

BOLETIM DO MUSEU NACIONAL

NOVA SÉRIE
RIO DE JANEIRO - BRASIL

ISSN 0080-3200

GEOLOGIA

Nº 75

15 DE OUTUBRO DE 2007

SHORT NOTE ON THE INGROUP RELATIONSHIPS OF THE TAPEJARIDAE (PTEROSAURIA, PTERODACTYLOIDEA)¹

(With 10 figures)

ALEXANDER W. A. KELLNER ²
DIOGENES DE ALMEIDA CAMPOS ³

ABSTRACT: The systematic status of some species of the clade Tapejaridae (Pterosauria, Pterodactyloidea) from the Romualdo and Crato members of the Lower Cretaceous Santana Formation (Araripe Basin) are reviewed. Several anatomical features, particularly on the palatal region and on the cranial crest, indicate the presence of four species in the Romualdo Member: *Tapejara wellnhoferi*, *Tupuxuara longicristatus*, *Tupuxuara leonardii* and *Thalassodromeus sethi*. One of the two species reported from the Crato Member, previously classified in the genus *Tapejara*, is relocated to a new genus, *Tupandactylus imperator*. The second species, "*Tapejara navigans*" is very similar to the previous one and possibly represents the same taxon. A subdivision of the Tapejaridae into the clades Tapejarinae and Thalassodrominae is proposed here.

Key words: Pterosauria. Tapejaridae. Lower Cretaceous. Araripe Basin. Brazil.

RESUMO: O status sistemático de algumas espécies do clado Tapejaridae (Pterosauria, Pterodactyloidea) encontrados nos membros Romualdo e Crato da Formação Santana (Cretáceo Inferior, Bacia do Araripe) é revisto. Diversas características anatômicas presentes particularmente na região palatal e na crista craniana indicam a presença de quatro espécies no Membro Romualdo: *Tapejara wellnhoferi*, *Tupuxuara longicristatus*, *Tupuxuara leonardii* and *Thalassodromeus sethi*. Uma das duas espécies de Tapejaridae do Membro Crato, anteriormente classificada no gênero *Tapejara* é realocada em um gênero novo, passando a ser designada *Tupandactylus imperator*. A segunda espécie, "*Tapejara navigans*" é muito similar à primeira e possivelmente representa o mesmo taxon. Neste trabalho é proposta a subdivisão dos Tapejaridae nos clados Tapejarinae e Thalassodrominae. Palavras chave: Pterosauria. Tapejaridae. Cretáceo Inferior. Bacia do Araripe. Brasil.

INTRODUCTION

The Tapejaridae was erected to accommodate two toothless pterosaur taxa from the Early Cretaceous Romualdo Member of the Santana Formation (Araripe Basin, Northeastern

¹ Submitted on August 3, 2007. Accepted on October 10, 2007.

² Museu Nacional/UF RJ, Departamento de Geologia e Paleontologia. Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil. E-mail: kellner@mn.ufrj.br.

Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

³ Museu de Ciências da Terra/DNPM. Avenida Pasteur, 404, Urca, 22290-240, Rio de Janeiro, RJ, Brasil. E-mail: dac@acd.org.br.

Brazil): *Tupuxuara longicristatus* Kellner & Campos, 1988 and *Tapejara wellnhoferi* Kellner, 1989 (KELLNER, 1989). Since then several other taxa have been included in this clade: *Sinopterus dongi* Wang & Zhou, 2002, *Sinopterus* (= *Huaxiapterus*) *jü* Lü & Yuan, 2005 and “*Huaxiapterus*” *corollatus* Lü, Jin, Unwin, Zhao, Azuma & Ji, 2006 from the Early Cretaceous deposits of China (WANG & ZHOU, 2002; LÜ & YUAN, 2005; LÜ *et al.*, 2006); “*Tapejara*” *imperator* Campos & Kellner, 1997, “*Tapejara*” *navigans* Frey, Martill & Buchy, 2003, and *Thalassodromeus sethi* Kellner & Campos, 2002 from the Santana Formation (CAMPOS & KELLNER, 1997; FREY *et al.*, 2003; KELLNER & CAMPOS, 2002). Besides the disagreement over tapejarid monophyly (e.g., UNWIN, 2003; KELLNER, 2003, 2004), recently MARTILL & NAISH (2006) have questioned the validity of the specific status of *Thalassodromeus sethi*, regarding this taxon as a “junior subjective synonym” of *Tupuxuara longicristatus*. In this paper we address this issue, presenting morphological differences that justify the distinction between the two species of *Tupuxuara* and *Thalassodromeus sethi*. We also discuss the taxonomic status of the species included in the genus *Tapejara* and propose the subdivision of the Tapejaridae in two new clades, the Tapejarinae and the Thalassodrominae.

TAPEJARINAE Kellner, 1989

Definition: All pterosaurs more closely related to *Tapejara wellnhoferi* than to *Thalassodromeus sethi*.

Diagnosis: Tapejarid pterosaurs with the rostral end downturned, bony portion of the premaxillary crest above the nasoantorbital fenestra low; posterior extension of the cranial crest low; and orbit positioned on a level only slighter below the dorsal margin of the nasoantorbital fenestra.

Included taxa: *Tapejara wellnhoferi*, *Tupandactylus imperator*, “*Tapejara navigans*”, *Sinopterus dongi*, *Sinopterus jü* and “*Huaxiapterus*” *corollatus*.

Tupandactylus n.gen.

Type species: *Tapejara imperator* Campos & Kellner, 1997 (Figs.1-2).

Etymology: *Tupan* or *Tupā*, god of the thunder in the Tupian culture and *dactylus*, from the Greek word *daktylos*, meaning finger.

Diagnosis: same as for the type species.

Tupandactylus imperator (Campos & Kellner, 1997) new combination

Holotype: almost complete skull housed in the Paleontological Collections of the Museu de Ciências da Terra (Departamento Nacional da Produção Mineral), Rio de Janeiro (MCT 1622-R).

Revised diagnosis: tapejarine pterosaur with large and high cranial sagittal crest formed by a basal ossified portion and an extensive area of soft tissue; premaxillary anterior portion of the crest large and high with distinct developed, dorsally oriented bony spine-like projection; posterior part of the ossified portion of the sagittal crest low and extended well behind the occipital region.

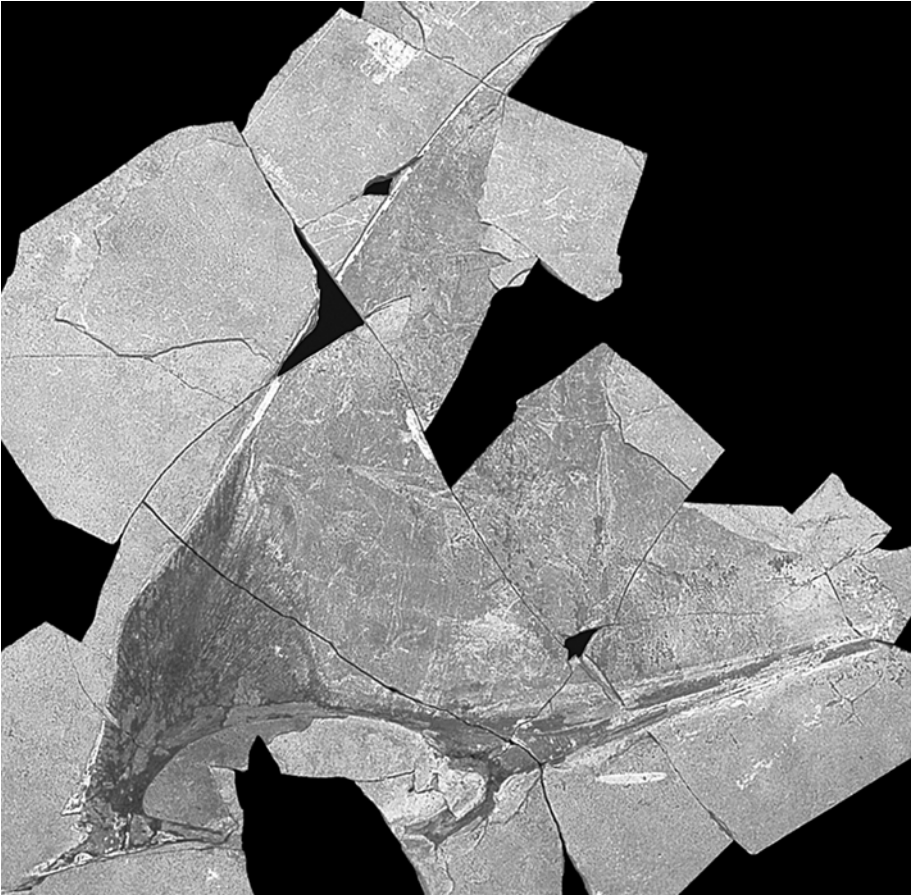


Fig.1- Photo of the skull of *Tupandactylus imperator* n.comb. (MCT 1622-R).

Remarks: With the description of *Tapejara wellnhoferi*, KELLNER (1989) has introduced the group (family) Tapejaridae. Based on the International Code of Zoological Nomenclature (article 36 - Principle of Coordination), the name established for a taxon at any rank in the family group is considered to simultaneously establish nominal taxa at all other ranks in the family group (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1999).

The genus *Tapejara* (type-species *Tapejara wellnhoferi*) was the second toothless pterosaur discovered in the Araripe Basin, found in the calcareous nodules of the Romualdo Member of the Santana Formation. At that time this taxon was known by one partial skull shown to be distinct from *Tupuxuara longicristatus* in several ways, particularly by the absence of a palatal ridge and a downturned anterior end of the rostrum (KELLNER, 1989), which was confirmed by additional specimens (WELLNHOFER & KELLNER, 1991).

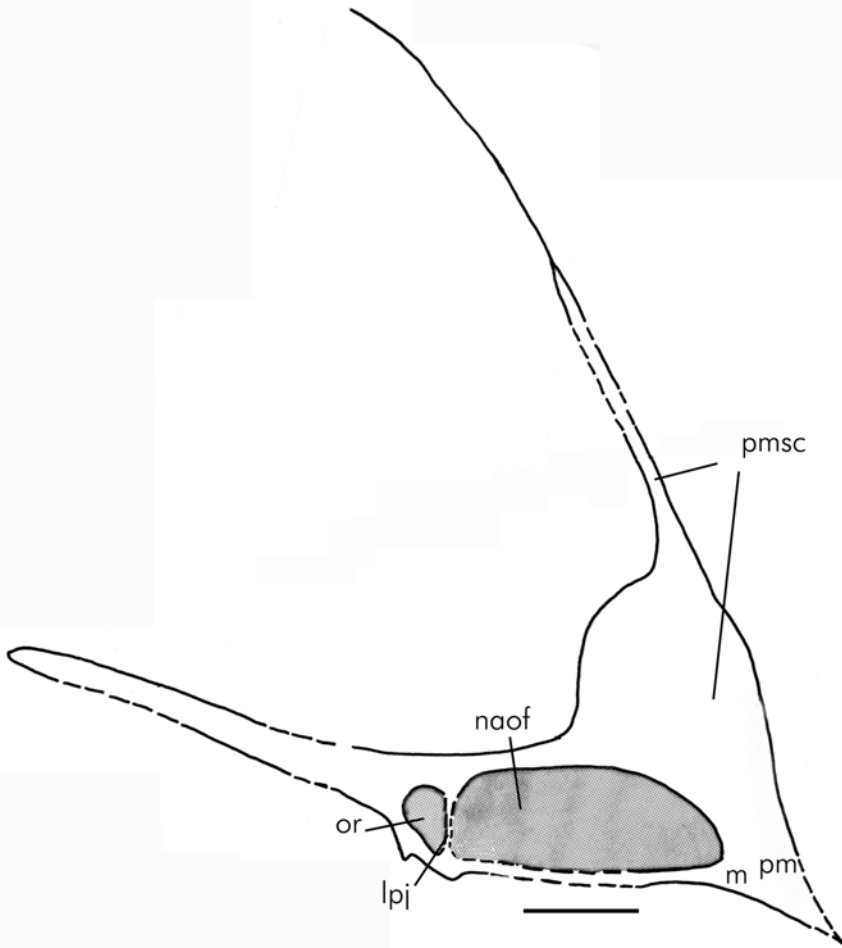


Fig.2- Skull of *Tupandactylus imperator* n. comb. (MCT 1622-R). Abbreviations: (lpi) lacrimal process of the jugal, (m) maxilla, (naof) nasoantorbital fenestra, (or) orbit, (pm) premaxilla, (pmsc) premaxillary sagittal crest. Scale bar = 100mm.

Some years later, a new tapejarid species was found in the Crato Member of the Santana Formation and referred to this genus - *Tapejara imperator* (CAMPOS & KELLNER, 1997). Since then more tapejarid material has been collected, not only from the Santana Formation (e.g., NUVENS *et al.*, 2002), but also from other deposits in Africa (WELLNHOFER & BUFFETAUT, 1999) and China (e.g., WANG & ZHOU, 2002; LÜ & YUAN, 2005), providing more information of those toothless pterosaurs. Previous phylogenetic analysis have shown *Tapejara wellnhoferi* and *Tupandactylus imperator* as monophyletic (KELLNER, 2003, 2004; UNWIN, 2003) and is here named Tapejarinae.

Comparison of the skull of *Tapejara wellnhoferi* with the one of *Tupandactylus imperator* indicates several morphological differences (see diagnosis above) and therefore a new genus to accommodate the Crato tapejarid is proposed. It should be noted that this result agrees with the phylogenetic analysis of MARTILL & NAISH (2006), where *Tapejara* turned out to be paraphyletic.

The systematic position of the second tapejarid from the Crato Member, "*Tapejara navigans*", based on two skulls (FREY *et al.*, 2003), is more problematical and depends on a close examination of the specimens referred to this taxon. The main distinct feature is the lack of the posterior expansion of the cranial crest present in *Tupandactylus imperator*. Examining the published pictures of "*Tapejara navigans*" it is clear that the posterior region of the skull in the referred specimen (SMNK PAL 2343) is broken, which apparently is also the case in the holotype (SMNK PAL 2344) as has been pointed out before (KELLNER, 2004). If indeed "*Tapejara navigans*" lacks the posterior extension of the cranial crest, it possibly represents a distinct taxon. Although the discussion of the phylogenetic analysis published by MARTILL & NAISH (2006) is beyond the scope of this paper, it is interesting to note that those authors got *Sinopterus* more closely related to other *Tapejara* species, with "*Tapejara navigans*" occupying a more basal position.

THALASSODROMINAE n. taxon

Definition: All pterosaurs more closely related to *Thalassodromeus sethi* than to *Tapejara wellnhoferi*.

Diagnosis: Tapejarid pterosaurs with a very high nasoantorbital fenestra and the bony portion of the sagittal crest starting on the anterior part of the skull and directed posteriorly larger than in other pterosaurs.

Included taxa: *Thalassodromeus sethi*, *Tupuxuara longicristatus* and *Tupuxuara leonardii*.

Remarks: *Tupuxuara longicristatus* was based on a partial skull and some wing elements (MN 6591-V) housed at the Museu Nacional/UFRJ in Rio de Janeiro. Among the diagnostic features of this species is the presence of a thin palatal ridge (Fig.3) and a pneumatic foramen on the dorsal surface of the first wing phalanx, close the base of the extensor tendon process (KELLNER & CAMPOS, 1988; KELLNER, 2004).

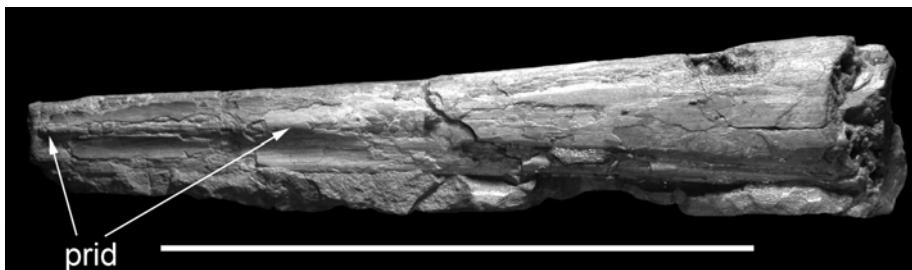


Fig.3- Palatal region of *Tupuxuara longicristatus* (MN 6591-V). Abbreviation: (prid) palatal ridge. Scale bar = 100mm.

Another toothless species from the Santana Formation, *Tupuxuara leonardii*, was erected based on a fragmentary cranial remain that was distinguished from other toothless pterosaurs (e.g., *Tupuxuara longicristatus*) by having a stronger, deeper and shorter palatal ridge (KELLNER & CAMPOS, 1994). A second specimen (Figs.4-5), housed at the Iwaki Coal and Fossil Museum in Iwaki, Japan (IMCF 1052), constituting of a partial skeleton including a complete skull was referred to this taxon (KELLNER, 2004) and provides extensive information of this species (Kellner and Hasegawa in prep).

MARTILL & NAISH (2006) questioned the taxonomic validity of *Tupuxuara leonardii* pointing out that the presence of a strong palatal ridge was variably present in *Azhdarcho*, citing BAKHURINA & UNWIN (1995). However, BAKHURINA & UNWIN (1995) did not point out the presence or absence of a palatal ridge in this taxon and the reproduced occlusal view of one lower jaw also lacks this feature. Furthermore, *Quetzalcoatlus* sp., the best know azhdarchid, lacks a palatal ridge (KELLNER & LANGSTON, 1996; *contra* MARTILL & NAISH, 2006).

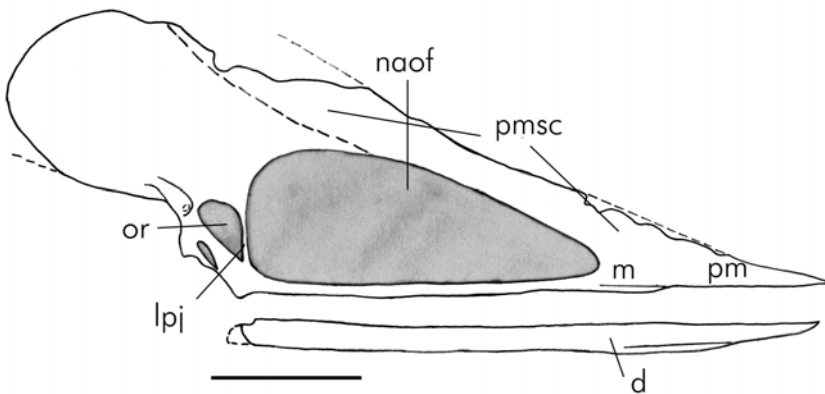


Fig.4- Skull and lower jaw of *Tupuxuara leonardii* (IMCF 1052). Abbreviations: (d) dentary, (lpi) lacrimal process of the jugal, (m) maxilla, (naof) nasoantorbital fenestra, (or) orbit, (pm) premaxilla, (pmsc) premaxillary sagittal crest. Scale bar = 200mm.

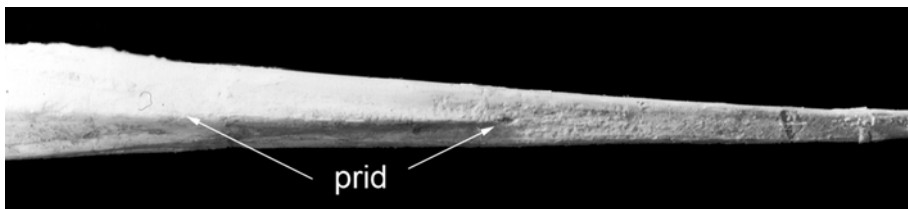


Fig.5- Palatal region of *Tupuxuara leonardii* (IMCF 1052). Abbreviation: (prid) palatal ridge.

Another large tapejarid from the Romualdo Member, *Thalassodromeus sethi* (Figs.6-10), was described by KELLNER & CAMPOS (2002) based on an almost complete skull and lower jaw, whose validity was also questioned by MARTILL & NAISH (2006). Six features were pointed out in the original description as diagnostic of this pterosaur: developed cranial crest (composed of premaxillae, frontal, parietal and supraoccipital) starting at the tip of the skull and extended posteriorly behind the occipital region; posterior end of the cranial crest “V” shaped; suture between premaxillae and frontoparietal portion of the crest rectilinear; anterior portion of the premaxillae and dentary with sharp dorsal and ventral edges; palatines before palatal ridge strongly concave; and posterior (occipital) region broader than in other tapejarids (width over quadrates 20% of squamosal to premaxilla length).

MARTILL & NAISH (2006) argued that the features regarding shape and size of the cranial crest in pterosaurs are not diagnostic, therefore dismissing the first two characters listed above. However, several authors have used the shape and size of cranial crests to distinguish pterosaurs at different taxonomic levels (e.g., CAMPOS & KELLNER, 1985; FREY *et al.*, 2003; KELLNER, 2003; UNWIN, 2003; WANG & ZHOU, 2002; LÜ & YUAN, 2005; LÜ *et al.*, 2006). Furthermore, the authors themselves use the shape of the cranial crest (“fingerlike crest on parietal” and distinct dentary crest) to establish the relationships of *Tapejara* and *Sinopterus* (MARTILL & NAISH, 2006: p.929).

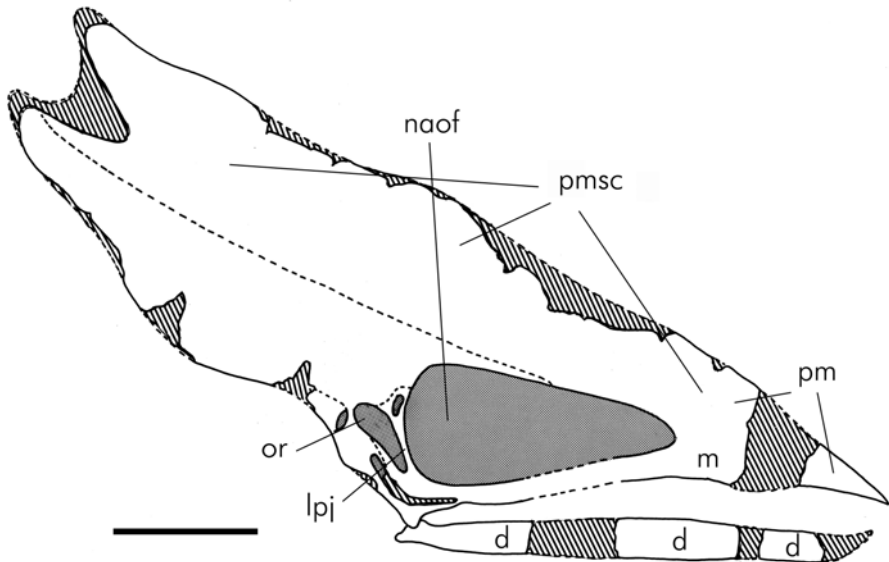


Fig.6- Skull and lower jaw of *Thalassodromeus sethi* (DGM 1476-R). Abbreviations: (d) dentary, (lpi) lacrimal process of the jugal, (m) maxilla, (naof) nasoantorbital fenestra, (or) orbit, (pm) premaxilla, (pmsc) premaxillary sagittal crest. Scale bar = 200mm.

Regarding the sharp ventral edge of the premaxillae and the sharp dorsal edge of the dentary present in *Thalassodromeus* (Fig.7), MARTILL & NAISH (2006) considered those features difficult to test since most azhdarchids have the skulls laterally compressed. This same justification was used regarding the distinct configuration of the palate (Figs.8,9) and the size of the occiput that are further differences between the former and *Tupuxuara* (KELLNER & CAMPOS, 2002). Actually most pterosaurs have their skulls laterally compressed and if one follows this line of reasoning, no tridimensional structures observed in well preserved specimens could be used to diagnose any of those volant archosaurs. Furthermore, the materials of the taxa involved are not compressed and *Tupuxuara* (both species) shows a convex palate and lacks a “scissors-like” configuration of the rostrum. MARTILL & NAISH (2006, p. 933) statement that *Zhejiangopterus linhaiensis* Cai & Wei, 1994 has the margins of the upper and lower jaw sharp as in *Thalassodromeus sethi* is in error.

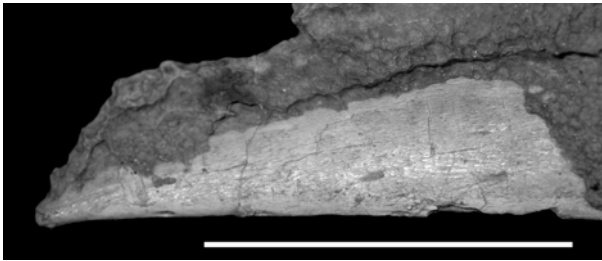


Fig.7- Anterior part of the left premaxilla of *Thalassodromeus sethi* (DGM 1476-R), in lateral view. Scale bar = 50mm.

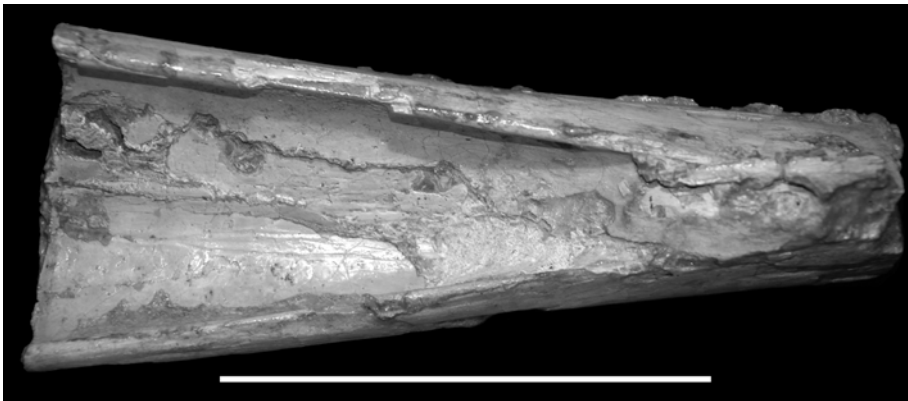


Fig.8- Palate of *Thalassodromeus sethi* (DGM 1476-R). Scale bar = 100mm.

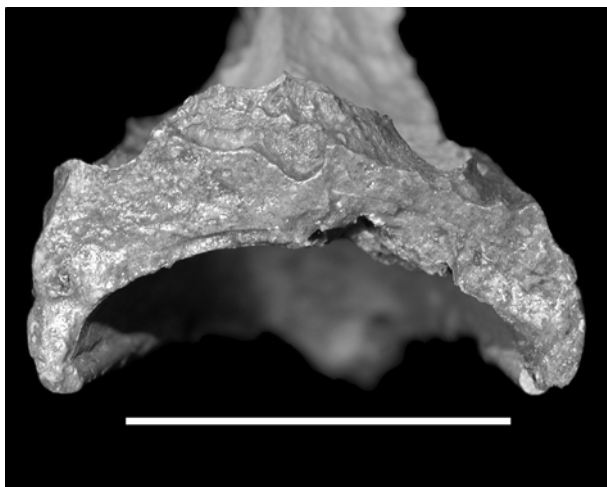


Fig.9- Transverse section of the skull of *Thalassodromeus sethi* (DGM 1476-R), showing the concave palate. Note that the dorsal region is still embedded in the calcareous matrix. Scale bar = 50mm.

There is one more feature, not listed by KELLNER & CAMPOS (2002) that distinguishes *Thalassodromeus sethi* from *Tupuxuara leonardii*: the ventral bar that makes the anterior portion of the nasoantorbital fenestra in *Thalassodromeus sethi* is thicker than in *Tupuxuara leonardii* (and also than in *Tupuxuara longicristatus*; Figs.4,6). Another interesting feature present in *Thalassodromeus sethi* is a peculiar opening on the basal part of the cranial crest (Fig.10). It is presently not clear if this paired opening is a distinct feature of this species or pathologic.

To conclude, the morphological differences between the two species of *Tupuxuara* and *Thalassodromeus* are not artifacts of preservation and cannot be explained as ontogenetic differences as suggested by MARTILL & NAISH (2006). Therefore the claim that *Thalassodromeus sethi* is as a junior synonym of one of the two species of *Tupuxuara* is unsubstantiated.

Notwithstanding their differences, *Tupuxuara* and *Thalassodromeus* share two features absent in other tapejarids: the large height of the nasoantorbital fenestra and the large bony component of the cranial sagittal crest. Those features indicate that they are more closely related to each other in respect to *Tapejara* (or *Sinopterus*), as has been established by previous phylogenetic analysis (KELLNER, 2004), for which the clade Thalassodrominae is here erected. Regarding the height of the nasoantorbital fenestra there is another pterodactyloid that also shows this feature: *Zhejiangopterus linhaiensis* described by CAI & WEI (1994). This species, however, is generally classified in the Azhdarchidae (e.g., UNWIN & LÜ, 1997; KELLNER, 2003) and according to the present hypothesis of tapejarid and azhdarchid relationships (e.g., WANG *et al.*, 2005), it developed this feature independently.

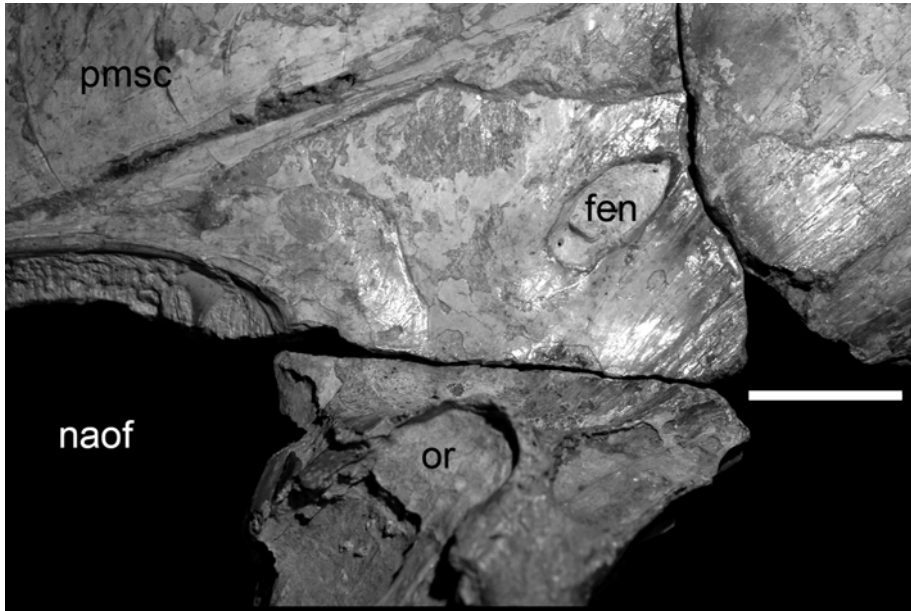


Fig.10- Detail of the left lateral view of the skull of *Thalassodromeus sethi* (DGM 1476-R). Abbreviations: (fen) fenestra, (naof) nasoantorbital fenestra, (or) orbit, (pmsc) premaxillary sagittal crest. Scale bar = 50mm.

TAPEJARIDAE FROM THE JIUFOTANG FORMATION

Except for an unpublished specimen from the Yixian Formation (WANG *et al.*, 2005), all tapejarid pterosaurs known so far from China were collected in the Jiufotang Formation. The first was *Sinopterus dongi*, based on a fairly complete skeleton (WANG & ZHOU, 2002). This species differs from other tapejarids by having a smaller nasoantorbital fenestra, the anterior part of the premaxillary crest less developed and the posterior extension of the cranial crest (formed by the premaxillae, supraoccipital, frontals and parietals) distinctively deflected upwards. A second species, "*Sinopterus gui*" Li, Lü & Zhang, 2003 was based on a small skeleton that differed from the previous one mainly by the supposed presence of a notarium (that is absent, see below), the lack of a cranial crest, and a comparatively smaller femur (LI *et al.*, 2003). However, a close examination of the holotype and only specimen of this taxon indicates that it belongs to a very young individual with a wing span around 0.64 m. There is no notarium and the ratio of the femur and tibia (fe/ti) is 0.642, closer to *Sinopterus dongi* (fe/ti= 0.712) and not 0.49 as originally proposed (LI *et al.*, 2003). Furthermore the skull is broken with the dorsal region not preserved; therefore if a cranial crest was or was not present cannot be established. Based on the observations above, there is no distinctive character separating "*Sinopterus gui*" from *Sinopterus dongi*, suggesting that it is a junior synonym of latter, representing an ontogenetically less mature individual.

Another tapejarid species, "*Huaxiapterus*" *jii* was erected by LÜ & YUAN (2005) based on an incomplete skeleton. The premaxillary crest of this taxon is slightly more pronounced than the one of *Sinopterus dongi* and the dentary is deeper, indicating that they are different species (LÜ & YUAN, 2005). However, the overall shape of the preserved elements, including the proportions of several postcranial bones are remarkably similar to *Sinopterus dongi*, suggesting that they do belong to the same genus as noted by WANG & ZHOU (2006). *Sinopterus jii* has an estimated wing span of 1.62 m, being, therefore, larger than *Sinopterus dongi* (wing span: 1.18m).

The last tapejarid from the Jiufotang Formation is "*Huaxiapterus*" *corollatus* that was based on a partial skeleton (LÜ *et al.*, 2006). According to the original description, the main difference from other tapejarids, particularly *Sinopterus jii*, is the particular hatchet-shaped expansion of the premaxillary crest above the anterior margin of the nasoantorbital fenestra. Based on the measurements provided by LÜ *et al.* (2006), the ratio between the lengths of several postcranial elements (e.g., humerus/wing metacarpal; ulna/ wing metacarpal; first wing phalanx/ femur) of "*Huaxiapterus*" *corollatus* differs from all other Chinese tapejarids, suggesting that it belongs to a distinct genus. Since *Huaxiapterus jii*, the type species of the genus *Huaxiapterus* is now referred to the genus *Sinopterus* (WANG & ZHOU, 2006), "*Huaxiapterus*" *corollatus* needs a new generic name.

FINAL CONSIDERATIONS

At present there is a debate about the monophyly of the Tapejaridae. Recently, LÜ *et al.* (2006) and MARTILL & NAISH (2006) have followed UNWIN (2003) in regarding *Tupuxuara* more closely related to the Azhdarchidae than to *Tapejara wellnhoferi*. Their main argument is the loss of the contact between metacarpals I-III and the carpus. Actually, there are three conditions of this character in pterosaurs: all metacarpals are attached to the carpus (the primitive condition), metacarpals II and III reduced (e.g. not reaching the carpus) and only metacarpals IV reaching the carpus (e.g., metacarpals I-III reduced). KELLNER (2004) pointed out that, despite using the supposed reduction of metacarpals I-III as a synapomorphy uniting *Tupuxuara* with Azhdarchidae, UNWIN (2003) regarded the condition of the former as unknown. MARTILL & NAISH (2006) acknowledged this, but pointed out the existence of unpublished specimens referable to *Tupuxuara* with metacarpals I-III reduced. To our knowledge, no specimens known to us that are referable to *Tupuxuara* (or Thalassodrominae) show the metacarpals I-III completely preserved to prove conclusively that those elements did not reach the carpus. The preserved portion of metacarpal I in the second specimen referred to *Tupuxuara leonardii* (IMCF 1052) indicates that this element is very long and was likely attached to the carpus, contradicting the information presented by MARTILL & NAISH (2006). In the original descriptions of the tapejarid *Sinopterus jii*, it was noted that the metacarpus III (more likely metacarpus I) reached the carpus while, according to LÜ *et al.* (2006) in the tapejarid "*Huaxiapterus*" *corollatus* metacarpals I-III are reduced, showing, at least, the ambiguous nature of this feature. Lastly, MARTILL & NAISH (2006) and LÜ *et al.* (2006) ignored that the loss of contact between metacarpals I-III is present in other pterodactyloid clades, such as in the Pteranodontidae (*Pteranodon*) and in the Nyctosauridae (BENNETT, 2001; KELLNER, 2003; UNWIN, 2003).

The discussion of the use of cranial crest for taxonomic purposes in pterosaurs has two quite distinct approaches - some authors using it and some discarding it. There are others, like MARTILL & NAISH (2006), that adopt a rather ambiguous posture criticizing authors that have used them but using them as well with, perhaps a different wording. Several species and supraspecific taxa are being distinguished by features present in cranial crests (e.g., FREY *et al.*, 2003; KELLNER, 2003; UNWIN, 2003; LÜ *et al.*, 2006) and the *a priori* dismissal of this source of information seems rather questionable.

Based on the morphological features present in *Tupuxuara longicristatus*, *Tupuxuara leonardii*, and *Thalassodromeus sethi*, all three species are regarded to be distinct from each other, thus confirming their status of valid and diagnosable species. Their distinctions were not only based on features of the cranial crests, but also on characteristics of the palatal region. We also would like to point out that if distinct anatomical features like the ones observed in *Tupuxuara* and *Thalassodromeus* are of no taxonomic value, then it might be very difficult to tell pterosaur species apart.

Lastly, MARTILL & NAISH (2006) raised the possibility of crests varying during ontogeny and proposed a specific developmental pattern for this structure in *Tupuxuara*. Note that the size of the skull measured from the tip of the premaxilla to the posterior edge of the squamosal of *Tupuxuara leonardii* (IMCF 1052) is larger (ca. 850 mm) than in *Thalassodromeus sethi* (ca. 798 mm), supposed to represent an adult and an old adult ontogenetic stage, respectively. Although discussing ontogenetic variation in cranial crests is an interesting idea, the model presented by MARTILL & NAISH (2006) lacks any empirical evidence and has to be regarded as speculative, at best.

ACKNOWLEDGMENTS

We would like to thank Wang Xiaolin and Zhou Zhonghe for allowing the examination of several pterosaur specimens housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP) and several discussions regarding the pterosaur fauna from the Jehol Biota, and Li Jian Jun for allowing the examination of the holotype of *Sinopterus gui*, housed in the Beijing Natural History Museum. We thank Marcelo Newton Trotta for many comments that improved the manuscript.

This research was partially funded by the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Rio de Janeiro (FAPERJ # E-26/152.885/2006), the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq #304965/2006-5), and the Brazilian Academy of Sciences.

REFERENCES

- BAKHURINA, N.N. & UNWIN, D.M., 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. **Historical Biology**, **10**:197-245.
- BENNETT, S.C., 2001. The osteology and functional morphology of the Late Cretaceous Pterosaur *Pteranodon*. **Palaeontographica Abt. A**, **260**:1-112.
- CAI, Z. & WEI, F., 1994. On a new pterosaur (*Zhejiangopterus linhaiensis* gen.et sp nov.) from Upper Cretaceous in Linhai, Zhejiang, China. **Vertebrata Palasiatica**, **32**:181-194.

CAMPOS, D.A. & KELLNER, A.W.A., 1985. Panorama of the Flying Reptiles Study in Brazil and South America. **Anais da Academia Brasileira de Ciências**, **57**(4):453-466.

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

FREY, E.; MARTILL.; D.M. & BUCHY.; M.C., 2003., A new species of tapejarid pterosaur with soft-tissue head crest. In: BUFFETAUT, E. & MAZIN, J.M. (Eds.) **Evolution and Paleobiology of Pterosaurs**. Geological Society, Special Publication 217, p.65-72.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1999. **International Code of Zoological Nomenclature (4th edition)**. The International Trust for Zoological Nomenclature 1999.

KELLNER, A.W.A., 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeast Brazil. **Anais da Academia Brasileira de Ciências**, **61**:439-446.

KELLNER, A.W.A., 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. In: BUFFETAUT, E. & MAZIN, J.M. (Eds.) **Evolution and Paleobiology of Pterosaurs**. Geological Society, Special Publication 217, p.105-137.

KELLNER, A.W.A., 2004. New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. **Ameghiniana**, **41**:521-534

KELLNER, A.W.A. & CAMPOS, D.A., 1988. Sobre um novo pterossauro com crista sagittal da Bacia do Araripe, Cretáceo Inferior do Nordeste do Brasil. **Anais da Academia Brasileira Ciências**, **60**:459-469.

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

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

KELLNER, A.W.A. & LANGSTON.; W. JR., 1996. Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from the Late Cretaceous Sediments of Big Bend National Park, Texas. **Journal of Vertebrate Paleontology**, **16**:222-231.

LI, J.J.; LÜ, J.C. & ZHANG, B.K., 2003. A new Lower Cretaceous sinopterid pterosaur from the western Liaoning, China. **Acta Palaeontologica Sinica**, **42**:442-446.

LÜ, J.; JIN, X.; UNWIN, D.; ZHAO, J.; 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 tapejarida pterosaurs. **Acta Geologica Sinica**, **80**:315-326.

LÜ, J. & YUAN, C., 2005. New tapejarid pterosaur from western Liaoning, China. **Acta Geologica Sinica**, **79**(4):453-458.

MARTILL, D.M. & NAISH, D., 2006. Cranial crest development in the azhdarchoid pterosaur *Tupuxuara*, with a review of the genus and tapejarid monophyly. **Palaeontology**, **49**:925-941.

NUVENS, P.C.; SAYÃO, J.M.; SILVA, H.P.; SARAIVA, A.S.F. & KELLNER, A.W.A., 2002. A coleção de pterossauros do Museu de Paleontologia de Santana do Cariri, Nordeste do Brasil. **Arquivos do Museu Nacional**, **60**:235-240.

UNWIN, D.M., 2003. On the phylogeny and evolutionary history of pterosaurs. In: BUFFETAUT, E. & MAZIN, J.M. (Eds.) **Evolution and Paleobiology of Pterosaurs**. Geological Society, Special Publication 217, p.139-190.

UNWIN, D.M. & LU, J., 1997., On *Zhejiangopterus* and the relationships of pterodactyloid pterosaurs. **Historical Biology**, **12**:199-210.

WANG, X.L.; KELLNER, A.W.A.; ZHOU., Z. & CAMPOS, D.A., 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. **Nature**, **437**:875-879.

WANG, X. & ZHOU, Z., 2002. "A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implication for biostratigraphy. **Chinese Science Bulletin**, **47**:1521-1528 (in Chinese; translation: Chinese Science Bulletin, 2003.48:16-23).

WANG, X. & ZHOU, Z., 2006. Pterosaur assemblages of the Jehol Biota and their implication for the Early Cretaceous pterosaur radiation. **Geological Journal**, **41**:405-418.

WELLNHOFER, P. & BUFFETAUT, E., 1999. Pterosaur remains from the Cretaceous of Morocco. **Paläontologische Zeitschrift**, **73**:133-142.

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

Universidade Federal do Rio de Janeiro
Reitor - Aloísio Teixeira

Museu Nacional
Diretor - Sérgio Alex K. Azevedo

Editores - Miguel Angel Monné Barrios, Ulisses Caramaschi

Editores de Área - Adriano Brillhante Kury, Alexander Wilhelm Armin Kellner, Andrea Ferreira da Costa, Cátia Antunes de Mello Patiu, Ciro Alexandre Ávila, Débora de Oliveira Pires, Guilherme Ramos da Silva Muricy, Izabel Cristina Alves Dias, João Alves de Oliveira, João Wagner de Alencar Castro, Marcela Laura Monné Freire, Marcelo de Araújo Carvalho, Marcos Raposo, Maria Dulce Barcellos Gaspar de Oliveira, Marília Lopes da Costa Facó Soares, Rita Scheel Ybert, Vânia Gonçalves Lourenço Esteves

Conselho Editorial - André Pierre Prous-Poirier (Universidade Federal de Minas Gerais), David G. Reid (The Natural History Museum - Reino Unido), David John Nicholas Hind (Royal Botanic Gardens - Reino Unido), Fábio Lang da Silveira (Universidade de São Paulo), François M. Catzefflis (Institut des Sciences de l'Évolution - França), Gustavo Gabriel Politis (Universidad Nacional del Centro - Argentina), John G. Maisey (Americam Museum of Natural History - EUA), Jorge Carlos Della Favera (Universidade do Estado do Rio de Janeiro), J. Van Remsen (Louisiana State University - EUA), Maria Antonieta da Conceição Rodrigues (Universidade do Estado do Rio de Janeiro), Maria Carlota Amaral Paixão Rosa (Universidade Federal do Rio de Janeiro), Maria Helena Paiva Henriques (Universidade de Coimbra - Portugal), Maria Marta Cigliano (Universidad Nacional La Plata - Argentina), Miguel Trefaut Rodrigues (Universidade de São Paulo), Miriam Lemle (Universidade Federal do Rio de Janeiro), Paulo A. D. DeBlasis (Universidade de São Paulo), Philippe Taquet (Museum National d'Histoire Naturelle - França), Rosana Moreira da Rocha (Universidade Federal do Paraná), Suzanne K. Fish (University of Arizona - EUA), W. Ronald Heyer (Smithsonian Institution - EUA)

Normalização - Vera de Figueiredo Barbosa

Diagramação e arte-final - Lia Ribeiro

Secretaria - Thiago Macedo dos Santos

Indexação - Biological Abstracts, ISI - Thomson Scientific, Ulrich's International Periodicals Directory, Zoological Record, NISC Colorado, Periodica, C.A.B. International

Tiragem - 650 exemplares

<http://acd.ufrj.br/~museuhp/publ.htm>
E-mail: mnbib@acd.ufrj.br

MUSEU NACIONAL
Universidade Federal do Rio de Janeiro
Quinta da Boa Vista, São Cristóvão
20940-040 - Rio de Janeiro, RJ, Brasil

Impresso na COPIARTE