AMEGHINIANA (Rev. Asoc. Paleontol. Argent.) - 41 (4): 521-534. Buenos Aires, 30-12-2004 ISSN 0002-7014

New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade

Alexander Wilhelm Armin KELLNER[1]

Abstract. A phylogenetic analysis indicates that the Tapejaridae is a monophyletic group of pterodactyloid pterosaurs, diagnosed by the following synapomorphies: premaxillary sagittal crest that starts at the anterior tip of the premaxilla and extends posteriorly after the occipital region, large nasoantorbital fenestra that reaches over 45% of the length between premaxilla and squamosal, lacrimal process of the jugal thin, distinct small pear-shaped orbit with lower portion narrow, and broad tubercle at the ventroposterior margin of the coracoid. Several cranial and postcranial characters indicate that the Tapejaridae are well nested within the Tapejaroidea, in sister group relationship with the Azhdarchidae. A preliminary study of the ingroup relationships within the Tapejaridae shows that *Tupuxuara* is more closely related to *Thalassodromeus* relative to *Tapejara*. At present tapejarid remains have been found in the following deposits: Crato and Romualdo members of the Santana Formation (Aptian-Albian), Araripe Basin, Brazil; Jiufotang Formation (Aptian), Jehol Group of western Liaoning, China; and in the redbeds (Cenomanian) of the Kem Kem region, Morocco. An incomplete skull found in the Javelina Formation (Maastrichtian), Texas also shows several tapejarid features and might be a member of this clade. Although information is still limited, the present distribution of the Tapejaridae indicates that this clade of pterosaurs was not exclusive of Gondwana, and was more widespread than previously known.

Resumen. NUEVA INFORMACIÓN SOBRE LOS TAPEJARIDAE (PTEROSAURIA, PTERODACTYLOIDEA) Y DISCUSIÓN SOBRE LAS RELACIONES DE ESTE CLADO. Un análisis cladístico realizado indica que Tapejaridae es un grupo monofilético de los pterosaurios pterodactiloideos y está diagnosticado por las siguientes sinapomorfías: cresta sagital del premaxilar comienza en el borde anterior del premaxilar y se extiende posteriormente hasta la región occipital, gran fenestra nasoantorbital que alcanza el 45% de la extensión entre el premaxilar y escamosal, proceso lacrimal del yugal delgado, órbita pequeña en forma de pera con la porción inferior estrecha, y un amplio tubérculo en el margen ventro posterior del coracoide. Ciertos caracteres craneanos y postcraneanos indican que los Tapejaridae pueden agruparse dentro de los Tapejaroidea en una relación de grupo hermano con los Azhdarchidae. Un estudio preliminar de las relaciones del grupo interno dentro de los Tapejaridae muestra que *Tupuxuara* está más cercanamente relacionado a *Thalassodromeus* que a *Tapejara*. Hasta el presente los restos de tapejáridos han sido hallados en los siguientes depósitos: en los miembros Crato y Romualdo de la Formación Santana (Aptiano-Albiano), Cuenca de Araripe, Brazil; Formación Jiufotang (Aptiano), Grupo Jehol, de Liaoning occidental, China; y en las capas rojas (Cenomaniano) de la region de Kem Kem, Marruecos. Un cráneo incompleto hallado en la Formación Javelina (Maastrichtiano), Texas también muestra varios caracteres de los tapejáridos y podría pertenecer a este clado. A pesar que la información es aún limitada la presente distribución de los Tapejaridae sugiere que este clado de pterosaurios no fue exclusivo del Gondwana y estuvo más ampliamente distribuido de lo que previamente se había conocido.

Keywords. Pterosauria. Pterodactyloidea. Tapejaridae. Phylogenetic analysis. Cretaceous.

Palabras clave. Pterosauria. Pterodactyloidea. Tapejaridae. Análisis filogenético. Cretácico.

Introduction

In 1988 a toothless pterosaur from the Early Cretaceous Santana Formation, *Tupuxuara longicristatus* Kellner and Campos, was described and regarded to represent an (at that time) unknown clade of the Pterodactyloidea (Kellner and Campos, 1988). One year later, a second toothless flying reptile from the same deposit (*Tapejara wellnhoferi* Kellner) was discovered and, together with *Tupuxuara*, classified in a new clade named Tapejaridae, whose relationships with other pterodactyloid groups remained uncertain (Kellner, 1989). Based on other specimens from the Santana Formation, Kellner and Campos (1992) suggested that tapejarids and azhdarchids were in sister group relationship, a hypothesis that was supported by latter studies (Kellner and Hasegawa, 1993; Kellner and Langston, 1996; Kellner, 1996; 2001; 2003). The monophyly of the Tapejaridae was accepted by subsequent workers (e.g., Unwin, 1995; Wellnhofer and Buffetaut, 1999; Frey and Tischlinger, 2000; Wang and Zhou, 2002),

---

[1] Paleovertebrate Sector, Department of Geology and Paleontology, Museu Nacional/UFRJ; Quinta da Boa Vista, São Cristóvão, Rio de Janeiro, RJ, 20940-040 Brasil. Fellow CNPq. *kellner@mn.ufrj.br*

AMGHB2-0002-7014/04$00.00+.50

but has been recently questioned (*e.g.*; Unwin and Lü, 1997; Unwin, 2000; 2003).

Here I review the evidence pro and against the monophyly of the Tapejaridae. I also present new information on several tapejarid and closely related species and present a new phylogenetic analysis that includes some recently described taxa tentatively referred to this and related pterodactyloid clades.

Abbreviations. BSP-Bayerische Staatssammlung fur Paläontologie und Historische Geologie, Munich. MCT-Museu de Ciências da Terra, Rio de Janeiro. MN-Museu Nacional/UFRJ, Rio de Janeiro. DNPM-National Department of Mineral Production, Rio de Janeiro. SMNK-Staatliches Museum für Naturkunde, Karlsruhe.

Phylogenetic analysis

In order to access the question of tapejarid monophyly, I performed a phylogenetic analysis which is an extension of the study published by Kellner (2003), with the addition of taxa and characters (see appendices). Among the taxa added are *Thalassodromeus sethi* Kellner and Campos, regarded as a tapejarid (Kellner and Campos, 2002a) and *Zhejiangopterus linhaiensis* Cai and Wei, first regarded as a member of the Nyctosauridae (Cai and Wei, 1994) but reclassified as an azhdarchid by Unwin and Lü (1997). The search was executed using PAUP 4.0b10 for Microsoft Windows (Swofford, 2000). The large dataset (3 outgroups + 42 pterosaur taxa; 80 characters, several multistate) dictated the heuristic search option. Characters were given equal weight and treated unordered (ACCTRAN setting). The first search conducted by PAUP including all three outgroups (*Ornithosuchus longidens* (Huxley), *Herrerasaurus ischigualastensis* Reig and *Scleromochlus taylori* Woodward) produced 6229 equally parsimonious trees with a length of 177 steps. When *Scleromochlus taylori* is excluded, PAUP finds 2095 trees (with 177 steps; consistency index=0.7627; retention index=0.9099; rescaled consistency index=0.6940). In both cases the topology of the consensus tree is the same (figure 1). The result indicates that the Tapejaridae are a monophyletic entity that has a sister group relationship with the Azhdarchidae.

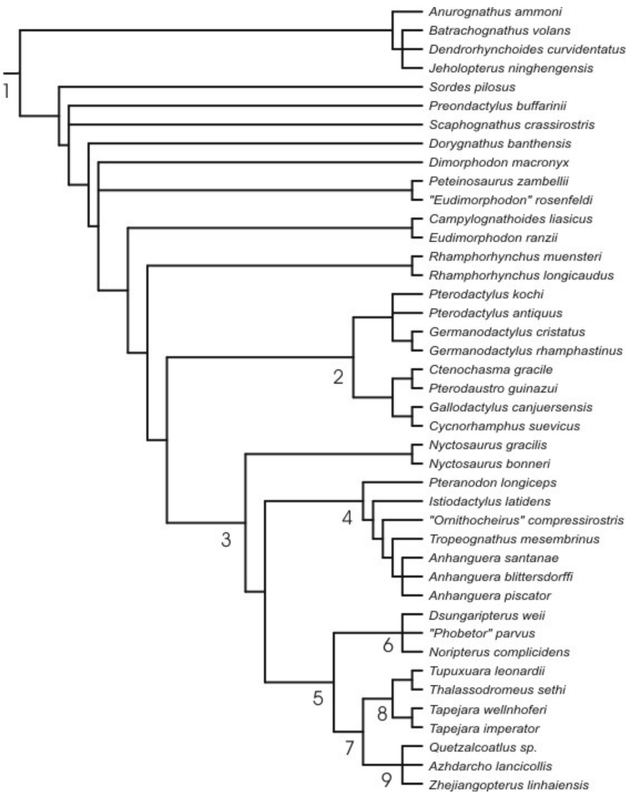

Figure 1. Strict consensus cladogram of the most parsimonious trees recovered in the cladistic analysis. Outgroups were excluded from the figure / *Cladograma del consenso estricto de los tres árboles más parsimoniosos obtenidos en el análisis cladístico. Los grupos externos fueron excluidos de la figura.* 1, Pterodactyloidea; 2, Archaeopterodactyloidea; 3, Dsungaripteroidea; 4, Pteranodontoidea; 5, Tapejaroidea; 6, Dsungaripteridae; 7, Azhdarchoidea; 8, Tapejaridae; 9, Azhdarchidae. See text for details.

Discussion of tapejarid monophyly

When the Tapejaridae was erected, Kellner (1989) presented three features diagnosing this clade of toothless pterosaurs: large sagittal crest on the anterior part of the skull extending backwards, very large nasoantorbital fenestra occupying nearly half the length of the skull, and rostrum downturned. With the discovery of *Tupuxuara leonardii* Kellner and Campos and *Tapejara imperator* Campos and Kellner, it became clear that the downward projected rostrum is only prominent in *Tapejara* and is now regarded as an apomorphy of that genus (character 4.1). The species *Sinopterus dongi* Wang and Zhou, from Cretaceous strata of the Liaoning province in China and assigned to the Tapejaridae also has a downturned rostral end, but shows a smaller inclination than *Tapejara* (Wang and Zhou, 2002).

Compared to the length between the tip of the premaxilla and the squamosal, the nasoantorbital fenestra in tapejarids is longer than in any other pterosaur (character 8.2), reaching about 45% in *Tapejara wellnhoferi* (figure 3) and *Sinopterus dongi*, half the size in *Thalassodromeus sethi* (figure 5) around 55% in *Tupuxuara leonardii* (figure 4) and being largest in *Tapejara imperator* (around 60%, figure 2). Although no detailed measurements are possible for *Tupuxuara longicristatus* (Kellner and Campos, 1988) and the Javelina tapejarid (figure 7, see section Composition of

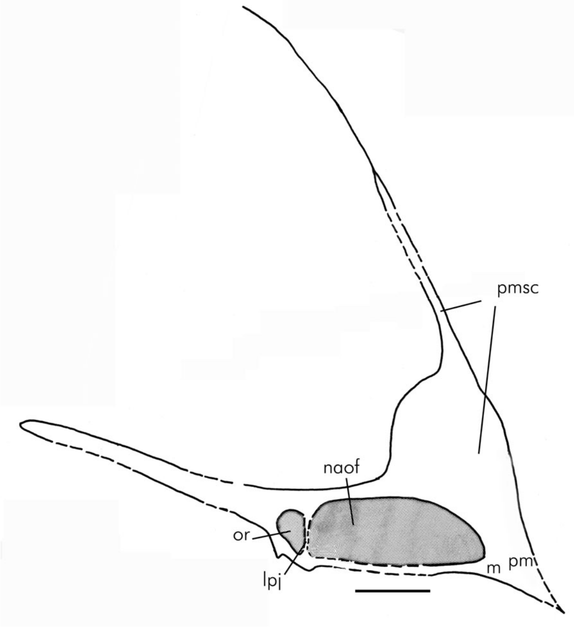

Figure 2. Skull of *Tapejara imperator*. Abbreviations: lpj, lacrimal process of the jugal; m, maxilla; naof, nasoantorbital fenestra; or, orbit; pm, premaxilla; pmsc, premaxillary sagittal crest. Scale bar = 50 mm / *Cráneo de* Tapejara imperator. *Abreviaturas: lpj, proceso lacrimal del yugal; m, maxilar; naof, fenestra nasoantorbital; or, órbita; pm, premaxilar; pmsc, cresta sagital del premaxilar. Escala: 50 mm.*

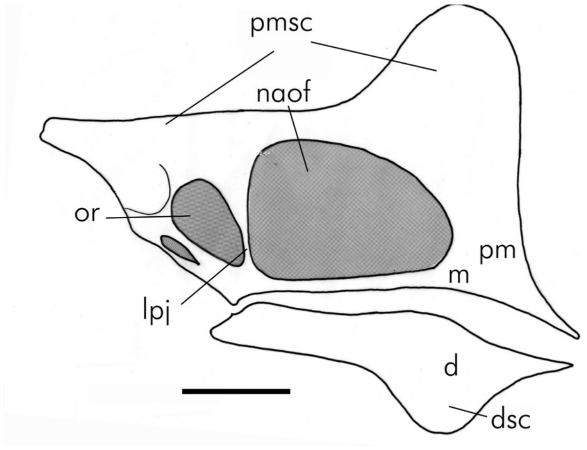

Figure 3. Skull and lower jaw of *Tapejara wellnhoferi*. Abbreviations: d, dentary; dsc, dentary sagittal crest; lpj, lacrimal process of the jugal; m, maxilla; naof, nasoantorbital fenestra; or, orbit; pm, premaxilla; pmsc, premaxillary sagittal crest. Scale bar = 50 mm / *Cráneo y mandíbula de* Tapejara wellnhoferi. *Abreviaturas: d, dentario; dsc, cresta sagital del dentario; lpj, proceso lacrimal del yugal; m, maxilar; naof, fenestra nasoantorbital; or, órbita; pm, premaxilar; pmsc, cresta sagital del premaxilar. Escala: 50 mm.*

the Tapejaridae), it is clear that in both the nasoantorbital fenestra is very long (particularly considering the preserved cranial part anterior to the beginning of the nasoantorbital fenestra) and compatible to the condition found in other tapejarids. In most pterodactyloid pterosaurs the size of the nasoantorbital fenestra relative to the premaxillary-squamosal length varies from one third (*e.g.*, *Pterodactylus*, *Anhanguera*, *Tropeognathus*, *Dsungaripterus*) to less than 20% (*Pterodaustro* and *Pteranodon*). The pteranodontoid *Istiodactylus* (formerly known as "*Ornithodesmus*") apparently also has a long (and unusual) nasoantorbital fenestra (Wellnhofer, 1978; Howse *et al.*, 2001), but the cranial reconstruction of this taxon is not certain (see Hooley, 1913). In any case, according to the present hypothesis the long antorbital fenestra of *Istiodactylus* and tapejarids has evolved independently. In *Quetzalcoatlus* sp. and *Zhejiangopterus* (the only azhdarchids where the skull is known) the size of this opening reaches respectively about one third (Kellner and Langston, 1996) and 40% (Cai and Wei, 1994; Unwin and Lü, 1997) of the premaxilla-squamosal length.

Regarding Kellner's (1989) second character, all tapejarids where complete cranial material is available bear a long sagittal crest made mostly by the premaxillae that starts at the beginning of the skull and extends backwards (character 13.4; figures 2-5). *Tupuxuara longicristatus* also has a very large cranial crest, although the exact posterior extension in this species is unknown. Other pterosaurs that show premaxillary crests differ by having this structure either confined to the anterior portion of the skull (Anhangueridae) or shifted posteriorly starting close to the anterior (*Germanodactylus*, "*Phobetor*", *Dsungaripterus*) or posterior (*Quetzalcoatlus* sp.) margin of the nasoantorbital fenestra. The azhdarchid *Zhejiangopterus* apparently lacks a cranial crest (Cai and Wei, 1994; Unwin and Lü, 1997).

Within tapejarids, the shape of the cranial crests varies. In *Tapejara wellnhoferi* and *Tapejara imperator*

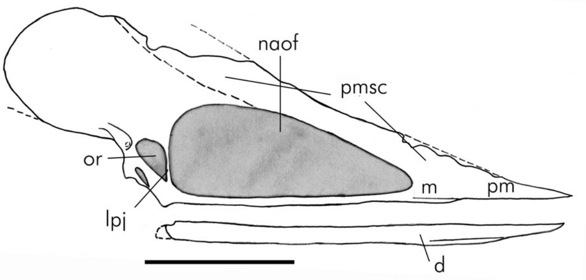

Figure 4. Skull and lower jaw of *Tupuxuara leonardii*. Abbreviations: d, dentary; lpj, lacrimal process of the jugal; m, maxilla; naof, nasoantorbital fenestra; or, orbit; pm, premaxilla; pmsc, premaxillary sagittal crest. Scale bar = 200 mm / *Cráneo y mandíbula de* Tupuxuara leonardii. *Abreviaturas: d, dentario; lpj, proceso lacrimal del yugal; m, maxilar; naof, fenestra nasoantorbital; or, órbita; pm, premaxilar; pmsc, cresta sagital del premaxilar. Escala: 200 mm.*

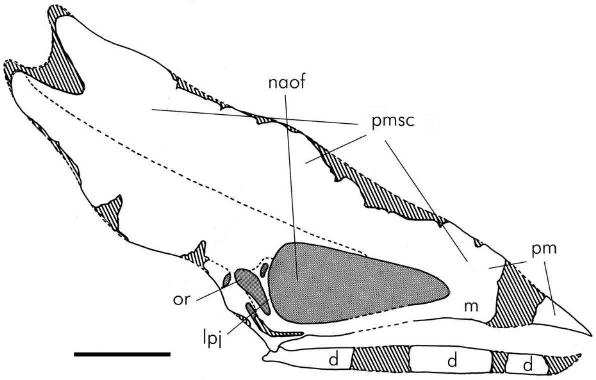

Figure 5. Skull and lower jaw of *Thalassodromeus sethi*. Abbreviations: d, dentary; lpj, lacrimal process of the jugal; m, maxilla, naof, nasoantorbital fenestra; or, orbit; pm, premaxilla; pmsc, premaxillary sagittal crest. Scale bar = 200 mm / *Cráneo y mandíbula de* Thalassodromeus sethi. *Abreviaturas: d, dentario; lpj, proceso lacrimal del yugal; m, maxilar; naof, fenestra nasoantorbital; or, órbita; pm, premaxilar; pmsc, cresta sagital del premaxilar. Escala: 200 mm.*

the premaxillary crest is anteriorly tall and expanded with a subvertical anterior margin, getting low towards the posterior region (at the middle portion of the nasoantorbital fenestra) and extends posteriorly well after the occiput (figures 2-3). In *Tupuxuara* (*Tupuxuara longicristatus* and *Tupuxuara leonardii*), *Thalassodromeus sethi* and the Javelina tapejarid the premaxillary crest is expanded above the entire dorsal border of the nasoantorbital fenestra. In *Thalassodromeus sethi* this crest is more developed (also above the nasoantorbital fenestra) and expands posteriorly terminating in a V-shaped structure, differing from *Tapejara* and *Sinopterus* (this condition in *Tupuxuara* and the Javelina tapejarid is unknown).

Another synapomorphy of tapejarids is the thin subvertical lacrimal process of the jugal (character 18.1; *e.g.*, *Tapejara*, *Tupuxuara leonardii*, *Thalassodromeus*) that is broader in azhdarchids (*Quetzalcoatlus* sp., *Zhejiangopterus*), dsungaripterids (*Dsungaripterus*, "*Phobetor*"), anhanguerids (*Anhanguera*, *Tropeognathus*), *Pteranodon*, and archaeopterodactyloids (*e.g.*, *Pterodactylus*, *Ctenochasma*). Apparently *Istiodactylus* also has a very thin lacrimal process of the jugal (Wellnhofer, 1978), but in this taxon it is inclined posteriorly (character 18.2), differing from the tapejarid condition.

Tapejarids further differ from all other pterosaurs by having a distinct and comparatively small pear-shaped orbit (character 10.1), with the lower portion formed by the lacrimal, and the postorbital processes narrow and the main axis running in a dorsoposterior-ventroanterior direction (*e.g.*, *Tupuxuara leonardii*, *Tapejara* and *Thalassodromeus*). This contrasts with the more rounded orbit of all other pterodactyloid pterosaurs such as azhdarchids (*Quetzalcoatlus*, *Zhejiangopterus*), *Pteranodon* (placed higher in the skull), archaeopterodactyloids (comparatively larger) and dsungaripterids (circular and placed very high in the skull).

Although the postcranials of the Tapejaridae were not described in detail, this study found one synapomorphic feature of this clade: the presence of a well developed and broad tubercle situated at the ventroposterior margin of the coracoid (character 57.1), observed in *Tapejara wellnhoferi* and *Tupuxuara leonardii*. This feature is absent in *Pteranodon* and *Nyctosaurus*, and differs from the extended coracoidal flange (character 56.1) present in the azhdarchids *Quetzalcoatlus* sp. (Kellner and Langston, 1996) and *Zhejiangopterus* (Unwin and Lü, 1997). This process is much smaller in anhanguerids (Wellnhofer, 1991a; Kellner and Tomida, 2000) while the condition in dsungaripterids is unknown.

In a recently published phylogenetic analysis, Unwin (2003) argued that the Tapejaridae are paraphyletic, an idea mentioned earlier (Unwin and Lü, 1997; Unwin, 2000). Although the discussion of the phylogeny proposed by Unwin (2003) is not the purpose of this paper, there are a few comments to be made.

This author adopts a composite terminal taxon method in order to maximize information and diminish missing data, allowing "poorly known taxa to contribute (with) phylogenetic information" (Unwin, 2003: 146). In practice this means to use species based on incomplete material that are assumed to belong to the same supraspecific taxon (*e.g.*, genus, "family") and use them as a terminal taxon. This approach, however, is questionable based on its pre-assumptive nature: all supraspecific taxa ("families", "subfamilies") are assumed *a priori* to be monophyletic. Although this might be the case for some, no test if the putative clades are indeed monophyletic is presented. Some of Unwin's *a priori* decisions of which supraspecific terminal taxa are or are not "well established" and "uncontroversial" are questionable (*e.g.*, Dimorphodontidae, Scaphognathidae, Ornithocheiridae) and do not find support in the literature (*e.g.*, Wellnhofer, 1978; 1991b; Campos and Kellner, 1985; Howse, 1986; Bennett, 1989; Unwin, 1995; Dalla Vecchia, 1998; Kellner, 1996; 2001; Kellner and Tomida, 2000).

Another fundamental contradiction of this approach is the justification that information is maximized by the inclusion of poorly known taxa: if one species is regarded as poorly known, how sure can one be about its assignment to a monophyletic entity? Furthermore, subsequent workers that wish to exam-

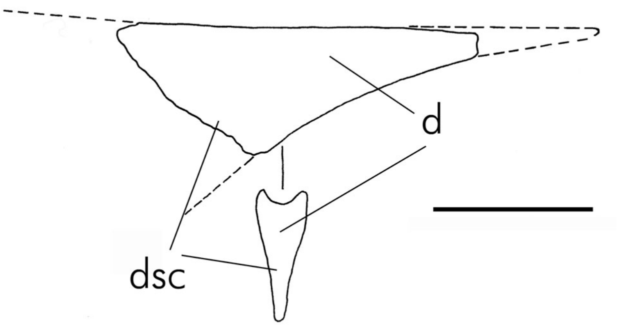

Figure 6. Incomplete tapejarid lower jaw from the Kem Kem region, Morocco, in right lateral view and cross section (based on Wellnhofer and Buffetaut, 1999). Abbreviations: d, dentary; dsc - dentary sagittal crest. Scale bar = 30 mm / *Mandíbula incompleta del taperájido proveniente de la región de Kem Kem, Marruecos, en vista lateral derecha y en sección (basado en Wellnhofer y Buffetaut, 1999). Abreviaturas: d, dentario; dsc, cresta sagital del dentario. Escala: 30 mm.*

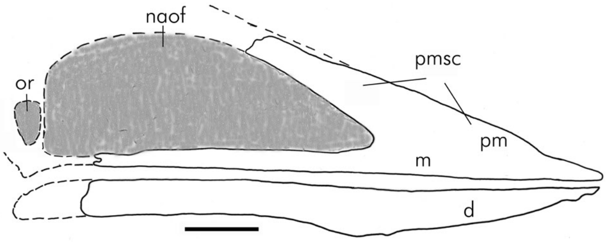

Figure 7. Skull and lower jaw a possible tapejarid from the Javelina Formation, Texas (based on Wellnhofer, 1991b). Abbreviations: d, dentary; m, maxilla; naof, nasoantorbital fenestra; or, orbit; pm, premaxilla; pmsc, premaxillary sagittal crest. Scale bar = 100mm. / *Cráneo y mandíbula de un posible taperájido de la Formación Javelina, Texas (basado en Wellnhofer, 1991b). Abreviaturas: d, dentario; m, maxilar; naof, fenestra nasoantorbital; or, órbita; pm, premaxilar; pmsc, cresta sagital del premaxilar. Escala: 100 mm.*

ine the character distribution in detail will have difficulties establishing which character state was actually observed in which species of the composite supraspecific terminal taxon. As an example, Unwin (2003) scores the presence of a notarium (character 31.1) in the "Ornithocheiridae"; however, most members of this supposed monophyletic group either lack postcranial elements (*e.g.*, *Ornithocheirus simus*, *Anhanguera blittersdorffi* Campos and Kellner) or are based on ontogenetically immature individuals where the presence of a notarium (although possible) cannot be demonstrated (*e.g.*, *Anhanguera piscator* Kellner and Tomida).

Regarding the Tapejaridae, Unwin (2003) considered this clade to be paraphyletic, with *Tupuxuara* closer related to the Azhdarchidae than to *Tapejara*, an assumption he made earlier (Unwin and Lü, 1997). Although having cited (and presumable access to) the phylogenetic analysis performed by Kellner (1996; a Ph.D. dissertation), Unwin (2003) did not discuss the character distribution of that study, considering it "unpublished". A summary of Kellner's phylogenetic analysis was reproduced in another publication (Kellner, 2001), which was also not used by him. The two features supposedly supporting the *Tupuxuara* - Azhdarchid clade (= "Neoazhdarchia" of Unwin, 2003) are: presence of a notarium and the loss of contact between metacarpals I-III to the distal syncarpal. Both features were used in a cladistic context previously (*e.g.*, Kellner, 1996; 2001) and also in the present study.

Regarding the notarium (character 44 in the present analysis), this feature is absent in primitive pterosaurs and in the Archaeopterodactyloidea (= primitive pterodactyloids *sensu* Kellner, 1996; figure 1, node 2), but widespread within derived pterodactyloids (*e.g.*, *Nyctosaurus*, *Pteranodon*, *Istiodactylus*, *Dsungaripterus*). It is correct that *Tapejara wellnhoferi* lacks a notarium as was pointed out previously (Kellner, 1996), but it should be noted that this taxon is only known by very young individuals. A notarium is further absent in the anhanguerids *Anhanguera santanae* (Wellnhofer) and *Anhanguera piscator,* both also only known by ontogenetically immature animals. In the present analysis the presence of a notarium is regarded as a synapomorphy of a more inclusive group, the Dsungaripteroidea (figure 1, node 3), corroborating with previous studies (Young, 1964; Kellner, 1996; 2001; 2003).

Regarding the articulation of the metacarpals I to III with the carpus (character 71 in the present analysis) in none of the specimens of *Tupuxuara*, *Tapejara* or azhdarchids to which I had access this region is sufficiently preserved to allow any conclusive statement. Curiously, according to Unwin's data matrix (Unwin, 2003: table 3; character 37), the condition of this feature is unknown in *Tupuxuara* and therefore it is not clear how it can be considered a synapomorphy uniting this taxon with the Azhdarchidae.

Lastly, although Unwin (2003) pointed out that *Tapejara* is short-faced, mentioning that *Tupuxuara* and Azhdarchidae share the derived condition of having the rostrum forming "more than 88% of the skull length", he did not use this character in his analysis. Although *Tapejara* indeed comprises short-faced animals, as has been pointed out before (Kellner, 1989), the basic configuration and proportions of the lateral margin of the skull in *Tupuxuara* and azhdarchids are quite distinct: *Tupuxuara* has a longer nasoantorbital fenestra and the rostral part of the skull anterior to the nasoantorbital fenestra is much shorter. A similar configuration is observed in *Tapejara* and *Thalassodromeus*, reinforcing the hypothesis that those taxa form a monophyletic entity.

Relationships of the Tapejaridae

Kellner and Campos (1992) were the first to suggest a sister group relationship between the Tapejaridae and the Azhdarchidae. Latter, Kellner and Hasegawa (1993) suggested that *Dsungaripterus* (Dsungaripteridae) was the next closest related taxon to tapejarids and azhdarchids, what has been confirmed by subsequent studies (Kellner, 1996; 2001; 2003) and followed by other workers (*e.g.*, Unwin, 1995).

Tapejarids share several features with the Dsungaripteridae and the Azhdarchidae, forming the clade Tapejaroidea (figure 1: node 5). Among those is the backwards extending supraoccipital (character 25.1) present in *Dsungaripterus*, "*Phobetor*", *Tapejara*, *Tupuxuara leonardii*, *Thalassodromeus* and probably also in the azhdarchid *Zhejiangopterus* (Cai and Wei, 1994; Unwin and Lü, 1997; condition in *Quetzalcoatlus* unknown). No other pterosaur shows this feature, including *Pteranodon* that has a large cranial crest extending backwards (Bennett, 2001).

Regarding the postcranial skeleton, tapejarids (where known) have the medial crest of the humerus massive, with a developed proximal ridge (*e. g.*, *Tapejara* sp., *Tupuxuara leonardii*). This character (65.2) is also present in *Dsungaripterus*, *Noripterus* and *Quetzalcoatlus*. Furthermore tapejarids, azhdarchids and dsungaripterids have the humerus about or less than 80% of femur length (character 60.0) which is a reversal to the primitive state (Kellner, 1996; 2001).

There are other features potentially shared by those groups such as the presence of a low and elongated frontal crest (character 19.2; apparently absent in *Zhejiangopterus*, condition of *Quetzalcoatlus* unknown) and expanded distal ends of the paroccipital processes (27.1; condition in azhdarchids unknown).

The members of the Tapejaridae lack several derived features of the clade Dsungaripteridae (*sensu* Kellner, 1996; 2003; figure 1, node 6), such as the comparatively small and rounded orbit that is positioned very high in the skull (character 9.1), the presence of a suborbital opening (character 12.1), the position of the premaxillary sagittal crest (character 13.3; displaced backwards, near the anterior margin of the nasoantorbital fenestra), the posterior ventral expansion of the maxilla (character 15.1), and the presence of a particular dsungaripterid dentition, which is formed by teeth with a broad, oval base that are absent from the anterior portion of the jaws (character 36.1) and has the largest maxillary teeth positioned posteriorly (character 37.1; Young, 1964, 1973; Bakhurina, 1982; Wellnhofer, 1991b; Kellner, 1996; 2001; 2003).

Up to date, there are only two synapomorphies that indicate a sister group relationship between tapejarids and azhdarchids, forming the clade Azhdarchoidea (figure 1, node 7). The first is the very unusual position of the orbit, which is situated lower than the dorsal rim of the nasoantorbital fenestra (character 11.1; Kellner and Campos, 1992; Kellner and Langston, 1996). Originally Kellner (1989) regarded the particular position of the orbit as diagnostic of *Tapejara wellnhoferi*, but more complete cranial material of the tapejarids *Tupuxuara* (Kellner and Hasegawa, 1993) and *Thalassodromeus* (Kellner and Campos, 2002a, 2002b), and the azhdarchids *Quetzalcoatlus* sp. (Kellner and Langston, 1996) and *Zhejiangopterus* (Cai and Wei, 1994) showed that this character diagnoses a more-inclusive group. Although there is some variation in the position of the orbit within the Pterosauria (*e.g.*, Wellnhofer, 1978), no other species approaches the condition found in azhdarchoids. The second synapomorphy uniting tapejarids and azhdarchids is the proportion the second phalanx of manual digit IV that is more than one third smaller than first one (character 74.3).

According to Howse (1986), the Azhdarchidae (Nessov, 1984; Padian, 1984) is diagnosed by the following features: midcervical vertebrae extremely elongated (character 48.2) and neural spines of the midcervical vertebrae extremely reduced or absent (character 50.3). In this analysis another synapomorphy of this clade was recognized: the presence of a deep coracoidal flange (character 56.1), present in *Quetzalcoatlus* sp. (Kellner and Langston, 1996) and *Zhejiangopterus* (Unwin and Lü, 1997). Besides the synapomorphies above, the cervical vertebrae of azhdarchids lack a lateral pneumatic foramen on the centrum (47.0) which is present and widespread among other pterodactyloids, including tapejarids.

Composition of the Tapejaridae

Most members of the clade Tapejaridae were found in the Early Cretaceous Santana Formation of the Araripe Basin, northeast Brazil. This unit is divided into three members, from base to top: Crato, Ipubi and Romualdo (Beurlen, 1971). As pointed out several times in the literature, the Santana Formation comprises two distinct *lagerstätten* formed respectively by the laminated limestone layers of the Crato Member and the limestone concretions embedded in shales of the Romualdo Member. Both are very rich in fossils (see Maisey, 1991, for a review), including pterosaurs, and were deposited during the Aptian - Albian (Pons *et al.*, 1990).

Up to date the only tapejarid described from the Crato Member is *Tapejara imperator* (figure 2), known from one complete skull (MCT 1622-R) housed at the Museu de Ciências da Terra (MCT) of the National Department of Mineral Production (DNPM) in Rio de Janeiro (Campos and Kellner, 1997). Another skull (still undescribed) that possibly belongs to this taxon is housed at the Staatliches Museum für Naturkunde (Karlsruhe). *Tapejara imperator* had a wingspan between 2 and 3 meters. Among the diagnostic features, this taxon has a very large and high cranial crest, which is the proportionally largest cranial structure found in any known vertebrate (fossil or recent). This crest has the basal portion fully ossified and is expanded anteriorly. The upper portion consists mostly of soft tissue that is supported anteriorly by a long and laterally compressed strip of bone formed by the premaxilla. Posteriorly the crest is formed mainly by the parietal that extends backwards almost doubling the length of the skull. The contact surface between the bony and soft portion of the crest is formed by small rod-like structures, which functions are unknown. It is possible that this region was still ossifying and that at least part of the crest became more rigid during the aging of the animal.

Another apomorphic feature of *Tapejara imperator* is the length of the nasoantorbital fenestra. Although the extent of the nasoantorbital fenestra is a synapomorphy of the Tapejaridae (Kellner, 1995), *Tapejara imperator* took this to an extreme, with the nasoantorbital fenestra occupying almost 60% of the skull length between the tip of the premaxilla and the posterior border of the squamosal. The rostral end formed by the premaxilla/maxilla (no suture between those bones could be identified) is downturned. If the lower jaw (not preserved) had a dentary ventral sagittal crest as *Tapejara wellnhoferi* (figure 3) cannot be ascertained at this point.

Frey and Tischlinger (2000) figured two other skulls (lacking the lower jaw) from tapejarids found in the Crato deposits. According to them, those specimens belong to a new taxon, differing from *Tapejara imperator* by lacking the large posterior extension of the cranial crest. Based on the published features, it is not clear if the posterior end of those specimens is complete (particularly in SMNK 2343 PAL), which are otherwise very similar to the type material of *Tapejara imperator*, including the long nasoantorbital fenestra and the downturned rostral end.

There are several (most undescribed) specimens from the Crato *lagerstätte* composed of postcranial elements (lacking skull), some of which were referred to the Tapejaridae (Sayão and Kellner, 1998; Nuvens *et al*., 2002). Martill and Frey (1999) regarded a partial wing from this deposit as a possible representative of the Azhdarchidae, mainly based on the "T" shaped cross section of the second and third wing phalanges. Such features, however, are also present in tapejarids and the presence of azhdarchids in the Santana Formation needs further confirmation.

The Romualdo *lagerstätte* comprises several tapejarid specimens, including *Tapejara wellnhoferi* (figure 3). It is the second smallest member of this clade known to date, with a wingspan around 1.5 meters (Kellner, 1989). The first description of this species was based on a partial skull (MN 6595-V), presently housed at the Museu Nacional (MN), but several more were found (*e.g.*, Wellnhofer and Kellner, 1991), making this the best represented pterosaur of the Santana Formation. *Tapejara wellnhoferi* is the shortest-faced pterodactyloid (more than *Tapejara imperator*) known to date, which is one of the diagnostic features of this taxon. Unfortunately, in none of the specimens the cranial crest is complete. This structure starts at the beginning of the anterior part of the skull rising steeply and reaching an almost subvertical condition. Based on AMNH 24440, somewhere above the middle part of the nasoantorbital fenestra, this crest reduces its height and extends posteriorly tapering towards the rear of the skull behind the occipital region. It is possible that a soft extension above the bony part of the crest such as the one found in *Tapejara imperator* (but perhaps less developed) was also present in *Tapejara wellnhoferi*. The latter, however, lacks the particular anterior thickened edge of the premaxillae that turn into a flattened long dorsoposteriorly oriented stripe of bone present in *Tapejara imperator* (figure 2).

The main features shared by *Tapejara imperator* and *Tapejara wellnhoferi* are the downturned rostral end of the premaxilla/maxilla and the steep anterior margin of the cranial sagittal crest. Other features observed in *Tapejara wellnhoferi* are a well developed strong ventral crest on the dentary (specimens AMNH 24440; MN 6597-V) and a distinct medial bump in the palatal region followed by a medial foramen (Kellner, 1989; Wellnhofer and Kellner, 1991). If those features are also present in *Tapejara imperator* is presently unknown.

Another toothless pterosaur from the Romualdo deposits is *Tupuxuara longicristatus*, known from a partial skull, wing-metacarpal and first wing phalanx of both sides (MN 6591-V) housed at the Museu Nacional (MN), Rio de Janeiro (Kellner and Campos, 1988). The holotype represents an animal with an estimated wingspan around 2.5 to 3 meters, and shows a well developed cranial crest above the nasoantorbital fenestra, whose posterior extension is unknown. Among the diagnostic features of this taxon are the presence of a thin palatal ridge and the presence of one pneumatic foramen perforating the basal portion of the extensor tendon process of the first wing phalanx (Kellner and Campos, 1988).

A second species of *Tupuxuara* (*T. leonardii*) was described based on a fragmentary cranial material consisting of a small portion of the rostrum that also bears a sagittal crest (Kellner and Campos, 1994) which is permanently housed at the Museu Nacional (MN 6592-V; cast: MCT 1495-R). This taxon can be distinguished from *Tupuxuara longicristatus* essentially by the presence of a strong ridge on the palate that does not reach the anterior portion of the skull. Later Kellner and Hasegawa (1993) reported a second specimen (figure 4) formed by a partial skeleton that includes a complete skull and lower jaw, representing a pterosaur with a wingspan of around 4.5 meters (Kellner and Hasegawa, in prep). This second specimen has the palatal region under the nasoantorbital fenestra strongly convex, which in *Tupuxuara longicristatus* is less convex. *Tupuxuara leonardii* also lacks a well developed pneumatic foramen on the base of the extensor tendon process (present in *Tupuxuara longicristatus*).

The last described member of the Tapejaridae from the Romualdo Member is *Thalassodromeus sethi* (figure 5). This taxon is known from an almost complete skull and lower jaw (DGM 1476-R) housed at the Museu das Ciências da Terra that represents an animal with a wingspan ranging between 4.2 and 4.5 meters (Kellner and Campos, 2002a,b). The cranial crest of this species is very large and extends posteriorly with a V-shaped termination. This crest is formed by premaxilla, frontal, parietal and supraoccipital and is fully ossified. There might have been a soft extension above the crest in some areas, which extent cannot be determined. The diagnostic features of *Thalassodromeus* are as follows: rectilinear suture between the premaxillae and the frontoparietal portion of the crest (contrary to the curved condition of *Tupuxuara leonardii*), strongly concave palatines posterior to the palatal crest, occipital region comparatively broader than in other tapejarids (width over quadrates about 20% of the squamosal-premaxilla length), and sharp dorsal and ventral edges of the premaxilla and dentary, giving the rostral end a scissors-like aspect. *Thalassodromeus* lacks a ventral dentary sagittal crest.

According to the present phylogenetic analysis, *Thalassodromeus* and *Tupuxuara* are more closely related in respect to *Tapejara*. This relationship has to be regarded as preliminary since no character used in the present analysis unambiguously supports this relationship. Among the features observed in *Tapejara* that are not present in *Tupuxuara* and *Thalassodromeus* is the downturned rostral end of the premaxillae/maxillae and the dentary bony crest (condition of *Tapejara imperator* unknown). On the other hand, *Thalassodromeus* and *Tupuxuara* have a palatal ridge which is absent in *Tapejara wellnhoferi* (condition of *Tapejara imperator* unknown). While proximal part of the humerus of *Tupuxuara leonardii* has a pneumatic foramen present on the ventral side, *Tapejara wellnhoferi* has two - one on the ventral and a second on the dorsal side. Other feature that might unite *Thalassodromeus* and *Tupuxuara* is the large posterior end of the nasoantorbital fenestra (figures 4, 5), which in *Tapejara* is comparatively lower (figures 2, 3). Lastly, *Thalassodromeus sethi* and *Tupuxuara leonardii* have the main part of the crest formed by bone, contrasting to *Tapejara imperator* (and perhaps also *Tapejara wellnhoferi*) where the sagittal crest has a large component of soft tissue.

Still from the Romualdo Member, Wellnhofer (1985) described some postcranial elements (carpus, radius and ulna) designating the species *"Santanadactylus" spixi* and referring it to the Ornithocheiridae. Despite the nomenclature problems surrounding the Ornithocheiridae (see Kellner and Tomida, 2000; Unwin, 2003), the carpus, particularly the distal carpal series, is similar to the correspondent bones of *Dsungaripterus* (Bennett, 1989) and tapejarids, being referred to the latter by Kellner (1995). If those elements belong to one of the taxa known from cranial material only cannot be established at this point.

Besides the Santana Formation, there are a few other deposits where tapejarids have been recovered. Among them is the Kem Kem region of southern Morocco, where extensive collecting activities has taken place in the last years. Most sites are situated in Hamada du Guir near the town of Taouz that show extensive outcrops with fossiliferous red beds. The age of those layers was not yet established precisely, but most authors regard them as Cenomanian (*e.g.*, Wellnhofer and Buffetaut, 1999). Among the fossil vertebrates found to date are dinosaurs (Russell, 1996; Sereno *et al.*, 1996) and turtles (Tong and Buffetaut, 1996). Pterosaurs have also been discovered, including azhdarchids (Kellner and Mader, 1996) and anhanguerids (Mader and Kellner, 1999). Wellnhofer and Buffetaut (1999) described some isolated jaw elements of toothless pterosaurs. Among those is one fragment of a mandibular symphysis (BSP 1977 I 67; figure 6) housed at the Bayerische Staatssammlung für Paläontologie und Historische Geologie (Munich) referred by those authors to the Tapejaridae. Although the specimen is incomplete, it is clear that it had a sagittal crest. If the authors are correct in their identification that this specimen belongs to a lower jaw, then this sagittal crest corresponds to the ventral dentary crest. Such a structure is absent in *Thalassodromeus* and *Tupuxuara*, but present in *Tapejara*. Furthermore the dorsal surface of the dentary in the Moroccan tapejarid is concave (contrary to sharp blade of *Thalassodromeus* and the flat surface found in *Tupuxuara*), similar to *Tapejara* suggesting that both are probably closely related. The Moroccan specimen is larger than *Tapejara wellnhoferi* and comparable in size to *Tapejara imperator* (Wellnhofer and Buffetaut, 1999).

A rather unusual find of a tapejarid was done by Wang and Zhou (2002). The specimen comes from the Jiufotang Formation of western Liaoning, China, which, together with the basal Yixian Formation forms the Jehol Group. The age of those rocks is Early Cretaceous, with the deposits of the Jiufotang Formation considered as Aptian (Wang and Zhou, 2002). The region of Liaoning is particularly interesting since it had furnished a large quantity of well preserved fossils like angiosperms, invertebrates, fishes, amphibians, turtles, lizards, crocodylomorphs, dinosaurs including avian and non-avian theropods (see Wang *et al.*, 2000 for a review). Several pterosaur specimens have been found in both formations of the Jehol Group, among which is a partial skeleton named by Wang and Zhou (2002) *Sinopterus dongi*. Due to the unfused carpal series it seems that this taxon is represented by a young animal, being the smallest tapejarid known to date with a wingspan of 1.2 meters. Wang and Zhou (2002) listed several diagnostic features of *Sinopterus*, among which a comparatively low premaxillary crest (lower than in all other tapejarids). *Sinopterus dongi* has a ventral dentary crest that, despite being lower than in *Tapejara wellnhoferi* (and the Moroccan tapejarid), indicates that they are close related relative to other tapejarids (*e.g.*, *Tupuxuara*, *Thalassodromeus*).

There is still another specimen that appears to be a member of the Tapejaridae. The material consists of an incomplete skull and jaw (TMM 42489-2, figure 7) recovered from the Javelina Formation, Big Bend National Park, Texas, housed in the Texas Memorial Museum, University of Texas, Austin. This unit represents continental deposits of Maastrichtian age that yielded the azhdarchids *Quetzalcoatlus northropi* (Lawson, 1975a,b) and a second closely related taxon represented by several specimens including cranial and postcranial material (Kellner and Langston, 1996). Lower in the section and closer to the basal part of the Javelina Formation another incomplete pterosaur skull was recovered. This material was figured by Wellnhofer (1991b) and mistakenly referred to *Quetzalcoatlus*, as pointed out by Kellner and Langston (1996). It is clear from this picture that TMM 42489-2 has a large nasoantorbital fenestra and bears a sagittal premaxillary crest that extends backwards. Those features contrast with the skull of the azhdarchid *Quetzalcoatlus* sp. (Kellner and Langston, 1996) but indicate that TMM 42489-2 likely represents a tapejarid, being the youngest record of the clade. This occurrence extends the range of the Tapejaridae to the top of the Late Cretaceous.

Conclusions

The monophyly of the Tapejaridae is well supported by four cranial characters and one postcranial feature (a broad tubercle situated at the ventroposterior margin of the coracoid). The present analysis shows that the Tapejaridae share several unique features with the Dsungaripteridae and the Azhdarchidae and their close relationship is presently well supported. Up to date there are only two unambiguous features indicating a sister group relationship between tapejarids and azhdarchids (position of the orbit and proportional size of the first and second wing phalanges). Perhaps with more detailed description of the postcranial elements of both, azhdarchids (*e.g.*, *Zhejiangopterus*, *Quetzalcoatlus* sp.) and tapejarids (*e.g.*, *Tupuxuara leonardii*, *Tapejara wellnhoferi*, *Sinopterus dongi*), more evidences of this relationship might turn to light.

Up to date, remains of tapejarids have been found in Brazil, Africa and China. A tapejarid is also likely present in the Javelina Formation, United States (Wellnhofer, 1991b: p. 144), extending the temporal range of this clade from the Aptian to the Maastrichtian. The occurrence of tapejarids in Africa was already expected (Kellner, 1994), but the occurrence in China is somewhat surprising and has to be analyzed in more detail. In any case, the current distribution of this pterosaur clade indicate that it was not restricted to the Gondwana but is more widely distributed (China, North America).

At this point the ingroup relationships of tapejarids is not known in detail. *Tapejara wellnhoferi* and *Tapejara imperator* share one synapomorphy, forming a monophyletic entity. Based on the presence of a strong ventral dentary crest, the Moroccan tapejarid and *Tapejara wellnhoferi* (condition of *Tapejara imperator* is not known) are possibly closely related relative to *Tupuxuara* and *Thalassodromeus*. *Sinopterus*, the Chinese tapejarid, might be closely related to *Tapejara* as well, but a detailed description of this taxon is needed to confirm its relationships. *Tupuxuara longicristatus* and *Tupuxuara leonardii* are also monophyletic. *Thalassodromeus sethi* shares some features with *Tupuxuara*, and both are here considered sister taxa relative to *Tapejara*.

Lastly, it is worth to mention that Sayão and Kellner (2001) referred a cervical vertebra from Tendaguru (Tanzania, Africa) to the Azhdarchidae, extending the temporal range of this clade back to the Late Jurassic (Kimmeridgian-Tithonian). If this is confirmed, due to the sister group relationship of the Tapejaridae and the Azhdarchidae, the record of tapejarids has to go back from the Aptian to the Late Jurassic.

Acknowledgments

I thank the following curators for allowing the examination of specimens housed in their institutions: Wann Langston Jr. (Texas Memorial Museum, University of Texas, Austin), Eberhard "Dino" Frey (Staatliches Museum für Naturkunde, Karlsruhe), Peter Wellnhofer (Bayerische Staatssammlung fur Paläontologie und historische Geologie, Munich), Angela Milner (British Museum, Natural History, London), Yoshikazu Hasegawa (Gunma Museum of Natural History, Gunma), Nabana Satoshi (Iwaki Fossil and Coal Museum, Iwaki) and Diogenes de Almeida Campos (Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro). I profited from discussions with several researchers, particularly Diogenes de Almeida Campos (MCT), Wann Langston (Austin, Texas), Christopher Bennett (Univ. of Bridgeport) and David Peters (Saint Luis, Missouri). This project was partially founded by the Conselho Nacional de Desenvolvimento Cientifico e Tecnológico (CNPq) and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ). I thank Fernando Suárez (Sociedad Paleontologica de Chile, Santiago) for the invitation to contribute to the special volume of the "Primer Congresso Latinoamericano de Paleontologia de Vertebrados", Maureen T. Craik (Museu Nacional, Rio de Janeiro) for help with the text, and Renata de Oliveira Cardoso and Vanessa Dorneles Machado (Museu Nacional, Rio de Janeiro) for the drawings that illustrate this paper. Lastly my special thanks to Richard A. Fariña (Universidad de La República, Montevideo, Uruguay) representing the editors of this volume, as well as Marcelo Reguero (Museo de La Plata), editor of *Ameghiniana*, for the patience regarding many missed deadlines to conclude this project.

References

Bakhurina, N.N. 1982. A pterodactyl from the Lower Cretaceous of Mongolia. *Paleontological Journal* 4: 105-109.

Bennett, S.C. 1989. A pteranodontid pterosaur from the early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *Journal of Paleontology* 63: 669-667.

Bennett, S.C. 2001. The osteology and functional morphology of the Late Cretaceous Pterosaur *Pteranodon*. *Palaeontographica*, Abt. A 260: 1-112.

Beurlen, K. 1971. As condições ecológicas e faciológicas da formação Santana nachapada do Araripe (Nordeste do Brasil). A*nais da Academia Brasileira de Ciências* 43 (supl.): 411-415.

Cai, Z. and 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. and Kellner, A.W.A. 1985. Panorama of the Flying Reptiles Study in Brazil and South America. *Anais da Academia Brasileira de Ciências* 57: 453-466.

Campos, D. A. and 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.

Dalla Vecchia, F.M. 1998. New observations on the osteology and taxonomic status of *Preondactylus buffarinii* Wild, 1984 (Reptilia, Pterosauria). *Bolletino della Societa Paleontologica Italiana* 36: 355-366.

Frey, E. and Tischlinger, H. 2000. Weichteilanatomie der Flugsaurierfüsse und Bau der Scheitelkämme: neue Pterosaurierfunde aus den Solnhofener Schichten (Bayern) und der Crato-Formation (Brasilien). *Archaeopteryx* 18: 1-16.

Hooley, R. W. 1913. On the skeleton of *Ornithodesmus* latidens, an Ornithosaur from the Wealden shales of Atherfield (Isle of Wight). *Quarterly Journal of the Geological Society* 69: 372-422.

Howse, S.C.B. 1986. On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria). *Zoological Journal of the Linnean Society* 88: 307-328.

Howse, S.C.B., Milner, A.R. and Martill, D.M. 2001. Pterosaurs. In: D. M. Martill and D. Naish (eds.), *Dinosaurs of the Isle of Wight*. The Paleontological Association, London. pp. 324-335.

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. 1994. Comments on the paleobiogeography of Cretaceous archosaurs during the opening of the South Atlantic Ocean. *Acta Geologica Leopoldensia* 39: 615-625.

Kellner, A.W.A. 1995. The relationships of the Tapejaridae (Pterodactyloidea) with comments on pterosaur phylogeny. In: A. Sun and Y. Wang (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Short Papers. Beijing, China Ocean Press, pp. 73-77.

Kellner, A.W.A. 1996. *Description of new material of Tapejaridae and Anhangueridae (Pterosauria, Pterodactyloidea) and discussion of pterosaur phylogeny, Ph.D.* Thesis, Columbia University (available through UMI - University Microfilms International/ ProQuest).

Kellner, A.W.A. 2001. *New hypothesis of Pterosaur Phylogeny*. In: L.M. Barros, P.C. Nuvens and J.B.M. Filgueira (eds.), I e II Simpósios sobre a Bacia do Araripe e bacias interiores do Nordeste, Comunicações. Crato, pp. 249-258.

Kellner, A.W.A. 2003. Pterosaur phylogeny and comments on the evolutionary history of he group. In: E. Buffetaut and J.M. Mazin (eds), *Evolution and Paleobiology of Pterosaurs*. Geological Society, Special Publication 217, pp. 105-137

Kellner, A.W.A. and 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 de Ciências* 60: 459-469.

Kellner, A.W.A. and Campos, D.A. 1992. A new Tapejarid from the Santana Formation (Lower Cretaceous) from the Araripe Basin, Northeast Brazil. *Journal of Vertebrate Paleontology* 12 (Suppl. 3): 36A-37A.

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

Kellner, A.W.A. and Campos, D.A. 2002a. 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. and Campos, D.A. 2002b. Form, function, and the flight of the pterosaur-response. *Science* 297: 2207-2208.

Kellner, A.W.A. and Hasegawa, Y. 1993. Postcranial skeleton of *Tupuxuara* (Pterosauria, Pterodactyloidea, Tapejaridae) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology* 13(3, suppl.): 44A (abstract).

Kellner, A.W.A., and 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.

Kellner, A.W.A. and Mader, B.J. 1996. First report of Pterosauria (Pterodactyloidea, Azhdarchidae) from Cretaceous rocks of Morocco. *Journal of Vertebrate Paleontology* 16 (suppl. to 3): 45A.

Kellner, A.W.A. and Tomida, Y. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), Northeastern Brazil. *National Science Museum Monographs* 17: 1-135.

Lawson, D.A. 1975a. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. *Science* 187: 947-948.

Lawson, D. A. 1975b. Could pterosaurs fly? *Science* 188: 676-677.

Mader, B.J. and Kellner, A.W.A. 1999. A new anhanguerid pterosaur from the Cretaceous of Morocco. *Boletim do Museu Nacional, Geologia* 45: 1-11.

Maisey, J.G. (ed.) 1991. *Santana Fossils: an illustrated atlas.* T.F.H. Publications, Neptune City, 459 pp.

Martill, D. and Frey, E. 1999. A possible azhdarchid pterosaur from the Crato Formation (Early Cretaceous, Aptian) of northeast Brazil. *Geologie en Mijnbouw*, 78: 315-318.

Nessov, L. A. 1984. Upper Cretaceous pterosaurs and birds from central Asia. *Paleontological Journal* 1: 38-49.

Nuvens, P.C., Sayão, J.M., Silva, H.P., Saraiva, A.S. F. and Kellner, A.W.A. 2002. A coleção de pterossauros do Museu de Paleontologia de Santana do Cariri, Norderste do Brasil. *Arquivos do Museu Nacional* 60: 235-240.

Padian, K. 1984. A large pterodactyloid pterosaur from the Two Medicine Formation (Campanian) of Montana. *Journal of Vertebrate Paleontology* 4: 516-524.

Pons, D., Berthou, P.Y. and Campos, D.A. 1990 - *Quelques observations sur la palynologie de l'Aptien Supérieur et de l'Albien du bassin d'Araripe (N. E. du Brésil).* In: D.A. Campos, M.S.S. Viana, P.M. Brito, and G. Beurlen (eds.), Atas do 1º Simpósio sobre a bacia do Araripe e bacias interiores do Nordeste, Crato, Ceará: 241-252.

Russell, D.A. 1996. Isolated dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. *Bulletin du Musée Nationale d' Historie Naturelle.* Paris, (4) sect. C, 18: 349-402.

Sayão, J.M. and Kellner, A.W.A. 1998. Pterosaur wing with soft tissue from the Crato Member (Aptian-Albian), Santana Formation, Brazil. *Journal of Vertebrate Paleontology* 15(suppl. to 3): 75A.

Sayão, J.M. and Kellner, A.W.A. 2001. New data on the pterosaur fauna from Tendaguru (Tanzania), Upper Jurassic, Africa. *Journal of Vertebrate Paleontology* 21(suppl. to 3): 97A.

Sereno, P.C., Dutheil, D.B., Jarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J. and Wilson, J.A. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* 272: 986-991.

Swofford, D.L. 2000. PAUP: *Phylogenetic Analysis Using Parsimony, Version 4.0B10* (for Microsoft Windows). Sinauer Associates, Inc. Sunderland, Massachusetts.

Tong, H. and Buffetaut, E. 1996. A new genus and species of pleurodiran turtle from the Cretaceous of southern Morocco. *Neues Jahrbuch für Geologie un Paläontologie*, Abh. 199: 133-150.

Unwin, D.M. 1995. Preliminary results of a phylogenetic analysis of the Pterosauria (Diapsida:Archosauria). In: A. Sun and Y. Wang (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota,* Short Papers. Beijing, China Ocean Press, pp. 69-72.

Unwin, D.M. 2000. On the systematic relationships of Cearadactylus atrox, an enigmatic Early Createaceous pterosaur from the Santana Formation of Brazil. Mitt. Mus. Nat.kd. Berl., Geowiss. *Reihe* 5: 239-263.

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: 139-190.

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

Wang, X. and 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.-L, Wang, Y.-Q., Zhou, Z.-H., Jin, F., Zhang, J.-Y., and Zhang, F. 2000. Vertebrate Faunas and Biostratigraphy of the Jehol Group in western Liaoning, China. *Vertebrata PalAsiatica* 38 (suppl.): 41-56.

Wellnhofer, P. 1978. *Pterosauria. Handbuch der Palaeoherpetologie*, Teil 19. Stuttgart: Gustav Fischer Verlag, 82 pp.

Wellnhofer, P. 1985. Neue Pterosaurier aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. *Palaeontographica* 187: 105-182.

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

Wellnhofer, P. 1991b. *The illustrated encyclopedia of pterosaurs*. London, Salamander Books, 192 pp.

Wellnhofer, P. and Buffetaut, E. 1999. Pterosaur remains from the Cretaceous of Morocco. *Paläontologische Zeitschrift* 73: 133-142.

Wellnhofer, P. and Kellner 1991. A.W.A. The skull of *Tapejara wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, Northeastern Brazil. Mitt. Bayer. Staatsslg. *Paläont. hist. Geol.*, 31: 89-106.

Young, C.C. 1964. On a new pterosaurian from Sinkiang, China. Vertebr. *Palasiatica* 8: 221-256.

Young, C.C. 1973. [Reports of Paleontological Expeditions to Sinkiang (II). Pterosaurian Fauna from Wuerho, Sinkiang]. Mem. Inst. Vert. Palaeont. *Paleoanthr. Acad. Sin.*, 11: 18-35 (in Chinese).

Recibido: 25 de marzo de 2004.
Aceptado: 10 de noviembre de 2004.

APPENDIX 1

CHARACTER LIST (per anatomical region)

Skull

1. Dorsal margin of the skull: 0 - straight or curved downward; 1 - concave; 2 - only rostrum curved upward.

2. Upper and lower jaw: 0 - laterally compressed; 1 - comparatively broad.

3. Rostral part of the skull anterior to the external nares: 0 - reduced; 1 - elongated (less than half of skull length); 2 - extremely elongated (more than half of skull length).

4. Rostral end of premaxillae/maxillae downturned: 0 - absent; 1 - present.

5. Process separating the external nares: 0 - broad; 1 - narrow.

6. Position of the external naris: 0 - above the premaxillary tooth row; 1 - displaced posterior to the premaxillary tooth row.

7. Naris and antorbital fenestra elongated and reduced relative to the orbit: 0 - absent; 1 - present.

8. Naris and antorbital fenestra: 0 - separated; 1 - confluent, shorter than 45% of the skull length; 2 - confluent, longer than 45% of the skull length.

9. Orbit comparatively small and positioned very high in the skull: 0 - absent; 1 - present.

10. Orbit pear-shaped: 0 - absent; 1 - present.

11. Position of the orbit relative to the nasoantorbital fenestra (naris + antorbital fenestra): 0 - same level or higher; 1 - orbit lower than the dorsal rim of the nasoantorbital fenestra.

12. Suborbital opening: 0 - absent; 1 - present.

13. Premaxillary sagittal crest: 0 - absent; 1 - confined to the anterior portion of the skull; 2 - high, displaced backwards, near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit, and extending backwards; 3 - low, displaced backwards near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit but not extending backwards; 4 - starting at the anterior portion of the skull and extended posteriorly above the occipital region; 5 - starting at the posterior half of the nasoantorbital fenestra; 6 - low, postioned in the middle portion of the rostrum not reaching the nasoantorbital fenestra; 7 - low, positioned in the middle portion of the rostrum extending until the middle part of the nasoantorbital fenestra.

14. Tip of the premaxilla expanded: 0 - absent; 1 - present, with premaxillary end high; 2 - present, with premaxillary end dorsoventrally flattened.

15. Posterior ventral expansion of the maxilla: 0 - absent; 1 - present.

16. Nasal process: 0 - absent, 1 - placed on the lateral side of the skull, long, straight, and directed ventrally (not fused with maxillae); 2 - placed laterally, reduced; 3 - placed medially, long; 4 - placed medially, reduced.

17. Foramen on nasal process: 0 - absent; 1 - present.

18. Lacrimal process: 0 - broad 1 - thin, subvertical; 2 - thin, strongly inclined posteriorly.

19. Bony frontal crest: 0 - absent; 1 - low and blunt; 2 - low and elongated; 3 - high and expanded posteriorly.

20. Bony parietal crest: 0 - absent; 1 - present, blunt; 2 - present, laterally compressed and posteriorly expanded, with a rounded posterior margin; 3 - present, constituting the base of the posterior portion of the cranial crest.

21. Posterior region of the skull rounded with the squamosal displaced ventrally: 0 - absent; 1 - present.

22. Position of the quadrate relative to the ventral margin of the skull: 0 - vertical or subvertical; 1 - inclined about 120º backwards; 2 - inclined about 150º backwards.

23. Position of the articulation between skull and mandible: 0 - under the posterior half of the orbit or further backwards; 1 - under the middle part of the orbit; 2 - under the anterior half of the orbit.

24. Helical jaw joint: 0 - absent; 1 - present.

25. Supraoccipital: 0 - does not extend backwards; 1 - extends backwards.

26. Foramen pneumaticum piercing the supraoccipital: 0 - absent; 1 - present.

27. Expanded distal ends of the paroccipital processes: 0 - absent; 1 - present.

28. Basisphenoid: 0 - short; 1 - elongated.

29. Palatal ridge: 0 - absent; 1 - discrete, tapering anteriorly; 2 - strong, tapering anteriorly; 3 - strong, confined to the posterior portion of the palate.

30. Maxilla excluded from the internal naris: 0 - absent; 1 - present.

31. Opening between pterygoids and basisphenoid (interpterygoid opening): 0 - absent or very reduced; 1 - present and larger than subtemporal fenestra; 2 - present but smaller than subtemporal fenestra.

32. Mandibular symphysis: 0 - absent or very short; 1 - present, at least 30% of mandible length.

33. Anterior tip of the dentary downturned: 0 - absent; 1 - present

34. Tip of the dentary projected anteriorly: 0 - absent; 1 - present

35. Dentary bony sagittal crest: 0 - absent; 1 - blade-like and short, placed anteriorly; 2 - massive and deep.

36. Position and presence of teeth: 0 - teeth present, evenly distributed along the jaws; 1 - teeth absent from the anterior portion of the jaws; 2 - teeth confined to the anterior part of the jaws; 3 - jaws toothless.

37. Largest maxillary teeth positioned posteriorly: 0 - absent; 1 - present.

38. Variation in the size of the anterior teeth with the 5th and 6th smaller than the 4th and 7th: 0 - absent; 1 - present.

39. Teeth with a broad and oval base: 0 - absent; 1 - present.

40. Multicusped teeth: 0 - absent; 1 - present.

41. Peg-like teeth: 0 - absent; 1 - present, 15 less on each side of the jaws; 2 - present, more than 15 on each side of the jaws.

42. Long slender teeth: 0 - absent or less than 150; 1 - present, more than 150.

43. Laterally compressed and triangular teeth: 0 - absent; 1 - present.

Axial skeleton

44. Notarium: 0 - absent; 1 - present.

45. Atlas and axis: 0 - unfused; 1 - fused.

46. Postexapophyses on cervical vertebrae: 0 - absent, 1 - present.

47. Lateral pneumatic foramen on the centrum of the cervical vertebrae: 0 - absent; 1 - present.

48. Midcervical vertebrae: 0 - short, sub-equal in length; 1 - elongated; 2 - extremely elongated.

49. Cervical ribs on midcervical vertebrae: 0 - present; 1 - absent.

50. Neural spines of the midcervical vertebrae: 0 - tall, blade-like; 1 - tall, spike-like; 2 - low, blade-like; 3 - extremely reduced or absent.

51. Number of caudal vertebrae: 0 - more than 15; 1 - 15 or less

Pectoral girdle

52. Length of the scapula: 0 - subequal or longer than coracoid; 1 - scapula shorter than coracoid (1 > sca/cor > 0.80); 2 - substantially shorter than coracoid (sca/cor < 0.80).

53. Proximal surface of scapula: 0 - elongated; 1 - sub-oval.

54. Shape of scapula 0 - elongated; 1 - stout, with constructed shaft.

55. Coracoidal contact surface with sternum: 0 - no developed articulation surface; 1 - articulation surface flattened, lacking posterior expansion; 2 - articulation surface oval, with posterior expansion.

56. Deep coracoidal flange: 0 - absent; 1 - present.

57. Broad tubercle on ventroposterior margin of coracoid: 0 - absent; 1 - present.

58 - Cristospine: 0 - absent; 1 - shallow and elongated; 2 - deep and short.

Forelimb

59. Proportional length of the humerus relative to the metacarpal IV (hu/mcIV): 0 - hu/mcIV > 2.50; 1 - 1.50 < hu/mcIV < 2.50; 2 - 0.40 < hu/mcIV < 1.50; 3 - hu/mcIV < 0.40.

60. Proportional length of the humerus relative to the femur (hu/fe): 0 - hu/fe =0.80; 1 - 1.4 > hu/fe > 0.80; 2 - hu/fe > 1.40.

61. Proportional length of the humerus plus ulna relative to the femur plus tibia (hu+ul/fe+ti): 0 - humerus plus ulna about 80% or less of femur plus tibia length; (hu+ul/fe+ti < 0.80); 1 - humerus plus ulna larger than 80% of femur plus tibia length (hu+ul/fe+ti > 0.80).

62. Pneumatic foramen on the ventral side of the proximal part of the humerus 0 - absent; 1 - present.

63. Pneumatic foramen present on dorsal side of the proximal part of the humerus: 0 - absent; 1 - present.

64. Deltopectoral crest of the humerus: 0 - reduced, positioned close to the humerus shaft; 1 - enlarged, proximally placed, with almost straight proximal margin; 2 - subrectangular, extending down the humerus shaft for at least 30% of humerus length; 3 - distally expanded; 4 - enlarged, hatchet shaped, proximally placed; 5 - enlarged, hatched shaped, positioned further down the humerus shaft; 6 - enlarged, warped; 7 - long, proximally placed, curving ventrally.

65. Medial (= ulnar) crest of the humerus: 0 - absent or reduced; 1 - present, directed posteriorly; 2 - present, massive, with a developed proximal ridge.

66. Distal end of the humerus: 0 - oval or D-shaped; 1 - subtriangular.

67. Proportional length of the ulna relative to the metacarpal IV (ul/mcIV): 0 - ulna 3.6 times longer than metacarpal IV (ul/mcIV > 3.6); 1 - length of ulna between four and two times the length of metacarpal IV (3.6 > ul/mcIV > 2); 2 - ulna less than two times the length of metacarpal IV (ul/mcIV < 2).

68. Diameter of radius and ulna: 0 - subequal; 1 - diameter of the radius about half that of the ulna; 2 - diameter of the radius less than half that of the ulna.

69. Distal syncarpals: 0 - unfused; 1 - fused in a rectangular unit; 2 - fused in a triangular unit.

70. Pteroid: 0 - absent; 1 - shorter than half the length of the ulna; 2 - longer that half the length of the ulna.

71. Metacarpals I - III: 0 - articulating with carpus; 1 - metacarpal III articulates with carpus, metacarpals I and II reduced; 2 - not articulating with carpus.
72. Proportional length of the first phalanx of manual digit IV relative to the metacarpal IV (ph1d4/mcIV): 0 - both small and reduced; 1 - both enlarged with ph1d4 over double the length of mcIV; 2 - both enlarged with ph1d4 less than twice the length of mcIV.
73. Proportional length of the first phalanx of manual digit IV relative to the tibiotarsus (ph1d4/ti): 0 - ph1d4 reduced; 1 - ph1d4 elongated and less than twice the length of ti (ph1d4/ti smaller than 2.00); 2 - ph1d4 elongated about or longer than twice the length of ti (ph1d4/ti subequal/larger than 2.00).
74. Proportional length of the second phalanx of manual digit IV relative to the first phalanx of manual digit IV (ph2d4/ph1d4): 0 - both short or absent; 1 - elongated with second phalanx about the same size or longer than first (ph2d4/ph1d4 larger than 1.00); 2 - elongated with second phalanx up to 30% shorter than first (ph2d4/-ph1d4 between 0.70 - 1.00); 3 - elongated with second phalanx more than 30% shorter than first (ph2d4/ph1d4 smaller than 0.70).
75. Proportional length of the third phalanx of manual digit IV relative to the first phalanx of manual digit IV (ph3d4/ph1d4): 0 - both short or absent; 1 - ph3d4 about the same length or larger than ph1d4; 2 - ph3d4 shorter than ph1d4.
76. Proportional length of the third phalanx of manual digit IV relative to the second phalanx of manual digit IV (ph3d4/ph2d4): 0 - both short or absent; 1 - ph3d4 about the same size or longer than ph2d4; 2 - ph3d4 shorter than ph2d4.

Hindlimb

77. Proportional length of the femur relative to the metacarpal IV (fe/mcIV): 0 - femur about twice or longer than metacarpal IV (fe/mcIV > 2.00); 1 - femur longer but less than twice the length of metacarpal IV (1.00 < fe/mcIV < 2.00); 2 - femur about the same length or shorter thanmetacarpal IV (fe/mcIV < 1.00).
78. Length of metatarsal III: 0 - more than 30% of tibia length; 1 - less than 30% of tibia length.
79. Fifth pedal digit: 0 - with four phalanges; 1 - with 2 phalanges 2 - with 1 or no phalanx (extremely reduced).
80. Last phalanx of pedal digit V: 0 - reduced or absent; 1 - elongated, straight; 2 - elongated, curved; 3 - elongated, very curved (boomerang shape).

APPENDIX 2. Data matrix

Ornithosuchus longidens (Huxley)	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
Herrerasaurus ischigualastensis Reig	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000020
Scleromochlus taylori Woodward	000??00000	0000000000	0?????????	0?000?0000	0???00?0??	????00?0??	?0?0??????	??????????
Anurognathus ammoni Döderlein	0100100??0	??0000000?	??????????	?000000000	1000???0??	1???????01	1??10000?1	011???001?
Batrachognathus volans Rjabinin	?100100???	??00000?0?	?????????0	?000000000	100??0?0?0	??001????2	1??10?????	??????????
Dendrorhynchoides curvidentatus (Ji and Ji)	010010????	??0000??0?	??????????	??00000000	1000???00?	10?0100?02	1??1??00?1	01122200??
Jeholopterus ningchengensis Wang, *et al.* Zhou, Zhang and Xu	010010????	??000???00	??0???????	??00000000	1000???00?	1000100?02	1??1??00?1	0112221011
Sordes pilosus Sharov	0010010000	0000000000	000?0?0???	?000000000	?000?0?000	0000100?01	1??10000?1	0111110013
Preondactylus buffarinii Wild	001001000?	0000000?00	000???????	?00000?00?	0000???0??	0???????11	1??1??10?1	01111100??
Scaphognathus crassirostris (Goldfuss)	0010010000	0000000000	00000?0000	1?00000000	0000?00000	0000100111	10010010?1	0111110013
Dorygnathus banthensis (Theodori)	0010010000	0000000000	00000?0???	1101000000	0000???000	000010??11	10030010?1	0111111013
Dimorphodon macronyx (Buckland)	0010010000	0000000000	000?0?0???	?000000000	0000?00000	000010??11	1001001111	0111111011
Peteinosaurus zambellii ? Wild	0????????	??????????	??????????	?????00?01	0000??????	00001???11	1??10011?1	0111110011
"*Eudimorphodon*" *rosenfeldi* Dalla Vecchia	??????????	????????00	?????000??	????????01	??00??????	????????11	1?????1???	011211101?
Campylognathoides liasicus (Quenstedt)	0010010000	0000000000	00000?0001	1010000000	0000000000	0000100111	10020011?1	0121221010
Eudimorphodon ranzii Wild	0010010000	0000000000	000?0?0???	?010000001	0000?0000?	0000100?11	?0020011?1	0?????1???
Rhamphorhynchus muensteri (Goldfuss)	0010011000	0000000000	0110000001	1101000000	0000000000	0000100111	10040011?1	0122221012
Rhamphorhynchus longicaudus (Munster)	0010011000	0000000000	01100?000?	?101000000	000000?000	0000100111	10040011?1	0122221012
Pterodactylus kochi (Wagner)	0010010100	0000010000	121?0?0?0?	?100000000	2000000112	1000100121	10070021?2	0212222020
Pterodactylus antiquus (Soemmerring)	0010010100	0000010000	121?0?0?0?	?100000000	2000000112	1000100121	10070021?1	0212222020
Germanodactylus cristatus (Wiman)	0010010100	0030010000	121?0?0???	?100000000	2000???11?	?000100?21	1??7?021??	?2122221??
Germanodactylus rhamphastinus (Wagner)	0010010100	0030010000	121?0?????	??00000000	2000???11?	??001???21	1??7?021??	?21???2???
Ctenochasma gracile Oppel	102001010?	0000000?00	121?0?0???	?100000000	010??00112	??001???21	1??7??21??	?212??2020
Pterodaustro guinazui Bonaparte	1020010100	0000010000	121?0?0???	?100000000	010???0112	1?001???21	1??7?02?1?	?212222020
Gallodactylus canjuersensis Fabre	101001010?	000020?02	??1???0???	???0020000	000??0????	?0001?????	??????????	??1222?1??
Cycnorhamphus suevicus (Quenstedt)	1010010100	0000020002	121???0?0?	?100020000	000?00?112	?0001???21	0??70021??	02122221??
Nyctosaurus gracilis (March)	0010010100	0000000000	0?110?0101	2100030000	0001110010	1000100131	11050?2122	22222220??
Nyctosaurus bonneri Miller	0010010100	0000000000	0?1?0?0???	?100030000	0001?1?010	????????31	???50?????	2222222???
Pteranodon longiceps Marsh	1020010100	0000040033	0121010101	2100030000	0001111011	1110100121	1106112122	2222222020
Istiodactylus latidens (Seeley)	00100102?0	??00?002??	???0????0?	?100000000	0011?1?0??	?1111002?1	???611?2??	???1??????
"*Ornithocheirus*" *compressirostris* (Owen)	0010?1????	??000?????	????????1?	??00000000	000???????	??????????	??????????	??????????
Tropeognathus mesembrinus Wellnhofer	0010010100	00110??011	0121010121	2100100000	000???????	??????????	??????????	??????????

Anhanguera santanae (Wellnhofer)	0010010100	0011031011	0121010111	2100?00100	0000111011	1211200???	?01611?22?	1?????????
Anhanguera blittersdorffi Campos and Kellner	0010010100	00110??011	0121010111	2100100100	000???????	??????????	??????????	??????????
Anhanguera piscator Kellner and Tomida	0010010100	0011031011	01210101?1	2100100100	0000111011	1211200221	101611222?	1?????2120
Dsungaripterus weii Young	2010010110	0120100023	0121111101	2100011010	0001111010	100010?220	0??7?0211?	0212222120
"*Phobetor*" *parvus* (Bakhurina)	0010010110	0120100023	012?1?1???	?100011010	000???????	??????????	????????1?	??????????
Noripterus complicidens Young	??????????	??????????	??????????	????????10	00??11010	????????20	001720211?	?212??2120
Tupuxuara leonardii Kellner and Campos	0010010201	10400??123	0121111131	2100030000	0001111010	?000101220	010720211?	?213??2???
Thalassodromeus sethi Kellner and Campos	0010010201	1040040123	0121111131	2100030000	000???????	??????????	??????????	??????????
Tapejara wellnhoferi Kellner	0011010201	10400??123	0120111101	2100230000	0000?11010	?000101?20	0117202112	?21???2120
Tapejara imperator Campos and Kellner	0011010201	10400??123	012?1?????	?????30000	000???????	??????????	??????????	??????????
Quetzalcoatlus sp.	0010010100	10500000??	?121????01	?100030000	0001110213	?000110?20	010720211?	?213222?20
Azhdarcho lancicollis Nessov	??????????	??????????	??????????	?????30000	00?1110213	??????????	?107?0????	??????????
Zhejiangopterus linhaiensis Cai and Wei	0010010100	100000000?	012?1?????	??00030000	00011??213	?000?10?20	0??7??21?2	?213??2???