

Brasileodactylus (Pterosauria, Pterodactyloidea, Anhangueridae); an update

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Summary

The majority of the toothed pterosaurs from the Araripe Basin in Brazil (Santana and Crato Formations) have premaxillary sagittal crests and dentary sagittal crests. A few skulls, however, lack such crests and ever since these fossils have been published, discussion continues whether these are independent taxa, ontogenetic variants or sexual dimorphics of other taxa. The present work presents an update, discussing the dentition and other morphological features, previously unnoticed, in order to evaluate the systematic position of the taxon.

Samenvatting

Het merendeel van de getande pterosauriërs die afkomstig zijn uit het Araripe Basin in Brazilië (Santana en Crato Formaties) hebben een premaxilla sagittale kam en een dentary sagittale kam. Er zijn echter een paar taxa die geen kammen hebben op deze plekken op de schedel en vanaf het allereerste moment dat deze fossielen bekend waren, is er gespeculeerd of deze een geldig taxon zijn of dat deze dieren ontogenetische of sexueel dimorfische varianten zijn van andere taxa. Deze bijdrage presenteert een update waarin het gebit gepresenteerd en kort besproken wordt, alsmede enkele morfologische kenmerken die eerder over het hoofd werden gezien, met als doel de systematische positie van het taxon *Brasileodactylus* te evalueren.

Introduction

Ever since the first pterosaur was discovered, this extraordinary group of vertebrates has been the subject of much debate and discussion. This is partly due to the fact that the pterosaur skeleton is extremely fragile and as a consequence, there are only relatively few fossils and even fewer well preserved complete specimens which have been adequately prepared. Nowadays, there are a few major sites for pterosaurs, of which the Araripe basin in Brazil is the most important one.

The aim of the present work is to present an update of the toothed pterodactyloid taxon *Brasileodactylus* on the basis of the skull, since long the most distinctive element in the pterosaur skeleton. Consequently, only comparable taxa from Brazil will be discussed of which cranial material is known and therefore *Arthurdactylus conandoylei* Frey & Martill, 1994, *Araripedactylus castilhoi* Price, 1971, *Araripedactylus dehmi* Wellnhofer, 1977, *Santanadactylus brasiliensis* De Buissonjé, 1980, *Santanadactylus pricei* Wellnhofer, 1985 and *Santanadactylus spixi* (Wellnhofer, 1985) are left out.

Dentition is sometimes used for systematic purposes (especially Unwin (2001) used the relative size, but the material he used is extremely fragmented and no reliable picture of the entire dentition can be obtained), although the

measurements are most of the time not included (exceptions are Fastnacht (2003), Lee (1994) and Veldmeijer (2003b)). Therefore, measurement of teeth and alveoli are included in the present work and discussed. A few problems, however, occur which complicate the taxonomic issue.

Materials and methods

The following specimens are used for comparison:

- Skull of *Anhanguera blittersdorffi*, MN-4805-V
- Skull and mandible of referred specimen of *Anhanguera blittersdorffi*, n. 40 Pz-DBAV-UERJ
- Skull *Anhanguera santanae*, AMNH 22555
- Mandible *Anhanguera* sp., AMNH 22573
- Mandible *Anhanguera* sp., SAO 200602
- Anhanguerid skull in the Iwaki Museum, IMNH 1053
- Skull and mandible cf. *Brasileodactylus araripensis*, MN-4797-V
- Anterior part mandible *Brasileodactylus araripensis*, MN-4804-V
- Anterior part mandible *Brasileodactylus ?araripensis*, MN-6517-V
- Skull and mandible *Brasileodactylus* sp., AMNH 24444
- Partial skull *Brasileodactylus* sp., BSP 1991 I 27
- Anterior part skull *Coloborhynchus clavirostris*, BMNH 1822

- Mandible *Coloborhynchus robustus*, BSP 1987 I 47
- Skull and mandible *Coloborhynchus piscator*, NSM-PV 19892
- Anterior parts skull and mandible *Coloborhynchus robustus*, SMNK 2302 PAL
- Skull *Coloborhynchus* sp, MN-4735-V
- Skull *Coloborhynchus* sp, SAO 16494
- Skull and mandible ?*Coloborhynchus* sp., MN-6687-V
- Skull ?*Coloborhynchus* sp, MN-6503-V
- Mandible ?*Coloborhynchus* sp., MN-6687-V
- Skull and mandible *Coloborhynchus spielbergi*, RGM 401880
- Skull and mandible *Criorhynchus mesembrinus*, BSP 1987 I 46
- Mandible cf. *Criorhynchus mesembrinus*, SMNS 56994
- Undescribed skeleton of a crestless pterosaur in the Kitakyushu museum

Institutional abbreviations:

BMNH = British Museum of Natural History, London; BSP = Bayerische Staatsammlung für Paläontologie und historische Geologie, Munich; IMNH = Iwaki Museum of Coal Mining & Fossils, Iwaki; MN = Museu Nacional, Rio de Janeiro; NSM = National Science Museum, Tokyo; Pz-DBAV-UERJ = Geological Museum University of Rio de Janeiro; RGM = Nationaal Natuurhistorisch Museum (Naturalis), former Rijksmuseum voor Geologie en Mineralogie, Leiden; SAO = Sammlung Oberli, St. Gallen; SMNK = Staatliches Museum für Naturkunde,

Karlsruhe; SMNS = Staatliches Museum für Naturkunde, Stuttgart.

All measurements of alveoli and diastemae have been taken laterally except for the anterior and anterolateral alveoli. These are measured lateral-lateral and anterolateral-ventrolateral respectively. The patterns are visualised in a graph (graph 1 & 2).

The known specimens

Type specimen of *Brasileodactylus* and holotype of *Brasileodactylus araripensis* (Fig. 1).

Order Pterosauria Kaup, 1834
Suborder Pterodactyloidea Plieninger, 1901
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



Fig 1 Type specimen of *Brasileodactylus* and holotype of *Brasileodactylus araripensis*, MN 4804-V. Courtesy of Museu Nacional, Rio de Janeiro, Brasil. Photograph by E. Endenburg / A.J. Veldmeijer

Type specimen van *Brasileodactylus* en holotype van *Brasileodactylus araripensis*, MN 4804-V. Met dank aan Nationaal Museum, Rio de Janeiro, Brazilië. Foto door E. Endenburg / A.J. Veldmeijer



Fig 2 The Crato specimen, MN 4797-V. Courtesy of Museu Nacional, Rio de Janeiro, Brasil. Photograph by E. Enderburg / A.J. Veldmeijer

Het Crato stuk, MN 4797-V. Met dank aan het Nationaal Museum, Rio de Janeiro, Brazilië. Foto door E. Enderburg / A.J. Veldmeijer

des Unterkiefers (distaler Teil), die sich in proximaler Richtung verbreitet. Alveolen mit elliptischer und rundlicher Form, Zahnabstände vergrößern sich in proximaler Richtung. Bezahnung bis an die Unterkieferspitze, Zähne schmal und spitz, nach vorne stehend." (For 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 anterolateral and the third pair of alveoli lateral. The dentary sagittal groove has small anterolaterally extending sub-grooves.

Discussion of diagnosis: Kellner & Tomida (2000: 103) evaluated *Brasileodactylus* and came to the conclusion that "4) rostral end expand from the 3rd alveoli, forming a flat surface. 5) medial groove on the dorsal part of the symphysis, star-

ting on the rostral tip and widening caudally." have to be regarded as apomorphies of *Brasileodactylus*." They regard the *degree* of expansion as apomorph (ibidem: 103). Kellner (1984) regards *Brasileodactylus* as Ornithocheirid. The rostral end starts to expand between the third and fourth alveoli, which is 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, very similar to the situation in *Anhanguera*, and is not consistent with the robust expansion in *Coloborhynchus*. 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*; both second and third pairs are orientated anterodorsally. The remaining alveoli are placed strongly laterodorsally, relative to, for instance,



Fig 3 The New York specimen, AMNH 24444. Courtesy of AMNH, New York. Photograph by E. Endenburg/A.J. Veldmeijer

Het stuk uit New York, AMNH 24444. Met dank aan AMNH, New York. Foto door E. Endenburg / A.J. Veldmeijer

comparable alveoli in *Coloborhynchus* as preliminary results of study in progress suggests.

In general, the alveoli are small. The first tooth is the smallest, after which the tooth size increases.

The third alveolus is the largest of the alveoli found in the distal expansion; the following alveoli decrease in size continuously but the size increases again steadily from the sixth alveolus

onwards. This results in the ninth alveolus being as large as the third one (remarkable is Kellner's statement on the teeth, as they are not preserved in the specimen).

The small sub-grooves of the dentary sagittal groove are only seen in *Brasileodactylus* (holotype and SMNS 55414) and are regarded as apomorphy. Finally, the symphysis is extremely elongated relative to other Brazilian pterosaurs like *Anhanguera* (for instance, Veldmeijer *et al.*, in press a), *Criorhynchus* (Wellnhofer, 1987; Veldmeijer, 2002; Veldmeijer & Hense, 2004) and *Coloborhynchus* (for instance, Kellner & Campos, 2000; Veldmeijer, 2003b).

Although we think that the absence of features should not be used in a diagnoses, the absence of crests seems to be important in the studied taxa. Most pterosaurs from this area have crests, premaxillary as well as dentary. Though recently a new pterosaur has been published (Frey *et al.*, 2003) without premaxillary and dentary sagittal crests but with a parieto-occipital crest, discussed in more detail below. So far, *Cearadactylus* and *Brasileodactylus* are the only genera without the premaxillary and dentary crests.

The Crato specimen (MN 4797-V; Fig. 2)

Various fossils have been assigned to *Brasileodactylus*. The fossil in Figure 2, originating from the Crato Formation of the Araripe plateau (in the collection of the Museu Nacional, Rio de Janeiro; MN 4797-V), has been assigned to the genus by Sayão & Kellner (2000) as *Brasileodactylus* sp. mainly on the basis of the absence of crests and the presence of a mandibular groove. However, a mandibular groove starting at the tip of the dentary can be found in other pterosaurs as well (for instance, *Coloborhynchus robustus*), but the type specimen of *Brasileodactylus* as well as the mandible in the Stuttgarter collection (see below) clearly shows small anterolateral running sub-grooves. Due to the fact that the fossil is severely deformed by compression, it cannot be determined whether these peculiar sub-grooves are present or not. Furthermore, it is difficult to determine the exact position of the alveoli, due to the deformation, although at least the second and third right alveolus seem to be in a laterodorsal position rather than anterolateral and lateral respectively. According to the authors, the most anterior portion is expanded, containing the

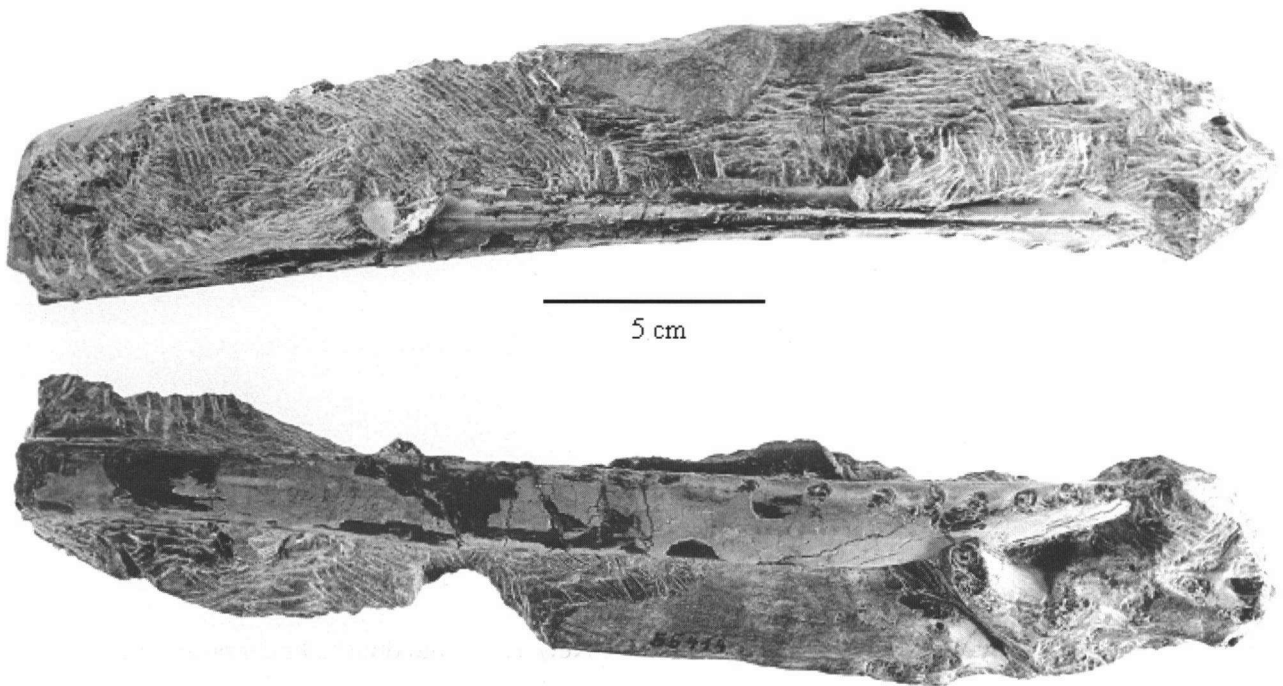


Fig 4 The Stuttgarter mandible, SMNS 55414. Courtesy of SMN, Stuttgart. Photograph by R. Harling

De onderkaak uit Stuttgart, SMNS 55414. Met dank aan SMN, Stuttgart. Foto door R. Harling

largest teeth, although it is not stated which ones exactly. However, the graph shows that the second to fourth alveoli are the biggest together with the seventh alveolus (see below).

The measurements are comparable to the type specimen of *Brasileodactylus* and holotype of *Brasileodactylus araripensis* (MN 4804-V), although slight differences can be noticed (for instance, the first and sixth alveolus). A major difference is seen in the measurements of the eighth, tenth and eleventh alveolus, which are decreasing in size relative to the previous alveoli. This contrasts with the holotype (MN 4804-V), which shows an increase in alveolar diameter, relative to the preceding ones.

The dentition of the skull shows a comparable pattern as seen for the mandible, but with two distinct differences. The third alveolus is clearly the biggest; the differences in measurement of this and the other alveoli are distinctly bigger than seen in the mandible. Furthermore, the eleventh alveolus is the smallest in the mandible, but in the skull, the smallest alveoli are the fifth and sixth; the size of the eleventh alveolus equals that of the tenth and are of comparable size to the fifth and sixth.

The New York specimen (AMNH 24444; Fig. 3)

The fossil in the collection of the American Museum of Natural History (AMNH 24444), preliminary described by Veldmeijer (2003a) as *Brasileodactylus* sp. has been assigned to this genus for several characters, among which the

most important ones are the lack of maxillary and dentary sagittal crests and the teeth. However, in due course the published table (Veldmeijer, 2003a: 11) should be revised because more details can be added after complete preparation of the fossil. The complete preparation of this specimen, which at this moment is being undertaken in The Netherlands, is important, because relevant characteristic features, such as the exact position of the first three alveoli, a possible expansion of the jaws and the sub-grooves, are obscured by matrix. Recently, a new genus and species has been published, which originates from the Crato member (Fig. 4), *Ludodactylus sibbicki* Frey *et al.* 2003 (in the collection of the Staatliches Museum für Naturkunde Karlsruhe, Germany) that looks remarkably similar to *Brasileodactylus* sp. (teeth, crestless dentary and premaxilla) but seems to differ in the presence of a parieto-occipital crest, seemingly lacking in the AMNH 24444 specimen. However, the dorsal view of the cranium (Veldmeijer, 2003a: figures 3 and 4) shows a possible start of a parieto-occipital crest (referred to as frontoparietal crest in Veldmeijer, 2003a). The crest might have been broken off, so the exact shape and its extend cannot be determined. Detailed research of *Ludodactylus sibbicki*, currently in progress, will possibly shed light on the attachment of the crest to the skull. Only after the full preparation of AMNH 24444 a detailed comparison can be done and conclusions be drawn. The first alveolus of the mandible is comparable to the size of this alveolus in the other discussed specimens, but the second, third and

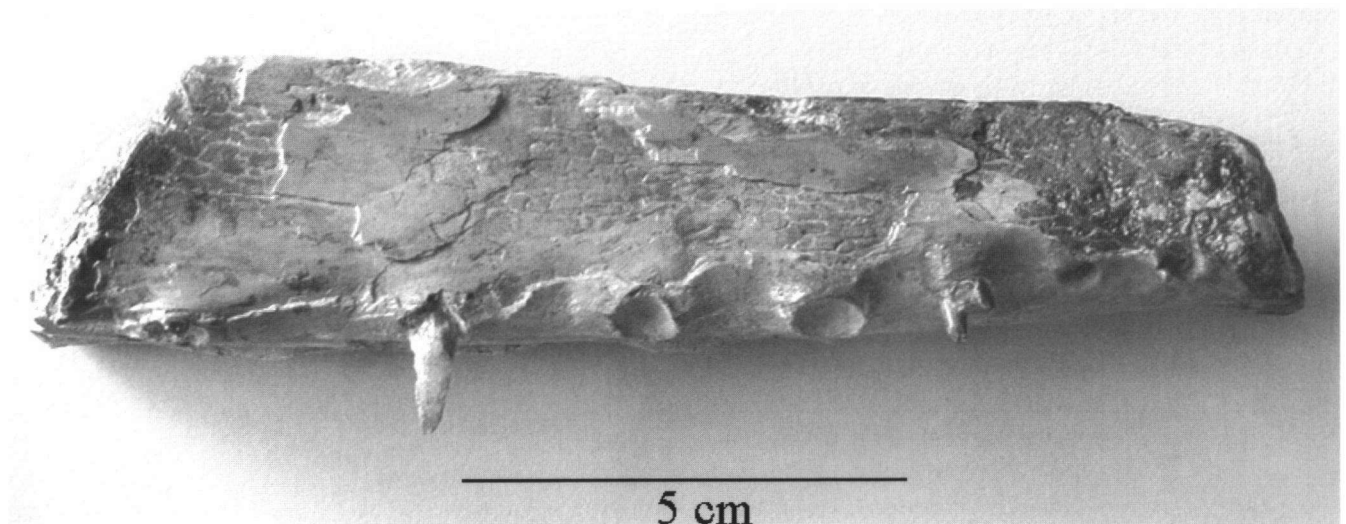


Fig 5 The Munich specimen, BSP 1991 I 27. Courtesy of BSP, Munich. Photograph by A. 't Hooft

Het stuk uit München, BSP 1991 I 27. Met dank aan BSP, München. Foto door A. 't Hooft

fourth alveoli are substantially smaller; the fifth alveolus is bigger and equals the size of the first. The position of the alveoli could not be established due to the unprepared state; the mandible faces lateroventrally, limiting necessary visibility to describe alveolar position as well as reliable measurements.

The right side of the skull is exposed, allowing the measurement of 26 alveoli. The alveoli are small with bigger measurements for the second, third, fourth, ninth and sixteenth alveoli. These are substantially bigger than the corresponding alveoli in the mandible; most others are smaller, except for the eleventh alveolus. Although the ninth and sixteenth alveolus are bigger relative to the previous and following ones, they still are smaller relative to the second, third and fourth alveoli. The biggest alveoli of the skull are positioned opposite to the smallest alveoli of the mandible; a pattern, if confirmed after preparation, that is not seen in the other discussed specimen that includes cranial alveoli (MN 4797-V). Differences with the alveolar pattern in the skull of MN 4797-V are clear. MN 4797-V has a distinct larger third alveolus where AMNH 24444 has a larger ninth alveolus, lacking in MN 4797-V.

The Stuttgarter mandible (SMNS 55414; Fig. 4)

This small, partly prepared but largely complete mandible in the Staatliches Museum für Naturkunde, Stuttgart (SMNS 55414, Veldmeijer *et al.*, in review), has been assigned to *Brasileodactylus* as well, as it clearly shows diagnostic features for this genus. The extremely elongated mandible clearly shows the dorsoventrally compressed anterior part with the expansion, the particular position of the first three alveoli and the mandibular groove with sub-grooves. This specimen differs from *Brasileodactylus araripensis* in its smaller size and in its distal expansion which is longer and smoother, although the authors do not think that the differences may justify the erection of a new species.

SMNS 55414 shows a small first alveolus (the smallest of all known specimens) and a large second alveolus (the biggest of all known specimens); this contrast with MN 4804-V which has the third alveolus as its biggest. The following alveoli (up to the seventh) follows the pattern and approximate size as seen in the holotype of *Brasileodactylus araripensis*; the eighth, ninth and tenth alveolus show the opposite pattern and are slightly smaller.

The Munich specimen (BSP 1991 I 27; Fig. 5)

The material housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany is tentatively classified as *Brasileodactylus* by Veldmeijer *et al.* (in review). The material consist largely of post-cranial material and includes only a small portion of the crestless maxilla; a direct comparison between this specimen and the type specimen is not possible, because the Munich materials do not include the mandible. Nevertheless, in assigning the specimen to *Brasileodactylus* on the basis of the comparable dentition (which is clearly distinct from the dentition in *Cearadactylus*) and the crestless maxilla (only occurring in this taxon as well as in *Cearadactylus*), the authors presented the first fully prepared post-cranial material thus avoiding the establishment of another taxon.

We interpret the first alveolus visible as the fourth one on the left side. If however, we compare the measurements of this specimen with those of MN 4797-V the following observations can be made. The first four measurements of BSP 1991 I 27 are comparable to those in MN 4797-V. After that, the differences are slightly bigger. This questions the conclusions by Veldmeijer *et al.* (in review), whether the fourth alveolus is indeed the fourth and not the third because then the curves would be more or less equal in pattern. We also have to take into account that the data of the Munich maxilla is based on average measurements of both sides, in contrast to MN 4797-V which is only based on the right side. Differences with AMNH 24444 is basically the same as described for MN 4797-V.

Diastemae

The diastemae of the measured mandibles show a remarkably uniform picture, i.e. a strong increase in size posteriorly, despite some small fluctuations. As with the alveoli, the specimen AMNH 24444 differs on this point (for the explanation, see the description of the alveolar pattern).

The pattern of the sizes of the diastemae of the skull in MN 4797-V is remarkable similar, despite small differences, to those of the mandible. Again, a difference can be noted for AMNH 24444. Here, a steady increase in diastemae size can be seen until the diastema 7-8. The following diastemae decrease in size at least until diastema 9-10 after which the diastemae increase in size; it remains uncertain whether this starts with

diastema 10-11 or with the following. Another strong decrease in size occurs with diastemae 14-15 and 15-16 after which again a strong increase in size occurs. A last a sharp decrease can be seen with diastemae 19-20 and 20-21, after which for the last time an increase in size can be noted, but far less relative to the foregoing ones.

This means that, when the fluctuations are included, the size of diastemae increases first posteriorly, but decreases from diastema 10-11 or 11-12. Full preparation of the specimens, allowing the measurement of the left side, is needed in order to confirm this deviating pattern. The pattern of diastemae in BSP 1991 I 27 is, despite small fluctuations, in line with the pattern seen in MN 4797-V, except for the decrease in size, which starts later relative to the others (with diastema 11-12 instead of 10-11 for MN 4797-V), but differ markedly with AMNH 24444. These differences are more or less the same as explained with the comparison of the New York specimen with the Crato specimen.

Discussion

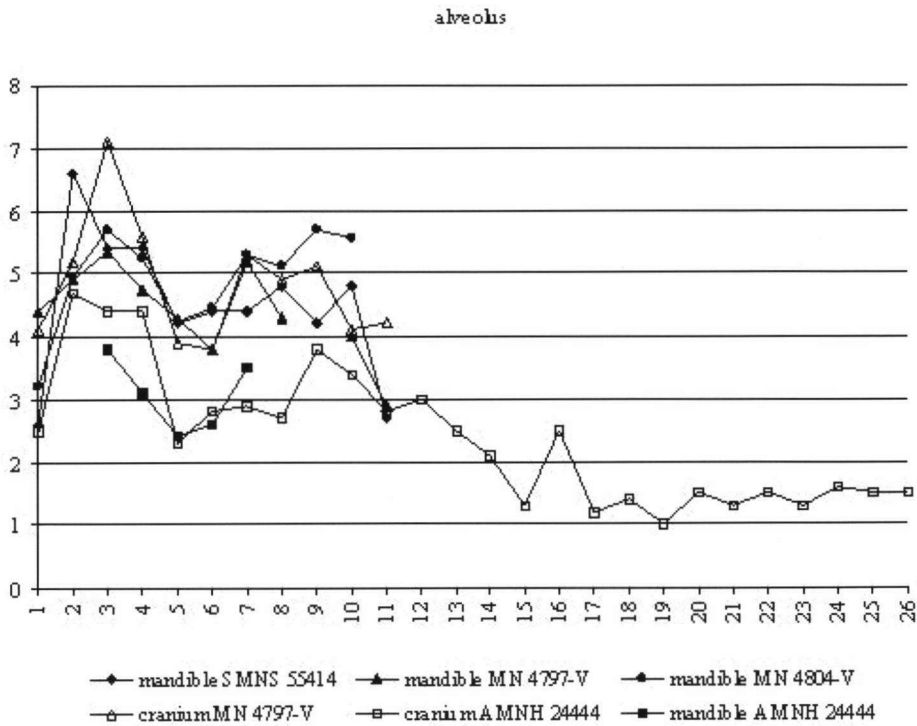
Firstly, in many cases teeth are not preserved and the alveolar diameter serves as indicator of tooth size, though there need not necessarily be a positive relation between alveolar size and tooth size; a large diameter of the alveolus could mean a long, perhaps fanglike tooth, but a short, bulb-like tooth could have been possible as well. On the other hand, the teeth of the taxa discussed here all have a comparable dentition inferred from the few (remnants) of teeth and the assumption that the bigger the alveolus, the longer the tooth, is reasonable. The second problem is that measurements of the teeth/alveoli and diastemae almost never have been published (exceptions are Fastnacht, 2001; Lee, 1994; Veldmeijer, 2003b), rendering scientific evaluation impossible. Therefore, the data of the herein described specimens have been presented, shortly described and discussed as well as important morphological peculiarities.

The situation on family (in a narrow sense) level 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 (for instance Unwin, 2001) but this is based on the difference in view of the assignment of the type

species for Ornithocheiridae (Kellner, 1990; for an overview, see Kellner & Tomida, 2000). As pointed out elsewhere (Veldmeijer, 2003b), Anhangueridae is regarded as a valid taxon and different from Ornithocheiridae; we agree with the designation of *Ornithocheirus compressirostris* as type species of Ornithocheiridae (see Kellner & Tomida, 2000). The acceptance of the *O. compressirostris* as the type species for Ornithocheiridae forces to include *Brasileodactylus* in Anhangueridae, as the laterally compressed jaws that strongly decrease in width in anterior direction resulting in a sharp pointed beak in Ornithocheiridae, contrast distinctly from the expanded and dorsoventrally compressed jaws in *Brasileodactylus*.

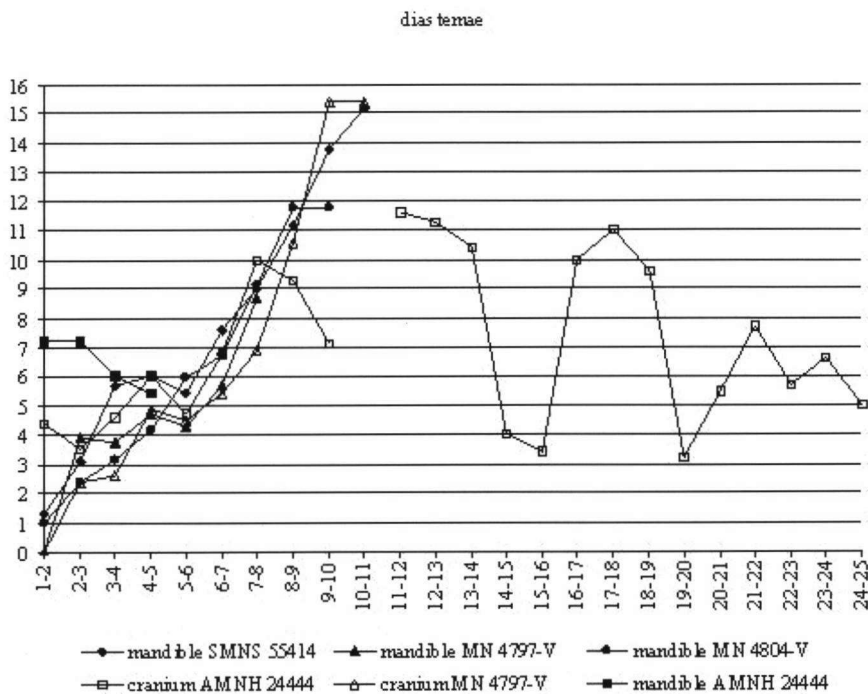
Various authors have suggested *Brasileodactylus* being synonymous with *Anhanguera* (Unwin, 2001 although in a later paper, Unwin (2002) still refers to it as *Brasileodactylus araripensis*) or even *Coloborhynchus* (Frey *et al.*, 2003). As remarked by Veldmeijer & Signore (2004) "The explanation of 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 different species unless proven (and not suggested) otherwise", hence the designation as *Brasileodactylus*. *Brasileodactylus* is here regarded as a valid taxon, on the basis of lack of a premaxillary sagittal crest and a dentary sagittal crest and the presence of the unique configuration of dentition and morphology of the dorsal aspect of the lower jaw, as pointed out above. The hitherto most complete cranial dentition cannot be assigned to *Brasileodactylus* with full confidence yet (Veldmeijer, 2003a), but the features of the dentition of the upper and lower jaw in MN 4797-V show a more erratic pattern of the skull, with larger differences in diameter of alveoli: the second, third and fourth alveoli are the biggest, followed by two smaller ones, after which again bigger ones, but less big than the second until fourth alveoli, follow. Comparison with other taxa (mainly *Anhanguera* and *Coloborhynchus*) will have to shed light on the conformities and differences in dentition of these closely related taxa and whether dentition patterns can be used to differentiate on a certain taxonomic level.

Furthermore, it can be suggested that if AMNH 24444 can be classified as *Brasileodactylus* as suggested in the preliminary description and if it



The dentition pattern of the various specimens showing the size distribution of the alveoli as described in the text; Y-axis size in mm, X-axis number of alveolus

Het dentitiepatroon van de verschillende specimens met de grootte-verdeling van de alveolen (tandkassen) zoals beschreven in de tekst; Y-as grootte in mm, X-as nummer van de alveole



The dentition pattern of the various specimens showing the size distribution of the diastemae as described in the text; Y-axis size in mm, X-axis number of diastema

Het dentitiepatroon van de verschillende specimens met de grootte-verdeling van de diastemen (tandenloze ruimtes) zoals beschreven in de tekst; Y-as grootte in mm, X-as nummer van het diastem

can be established that AMNH 24444 and *Ludodactylus sibbicki* are the same (which seems to be so on the basis of the preliminary observations on the half prepared holotype by the first author in 1998), *Ludodactylus sibbicki* should be re-named as *Brasileodactylus* (either *Brasileodactylus araripensis* or *Brasileodactylus sibbicki*).

Finally, the generally larger alveoli in the skull of AMNH 24444 relative to MN 4797-V might be explained by the fact that AMNH 24444 is ontogenetically younger relative to MN 4797-V. This however, cannot be the explanation for the large difference in size between AMNH 24444 and BSP 1991 I 27, as the latter is regarded as not fully grown as well.

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