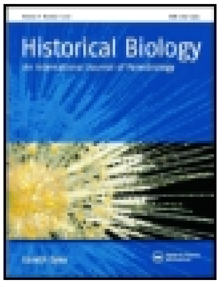

Historical Biology: An International Journal of Paleobiology

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ghbi20

On wing disparity and morphological variation of the Santana Group pterosaurs

Bruno Cavalcanti Vila Nova [a] & Juliana Manso Sayão [b]

[a] Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de Sao Paulo, Avenida Bandeirantes 3900, Ribeirao Preto, 14040-901, Sao Paulo, Brazil

[b] Centro Acadêmico de Vitória, Universidade Federal de Pernambuco, Rua Alto do Reservatório, S/N - Bela Vista, Vitória de Santo Antão, 55608-680, Pernambuco, Brazil

To cite this article: Bruno Cavalcanti Vila Nova & Juliana Manso Sayão (2012): On wing disparity and morphological variation of the Santana Group pterosaurs, Historical Biology: An International Journal of Paleobiology, DOI:10.1080/08912963.2012.658386

To link to this article: http://dx.doi.org/10.1080/08912963.2012.658386

Historical Biology
iFirst article, 2012, 1–8

On wing disparity and morphological variation of the Santana Group pterosaurs

Bruno Cavalcanti Vila Nova[a]* and Juliana Manso Sayão[b]

[a]*Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de Sao Paulo, Avenida Bandeirantes 3900, Ribeirao Preto 14040-901, Sao Paulo, Brazil;* [b]*Centro Acadêmico de Vitória, Universidade Federal de Pernambuco, Rua Alto do Reservatório, S/N - Bela Vista, Vitória de Santo Antão, 55608-680, Pernambuco, Brazil*

(*Received 30 November 2011; final version received 13 January 2012*)

Pterosaurs were widely spread throughout the Mesozoic Era, populating the whole world. Among this great diversity, two groups are commonly found in Brazil: the Anhangueridae and Tapejaridae. These can be mainly identified by cranial synapomorphies. However, because of the fragility of the pterosaur skeleton and rarity of the fossilisation process, the fossils found are usually incomplete, which hampers a proper taxonomic identification of the specimens. The specific proportions of these two groups of pterosaurs were obtained from bibliographic data and measurements of specimens. Eight Anhangueridae-like and seven Tapejaridae were used: *Anhanguera piscator*, *Anhanguera santanae*, *Anhanguera spielbergi*, *Araripesaurus castilhoi*, *Barbosania gracilisrostris* and three Anhangueridae sp. indet.; *Sinopterus dongi*, *Tapejara wellnhoferi* and five Tapejaridae sp. indet. We find that proportions of the humerus, wing metacarpal, first phalanx of the wing digit, femur and tibia are sufficient to identify partial remains of Araripe pterosaurs. A principal component analysis shows that each clade has different, non-overlapping scores in the studied ratios and these can be used with precision. Specific bone ratios for fast identification of anhanguerids and tapejarids are given, opening a broader way to diagnostic fragmentary bones.

Keywords: Pterosauria; apendicular skeleton; bone ratios; linear morphometry; Anhangueridae; Tapejaridae

1. Introduction

Pterosaurs are an extinct group of flying reptiles, which have evolved during the Mesozoic Era. The group evolved into various species and spread throughout the whole world (Wellnhofer 1991a; Hammer and Hickerson 1999; Kellner 2006; Barrett et al. 2008; Sayão et al. 2011). However, pterosaur palaeobiogeography is not fully understood, since most of the phylogenetic data are incomplete and do not include all known species (Butler et al. 2009; Sayão et al. 2011). Among this great distribution, the Brazilian pterosaurs are known worldwide, bearing some of the most important discoveries within the group (Kellner and Tomida 2000; Kellner and Campos 2002; Unwin and Martil 2007). In this scenario, the Anhangueridae and closely related taxa, and the Tapejaridae clade are the most common pterosaur groups found in Brazil (Kellner and Campos 2000). The Anhangueridae are also found in Africa (Mader and Kellner 1999; Wellnhofer and Buffetaut 1999; Elias et al. 2007), Australia (Molnar and Thulborn 1980; Molnar 1982, 1987; Long 1998), Europe (e.g. Barrett et al. 2008) and China (Wang and Zhou 2003b), showing a cosmopolitan distribution during the Cretaceous period (Barrett et al. 2008; Rodrigues and Kellner 2008; Sayão et al. 2011). The Tapejaridae also present a broad distribution with specimens found in Africa (Wellnhofer and Buffetaut 1999; Kellner 2010), China (Li et al. 2003; Wang and Zhou 2003a, 2003b; Lü and Yuan 2005; Lü et al. 2006, 2007), Morocco (Pinheiro et al. 2011) and Spain (Vullo et al. 2009). Apart from the Brazilian and Chinese specimens, most of the group's record consists of fragmentary material making identification difficult (Wellnhofer 1991b; Nuvens et al. 2002; Buffetaut and Mazin 2003; Unwin 2003). Since most of the synapomorphies of both groups are cranial, the identification of the remains is even more difficult, resulting in many 'Pterodactyloidea indet'.

The use of bone lengths for diagnosis is a common way to establish morphological classification of pterosaurs (Wellnhofer 1991a; Martill and Frey 1999; Nuvens et al. 2002; Lü et al. 2009; Wang et al. 2009; Eck et al. 2011), and also as discrete characters in Mesozoic birds (Chiappe 1995, 1996; Forster et al. 1998; Ji et al. 1998; Padian and Chiappe 1998). Bones can be crushed during burial, but they have some advantages, since only a few are required for identification. To a large extent, the proportions of wing bones determine planform and wing deformations during flight. Early anatomists noted variations in the relative proportions of proximal wing elements (humerus, radius and ulna), and remarked on the distribution of this variation within birds (Beddard 1898; Steiner 1917; Boker 1927; Marples 1930). The proportions of the proximal wing elements have been used in the morphological classification of Aves (Verheyen 1961) and could be used for other flying vertebrates such as pterosaurs. The fossilisation of

---

*Corresponding author. Email: bruno.vilanova@gmail.com

ISSN 0891-2963 print/ISSN 1029-2381 online

http://dx.doi.org/10.1080/08912963.2012.658386
http://www.tandfonline.com

pterosaur skeletons with skulls and post-cranial parts would have been a rare event (Kellner 1994; Kellner and Tomida 2000). Therefore, a valid method to identify skeletons without cranial material is necessary. The use of linear morphometry is proven as a good source of information, since bone lengths and proportions are more easily identified, even in fossil taxa (Dyke et al. 2006; Eck et al. 2011; Elgin and Frey 2011). The linear measurements are repeatable in different specimens and capable of elucidating significant differences without the need of form preservation from the studied organism (Astúa 2003). The aim of this work is to analyse ratios and relations that could be used in the identification and diagnostic of the Anhangueridae-like and Tapejaridae groups, where only fragments from their appendicular skeletons are present.

2. Material and methods

Pterosaur fossils were analysed from the current bibliography as well as samples housed in the Museu Nacional/UFRJ. Fifteen specimens were selected, eight anhanguerids and related toothed pterosaurs (for clarity, all toothed pterosaurs are called anhanguerids in this paper) and seven tapejarids (Table 1). All the species identification used were provided by the authors on the available literature. For collection material, we recurred for the institution's description. These were chosen because at least three of the following bones with the total length preserved were present: humerus, radius, ulna, wing metacarpal, any of the four phalanges of wing digit, femur or tibia. We also compared the relationship of the appendicular skeleton of five specimens that belong to different groups, chosen to make a comparison with the results obtained for the studied specimens and to determine if the diagnostic data found were species specific or a common feature shared with all pterosaurs. One Ctenochasmatidae (BPM 0002), three Nyctosauridae (M1323, M1325, M1328) and one Pterodactylidae (*H. gracilis*, holotype: IVPP V11726). These taxa were selected for being described with precise measurements for all the apendicular bones, greatly improving the analysis.

We measured the total length of each bone, and the relationship between all the bones was calculated and compared. For the bone ratios, up to 5% of variation in the same clade was deemed acceptable for precise diagnosis. If a bigger difference was observed, we discarded the ratio. To separate both groups, we used a variation of at least 10% in each ratio. These values were chosen to have a good security margin on the identification (Hammer and Harper 2006). To test the validity of the data, we inserted the ratios in the PAST version 1.95 program (Hammer et al. 2001) using a principal component analysis (PCA). The analysis created a plot where the influence of each bone in the wing length could be identified, as part of two main components (Components 1 and 2 are, respectively, the *X*- and *Y*- axis of the graphic). The PCA was used to support the diagnostic separation of the Anhangueridae from the Tapejaridae.

2.1. Abbreviation list

humerus (hu), radius (rd), ulna (ul), metacarpal I (mcI), metacarpal II (mcII), metacarpal III (mcIII), metacarpal IV (mcIV), first phalanx of the wing digit (ph1d4), second phalanx of the wing digit (ph2d4), third phalanx of the wing digit (ph3d4), fourth phalanx of the wing digit (ph4d4), femur (f) and tibia (t).

2.2. Institutional abbreviations

American Museum of Natural History, NY, USA (AMNH); National Science Museum, Tokyo, Japan (NSM); Nationaal Natuurhistorisch Museum, Leiden, Netherlands (RGM); Museu Nacional/UFRJ, Rio de Janeiro, Brazil (MN); Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil (DNPM); Museu de Paleontologia de Santana do Cariri, Santa do Cariri, Brazil (MPSC); Zhejiang Museum of Natural History, Zhejiang, China (M); Institute of Vertebrate Paleontology and Paleoanthropology, China (IVPP); Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany (SMNK); Museum of Natural History Sintra, Portugal (MNHS).

3. Results

Nine of the tested ratios could be used for diagnostic purposes. They were mainly related to humerus, fourth

Table 1. Selected specimens used in the study. See abbreviation list for institution of origin.

Anhangueridae		Tapejaridae	
Araripesaurus castilhoi	DNPM: 529-R	*Sinopterus dongi*	IVPP V13363
Anhanguera piscator	NSM-PV 19892	*Tapejara wellnhoferi*	SMNK PAL 1137
Anhanguera santanae	AMNH 22555	Tapejaridae indet.	MN 4729-V
Anhanguera spielbergi	RGM 401 880	Tapejaridae indet.	MN 6527-V
Barbasonia gracilirostris	MNHS/00/85	Tapejaridae indet.	MN 6532-V
Anhangueridae indet.	MN 4809-V	Tapejaridae indet.	SMNK PAL 2342
Anhangueridae indet.	SMNK PAL 1132	Tapejaridae indet.	SMNK PAL 3855
Anhangueridae indet.	MPSC R-739		

Table 2. Main values of bone ratios for Anhangueridae and Tapejaridae.

Anhangueridae	Taperjaridae
$\mathrm{mcIV/ph1d4} = 0.4$	$\mathrm{mcIV/ph1d4} = 0.6$
$\mathrm{mcIV/hu} = 1.00$	$1.30 < \mathrm{mcIV/hu} < 1.60$
$\mathrm{ph4d4/hu} = 0.6$	$\mathrm{ph4d4/hu} < 0.6$
$0.51 < \mathrm{f/hu} < 0.99$	$\mathrm{f/hu} = 1.20$
$\mathrm{f/rd} < 0.75$	$\mathrm{f/rd} > 0.8$
$\mathrm{f/ul} < 0.70$	$\mathrm{f/ul} > 0.8$
$\mathrm{t/hu} = 1.00$	$\mathrm{t/hu} = 1.7$
$\mathrm{t/rd} < 1.00$	$\mathrm{t/rd} > 1.00$
$\mathrm{t/ul} < 1.00$	$\mathrm{t/ul} > 1.00$

metacarpal, first phalanx of the wing digit and hind limb (femur and tibia) (Table 2).

According to *Anhanguera piscator*, *Anhanguera spielbergi* and *Anhanguera santanae* in the anhanguerids (Figure 1), the fourth metacarpal showed about 40% of the first wing phalanx length ($\mathrm{mcIV/ph1d4} \approx 0.40$). They also present humerus and fourth metacarpal with approximately the same length ($\mathrm{mcIV/hu} \approx 1.00$). While in the tapejarids MPSC R-739, MN 4729-V and *Sinopterus dongi*, the fourth metacarpal bears 70% of the first wing phalanx ($\mathrm{mcIV/ph1d4} \approx 0.70$). In that group, the previous bone is also 50% longer than the humerus ($\mathrm{mcIV/hu} \approx 1.50$).

With regard to the fourth wing phalanx and the humerus, all the specimens in the tapejarids showed the fourth phalanx lesser than 60% of humerus length ($\mathrm{ph4d4/hu} < 0.60$), while all the specimens in the anhanguerid showed a fourth phalanx greater than 60% of the humerus ($\mathrm{ph4d4/hu} > 0.60$).

Using both anterior and posterior limbs, we can see a pattern with the radius, ulna, femur and tibia (Figure 2). Considering anhanguerids, the femur ranges from half the length of humerus in *A. santanae* to almost its length, as observed in *A. spielbergi* ($0.5 < \mathrm{f/hu} < 1.0$). Still in the humerus ratios, this bone has a similar length to the tibia ($0.89 < \mathrm{t/hu} < 1.22$). The femur is always shorter than 75% of radius ($\mathrm{f/rd} < 0.75$ – higher value of 71% in *A. spielbergi*). It is also smaller than 70% of ulna ($\mathrm{f/ul} < 0.70$ – higher value of 69% also in *A. spielbergi*). The tibia is always shorter than radius ($\mathrm{t/rd} < 1.00$ – higher value of 88% in *A. spielbergi*) and shorter than ulna ($\mathrm{t/ul} < 1.00$ – higher value of 86% in *A. spielbergi*).

With regard to tapejarids, the tibia is big, being almost twice the humerus length ($\mathrm{t/hu} \approx 1.7$). It is also larger than the radio ($\mathrm{t/rd} > 1.00$) and the ulna ($\mathrm{t/ul} > 1.00$). Conversely, the femur is not as large as the tibia, being only

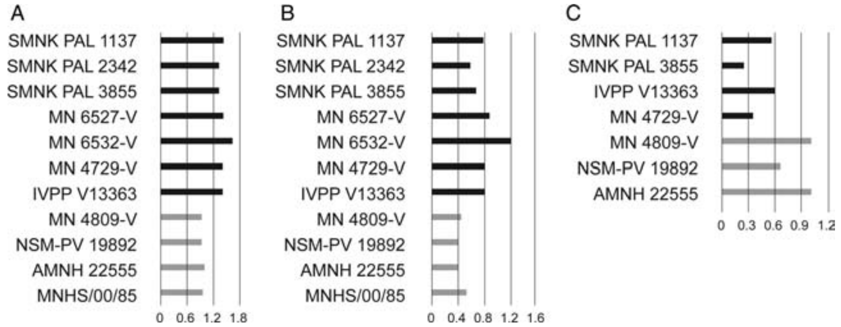

Figure 1. Bone relations of forelimb elements: (A) metacarpal IV with humerus; (B) metacarpal IV with the first phalanx of the wing digit; (C) fourth phalanx of the wing digit with the humerus. Specimens bearing preserved bones in each graph, with tapejarids (black) top, and anhanguerids (light grey) below.

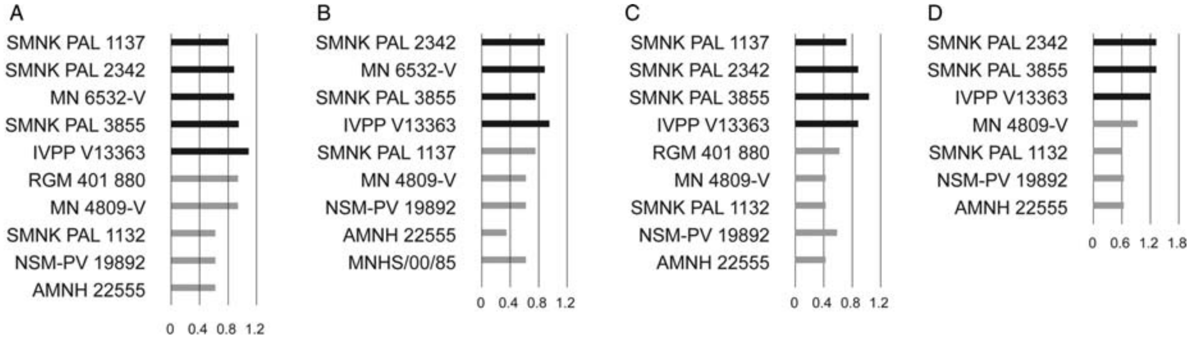

Figure 2. Bone relations of fore and hind limbs elements: (A) femur with the radio; (B) femur with the ulna; (C) tibia with the radio; (D) tibia with the ulna. Specimens bearing preserved bones in each graph, with tapejarids (black) top, and anhanguerids (light grey) below.

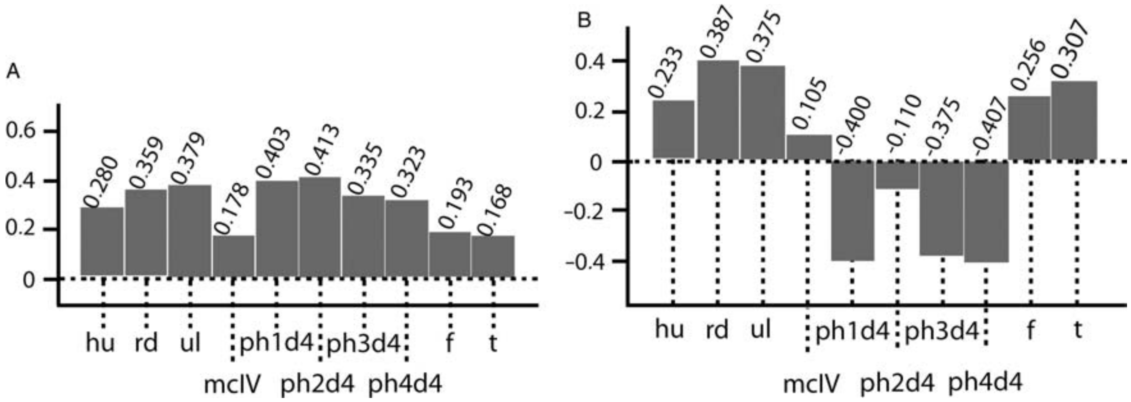

Figure 3. Weight of each appendicular bone, showing the influence in (A) Principal Component 1; (B) Principal Component 2.

20% greater than the humerus (f/hu ≈ 1.2). The femur has at least 75% of the radius size (f/rd > 0.75 – smaller value of 81% in *Tapejara wellnhoferi*). In this group, the femur is greater than 70% of the ulna (f/ul > 0.70 – smaller value of 84% in *S. dongi*).

Using the ratios, we performed the PCA originating at the Components 1 and 2. They were established calculating the influence of each bone on the wing total length, and comprise 92% of the wing variation among the studied specimens (Figure 3). With this PCA we could separate the specimens of Anhangueridae and Tapejaridae in two different clusters, related to limb length (Figure 4). It also confirms that the rate values are specifics for each group.

4. Discussion

The wing of pterosaurs consists of the forelimb bones with a number of significant morphological modifications, including elongation, reduction, fusion and complete loss of certain elements (Wellnhofer 1991a). This creates considerable differences in the shape of bones, and consequently in the construction of the wing within taxa (e.g. Prondvai and Hone 2008). With regard to hind limbs this peculiarity is also observed, with the azhdarchoids presenting larger attachment area for abductor muscles of the femur, as a partial consequence of an increased terrestrial lifestyle (as recently reaffirmed by Eck et al. 2011). Using this arrangement, histological studies have showed that anhanguerids and tapejarids exhibit bones

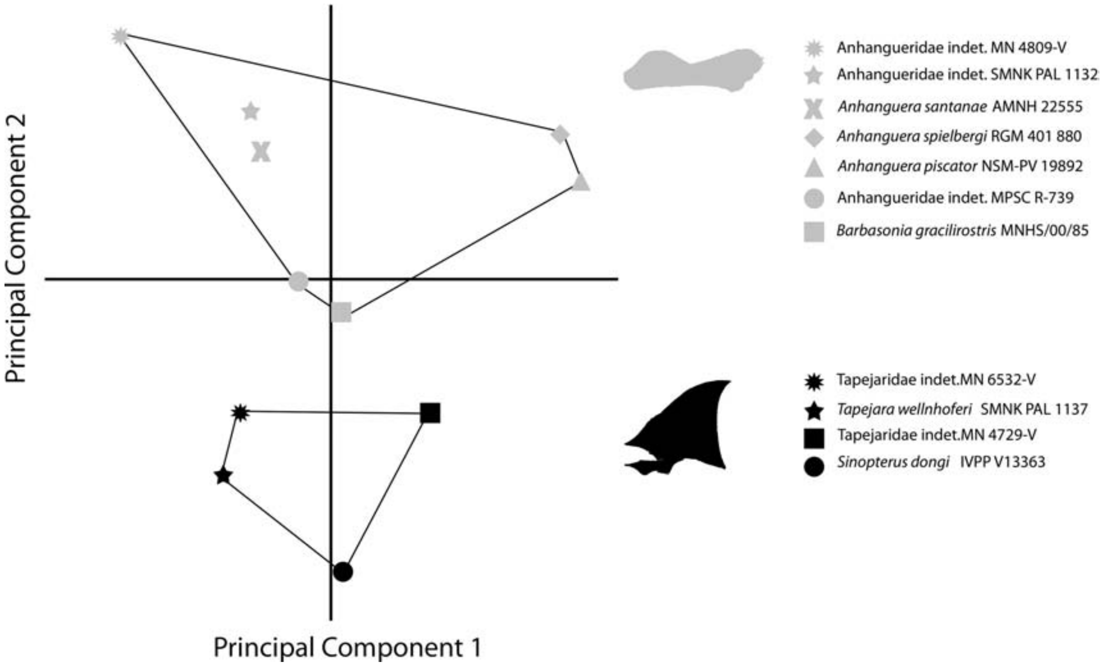

Figure 4. Principal components analysis of linear measurement of wing bones of species of Anhangueridae (light grey) and Tapejaridae (black).

with different growth rates, showing a histovariability among the wing (Sayão 2003). The same pattern was observed in the limb bones as well as in the mid-series cervical vertebrae of the Argentinean Ctenochasmatidae *Pterodaustro guiñazui* (Codorniú and Chiappe 2004; Chinsamy et al. 2009). It is likely that similar allometric changes might have occurred in other pterodactyloid pterosaurs (Codorniú 2007). Therefore, differences in flight methods and terrestrial lifestyle could have direct influences in bone structures. These data indicate that species can have different bone ratios, being useful for group identification (Figure 5). The use of bone ratios for the identification of pterosaur groups allows precise diagnostics, and was highly used as taxonomic criteria in previous papers (Wellnhofer 1991a; Martill and Frey 1999; Kellner and Tomida 2000; Nuvens et al. 2002; Sayão and Kellner 2006; Andres and Ji 2008; Wang et al. 2009; Lü et al. 2010; Eck et al. 2011; Elgin and Frey 2011; Vila Nova et al. 2011).

The basal forms of pterosaurs have a short wing metacarpal, which is longer in more derived pterodactyloids (Prondvai and Hone 2008). Even among this group, there is a variation within some clades, already stated in the literature. Elgin and Frey (2011) distinguished the pteranodontoid SMNK PAL 3854 from other pteranodontoid and nyctosaurid pterosaurs by the relative shortness of the wing metacarpal, and from the Istiodactylidae by a set of ratios that lie out with the observed range of values known for these taxa. If we compare the ratio values for the studied groups in this analysis (Ctenochasmatidae, Nyctosauridae and the Pterodactylidae *H. gracilis*), a few similarities can be noticed. The wing metacarpal has almost the same length as the humerus in Ctenochasmatidae (hu/mcIV = 0.90), a value close to Anhangueridae (hu/mcIV ≈ 1.00). The humerus is smaller than wing metacarpal in *H. gracilis* (hu/mcIV = 0.78) and shows a close value to Tapejaridae (hu/mcIV ≈ 0.68). The close value in both situations (10% of difference) does not negate the use of the hu/mcIV ratio as a diagnostic tool for the two treated groups, in regard to Araripe pterosaurs. The humerus to femur ratio has a broad range in the studied groups, with the humerus reaching 150% of femur length in Ctenochasmatidae (hu/f = 1.60) and only 60% of the femur in the Nyctosauridae (hu/f = 0.60). The relation of femur with radius and ulna was also highly variable, with Ctenochasmatidae showing a femur with half the length of the radius and ulna (f/rd = 0.56 and f/ul = 0.56 respectively), while in Nyctosauridae the sizes are similar (f/rd = 0.95 and f/ul = 0.95).

The Tapejaridae wings are generally composed of the first wing phalanx, which represents the longest part of the anterior limb, and also have a reduction in size towards the fourth phalanx, which is very short (Kellner 2003). This can be easily seen in some cases, as in the MN 4729-V specimen, in which the first wing phalanx reaches six times the length of the fourth (ph1d4/ph4d4 = 6.05). In *S. dongi* the ratio is not so high (ph1d4/ph4d4 = 3.78), though it is bigger than that in the Anhangueridae (ph1d4/ph4d4 = 2.32 in *A. santanae*; ph1d4/ph4d4 = 2.98 in *A. piscator*) and also in *H. gracilis* (ph1d4/ph4d4 = 3.20). Still regarding the first wing phalanx, some authors use its relative size to the wing metacarpal as taxonomic criteria for Pterodactyloidea (character 101 of Andres and Ji 2008; character 81 of Wang et al. 2009). However, our analysis

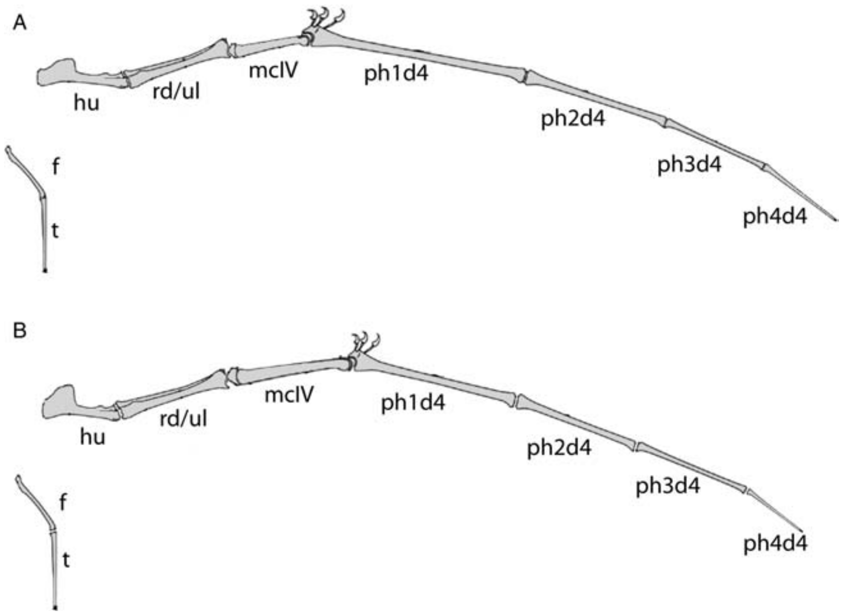

Figure 5. Relative size of each bone in the studied groups: (A) Anhangueridae; (B) Tapejaridae.

can distinguish the Anhangueridae from the Tapejaridae, both Pterodactyloidea, using the mcIV/ph1d4 ratio more precisely than these previous attempts. The identification of anhanguerids and tapejarids has the potential to refine and enhance current phylogenetic matrixes.

The most derived pterosaurs showed a hypertrophy of anterior limbs and a hypotrophy of hind limbs (Wellnhofer 1991a; Dyke et al. 2006). In the Anhangueridae clade, this relationship is ambiguous as the femur is slightly shorter than the humerus (f/hu $\approx$ 0.90) and the tibia has a similar length ($0.89 <$ t/hu < 1.22). In tapejarids, however, a group proximately related to Azhdarchidae, one of the most derived pterosaur group (Kellner 2003; Unwin 2003; Andres and Ji 2008), the femur is notably larger than humerus (f/hu < 1.20) and the tibia has almost half the length of the humerus (t/hu < 1.75). A very interesting characteristic can be seen in the hind limbs: the tibia is lesser than the radius (t/rd < 1.00) and ulna (t/ul < 1.00) only in anhanguerids, while in all the other studied groups, the tibia is greater than the radius and ulna (t/rd > 1.00; t/ul > 1.00). According to Eck et al. (2011), and confirmed by our analysed specimens, the bivariate ratios based on the tapejarids hind limb length indicate that all species showed similar to identical values, where the tibia varies between 1.38 and 1.68 the femur length. Thus, the similarity of these bivariate ratios between Brazilian and Chinese tapejarids for a variety of long bones suggests that similar rates of bone development occurred in all tapejarid pterosaurs, although slight differences in ratios noted by Lü et al. (2009) between specimens of *S. dongi* may indicate that there was a slight variety in intraspecific growth rates, at least for the humerus, femur, mc IV and tibia. Were the bones to develop at a significantly different rate between species, then they would be clearly manifested given the overall closeness of physical size between individual specimens (Eck et al. 2011).

The humerus and wing metacarpal ratio can be used as a diagnostic tool for Tapejaridae. When applied for Anhangueridae, the value is similar to the one found in Nyctosauridae, and therefore is not exclusive to the former. In addition, the tibia with radio/ulna ratio can be used to identify anhanguerids, but not for tapejarids. In this group, the relation is similar to the one of *H. gracilis*, and must be used with caution. These ratios should be carefully applied in areas where both families are registered; for example in the Chinese Jehol Group, which bears both Tapejaridae and Pterodactylidae. However, *H. gracilis* occurs in the older Yixian Formation, while *S. dongi*, a tapejarid, comes from the younger Jiufotang Formation (Wang and Lü 2001; Wang and Zhou 2003b). Until now, there has not been any region that presents both Anhangueridae and Nyctosauridae (Barrett et al. 2008). The presence of *Nyctosaurus lamegoi* in the Paraiba Basin, and the *Anhanguera* genus in the Araripe Basin are the closest registers, despite being separated by almost 50 million years (Price 1953; Kellner and Campos 1988; Kellner and Tomida 2000).

Since each principal component has different weights for each bone, the PCA was able to establish two separate clusters for each group. The two principal components used in the PCA separated the clusters mainly in the horizontal axis, correlated to the PC1. Because most part of pterosaur wing is related to wing phalanges (Wellnhofer 1991a; Bennett 2001; Prondvai and Hone 2008), a variation in these bones greatly influences the PCA. The different weights for each bone in both principal components can explain the variation in clusters (Peres-Neto et al. 2003), since the PC1 has more influence from the wing phalanges than the PC2. Our data show that tapejarids wings have a difference in phalanges size that is more evident than in anhanguerids, which separate both groups according to the present analysis.

To a large extent, the proportions of wing bones determine planform and wing deformations during flight in birds, which influences the species lifestyle (Nudds et al. 2004), and likely had the same influence in pterosaurs. Besides the taxonomic potential, these variations may be related to differences in habitat of the analysed pterosaurs. In ornithocheiroids, the estimated length of the wing spar, combined with the short length of the hind limbs forming a high aspect ratio, indicates a lifestyle of relatively fast, open water glider, using dynamic or thermal soaring (Chatterjee and Templin 2004). Adding more specimens to the dataset can confirm this hypothesis, which can be verified in further studies.

5. Conclusion

We obtained distinctive relations for the Anhangueridae and Tapejaridae groups, especially using humerus, wing metacarpal, first phalanx of wing digit, femur and tibia. These results indicate that it is possible to identify both groups, using only bone ratios. The PCA clearly shows that each clade has different, non-overlapping scores on both principal components. Therefore, those variables with major weight on each of the principal components can be used to identify them.

With these values, it is possible to identify both groups, using a few specific bones. Table 2 shows which pair of bones can be used to identify individuals. Therefore, if a combination of humerus, wing metacarpal, first and last phalanx of wing digit, radius, ulna, femur and tibia is preserved, it is possible to associate these remains to one of the most usual Brazilian pterosaur clades, thus aiding in the resolution of identifying ambiguously identified bones.

Acknowledgements

The authors thank Dr Diego Astúa (Universidade Federal de Pernambuco) for helping with early versions of the manuscript, Dr Haydon Mort (Universidade Federal de Pernambuco) for reviewing and improving the English version, Dr Alexander W.A. Kellner (Museu Nacional/UFRJ) and Dr Antônio Alamo Feitosa Saraiva (Universidade Regional do Cariri) for the access to specimens at the Museu Nacional/UFRJ and Museu de Paleontologia de Santana do Cariri, Matheus Barbosa for Figures 1 and 2, and Dr Taíssa Rodrigues and Dr Christopher Bennett for reviewing and improving the manuscript. This project was partially funded by Pro-Reitoria de Pesquisa e Pós-Graduação da Universidade Federal de Pernambuco and CNPq (Fellowship to Juliana M. Sayão 1) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES (Fellowship to Bruno C. Vila Nova).

References

Andres B, Ji Q. 2008. A new pterosaur from the Liaoning province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. Palaeontology. 51(2):453–469.

Astúa D. 2003. A morfometria geométrica e a 'revolução na morfometria' – Localizando e visualizando mudanças na forma dos organismos. Bioletim. Ano III(Número 3):5.

Barrett PM, Butler RJ, Edwards NP, Milner AR. 2008. Pterosaur distribution in time and space: an atlas. Zitteliana. B 28:61–107.

Beddard FE. 1898. The structure and classification of birds. 1st ed. London: Longmans Green.

Bennett SC. 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Palaeontographica Abt. A 260: 1–153.

Boker H. 1927. Die biologische Anatomie der Flugarten der Vogel und ihre Phylogenie. J Ornith. 75:304–371.

Buffetaut E, Mazin JM. 2003. Evolution and palaeobiology of pterosaurs [special publications]. Geol Soc Lond. 217:335–342.

Butler RJ, Barrett PM, Nowbath S, Upchurch P. 2009. Estimating the effects of sampling biases on pterosaur diversity patterns: implications for hypotheses of bird/pterosaur competitive replacement. Paleobiology. 35(3):432–446.

Chatterjee S, Templin RJ. 2004. Posture, locomotion, and paleoecology of pterosaurs [special paper]. Geol Soc Am. 376:1–64.

Chiappe LM. 1995. The phylogenetic position of the Cretaceous birds of Argentina: Enantiornithes and *Patagopteryx deferrariisi*. CFS. 181: 55–63.

Chiappe LM. 1996. Late Cretaceous birds of southern South America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi*. Münch Geowissen Abh. 30:203–244.

Chinsamy A, Codorniú L, Chiappe L. 2009. Palaeobiological implications of the bone histology of *Pterodaustro guinazui*. Anat Rec. 292:1462–1477.

Codorniú L. 2007. Evidencias de cambios aloméricos en las cervicales de *Pterodaustro guinazui* (Pterosauria, Pterodactyloidea). Ameghiniana, Complemento de Resúmenes. Capital Federal: Asociación Paleontológica Argentina. 44:10.

Codorniú L, Chiappe LM. 2004. Early juvenile pterosaurs (Pterodactyloidea: *Pterodaustro guinazui*) from the Lower Cretaceous of central Argentina. Can J Earth Sci. 41:9–18.

Dyke GJ, Nudds RL, Rayner JMV. 2006. Limb disparity and wing shape in pterosaurs. J Evol Biol. 19:1339–1342.

Eck K, Elgin RA, Frey E. 2011. On the osteology of *Tapejara wellnhoferi* KELLNER 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE-Brazil. Swiss J Palaeontol. 130(2):277–296.

Elgin RA, Frey E. 2011. A new ornithocheirid, Barbosania gracilirostris gen. et sp. nov. (Pterosauria, Pterodactyloidea) from the Santana Formation (Cretaceous) of NE Brazil. Swiss J Palaontol. 130(2): 259–275.

Elias FA, Bertini RJ, Medeiros MA. 2007. Pterosaur teeth from the Laje do Coringa, middle Cretaceous, São Luíz-Grajaú Basin, Maranhão state, Northern-Northeastern Brazil. Rev Bras Geosci. 37(2):1–9.

Forster CA, Sampson SD, Chiappe LM, Krause DW. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. Science. 279:1915–1919.

Hammer O, Harper DAT. 2006. Paleontological data analysis. Oxford: Blackwell.

Hammer O, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron. 4(1):9.

Hammer WR, Hickerson WJ. 1999. Gondwana Dinosaurs from the Jurassic of Antarctica. Paper presented at the proceedings of the 2nd Gondwanan Dinosaur Symposium, Tokyo, Japan

Ji Q, Currie P, Norell MA, Ji SA. 1998. Two feathered dinosaurs from northeastern China. Nature. 393:753–761.

Kellner AWA. 1994. Remarks on Pterosaur Taphonomy and Palaeoecology. Acta Geol Leopol. 39(17):175–189.

Kellner AWA. 2003. Pterosaur phylogeny and comments on the evolutionary history of the group [special publications]. In: Buffetaut E, Mazin J-M, editors. Evolution and palaeobiology of pterosaurs. Vol. 217. London: Geological Society. p. 105–137.

Kellner AWA. 2006. Pterossauros – os senhores do céu do Brasil. Rio de Janeiro: Vieira e Lent.

Kellner AWA. 2010. Comments on the Pteranodontidae (Pterosauria, Pterodactyloidea) with the description of two new species. An Acad Bras Ciênc. 82(4):1063–1084.

Kellner AWA, Campos DA. 1988. Sobre um novo pterossauro com crista sagital da Bacia do Araripe, Cretáceo Inferior do Nordeste do Brasil. An Acad Bras Ciênc. 60:459–469.

Kellner AWA, Campos DA. 2000. Brief review of dinosaur studies and perspectives in Brazil. An Acad Bras Ciênc. 72(4):509–538.

Kellner AWA, Campos DA. 2002. The function of the cranial crest and jaws of a unique pterosaur from the early Cretaceous of Brazil. Science. 297(5580):389–392.

Kellner AWA, Tomida Y. 2000. Description of a new specie of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian – Albian), Northeastern Brazil. Natl Sci Museum Monogr. 17:1–135.

Li JJ, Lü JC, Zhang BK. 2003. A new Lower Cretaceous Sinopterid pterosaur from the Western Liaoning, China. Acta Palaeontol Sin. 42(3):442–447.

Long JA. 1998. Dinosaurs of Australia and New Zealand and other animals of the Mesozoic Era. Cambridge: Harvard University Press.

Lü J, Azuma Y, Dong Z, Barsbold R, Kobayashi Y, Lee YN. 2009. New material of dsungaripterid pterosaurs (Pterosauria: Pterodactyloidea) from western Mongolia and its palaeoecological implications. Geol Mag. 146(5):690–700.

Lü J, Gao Y, Xing L, Li Z, Ji Q. 2007. A new species of *Huaxiapterus* (Pterosauria: Tapejaridae) from the Early Cretaceous of Western Liaoning, China. Acta Geol Sin. 81(5):683–687.

Lü J, Jin X, Unwin DM, Zhao L, Azuma Y, Ji Q. 2006. A new species of *Huaxiapterus* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of Western Liaoning, China with comments on the systematics of Tapejarid pterosaurs. Acta Geol Sin. 80(3):315–326.

Lü J, Unwin DM, Jin X, Liu Y, Ji Q. 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. Proc R Soc. B 277(1680):383–389.

Lü J, Yuan C. 2005. New tapejarid pterosaur from Western Liaoning, China. Acta Geol Sin. 79(4):453–458.

Mader BJ, Kellner AWA. 1999. A new anhanguerid pterosaur from the Cretaceous of Morocco. Bol Mus Nac. 45:1–11.

Marples BJ. 1930. The proportions of birds' wings and their changes during development. Proc Zool Soc Lond. 100(4):997–1008.

Martill DM, Frey E. 1999. A possible azhdarchid pterosaur from the Crato Formation (Early Cretaceous, Aptian) of Northeast Brazil. Geol Minjnbouw. 78:315–318.

Molnar RE. 1982. A catalogue of fossil amphibians and reptiles in Queensland. Mem Qd Mus. 20:613–633.

Molnar RE. 1987. A pterosaur pelvis from western Queensland. Australia. Alcheringa. 11:87–94.

Molnar RE, Thulborn RA. 1980. First pterosaur from Australia. Nature. 288:361–363.

Nudds RL, Dyke GJ, Rayner JMV. 2004. Forelimb proportions and the evolutionary radiation of Neornithes. Proc R Soc Lond Ser. B 271 (suppl. 5):324–327.

Nuvens PC, Sayão JM, Silva HP, Saraiva AAF, Kellner AWA. 2002. A coleção de pterossauros do Museu De Paleontologia De Santana

Do Cariri, nordeste do Brasil. Arquivos Do Museu Nacional, Rio de Janeiro. 60(3):235–240.

Padian K, Chiappe LM. 1998. The origin and early evolution of birds. Biol Rev. 73(1):1–42.

Peres-Neto PR, Jackson DA, Somers KM. 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. Ecology. 84:2347–2363.

Pinheiro FL, Fortier DC, Schultz CL, De Andrade JAFG, Bantim RAM. 2011. New information on *Tupandactylus imperator*, with comments on the relationships of Tapejaridae (Pterosauria). Acta Palaeontol Pol. 56(3):567–580.

Price LI. 1953. A presença de Pterosauria no Cretáceo Superior do Estado da Paraíba. Notas Preliminares Estudos, Divisão Geologia do DNPM. 71:1–12.

Prondvai E, Hone DWE. 2008. New Models for the wing extension in pterosaurs. Hist Biol. 20(4):237–254.

Rodrigues T, Kellner AWA. 2008. Review of the pterodactyloid pterosaur *Coloborhynchus*. Zitteliana. B 28:219–228.

Sayão JM. 2003. Histovariability in bones of two pterodactyloid pterosaurs from the Santana Formation, Araripe Basin, Brazil: preliminary results [special publications]. In: Buffetaut E, Mazin J-M, editors. Evolution and palaeobiology of pterosaurs. Vol. 217. London: Geological Society. p. 335–342.

Sayão JM, Kellner AWA. 2006. Novo esqueleto parcial de pterossauro (Pterodactyloidea, Tapejaridae) do Membro Crato (Aptiano), Formação Santana, Bacia do Araripe, Nordeste do Brasil. Estudos Geológicos. 16:16–40.

Sayão JM, Vila Nova BC, Romano PSR. 2011. Paleontologia de Vertebrados: Relações entre América do Sul e África. Chapter: Considerações sobre os padrões de distribuição geográfica dos Pterodactyloidea (Archosauria, Pterosauria). Rio de Janeiro: Editora Interciência.

Steiner H. 1917. Das Problem der Diastataxie des Vogelflügels. Jena Z Naturwissen. 55:221–496.

Unwin D. 2003. On the phylogeny and evolutionary history of pterosaurs [special publications]. In: Buffetaut E, Mazin J-M, editors. Evolution and palaeobiology of pterosaurs. Vol. 217. London: Geological Society. p. 139–190.

Unwin D, Martill DM. 2007. The Crato fossil beds of Brazil: window into an ancient world. Chapter 17, Pterosaurs of the Crato Formation. Cambridge: Cambridge University Press. p. 475–524.

Verheyen R. 1961. A new classification for the non-passerine birds of the world. Bull Inst R Sci Nat Belg. 37:1–36.

Vila Nova BC, Saraiva AAF, Moreira JKR, Sayão JM. 2011. Controlled excavations in the Romualdo Formation Lagerstätte (Araripe Basin, Brazil) and pterosaur diversity: remarks based on new findings. Palaios. 26(3):173–179.

Vullo R, Marugán-Lobon J, Buscalioni A, Moratalla JJ. 2009. The first tapejarid pterosaur from Europe. 69th Society of Vertebrate Paleontology Annual Meeting. J Vert Paleont. 29(3):196A.

Wang X, Kellner AWA, Jiang S, Meng X. 2009. An unusual long-tailed pterosaur with elongated neck from western Liaoning of China. An Acad Bras Ciênc. 81(4):793–812.

Wang X, Lü J. 2001. Discovery of a pterodactyloid pterosaur from the Yixian Formation of western Liaoning, China. Chin Sci Bull. 46(13): 1112–1117.

Wang X, Zhou Z. 2003a. A new pterosaur (Pterodactyloidea, Tapejaridae) from the early Cretaceous Jiufotang formation of western Liaoning, China and its implications for biostratigraphy. Chin Sci Bull. 48(1):16–23.

Wang X, Zhou Z. 2003b. Two new pterodactyloid pterosaurs from the early Cretaceous Jiufotang formation of western Liaoning, China. Vertebrat Palasiatic. 41(1):34–41.

Wellnhofer P. 1991a. The illustrated encyclopedia of pterosaurs. London: Salamander Books. p. 192.

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

Wellnhofer P, Buffetaut E. 1999. Pterosaur remains from the Cretaceous of Morocco. Paläont Z. 73:133–142.