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Description of Pterosaurian (Pterodactyloidea: Anhangueridae, *Brasileodactylus*) remains from the Lower Cretaceous of Brazil

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A near-complete mandible (SMNS 55414) and a partial skeleton, including a fragment of maxilla (BSP 1991 I 27), from the Lower Cretaceous Santana Formation (Romualdo Member) of Brazil are described and classified. Both have been assigned to *Brasileodactylus*. The results are being viewed in the light of the ongoing discussion about Ornithocheiridae-Anhangueridae problem as pinpointed by Veldmeijer (2006). Note, however, that due to the long time it took the editors to publish the present work, recent literature, such as Rodrigues & Kellner (2008), is not included in the discussion.

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Key words: *Brasileodactylus*, *Anhanguera*, *Coloborhynchus*, *Criorhynchus*, *Anhangueridae*, *Ornithocheiridae*, Lower Cretaceous, Santana Formation, Romualdo, Chapada do Araripe

INTRODUCTION

The Staatliches Museum für Naturkunde in Stuttgart, Germany possesses various specimens of pterosaurs, rhamphorhynchoids as well as pterodactyloids, from Germany. Besides these 'native' pterosaur fossils, the collection incorporates pterosaur remains from the Santana Formation, Brazil. The bulk of the material has been previously described (Veldmeijer 2002, but see Veldmeijer 2006); the remaining elements, a small, almost complete mandible and attached vertebrae with the registration number SMNS 55414, are presented in this chapter.

The Bayerische Staatssammlung für

Paläontologie und Geologie in Munich, Germany houses one of the largest pterosaur collections in the world. The collection includes rhamphorhynchoids as well as pterodactyloids from Germany. Furthermore, the collection incorporates pterosaur remains from the Santana Formation, Brazil. The bulk of the material has been described previously (Wellnhofer 1985, 1987, 1991), except for a partial skeleton (BSP 1991 I 27) presented here.

The mandible from the Stuttgarter museum is the most complete mandible of the genus *Brasileodactylus* so far. The material from the Munich collection is especially important

because of the non-crested skull. The aim of the present work is to present a description and classification of the material, which is the most complete hitherto known of *Brasileodactylus*. The comparison is limited to the toothed taxa from Brazil with the exception of type specimens and holotypes from other areas (viz. Cambridge Greensands, England). Comments are made on the taxonomy of the Brazilian Cretaceous pterosaurs.

ABBREVIATIONS

cond.	condyle
co.	cotyle
d.sag.gr.	dentary sagittal groove
del.cr.	deltpectoral crest
ex.p.	exapophyses
pn. for.	pneumatic foramen
h.	head
hyp.	hypapophysis
d.	indented
n.c.	neural canal
n.s.	neural spine
pal.sag.r.	palatinal sagittal ridge
po.z.	postzygapophyses
post.tub.	posterior tuberosity
pr.z.	prezygapophyses
r.t.	replacement tooth
s.gr.	side-grooves
t.p.	transverse processes
tub.	tuberculum

THE MANDIBLE IN THE STUTTGART COLLECTION

Preservation

The specimen (SMNS 55414) is a nearly complete lower jaw, lacking the retroarticular processes. The specimen is still embedded with its left lateral aspect. The matrix obscures the alveoli at this side. It is not clear whether the left ramus is still embedded in the matrix; it might be broken. The right ramus is partially obscured, especially at its medial aspect. The condition of the preserved mandibular part is good and only parts of the dorsal aspect are slightly damaged, resulting in an unclear den-

tary sagittal groove at some places. All teeth are broken at the alveoli, but remnants are visible in some of the alveoli (sixth to ninth). Remnants of the first pair of teeth are still visible in the matrix.

Attached to the matrix are three vertebrae, which are, judging from the elongated centra, cervicals of the midseries. The vertebrae are still largely embedded; one, however, is prepared for a large part but the postexapophyses are not preserved. It is assumed that the vertebrae and mandible belong to the same individual. Due to the incompleteness and unprepared state, no further attention is given to the vertebrae. Bennett (1994) remarked that the vertebrae are like those of *Ornithocheirus*, as presented by Owen (1861, note that Bennett erroneously refers to Owen's supplement no. III to the monograph on the fossil reptilian, as Owen 1860, but this supplement was published in 1861). However, the conclusion based on this is premature because the largely embedded state of the vertebrae in SMNS 55414 prohibits a detailed comparison.

Systematic palaeontology

(Figs. 1, 2; Tables 1, 2)

Family ?Anhangueridae CAMPOS & KELLNER, 1985

Genus *Brasileodactylus* KELLNER, 1984

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

Diagnosis *Brasileodactylus* as diagnosed by Kellner, 1984 (580): "Pterosauriër mit Unterkiefer gebildet aus einer länglichen am Ende abgerundeten Symphyse, leicht nach oben gebogen, triangulärem Querschnitt, Schmälerung ab dem proximalen Teil, wobei eine Verbreiterung an dem distalen Bereich ab der dritten Alveole existiert, die eine flache Oberfläche bildet. Vorhandensein einer medialen Furche an der Dorsalseite der Symphyse, sehr ausgeprägt ab dem Beginn des Unterkiefers (distaler Teil),

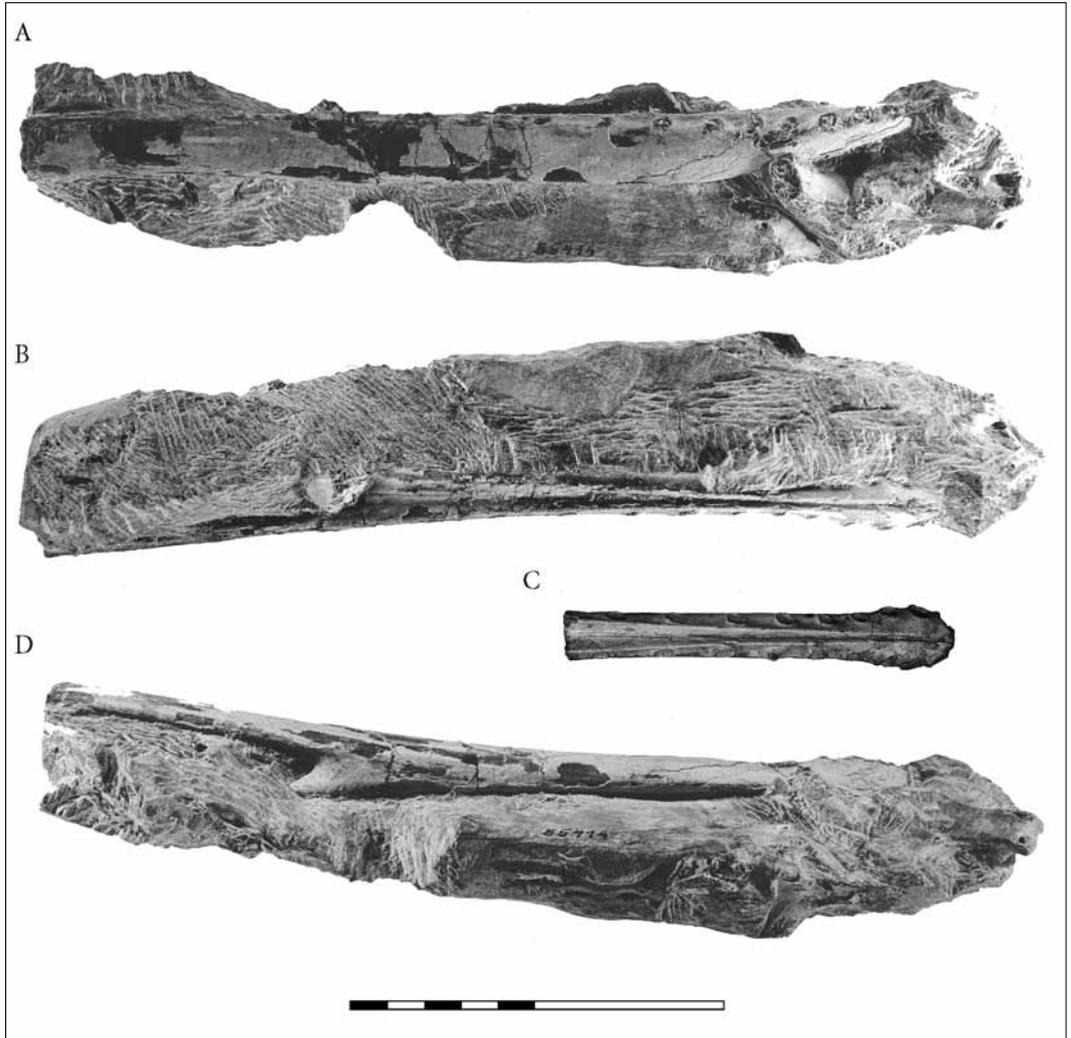


Figure 1 *Brasileodactylus araripensis* (SMNS 55414). Mandible in various views **A**: right lateral; **B**: dorsal; **D**: ventral. **C** is the dorsal view of the holotype (MN 4804-V), housed in the MN, Rio de Janeiro. [Photographs A, B, D by R. Harling. Courtesy of SMN, Stuttgart; photograph C by E. Eendenburg/A.J. Veldmeijer. Courtesy of MN, Rio de Janeiro]

Table 1 *Brasileodactylus araripensis* (SMNS 55414). Measurements of the mandible in mm (*: approximate)

Length, as preserved	252
Length symphysis–anterior aspect	174
Width at symphysis	20*
Width at third and sixth alveolus respectively	15*/12*
Thickness ramus	5*
Height at third/ninth alveolus respectively	11.7/19.7

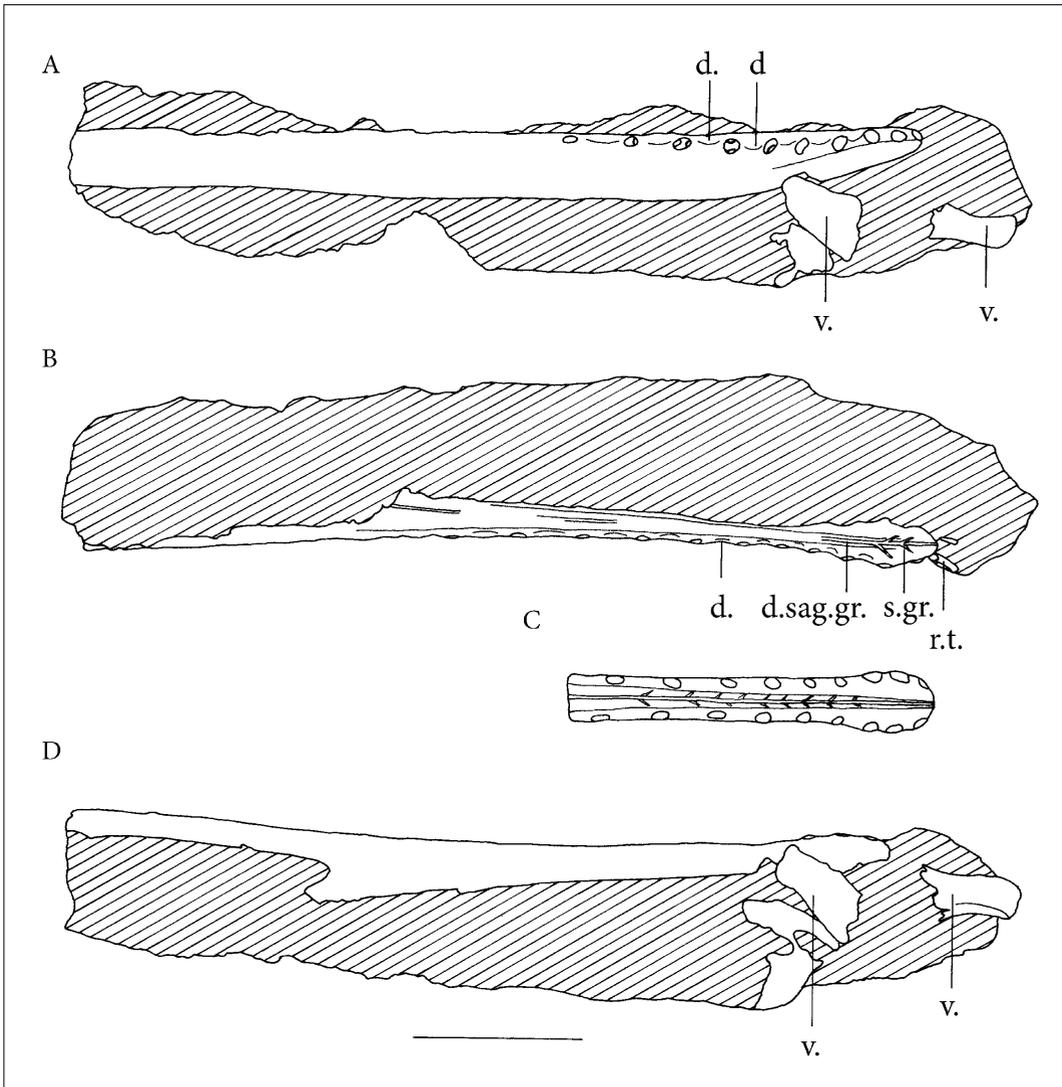


Figure 2. *Brasileodactylus araripensis* (SMNS 55414). Mandible in various views. **A**: right lateral; **B**: dorsal; **D**: ventral. **C** is the dorsal view of the holotype (MN 4804-V), housed in the MN, Rio de Janeiro. [Drawings by A.J. Veldmeijer; C is after Kellner (1984)]

die sich in proximaler Richtung verbreitet. Alveolen mit elliptischer [sic] und rundlicher Form, Zahnabstände vergrößern sich in proximaler Richtung. Bezahnung bis an die Unterkieferspitze, Zähne schmal und spitz, nach vorne stehend." English translation see Kellner & Tomida (2000: 102).

Emended diagnosis Combination of first pair of alveoli positioned at the anterior aspect; the

second pair of alveoli positioned anterolaterally and the third pair of alveoli laterally. The dentary sagittal groove has small anterolaterally extending side-grooves.

Discussion of diagnosis Kellner & Tomida (2000: 103) evaluated *Brasileodactylus* and came to the conclusion that "(4) rostral end expand from the third alveoli, forming a flat surface. (5) medial groove on the dorsal part

Table 2 *Brasileodactylus araripensis* (SMNS 55414). Measurements of dentition of the mandible in mm. (*: approximate)

Alveoli		Diastemae	
Number	Diameter	Number	Size
1	2.6*	1–2	1.3*
2	6.6	2–3	3.1
3	5.4	3–4	5.7
4	5.4	4–5	6.0
5	4.2	5–6	5.4
6	4.4	6–7	7.6
7	4.4	7–8	9.0
8	4.8	8–9	11.2
9	4.2	9–10	13.8
10	4.8	10–11	15.2*
11	2.7*		

of the symphysis, starting on the rostral tip and widening caudally” have to be regarded as apomorphies of *Brasileodactylus*. They regard the degree of expansion as apomorph (*ibidem*). Kellner (1984) regard *Brasileodactylus* as Ornithocheiridae. The rostral end starts to expand between the third and fourth alveoli, while between the fourth and fifth alveoli in *Anhanguera* and *Coloborhynchus*. However, the expansion in SMNS 55414 starts between the fourth and fifth alveolus as well. The expansion in *Brasileodactylus* is small but distinct, contrasting the robust expansion in *Coloborhynchus*, and equals the situation in *Anhanguera*. The configuration of the alveoli in the anterior part of the jaw, roughly the spoon-shaped expansion, is not seen in other pterosaurs. The first three pairs of alveoli are at the anterior, anterolateral and lateral aspect respectively (these are positioned anterodorsally and laterodorsally in *Anhanguera* and *Coloborhynchus*; the second and third pairs being orientated anterodorsally). The small side-grooves of the dentary sagittal groove are only seen in *Brasileodactylus* and are regarded as apomorph. The ‘?’ with the designation Anhangueridae will be explained in the discussion below.

***Brasileodactylus araripensis* KELLNER, 1984**

Holotype Anterior part of mandible, MN 4804–V, Museu Nacional, Rio de Janeiro, Brazil.

Diagnosis As for genus.

Description

SMNS 55414 agrees with the former descriptions of *Brasileodactylus* (Kellner 1984; Sayão & Kellner 2000). The long and slender lower jaw (Figs 1, 2; Tables 1, 2) is anteriorly slightly expanded and dorsally flattened, which results in a flat, spoon-shaped part. This expansion starts between the fourth and fifth alveolus. The jaw has its smallest width immediately posterior to the expansion but widens continuously posteriorly, including the rami. No sutures are observed.

Seen from a dorsal perspective, a dentary sagittal groove (d.sag.gr.), starting at the anterior aspect, continuously increases in width posteriorly and deepens as well. The sloping sides slightly bulge at the dorsal surface. At several points, the groove has small side-grooves (s.gr.), which are orientated anterolaterally. These side-grooves are not limited to the sloping faces of the groove, as in the holotype. Instead, some extend over it.

The first pair of alveoli is positioned at the anterior aspect whereas the second is positioned anterolaterally. The third and fourth alveoli are situated at the lateral aspect (the fourth slightly more laterodorsally) and the subsequent alveoli are positioned increasingly laterodorsally. The alveoli until the tenth point slightly anterodorsally rather than straight dorsally. The specific position of the first three pairs (respectively anterior, anterolateral, lateral) is not seen in any other pterosaur and can be regarded as apomorph for *Brasileodactylus*. The alveoli are slightly elliptical but almost circular in cross-section (with the long axis in an anteroposterior direction). From a laterodorsal position, the area between the alveoli and the diverging dentary sagittal groove at the dorsal aspect, is indented (d.). A replacement tooth can be seen at the posterior aspect of the first tooth right (r.t.).

Comparison and discussion

The presence of teeth excludes the classification as Tapejaridae. For the same reason, the specimen cannot be referred to the edentulous Azhdarchidae.

Comparison with the remaining, toothed, taxa from Brazil is limited to those that include cranial material. The various *Anhanguera* and *Coloborhynchus* species as well as *Criorhynchus* can be excluded from classificatory comparison because these genera all have premaxillary dentary crests; a feature which is not present in SMNS 55414. The remaining taxa are *Brasileodactylus araripensis* KELLNER, 1984, *B. cf. araripensis* SAYÃO & KELLNER, 2000 and *B. sp. indet.* VELDMEIJER, 2003b, *Cearadactylus atrox* LEONARDI & BORGOMANERO, 1985 and *Cearadactylus? ligabuei* DALLA VECCHIA, 1993. The presence of a crest cannot be excluded in *Cearadactylus atrox* (see Kellner & Tomida 2000). *Cearadactylus? ligabuei* has no crest, but doubts have been raised whether the parts of which the specimen consists, actually belong to one individual (*ibidem*, but see Unwin 2002); comparison should be viewed in this light. Therefore, it is difficult to use this specimen in comparative

anatomy. Differences between SMNS 55414 and *Cearadactylus* are the dorsal bending of the snout, as seen in *C.? ligabuei* (but not in *C. atrox*). The dentition pattern is not known in *Cearadactylus*. There is a slight anterior expansion of the anterior part of the mandible. Another difference between *C. atrox* and SMNS 55414 is seen in the morphology of the anterior part of the mandible, which shows a gap between upper and lower jaws when closed in *C. atrox*. It is, however, pointed out by Kellner & Tomida (2000) that this can only be observed after complete preparation and they suggest that the gap is far less pronounced than originally proposed.

Comparable features are the dorsoventrally compressed jaws (again not entirely excluded for *Cearadactylus atrox*). The number of teeth in the mandible of *Cearadactylus* is larger (28 in *C. atrox* and at least 22 in *Cearadactylus? ligabuei* based on the number of teeth in the skull). The skull in *C.? ligabuei* has a premaxillary sagittal ridge, which, as is assumed, corresponds with a dentary sagittal groove. If this is so, the groove did not start at the anteriormost aspect but rather more posteriorly, as seen in *Coloborhynchus robustus* (WELLNHOFER, 1987) (SMNK 2302 PAL; Fastnacht 2001).

Various fossils are known that are referred to as *Brasileodactylus*. However, comparison is limited to the holotype (Kellner 1984) and *B. cf. araripensis*. Comparison with *Brasileodactylus sp. indet.* (Veldmeijer 2003b: this New York specimen is currently under study) is limited because this fossil is still largely embedded, obscuring the dorsal and anterior aspects (which contain most of the diagnostic features). Comparison with *Brasileodactylus* reveals a high degree of resemblance. SMNS 55414 and the two mentioned specimens, have in common the slight anterior expansion of the dorsoventrally compressed anterior part, the lack of a dentary sagittal crest and the presence of a posterior widening dentary sagittal groove, which starts at the anteriormost aspect. Also visible in the holotype as well as the Stuttgarter mandible are the dentary side-grooves; a feature not seen

in other pterosaurs. Furthermore, the holotype and the specimen described in the present work have the anterior aspect with the three pairs of alveoli in common. Both the holotype and SMNS 55414 show the indented areas between the alveoli and dentary sagittal groove (a feature also seen in *Coloborhynchus robustus* SMNK 2302 PAL). This is not visible in the confer-specimen, which is due to the severe compaction of this fossil. The expansion of the anterior part of the mandible in SMNS 55414, however, is more pronounced and the jaw is comparatively more slender than the holotype (not clearly visible in the confer-specimen). Based on the small piece, the holotype seems to widen less strongly relative to SMNS 55414. Differences with *Ludodactylus sибbicki* FREY *et al.* 2003 are the fact that the lower jaw in this new species seems not expanded (but this cannot be ruled out entirely) and dorsoventrally compressed. The first three alveoli are positioned anterodorsally rather than anterolaterally and laterally. Apparently, *L. sибbicki* lacks the small side-grooves of the mandibular sagittal groove.

From the comparison it can be concluded that SMNS 55414 must be classified as *Brasileodactylus*. The only known species, *B. araripensis* consist of the anteriormost part and the differences with the described mandible are small (basically only the degree of posterior width and pronounced anterior expansion). This, however, does not warrant the establishment of a new species; the posteriorly increasing width in the Stuttgarter mandible seems to be stronger but cannot be properly compared with the incomplete holotype. Furthermore, it is assumed that the overall larger size of the holotype is to be regarded as variation within the species.

THE PARTIAL SKELETON IN THE MUNICH COLLECTION

Preservation

The fossil (BSP 1991 I 27) is a partial skeleton and consists of the anterior part of the maxilla

(lacking the anteriormost part), the proximal parts of both humeri (from the deltopectoral crest onwards), both complete scapulae, both complete coracoids, the distal part of the first wing finger phalanx, the proximal part of the second phalanx of the wing finger, the sixth to ninth almost complete cervical vertebrae, the first to tenth complete dorsal vertebrae (numbers nine and ten are broken and incomplete respectively), four pieces of rib, the left pubis, the dorsal piece of right ischium (including anteroventral part of acetabulum) and the anterodorsal piece of the left ischium and seven small fragments of vertebrae.

The anterior end of the maxilla is worn, showing rounded edges. This suggests that this end was sticking out of the matrix and eroded by water. This kind of wear is also seen in material from the Cambridge Greensands. Of the vertebrae, the sixth and seventh cervical vertebrae are not complete. Parts of the left postzygapophysis, exapophyses and the neural spine lack in the sixth cervical. The surface of the left lateral side lacks the outer bone layer, displaying a rough surface. The seventh cervical is even less complete, lacking a large part of the posterior condyle and exapophysis, the right prezygapophysis and the neural spine. The postzygapophysis at the right side is slightly damaged. The eighth cervical is complete but ventrally, the rim of the anterior cotyles is a little damaged. Most of the dorsals are slightly damaged; often pieces of the neural spines and the tips of the transverse processes lack. Only three ribs are partially preserved; the right one of the first dorsal vertebra is almost complete. Of the humeri, only the proximal parts, including the attachment of the deltopectoral crest, a feature which is often seen with humeri (e.g. De Buissonjé 1980; Wellnhofer 1991), have survived. The left one is almost intact, save some minor damage at the head; the right one is damaged at the inner side of the deltopectoral crest and at the posterior tuberosity.

Systematic palaeontology and description

(Figs. 3-11; Tables 3-11)

Brasileodactylus sp. indet.

Maxilla (Figs. 3, 4; Tables 3, 4)

The crestless maxilla, lacking the anterior-most tip, is slender, and broadens in posterior

direction. The preserved anterior end of the rostrum shows the beginning of an anterior expansion, the dimensions of which cannot be established. Seen from ventral, small foramina insert especially towards the expansion; from lateral view, the expansion starts immediately anterior to a narrowed area, containing three alveoli regarded as the fifth to seventh alveolus on the basis of the comparison with

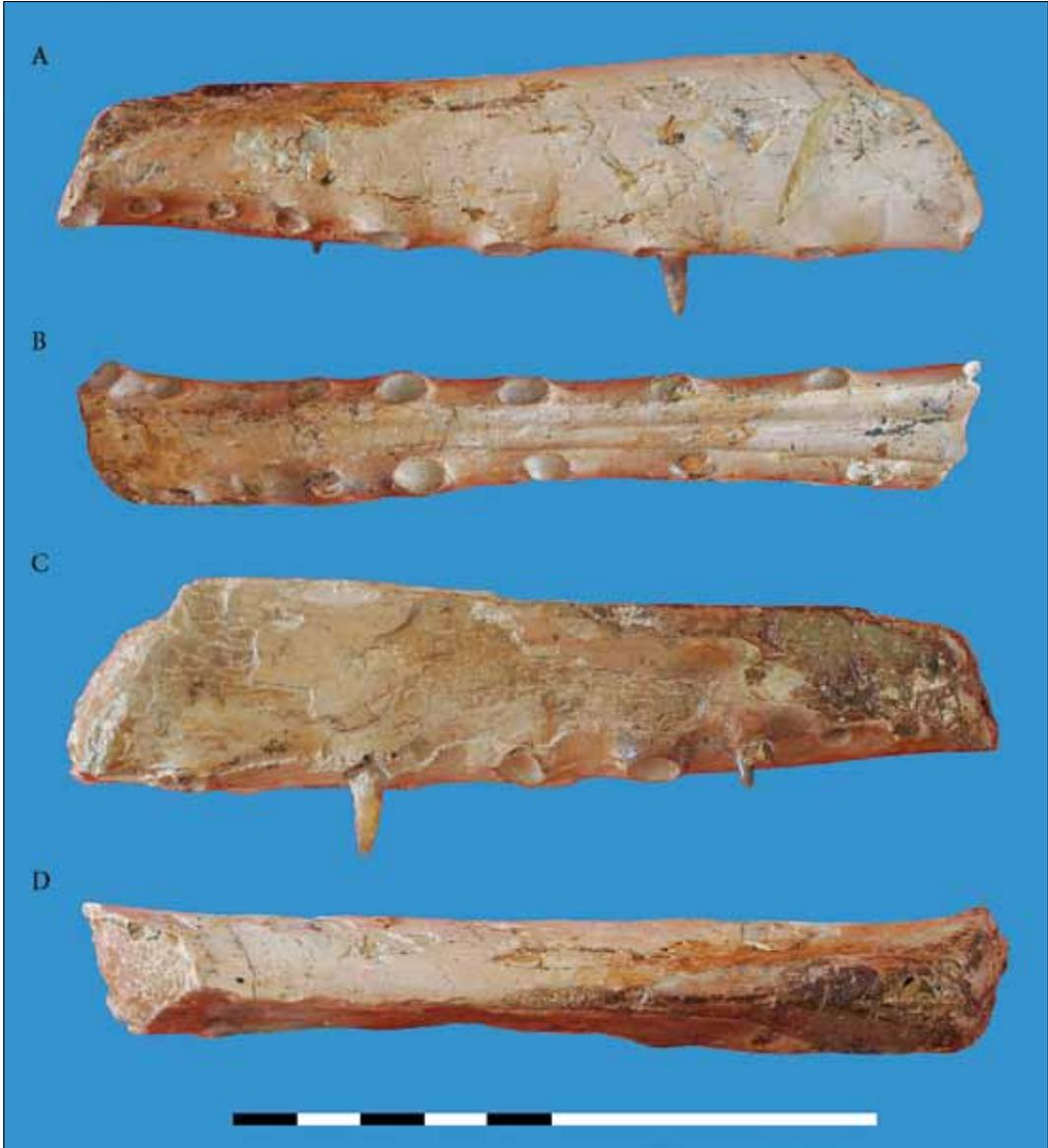


Figure 3 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Rostrum in various views. **A**: left lateral; **B**: ventral; **C**: right lateral; **D**: dorsal. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Eendenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

complete specimens. The preserved alveolus at the posterior beginning of the expansion of the left side is substantially bigger relative to the three alveoli in the retracted area and is bigger relative to the other alveoli as well. The three alveoli in the retracted area are amongst the smallest preserved. The alveoli are increasingly wider spaced in posterior direction. Some alveoli have erupting teeth preserved (the fifth and eleventh alveolus right and the sixth and tenth left). Only one fully erupted tooth is visible (tenth right): it points ventrally and faces slightly anteromedially. The cross-section is elliptical, with the inner (lingual) aspect flattened. Seen from ventral, at the posterior beginning of the retractions, anteroposterior ridges start that separate the tooth-bearing sides from the palate. Slightly posterior to this beginning emerges a small but distinct palatal sagittal ridge (pal.sag.r.), which widens slightly and becomes less well-defined posteriorly. In posterior direction, the dorsal border extends continuously dorsally. The cross-section is triangular.

Comparison *Criorhynchus* is one of the many taxa from the Cambridge Greensands that fuels long lasting discussions and many reviews. More recently, Fastnacht (2001) regards *Criorhynchus* a valid taxon, whereas Unwin (2001) does not and refers to Fastnacht's type specimen as *Ornithocheirus*, regarding it type specimen of Ornithocheiridae. Veldmeijer (2003a) refers to the Brazilian specimen as "*Criorhynchus*" *mesembrinus*. In doing so, he acknowledged the dichotomy but realised that only a detailed evaluation can shed light on this very complicated issue before accepting or

refuting one of the conclusions. In the present work, however, *Criorhynchus* is regarded a valid taxon (as a result of accepting *O. compressirostris* (OWEN, 1851) as type specimen of Ornithocheiridae, see Veldmeijer *et al.* (2006). The specimen recovered from the Cambridge Greensands is a small anterior piece of the rostrum of only few cm long and cannot be compared with BSP 1991 I 27 because this has no anterior parts preserved. Comparison is therefore concentrated on the Munich skull and mandible (BSP 1987 I 46) recovered from the Araripe basin. The presence of a premaxillary sagittal crest, which starts at the blunt anterior aspect, contrasts with the non-crested jaw of BSP 1991 I 27. In *Criorhynchus mesembrinus* (WELNHOFER, 1987), the palatal sagittal ridge is much stronger (even extending ventrally beyond the tooth-bearing ridges) and extends far anteriorly. The teeth in *Cr. mesembrinus* do not show a strong variation in size as seen in the Munich material but the alveoli can not be regarded completely isometric as suggested by Fastnacht (2001). The skull has no retracted ventral margins with smaller teeth.

Several skulls from the Araripe basin have been described and classified as species of *Coloborhynchus*. The type specimen, however, originates from England. In general, *Coloborhynchus* differs from BSP 1991 I 27 in the fact that *Coloborhynchus* has a premaxillary sagittal crest that starts at the anterior rostral margin. Other characteristics, such as the blunt anterior margin with teeth, cannot be compared due to the incompleteness of the material described here.

Comparison with *Coloborhynchus clavirostris* OWEN, 1874 is limited, because of

Table 3 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of the rostrum in mm. (*: approximate)

Length, as preserved	140
Width at anterior and posterior end respectively	21/19
Width between alveoli 3–4	20
Width between alveoli 6–7	16
Height at anterior and posterior end respectively	20*/31

the fact that the specimen is the anteriormost part of the skull, which is not preserved here. *Coloborhynchus clavirostris* has a premaxillary sagittal crest and a prominent palatal sagittal ridge, which extends much further anteriorly (almost until the anterior aspect). BSP 1991 I 27 has no crest and although the palatal ridge is distinct, it is more delicate and does not extend as far anteriorly. The senior author studied a referred skull of *Coloborhynchus araripensis* (see Kellner & Tomida 2000). The skull in having a flat rostrum with the first pair of teeth projecting, clearly shows features characteristic for *Coloborhynchus*. The holotype of *C.*

araripensis (Wellnhofer 1985) did not have the anterior part preserved that could be compared with the fossil described here. Except for the presence of the crest, the two specimens show a palatal ridge that extends in the same way and *Co. araripensis* also shows the retracted margin, containing three alveoli (5-7).

Comparison with the holotype of *Coloborhynchus robustus* is not possible due to the fact that this is only a lower jaw. The Karlsruhe specimen, however, (SMNK 2302 PAL), consist of the anterior parts of the mandible as well as the cranium (Fastnacht 2001). *Coloborhynchus robustus* differs, besides the

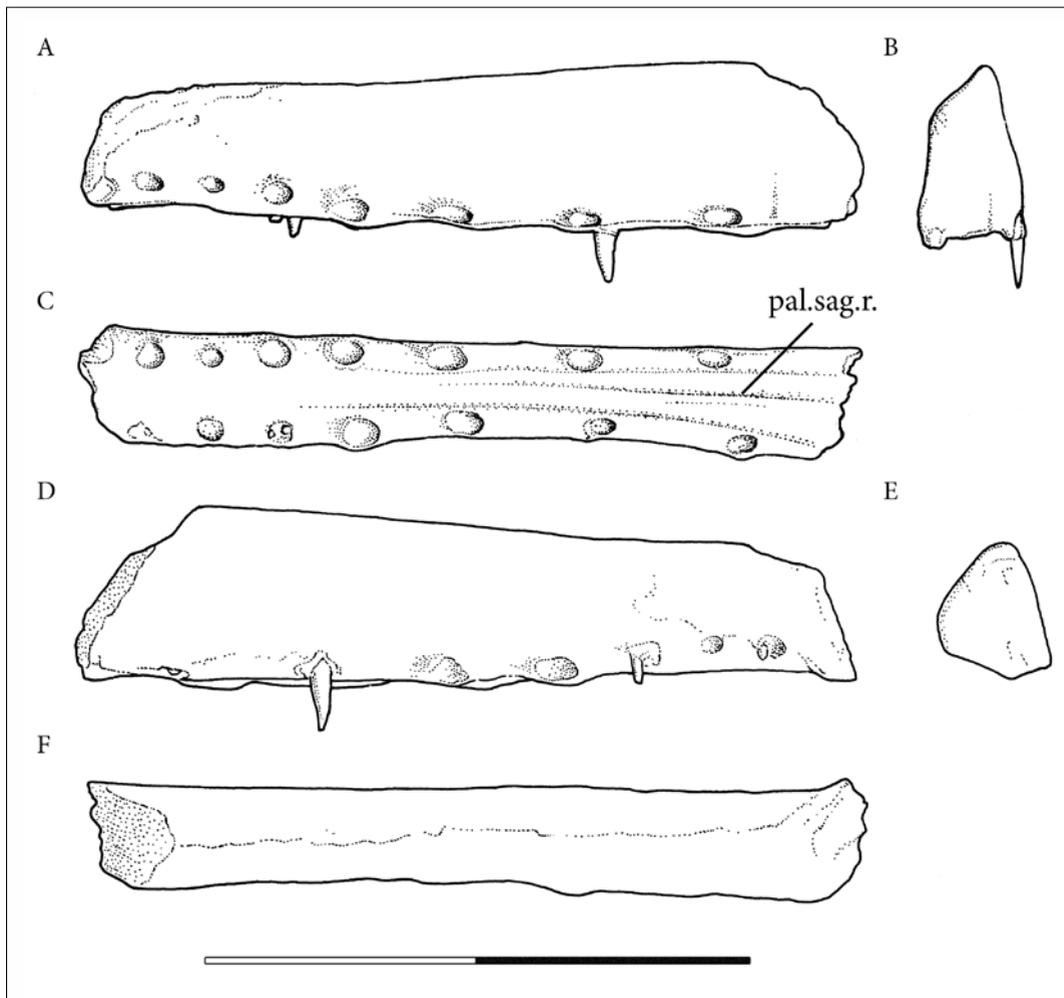


Figure 4 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Rostrum in various views. **A**: left lateral; **B**: posterior cross-section; **C**: ventral; **D**: right lateral; **E**: anterior cross-section; **F**: dorsal. Scale bar = 10 cm. [Drawings by A.M. Hense]

Table 4 *Brasileodactylus* sp. *indet.* (BSP 1991 I 27), measurements of dentition of the rostrum in mm. (*: approximate)

Number	Alveoli		Number	Diastemae	
	Diameter left	Diameter right		Size left	Size right
4	7.5*	–	4–5	3.5	–
5	5.3	5.1	5–6	6.6	6.1
6	4.1	4.5	6–7	6.0	6.5
7	5.5	5.8	7–8	8.1	7.5
8	6.9	7.5	8–9	11.4	12.6
9	7.5	6.3	9–10	15.5	16.1
10	6.5	5.9*	10–11	17.8	21.3
11	6.1	5.6			

crest, because it has a robust expanded anterior part and the jaw is not dorsoventrally flattened. A palatinal sagittal ridge might have been present, but would not extend far anteriorly. On the other hand, the ventral margin of the premaxilla is slightly retracted in which alveoli 5–7 are situated and this compares well with BSP 1991 I 27.

Coloborhynchus piscator (KELLNER & TOMIDA, 2000) differs besides the presence of a premaxillary sagittal crest, because of a relatively slight expanded anterior part, the much bigger size and the lack of a retracted ventral premaxillary margin. *Coloborhynchus spielbergi* VELDMEIJER, 2003a has a large premaxillary sagittal crest, a medially expanded anterior part and a slightly upwards bent snout. The ill-defined palatinal sagittal ridge extends until well onto the expanded part.

Cearadactylus atrox is not prepared three-dimensionally, thus important features might still be obscured. Furthermore, as mentioned previously, the fossil is in bad shape, which resulted in the rejection of few characters (Kellner & Tomida 2000).

Cearadactylus? ligabuei shows some comparable characters, but the specimen has a dubious reputation (see above). Nevertheless, the premaxilla has no crest and in this it compares well with the Munich specimen. Both fossils show a retraction in which smaller alveoli are positioned. However, the overall size of *C. ligabuei* is bigger and the dentition

of *Cearadactylus* and the specimen described clearly differ, the former being much bigger in general.

Anhanguera has also a premaxillary sagittal crest and differs therefore from the presented material. In *Anhanguera* the crest does not start at the anteriormost margin but more posteriorly. The snout anterior to the crest is dorsoventrally compressed. *Anhanguera blittersdorffi* CAMPOS & KELLNER, 1985 differs, besides the presence of a crest, in the fact that it has no retracted margin.

Comparison with *Anhanguera santanae* (WELNHOFER, 1985) is limited, because the holotype (BSP 1982 I 90) lacks the anterior portion. Still the beginning of a crest is visible. The second specimen of *A. santanae* (AMNH 22555, Wellnhofer 1991; see Veldmeijer 2003a for a discussion on the classification of the holotype and *A. santanae* in the AMNH collection) clearly shows the palatinal sagittal ridge, extending almost until the anterior aspect; the premaxilla has no retracted area.

Brasileodactylus is one of the first described pterosaurs from the region, based on cranial material. *Brasileodactylus* is one of the two specimens known from the basin (together with *Cearadactylus*) lacking a premaxillary sagittal crest. The type specimen of *Brasileodactylus* and holotype of *B. araripensis* consists of the anterior part of the mandible. Comparison with the Munich material is therefore not possible. The specimen described by Sayão & Kellner

(2000), originating from the Crato Member, consists of the anterior parts of the rostrum and mandible. The rostrum does not have a crest and no retraction of the ventral margin of the premaxilla. Sayão & Kellner (2000: 4) mention that: “Despite the fact that MN 4797–V was submitted to lateral compression during the fossilization process, it can be observed that the most anterior portion is expanded.” The ventral aspect of the skull is obscured. However, because the lower jaw has a groove, which extends until the anterior aspect (note that Sayão & Kellner (2000: 2) erroneously mention the presence of a medial ridge on the dorsal aspect of the lower jaw) it can only be tentatively assumed that the specimen has a corresponding sagittal ridge at the palate but absolute certainty cannot be obtained. The largely unprepared state of *Brasileodactylus* sp. indet. (AMNH 24444; Veldmeijer 2003b) did not allow a detailed comparison at the time, but at present the fossil is entirely prepared and under study. However, the specimen lacks a premaxillary sagittal crest and the anteriormost tip of the rostrum is dorsoventrally flattened. In this it compares well with the Munich material. The retraction of the ventral margin cannot be observed because this area is damaged at the exposed right side.

Comparison with the recently described *Ludodactylus sibbicki* shows that none of the specimens possess a premaxillary crest. On the other hand, the teeth seem to be bigger relative to BSP 1991 I 27 but no measurements are given of the dentition (and the fossil in general). The jaws are likely not expanded. Seen from lateral, the dorsal line of the maxilla in *Ludodactylus* is slightly concave, contrasting with the Munich mandible which has a straight edge that slopes towards the front continuously. Further comparison is hindered by the fact that *Ludodactylus* is compressed and not fully prepared, obscuring the ventral aspect.

Cervical vertebrae (Fig. 5; Table 5)

The general anatomical features compare well with previously described cervical vertebrae (Kellner & Tomida 2000; Veldmeijer 2003a; Wellnhofer 1985, 1991). The sixth and seventh

cervicals are somewhat similar to each other. They are strongly procoelous, with large neural spines. Large pneumatic foramina can be found at the lateral sides of the centra. The eighth and ninth cervicals are more similar to the dorsals; their centra are shorter and their neural spines are blunter and higher. Besides, they possess large attachment areas for ribs.

Sixth cervical vertebra (Fig. 5; Table 5)

The sixth cervical has a long, elongated centrum, which is, seen from ventral, strongly restricted in width in the middle. The centrum is slightly concave. Anteroventrally, a strongly developed hypapophysis (hyp.) is present, which fades continuously in posterior direction and disappears at approximately one third of the length of the centrum. The strongly concave cotyle (co.) has the characteristic triangular-like shape with a slightly indented middle part surrounded by a pronounced upper edge. The lateral edges continue at the ventral surface of the centrum where they end in small, elongated concave surfaces, orientated anterolaterally, likely for the attachment of the tuberculum (tub.) of a small cervical rib. The cotyle is laterally and slightly dorsally flanked by the prezygapophyses (pr.z.), displaying large anterodorsally and medially orientated articular surfaces, which are oval in shape. Posterior to the surfaces, a distinct protrusion points anteroventrally with a slight anterior orientation. Dorsally of the neural canal (n.c.) are two irregularly-shaped pneumatic foramina.

Seen from lateral, the centrum has two large foramina on each side. These foramina are separated from each other by a bony bar. The edges of the ventral surface run into the exapophyses (ex.p.), which extend dorsally and posteriorly. The flat posteroventral surfaces are incomplete, although only small parts are lacking. Although damaged, the size seems relatively large compared to known examples. Between these exapophyses and ventral to the condyle (cond.) is an ill-defined bean-shaped dent for the reception of the hypapophysis of the subsequent cervical. It is situated at the transition of the centrum and the ventral sur-

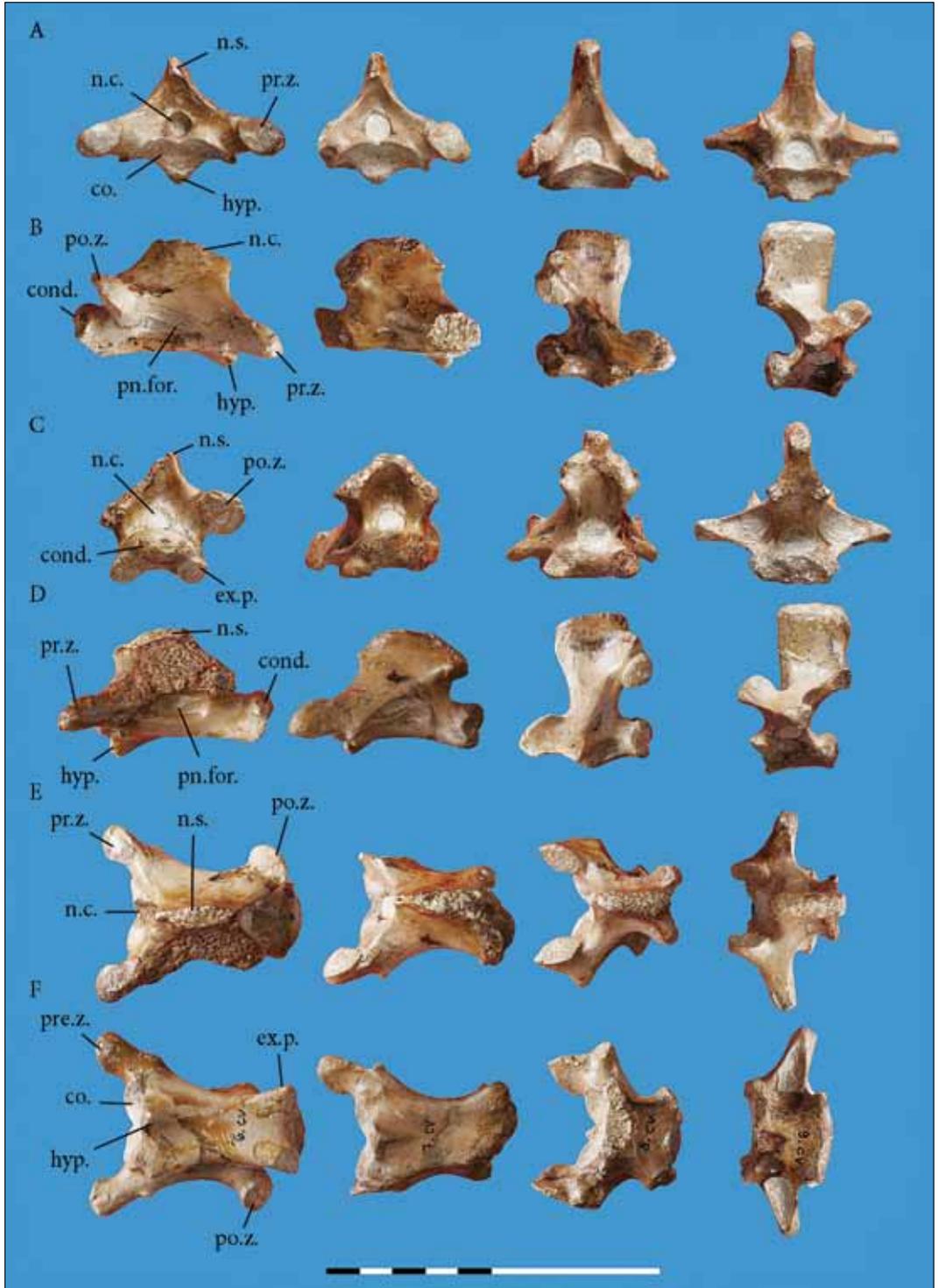


Figure 5 *Brasileodactylus* sp. indet. (BSP 1991 I 27). From left to right, sixth to ninth cervical vertebrae in various views. **A**: anterior; **B**: right lateral; **C**: posterior; **D**: left lateral; **E**: dorsal; **F**: ventral. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Enderburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

face of the condyle. The condyle is oval and smoothly rounded in dorsoventral plane; it is also rounded at the lateral sides, though less so. The condyle is laterodorsally flanked by the postzygapophyses (po.z.). The relatively large and flat ventral surfaces of these processes face posteroventrally and bear some ridges; cartilaginous tissue connected the processes with the subsequent vertebrae. The slightly oval neural canal lies deep between the postzygapophyses and is laterally flanked by foramina.

Comparison Differences between the sixth cervical in BSP 1991 I 27 and *Anhanguera santanae* are slight. The maximal width is larger in the Munich specimen. Seen from ventral, the hypapophysis is stronger and the centrum is more concave in BSP 1991 I 27. The postzygapophyses are larger. Seen from anterior, two pneumatic foramen are seen dorsal to the neural canal whereas there is only one, albeit larger, in *An. santanae*.

The sixth cervical in *Coloborhynchus piscator* is substantially larger in all respects, but Kellner & Tomida (2000) give no morphological description of the cervical. According to the authors (Kellner & Tomida 2000: 33) “[...] the lateral side {of the seventh cervical} shows that the lateral pneumatic foramen is divided by a bony bar, as in the seventh cervical of AMNH 22555 [...] and can be used to identify cervical 7, at least in *Anhanguera* [...]” However, also the sixth cervical of the Munich specimen displays such a bar, albeit tiny. The bar in the seventh cervical of the Munich specimen is, as seen in *Co. piscator* and *Anhanguera santanae*, much more robust.

Seventh cervical vertebra (Fig. 4; Table 5)

The description of the seventh cervical vertebra presents the differences with the sixth cervical. The centrum is shorter and the exapophyses are extending less ventrally. The posterior aspect is smaller; the neural canal is more circular and the ventral portion of the arch is deeper. The postzygapophyses are situated higher and extend less laterally. The large neural canal is also apparent at the anterior aspect. The sur-

faces of the prezygapophyses are slightly narrower; the protrusion posterior to the surfaces is more distinct. Seen from lateral, the two foramina are of different sizes; the dorsal one is far bigger relative to the ventral one and they are separated by a distinct and stout bony bar.

Comparison As with the previous cervical, differences between the presented cervical and *Anhanguera santanae* are slight. The size difference is, again, negligible. The centrum, seen from ventral, is more concave in the Munich material and the hypapophysis is stronger. The protrusions posterior to the articular surfaces of the prezygapophyses seem to be stronger developed in BSP 1991 I 27, but due to the incompleteness of the cervical of *A. santanae*, this statement is tentative. Seen from lateral, the foramina in the Munich cervical are smaller.

The seventh cervical in *Coloborhynchus piscator* is incomplete, which is the reason for the lack of measurements. However, based on own observations, it can be concluded that the width over the postzygapophyses is larger in *Co. piscator*. The overall measurements of the seventh cervical in *Co. spielbergi* is slightly larger. Seen from ventral, the centrum in the Munich material is more concave and the hypapophysis is stronger developed. Seen from lateral, the prezygapophyses extend more abrupt laterally from the centrum in *Co. spielbergi*; the anterior part however, containing the articular surfaces, turns stronger medially. The articular surfaces are orientated less dorsally and face stronger anteriorly. The cervical of *Co. spielbergi* does not show signs of the protrusion posterior to the articular surfaces of the prezygapophyses; also the small, elongated concave surfaces at the centrum which supposedly served for the reception of the tuberculum of the rib is not present. On the other hand, the left side of the Leiden cervical vaguely shows a line at the same position as the concave ventral border of the prezygapophysis in BSP 1991 I 27, between the protrusion for the reception of the tuberculum and the anterior articular surface of the prezygapophysis. The pneumatic foramina are smaller in *Co. spielbergi*.

Table 5 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of the cervical vertebrae in mm. (*: approximate)

	sixth	seventh	eighth	ninth
Length centra	47	40	25	20
Length over zygapophyses	58	50*	37	–
Width over postzygapophyses	42*	28*	21	–
Width over prezygapophyses	49	42*	33	28

Eighth cervical vertebra (Fig. 5; Table 5)

The following cervicals are completely different from the previous ones, despite the fact that they possess broad oval cotyles and condyles as well as large zygapophyses. The flat centrum is shorter than it is wide. The cotyle is oval rather than triangular in shape and lacks a hypapophysis. The dorsal rim of the cotyle is pronounced. The articular surfaces for the cervical rib are distinctly larger. Seen in anterior view, the cotyle is laterodorsally flanked by mediodorsally oriented prezygapophyses. The prezygapophyses have slightly convex and oval surfaces. The ventral portion of the neural arch is deep and extends dorsally from the centrum. Clear ridges extend from the prezygapophyses mediodorsally towards the neural spine. Seen from lateral view, two small foramina insert in the centrum; the dorsal one is slightly larger than the ventral one.

The condyle is less convex and, although clearly oval, it is less obvious relative to the previous cervicals. The exapophyses are wide but short. The dorsal border of the condyle is dented. The neural canal is circular and relatively large. The neural spine (n.s.) is higher, extends far more posteriorly and large prominent postzygapophyses are positioned high on the spine, flanking the ventral portion of the neural arch laterodorsally. The large flat surfaces of these postzygapophyses are oval; they face lateroventrally and short processes are situated laterodorsally to them. At the posterior edge of the transverse process there is a foramen, lateral to the neural canal. Seen from ventral, small foramina insert approximately halfway the centrum and the attachment area for the capitulum of the rib. The transverse process ends in an articular surface for the

reception of the capitulum of the rib. The articular surface of the reception of the tuberculum of the cervical rib is placed at the lateroventral edge of the cotyle.

Comparison Again, the size difference between the eighth cervical in BSP 1991 I 27 and that of *Anhanguera santanae* is negligible. Seen from ventral view, the ridge that separates the condyle from the ventral aspect in *A. santanae* is not present in BSP 1991 I 27. Instead, the condyle extends slightly onto the ventral surface; the exapophyses extend stronger in lateroventral direction. The dent, anterior to the ridge, is distinct in *A. santanae* but is lacking in the Munich material. Seen from anterior, the cotyle in BSP 1991 I 27 has a dent in the dorsal rim; this is not visible in *A. santanae*. The cotyle in the latter, however, is slightly larger in dorsoventral plane.

The eighth cervical in *Coloborhynchus piscator* is substantially larger in all respects. The centrum is not fused, contrasting with the fused state of the Munich cervical, despite the fact that both animals were not yet fully grown when they died. The eighth cervical in *Coloborhynchus spielbergi* is longer but especially wider over the prezygapophyses. The proximal parts of the ribs are still attached to the cervical; the sutures are clearly visible. Seen from ventral view, the exapophyses are less pronounced relative to BSP 1991 I 27. From anterior, the prezygapophyses have a higher position in *Co. spielbergi* and the neural arch is less deep. The pneumatic foramina at the posterior aspect of the lateroventrally descending prezygapophyses are not seen in *Co. spielbergi*. The dorsal rim of the cotyle is substantially more pronounced in BSP 1991 I 27

but *Co. spielbergi* has a dent in the dorsal rim as well (contrary to *A. santanae*).

Ninth cervical vertebra (Fig. 5; Table 5)

This ninth cervical differs considerably from the former; again the description focuses on the differences between the two. The cotyle is oval but the middle is more strongly dented and the lateral sides are pointed. A small rectangular process is situated at the ventral rim; if this process is to be regarded as a hypapophysis, it differs considerably from the ones seen at the midcervicals in the fact that the latter ones are far stronger and pointed. The process is laterally flanked by small protrusions, which are the attachment areas for ribs. The ventral portion of the neural arch is slightly sunken and there are no ridges that extend from the prezygapophyses mediodorsally towards the neural spine. The prezygapophyses face almost entirely medially and the surfaces are completely smooth. They are positioned higher up in respect to the eighth cervical. Ventral to them are two small foramina.

The transverse processes (t.p.) appear lightly constructed; indeed, much more so than in the eighth cervical. They face posterolaterally instead of lateroventrally and anteriorly as seen in the eighth cervical. The processes are stout and robust. Seen in lateral view, the foramina in the centrum are distinctly smaller.

Seen in ventral view, the centrum is again short compared to the midcervicals, but it is almost as wide as long and slightly concave. The condyle is only weakly convex and the exapophyses are slight bulges in the laterodorsal corners. The dorsal border is indented; the indentation is smaller but sharply defined. The large neural canal is rounded triangular. The neural spine is higher but less wide in anterior-posterior plane. The postzygapophyses are considerably smaller and lack the laterodorsal processes.

Comparison The ninth cervical in *Santanadactylus brasiliensis* DE BUISONJÉ, 1980 (this notarium is included in the genus on the basis of its size) is fused with the first dorsal

of the notarium, but Wellnhofer *et al.* (1983) does not regard it as part of the notarium. The cervical is incomplete which hinders a detailed comparison with the material described in the present work. The size is comparable to the Munich specimen.

The ninth cervical in *Anhanguera santanae* (AMNH 22555) is not entirely fused with the following vertebra but the exact state of fusion is difficult to determine due to the fact that it has not been prepared entirely. The size is comparable (contra Wellnhofer 1991) to BSP 1991 I 27 but the prezygapophyses in the Munich cervical are more distinct, protruding slightly more in anterior direction and separating more clearly from the transverse process. From anterior view, the pneumatic foramina on each side of the neural canal and ventral to the prezygapophyses are larger in *A. santanae*; there is one foramen on each side (contra Kellner & Tomida 2000). In BSP 1991 I 27, the left side has two small foramina whereas the right side has only one.

Coloborhynchus piscator has a larger ninth cervical, which is not fused to other cervicals or dorsals. The suture between the neural arch and centrum is still visible, contrasting with the condition in the Munich specimen. Furthermore, Kellner & Tomida (2000) mention the presence of two small foramina at the anterior aspect, on each side of the neural canal. As mentioned above, BSP 1991 I 27 has only two foramina on the left side. The ninth cervical in *Coloborhynchus spielbergi*, which is of comparable size to BSP 1991 I 27, is firmly co-ossified with the notarial dorsals. Veldmeijer (2003a) regards the cervical as part of the notarium. Unfortunately, the vertebra is damaged, which limits the extent of a detailed comparison. The foramina on each side of the neural canal consist of one big and few small ones. The small remnants of the transverse processes in *Co. spielbergi* suggest a less ventral and posterior orientation, although no certainty can be obtained. The neural spine is less stout in the Munich cervicals.

In general, the cervical vertebrae of BSP 1991 I 27 does not account for an identification

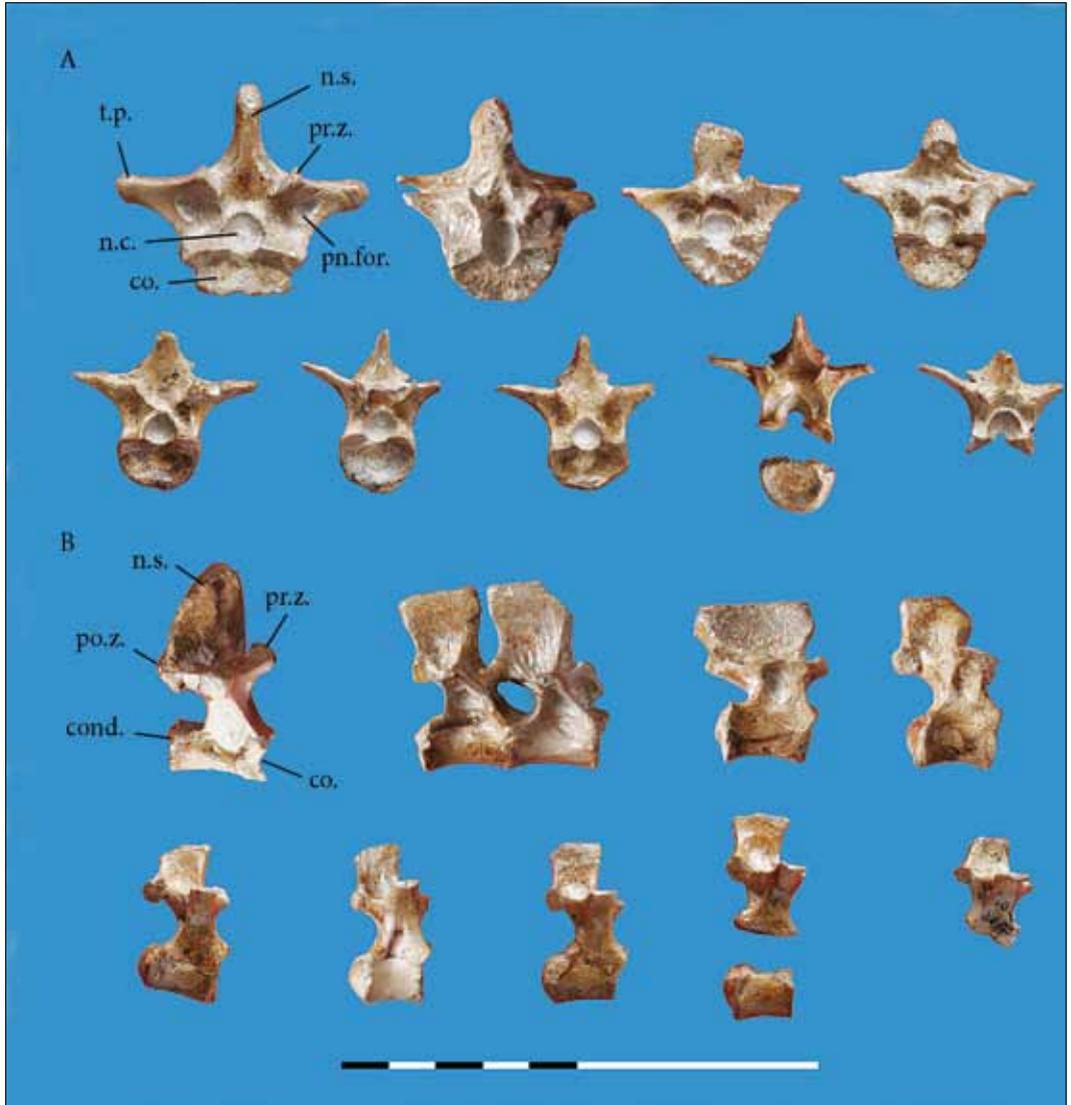


Figure 6 *Brasileodactylus* sp. indet. (BSP 1991 I 27). From left to right, first to tenth dorsal vertebrae in **A**: anterior; **B**: right lateral. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Eendenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

at species level: vertebrae morphology seems conserved throughout pterosaur species. It is noted, however, that not all vertebrae were completely fused.

Dorsal vertebrae (Fig. 6; Table 6)

The general anatomical features compare well with previously described dorsal vertebrae (Veldmeijer 2003a; Wellnhofer 1985, 1991). The dorsals display strong similar morphology, although they got increasingly smaller. The

first dorsals (and the last cervical), however, are often fused into a notarium. All dorsals display the demarcation between the neural arch and the centrum, but the sutures become clearer with each subsequent posterior dorsal. The neural arch and the centrum of the ninth and tenth dorsal are not fused. Individual attention is given to the first six dorsals.

The description of this first dorsal vertebra concentrates on the differences with the ninth cervical. This vertebra, the first true dorsal,

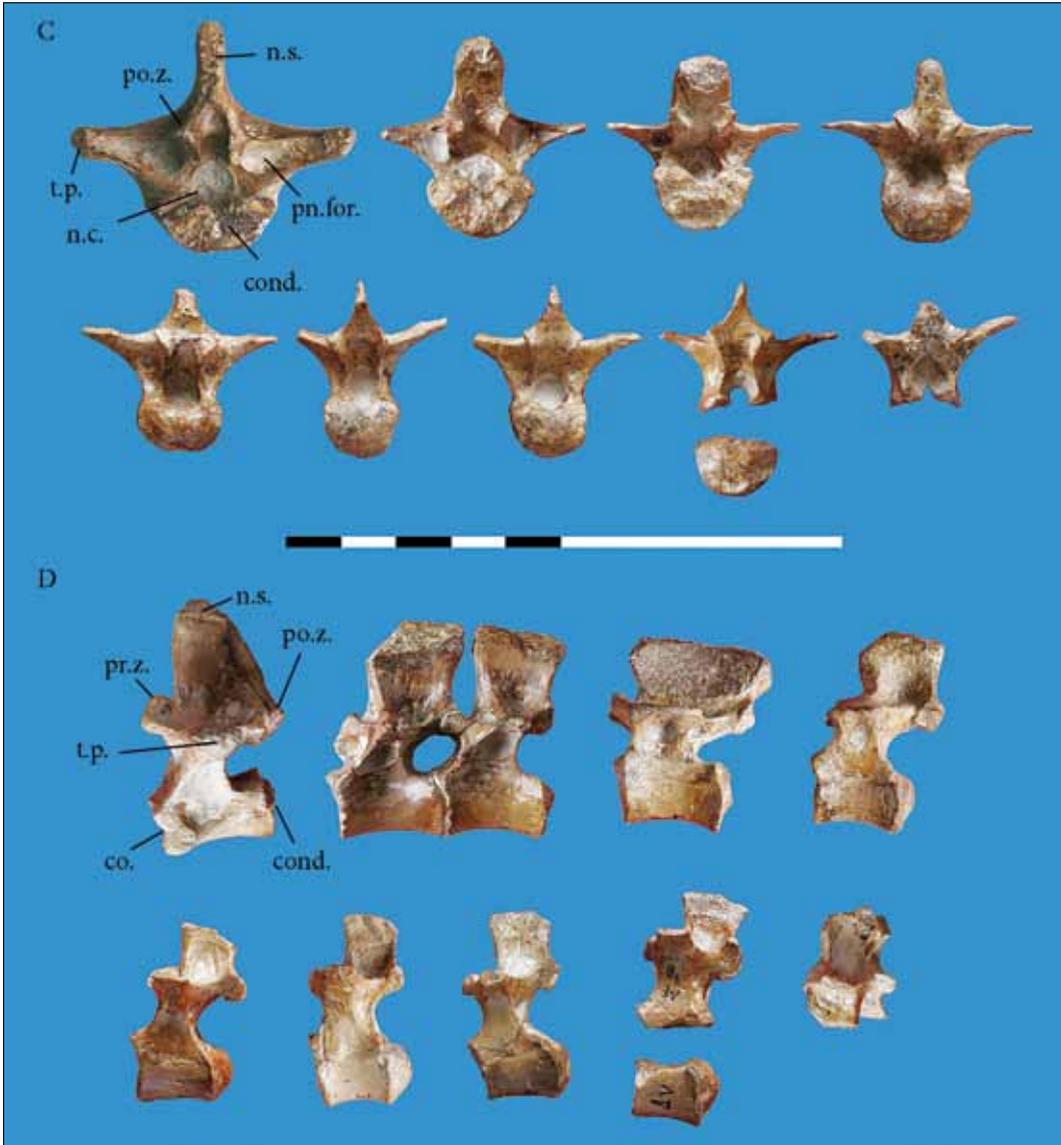


Figure 6 (continued) *Brasileodactylus* sp. indet. (BSP 1991 I 27). From left to right, first to tenth dorsal vertebrae in **C**: posterior; **D**: left lateral. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Eendenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

compares with the last cervical but in general the vertebra is smaller. The cotyle is shallow and only the mediodorsal rims are protruding. There is no hypapophysis and the lateral protrusions are only faint traces. Seen from anterior, the ventral portion of the neural arch, having an almost circular neural canal, is slightly sunken. The orientation of the prezygapophyses is comparable with those in the ninth

cervical but they are considerably smaller. Large foramina are situated lateroventral to the prezygapophyses. The transverse processes extend posterolaterally. These processes in the ninth cervical are oriented in the same direction but slightly more posteriorly. Foramina are situated at the anterolateral sides of the neural spine (which is thinner than in the ninth cervical) and mediodorsally to the prezygapophyses.

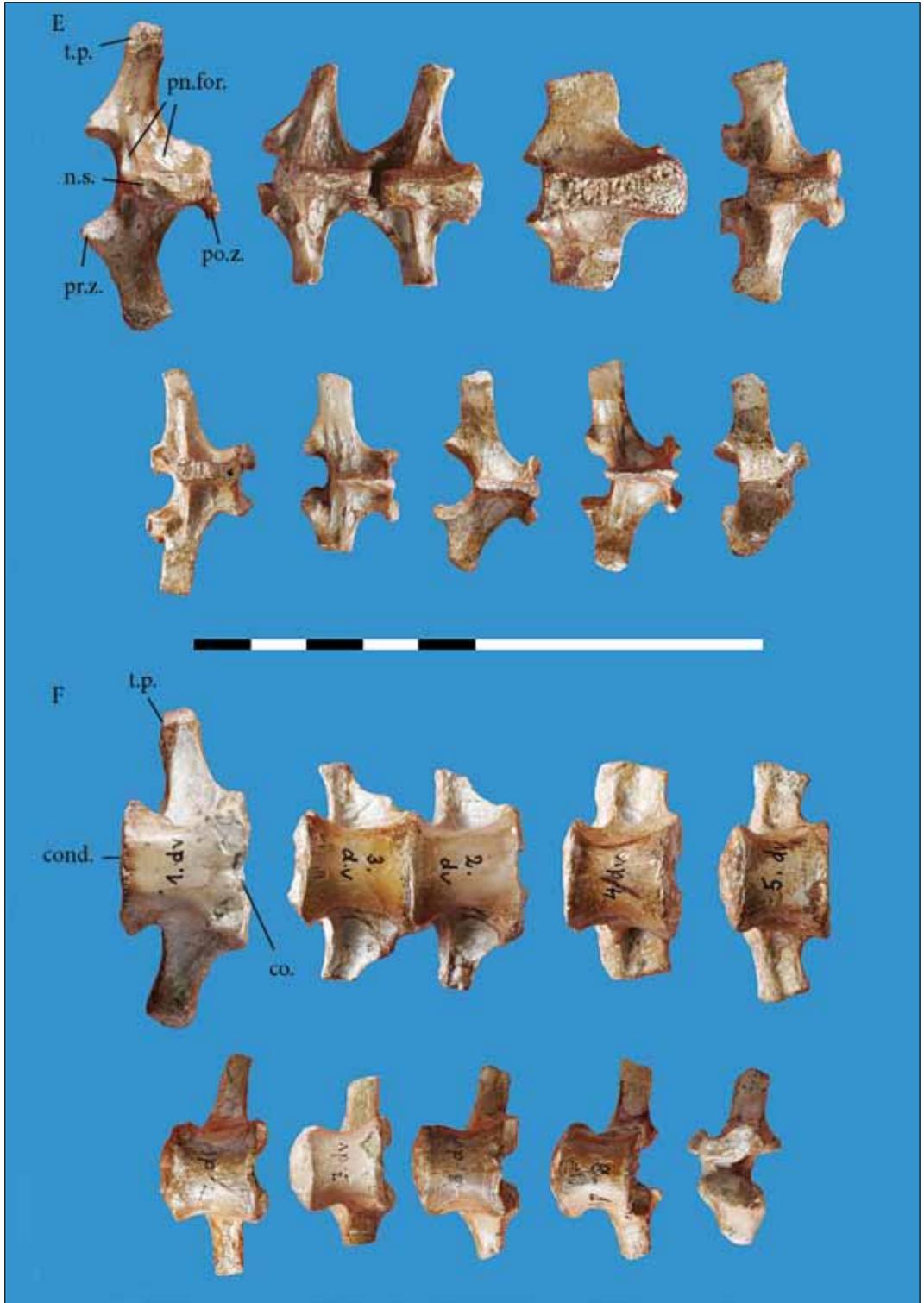


Figure 6 (continued) *Brasileodactylus* sp. indet. (BSP 1991 I 27). From left to right, first to tenth dorsal vertebrae in **E**: dorsal; **F**: ventral. Scale bar = 10 cm. [Photographs by A. 't Hoof, reworked by E. Enderburg/A.J. Veldmeijer; Courtesy of BSP, Munich]

Table 6 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of the dorsal vertebrae in mm. Remark: right transverse process of the third dorsal is complete. (*: approximate)

	first	second	third	fourth	fifth	sixth	seventh	eighth	ninth	tenth
Length centra	19	17	17	19	17	16	15	14	13	–
Height	41*	36	34	30*	34	31*	32	32	32*	–
Width over transverse processes	51*	36*	36*	36	40	38	29*	32*	34	30*
Width over postzygapophyses	13	11	12	13	13	12	12	12	12	13*
Width over prezygapophysis	18	14	11	12	14	13	12	13	13	13
Length neural spine	–	17*	16	24*	14*	10*	10	11*	12*	8*
Thickness neural spine (dorsalmost)	5*	4*	6	10*	5	4*	2	3	2	3*

The centrum has a more elongated appearance; it is longer than wide. The condyle is almost smooth and there are no exapophyses. Seen from posterior view, the ventral portion of the neural arch is deeply sunken with a strongly protruding posterior side of the neural spine. The postexapophyses are situated close together and the surfaces are facing less laterally; instead they face posterolaterally and slightly posteroventrally.

The fused second and third dorsal vertebrae are comparable to the first dorsal, despite being of overall smaller dimensions. In general, the vertebrae are even more lightly built, with more and larger foramina. The cotyle of the second dorsal lack the lateral protrusions entirely and the neural canal is slightly elongated and circular. The prezygapophyses are lower on the transverse processes and the surfaces are turned slightly outwards, viz. anteriorly. The transverse processes are thinner and less wide. The neural spine of the second dorsal equals the spine of the first in morphology although it is slightly less high. The neural spine of the third, however, becomes thicker posteriorly, starting from halfway the anterior-posterior width, and its height decrease. The centrum of the second and third dorsals are more strongly concave relative to the first.

The fourth dorsal differs from the previous ones in the fact that the dorsal is more stout. There are foramina in the same places (flank-

ing the neural canal at the anterior aspect laterally, ventrally and posteroventrally to the transverse processes and flanking the neural canal at the posterior aspect laterally) but they are less numerous and smaller in size. The transverse processes are flat, broad and relatively short. Seen from lateral, the anterior corner has distinct articular surfaces for the capitulum of the rib. The thick neural spine is much more robust and contains the oval, slightly saddle-shaped scapula articulation surfaces. The centrum is even more concave.

The fifth dorsal is less robust than the fourth and is more comparable to the second and third dorsals. The neural spine is of limited height and smaller. The transverse processes are still short, broad and flat but less so than seen in the fourth dorsal; their orientation is completely lateral, although they are slightly tilted in anterodorsal direction. The thin bony flange between the process and the cotyle, as so prominent in the second dorsal, is almost absent, resulting in a 'freestanding' transverse process. The foramina are larger in respect to those in the fourth dorsal and of comparable size as those of the second, including the large foramina dorsal to the prezygapophyses. The prezygapophyses are small and the surfaces are slightly anterodorsally orientated. The postzygapophyses are more prominent and lack foramina at the transverse processes, lateroventral to the postzygapophyses, in contrast to the situation in the third and fourth ones.

The sixth to tenth dorsals continuously decrease in overall size. The cotyles and condyles are strongly concave and convex, respectively. The neural spines are thinner and the transverse processes smaller (anterior-posterior). There are no articular surfaces for ribs anymore. The prezygophyses are oriented mediodorsally.

Comparison Comparison with the dorsals in *Anhanguera santanae* is limited due to the damaged state of the material but the remnants suggest a high degree of resemblance, morphologically as well as biometrically. The specimens of *Anhanguera* that includes these parts of the post-cranial skeleton (besides AMNH 22555 also BSP 1982 I 91), never show the dorsals fused into a notarium. This is also the case with BSP 1991 I 27, although two vertebrae already started to fuse. Posteriorly, from the seventh dorsal onwards, the dorsals in *Anhanguera* tend to decrease in size more rapidly relative to BSP 1991 I 27 (on the basis of the length of the neural spine; the only measurement given for AMNH 22555 by

Wellnhofer 1991). Wellnhofer (1991) counted 13 dorsals in AMNH 22555; the number in BSP 1991 I 27 is ten, but the unfused remnants of at least two more vertebrae is among the material. The largely unprepared and damaged state of *A. santanae* (BSP 1982 I 91) limits the comparison as well, but suggests a high degree of similarity.

On the comparison with the notarium in *Santanadactylus brasiliensis* see the comparison with the ninth cervical, the first vertebra of the notarium. We can note that morphologically, the material is highly comparable but the notarial dorsals are larger (on the basis of the measurements of the centra) than the same dorsals in the Munich material; the free dorsals (numbers six to nine) are slightly larger as well, but the difference is less pronounced. These dorsals in *S. brasiliensis*, however, do not decrease in size as is visible in the material described in this work.

The dorsals in *Coloborhynchus spielbergi* differ especially in their overall larger size, besides the fact *Co. spielbergi* has a true notarium. The only dorsals preserved in



Figure 7 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Ribs in various views. **A**: cervical rib in posterior and anterior aspect; **B**: right and left dorsal rib in posterior aspect; **C**: right and left dorsal rib in anterior aspect. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Endenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

Table 7 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of the ribs in mm.

ninth cervical rib, left	Length, as preserved, without bending	74
	Width over articular facets	23
first dorsal rib, right	Length, without bending	109
	Length, with bending	115
	Width over articular facets	28

Coloborhynchus piscator are the first five, which are comparable in length and morphology to *Co. spielbergi*, but, in contrast to it, show largely unfused centra. They are larger than the dorsals in BSP 1991 I 27.

The attachment area for the scapula is positioned at the fourth dorsal in all discussed *Anhanguera* and *Coloborhynchus* specimens, as is the case in BSP 1991 I 27. This differs from the situation in *Arthurdactylus conan-doylei* FREY & MARTILL, 1994, in which the notarium consists of three fused spines (nothing can be said on the centra), two serving as attachment area for the scapula. Although Frey & Martill (1994: 395) admit that “[...] nothing can be said about the vertebrae anterior to the preserved part of the notarium. The fact that these vertebrae are missing indicates that there was probably no fusion at all” they nevertheless use the fusion of these three in their diagnosis of *Arthurdactylus*. The unfused state of notaria is generally regarded as an ontogenetic rather than a morphological character.

Ribs (Fig. 7; Table 7)

Three (pieces of) ribs are part of the remains. One of these is the proximal two thirds of the rib of the ninth cervical. In articulation with the cervical, the rib extends posterolaterally. The shaft of the double headed rib extends lateroventrally and is distinctly curved. The shaft is thin: 4.5 mm. The tuberculum is small and situated close to the shaft; the tubercular articulation is oval and flat. The triangular capitulum is more pronounced and extends from the shaft of the rib; the shaft has a flat ventral surface that transforms into the small ventral aspect of the shaft of the rib proper. The capitular articulation is strongly con-

vex. The surrounding bone of both processes are rugose, which likely is, as suggested by Bennett (2001), an indication of the fusion of the rib to the vertebra. A pneumatic foramen is situated between the capitulum and tuberculum at the posterior surface.

One set of ribs is preserved, which is to be regarded as notarial rib, though the first dorsal was not fused into a notarium. The ribs are of comparable size to the previously described cervical rib and the curvature is comparable as well. The shaft extends lateroventrally and is also bent in posterior direction. The capitular shaft extends stronger ventrally and the big capitular articulation is convex and oval. The tuberculum (tub.), positioned at the shaft, is bigger than the capitular articulation with a flat and almost circular articulation. Also with these notarial ribs, rings of rugose bone are situated along the margins of the articulations, suggesting the fusion of the ribs and the notarial dorsal.

Comparison Comparison with the partly prepared ribs in *Anhanguera santanae* reveal a high degree of similarity. This is also true for the fragments of ribs in *Coloborhynchus spielbergi*. The ribs in *Coloborhynchus piscator* are slightly larger but morphologically highly comparable.

Scapula and coracoid (Fig. 8; Table 8)

The general morphology of the bones of the shoulder girdle agrees with that described for other pterosaurs from the Araripe Basin (Kellner & Tomida 2000; Veldmeijer 2003a; Wellnhofer 1991). The scapula is the shortest of the two and a stout bone. Both scapulae are complete, although one is damaged medially.



Figure 8 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Left and right scapula in various views. **A**: dorsal; **B**: posterior; **C**: anterior; **D**: medial; **E**: ventral and **F**: lateral. Left and right coracoid in various views. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Eendenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

The shaft is restricted and the proximal articular surface expanded. A deep pit is visible on the proximal articular surface. The articular surfaces with the coracoid are strongly expanded as well. The coracoid is far less stout but longer. The articular surfaces, with the sternum as well as with the scapula, are small.

Comparison As already stated, the scapulae and coracoids share the same general morphology as the described species of *Coloborhynchus* and *Anhanguera*. However, the shoulder bones are firmly fused in *Coloborhynchus spielbergi*, contrasting with the unfused state in the Munich specimen as well as in the other *Coloborhynchus* and *Anhanguera* species.

The bones in *Coloborhynchus spielbergi* and *Co. piscator* have slightly larger overall dimensions; the bones in *Anhanguera* are of



Figure 8 (continued) *Brasileodactylus* sp. indet. (BSP 1991 I 27). Left and right scapula in various views. **G:** lateral; **H:** ventral; **I:** posterior; **J:** dorsal; **K:** medial and **L:** anterior. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Endenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

Table 8 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of the scapula and coracoid in mm.

Scapula	Length, without bending	94
	Width head	25
	Height head	17
Coracoid	Length, without bending	125
	Width head	18
	Height head	17
Scapulocoracoid	Length articulated scapulocoracoid, distal	244

comparable size. Shoulder bones, fused into a scapulocoracoid, have been described for *Santanadactylus brasiliensis*. Comparison is hindered by the fact that this specimen is largely incomplete.

Humerus (Fig. 9; Table 9)

Humeri of Brazilian pterosaurs are relatively common in the fossil record and general morphology of the here presented humeri agree with former descriptions (especially Kellner & Tomida 2000; Veldmeijer 2002, 2003a;

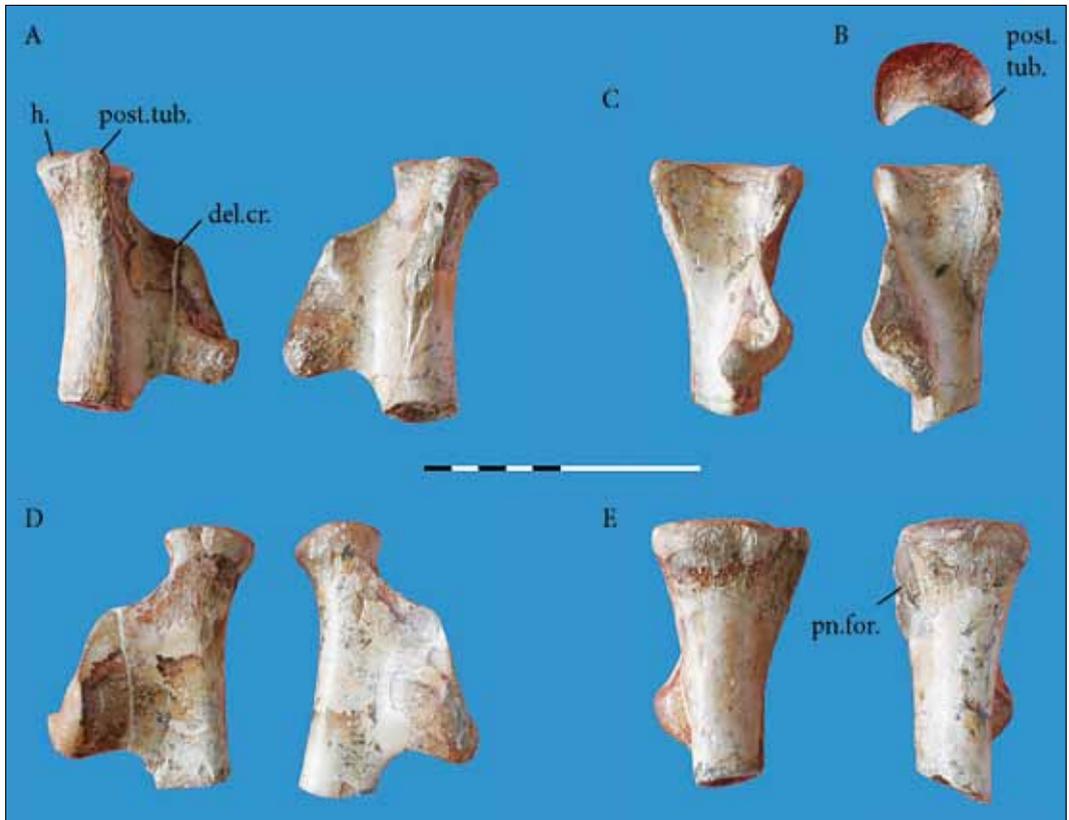


Figure 9 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Left and right humerus in various views. **A**: posterior; **B**: proximal; **C**: ventral; **D**: anterior and **E**: dorsal. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Endenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

Table 9 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of right humerus in mm.

Length, as preserved	95
Width head	43
Height head	29
Maximum height deltopectoral crest	60
Distance distal edge crest–head	80
Diameter shaft	25 × 27

Wellnhofer 1985, 1991). In general, they are comparatively short, but robust, are expanded at their proximal and distal ends and have a prominent deltopectoral crest.

The head (h.) is elongated anteroposteriorly. The articulation surface is kidney-shaped without a ridge. The depression of the head lies ventrally and continues slightly at the ventral surface, where it is limited by a small ridge, which probably served as an insertion for joint-stabilising ligaments. Seen from ventral view, the area distal to this ridge and posteromedial to the deltopectoral crest is depressed.

The posterior tuberosity (post.tub.) extends from the shaft towards the head. It is a large expansion, relative to the head, but substantially smaller relative to the deltopectoral crest. Seen from dorsal, a pneumatic foramen inserts in the tuberosity proximally.

The deltopectoral crest (del.cr.) extends laterally, starting as a thin proximal flange and continuing with a curve inwards (i.e. in posterior direction) towards the ventral end of the crest. The margin of the flange has a distinct convex bend at the place where the flange changes its inward direction into more outward (i.e. in anterior direction) bending. The lateral end is greatly thickened and curves anterolaterally towards the shaft. The concave inner surface has prominent scars for muscle attachment.

Comparison The humerus of *Anhanguera santanae* compares morphologically as well as biometrically well with the Munich material, although the ventral rim of the deltopectoral crest has a less strong convex bend in *Anhanguera* relative to BSP 1991 I 27. The ventralmost tip of the crest curves stronger

inwards in *Anhanguera*.

The humerus of *Santanadactylus brasiliensis* differs especially in the fact that the head is more bulbous dorsoventrally. The humeral head in *Santanadactylus* is directed stronger in dorsal direction. This latter feature can be seen in the humerus of *Santanadactylus pricei* WELLNHOFER, 1985 as well; however, the strong convex bend of the rim of the deltopectoral crest, not seen in the other species of *Santanadactylus*, is clearly visible here but the flange does not have a strong inwards (i.e. posterior) direction. This humerus is also much smaller.

The humerus of *Coloborhynchus araripensis* differs also especially in the fact that the head is more bulbous dorsoventrally. A clear ridge is positioned at the anterodorsal edges of the head, lacking in the Munich material. The humerus described here has the same morphology as *Coloborhynchus piscator* but the latter is larger in overall dimensions. Comparison with the humerus of *Coloborhynchus spielbergi* is limited due to the fact that the humerus in the latter is relatively damaged, especially the deltopectoral crest. However, the remaining part of the crest seems to incline inwards (i.e. posteriorly) far less and the convex bend of the rim of the crest is faint. An ill-defined ridge is noticed at the humeral head, though this can hardly be the same ridge as described in *Santanadactylus*, since its position and shape is quite different. Nevertheless, a comparable ridge has not been described in BSP 1991 I 27.

Wing finger phalanges (Fig. 10; Table 10)

Only small parts of the hyperelongated phalanges of the right wing finger are among



Figure 10 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Distal part of the first wing finger phalanx right in various views. **A**: dorsal; **B**: posterior; **C**: ventral; **D**: anterior; **E**: distal. Proximal part of the second wing finger phalanx right in various views. Scale bar = 10 cm. [Photographs by A. 't Hooft, reworked by E. Endenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

the remains; the distal end of the first phalanx and the proximal end of the second phalanx of the wing finger are preserved. Both bones show rugose areas near the articular surfaces.

In dorsal view, the first phalanx is flat, but seen from ventral it is convex. The cross-section of the distal part of the first phalanx is rounded triangular; the bone is slightly thicker at the edges (3.5 mm versus 1.3 mm) (*cf.* Frey & Rieß 1981). In distal direction, the shaft increases in all directions towards the articular surface. The articular surface is expanded towards the proximal and the surface is strong convex.

The oval articular surface of the second phalanx is concave and expanded posteriorly; it corresponds perfectly with the convex surface of the first phalanx. The bone is distinctly smaller. The phalanx is slightly bent in ventral direction. Seen from ventral, the shaft exhibits a longitudinal groove, resulting in an irregular triangular cross-section.

Comparison Only few wing finger phalanges have been published, of which only some are complete (Wellnhofer 1985, 1991); various others are incomplete (Frey & Martill 1994; Kellner & Tomida 2000) or incom-



Figure 10 (continued) *Brasileodactylus* sp. indet. (BSP 1991 I 27). Distal part of the first wing finger phalanx right in various views. **F**: proximal; **G**: dorsal; **H**: anterior; **I**: ventral; **J**: posterior; **K**: distal. Scale bar = 10 cm. [Photographs by A. 't Hoof, reworked by E. Endenburg/A.J. Veldmeijer; Courtesy of BSP, Munich]

Table 10 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of the first and second phalanges of the right wing finger in mm.

first phalanx wing finger	Length, as preserved	130
	Width head	47
	Height head, as preserved	21
	Diameter shaft	18 x 27
second phalanx wing finger	Length, as preserved	212
	Width head	47
	Height head	22
	Diameter shaft	19 x 12

pletely prepared. The comparison of the distal articular area of the first phalanx reveals great similarity with the known specimens. The complete second phalanx of the wing finger in *Coloborhynchus piscator* has not been illustrated, but on the basis of own observations by the senior author, it can be concluded that the two phalanges share the same morphology. The second phalanges in *Santanadactylus pricei* differ in the fact that these do not exhibit the longitudinal groove, seen in the Munich material and in *Co. piscator*. It is interesting to note that this configuration of the second phalanx is considered by Martill & Frey (1999) as a character diagnostic for the pterodactyloid family Azhdarchidae.

Pelvic girdle (Fig. 11; Table 11)

Three parts are preserved of the pelvic girdle. The left pubis, a laterally compressed bone and relatively long, is preserved. The morphology compares well with previously-described specimens (Kellner & Tomida 2000; Veldmeijer 2003a; Wellnhofer 1988). The dorsal part is strong and massive and closes the acetabulum posteroventrally; the ventral plate is gradually more compressed ventrally and has a twisted appearance.

Table 11 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Measurements of the left pubis in mm.

Length	52
Width, ventral	31



Figure 11 *Brasileodactylus* sp. indet. (BSP 1991 I 27). Parts of the pelvis. **A**: left pubis; **B** and **C**: parts of the left and right ischium. Scale bar = 5 cm. [Photographs by A. 't Hooft, reworked by E. Eendenburg/A.J. Veldmeijer. Courtesy of BSP, Munich]

The other remnant is the dorsalmost part of the left ischium; the part makes up the anteroventral part of the acetabulum. It is broken at the rim. The anterodorsal corner of the right ischium is the third part. Also this bone compares well with previous descriptions.

DISCUSSION

As explained previously, the material housed in the Stuttgart and Munich collections is only compared with toothed taxa from Brazil and, if necessary, with taxa from the Cambridge Greensands, England. The morphology of the lower jaw SMNS 55414 separates it from all known mandibles, except *Brasileodactylus*. The Munich specimen, lacking a mandible, has been assigned to *Brasileodactylus* because of the lack of a premaxillary crest (only seen in *Cearadactylus* and *Ludodactylus*), but the dentition is clearly distinct from *Cearadactylus*. It has not been assigned to *Ludodactylus* due to the stronger teeth in this new genus as well as the non-expanding configuration of the jaws.

Various authors have suggested *Brasileodactylus* to be synonymous with *Anhanguera* (Unwin 2001) or *Coloborhynchus* (Frey *et al.* 2003). As remarked by Veldmeijer & Signore (2004) "The explanation of the supposed difference as the result of ontogeny, sexual dimorphism or variation cannot be proven, mainly due to the scanty fossil record (most of the species are represented by only one (published) specimen, often consisting only of parts of the skull); the fossils should therefore be treated as a different species unless proven (and not just suggested) otherwise." On the other hand, as pointed out elsewhere (Kellner & Tomida 2000; Veldmeijer *et al.* 2005; Veldmeijer & Signore 2004), *Brasileodactylus* is a valid taxon, exhibiting unique configuration of dentition and morphology of the dorsal aspect of the lower jaw, as explained in the emended diagnosis.

The situation on family level of the Brazilian pterosaurs (family in the traditional sense) is complex. The Ornithocheiridae are primarily composed of taxa from the Cambridge Greensands; the Anhangueridae mainly from

taxa from the Araripe Basin. The two taxonomic units have been synonymised by various authors (e.g. Unwin 2001) but this is based on the difference in view of the assignment of the type species for Ornithocheiridae with authors who regard them separated (Kellner 1990; for an overview see Kellner & Tomida 2000). It is beyond the scope of the present work to untangle this complicated issue but we regard Anhangueridae as valid and different from Ornithocheiridae, in this agreeing with the designation of *Ornithocheirus compressirostris* as type species of Ornithocheiridae (see Kellner & Tomida 2000; Veldmeijer *et al.* 2006).

The present work has no intention to give a full pterosaur phylogeny, but rather wants to pinpoint some flaws in the analysis of pterosaurian remains thus far. If we accept the diagnosis for Anhangueridae as presented by Campos & Kellner (1985, but see Veldmeijer 2006), *Brasileodactylus* cannot be assigned to it due to the lack of crests. But it is clear that *Brasileodactylus* shares many features with *Coloborhynchus* and *Anhanguera* (anterior expansion of the jaws, dentition pattern, mandibular groove (even though the morphology varies in the various taxa) and post-cranial characteristics as well), making a classification close to the Anhangueridae obvious. The type specimen of the Ornithocheiridae is crestless as well, but the overall morphology of the jaw differs far more (see Veldmeijer 2006) from *Brasileodactylus*. None of the existing models create a satisfying solution (Kellner 2003; Unwin 2003). The creation of a new family including the crestless taxa (thus *Brasileodactylus*, *Cearadactylus* and also *Ludodactylus*) which are closely related to the Anhanguerids (closer than to the non-crested Ornithocheirids) seems to be an option. The alternative would be a subfamily, together with the Anhanguerids, within a larger group, based on dental characters. However, as shown above, this would lead to exclusion of *Criorhynchus*, even though the non-dental morphology clearly shows a close relationship. Until more complete material of especially *Brasileodactylus* has been published, it seems

irresponsible to erect such a group; therefore, reference to classification is marked with ‘?’.

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