic than the pattern of the mandible. The wide diastema between tooth 15 and 16 on the right side is probably a result of restoration. Most probably, there was an alveolus, which would result in at least 19 teeth on one half of the skull.

*Comparison* — The second to fourth alveoli in *Co. clavirostris* are far more laterally placed relative to the subsequent teeth and relative to these alveoli in *Co. spielbergi*. The alveolar size of *B. cf. araripensis* (MN 4797-V) varies less, but the pattern is comparable.

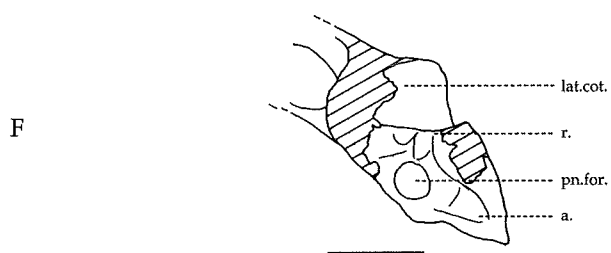
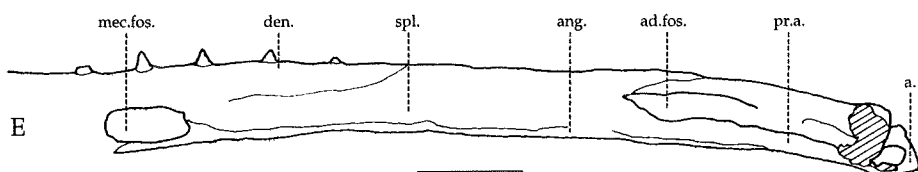
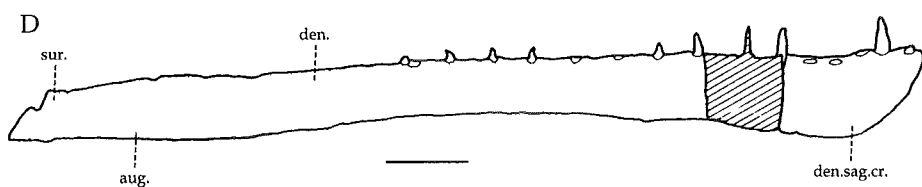
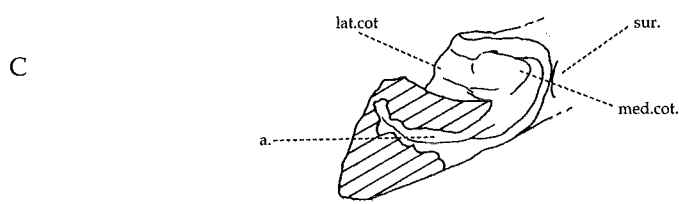
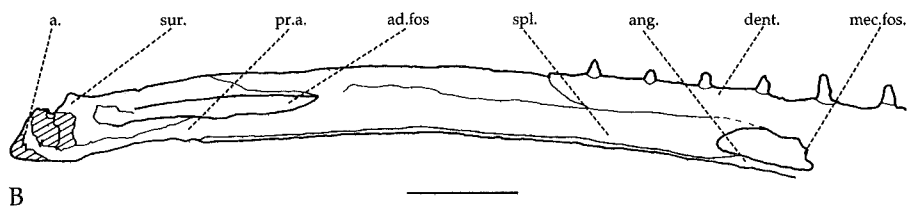
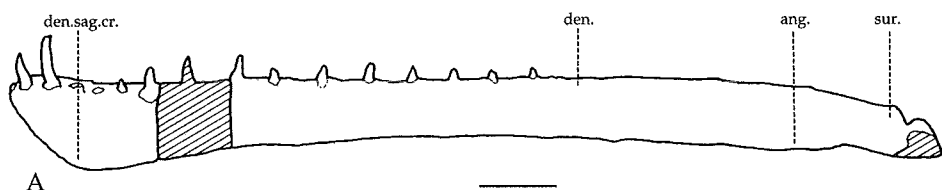
The number of alveoli in *Ce. atrox* is less (30-32 against at least 36 in *Co. spielbergi*), but the number of teeth in *Ce.? ligabuei*, at least 22 in each side, exceeds the number in *Co. spielbergi*. *Ce.? ligabuei* has a first pair at the anterior aspect that are positioned slightly more dorsal relative to the subsequent alveoli. The second pair is transitional, being placed anteroventrally, resembling *Anhanguera*.

*Anhanguera blittersdorffi* (MN 4805-V) has 52 alveoli, which exceeds the number in *Co. spielbergi* markedly. The largest pair of alveoli in *An. blittersdorffi* (MN 4805-V) is the tenth and the alveolar pattern is less erratic relative to *Co. spielbergi*. However, the third tooth of the referred specimen of *An. blittersdorffi* (n. 40 Pz-DBAV-UERJ) is, as in *Co. spielbergi*, the largest, but the alveolar pattern is far less erratic relative to the holotype and *Co. spielbergi*. The number of alveoli is less than is seen in the holotype (44 in total).

The number of alveoli in *Co. araripensis* (SAO 16494) is 36, which is the minimal number in *Co. spielbergi*. The dentition pattern is less erratic and the position of the alveoli two to six is stronger anteroventrally.

*A. santanae* has a less distinct variation in alveolar size. The number of alveoli is estimated (both skulls are incomplete) at 40 (Wellnhofer, 1991b).

The dentition in "*Cr.*" *mesembrinus* (BSP 1987 I 46) lacks distinct variation in alveolar size and the position of the alveoli is, in general, less laterally and there are less alveoli than *Co. spielbergi* (14 in each side; *contra* Wellnhofer, 1987). The number of teeth in *Co. robustus* is not known. However, the pattern is comparable to the new



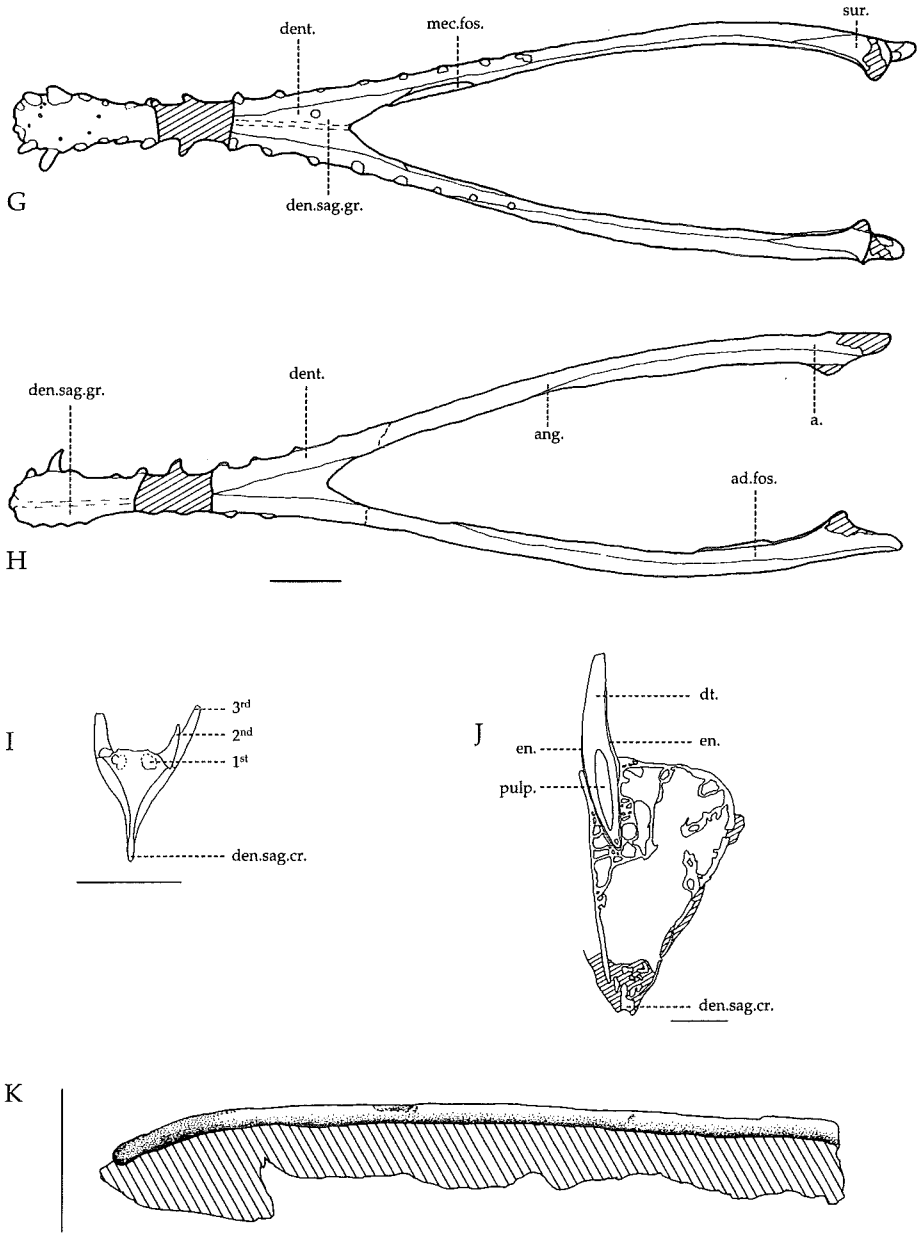


Fig. 4. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the mandible in various aspects (with details separately). A: mandible, left lateral; B: left ramus, medial; C: left retroarticular process, posteromedial view (scale bar = 20 mm); D: mandible, right lateral; E: right ramus, medial; F: right retroarticular process, posteromedial view (scale bar = 20 mm); G: mandible, dorsal; H: mandible, ventral; I: mandible, anterior; J: cross section of the mandible (anterior aspect with longitudinal section of tooth seven, right side: scale bar = 10 mm); K: piece of ?ceratobranchial (scale bar = 20 mm). Scale bar = 50 mm (unless mentioned otherwise). Drawings by the author.

species, although the second and third alveoli in *Co. robustus* are the largest against the third, fourth and ninth in *Co. spielbergi*.

The number of teeth in *Co. piscator* is 40 (observed on the cast) and the dentition pattern is comparable to *Co. spielbergi*, although there are differences between the seventh, eighth and ninth alveolus. These are of comparable size in *Co. spielbergi* and vary distinctly in *Co. piscator*.

#### *Frontal (fr.)*

The suture medial between the left and right frontal is well developed and forms a shallow ridge. Seen from posterior, the suture continues far between the two parietals (figs. 2E, F; Pl. 2C).

*Comparison* — The frontoparietal crest is more strongly developed in *An. blittersdorffi* (fig. 3E) and *Co. araripensis* (figs. 3F, G) than *Co. spielbergi*. The crest in *An. santanae* (figs. 3H, I) is longer and slightly more distinct. It is weak in *Co. piscator* (fig. 3L) and comparable to *Co. spielbergi*.

#### *Parietal (par.)*

The left and right parietals fuse posterior to the suture of the frontal and dorsal to the lower temporal fenestra (l.t.f.; figs. 2A-F; Pl. 2A-C).

*Comparison* — The parietal in *Co. spielbergi* is more strongly concave than that of *An. santanae* (figs. 3H, I). The short and blunt parietal crest (par.cr.) seen in "*Cr.*" *mesembrinus* (BSP 1987 I 46; fig. 3J) is nearly absent in *Co. spielbergi*.

#### *Lacral (lac.)*

The posterior edge of the lacrimal forms a curve that points into the orbit (figs. 2B, D, F; Pl. 2A-C). An opening, the lacrimal fossa (lac.fos.), is situated in the middle of the lacrimal and is bean-shaped, with its recess anteriorly. From here a ridge extends concavely towards the orbit (or), separating the lacrimal from the lacrimal process. At the end of this ridge is a small opening, interpreted as the ductus lacrimalis (duc.lac.).

*Comparison* — The lacrimal process in *An. blittersdorffi* (fig. 3E) is comparatively small and long, and the lacrimal fossa is somewhat larger. The small fossa posteroventral to the lacrimal fossa is not seen in *Co. spielbergi*.

Assuming that the lacrimal is complete in *Co. spielbergi*, it is shorter compared to *Co. araripensis* (figs. 3F, G) but the process that points into the orbit is more massive. *Coloborhynchus araripensis* has a small fossa dorsal to the larger lacrimal fossa.

"*Criorhynchus*" *mesembrinus* (BSP 1987 I 46; fig. 3J) lacks a lacrimal with a process that points into the orbit. The lacrimal fossa in *Co. piscator* (fig. 3L) is larger and the process pointing into the orbit is substantially smaller.

#### *Postfrontal (po.fr.)*

The postfrontal forms the posterodorsal edge of the orbit, and is sandwiched between the frontal and the postorbital (figs. 2D, F; Pl. 2B, C). The postfrontal is arched slightly posteroventrally towards the inner side of the orbit.

*Comparison* — According to Kellner & Tomida (2000) the presence of this bone is uncertain in *Co. piscator* (fig. 3L).

*Postorbital* (po.or.)

The postorbital is a triradiate bone of which the rays extend anteroventrally (the jugal process), posteroventrally (the squamosal process) and dorsally (the frontal process) (figs. 2B, C, F; Pl. 2A-C). The postorbital closes the orbit posteriorly and the lower temporal fenestra dorsally.

*Comparison* — The jugal process of the postorbital in *An. blittersdorffi* (fig. 3E) extends more laterally, giving the skull, seen in dorsal view, a somewhat broader appearance.

*Jugal, quadratojugal* (j., q.j.)

The processes of the triradiate jugal extend dorsally (lacrimal process), posterodorsally (postorbital process) and anterodorsally (maxillar process) (figs. 2D, F; Pl. 2B, C). The quadratojugal is sandwiched between the jugal and the quadrate (q.).

*Comparison* — The maxillar process of the jugal in *Co. piscator* (fig. 3L) is extremely long and slender in contrast to the short and robust process in *Co. spielbergi*.

*Squamosal* (sq.)

The squamosal consists of three rays, the parietal, postorbital and otic processes that originate in the broad, well-developed centrum (figs. 2B, D, H; Pl. 3A, B, D). The centrum is twisted diagonally posteroventrally to anterodorsally. Seen in ventral view, the otic process overlaps the quadrate. The otic process broadens anteriorly, with its largest width at two thirds of the length of the ventral aspect of the centrum of the squamosal. Beyond this point the angle of the squamosal changes and the bone continues anterolaterally. The squamosal lies against the opisthotic and the supraoccipital, and forms the junction between the opisthotic, the quadrate, the parietal and the postorbital.

*Comparison* — The edge of the otic process is sharper and extends more strongly dorsally in *Co. spielbergi* and *An. santanae* (AMNH 22555) relative to *An. santanae* (BSP 1982 I 90).

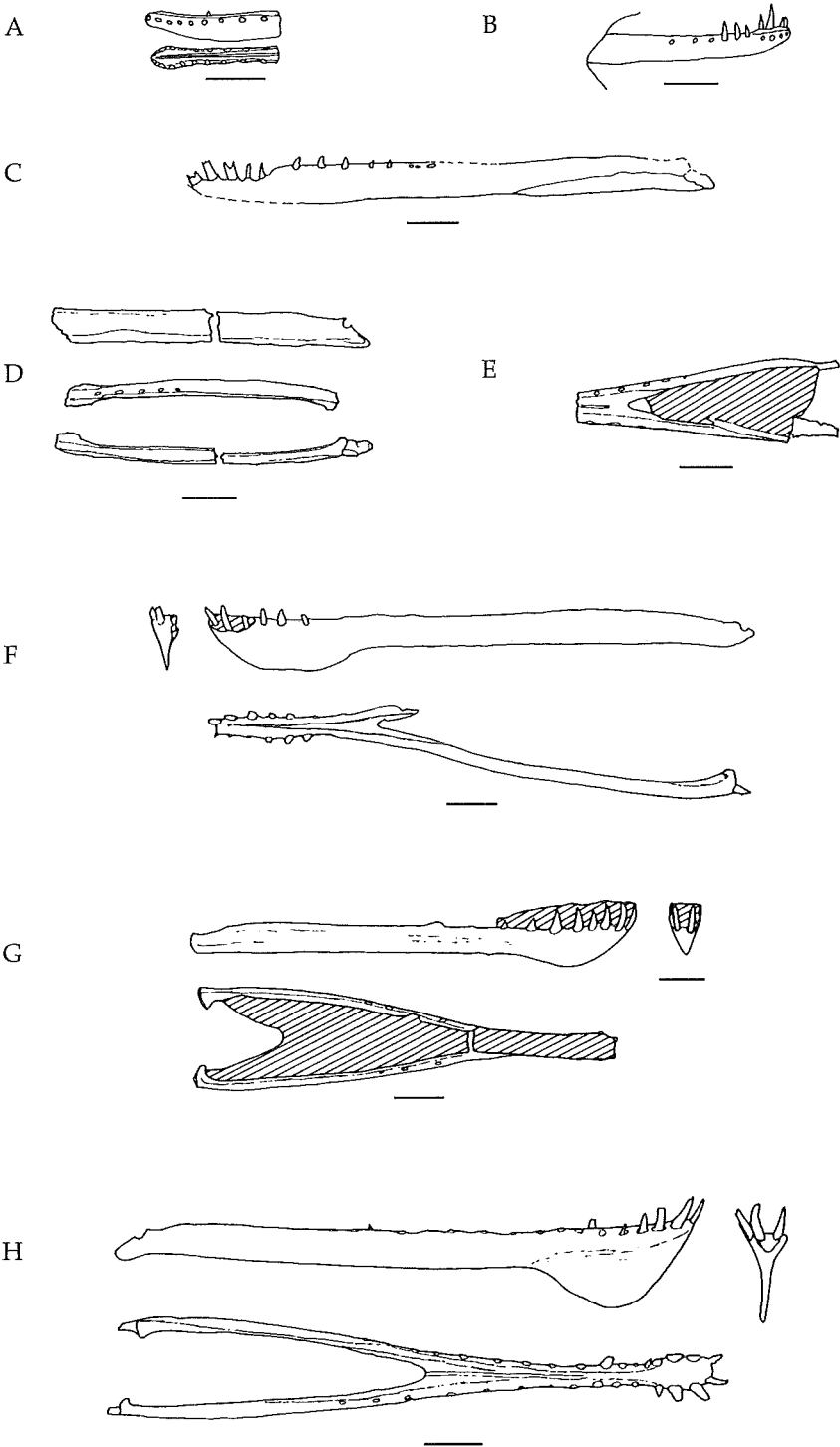
*Palatine* (pal.)

The palatine is in contact with the maxilla laterally, but the exact borders, both anteriorly and posteriorly, cannot be determined (fig. 2G; Pl. 2D). The palatine is recessed slightly relative to the palatine. Posteriorly, the palatine limits the choanae (ch.). More anteriorly, it has a small and low sagittal ridge (pal.sag.r.) that has its counterpart on the mandible. This ridge is most obvious between teeth 5 and 10. Posterior to tooth 10, the ridge disappears.

*Comparison* — Comparison with the palatal region of *Ce. atrox* is not possible. But the palatine of *Ce.? ligabuei* (fig. 3D) has a clear sagittal ridge extending far anteriorly and extend laterally at the posterior expansion.

*Anhanguera blittersdorffi* (fig. 3E) has a distinct palatal sagittal ridge, extending to the anterior border of the choanae. In the referred specimen, it extends anteriorly until the expansion, and fades between the fourth and fifth alveolus.

*Coloborhynchus araripensis* (figs. 3F, G) has a ridge at the palatine, but this is less distinct relative to "*Cr.*" *mesembrinus* (BSP 1987 I 46; fig. 3J) and *An. blittersdorffi* (fig. 3E). It is still stronger relative to *Co. spielbergi*.



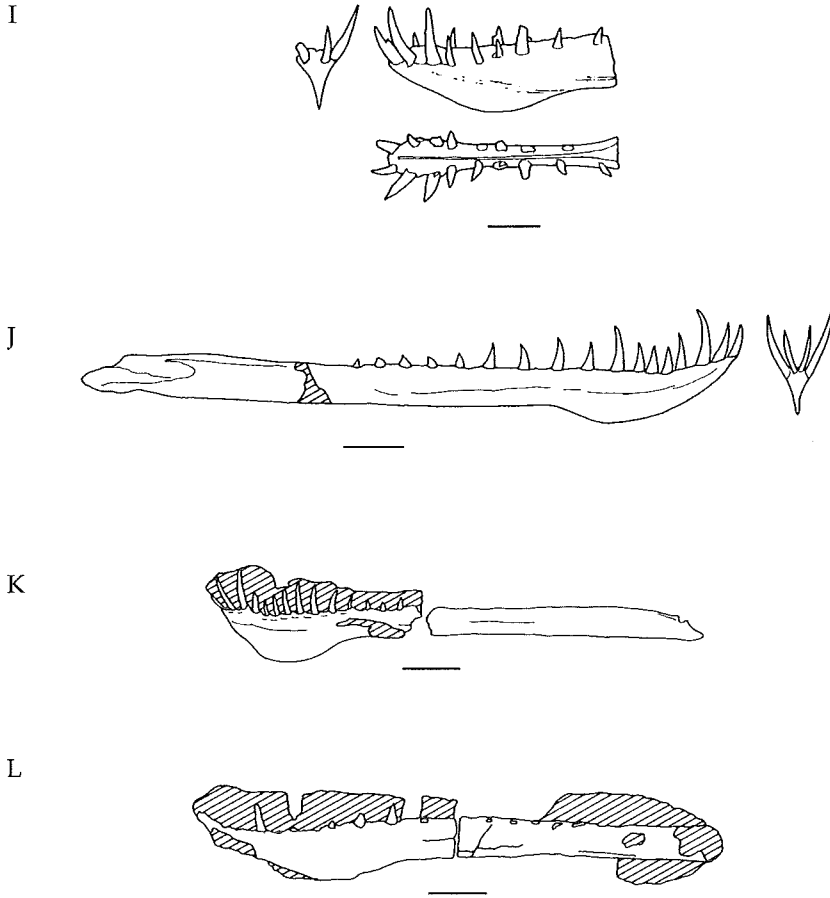


Fig. 5. Mandibles of compared pterosaurs in various aspects. A: *B. araripensis* (MN 4804-V: after Kellner & Tomida, 2000, p. 103); B: *B. cf. araripensis* (MN 4797-V); C: *Ce. atrox*; D: *Co. araripensis* (BSP 1982 I 89); E: *An. santanae* (BSP 1982 I 90); F: "*Cr.*" *mesembrinus* (BSP 1987 I 46); G: cf. "*Cr.*" *mesembrinus* (SMNS 56994); H: *Co. robustus* (BSP 1987 I 47); I: *Co. robustus* (SMNK 2302 PAL), J: *Co. piscator* (reconstructed, after Kellner & Tomida, 2000, p. 10, 23); K: *Anhanguera* sp. (SAO 200602); L: *Anhanguera* sp. (AMNH 22573). Scale bar = 50 mm. Drawings by E. Endenburg and the author.

The palatinal ridge is most obvious between tooth 6 and 11 in *An. santanae* (AMNH 22555) and between tooth 5 and 10 in *Co. spielbergi*. Although none of the specimens have a strongly developed palatinal sagittal ridge, the ridge of *Co. spielbergi* is weakest.

In "*Cr.*" *mesembrinus* (BSP 1987 I 46; fig. 3J) the "palate is elevated to a high medial ridge fitting into a corresponding deep sulcus on the mandibular symphysis" (Wellnhofer, 1987, p. 179), contrasting with the almost absent ridge in *Co. spielbergi*. No palatinal sagittal ridge can be observed in *Co. robustus* (SMNK 2302 PAL; fig. 3K), which is probably due to only the anterior part being preserved. A depressed medial

area evolves between the eighth and ninth left alveolar pair in this species. If *Co. robustus* had a palatal ridge, it did not extend far anteriorly. The distinction between the depressed medial area and tooth-bearing maxillae is more distinct relative to *Co. spielbergi*.

#### *Pterygoid* (pt.)

The pterygoid is triangular (figs. 2E, G; Pl. 3C, D). The interpterygoid vacuity (in.pt.vac.) is comparatively large. Both pterygoids are firmly united with the quadrate, posterolateral to the vacuity.

*Comparison* — The pterygoid in *An. blittersdorffi* (fig. 3F) has a distinct foramen, which is not seen in *Co. spielbergi*. *Coloborhynchus araripensis* (figs. 3F, G) has a small process at the pterygoid that is directed towards the subtemporal fenestra (s.t.f.), which cannot be observed in *Co. spielbergi*. However, this may be a preservational artifact.

#### *Quadrate* (q.)

The anterior aspect of the quadrate is directed anteroventrally and lies ventral to the quadratojugal and the jugal (figs. 2D, H; Pl. 2B, D). Seen from a ventral aspect, the quadrate is a thin, bar-like bone with the, damaged, condyloid process situated anteriorly. Parts of the fragile, thin, bony lamella (lam.) are still in place in the anterior corner of the cranioquadrate opening (cr.q.op.). The lamella is situated at the inner side of the quadrate, starts at the side of the basisphenoid and extends more than halfway along the posterior extending process of the quadrate. A foramen is situated in the anteromedial corner.

*Comparison* — The foramen in the anteromedial corner, at the junction with the basisphenoid, is absent in *An. blittersdorffi* (fig. 3E), *Co. araripensis* (fig. 3G) and "*Cr.*" *mesembrinus* (BSP 1987 I 46; fig. 3J). The reconstructed width of the skull of *C. spielbergi* is larger relative to the other taxa discussed herein, except "*Cr.*" *mesembrinus* (Table 4).

#### *Basisphenoid, interorbital septum* (b.sph., in.sep.)

The basisphenoid is orientated anteroventrally and narrows posteriorly, where it is in contact with the basioccipital (b.o.), and penetrates this bone between the left and right vagus foramen (v.for.) (figs. 2H, J; Pl. 2D). Anteriorly, the basisphenoid limits the interpterygoid vacuity. The interorbital septum lies dorsal to the basisphenoid inside the braincase and is a dorsally-trending, small bony plate that forms a small elliptical opening against the back wall of the braincase.

*Comparison* — Posteriorly, the lateral expansion of the basisphenoid in *An. blittersdorffi* (fig. 3E) is more abrupt and stronger than in *Co. spielbergi*. In the holotype of *An. blittersdorffi* (MN 4805-V) the bone is not completely fused with the quadrate anteriorly, in contrast to the referred specimen (n. 40 Pz-DBAV-UERJ) and *Co. spielbergi*. The lateral expansion of the basisphenoid is anteriorly and posteriorly stronger in "*Cr.*" *mesembrinus* (BSP 1987 I 46; fig. 3J).

#### *Basioccipital, opisthotic, exoccipital* (b.o., op., ex.o.)

The complete borders between these three bones cannot be determined, due to the very high degree of ossification obliterating the sutures (fig. 2H; Pl. 2D). However, small parts of the sutures between the basisphenoid, basioccipital and exoccipital are



still visible, and the entire posterodorsal suture of the opisthotic can be traced. Morphological these bones are comparable to those of previously described taxa.

#### *Supraoccipital* (sup.o.)

Posteroventrally, the skull is closed by the supraoccipital, the element that forms the dorsal margin of the posttemporal fenestra (p.t.f.) and foramen magnum (for.mag.) (fig. 2H; Pl. 2D). The posterior of the supraoccipital joins the parietal, which is overlapped by the parietal process of the squamosal. Posteriorly, the supraoccipital has a medial and strongly developed, bulb-shaped protrusion that extends anteroventrally into a ridge (o.sag.ri.) that fades towards the foramen magnum. At both sides of the ridge are posteromedially orientated pneumatic foramina.

*Comparison* — The holotype of *An. blittersdorffi* (MN 4805-V; fig. 3E) has a strongly developed occipital sagittal ridge which is even stronger developed in the referred specimen (n. 40 Pz-DBAV-UERJ). The occipital region in the latter is wider relative to the holotype as well as to *Co. spielbergi*.

The occipital sagittal ridge in "*Cr.*" *mesembrinus* (BSP 1987 I 46; fig. 3K) is distinctly robuster than that of *Co. spielbergi*. The posteroventral aspects of the skull in *Co. araripensis* (SAO 16494; fig. 3B), *An. santanae* (BSP 1982 I 90; fig. 3H) and *Co. piscator* (fig. 3L) are steeper relative to *Co. spielbergi* and *An. santanae* (AMNH 22555; fig. 3I). The occipital sagittal ridge in *Co. piscator* is weaker.

#### *Skull openings*

The shape of many of the skull openings at the ventral aspect cannot be determined because of the fragmented nature of the Leiden skull (figs. 2A, F, J; Pl. 3A-D). The skull openings of others specimens are also poorly preserved.

*Comparison* — The interpterygoid vacuity in *Co. spielbergi* is wider relative to that of *An. blittersdorffi* (fig. 3E) and *Co. araripensis* (figs. 3F, G). The lower temporal fenestra in *An. blittersdorffi* (fig. 3E) is more oblong. The orbit in *Co. araripensis* (fig. 3G) is slightly wider and the orbit in "*Cr.*" *mesembrinus* (BSP 1987 I 46; fig. 3J) is more elliptical, contrasting with the oval orbit in *Co. spielbergi*. The ratio of the length of the nasoantorbital fenestra to length of the skull is lowest in *Co. araripensis*. This ratio in other taxa varies by only a few percent (Table 4).

#### *Mandible*

The morphology of the mandible is comparable to those of the known toothed pterosaurs except for the presence of crests (absent in some taxa) (figs. 4, 5; Pl. 3; Tables 5-7). The mandible is long and slender with a comparatively short symphysis and diverging rami. The rami display a strong posteromedial bending of the posterior half. Anteriorly, the jaw has a dentary sagittal crest, which is substantially smaller than the premaxillary sagittal crest. The length of the lower jaw is substantially larger than that of other species discussed herein. However, comparison with other taxa are limited because most mandibles are incomplete and/or only partially prepared.

#### *Dentary* (den.)

In medial view, the dentary starts immediately posterior to the last alveolus and forms the dorsal border of the Meckelian fossa (mec.fos.) (figs. 4A, B, D, E, G, H; Pl.

3A, B, D, E, G, H). The left and right dentaries meet each other anteromedially, forming the symphysis. In dorsal view, there is a shallow ill-defined dentary sagittal groove (den.sag.gr.). Towards the anterior spoon-shaped expansion, this groove widens and disappears. The tooth-bearing lateral edges protrude relative to the medial area. The dentary sagittal crest starts at the cross sectioned area, probably between alveolus seven and nine, and narrows ventrally continuously, ending in a ventralmost border 3 mm thick. The posterior view of the cross section (fig. 4J; Pl. 3J) demonstrates the strengthening of the ventral inner side of the crest.

*Comparison* — The dentary of *B. araripensis* (MN 4804-V; fig. 5A) lacks a sagittal crest and is spoon-shaped expanded, but less distinct than in *Co. spielbergi*. The dentary sagittal groove, which is defined sharply, is continuous to almost the anterior aspect, contrasting with the weak and short groove in *Co. spielbergi*.

The dorsal border up to the sixth alveolus inclines in a ventral direction in *Ce. atrox* (fig. 5C) and there is no dentary sagittal crest. The dentary is spatulate and more expanded than the premaxilla (Leonardi & Borgomanero, 1985).

The mandible of *An. blittersdorffi* (n. 40 Pz-DBAV-UERJ) is proportionally narrower than that of *Co. spielbergi* with a smaller dentary sagittal crest (Table 7). The configuration of the dorsal aspect (recessed medial area having a sagittal groove flanked by ridges) is comparable to *An. santanae* and the two other *Anhanguera* mandibles (see below), but differs from *Co. spielbergi*, which has an ill-defined dentary groove that is situated in the recessed medial area. The tooth-bearing edges are less clearly raised and separated from this medial area in *Co. spielbergi*. The dentary configuration in *An. blittersdorffi* is probably only seen in *Anhanguera* sp. (Veldmeijer, in review). The rami in *An. blittersdorffi* diverge straight and posterolaterally instead of with a posteromedial bending as seen in *Co. spielbergi*.

Wellnhofer (1985) mentioned a coronoid in *C. araripensis* (BSP 1982 I 89; fig. 5D), which is not observed in *Co. spielbergi*. However, this might be due to the high co-ossification of the latter. The rami in *Co. araripensis* (BSP 1982 I 89) are less strongly curved.

The reconstruction of the proportionally narrower (Table 7) mandible of *An. santanae* (BSP 1982 I 90; fig. 5E), is without a crest (Wellnhofer, 1985, 1991b). The anterior part, starting roughly 50 mm anterior to the symphysis, is missing in the holotype. Only the retroarticular process is preserved in *An. santanae* (AMNH 22555). Although the reconstruction of the skull was altered later (Wellnhofer, 1991b), Kellner & Tomida (2000) made no attempt to reconstruct the mandible. However, the reconstructions are hypothetical and there is no evidence for the presence of the crest or its position. If there was a crest, it is unlikely that it was placed posterior to the anterior aspect, allowing an analogy with *An. blittersdorffi* (n. 40 Pz-DBAV-UERJ) on the basis of the comparable position of the premaxillary sagittal crests (which has the dentary sagittal crest starting at the anterior aspect). Seen from a dorsal perspective, the tooth-bearing borders in *An. Santanae* are raised relative to the medial part. Medial to this recessed area is a dentary sagittal groove that is flanked by two parallel running, slightly raised ridges as seen in *A. blittersdorffi* (see above). The cross section of the symphyseal part is, as in the *Anhanguera* sp., rounded trapezoid, unlike the section of this region in *Co. spielbergi*.

The mandible of "*Cr.*" *mesembrinus* (fig. 5F, G) is proportionally smaller and the crest is shorter, albeit markedly deeper (Table 7). The anterior aspect has a small

depression mediodorsal to the two front teeth. The anterior part is almost not expanded. The sagittal groove is deep and posteriorly widening. The curvature of the rami is less.

The anterior margin of the mandible in the holotype of *Co. robustus* (BSP 1987 I 47; fig. 5H) is blunt and "forms an angle of c. 50° with the upper edge of the jaw" (Wellnhofer, 1987, p. 182). The anterior margin of *Co. spielbergi* is also blunt, and the dentary sagittal crest is far smoother and longer, but less deep relative to *Co. robustus* (Table 7). The dorsal aspect of the spoon-shaped anterior part is slightly concave in *Co. robustus* against slightly convex in *Co. spielbergi*. The dentary sagittal groove in *Co. robustus*, especially SMNK 2302 PAL (fig. 5I), is clearly defined and comparatively deep, which contrasts sharply with the ill-defined groove in *Co. spielbergi*. It extends further anteriorly in *Co. robustus*, until the anterior expanded part, widens posteriorly, starting approximately between the ninth and tenth alveolus (Veldmeijer, in review). This groove differs from the dentary groove in *Anhanguera*, having no flanking ridges and extending further anteriorly. In *Co. robustus* (BSP 1987 I 47), the symphysis starts at the 14<sup>th</sup> alveolus. This is with the 12<sup>th</sup> in *Co. spielbergi*, which results in a longer and therefore more slender appearance of the lower jaw of *Co. robustus* (Table 7).

Proportionally, the mandible of *Co. piscator* (fig. 5J) is narrower and the crest shorter but deeper (Table 7). The anterior tip in *Co. piscator* is curved upwards, and the rami are less strongly curved, unlike *Co. spielbergi*.

The proportions of the mandibles in the *Anhanguera* sp. (figs. 5K, L; Veldmeijer, in review) are comparable and differ from *Co. spielbergi* mainly because they have a shorter, but deeper, crest (Table 7). The different dentary sagittal groove was discussed above.

### Dentition

The teeth are still preserved although most are incomplete (figs. 4G-J; Pl. 3G-J; Table 6). The left side of the jaw contains 16 teeth, which is also the number of teeth on the right side (excluding the putative tooth numbered '15a', see below). They are distributed over the anterior half of the mandible. The alveoli are orientated laterodorsally and the two alveoli at the anterior aspect anteriorly. They are elliptic with their long axis longitudinally (except the first pair which are circular). Alveoli two to seven are orientated laterodorsally and slightly anteriorly. The teeth are curved posteromedially

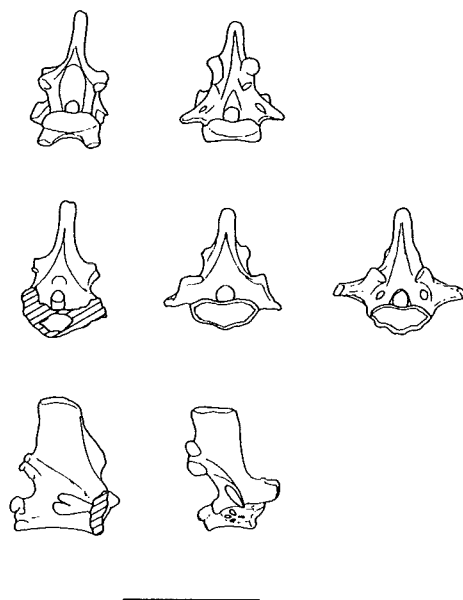


Fig. 6. Cervicals of a compared pterosaur in various aspects. Seventh, eighth and ninth cervicals (from left to right) of *An. santanae* (AMNH 22555: after Wellnhofer, 1991b, p. 56-57). Scale bar = 50 mm. Drawings by E. Enderburg and the author.

(based on the complete second and third on the left side and the third tooth on the right). The remaining alveoli are positioned dorsally and the teeth are curved postero-medially. The first and second alveoli are of comparable size, but smaller than the third. The description is based on the measurements taken at the left side. Alveoli 4-6, all of comparable size, are smaller than alveoli 1-3. Alveoli 7-8 are of comparable size to each other and are larger than alveoli 1, 2, 4-6 but smaller than alveolus 3. Alveoli 9-16 are of comparable size to 4-6. The alveoli are widely spaced although the first six less widely than the following (an average of 7 mm against an average of 29 mm). There is a continuous increase, save some small fluctuations, in the size of the diastema. Alveolus 16 of the right ramus is orientated more medially than all other alveoli whereas the putative alveolus posterior to alveolus 16 and numbered '15a', is orientated laterally. The expansion at this place on the lateral aspect is likely due to the root of the tooth in his alveolus, although the tooth itself is not preserved.

Tooth 7 of the right side is sectioned longitudinally, which provides a good view of the interior of the tooth (fig. 4J; Pl. 3J(i)). The lateral aspect of the tooth extends convexly into the alveolus. The medial aspect extends with a concave curvature until the alveolar margin, where it has its largest diameter (6.5 mm compared to 1.7 mm at the dorsalmost point, measured lateromedially) and continues almost straight into the alveolus. The diameter of the tooth decreases continuously ventrally. The tooth ends in a sharp edge. The large, oval space inside is the pulp cavity (pulp.). A small layer, comparable to enamel (en.), is observed between the alveolar margin and the dentine (dt.). This layer is continuous onto the crown, where it is very thin (less than 1 mm). The root is firmly embedded in the jaw by means of large quantities of small bony transverse joins. These joins form small compartments that serve as a base for the tooth. This structure is only present in the surroundings of the tooth; the rest of the jaw is hollow with a structure of bony transverse bars.

*Comparison* — The second to sixth alveoli are positioned more laterally in *B. araripensis* (MN 4804-V). The first pair of alveoli is placed more anteriorly. The differences in alveolar size are far less relative to *Co. spielbergi*.

The number of alveoli in *Ce. atrox* is smaller (28 against 32 in *Co. spielbergi*). At least 42 alveoli occur in *An. blittersdorffi* (n. 40 Pz-DBAV-UERJ), which is a substantially larger number relative to *Co. spielbergi* (32). The third alveolus is the biggest and the alveolar size decreases from the seventh alveolus continuously in size, against the large ninth alveolus in *C. spielbergi*. The pattern is less erratic and generally the alveoli are substantially smaller. The pattern of diastema size is more regular than in *Co. spielbergi* and size decreases from alveoli 10-11 onwards.

The alveoli in "*Cr.*" *mesembrinus* are set at the anterior and lateral edge, and face dorsally rather than laterodorsally as seen in *Co. spielbergi*. The alveoli are all comparable in size and twelve teeth are observed at both sides.

The pattern of dentition of the two *Co. robustus* specimens are comparable but the ninth alveolus in *Co. spielbergi* is of approximately the same size as the third. In the holotype of *Co. robustus* (BSP 1987 I 47) this is the eighth (although this alveolus is still substantially smaller). Alveoli 6 and 7 in *Co. robustus* (SMNK 2302 PAL) are slightly larger than alveoli 5 and 8, but still substantially smaller relative to the third alveolus. Furthermore, the increase in size of the diastemae is more severe in the latter specimen. In this, the holotype of *Co. robustus* and *Co. spielbergi* are more comparable. The former specimen also differs from *Co. spielbergi* by the large differences in measure-

ment ratios (Table 7). Both animals are full-grown but have a different number of teeth (18 against 15). Kellner & Tomida (2000, p. 118) mistakenly mentioned a "(height between the dorsal margin of the mandible and the ventral part of the sagittal crest [...])" of 760 mm. The depth of the crest measures 76 mm.

The alveoli in *Co. piscator* are more numerous, 38 against 32 in *Co. spielbergi*. The mandibular teeth in *Co. piscator* are generally larger than the teeth in the upper jaw, which is the other way around in *Co. spielbergi*. The variation in alveolar size is larger in *Co. piscator*. The pattern of diastemae size shows a distinct difference. The alveoli are increasingly less widely spaced from approximately halfway the dentition in *Co. piscator*, whereas the alveoli in *Co. spielbergi* are continuously wider spaced posteriorly, save a minor decrease between the last four alveoli.

The *Anhanguera* sp. has 38 teeth. The dentition pattern in the *Anhanguera* sp. is comparable to *An. blittersdorffi* although measurements are slightly greater and the graph is slightly more erratic. The pattern still contrasts with *Co. spielbergi* for reasons explained with *An. blittersdorffi*. The diastemae variation also differs from *Co. spielbergi* in the same way as the variation differs between *An. blittersdorffi* and *Co. spielbergi*.

#### *Surangular, angular* (sur., ang.)

The surangular extends further posteriorly than the cotyles and ends in a overhanging ridge dorsal to the cotyles (figs. 4A-E, G, H; Pl. 3A-E, G, H). The anterior aspect is orientated medially with a curve and ends in a sharp edge. Seen from a medial perspective, the anterior part ends in a sharp edge pointing anteroventrally. The exact position of the angular cannot be determined.

#### *Prearticular* (pr.a.)

Seen from a medial perspective, the left ramus has an element between the articular (a.), the Meckelian fossa, the splenial and the angular that is interpreted as the prearticular (figs. 4B, E; Pl. 3B-E). Posteriorly, the prearticular forms the edge of the retroarticular process. It confines the ventral sides of the surangular and the adductor fossa (ad.fos.), and forms a ridge at the latter. The prearticular is in contact with the angular dorsally.

#### *Splenial* (spl.)

The dorsal side of the splenial is confined by the dentary (figs. 4B, E; Pl. 3B, E). Seen from a medial perspective, the splenial continues anteriorly to the Meckelian fossa and forms its posterior border. Posteriorly, the splenial forms the anteroventral border of the adductor fossa.

*Comparison* — The splenial in *Co. araripensis* (BSP 1982 I 89) has several small pneumatic foramina, absent in *Co. spielbergi*.

#### *Retroarticular process*

The retroarticular process forms an edge with the mandible of 40° and is orientated posteroventrally (figs. 4C, F; Pl. 3C, D). The articular is relatively long and small in comparison with the ramus. It narrows posteriorly, and consists of the lateral and medial cotyle (lat.cot., med.cot., respectively) that is separated by a distinct posterolaterally and anteromedially orientated ridge. A large pneumatic foramen (for.) is situated posteroventrally to the medial cotyle.

*Comparison* — The holotype of *B. araripensis* retains the anterior part of the retroarticular process, but a more complete specimen currently under study by the author shows that the rami and especially the retroarticular process are, seen from dorsal, less strongly inclined. The mandible in *B. araripensis* has smaller dimensions overall.

Comparison of the mandible with *Co. araripensis* (BSP 1982 I 89: fig. 5D) indicates a more elongated articular relative to *Co. spielbergi* and the dorsal aspect of the articular is less steep and pointed. The articular in "*Cr.*" *mesembrinus* (BSP 1987 I 46: fig. 5F) is even shorter.

#### ?Ceratobranchials

A piece of slender bone is still attached to the matrix (fig. 4K; Pl. 3K). The cross section is circular, but one end of the bone is curved and flatter than the other extremity. Another piece (not illustrated) is a thin, almost straight fragment with an oval cross section. It is slightly bent, which becomes even clearer when it is connected with another part of the bone that is completely freed from the matrix (not illustrated).

*Comparison* — Comparison of these fragments reveals a strong resemblance and they are regarded as possible pieces of ceratobranchialia. The shape and size suggests that the bone is a piece of ceratobranchialia of the hyoid apparatus (*cf.* Veldmeijer, in review; Wellnhofer, 1985).

#### Axial skeleton

(Figs. 6-13; Pls. 4-8; Tables 8-13)

#### Cervical vertebrae

The seventh and eighth cervical vertebrae (the last two before the notarium) are similar to those described by previous authors (Wellnhofer, 1991b; Kellner & Tomida, 2000). However, the eighth cervical vertebra has pieces of the rib fused (Pl. 4; Table 8).

*Comparison* — Comparison with the cervicals of other taxa from Brazil is limited by the paucity of data. The seventh and eighth cervical in *An. santanae* (AMNH 22555; fig. 6) and *Co. spielbergi* are, apart from slight biometrical differences (the cervicals in *An. santanae* are overall smaller), similar despite the fact that the neural spine of the eighth cervical of the new species has a more convex anterior border and its prezygapophysis is comparatively more robust.

The cervical vertebrae in *Co. piscator* are, besides the size "essentially the same as in *Anhanguera santanae* (AMNH 22555)" (Kellner & Tomida, 2000, p. 34). However, the cervicals of *Co. piscator* (not illustrated) are longer and higher relative to *Co. spielbergi*. In contrast, the width over the pre- and postzygapophyses is larger in the latter species. Kellner & Tomida (2000) remarked that there is no fusion of the centra of the eighth and ninth cervical vertebrae, contrasting with the fused situation in *An. santanae* (AMNH 22555; *contra* the addition of 'apparently' by Kellner & Tomida, 2000, p. 34, because it is clearly visible that the centrum and neural arch of the eighth and ninth cervicals are completely co-ossified) and *Co. spielbergi*.

#### Notarium

The notarium consists of six vertebrae, which are firmly fused by their centra (c.), zygapophyses and neural spines (fig. 7; Pl. 5; Table 9). The neural spines form a stout

supraneural plate (sup.n.p.). The posterior half of this plate expands laterally, starting dorsal to the fourth vertebra and obtains its largest width dorsal to the fifth vertebra, which results in a stouter part. The scapular articulation (sc.art.) is situated at this bulbous part, which is in the middle of the supraneural plate, dorsoventrally, and posterodorsal to the fifth vertebra. The surfaces are oval and saddle-shaped. A large foramen is situated immediately posterior to the scapular articulation.

A ridge characterises the sutures between the centra. The sutures between the third and fourth, fourth and fifth, and fifth and sixth notarial vertebrae are even more distinct, and marked by a distinct bulging of the articular areas. Comparatively large foramina are visible between the centra.

The first vertebra of the notarium is the last cervical (number nine) and is firmly fused with the following notarial dorsals. The rounded triangular neural canal (n.c.) is flanked by pneumatic foramina immediately ventral to the prezygapophyses (pr.z.). The cotyle (co.) of this first vertebra is elliptical of shape and directed slightly anteroventrally. The part of the supraneural plate that belongs to this vertebra is thicker in comparison to the rest.

The transverse processes (t.p.) of the first three notarial dorsals are thick and their distal extremities narrow strongly relative to the transverse processes of the fourth dorsal. The transverse processes of the third and fourth notarial dorsals are situated slightly more posteriorly relative to the other vertebrae. The transverse processes of the last dorsal is orientated more anteriorly than the others, and the relatively big and flat transverse process is orientated slightly laterally, relative to the previous ones. The articular area for the rib (rib.) is oval, convex and orientated anteroventrally. The small part of the neural canal that is to distinguished from the damaged posterior aspect suggests a triangular shape.

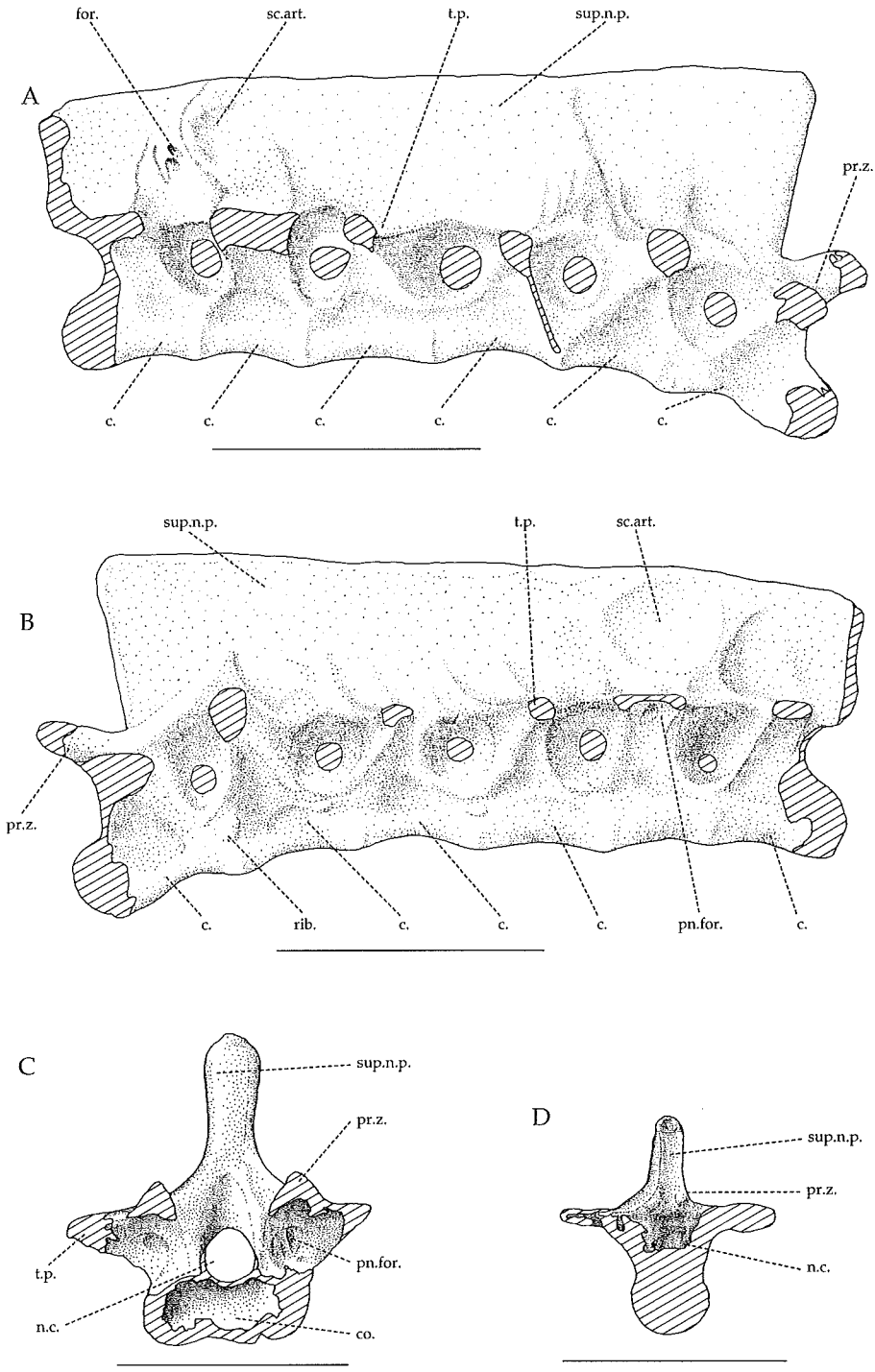
*Comparison* (fig. 8) — Few notaria from Brazil have been described (Frey & Martill, 1994; Wellnhofer *et al.*, 1983). The notarium in *Santanadactylus brasiliensis* de Buisonjé, 1980 (fig. 8) is included in this genus on the basis of its size (Wellnhofer *et al.*, 1983). The notarium is composed of five vertebrae because Wellnhofer *et al.*, (1983) concluded that the first notarial vertebra, i.e., the last cervical, does not take part in the notarium, in contrast with *Co. spielbergi*. The scapular articulation is situated dorsal to the fourth notarial dorsal, the same as in *Co. spielbergi*. The neural spines of the vertebrae in *Co. spielbergi* form a stout supraneural plate, but the neural spines in *S. brasiliensis* are not completely fused.

*Anhanguera santanae* (AMNH 22555) lacks a notarium. Another specimen of *An. santanae* (BSP 1982 I 91) lacks a co-ossified notarium (Wellnhofer, 1985, 1991b) too, as well as the juvenile *Co. piscator*. The scapular articulation, however, is situated at the fourth notarial dorsal in *An. santanae* (AMNH 22555) as well as in *Co. spielbergi*.

The notarium in *Arthurdactylus conandoylei* Frey & Martill, 1994, is characterized by "three fused neural spines, two of them serving as attachment site for the very broad scapulae" (Frey & Martill, 1994, p. 395).

## Dorsals

There are seven isolated dorsals (number 6-12), which are similar in morphology (fig. 9; Table 10). Therefore, the morphology of the sixth dorsal, which is the first free





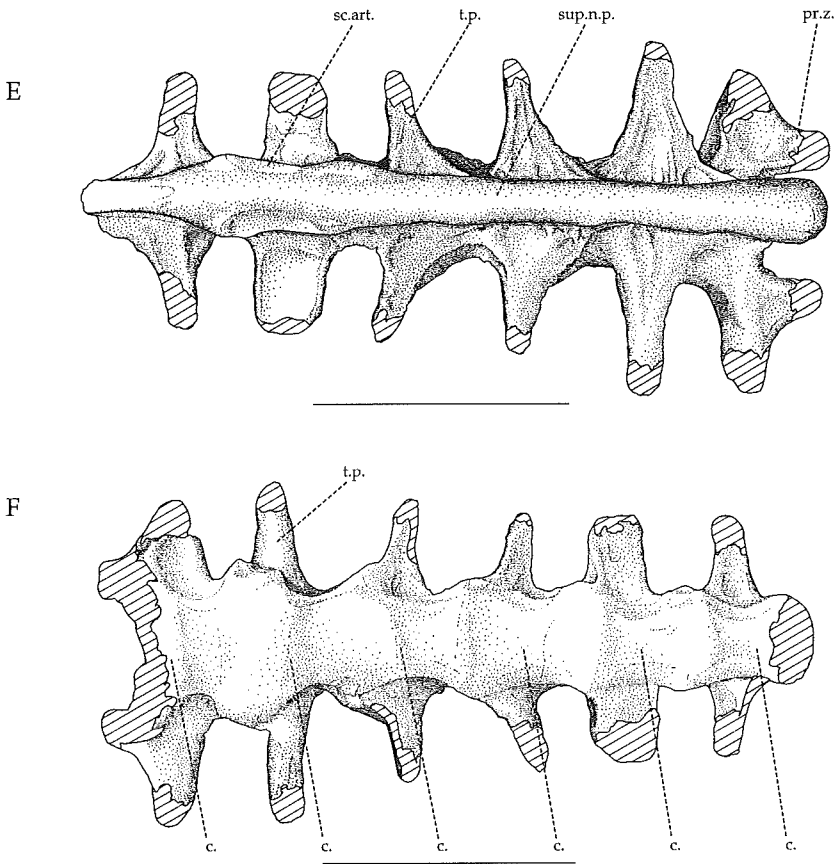


Fig. 7. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the notarium in various aspects. A: right lateral; B: left lateral; C: anterior; D: posterior; E: dorsal; F: ventral. (Note that only one transverse process is indicated). Scale bar = 50 mm. Drawings by the author.

dorsal, is described in detail and the subsequent dorsals are discussed by focussing on the differences with the sixth dorsal.

The neural spine (n.s.) of the sixth dorsal is high and slender, occupying 40% of the total height. The dorsal edge is slightly convex. The prezygapophyses, which are situated slightly ventrally relative to the postzygapophyses (po.z), point anterodorsally, but less so than the postzygapophyses. The prezygapophyses are located anterodorsally relative to the transverse processes. The area dorsal to the prezygapophyses and ventral to the neural canal is slightly sunken. The depressed area ventral and lateroventral to the postzygapophyses is large, but less deep relative to the seventh cervical. The comparatively large neural canal is circular and the bottom of the neural canal is deeply dented. The ventral aspects of the transverse processes extend concave towards the centrum and taper laterally. The lateralmost extremities point slightly ventrally. The articulation surface with the rib is slightly oval with its

pointed aspect orientated posteriorly and slightly posterodorsally. The elongated slender centrum has laterally expanding cotyles and condyles. The ventral aspect of the centrum is concave longitudinally and convex transversely. The condyle is convex and elliptical of shape. Seen from posteriorly, it partially obscures the neural canal. The cotyle is concave and bean-shaped, and the ventral and lateral edges are distinct swollen. The areas lateral to the neural canal taper ventrally. The dorsal margin of the cotyle changes into these areas lateral to the canal.

Dorsals seven to 12 differ from the sixth dorsal in having a more pos-

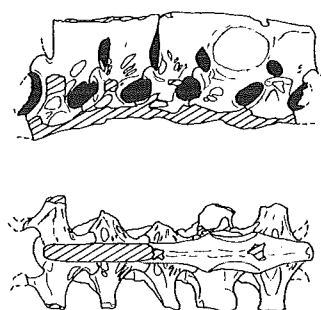


Fig. 8. Notarium of a compared pterosaur in various aspects. *S. brasiliensis* (V-201; after Wellnhofer *et al.*, 1983, p. 153). Scale bar = 50 mm. Drawings by E. Endenburg and the author.

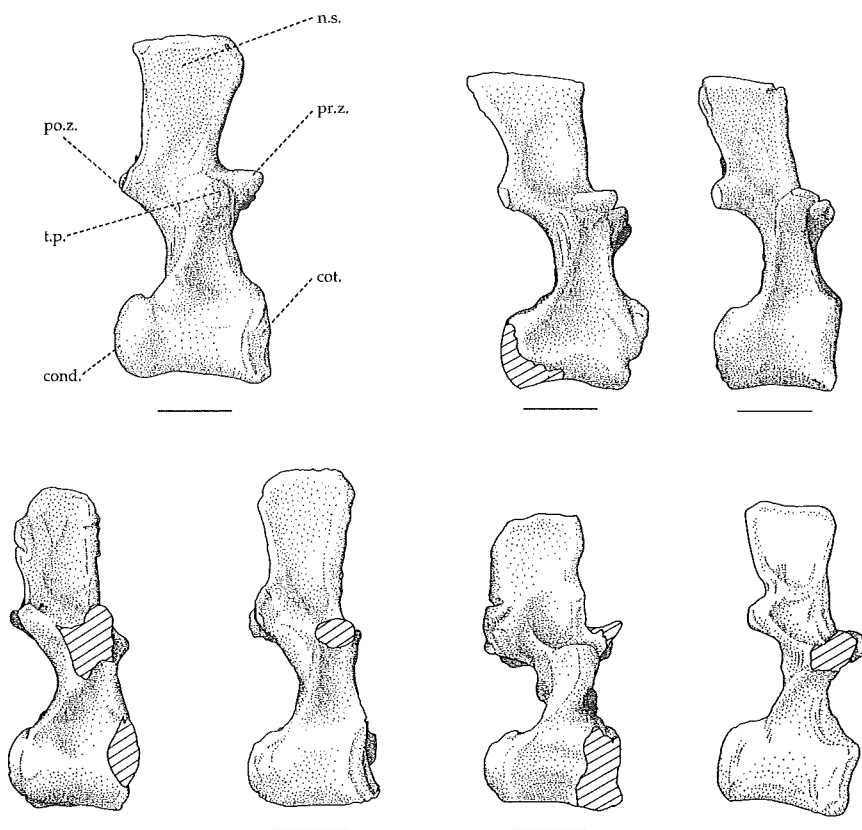


Fig. 9. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sixth up to and including the twelfth dorsal vertebrae in various aspects. A: right lateral. Scale bar = 10 mm. Drawings by the author.

terodorsal orientation of the posterior aspect of their neural spine. The prezygapophyses are situated slightly ventral to the transverse processes and are less close together. The area between these prezygapophyses is less deeply sunken. The postzygapophyses are less close together as well. The condyle is smaller laterodorsally as well as dorsoventrally. The centra are less elongated, but slightly more concave in sagittal plane.

*Comparison* — Unfortunately, no detailed comparison is possible with the dorsals in *An. santanae* (AMNH 22555) due to their damaged state. Wellnhofer (1991b) counted 13 dorsals in *An. santanae* (AMNH 22555). If this number is correct, it differs from the new species (12 dorsals). The comparison with another specimen of *An. santanae* (BSP 1982 I 91) suggests a high degree of resemblance. *Coloborhynchus spielbergi* has seven dorsals in total (12 with the dorsals of the notarium included and 16 when the dorsals of the pelvis are also counted). The only preserved, first five dorsals in *Co. piscator* are not fused into a notarium (see above).

Synsacrum

The synsacrum consist of at least six, but possibly seven, vertebrae, which are fused

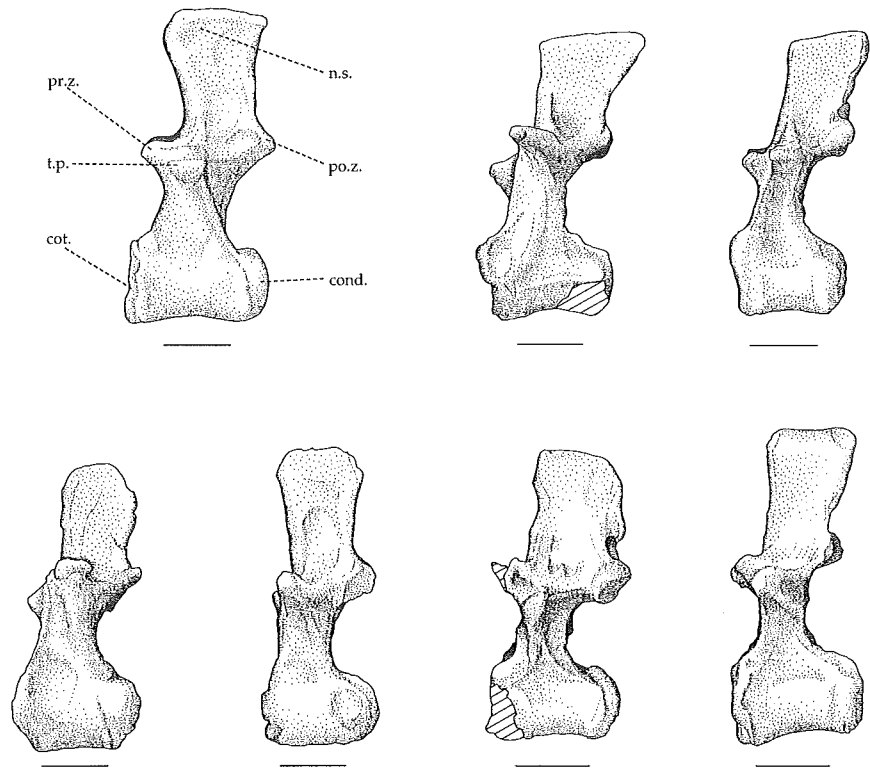


Fig. 9. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sixth up to and including the twelfth dorsal vertebrae in various aspects. B: left lateral. Scale bar = 10 mm. Drawings by the author.

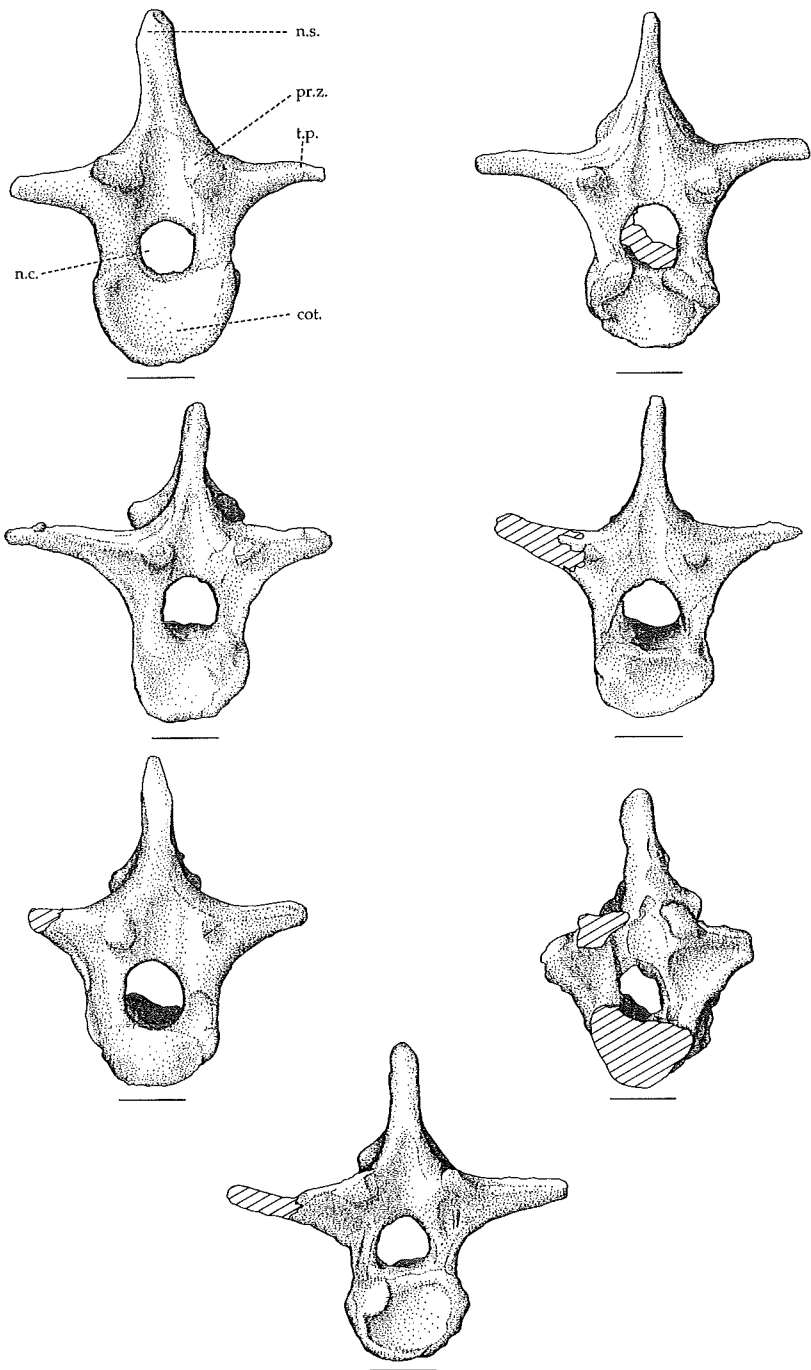


Fig. 9. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sixth up to and including the twelfth dorsal vertebrae in various aspects. C: anterior. Scale bar = 10 mm. Drawings by the author.

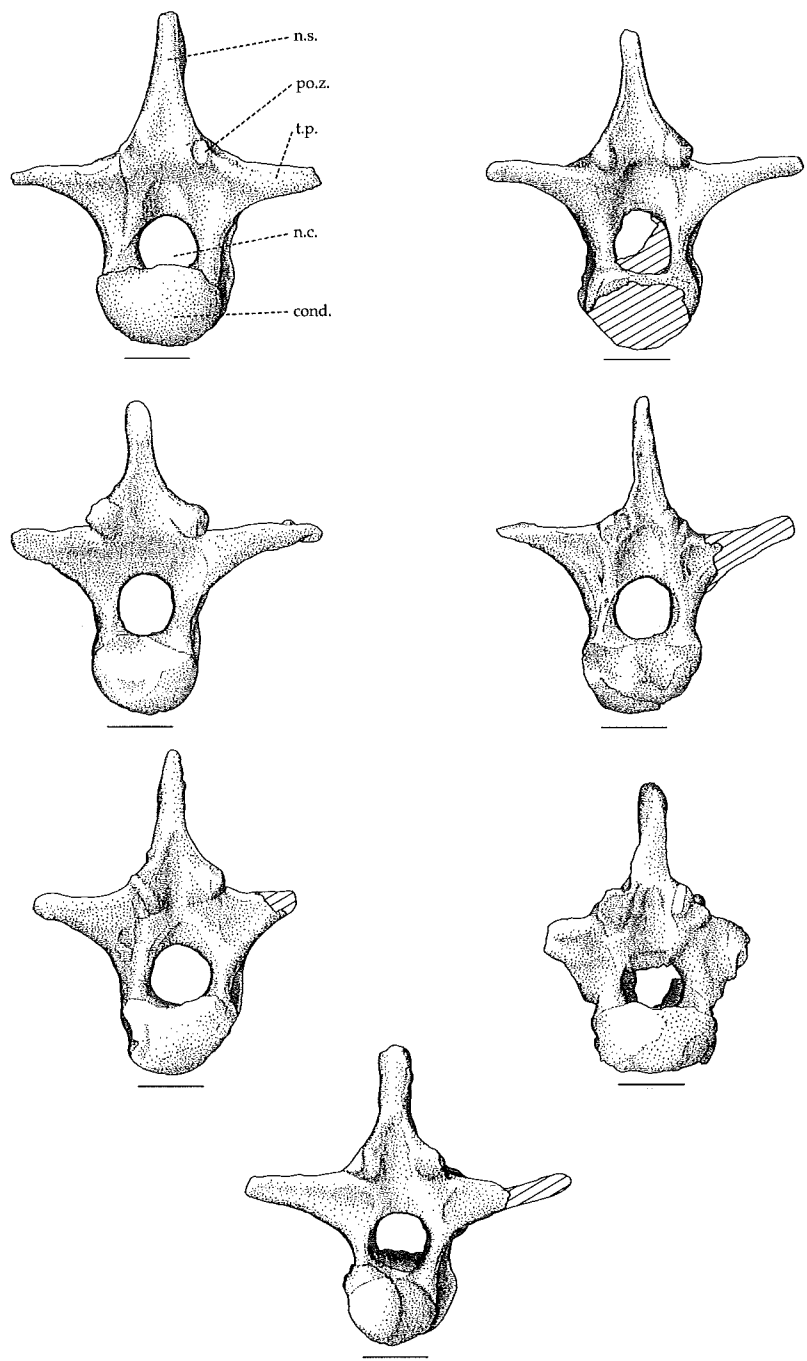


Fig. 9. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sixth up to and including the twelfth dorsal vertebrae in various aspects. D: posterior. Scale bar = 10 mm. Drawings by the author.

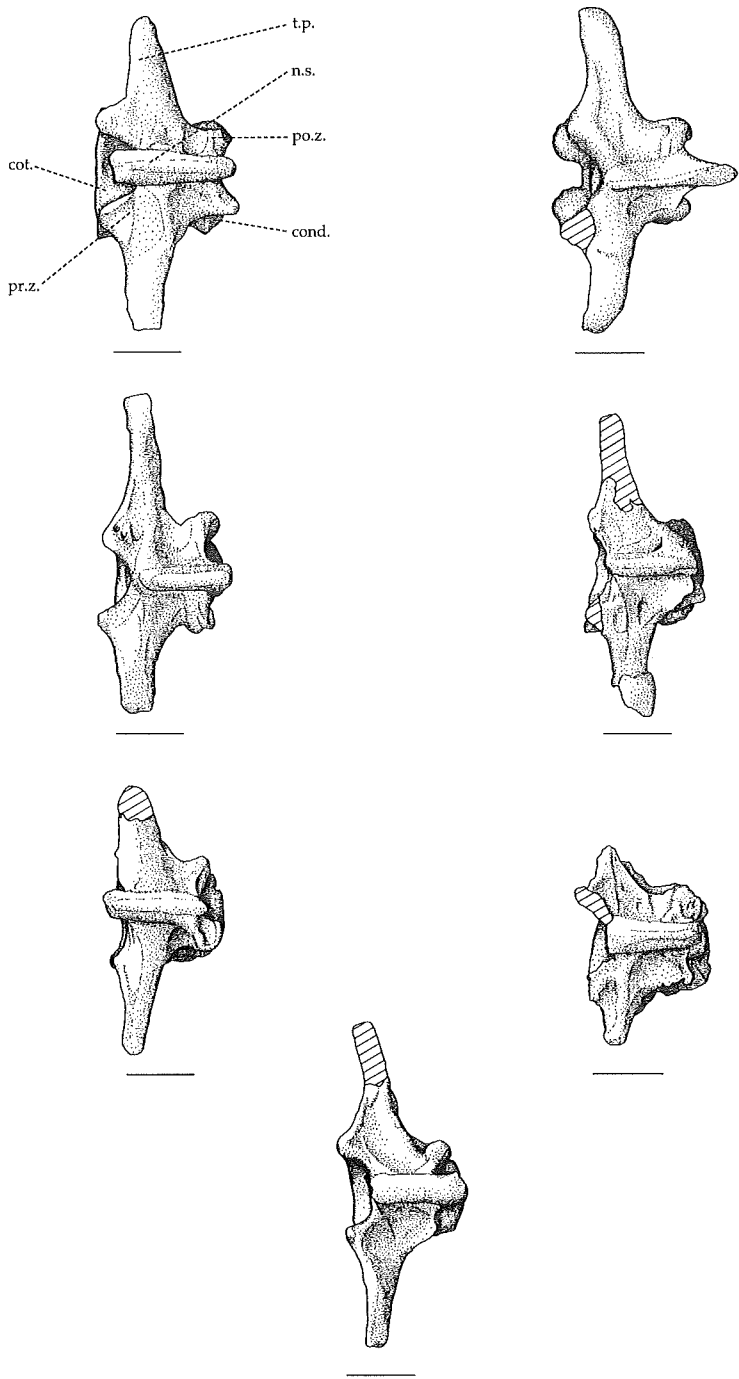


Fig. 9. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sixth up to and including the twelfth dorsal vertebrae in various aspects. E: dorsal. Scale bar = 10 mm. Drawings by the author.

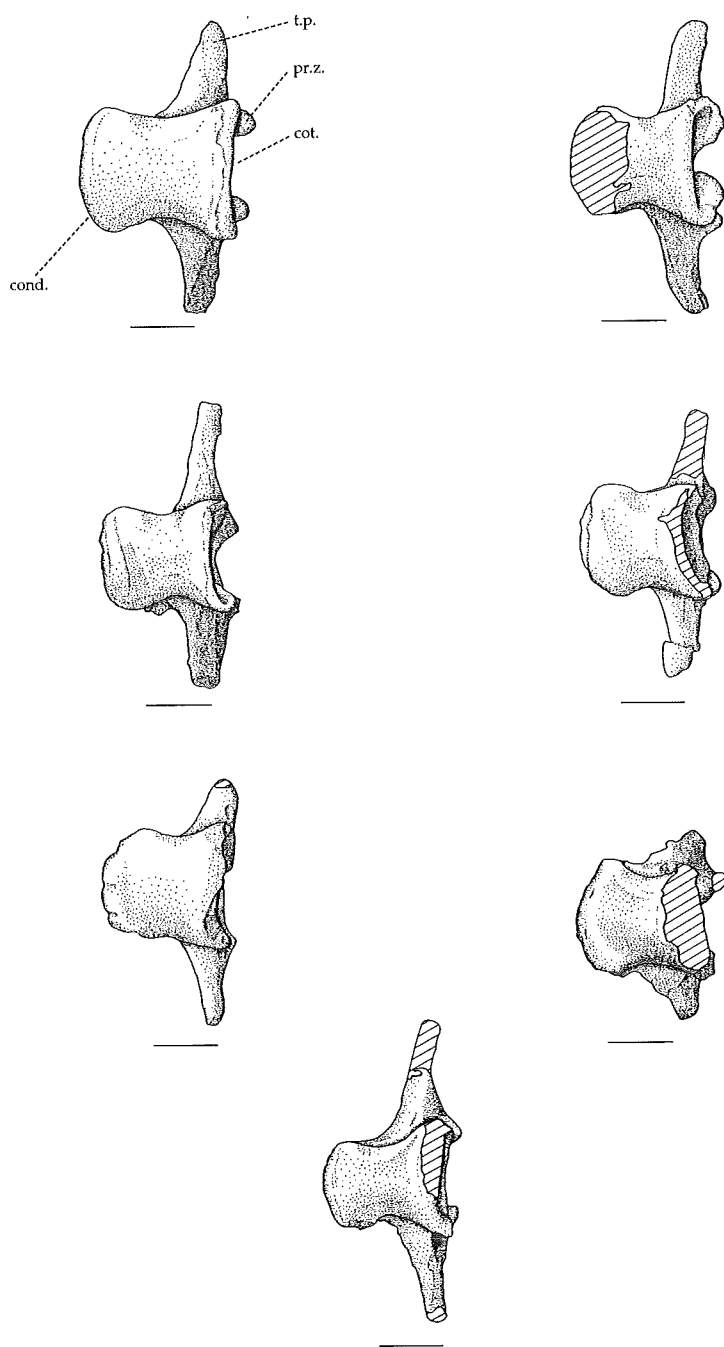


Fig. 9. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sixth up to and including the twelfth dorsal vertebrae in various aspects. F: ventral. Scale bar = 10 mm. Drawings by the author.

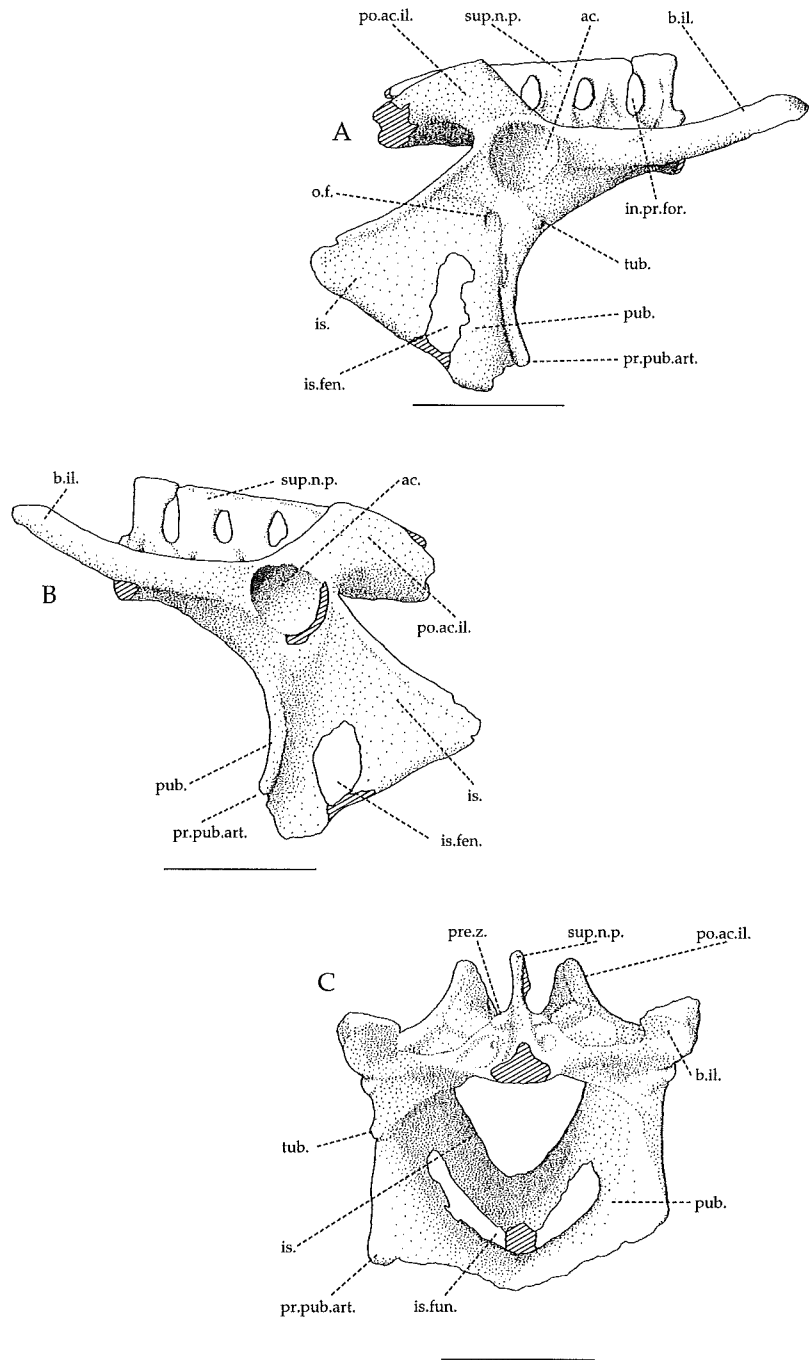
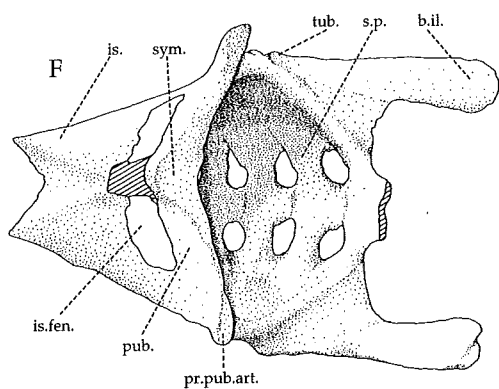
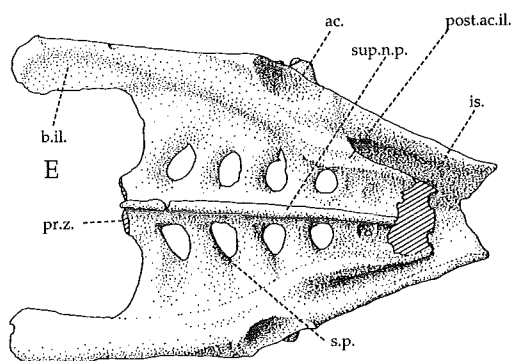
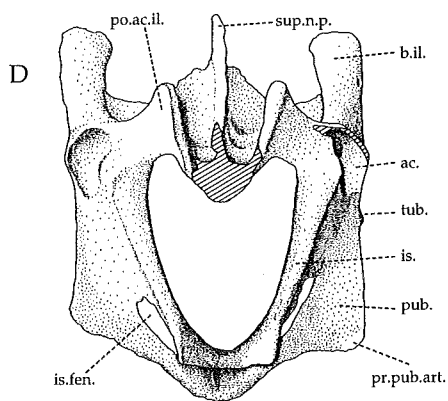


Fig. 10. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the pelvis in various aspects. A: right lateral; B: left lateral; C: anterior; D: posterior; E: dorsal; F: ventral. Scale bar = 50 mm. Drawings by the author.





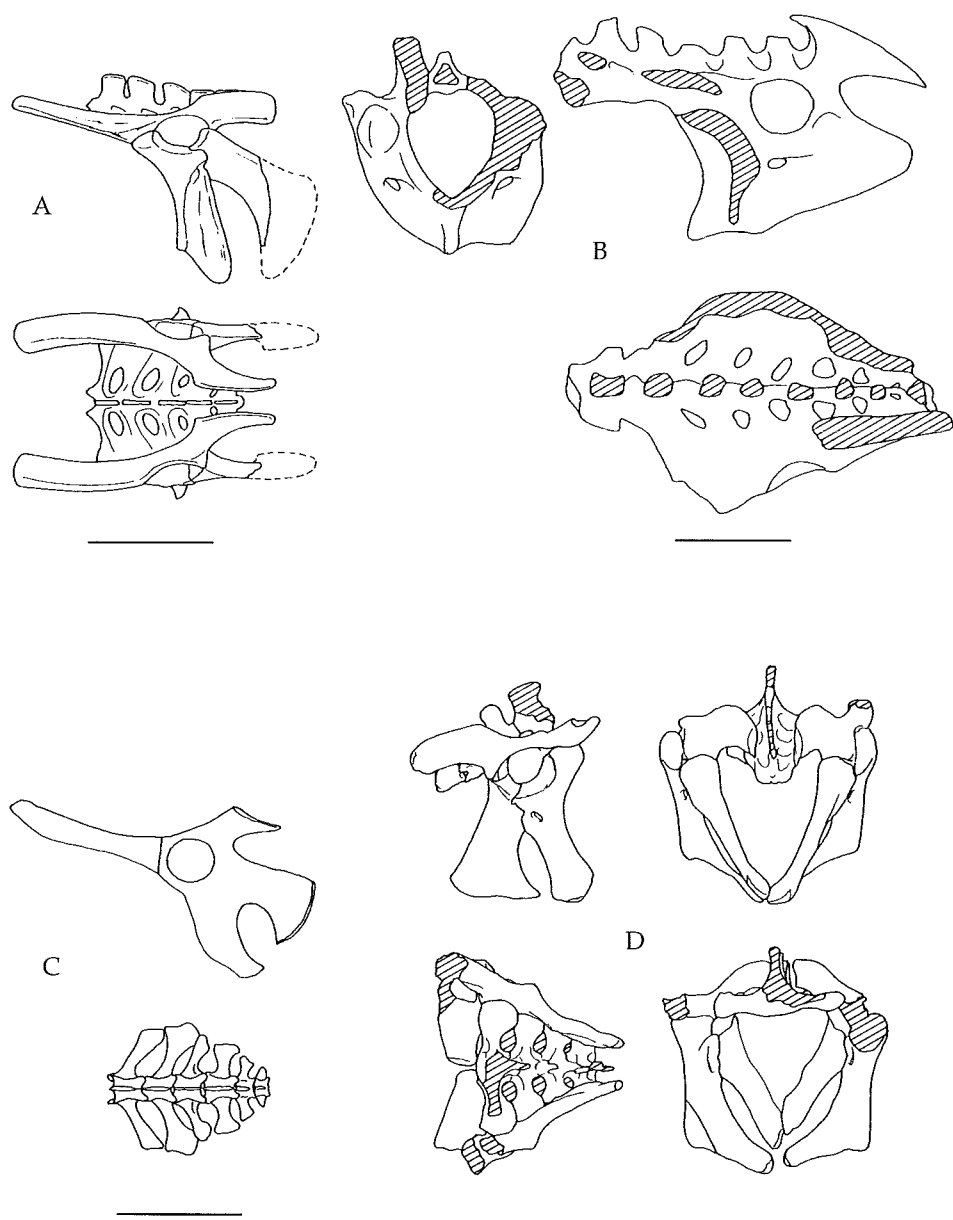


Fig. 11. Pelves of compared pterosaurs in various aspects. A: *An. santanae* (AMNH 22555; after Wellnhofer, 1988, p. 10); B: AMNH 22569 (after Bennett, 1990, p. 81); C: reconstruction of *Ar. conan-doylei* (SMNK 1132 PAL; after Frey & Martill, 1994, p. 393-394); D: *Co. piscator* (NSM-PV 19892; after Kellner & Tomida, 2000, p. 72-73). Scale bar = 50 mm. Drawings by the author.

with their centra and zygapophyses (fig. 10; Pl. 6; Table 11). The vertebrae are sacrals, characterized by the fused neural spines (though the spine of the first is not fused to the others), and the short, broad and fused transverse processes-sacral ribs (s.p.) which are firmly fused to pelvic girdle. It is unclear whether there is a seventh vertebra (caudal vertebra?) due to the damaged state of the posterior part of the synsacrum.

The sacral processes increase in width continuously towards the pelvic girdle. The oval openings between the subsequent processes decrease in size posteriorly. The length, i.e., the transverse measurement, of the processes is largest in the anteriormost of these vertebrae. The length of the processes of the subsequent vertebrae decreases continuously. The first sacral shows both prezygapophyses as well as an incomplete cotyle. The width of the centrum of the first vertebra is largest, whereas the width of the subsequent centra decreases. The dorsal extremities of the neural spines of the last five sacrals are fused with their dorsalmost edges, forming a dorsoventrally small, supraneural plate, with large oval interprocessal foramina (in.pr.for.) between the individual neural spines.

*Comparison* — The neural spines of the different sacrals are not fused in *An. santanae* (AMNH 22555; fig. 11A) (Wellnhofer, 1988, 1991b), but the fusion of the sacral processes with the pelvic girdle is equally complete. The synsacrum in AMNH 22555 consists of five sacrals.

In the partially preserved pterodactyloid pelvis AMNH 22569 (Bennett, 1990) (fig. 11B) the number of fused vertebrae is nine, but only five are sacrals. Though the centra are fused, the neural spines are broken and the presence of a supraneural plate in AMNH 22569 cannot be confirmed.

The unfused state of the sacral processes is one of the obvious differences between the badly preserved synsacrum in *Ar. conandoylei* (fig. 11C) and *Co. spielbergi*, besides the lack of a supraneural plate in the former. Furthermore, the openings between the sacral processes are larger in *Ar. conandoylei*.

*Co. piscator* (fig. 11D) possibly has five sacrals, against six in *Co. spielbergi*. The sacrals of *Co. piscator* are not fused, neither with their centra nor with their spines. The openings between the sacral processes are larger. The transverse size difference between the anterior and posterior vertebrae is comparatively larger relative to *Co. spielbergi*.

## Ribs

Four pieces of cervical rib (Pl. 7A; Table 12) are preserved, of which three still bear, albeit only partly, the proximal articulation areas. The four pieces are identified as a cervical rib because the capitulum has a strong ventral orientation and the rib itself is comparatively broad. The shaft, arched dorsally and caudally, has a strong oval cross section. The area between the capitulum and the tuberculum consists of very thin bone.

A small piece of hollow bone (Pl. 7B), highly oval and bent at one of the sides, is a piece of notarial rib (first right). The bending is orientated towards the proximal articular surface. The bone is broken slightly proximal to the beginning of the bending. Its width is 11 mm and its preserved length 100 mm.

*Comparison* — The pieces of cervical rib are nearly identical to those of *An. santanae* (AMNH 22555) and *Co. piscator*. The notarial ribs are the first one noticed in these pterosaurs, but were reported by Bennett (2001) in *Pteranodon*.

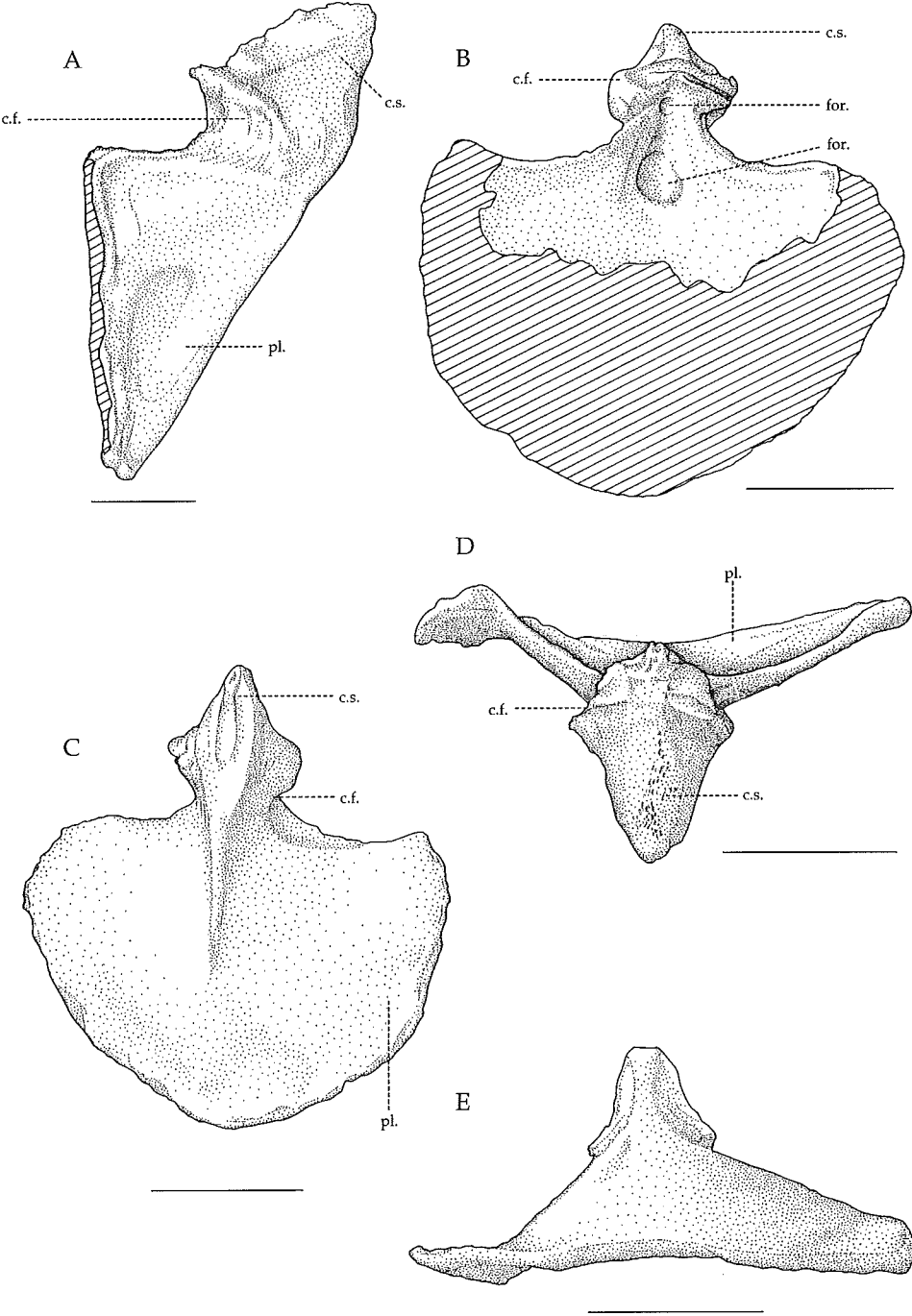


Fig. 12. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sternum in various aspects. A: right lateral; B: dorsal; C: ventral; D: anterior; E: posterior. Scale bar = 50 mm. Drawings by the author.

## Sternum

The sternum consists of a large, strongly developed anteroventral process and a large, thin posterior plate, which is slightly twisted in sagittal plane (fig. 12; Pl. 8; Table 13). The cristospine extends strongly ventrally and anteriorly relative to the posterior plate (pl.). Seen from a lateral position, the anterior part of the cristospine extends more horizontally than the posterior part, starting immediately anteroventrally of the coracoid facet (c.f.). Slightly posterior to this point the cristospine broadens, gaining its largest width halfway its length. The anterior aspect of the spine is orientated posterodorsally. The anteroventral aspect of the cristospine is slightly convex. The laterally sloping, anteroventral part ends at the lateral aspects of the cristospine in slightly swollen ridges. The cristospine is covered with muscle marks, most clearly visible at the anterior aspect.

The left anterior margin extends with a smooth concave curve towards the edge of the posterior plate and the anterolateral corner points anteriorly. The posterior plate is rounded triangular and in contact with the cristospine between the coracoid facets, which are anteriorly buttressed by stout, dorsally extending processes. These processes are separated from the facets by distinct swollen, lateral extending edges. The saddle-shaped coracoid facets are arranged symmetrically at the laterodorsal aspects and are orientated anteroventrally. A small sunken area posteromedial to the coracoid facets has a small foramen. A large foramen that opens into the body of the posterior plate is still partly filled with matrix.

*Comparison* — Although several unpublished sterna are known, only the sternum in *Co. piscator* (fig. 13) has been published, of which the posterior plate is less complete than that described above, although the cristospine is better preserved. The overall measurements in *Co. spielbergi* are larger. The posterior plate in *Co. piscator* is more rectangular instead of rounded triangular. The ventral aspect of the cristospine is flatter in *Co. spielbergi* (against convex in *Co. piscator*), but the ridge at the anterior aspect of the cristospine, extending from left to right and from dorsal to ventral, is more prominent in *Co. piscator*. Furthermore, *Co. spielbergi* lacks the small processes on the

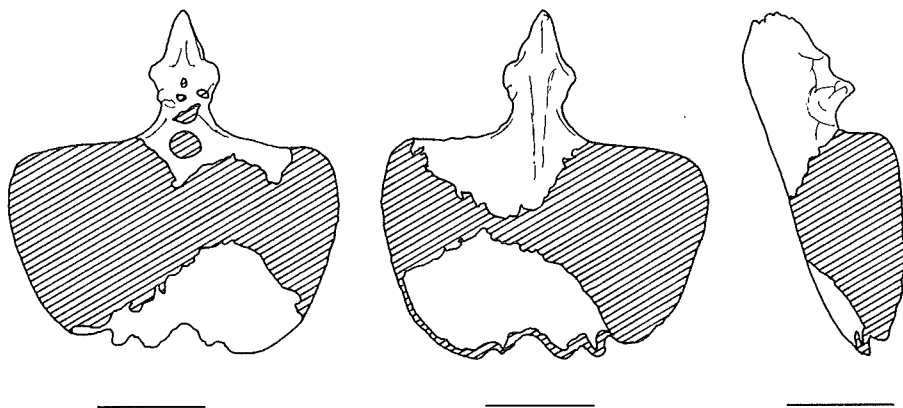


Fig. 13. Sternum of a compared pterosaur in various aspects. *Co. piscator* (NSM-PV 19892; after Kellner & Tomida, 2000, pp. 45, 47, 48). Scale bar = 50 mm. Drawing by the author.

anterior edge of the spine for the attachment of a supposedly cartilaginous extension, visible in *Co. piscator* (Kellner & Tomida, 2000).

Pectoral girdle and forelimb  
(Figs. 14-19; Pls. 9-14; Tables 14-20)

### Scapulocoracoid

The scapula and coracoid are firmly co-ossified and form a scapulocoracoid (Pl. 9; Table 14). The scapula is strong, thick and short, and the coracoid is much thinner and longer. The general morphology is well known and agrees well with previously described specimens (Kellner & Tomida, 2000; Wellnhofer, 1985, 1991b).

*Comparison* — The most important difference between the shoulder girdles in *An. santanae* (BSP 1982 I 91), *An. santanae* (AMNH 22555: fig. 14B) and *Co. spielbergi* is that in the latter it is firmly co-ossified into a scapulocoracoid, whereas it is not co-ossified in the *Anhanguera* species. Similarly, scapula and coracoid in *Co. piscator* (fig. 14C) share the same morphology as *Anhanguera*. However, the glenoid fossa in *Co. spielbergi* is deeper and more pronounced, and the shaft of the scapula is narrower than in the aforementioned taxa. The larger Cretaceous Pterodactyloidea possess a large longitudinal foramen at the posterior aspect of the scapulocoracoid (de Buissonjé, 1980). Wellnhofer (1991b) noticed such a foramen in *S. brasiliensis* (BSP 1987 I 65; fig. 14A). Though such a foramen is also observed at the scapulocoracoid in *Co. spielbergi*, it is a shallow one. The glenoid fossae in *Co. spielbergi* and in *An. santanae* (AMNH 22555) have more prominent overhanging borders than is seen in *S. brasiliensis*, and is more comparable to *Co. piscator*. The process at the anterior aspect of the coracoid is more prominent in *Co. spielbergi* than in *S. brasiliensis* (BSP 1987 I 65) and *Co. piscator*. The supraneural plate articulation in *C. spielbergi* is more circular when compared to the stronger elliptical surface in *S. brasiliensis* (BSP 1987 I 65). The scapular shaft is curved more strongly in *S. brasiliensis*.

The overall size is largest for *Co. spielbergi*. The length of the scapula is 38% of the total length of the scapulocoracoid. Despite the differences in mea-

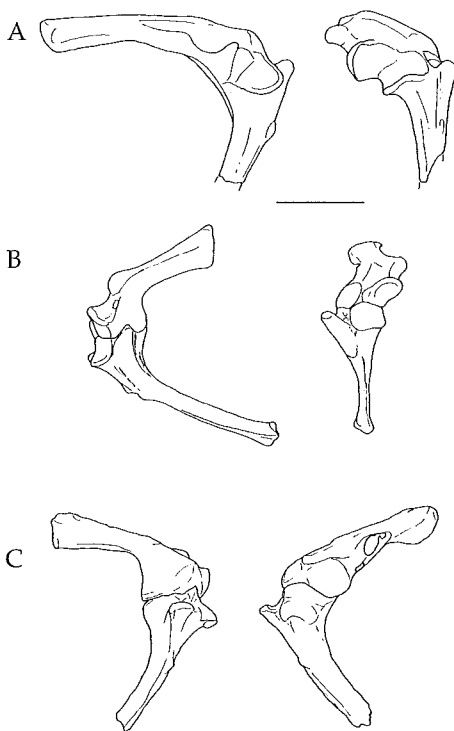


Fig. 14. Scapulocoracoids of compared pterosaurs in various aspects. A: *S. brasiliensis* (BSP 1987 I 65; after Wellnhofer, 1991b, p. 94); B: *An. santanae* (AMNH 22555); C: *Co. piscator* (NSM-PV 19892; after Kellner & Tomida, 2000, p. 50-51).

surements in various Cretaceous Brazilian pterosaurs, this ratio is always between roughly 35 and 40%. Also the length of the coracoid and the length of the scapulocoracoid are, as far as could be calculated, in comparable ratios, but larger than the ratio calculated for the scapula. This suggests that there is little space for variation in the ratios of the shoulder girdle.

## Humerus

The humerus is a part of the post-cranial skeleton that has been commonly described (e.g. Kellner & Tomida, 2000; Veldmeijer, 2002; Wellnhofer, 1985, 1991b) and a detailed description is therefore not presented. It is a comparatively short, but robust bone (fig. 15; Pl. 10; Table 15, 18). It has a convex head, expanded distal end and a large deltopectoral crest.

The head (h.) has a kidney-shaped and convex articular surface, and a feint, shallow ridge separates the concave ventral area from the convex dorsal area. The posterior tuberosity (post.tub.) extends towards the caput. It is a large expansion, relative to the caput itself, but substantially smaller relative to the deltopectoral crest (del.cr.). The transition between the shaft and the tuberosity is fluent but a difference in angle is noticeable between the head and the tuberosity. A large pneumatic foramen is situated at the dorsal aspect and penetrates the bone distally.

Seen from a ventral position, the deltopectoral crest starts as a thin ridge proximally, but develops into a broad plane ventrodistally. The plane of the strongly developed crest is rough and shows large junctures for the attachment of powerful muscles. The deltopectoral crest is slightly turned inwards (i.e., in a proximal direction) and the rim is straight, but the crest is incomplete and damaged at the rim.

In the anteroposterior plane, the extension of the proximal end is stronger than that of the distal end. A scar proximal to the deltopectoral crest at roughly three quarters of the length is identified as the supracondylar process (sup.pr.). Slightly posterior to this process is a second muscle scar, which is less pronounced. The distal aspect is dominated by the large pneumatic foramen, flanked by the capitulum (cap.) anteriorly and by the trochlea (tr.) ventrally.

*Comparison* — The humerus of the Leiden *Coloborhynchus* is the largest to be described. The deltopectoral crest in *Co. spielbergi* extends directly from the head, in contrast to *S. brasiliensis* (M 4894; fig. 16A), in which the extension of the crest starts distal to the humeral head, giving it a constricted appearance.

The most important difference between the humeri of *Co. araripensis* (BSP 1982 I 89; fig. 16B) and *Co. spielbergi* is that the "dünne proximale Rand dieses sehr kräftigen Fortsatzes geht mit konkaver Linie vom Humeruskopf aus" (Wellnhofer, 1985, p. 120). The thicker rim in *Co. spielbergi* does not extend as strongly concave from the head. The straight ventral edge of the deltopectoral crest in *Co. spielbergi* differs from the situation in *Co. araripensis* (BSP 1982 I 89) and *S. pricei* (BSP 1980 I 43, AMNH 22552; figs. 16D, E) (convex), and more closely resembles *S. brasiliensis*. However, the humerus of the Leiden specimen is damaged and little value can be credited to this feature. The middle portion of the deltopectoral crest is not bent inwards, i.e., in posterior direction, as severely as in *S. brasiliensis*. The almost straight ventral margin of the proximal and middle portions of the deltopectoral crest was regarded by Kellner & Tomida

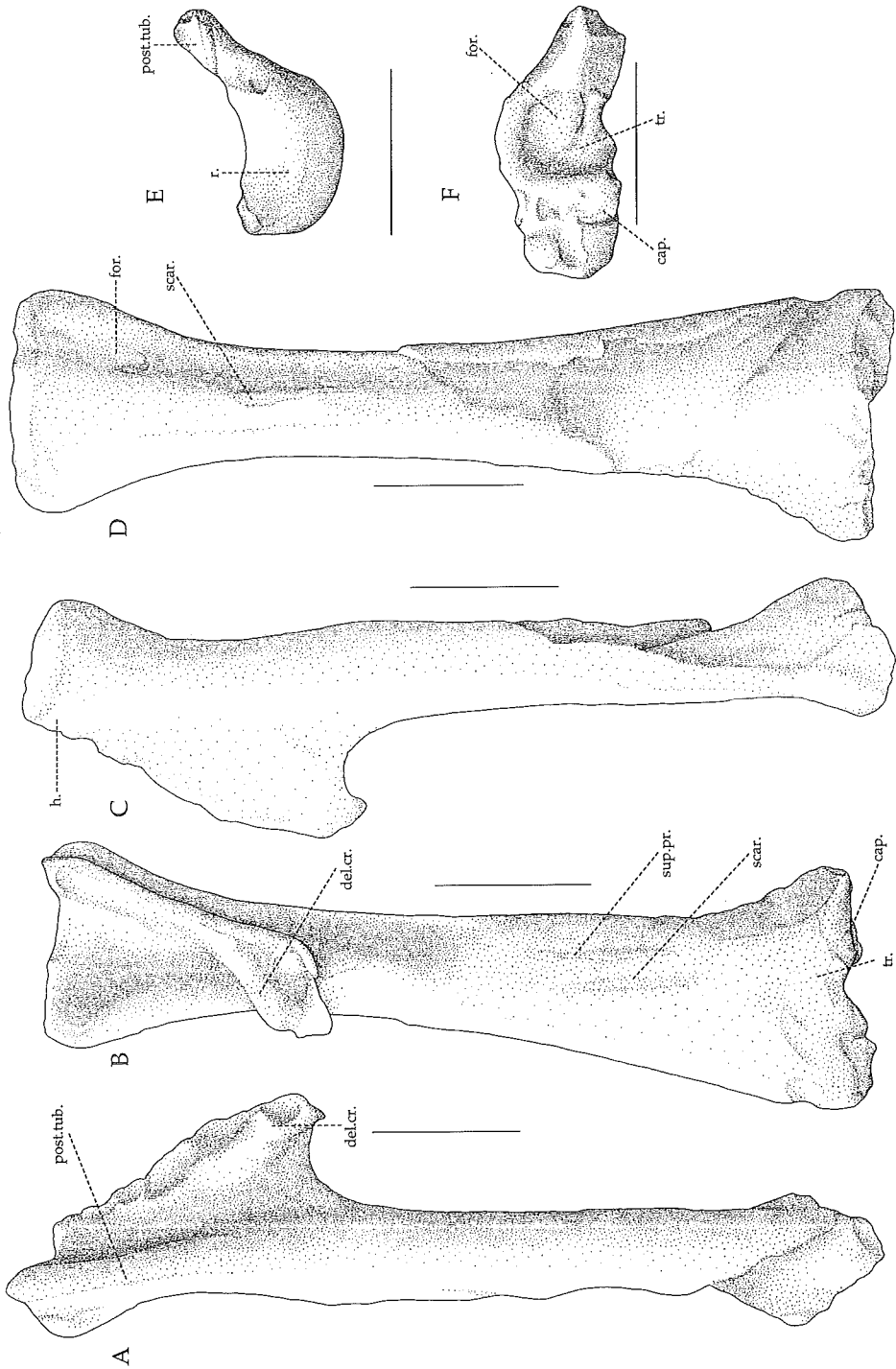


Fig. 15. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the left humerus in various aspects A: posterior; B: ventral; C: anterior; D: dorsal; E: proximal; F: distal. Scale bar = 50 mm. Drawings by the author.



(2000) as a possible apomorphy. The humeral head in *Santanadactylus* has a distinct ridge, which is absent in *Anhanguera*, but poorly defined in the Leiden *Coloborhynchus*. Kellner & Tomida (2000) suggested that this might be an ontogenetic feature developing towards maturity, as opposed to the view of Wellnhofer (1991b), who regarded this as a diagnostic feature in *Santanadactylus*. Due to the reclassification of *S. araripensis* as *Co. araripensis* by Veldmeijer (in review), this feature is seen in *Coloborhynchus* as well. The skeleton of the Leiden specimen displays a high degree of co-ossification and must be regarded as an adult, perhaps an older individual. Thus it is unlikely that the presence of a ridge is ontogenetic because this specimen lacks such a feature. Because of the degree of co-ossification it is suggested that the fusion of the epiphyses occurred very late in the ontogenetic sequence.

One humerus of *An. santanae* (AMNH 225525: fig. 16C) is known. The humeral head is more comparable to that of *Co. spielbergi* than the humerus of *Santanadactylus*; the lack of a distinct ridge is most conspicuous. However, the proximal edge is more strongly concave and the deltopectoral crest is stronger turned inwards (i.e., in a posterior direction). The posterior tuberosity is less strongly developed.

The humerus in *S. pricei* is substantially smaller than that of *Co. spielbergi* and the shaft has a stronger circular cross section. The ratio of the smallest width of the shaft to length of the humerus is slightly higher (13% against 12% in *Co. spielbergi*). The proximal aspect shows a broad and short posterior tuberosity relative to *Co. spielbergi*. The head is set stronger dorsally.

The humerus in *Co. piscator* (fig. 16F) is highly comparable to *Co. spielbergi*. The deltopectoral crest has a strongly concave rim and the crest is more strongly turned inwards.

## Ulna

The ulna is a long and comparatively robust bone (fig. 17; Pl. 11; Tables 16, 18). The shaft is straight and the ends are expanded. It has an elliptical cross section in the anteroposterior plane. No pneumatic foramen is observed, although the places where foramina are often situated (anterior aspect, close to the proximal articulation area) are damaged.

The proximal aspect is dominated by the cotyles, separated from each other by a ridge. Seen from the anterior, the biceps tubercle (b.t.) is strong developed and starts about 50 mm distal to the proximal aspect. It extends towards the trochlear cotyle (tr.cot.) at the proximal aspect. At the opposite side is a large, low protrusion, relative to the tubercle, which is the capitular cotyle (cap.cot.).

Seen from a ventral perspective, at approximately one third from the proximal aspect, a sharp ridge extends to the middle of the length of the bone. It has a smooth surface without roughness. It is tentatively suggested that this is an attachment for interosseus membrane (in.os.mem.) (see Bennett, 2001).

*Comparison* — The ulna is a comparatively featureless bone, which has a low diagnostic value (Veldmeijer, 2002), which is even further limited by the incompleteness of the Leiden specimen. Nevertheless, RGM 401 880 is the longest ulna from Brazil published so far.

The damaged distal end of *Co. spielbergi* hampers a detailed comparison with *Co. araripensis* (BSP 1982 I 89). The cross section of the ulna of *Co. araripensis* is circular.

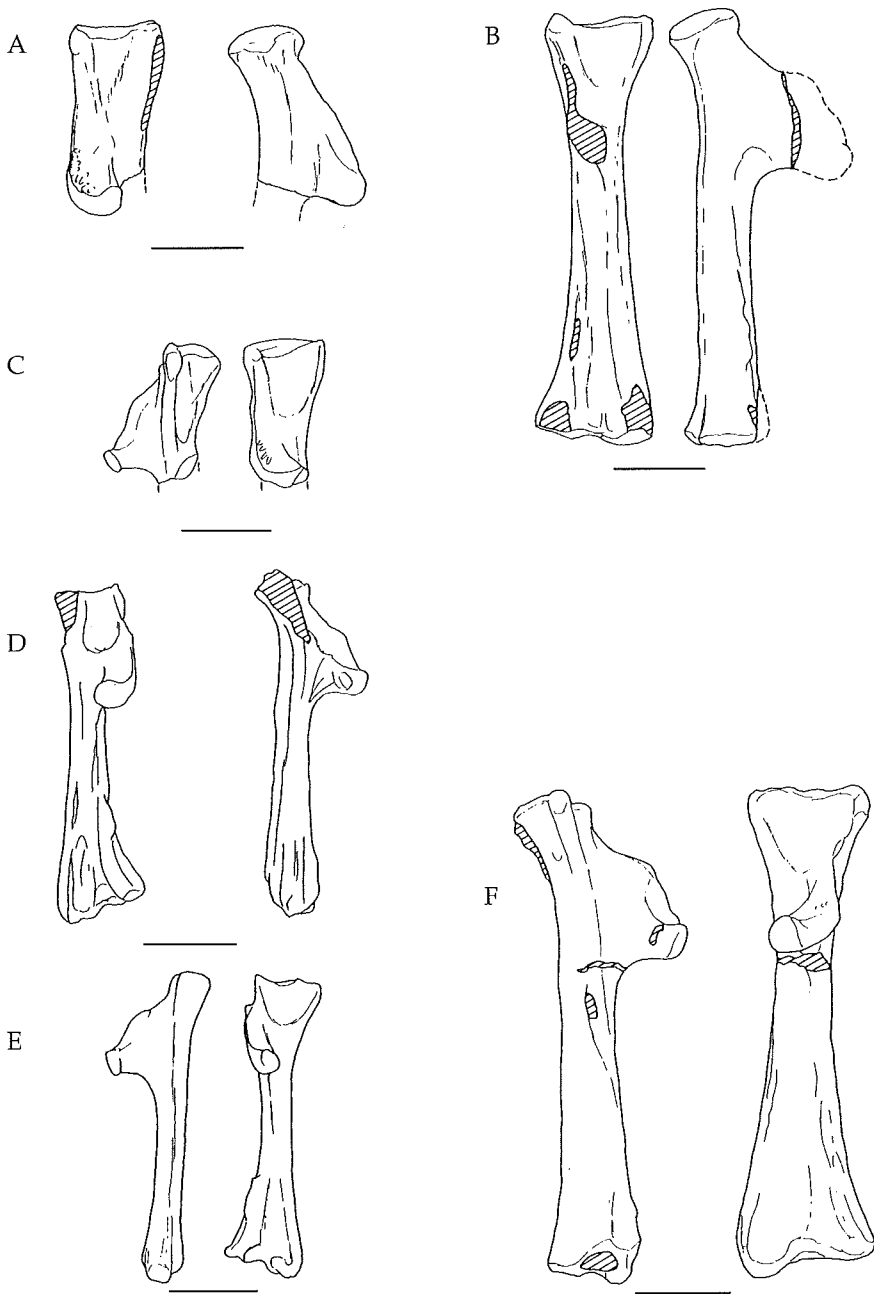


Fig. 16. Humeri of compared pterosaurs in various aspects. A: *S. brasiliensis* (M 4894; after Wellnhofer, 1985, p. 129); B: *Co. araripensis* (BSP 1982 I 89; after Wellnhofer, 1985, p. 121); C: *An. santanae* (AMNH 22555); D: *S. pricei* (BSP 1980 I 43); E: *S. pricei* (AMNH 22552); F: *Co. piscator* (NSM-PV 19892; after Kellner & Tomida, 2000, p. 53). Scale bar = 50 mm. Drawings by E. Enderburg and the author.

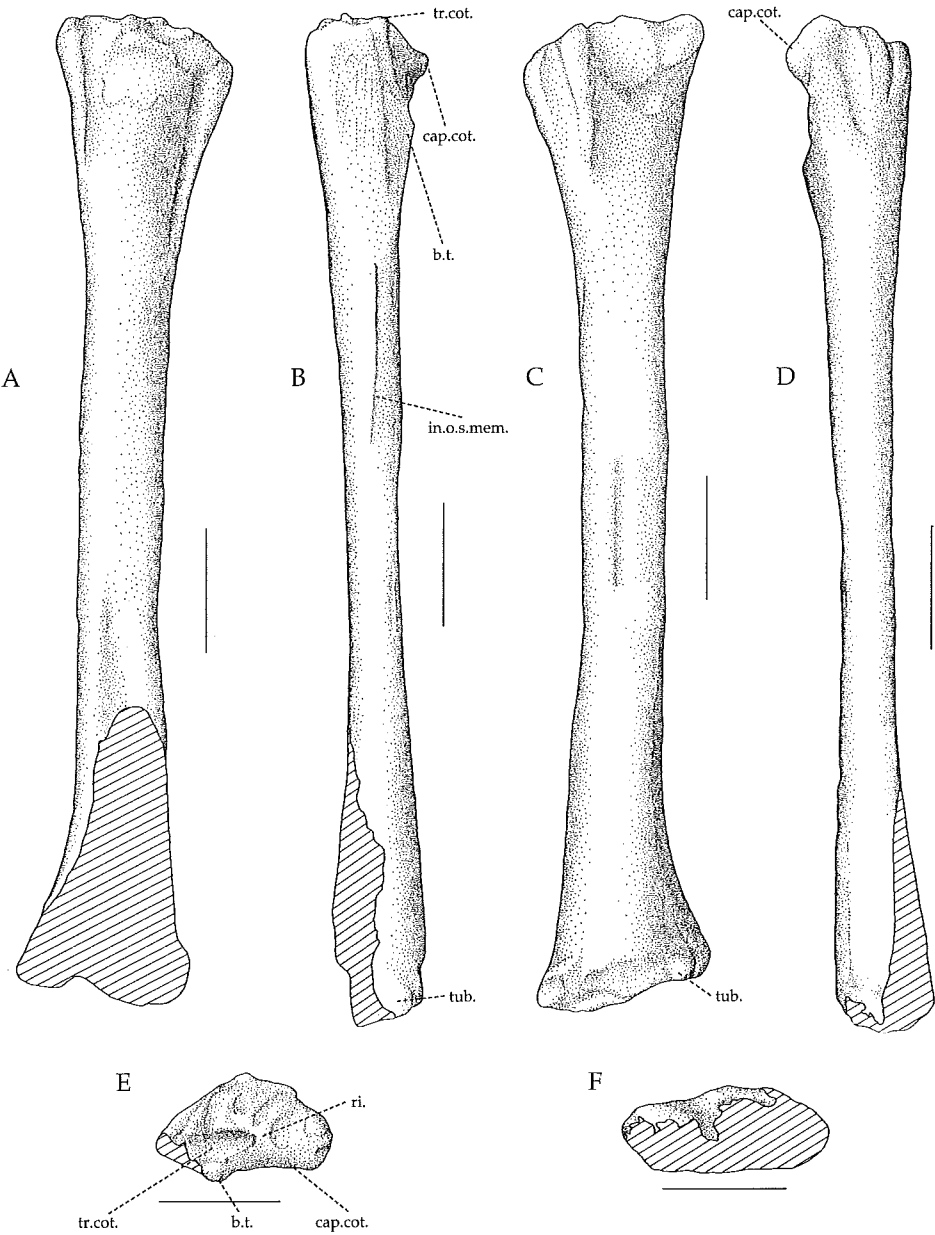


Fig. 17. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the left ulna in various aspects. A: posterior; B: ventral; C: anterior; D: dorsal; E: proximal; F: distal. Scale bar = 50 mm. Drawings by the author.

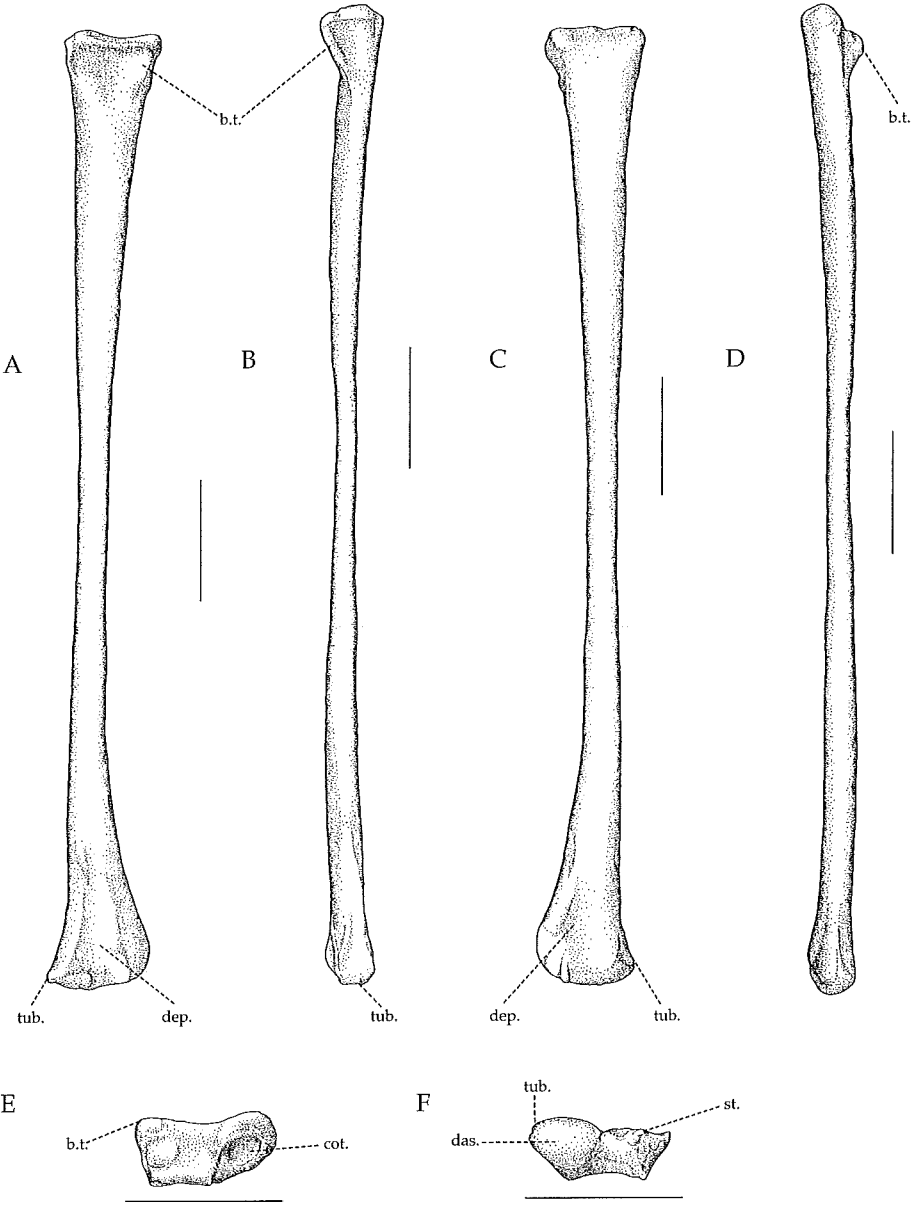


Fig. 18. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the left radius in various aspects A: posterior; B: ventral; C: anterior; D: dorsal; E: proximal; F: distal. Scale bar = 50 mm. Drawings by the author.

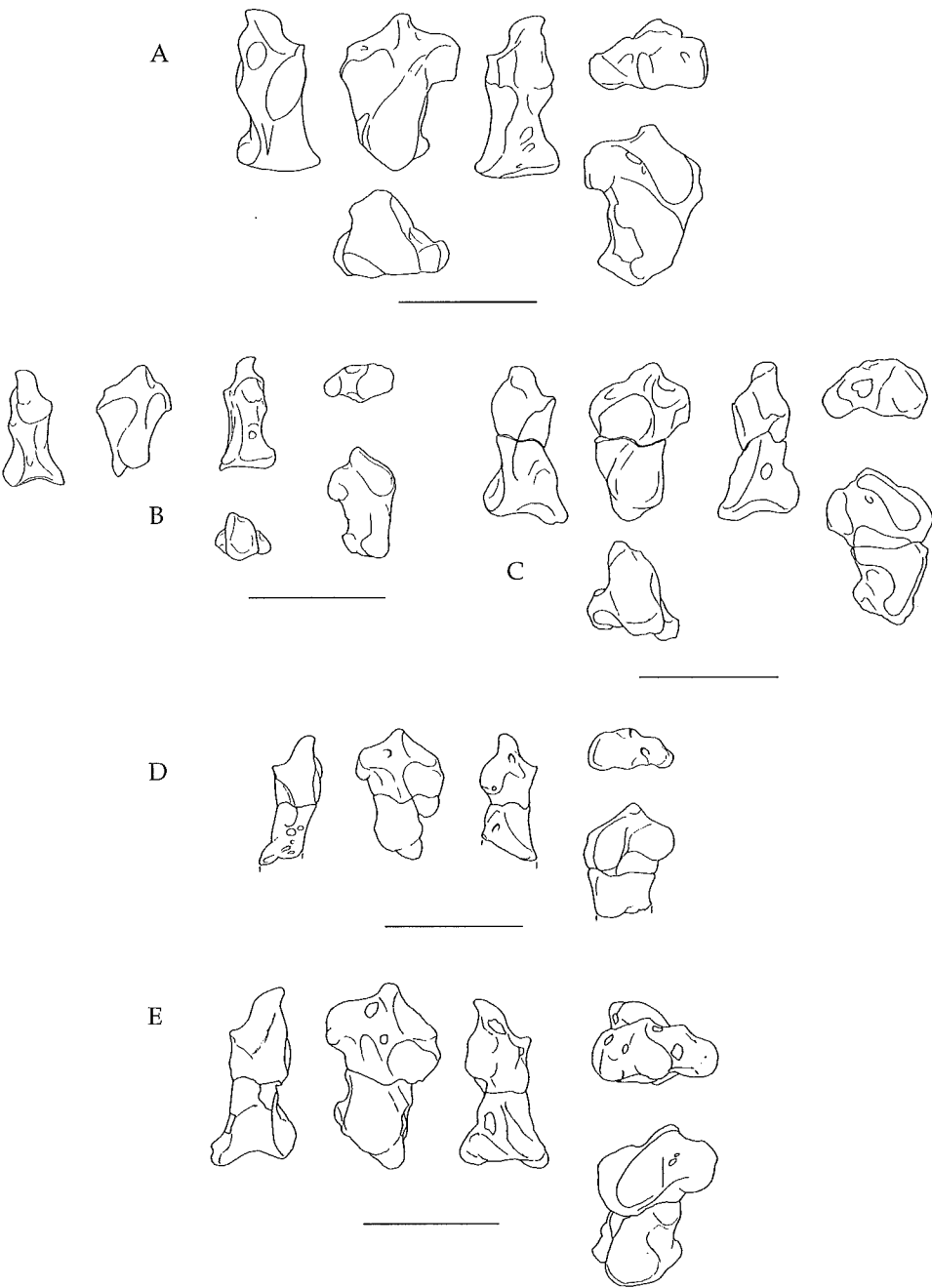


Fig. 19. Proximal syncarpals of compared pterosaurs in various aspect. A: *Co. araripensis* (BSP 1982 I 89; after Wellnhofer, 1985, p. 124); B: *S. pricei* (AMNH 22552); C: *An. santanae* (BSP 1982 I 90; after Wellnhofer, 1985, p. 161); D: *An. santanae* (AMNH 22555); E: *Co. piscator* (NSM-PV 19892; after Kellner & Tomida 2000, p. 59-62). Scale bar = 50 mm. Drawings by the author.

Differences with *S. pricei* are, besides the large size difference (the ulna of *S. pricei* is smaller), that the proximal end in *S. pricei* is less expanded, especially the side of the capitular cotyle. The shaft of the new species is less strongly bent and the cotyles at the proximal aspect are comparatively smaller.

The ulna in *An. santanae* (BSP 1982 I 90) shows a slight backward bending of the proximal end. The shaft has a circular cross section, against elliptical in *Co. spielbergi*.

The ulna in *Co. piscator* is comparable. The "sharp ventral crest on the distal articulation of ulna" (Kellner & Tomida, 2000, p. 7), mentioned as a diagnostic feature, is not depicted and hence no comparison can be done.

### Radius

The general morphology is similar to that of other described radii (Kellner & Tomida, 2000). The radius is the most slender bone of the ulna/radius complex (fig. 18; Pl. 12; Table 17, 18), having a diameter less than half of that of the ulna. The radius is slightly shorter than the ulna and the cross section is strong elliptical. Both ends expand in venterodorsal plane. The radius lies close to the ulna.

*Comparison* — The radius is large relative to the compared specimens. The radii in *Co. araripensis* (BSP 1982 I 89) and *S. pricei* show few differences to each other and *Co. spielbergi*. The biceps tubercle in *Co. spielbergi* is stronger developed and the radius in *S. pricei* is far more circular in cross section. The distal end in *S. pricei* is less expanded. The diameter is about half the diameter of the ulna.

The radius in *An. santanae* (BSP 1982 I 90) is very comparable to *Co. spielbergi*. The stop against bending (st.), however, is far more distinct in *Co. spielbergi*. The diameter in *An. santanae* (AMNH 22555) is larger than half the diameter of the ulna, but the measurements are made more closely to the distal end rather than the middle (= smallest width). The distal articulation surface in *Co. piscator* is less clearly defined and the stop is less pronounced. The ventral expansion is slightly stronger.

The ratio width-length of the radius varies substantially in various pterosaurs, whereas that of the ulnae does not. The biometric comparison of the humerus and ulna/radius of different Brazilian pterosaurs shows that the ratio length humerus to length ulna/radius (of the total length humerus/ulna/radius-complex; Table 18A) is comparable. Only the humerus in *Co. araripensis* (BSP 1982 I 89) is less than 40% of the total length. The different ratios in *Ar. conandoylei* are due to the different measurements of the humerus (Frey & Martill, 1994). More obvious differences are observed in the ratios of the length of the scapula, humerus and ulna/radius relative to the total length of the bones (Table 18B). The relative length of the scapula in *Ar. conandoylei* is shortest. In all but one species, *Co. piscator*, the scapula-humerus occupies about 50% of the total length of the scapula-humerus-ulna/radius, despite differences of the relative length of the scapula.

### Carpus

Carpal bones are robust and commonly preserved. Their general morphology in *Co. spielbergi* agrees with published material (Kellner & Tomida, 2000; Wellnhofer, 1985, 1991b) (Pl. 13; Table 19). In RGM 401 880, the proximal syncarpal is completely co-ossified.

*Comparison* — The proximal syncarpal in *Co. spielbergi* shows more resemblance to *Co. araripensis* (BSP 1982 I 89; fig. 19A) than to the various species of *Anhanguera*. In both *Co. spielbergi* and *Co. araripensis* the carpals are firmly fused.

The only preserved proximal syncarpal in a *Santanadactylus* is in *S. pricei* (AMNH 22552; fig. 19B). The articular facet with the radius is responsible for an extension dorsal to the ulnar tubercle. Consequently, the tubercle is situated more strongly ventrally relative to *Co. spielbergi*. Furthermore, seen from a distal perspective, the syncarpal becomes distinct smaller in a ventral direction. Although this is also visible in *Co. spielbergi*, it is less strongly developed. The overall size of the syncarpal in *S. pricei* is smaller.

The syncarpal is not completely fused in *An. santanae* (figs. 19C, D) and *Co. piscator* (fig. 19E). The syncarpal is comparable with *An. santanae* although the articular facet for the ulna is more clearly defined in *Co. spielbergi* and *An. santanae* (BSP 1982 I 89), than in *An. santanae* (AMNH 22555).

#### ?Metacarpals, phalanges and unguals

Two bones lie close to each other; as preserved the smaller one is one third of the length of the larger one (Pl. 14; Table 20). This larger bone fragment is straight and circular in shape. These two bones may be the first and third metacarpalia (cf. Wellnhofer, 1991b). Between the two fragments are traces of another bone, now lost, interpreted as the second metacarpal. Another piece of bone, though not illustrated, is attached at the reverse of the matrix. Its inner side reveals the trabecular system.

A small complete bone is identified as the third phalanx of the third digit, based on the comparison with *S. pricei* (AMNH 22552). A small piece of the second phalanx still contact the proximal end. The bone has a slender shaft, but broadens rapidly towards the proximal and distal ends. The proximal end is the more strongly developed. The shaft has a rounded square cross section. Seen from a distal perspective, a shallow groove continues onto the anterior aspect.

None of the claws can be assigned with certainty to a digit, which are not preserved. The curvature of the smallest claw is the strongest. A groove on both sides of the claw separates the flexor tubercles from the body. The flexor tubercles are comparatively shallow and most strongly developed in the smallest claw.

#### Pelvic girdle and hind limb

(Figs. 10, 20-21; Pls. 6, 15-16; Tables 11, 21-22)

#### Pelvic girdle

The anterior blade of the ilium (b.il.) is long (half the length in sagittal plane) and extends anteriorly with a curvature in a dorsal direction (fig. 10; Pl. 6; Table 11). Posteriorly, it tapers, reaching its smallest width at the articulation with the synsacrum. The blade is triangular in cross section of which the dorsal line declines medially with a slight concave course. The postacetabular process (po.ac.il.) develops dorsal to the anterior rim of the acetabulum (ac.), extends posteromedially-anterolaterally and reaches the highest point posterodorsal to the acetabulum. The dorsal border is convex. Ventrally, the postacetabular process is thickened posterodorsal to the acetabulum, where the ilium meets the ischium (is.). Sutures cannot be identified, but the

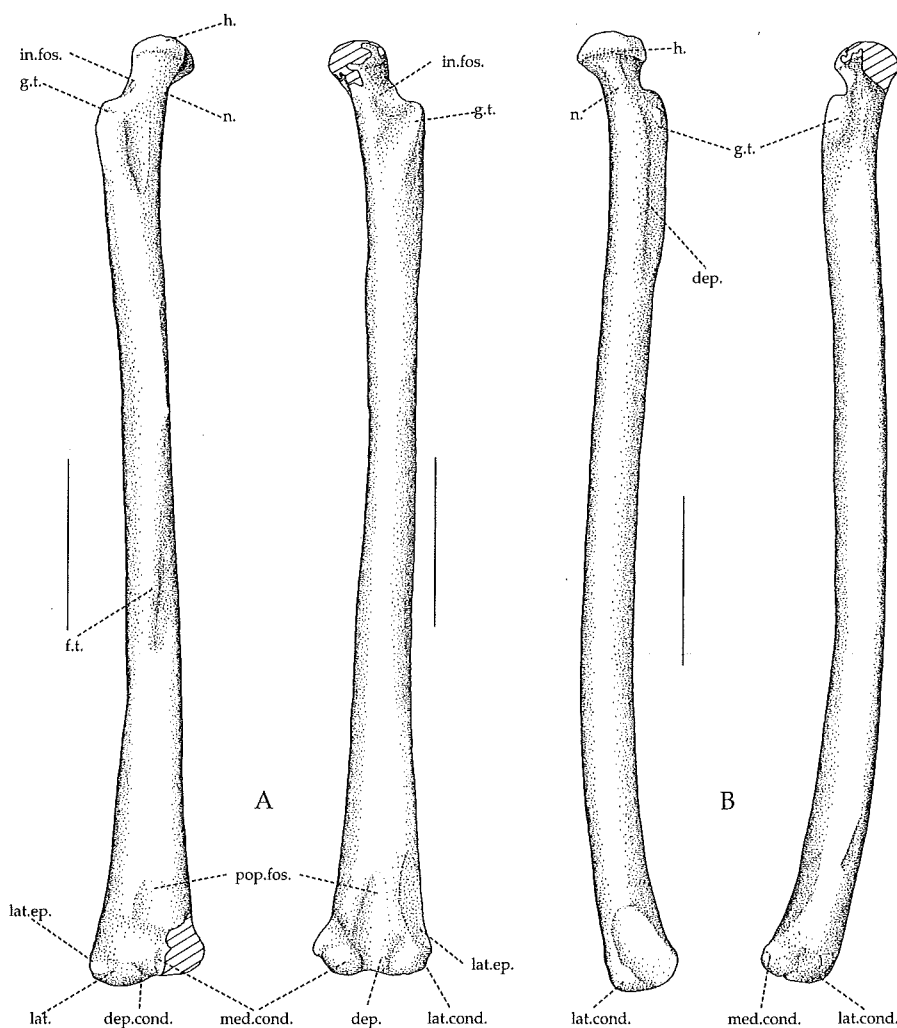
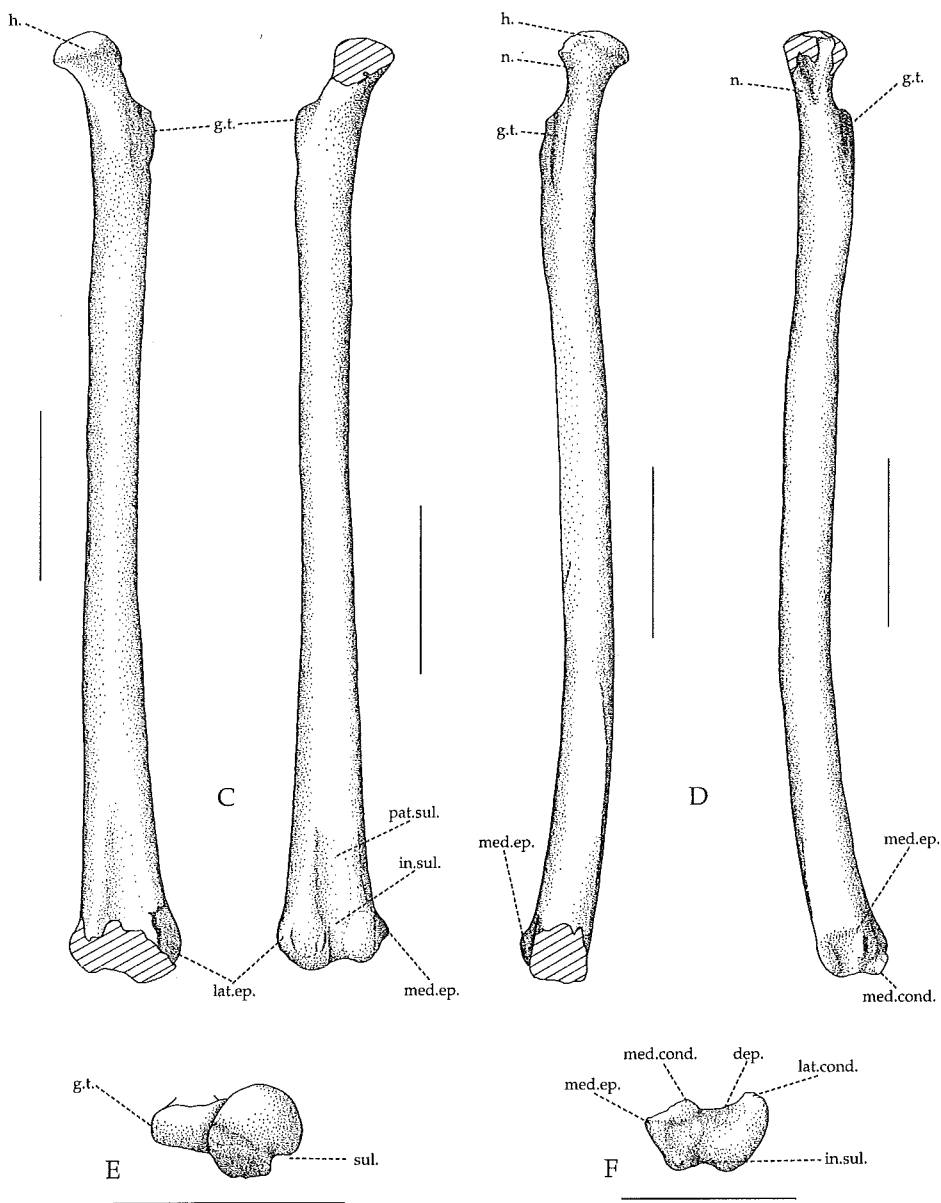


Fig. 20. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the femora in various aspects (left and right respectively). A: posterior; B: lateral; C: anterior; D: medial; E: proximal (left); F: distal (right). (Note that the proximal aspect of the right femur and the distal aspect of the left femur are not shown because these aspects are reconstructed.) Scale bar = 50 mm. Drawings by the author.

vaguely swollen line indicates that the ilium forms the dorsal half of the acetabulum.

The pubis (pub.) and ischium form the posterolateral and posterior aspects of the pelvis. The pubis extends from the area anteroventral to the acetabulum, the united sacral rib and transverse process, in a concave line in posteroventral direction. The pubis has a small, distinct tubercle ventral to the acetabulum. The dorsal part of the pubis forms the anteroventral part of the acetabulum. The obturator foramen (o.f.) is located





posteroventrally to the acetabulum in a slightly depressed area, which is created by the medial orientation of the posterior part of the pubis. The ventral aspect of the pubis, the articulation area for the prepubes, ends 55 mm ventral to the centrum of the acetabulum.

The ischium and pubis are partially fused and separated by an opening, the ischiopubic fenestra (is.fen.). Part of the suture between the ischium and pubis is visible posterodorsally and anteroventrally to the obturator foramen. No suture is visible

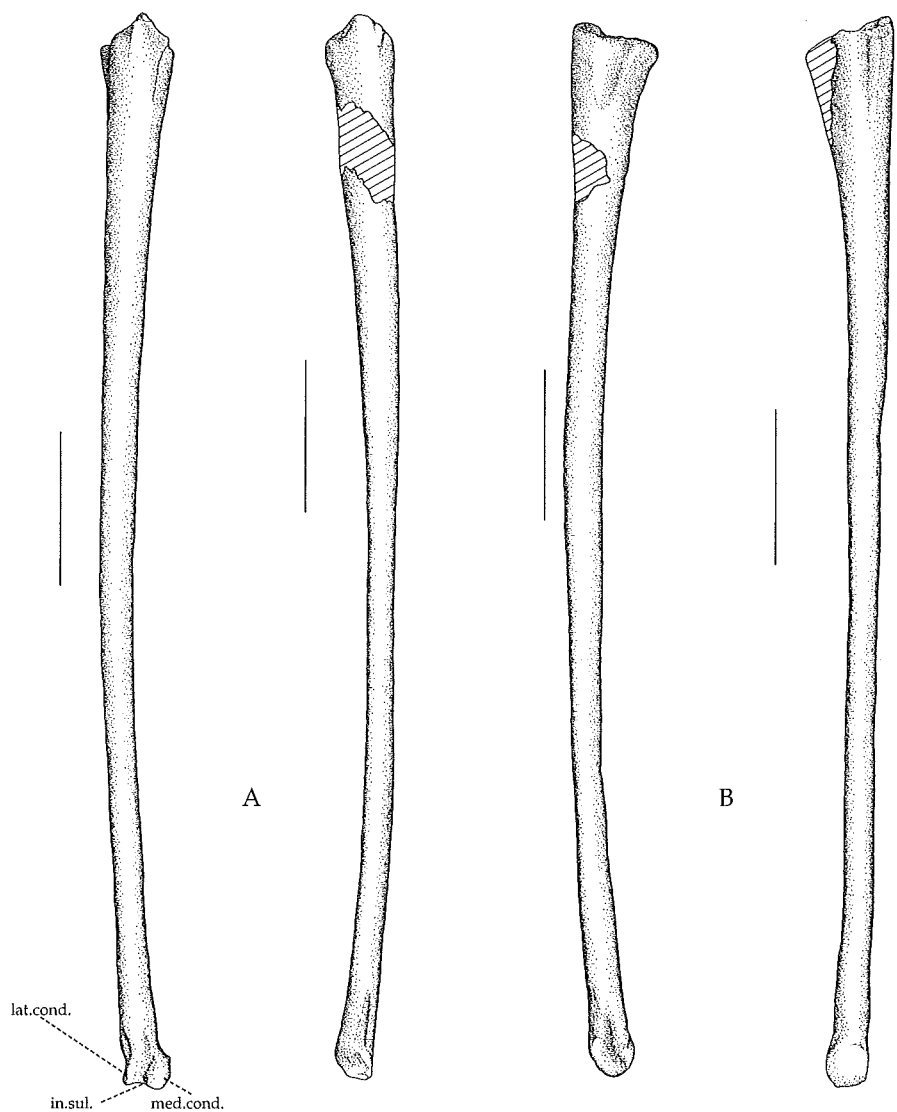
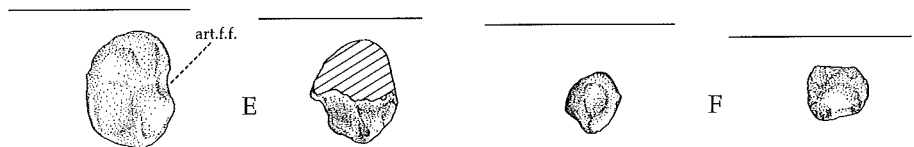
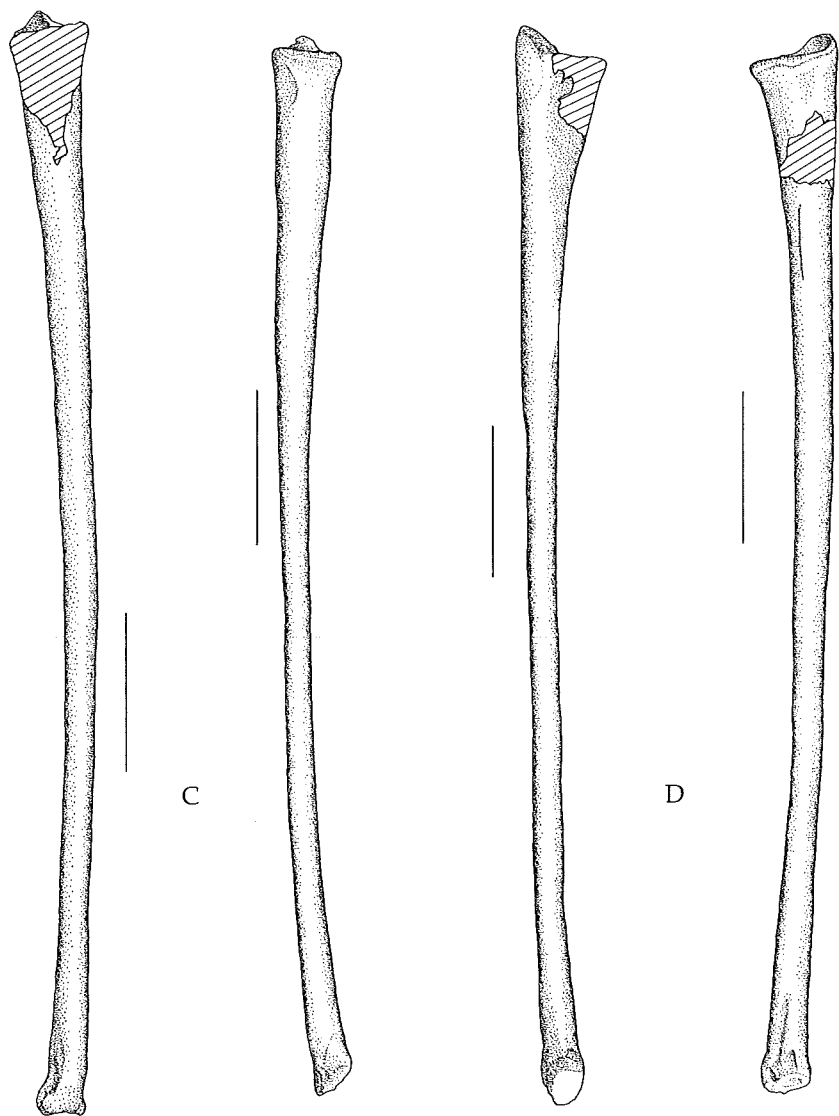


Fig. 21. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the tibiae in various aspects (left and right respectively). A: posterior; B: lateral; C: anterior; D: medial; E: proximal (left); F: distal (right). Scale bar = 50 mm. Drawings by the author.



in the acetabulum itself, but the swollen line indicates that the posteroventral part of the acetabulum consists of the ischium. The left and right ischia close the pelvis posteroventrally and establish a strong symphysis (sym.). The ischia taper posteroventrally, making a stronger angle than the two pubes, which close the pelvis ventrally. The ischial symphysis is V-shaped (anteroventrally) and forms a flat surface.

*Comparison* — Four pterosaur pelvises have been described from the Santana Formation. For a comparison between the pelvises of *Ar. conandoylei*, *An. santanae* (AMNH 22555) and AMNH 22569, see also Frey & Martill (1994). The pelvis of RGM 401 880 is larger relative to the compared specimens.

There are several distinct differences between the pelvis in *An. santanae* (AMNH 22555; fig. 11A) and *Co. spielbergi*. The ventral connection of the left and right pubis of the pelvis is not seen in *An. santanae*. The ischium and pubis in *Co. spielbergi* form an ischiopubic plate, also seen in AMNH 22569 (fig. 11B) and *Ar. conandoylei* (fig. 11C). The anterior blade of the ilium inclines more strongly medially in *An. santanae*.

Seen from a dorsal perspective, the reconstructed anterior blade of the ilium extends more strongly medially. The pelvis does not show an ischiopubic fenestra. It remains uncertain, despite the reconstructions of Bennett (1990) based on *Pteranodon* and of Frey & Martill (1994), whether the neural spines were fused into a supraneural plate. The "striking resemblance" observed by Bennett (1990, p. 81) between the Santana pelvis AMNH 22569 and that of *Pteranodon* (cf. Eaton, 1903, 1910) let Bennett to conclude that pelvises are non-diagnostic but this is likely a premature conclusion (cf. Frey & Martill, 1994). However, the pelvis AMNH 22569 is far more *Pteranodon*-like than any of the other pelvises.

The unfused state of the pelvis in *Co. piscator* (fig. 11D) is in contrast with the firmly fused condition in *Co. spielbergi*. Furthermore, the ventral symphysis of the left and right pubis is not seen in *Co. piscator*, as is the ventral symphysis of the left and right ischium. The anterior border of the postacetabular process extends more strongly ventrally, which results in a flatter course of the ilium. Although Kellner & Tomida (2000) did not present measurements of the pelvis, it could be deduced from the illustration that the overall size of *Co. piscator* is smaller.

## Femur

The femur is a short, relative to the ulna/radius, and slender bone, which is slightly bent (fig. 20; Pl. 15; Table 21). The head is separated from the shaft by a constricted neck.

The constricted neck (n.) extends into the greater trochanter (g.t.) at the lateral aspect of the femur. The proximal aspect of the strongly developed trochanter is slender relative to the femoral neck and shaft. Distally it widens to fuse with the shaft at 50 mm, measured from the proximal edge of the greater trochanter. The trochanter is flanked at the posterolateral and anteromedial aspects by distinct, shallow grooves. The depression between the head and the trochanter is identified as an intertrochanteric fossa (in.fos.). Approximately in the centre, at the posterior aspect, is the fourth trochanter (f.t.) consisting of a well-defined groove.

The lateral (lat.cond.) and medial (med.cond.) condyles are rounded protrusions at the distal end and posterior aspect. They are separated by a distinct intercondylar sulcus. The medial condyle is slightly more bulbous relative to the lateral condyle and extends further posterodistally. Small tubercles are situated laterodorsally to the later-

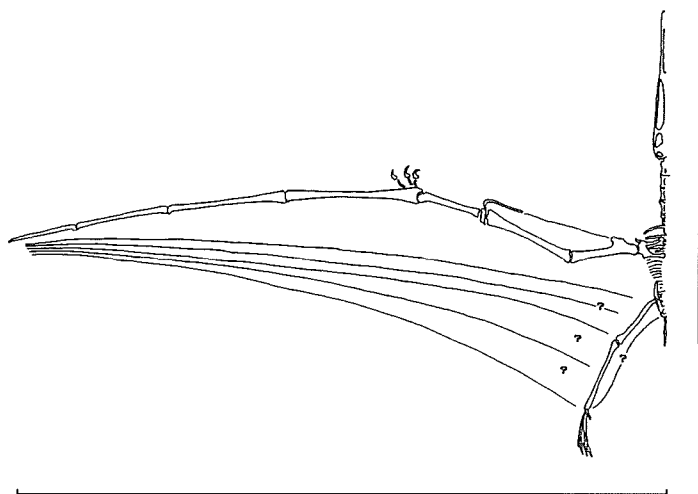


Fig. 22. The skeleton on scale as calculated. Drawing by the author.

al condyle (lat.ep.) and mediodorsally to the medial condyle (med.ep.). Seen from a posterior perspective, the epicondyles are separated by a large, but shallow, oval depression (pop.fos.) relative to the length of the condyles.

Seen from an anterior perspective, the patellar sulcus (pat.sul.) at the distal end is shallow compared to the more distally situated intercondylar sulcus (in.sul.). The lateral side of this sulcus is well defined.

*Comparison* — Femora of pterosaurs are not often reported, but a detailed description was provided by Kellner & Tomida (2000) with which the general morphology compares well. The femur in *Co. piscator* is shorter than that of *Co. spielbergi*. The sulcus at the head is deeper and longer in *Co. spielbergi*, and the patellar sulcus and popliteal sulcus are more distinct, as well as the features at the distal aspect.

#### Tibia

The tibia is more slender than the femur and slightly bent (fig. 21; Pl. 16; Table 22). The damaged distal end expands posteriorly and laterally. The lateral expansion is stronger relative to the posterior expansion. The lateral and medial condyles are separated by a gentle intercondylar sulcus.

*Comparison* — Tibiae are seldom preserved and the described tibiae of *Co. piscator* are the only ones from Brazil. The general morphology is however, highly comparable. The tibia of *Co. piscator* is shorter and the tuberosity at the posterior end lacks in *Co. spielbergi*.

### Discussion and conclusion

The Leiden pterosaur is not classified as *Criorhynchus* ("*Cr. mesembrinus*") because of the lack of expansion, the different configuration of the anterior aspect, the difference in

mandibular groove and the different dentition pattern. The most obvious difference between *Co. spielbergi* and *Brasileodactylus* are the lack of crests, the different mandibular groove and the anterior expansion. *Cearadactylus* differs because of the lack of crests and the differences in tooth-bearing parts. *Santanadactylus* differs in size and in having a distinct ridge at the humeral head. Comparison with *Ar. conandoylei* shows the size difference to be considerable and there are distinct differences in pelvii. *Coloborhynchus spielbergi* differs from *Anhanguera* mainly because of the morphology of the anterior part of the skull (blunt anterior aspect with teeth protruding and crest starting at the anterior aspect) and the configuration of the mandibular groove (the groove in *Anhanguera* is flanked by small ridges, in contrast to *Coloborhynchus*). Furthermore, the maxillae are slightly raised relative to the ventral aspect, in contrast to *Anhanguera* where this is distinct. The specimen (RGM 401 880) in the National Museum of Natural History, Leiden, the Netherlands, is regarded as *Coloborhynchus* because all the diagnostic features of the type genus are apparant (but see below). It is considered to be a new species, differing from *Co. clavirostris*, *Co. robustus*, *Co. araripensis* and *Co. piscator* in having markedly weaker (almost absent) mandibular groove and palatal ridge. The mandibular groove does not extend onto the anterior expansion as seen in *Co. robustus*. The rami in *Co. spielbergi* are distinctly bent. It is not clear if *Co. spielbergi* has a pterygoid process as seen in *Co. araripensis* due to the incompleteness of the palatal region in the RGM specimen. *Coloborhynchus spielbergi* and *Co. piscator* (the latter surely not fully grown but the largest known specimen) differ in size and morphology of the sterna. Furthermore, the dentition of the lower jaw in *Co. piscator* (the anterior eighth) is larger than the dentition of the skull. This, however, might be due to its ontogenetic state.

A detailed review of the Brazilian and Cambridge Greensand pterosaurs is beyond the scope of the present work. However, the following remarks on Brazilian pterosaurs are made in the light of the systematic classification of the present pterosaur and the new insights gained from its study.

According to Wellnhofer (1978), morphology of the sternum is diagnostic at the generic level. Because *Co. piscator* is a species of *Coloborhynchus* (see below), and the sternum of *Co. spielbergi* differs from that of *Co. piscator*, it is regarded as diagnostic at the species level.

Although post-cranial material is known to have a limited diagnostic value, humeri are often used to differentiate between pterosaurs, but their diagnostic value appears to be more limited than previously thought. Minor differences, as for instance the thickness of the proximal edge of the deltopectoral crest and its inward (i.e., posterior direction) orientation, might be explained as individual variation (see also Veldmeijer, 2002).

The diagnosis of the type specimen of *Coloborhynchus* needs reviewing. The depression at the anterior aspect is not seen in *Co. araripensis* (Veldmeijer, in review). Differences between *Anhanguera* and *Coloborhynchus* are limited. The expansion in *Coloborhynchus* is robust, but in *Anhanguera* is slight. The premaxillary crest in fully-grown specimens of *Anhanguera* starts distinct posterior to the tip of the snout and extends to the anterior border of the nasoantorbital fenestra. The tip of the snout is dorsoventrally compressed, leaving no space for teeth anteriorly. Only one species can be definitely assigned to *Anhanguera* (*An. blittersdorffi*), whereas *An. santanae* might be an immature stage of *Coloborhynchus* (see below).

All known species hitherto assigned to *Anhanguera* display an unfused state of the

skeleton (see below) except *An. blittersdorffi* (Campos & Kellner, 1985b), which is only represented by cranial material. Possibly, the skull was first to fuse completely and perhaps early in the ontogeny of pterodactyloids (Kellner & Tomida, 2000). This makes it uncertain whether *An. blittersdorffi* was an adult with a completely fused skeleton, as seen in *Co. spielbergi*, or close to adulthood with still unfused post-cranial parts.

The lack of a notarium in *An. santanae* (AMNH 22555) was explained thus by Wellnhofer (1991b, p. 58): "Allerdings ist eine Tendenz hierzu [co-ossification of the first five dorsals] erkennbar, so daß nicht auszuschließen ist, daß bei weiterem Wachstum bzw. höherem Lebensalter des Individuums eine Verschmelzung dieser Wirbel eingetreten wäre." The holotype and another specimen of *An. santanae* (BSP 1982 I 90 and 1982 I 91) and the described specimen of *Co. piscator* (Kellner & Tomida, 2000) all lack a co-ossified notarium. Further, the carpals of these specimens are unfused and in *Co. piscator* most bones are unfused throughout the skeleton; it is consequently regarded as juvenile (Kellner & Tomida, 2000). However, Wellnhofer (1985) initially used the incomplete fusion as a diagnostic feature for *Anhanguera* although he later regarded this feature as "ontogenetisch sehr spät einsetzenden Koossifizierung [...]" (Wellnhofer, 1991b, p. 99). It is generally accepted that incomplete fusion is ontogenetic rather than diagnostic, although the diagnosis of *Ar. conandoylei* is based for the major part on the degree of fusion (Frey & Martill, 1994). Kellner & Tomida (2000) pointed out that these features are possibly ontogenetic. The number of fossilized juvenile pterosaurs is large, perhaps even more specimens than adult animals. Apparently, being adult did not mean that the animal already had a completely co-ossified skeleton - should we speak, instead, of fully-grown or not?

Bennett (1993, 1994) regarded *Anhanguera* as sub-adults of *Co. araripensis* on the basis of the unfused elements. Although *An. santanae* is represented by non-adult specimens, *An. blittersdorffi* is regarded as adult (but see above) and can therefore not be seen as a sub-adult of *Co. araripensis*.

The comparison of *Anhanguera* and *Co. spielbergi* shows, besides the difference in degree of co-ossification, few distinct differences apart from the shape and position of the premaxillary sagittal crest. It is possible that, in aging, bone accumulated on the crest, especially anteriorly. This would explain the more posterior start of the crest in many specimens. In these specimens then, the bone did not accumulate at that point because the animal was not yet full-grown. This might also explain the concavity at the anterodorsal border of many of the crests. If the animal accumulated bone at the crest during the growing process, this might result in: larger crests as the animal gets closer to being fully grown, that is, the older it gets; a crest that, when the animal stopped growing, starts at the anteriormost aspect of the skull; and a flat anterior aspect from which teeth could possibly protrude, only seen in full grown animals and already in the not fully grown *Co. piscator*.

The first prediction is confirmed by *Co. spielbergi*, a fully-grown animal, of which the premaxillary crest is largest (in percent of the length of the cranium) relative to the compared *Anhanguera* species. The second prediction is supported by differences in the position of the crests. The premaxillary crest in *An. santanae* (AMNH 22555) starts substantially posterior to the anterior aspect of the skull. The crest in another specimen, SMNK 1136 PAL, referred to by Frey & Martill (1994) as *Anhanguera* sp. has a crest that starts far more anteriorly relative to *An. santanae* (AMNH 22555).

However, it does not start at the anteriormost edge of the skull as seen in the *Coloborhynchus* sp. The third prediction is supported by the two front teeth in *Anhanguera*, which often are already positioned dorsal to the imaginary line made by the rest of the teeth. This is apparent in *An. santanae* (AMNH 22555). It would take only slight alterations to create an anterior aspect as seen in *Coloborhynchus*. The anterior aspect in *Co. piscator* displays a high degree of similarity with *Co. robustus* (SMNK 2302 PAL). The dorsal margin therefore cannot be used as diagnostic feature, but might be ontogenetic.

Unfortunately, Kellner & Tomida (2000, p. 15) did not describe or illustrate the "texture of the bone surface" of the crests. However, there is no reason to believe that the crests were formerly covered with horny sheets as suggested by Kellner & Tomida (2000) nor extended with wattle-like structures. No trace of the supposed horny sheets is preserved despite the abundant records of the preservation of soft tissue from the Araripe basin. The crests display strong, well defined edges, in contrast to the crests of the skulls of those pterosaurs which did have soft tissue wattle-like extensions, like the Tapejaridae indet. in the collection of the Staatliches Museum für Naturkunde at Karlsruhe (Frey & Tischlinger, 2000; pers.obs.; Frey, pers. com.). Finally, no area of attachment can be detected at the crest. Suggestions for the texture of the surface, as described for the crests in *Co. spielbergi* (Pl. 2G), vary from copies of the internal trabecular system to the internal surface of the bony crests (Wellnhofer, pers. comm., on the basis of photographs) to the internal surface of very thin bone in which the outside, few tens of microns, has flaked away during preparation (Martill, pers. com., on the basis of photographs), rather than scars for the anchoring of sheets or soft tissue material. Mader & Kellner (1999) observed rugosities, meandering striations and shallow pits on the anterior part of the cranium of *Sirocopteryx moroccensis*. The description prohibits a comparison with the, in the present work described, condition. However, it seems not unlikely that the features are the same. Mader & Kellner (1999) interpreted the features as pathologic.

If we accept the theory on the creation of crests as a working hypothesis, it is tentatively suggested that the immature *An. santanae* might be young stages of *Coloborhynchus*, rather than *Santanadactylus* as suggested by Bennett (1993). The skull in *An. santanae* (BSP 1982 I 90) shows the posterior start of a crest. Because the anterior extension is not known, the crest cannot be used as diagnostic feature and the generic classification, as either *Anhanguera* or *Coloborhynchus*, is uncertain. Comparison of this specimen with *An. santanae* (AMNH 22555) shows some striking differences. The quadrate in AMNH 22555 is robuster, the lower temporal fenestra smaller, the nasal longer and wider, and the prefrontal extends less far posteriorly. The straight posteroventral back of the skull in *An. santanae* (BSP 1982 I 90) inclines more sharply, through which it has a higher appearance. The back of the skull in *Co. spielbergi* is more comparable to AMNH 22555 than to BSP 1982 I 90. Because the latter is the holotype, it can be questioned whether the classification of AMNH 22555 pterosaur as *An. santanae* is justifiable. The differences as explained are far less compared to the skull in *Co. spielbergi*. Though the skulls suggest close relationships, *Anhanguera* has a pointed snout, and a crest that does not start immediately anterior to the nasoantorbital fenestra and does not extend to the anterior aspect (but see above).

The reconstruction of the mandible in *An. santanae* (AMNH 22555) is not based on



studied material because a complete mandible with associated skull is not known, but rather based on the assumptions that because the animal has a premaxillary crest it had a dentary crest as well and since the premaxillary crest starts more posteriorly, the dentary crest starts more posteriorly as well. Neither of these assumptions is necessarily true. On the contrary, there are strong indications that the dentary crest in *Anhanguera* did not start posteriorly at all (*An. blittersdorffi*, referred specimen Kellner & Tomida, 2000; Veldmeijer, in review, pers.obs.), which makes the mandible less easy to diagnose. Differences between the mandible in *Coloborhynchus* and *Anhanguera* include the configuration of the groove at the ventral aspect, which is flanked with tiny raised ridges in the latter (Veldmeijer, in review).

From the above arguments, it may be that *An. piscator* should be classified as a species of *Coloborhynchus*. It is also relevant that the premaxillary crest in *An. piscator* runs all the way to the anterior aspect of the skull (*contra* Kellner & Tomida, 2000). Additional support is provided by the flat, though small, anterior aspect of the skull from which two teeth project that are positioned more dorsally relative to the subsequent teeth. It is beyond the scope of this work to discuss the classification of this specimen in detail but the large size alone (the juvenile specimen is as large as for instance the adult *Co. spielbergi*) points to a new, largest known species of the *Coloborhynchus* and is therefore referred to as *Co. piscator*.

Wellnhofer (1985) classified the remains of a large pterosaur (BSP 1982 I 89) as *Santanadactylus araripensis*. Kellner (1990) reclassified this material as *Anhanguera*, because, as stated by Kellner & Tomida (2000, p. 104): "the preserved dorsal portion of the premaxilla becomes gradually sharper toward the preserved rostral part of the skull, suggesting the presence of a sagittal crest rostral to the nasoantorbital fenestra." Apparently, the presence of a crest was the only reason for the reclassification of the specimen (Kellner & Tomida, 2000, p. 106; note that "Kellner (1990), [...], referred this taxon to *Anhanguera* (*A. araripensis*) as a member of the Anhangueridae, based on the dorsal margin of the premaxillary crest"). Neither, the presence of a crest nor the posterior start of a crest can be proven; consequently, the specimen cannot be referred to as *Anhanguera*. Conversely, the referred specimen has a crest, but the anterior aspect is distinctly different from *Anhanguera*. It resembles *Coloborhynchus* very closely and Veldmeijer (in review) pointed out the resemblance of the holotype (BSP 1982 I 89), the referred specimen (MN 4735-V; see Kellner & Tomida, 2000) and a complete skull in the Oberli collection Switzerland, (SAO 16494). Consequently, *S. araripensis* is reclassified as *Coloborhynchus araripensis*. In doing this, the suggestion that *S. araripensis* might be identical to *Brasileodactylus* (e.g., Wellnhofer, 1991a) can be rejected.

*Tropeognathus robustus* (Wellnhofer, 1987) was classified as *Anhanguera robustus* by Kellner & Campos (1989; see also Kellner & Tomida, 2000). However, Veldmeijer (1998), reclassified the mandible as *Co. robustus* on the basis of the comparison with *Co. spielbergi* and *Co. robustus* (SMNK 2302 PAL; see also Fastnacht, 2001).

*Tropeognathus mesembrinus* is distinct from all other *Coloborhynchus* and *Anhanguera* species. Though regarded as valid taxon by Kellner & Tomida (2000), a recent study by Fastnacht (2001) reclassified it as *Criorhynchus mesembrinus*.

Although ratios are helpful in pointing out differences they can only be used with reserve because pterosaurs display true allometry (Brower & Veinus, 1981) and there is still debate as to whether some specimens are juveniles, sub-adults or adults, so it is

even more difficult to establish ratios for a specific species. Further, there are too few specimens of the same species that are determined in order to have a statistically reliable picture.

The reconstruction of the feeding habits and the method of collecting food proposed for crested pterosaurs may be an oversimplification, since all pterosaurs with crests are thought to have collected food in the same way (for instance, Wellnhofer, 1991a). Although this might be true if the position and size of crests is related to age, it is odd that so little attention has been given to changes in functional morphology relative to the position and form of the crests. Crests were probably multifunctional and, may have been a instrument for recognition and courtship display, for example.

The following is a list of toothed pterosaurs from the Santana Formation. For a list of the compared material, which includes non-Brazilian specimen, see the inventory numbers and publications in Table 23.

*Anhanguera blittersdorffi*, *An. santanae*

*Brasileodactylus araripensis*

*Cearadactylus atrox*, *Ce.? ligabuei*

*Coloborhynchus robustus*, *Co. spielbergi*, *Co. araripensis*, *Co. piscator*

*Santanadactylus brasiliensis*, *S. pricei*, "*S.*" *spixi*

"*Criorhynchus*" *mesembrinus*

## Reconstruction

The relation between different parts of the skeleton depends on variables such as age and species. However, in making a reliable reconstruction it is assumed that the ratios of related animals are comparable, so variables within species may not be adequately considered.

Figure 22 shows different possible shapes of the wings. The preservation of the scapulocoracoid, humerus, ulna/radius and carpal allows an estimation of the wingspan. The length of the scapula (Table 14) is taken as a whole despite the angled position and, therefore, slightly smaller length in left lateral-right lateral plane. The humerus, ulna and radius are preserved in total length (Tables 15-17) as is the proximal syncarpal (Table 19). Furthermore, some length has to be taken into account for the cartilage. The length of the metacarpals and wing finger has to be reconstructed since these bones were not among those preserved.

The remains of *S. pricei*, *Co. piscator* and *Ar. conandoylei* contain the fourth metacarpal and preserved humeri that are close in length to those of *Co. spielbergi* (except for *S. pricei*). The measurement of the proximal syncarpal is taken from Wellnhofer (1991b). The length of the humerus in *S. pricei* is 167 mm and the length of the fourth metacarpal is 172 mm (Wellnhofer, 1991b). The length of the humerus in *Co. piscator* is 255 mm and the fourth metacarpal measures 256 mm (Kellner & Tomida, 2000). The length of the humerus in *Ar. conandoylei* is 230 mm and the length of the metacarpal 227 mm (Frey & Martill, 1994). Consequently, it can be assumed that the length of the fourth metacarpal, the biggest of the metacarpalia, is only slightly smaller in length relative to the humerus and must have been about 285 mm.

The wing finger in *S. pricei* has a total length of at least 1,108 mm, divided over four digits with lengths of 372, 324, 252 and 160 mm, respectively (Wellnhofer, 1991b). The length of the humerus + ulna/radius (412 mm) and the length of the complete wing finger are in the ratio of 1:2.7. The wing finger in *Ar. conandoylei* has a total length of 1,434 mm, divided over four digits with lengths of 445, 402, 312 and 275 mm, respectively (Frey & Martill, 1994). The length of the humerus + ulna/radius (542 mm) and the length of the complete wing finger are in the ratio of 1:2.6. The ratios calculated for the different pterosaurs are comparable. Therefore, a ratio of the length humerus + ulna/radius and the length of the complete wing finger of 1:2.6 is proposed for *Co. spielbergi*. The wing finger is reconstructed with a length of  $2.6 \times \text{length humerus}$  (290 mm) + length ulna/radius (410 mm). The total reconstructed length of the wing finger is 1,820 mm. The reconstructed span of one wing can be estimated by adding 130 (scapula) + 290 (humerus) + 410 (ulna) + 3 (carpal *An. santanae*) + 285 fourth metacarpal, reconstructed) + 1,820 (wing finger, reconstructed) mm, that is 2,938 mm. Allowing for some cartilage, the length of one wing, including the chest since the length of the scapula represents the circumference of the chest, might have been about 2,950 mm. The total wingspan is thus reconstructed at 5,900 mm.

The length of the animal, stretched from top to bottom, can be estimated by reference to the skeleton of *Co. piscator*, which includes the caudal vertebrae. The length of the skull in *Co. spielbergi* is 712 mm (Table 2). The preserved cervical vertebrae (Table 8), notarium (Table 9), dorsals (Table 10) and synsacrum (Table 11) have a total length of 72 (seventh and eighth cervical) + 135 (notarium) + 135 (dorsals) + approximately 165 (synsacrum) = 507 mm.

*Anhanguera santanae* (AMNH 22555) has a complete neck, of which the length of the cervicals that are not preserved in *Co. spielbergi*, the first to sixth, can be calculated as 223 mm (Wellnhofer, 1991b). The length of the seventh + eighth cervical (62.5 mm; Wellnhofer, 1991b) and the length of the first to sixth cervical, are in the ratio of 1:3.6.

*Coloborhynchus piscator* also has a complete preserved neck, of which the length of the cervicals that are not preserved in *Co. spielbergi*, are calculated at 218 mm (Kellner & Tomida, 2000). Assuming that the ratio between the height and length of the seventh cervical is 1:1.5, which is comparable to this ratio in *Co. spielbergi* (1:1.4) and *An. santanae* (AMNH 22555) (1:1.6), an estimated length of the seventh cervical in *Co. piscator* is 45 mm. The reconstructed length of the seventh + eighth cervical (45 + 28; Kellner & Tomida, 2000) and the length of the first up to and including sixth cervical are in the ratio of 1:3.0.

The length of the neck in *Co. spielbergi* is estimated to be 251 mm (76 [Table 8] 3.3), if it is assumed a ratio that is the average of those calculated in *An. santanae* and *Co. piscator*. Allowing some cartilage it seems reasonable to estimate the length of the neck as at least 255 mm.

The eleven caudal vertebrae in *Co. piscator* have a total length of 164 mm although it is not certain whether this was the complete tail (Kellner & Tomida, 2000). It is uncertain whether *Co. spielbergi* had a comparable tail. However, because of the close relationship between *Coloborhynchus* and *Anhanguera*, it is assumed that *Co. spielbergi* possessed a comparable tail. The length of the tail and the reconstructed length of the first eight cervicals of the neck in *Co. piscator* (see above) are in the ratio of 1:1.6.

Assuming a comparable ratio in *Co. spielbergi*, the tail might have been 156.8 mm long. Allowing for some cartilage, a length of 160 mm is assumed.

Consequently, the reconstructed length from the tip of the snout to the tip of the tail is estimated at  $712 + 255 + 135 + 140$  (dorsals and cartilage)  $+ 165 + 160 = 1,567$  mm. The wingspan and length does not take natural bendings of the skeleton into account.

### Acknowledgements

I thank John de Vos of the Nationaal Natuurhistorisch Museum, Leiden and Teylers Museum, Haarlem, the Netherlands, for offering for study the 'Brazilian' and 'German' pterosaurs in the collections of these museums. I thank him as well for making me familiar with palaeontology, reading the typescript, for his numerous ideas and comments and his assistance in finding grants.

I am grateful to the Stichting Molengraaff Fonds, which made it financially possible to visit the collections in Munich, Karlsruhe and Stuttgart (1998) and the Jan Joost ter Pelkwijk Fonds, which partly financed the visit to New York (2001). For another research project, but of great importance for the present work, the Stichting Molengraaff Fonds, the Jan Joost ter Pelkwijk Fonds and the Mej. A.M. Buitendijkfonds made it possible to study the collection in MN and DNPM, Rio de Janeiro, Brazil in 2002. The Nationaal Natuurhistorisch Museum, Leiden, is thanked for financing the costs involved in scanning the skull in Mainz, Germany (1998).

I thank the following persons for access to specimens under their care (in alphabetical order); D.A. Campos (Paleontological Collection of the Setor de Paleontologia do Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil), E. 'Dino' Frey (Staatliches Museum für Naturkunde, Karlsruhe, Germany), Geological Department Artis Zoo (Amsterdam, the Netherlands), A.W.A. Kellner (Museu Nacional, Rio de Janeiro, Brazil), M. Norell, C. Collins and I. Rutzky (American Museum of Natural History, New York, USA), A.C. Milner (the Natural History Museum, London, UK), J. van Veen and J. de Vos (Teylers Museum, Haarlem, The Netherlands), P. Wellnhofer (Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany) and R. Wild (Staatliches Museum für Naturkunde, Stuttgart, Germany).

I thank D.M. Unwin (Museum für Naturkunde der Humboldt-Universität, Berlin, Germany) and A.W.A. Kellner for reviewing the typescript. E. 'Dino' Frey, D.M. Martill (University of Portsmouth) and M. Fastnacht also made constructive comments. S.K. Donovan is thanked for the editing.

F. Dalla Vecchia (Istituto di Paleontologica, Università di Modena, Italy) is thanked for his efforts in trying to establish contact with the Centro Studi e Ricerche Ligabue, Venice, Italy, in order to study the Brazilian material. Unfortunately, the institute remained inaccessible. M. Fastnacht is thanked for his proposal and help taking CT-scans of the skull in 1998, and P. Stoeter and S. Boor (Department of Neuroradiology, University of Mainz, Germany) are thanked for providing the equipment and making the scans. A. 't Hooft is thanked for making the photographs and processing them for computerized use. Furthermore, I mention (in alphabetical order) J.E.M.F. Bos, J. Gamble/G. Mauricio/A. Keefer/R. Muller (all AMNH), A.M. Hense, M. van

Kuik, M. van Kuik-Woudstra, L. Veldmeijer, R. van Walsem (Egyptology Department, University of Leiden, the Netherlands) and R. van Zelst (NNM), for their support one way or the other.

Last but not least, I thank E. Endenburg for his continuous support and companionship, and his help with all kinds of things, from solving computer problems to drawing sketches, help that was and still is priceless.

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Appendix

Table 1: Sixty-nine percent of the specimen is complete. The figures in the tables are percentages of the total of the complete skeleton (heading 'original') and the amount of prepared bone (heading 'present') relative to the percentage of that bone of a complete skeleton. (From: de Buissonjé, 1993).

	original	present
skull	15	12
mandible	10	10
cervicals	7	2
dorsals	10	7
sacrum	6	6
ribs	5	2
wings	20	6
legs and feet	12	9
shoulder girdle	7	7
total	100	69

Table 2: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the skull in mm.

length skull	712
maximal width anterior spoon-shaped expansion (ventrally)	36
minimal width anterior spoon-shaped expansion (ventrally)	26
height premaxillary sagittal crest	109
length premaxillary sagittal crest	300
width over quadrates	150*
height of right orbit	97
height quadrate-occiput	130
length nasoantorbital fenestra	230
height nasoantorbital fenestra	60*
centrum occipital condyle-posterior skull	60
diameter occipital condyle (sagittal plane)	11

\*: approximate.

Table 3: *Coloborhynchus spielbergi* (RGM 401 880), measurements of alveoli and diastemae of the skull in mm.

left side					right side				
tooth	diameter	length of tooth	diastema	measure-ment	tooth	diameter	length of tooth	diastema	measure-ment
1	-	-	1-2	-	1	-	-	1-2	-
2	8.6	-	2-3	8.1	2	9.6	-	2-3	8.0
3	12.2	20.1	3-4	7.8	3	11.4	20.4	3-4	8.0
4	10.0	11.7	4-5	4.2	4	10.1	19.5	4-5	6.0
5	6.9	8.9	5-6	6.2	5	6.5	8.7	5-6	-
6	5.4	-	6-7	10.9	6	-	-	6-7	-
7	9.2	12.6	7-8	11.0	7	8.4	14.2	7-8	15.0
8	9.3	11.2	8-9	18.0	8	10.7	22.2	8-9	15*
9	10.8	11.5	9-10	20*	9	-	-	9-10	18*
10	-	-	-	-	10	6.9	-	10-11	15*
11	-	-	-	-	11	7.3	9.3	11-12	25.0
12	-	-	-	-	12	7.8	9.0	12-13	28.0
13	-	-	-	-	13	7.3	8.1	13-14	20*



14	-	-	-	-	14	7.5	8.2	14-15	17.0
15	-	-	-	-	15	7.6	6.6	15-16	45*
16	-	-	-	-	16	5.3	-	16-17	12.0
17	-	-	-	-	17	5.0	-	17-18	13.0
18	-	-	-	-	18	5.0	-	-	-

\*: approximate.

Table 4: Measurements and ratios of the skull of compared pterosaurs (in mm). All specimen are studied first hand of original material except for *Co. piscator* (cast in Museu Nacional, Rio de Janeiro, Brazil).

Measurements:	<i>An. blittersdorffi</i> (MN 4805-V)	<i>Co. araripensis</i> (BSP 1982 I 89)	<i>cf. Co. araripensis</i> (MN 4735-V)	<i>Co. araripensis</i> (SAO 16494)	<i>An. santanae</i> (BSP 1982 I 90)	<i>An. santanae</i> (AMNH 22555)	<i>"Cr." mesembrinus</i> (BSP 1987 I 46)	<i>Co. piscator</i> (MSM-PV 19892)
length	520	600*	680	535	520*	475	640	620
width over quadrates	80	98	121	80	98	-	137**	-
length premaxillary sagittal crest	200	-	290	220	-	125*	225	201
maximal height premaxillary crest	64	-	140	86	-	-	105	63
length nasoantorbital fenestra	160	160	170 <sup>#</sup>	148	156	162	220	190

Ratios:

width quadrate-total length skull: ( <i>Co. spielbergi</i> , RGM 401 880=21)	15	16	18	15	19	-	21	-
length premaxillary sagittal crest-total length skull: ( <i>Co. spielbergi</i> , RGM 401 880=42)	38	-	43	41	-	26	35	32
height -length premaxillary sagittal crest: ( <i>Co. spielbergi</i> , RGM 401 880=36)	32	-	48	39	-	-	47	31
length nasoantorbital opening-total length skull: ( <i>Co. spielbergi</i> , RGM 401 880=32)	31	27	25	28	30	34	34	31

\*: approximate, from Wellnhofer (1985); \*\*: from Wellnhofer (1987); <sup>#</sup> approximate.

Table 5: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the mandible and ?ceratobranchial in mm.

Mandible:	
length mandible	606
length retroarticular process-symphysis	355
thickness ramus at last alveolus	10
maximal width anterior spoon-shaped expansion (dorsally)	38
maximal width at symphysis	56
maximal width rami (laterally)	155
width over surangular	150
minimal width anterior to symphysis (dorsally)	25
maximal height of dentary sagittal crest	55
height at posterior most alveolus	55
length dentary sagittal crest	245
?Ceratobranchial:	
length, as preserved (illustrated fragment)	104
length, as preserved (not illustrated fragments)	35, 65
cross section (illustrated fragment)	2.5
cross section (not illustrated fragment)	2.5

Table 6: *Coloborhynchus spielbergi* (RGM 401 880), measurements of alveoli and diastemae of the mandible in mm.

left side					right side				
tooth	diameter	length of tooth	diastema	measurement	tooth	diameter	length of tooth	diastema	measurement
1	7.9	-	1-2	6.0	1	7.9	-	1-2	4.0
2	8.5	21.1	2-3	8.0	2	11.0	-	2-3	5.0
3	11.4	33.6	3-4	4.0	3	11.3	23.4	3-4	5.0
4	6.1	-	4-5	8.0	4	5.9	-	4-5	6.0
5	6.1	-	5-6	9.0	5	4.9	-	5-6	10.0
6	7.1	9.0	6-7	10.0	6	6.9	-	6-7	11.0
7	9.2	19.6	7-8	16*	7	7.0	19.8	7-8	n/a-
8	8.7	17.3	8-9	18*	8	n/a-	n/a-	8-9	n/a-
9	7.3	16.4	9-10	16.0	9	7.5	12.7	9-10	18.0
10	7.3	9.7	10-11	24.0	10	7.0	11.5	10-11	20.0
11	6.7	11.2	11-12	23.0	11	6.2	-	11-12	23.0
12	7.5	9.1	12-13	20.0	12	5.8	-	12-13	20.0
13	7.6	12.1	13-14	19.0	13	5.0	8.8	13-14	20.0
14	6.8	9.9	14-15	18.0	14	6.9	10.3	14-15	21.0
15	6.3	9.2	-	-	15	6.7	7.9	-	-
15a	n/a-	n/a-	15-15a	n/a-	15a	6.2	-	15-15a	18.1
16	6.4	7.8	15-16	19.0	16	5.5	5.0	15-16	22.0

\*: approximate, -: not preserved, n/a-: not applicable.

Table 7: Measurements and ratios of the mandible of compared pterosaurs in mm. All specimens are studied first hand except for *Co. piscator* (cast in Museu National, Ro de Janeiro, Brazil).

Measurements:

	<i>cf. An. blittersdorffi</i> (ref. spec. n. 40 Pz- DBAV-UER).)	<i>Co. araripensis</i> (BSP 1982 I 89)	<i>An. santanae</i> (BSP 1982 I 90)	<i>Anhanguera</i> sp. (SAO 200602)	<i>Anhanguera</i> sp. (AMNH 22573)	" <i>Cr.</i> " <i>mesembrinus</i> (BSP 1987 I 46)	<i>cf. "Cr." mesembrinus</i> (SMNS 56994)	<i>Co robustus</i> (BSP 1987 I 47)	<i>Co. robustus</i> (SMNK 2302 PAL)	<i>Co. piscator</i> (NSM-PV 19892)
Length	315	500*	460*	403	435**	540*	385	555	-	533##
length dentary sagittal crest	100	-	-	115	145**	126#	118	145#	170	145
depth dentary sagittal crest	-	-	-	40	40	51#	35	76#	62	50
width at symphysis	25	43	37	37	38	23#	34	33#	-	35

Ratios:

width at symphysis-total length mandible:										
( <i>Co. spielbergi</i> , RGM 401 880=9.2)	7.9	8.6	8.0	9.2	8.7	4.3	8.8	5.9	-	6.6
length dentary sagittal crest-total length mandible:										
( <i>Co. spielbergi</i> , RGM 401 880=40)	32	-	-	29	33	23	31	26	-	27
depth-length dentary sagittal crest:										
( <i>Co. spielbergi</i> , RGM 401 880=22)	-	-	-	35	28	40	30	52	36	34

\*: approximate, from Wellnhofer (1985); \*\*: approximate; #: from Wellnhofer (1987); ##: from Kellner & Tomida (2000).

Table 8: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the cervical vertebrae in mm.

	seventh cervical	eighth cervical
length centra (incl. postzygapophysis)	49	27
height	69	64
width over postzygapophyses	36	31*
width over prezygapophyses	52	45
width over transverse processes	-	60
maximal thickness neural spine	8.5	9

\*: approximate.

Table 9: *Coloborhynchus spielbergi* (RGM 401 880); measurements of the notarium in mm.

length (at centra)	135*
length supraneural plate	144
length centrum 1st vertebra (notarial cervical)	23
length centrum 2nd vertebra (notarial dorsal)	21
length centrum 3rd vertebra (notarial dorsal)	22
length centrum 4th vertebra (notarial dorsal)	22
length centrum 5th vertebra (notarial dorsal)	21
length centrum 6th vertebra (notarial dorsal)	26*
width centrum 1st vertebra (notarial cervical)	19
width centrum 6th vertebra (notarial dorsal)	14
width supraneural plate at 1st vertebra (notarial cervical)	12
width supraneural plate at 4th vertebra (notarial dorsal: anterior to scapular articulation)	13
width supraneural plate at 4th vertebra (notarial dorsal: posterior to scapular articulation)	16
width supraneural plate at 6th vertebra (notarial dorsal)	7
height anterior aspect	61
height posterior aspect	48
length scapular articulation	22
height scapular articulation	17

\*: approximate.

Table 10: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the dorsals in mm.

	6 <sup>th</sup>	7 <sup>th</sup>	8 <sup>th</sup>	9 <sup>th</sup>	10 <sup>th</sup>	11 <sup>th</sup>	12 <sup>th</sup>
length centra	23	19	17	18	19	20	19
height	49	45	45	47	49	43	44
width over transverse processes	47	49	48	46	41	32	50
width over postzygapophyses	18	15	18	12*	14	16	15*
width over prezygapophysis	21	21*	20	19*	19*	19*	19*
length neural spine	17	17	18	13	19	14*	13
thickness neural spine (dorsalmost)	3	2.5	3.5	2.5	2.5	4.5*	4*

\*: approximate.

Table 11: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the pelvis in mm.

total length	165*
length supraneural plate	98*
height pelvis posterodorsalmost point ischium-dorsal aspect	56
width illii (anteriormost)	18
width illii (posteriorly)	14
width over illii	106
width over anterior edges of acetabulae	99
width over posterior edges of acetabulae	78
width over postacetabular process (anteriorly)	40
width over postacetabular process (posteriorly)	23
width posterior to ischia	32
width at	99
height articulation for the prepubes-postacetabular process	95

\*: approximate.

Table 12: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the ribs in mm.

width mediolateral cervical ribs	10.5-12.0
length notarial rib (as preserved)	100

Table 13: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the sternum in mm.

width (measured dorsally)	135
width (measured ventrally)	180
length (measured dorsally)	200
length (measured ventrally)	180
width cristospine (ventral to coracoid facet)	23
height cristospine (at coracoid facet)	55
thickness posterior plate (left anterior margin)	3

Table 14: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the scapulocoracoid in mm.

width supraneural plate articulation	35
width shaft of the scapula	23
width sternal articulation	27
width shaft of the coracoid	14
length (measured laterally)	340
length scapula	130
length coracoid	175

Table 15: *Coloborhynchus spielbergi* (RGM 401 880), measurements of humerus in mm.

length	290
width proximal end	70
width distal end	83
width shaft, anterior aspect (begin of deltopectoral crest)	34
width shaft, ventral aspect (begin of deltopectoral crest)	37
width shaft - maximal height deltopectoral crest	69

Table 16: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the ulna in mm.

Length	410
minimal width, anterior aspect	35
minimal width, ventral aspect	22
maximal width anterior aspect, proximal end	75
maximal width ventral aspect proximal end	45

Table 17: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the radius in mm.

length	401
width, anterior aspect	12
width, ventral aspect	10
width anterior aspect over biceps tubercle	21
width proximal end (anterior aspect)	44
width proximal end (ventral aspect)	18
width distal end (anterior aspect)	40
width distal end (ventral aspect)	16

Table 18A: Ratios of humerus and ulna/radius of different Brazilian pterosaurs.

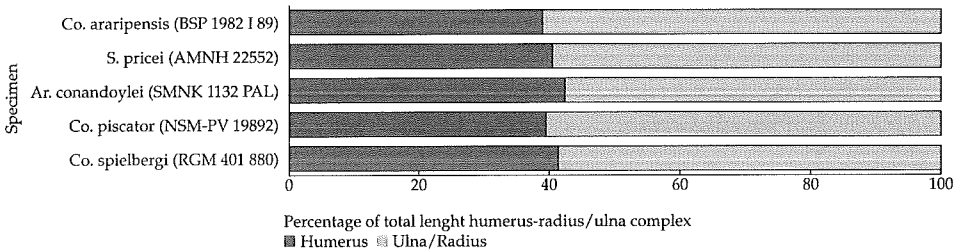


Table 18B: Ratios of scapula, humerus and ulna/radius of different Brazilian pterosaurs.

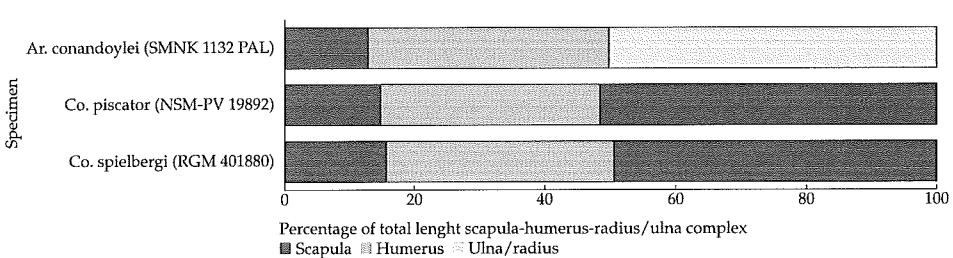


Table 19: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the proximal syncarpal in mm.

maximal width proximal aspect	50
minimal width proximal aspect	37
maximal width dorsal aspect	30
minimal width dorsal aspect	26
length (measured anterior-posterior)	73

Table 20: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the third phalanx of the third digit and unguals in mm.

?Metacarpals:		
length, longest		100
cross-section, longest		4.5
cross-section, smallest		3
Phalanx:		
length		28
width (anteroposterior plane)		2.5
width (dorsoventral plane)		3
Unguals:		
length		27-28
width at tuberculum		14-17
thickness of tuberculum		5-6

Table 21: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the femur in mm.

length	285
maximal diameter head, lateromedially	20
width at greater trochanter	22
width neck, anterior aspect	12
width shaft, anterior aspect	15
width shaft, lateral aspect	17
width distal end, anterior aspect	35

Table 22: *Coloborhynchus spielbergi* (RGM 401 880), measurements of the tibia in mm.

length	355
width shaft, lateral aspect	9
width shaft, anterior aspect	11
width proximal end, lateral aspect	30
width proximal end, anterior aspect	23
width distal end, lateral aspect	14
width distal end, anterior aspect	15

Table 23: Compared material in sequence of publication. Specimen marked with \*) are studied first hand.

*) <i>Coloborhynchus clavirostris</i>	BMNH 1822	Owen, 1874
*) <i>Santanadactylus brasiliensis</i>	UvA M 4894	de Buissonjé, 1980
<i>Santanadactylus brasiliensis</i>	V-201	Wellnhofer <i>et al.</i> , 1983
*) <i>Brasileodactylus araripensis</i>	MN 4804-V	Kellner, 1984
*) <i>Santanadactylus araripensis</i> =	BSP 1982 I 89	(Wellnhofer, 1985)
<i>Anhanguera araripensis</i> =		(Kellner, 1990)
<i>Coloborhynchus araripensis</i>		Veldmeijer, in review.
*) <i>Santanadactylus pricei</i>	BSP 1980 I 122	Wellnhofer, 1985
*) <i>Santanadactylus pricei</i>	BSP 1980 I 43	Wellnhofer 1985
*) <i>Santanadactylus pricei</i>	BSP 1980 I 120	Wellnhofer 1985
*) " <i>Santanadactylus</i> " <i>spixi</i>	BSP 1980 I 121	Wellnhofer 1985
*) <i>Araripesaurus santanae</i> =	BSP 1982 I 90	(Wellnhofer, 1985)
<i>Anhanguera santanae</i>		Kellner, 1990
*) <i>Araripesaurus</i> sp. =	BSP 1982 I 91	(Wellnhofer, 1985)

<i>Anhanguera santanae</i>		Wellnhofer, 1991b
*) <i>Araripesaurus</i> sp. =	BSP 1982 I 93 <sup>□</sup>	(Wellnhofer, 1985)
? <i>Anhanguera</i> sp.		Wellnhofer, 1991b
<i>Cearadactylus atrox</i>	CB-PV-F-093	Leonardi & Borgomanero, 1985
*) <i>Anhanguera blittersdorffi</i>	MN 4805-V	Campos & Kellner, 1985b <sup>□□</sup>
*) <i>Tropeognathus mesembrinus</i> =	BSP 1987 I 46	(Wellnhofer, 1987)
" <i>Criorhynchus</i> " <i>mesembrinus</i>		Fastnacht, 2001
*) <i>Tropeognathus robustus</i> =	BSP 1987 I 47	(Wellnhofer, 1987)
<i>Anhanguera robustus</i> =		(Kellner & Campos, 1989)
<i>Coloborhynchus robustus</i>		Veldmeijer, 1998
*) pterodactyloid	AMNH 22569	Bennett, 1990
*) <i>Anhanguera blittersdorffi</i> (ref. spec.)	n. 40 Pz-DBAV-UERJ	Campos & Kellner, 1985a
*) <i>Santanadactylus pricei</i>	BSP 1987 I 1	Wellnhofer, 1991b
*) <i>Santanadactylus araripensis</i> =	BSP 1987 I 66	(Wellnhofer, 1991b)
<i>Coloborhynchus araripensis</i>		Veldmeijer, in review
*) <i>Santanadactylus brasiliensis</i>	BSP 1987 I 65	Wellnhofer, 1991b
*) <i>Anhanguera</i> sp. =	AMNH 22555	(Wellnhofer, 1988)
<i>Anhanguera santanae</i>		Wellnhofer, 1991b
*) <i>Santanadactylus pricei</i>	AMNH 22552 <sup>Δ</sup>	Wellnhofer, 1991b
<i>Cearadactylus? ligabuei</i>	CCSRL 12692/12713	Dalla Vecchia, 1993
<i>Arthurdactylus conandolei</i>	SMNK 1132 PAL <sup>ΔΔ</sup>	Frey & Martill, 1994
<i>Siroccopteryx moroccensis</i>	LINHM 016	Mader & Kellner, 1999
◇ <i>Anhanguera piscator</i> =	NSM-PV 19892	(Kellner & Tomida, 2000)
<i>Coloborhynchus piscator</i>		present work
*) <i>Anhanguera araripensis</i> (ref. spec.) =	MN 4735-V	(Kellner & Tomida, 2000)
<i>Coloborhynchus araripensis</i>		Veldmeijer, in review.
*) <i>Brasileodactylus</i> cf. <i>araripensis</i>	MN 4797-V	Sayão & Kellner, 2000
*) <i>Coloborhynchus robustus</i>	SMNK 2302 PAL	Fastnacht, 2001
*) Cf. " <i>Criorhynchus</i> " <i>mesembrinus</i>	SMNS 56994	Veldmeijer, 2002
*) <i>Coloborhynchus araripensis</i>	SAO 16494	Veldmeijer, in review
*) <i>Anhanguera</i> sp.	SAO 200602	Veldmeijer, in review
*) <i>Anhanguera</i> sp.	AMNH 22573	Veldmeijer, in review

<sup>□</sup> Wellnhofer (1991b) refers erroneously to this specimen as BSP 1982 I 92.

<sup>□□</sup> The specimen was first mentioned by Campos (1983).

<sup>Δ</sup> Note that Kellner & Tomida (2000) erroneously refer to this specimen as AMNH 22555.

<sup>ΔΔ</sup> Note that Kellner & Tomida (2000) mistakenly refer to this specimen as SMNK 1133 PAL.

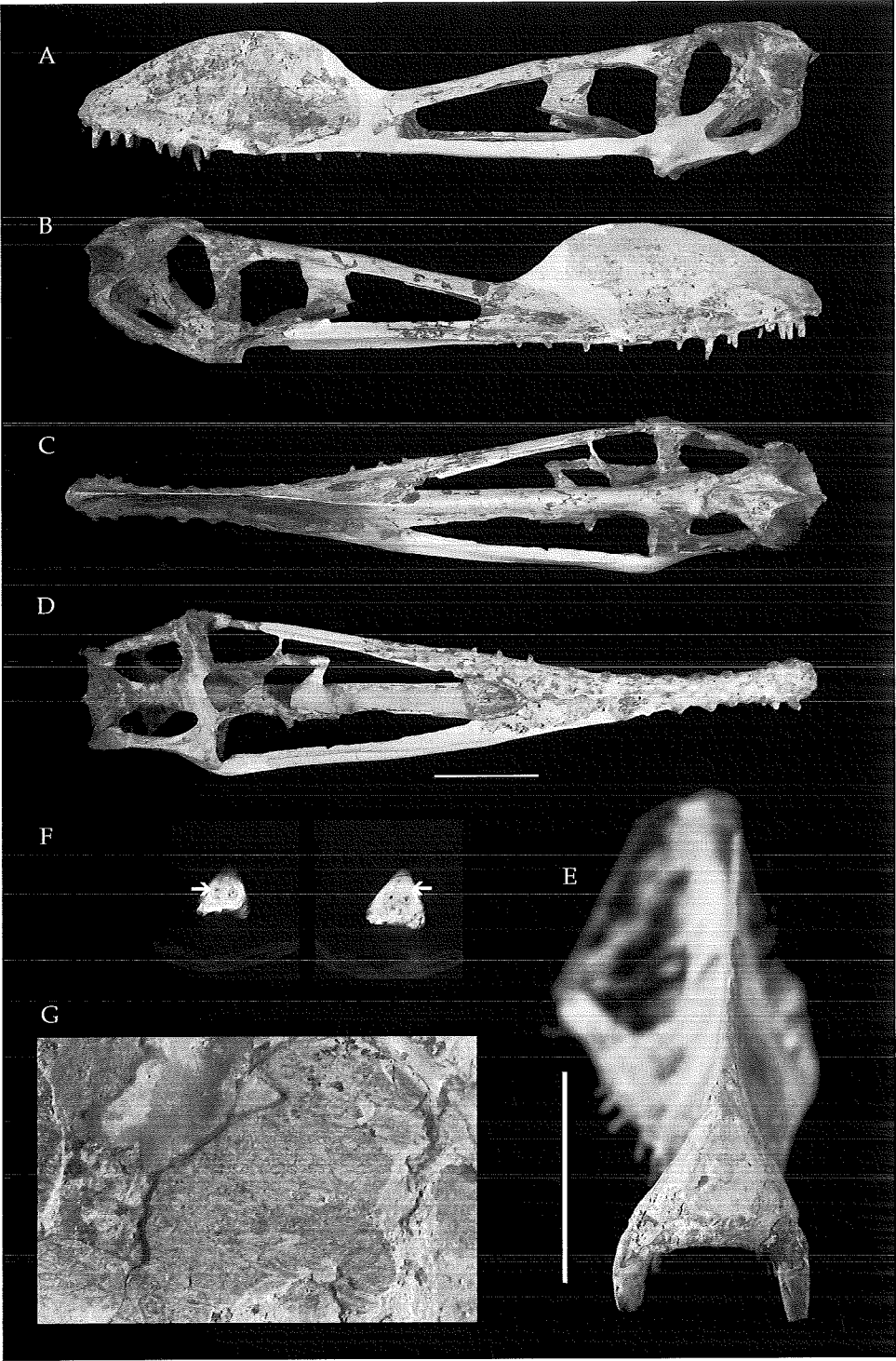
<sup>◇</sup> A cast was studied at the Museu Nacional, Rio de Janeiro, Brazil.



Pl. 1. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the skeleton embedded in nodules. The sides of a nodule that connected to another nodules were marked by characters in red ink. Photographer unknown.

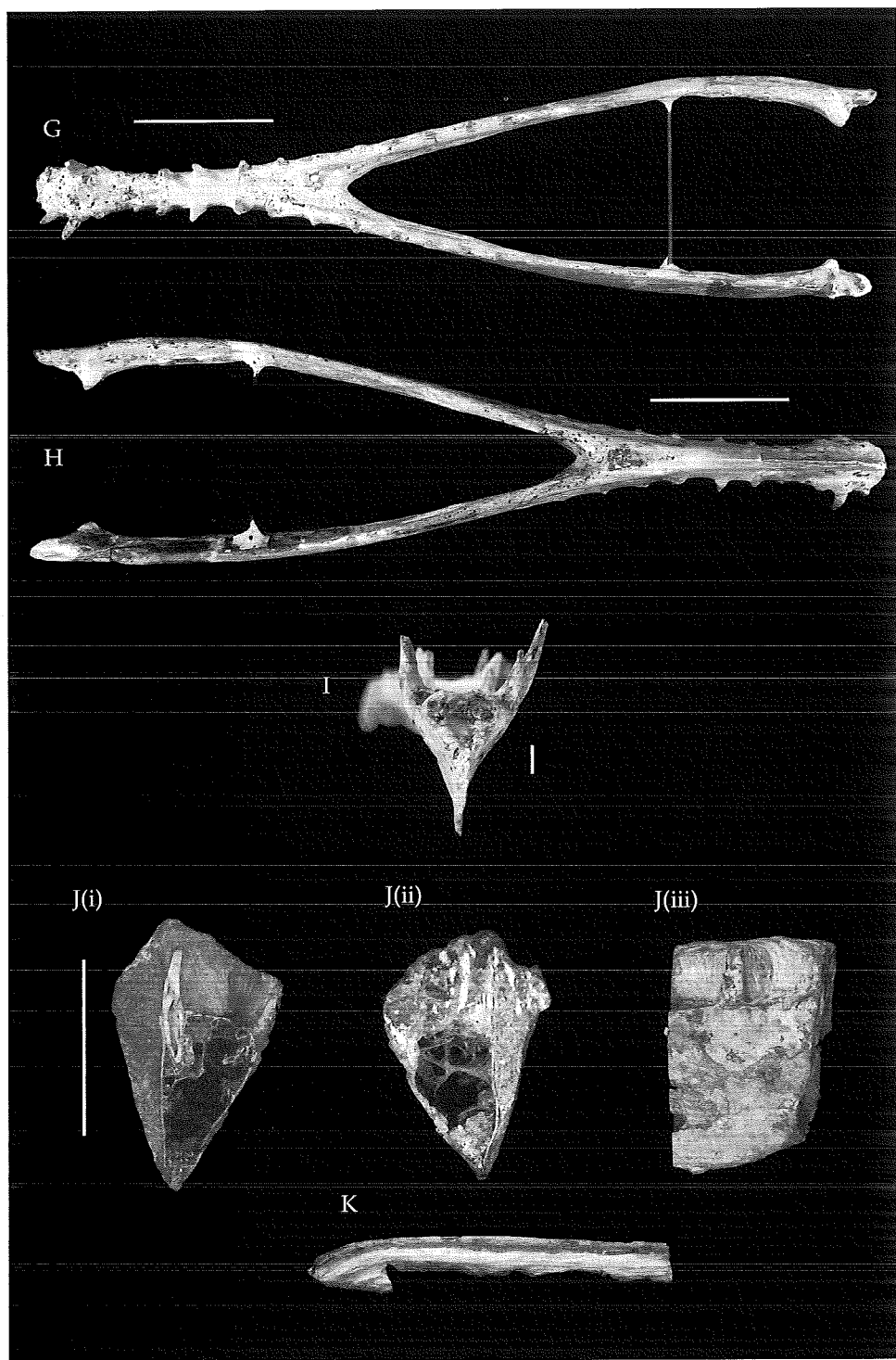
Pl. 2. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the skull in various aspects. A: left lateral; B: right lateral; C: dorsal; D: ventral; E: anterior (scale bar = 50 mm); F(i, ii): CT-scans of anterior aspect; G: network of grooves at the premaxillary crest. Photograph F: S. Boor and P. Stoeter (Department of Neuroradiology of the University of Mainz, Germany). Scale bar = 100 mm (unless mentioned otherwise). All other photographs by A. 't Hooft.



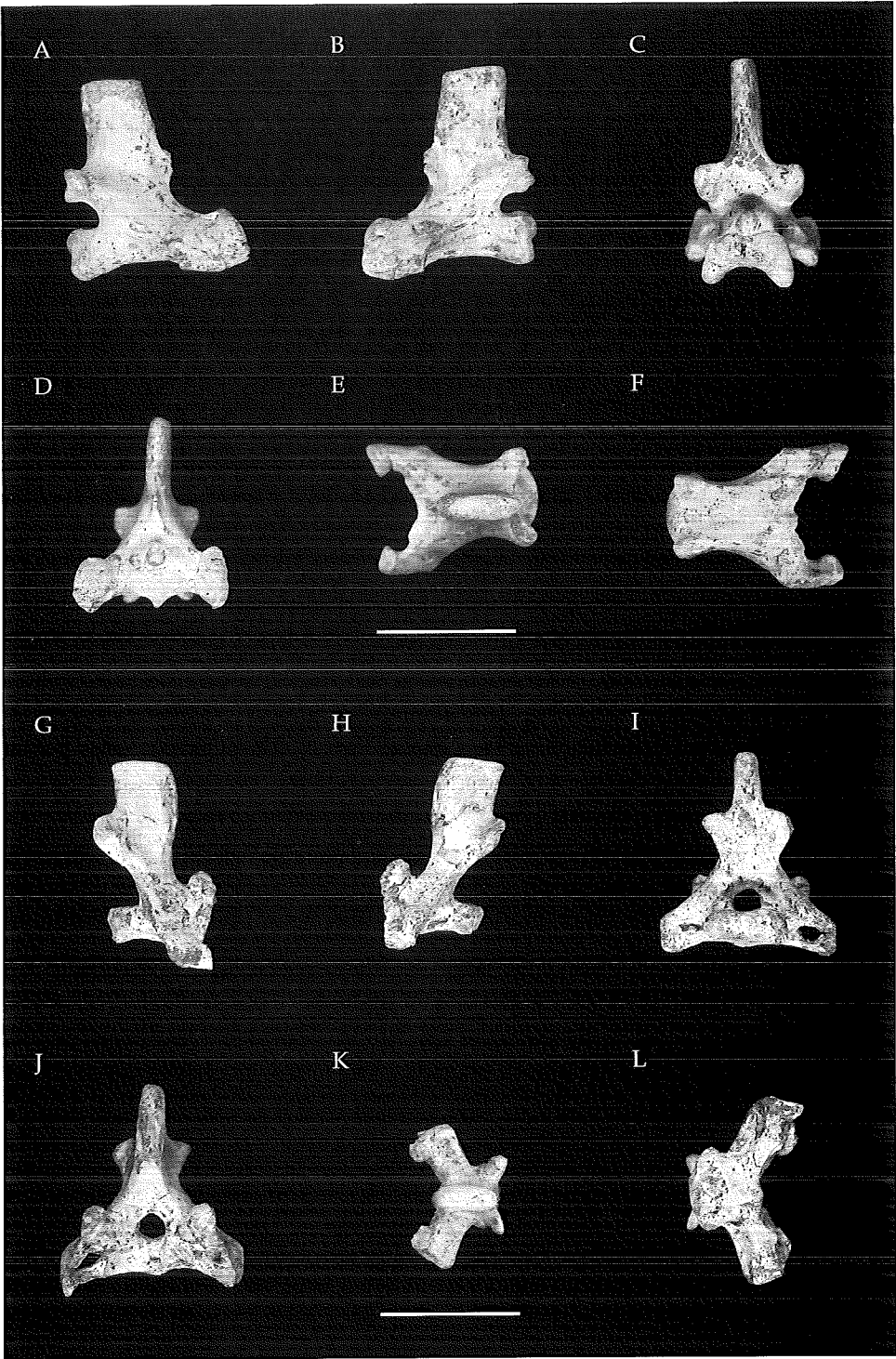




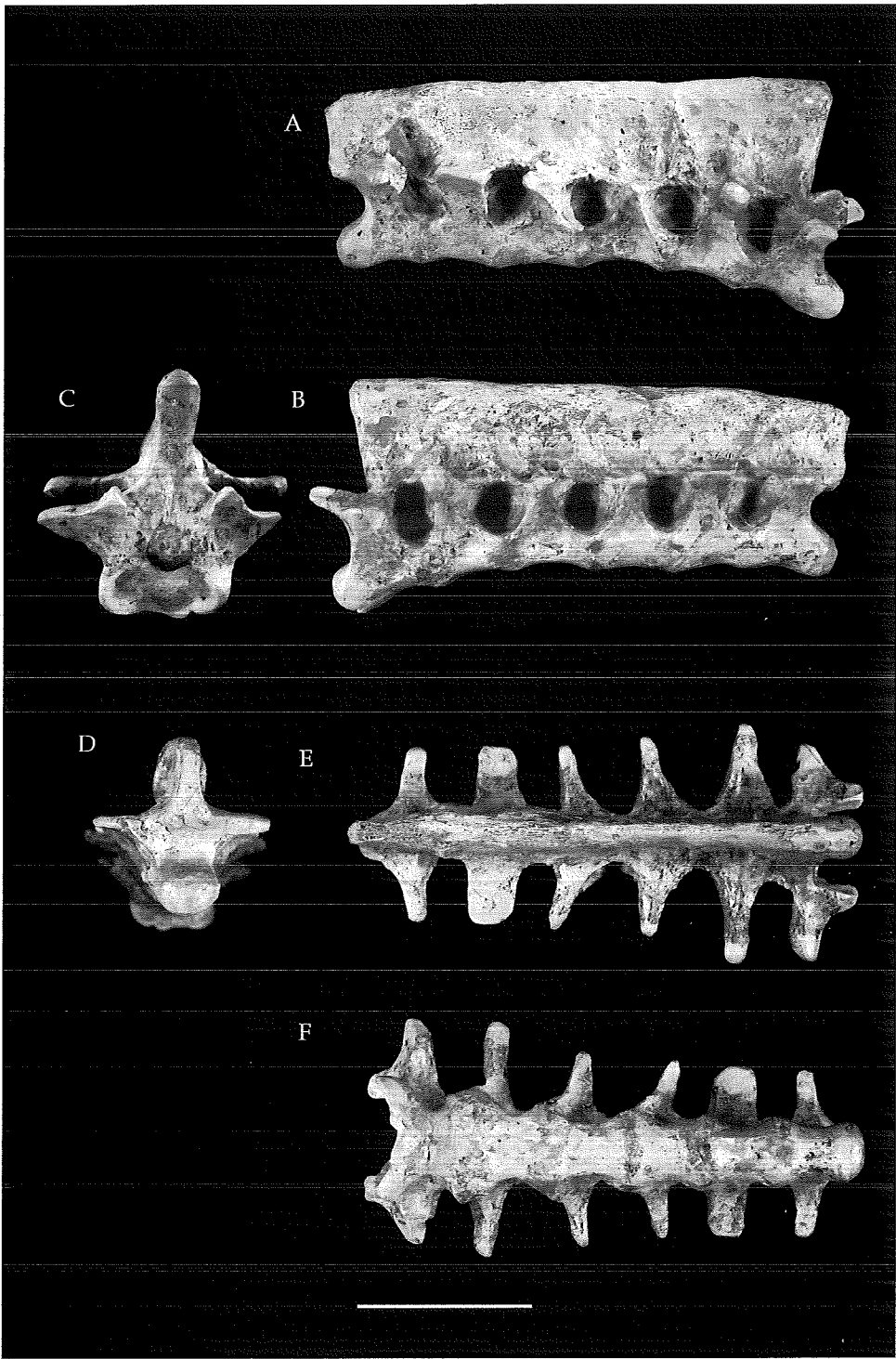
Pl. 3. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the mandible in various aspects. A: left lateral; B: left ramus, medial; C: left posterior articular area (scale bar = 10 mm); D: right lateral; E: right ramus, medial; F: right posterior articular area (scale bar = 10 mm); G: dorsal; H: ventral; I: anterior (scale bar = 10 mm); J: cross-section of the mandible in anterior (i), posterior (ii), and left lateral (iii) aspects (scale bar = 50 mm); K: largest part of ?ceratobranchial. Scale bar = 100 mm (unless stated otherwise). Photographs by A. 't Hooft.

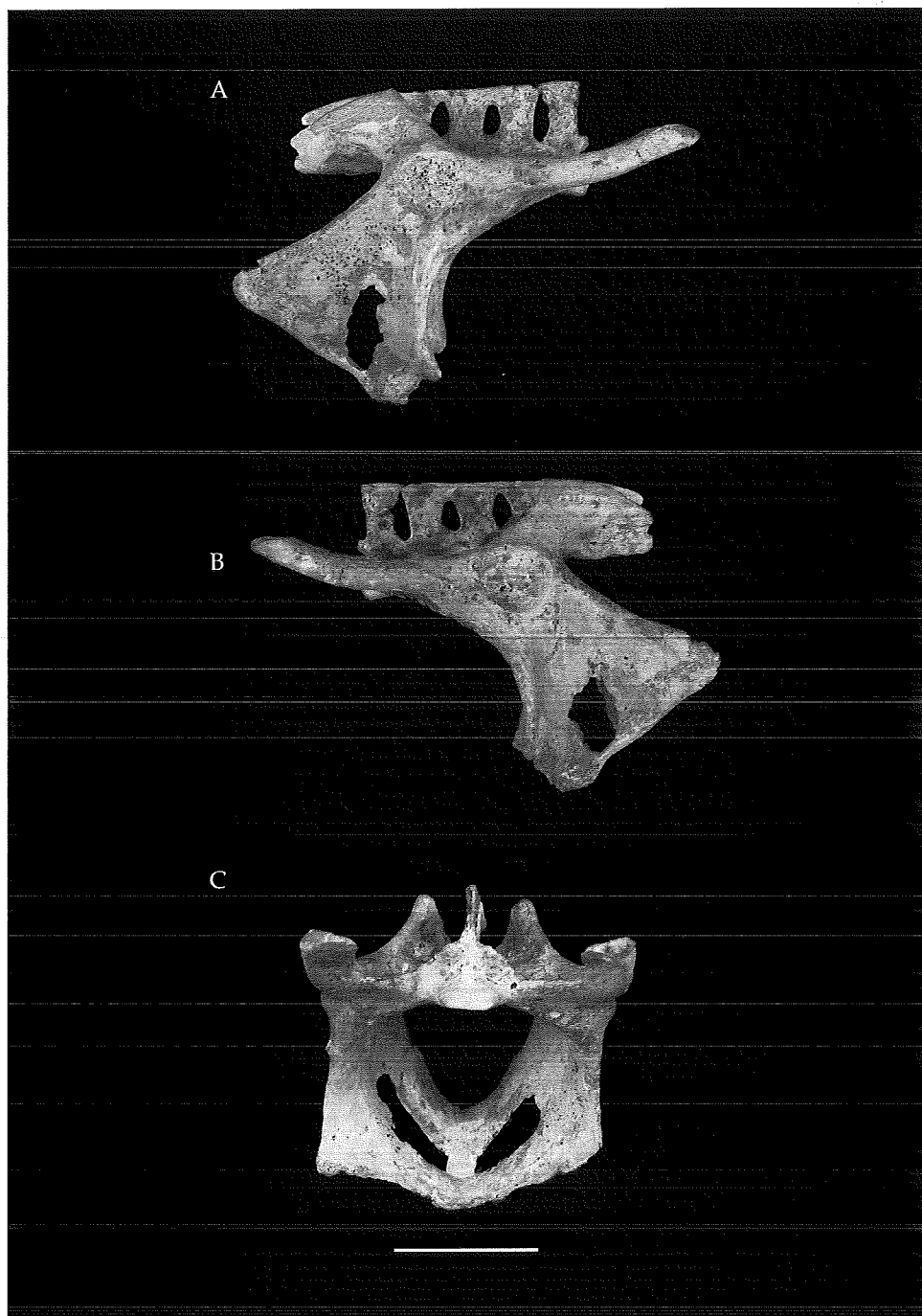


Pl. 4. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the seventh and eighth cervical in various aspects. Seventh cervical: A: right lateral; B: left lateral; C: anterior; D: posterior; E: dorsal; F: ventral. Eighth cervical: G: right lateral; H: left lateral; I: anterior; J: posterior; K: dorsal; L: ventral. Scale bar = 50 mm. Photographs by A. 't Hooft.



Pl. 5. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the notarium in various aspects. A: right lateral; B: left lateral; C: anterior; D: posterior; E: dorsal; F: ventral. Scale bar = 50 mm. Photographs by A. 't Hooft.





Pl. 6. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the pelvis in various aspects. A: right lateral; B: left lateral; C: anterior; D: posterior; E: dorsal; F: ventral. Scale bar = 50 mm. Photographs by A. 't Hooft.

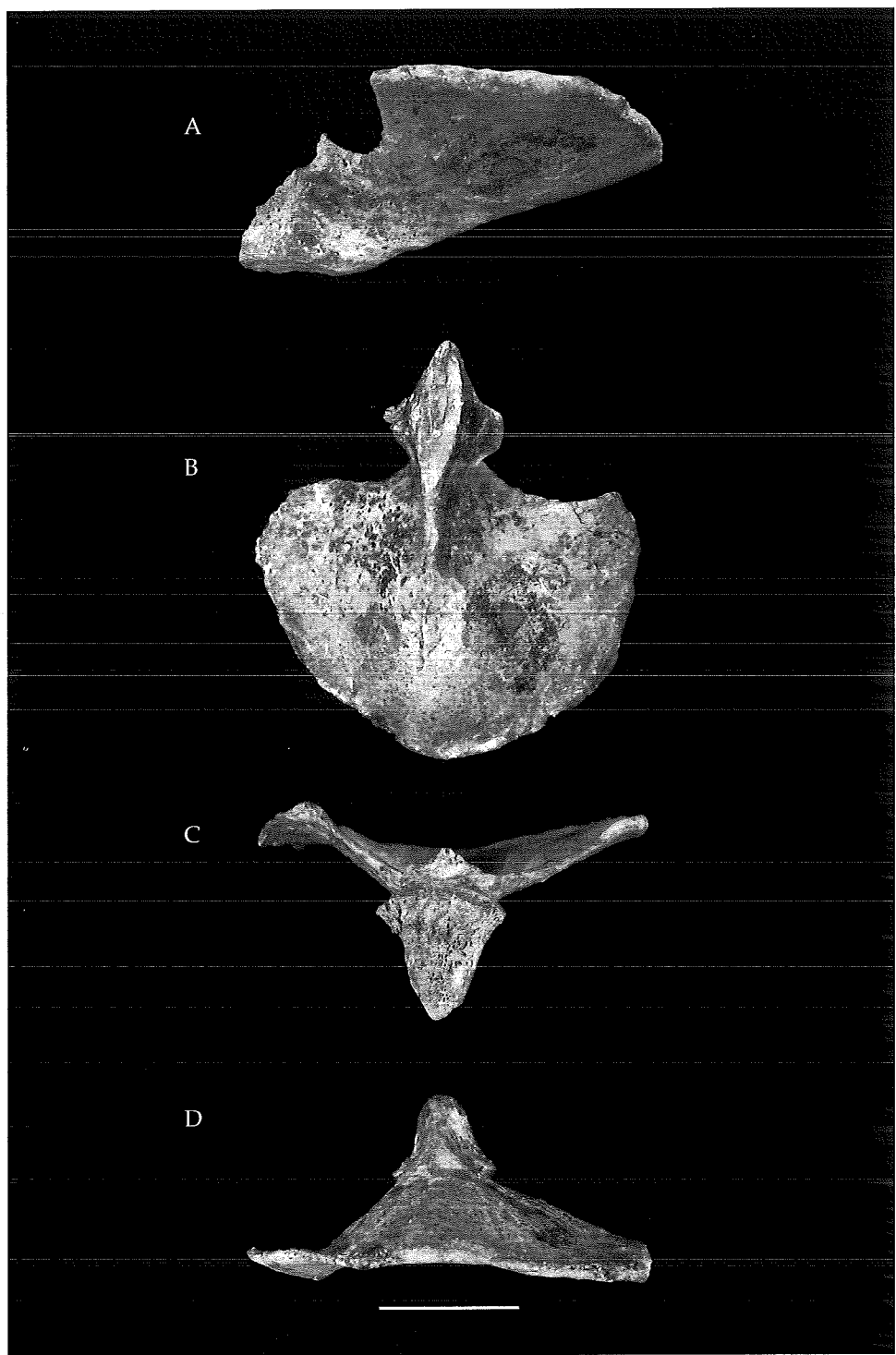




Pl. 7. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880). A: four pieces of cervical rib anterior aspect (scale bar = 20 mm). B: the first notarial rib right in various aspects. From top to bottom: lateral; medial; dorsal; ventral. (scale bar = 30 mm). Photographs by A. 't Hooft.



Pl. 8. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the sternum in various aspects. A: left lateral; B: ventral; C: anterior; D: posterior (Note that the dorsal aspect is not included because it is largely covered with matrix). Scale bar = 50 mm. Photographs by A. 't Hooft.



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Pl. 9. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the scapulocoracoids in various aspects (left and right respectively). A: posterior; B: lateral; C: anterior; D: dorsal. Scale bar = 50 mm. Photographs by A. 't Hooft.





Pl. 10. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the left humerus in various aspects. A: posterior; B: ventral; C: anterior; D: dorsal; E: proximal; F: distal. Scale bar = 50 mm. Photographs by A. 't Hooft.

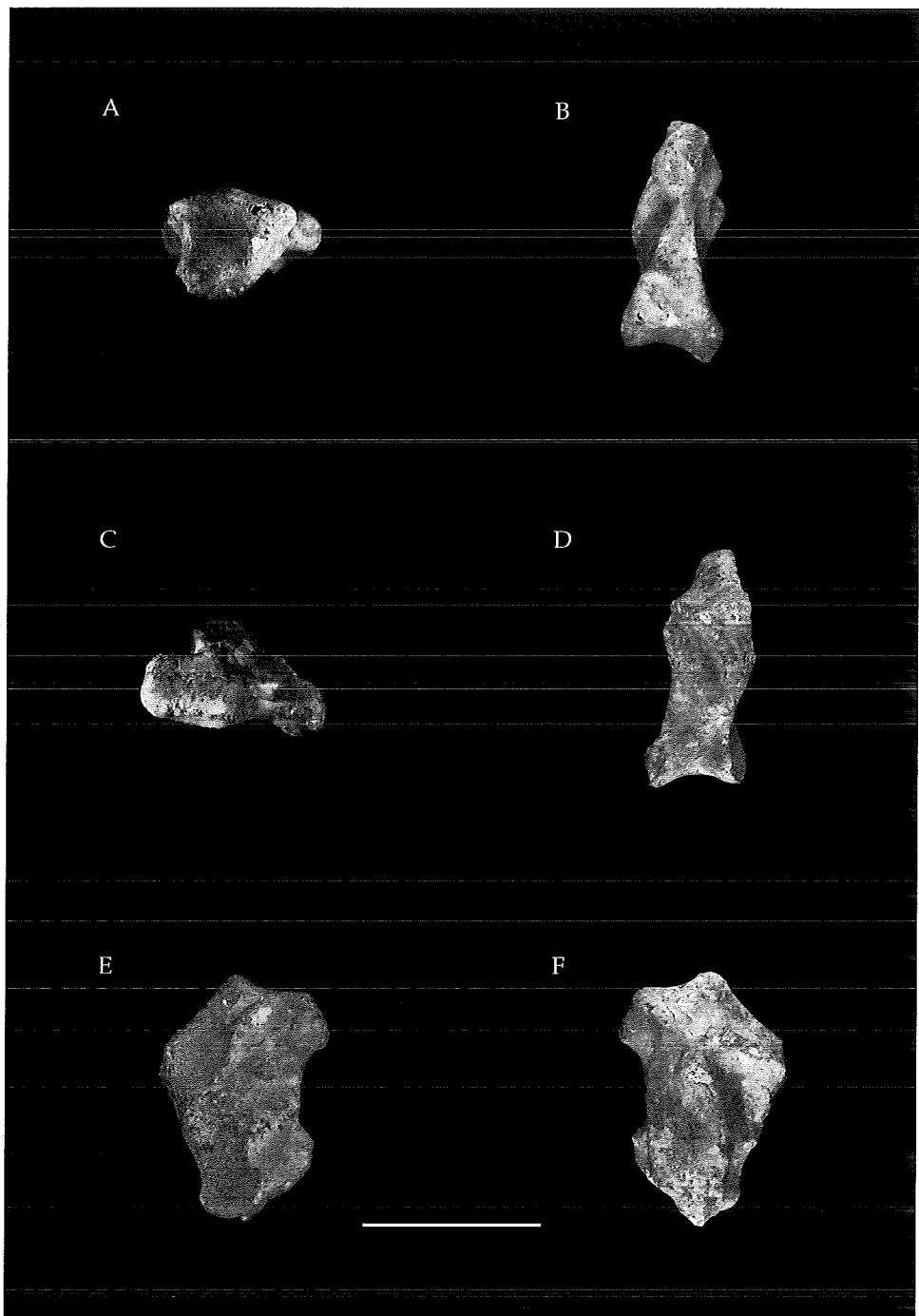




Pl. 11. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the left ulna in various aspects. A: posterior; B: ventral; C: anterior; D: dorsal; E: proximal; F: distal. Scale bar = 50 mm. Photographs by A. 't Hooft.

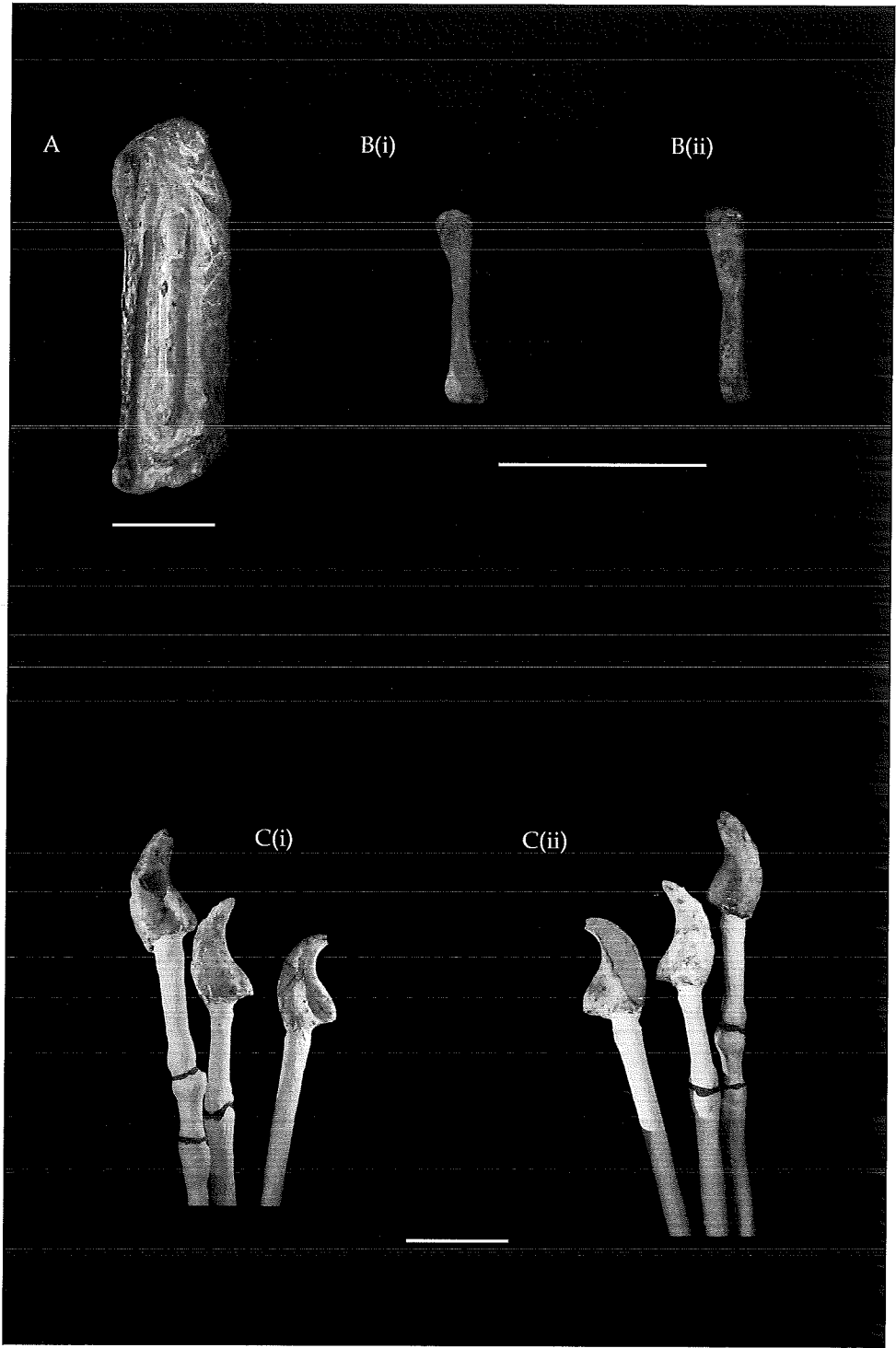


Pl. 12. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the left radius in various aspects; A: posterior; B: ventral; C: anterior; D: dorsal; E: proximal; F: distal. Scale bar = 50 mm. Photographs by A. 't Hooft.



Pl. 13. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the left proximal syncarpal in various aspects. A: posterior; B: ventral; C: anterior; D: dorsal; E: proximal; F: distal. Scale bar = 50 mm. Photographs by A. 't Hooft.

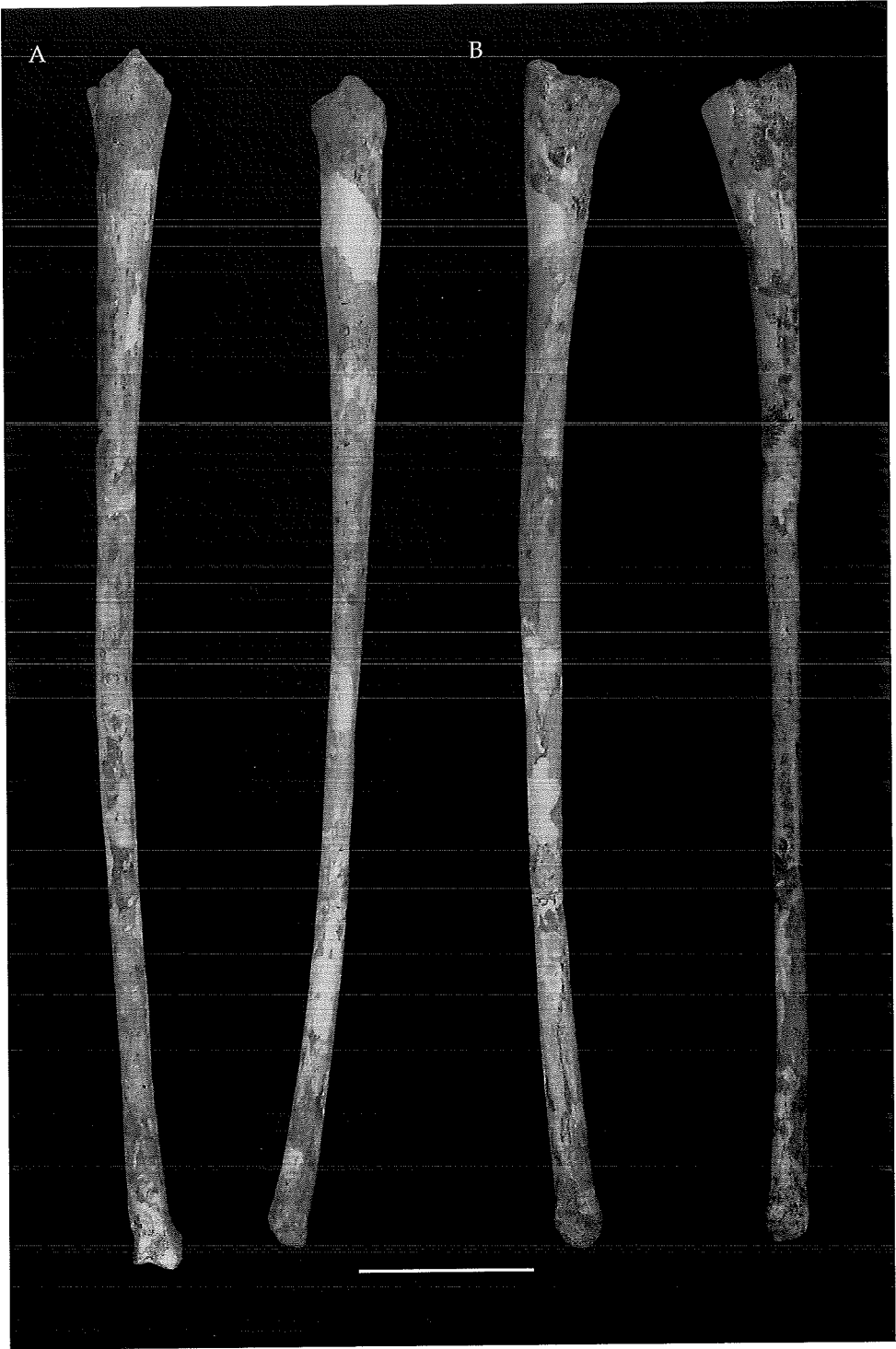
Pl. 14. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), ?Metacarpals, phalanges and unguals. A: First and third ?metacarpalia. B: Third phalanx with partially preserved and attached second phalanx in i) ventral and ii) anterior aspects. C: Unguals in (i) anterior and (ii) posterior aspects. Scale bar = 30 mm. Photographs by A. 't Hooft.





Pl. 15. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the femora in various aspects (left and right respectively). A: posterior; B: lateral; C: anterior; D: medial; E: proximal (left) (scale bar = 30 mm); F: distal (right) (scale bar = 30 mm). (Note that the proximal aspect of the right femur and the distal aspect of the left femur are not shown because these aspects are reconstructed.) Scale bar = 50 mm (unless stated otherwise). Photographs by A. 't Hooft.









Pl. 16. *Coloborhynchus spielbergi* sp. nov. (RGM 401 880), the tibiae in various aspects (left and right respectively). A: posterior; B: lateral; C: anterior; D: medial; E: proximal (left) (scale bar = 30 mm); F: distal (right) (scale bar = 30 mm). Scale bar = 50 mm unless stated otherwise. Photographs by A. 't Hooft.

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