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New information on the pterosaur *Tupandactylus imperator*, with comments on the relationships of Tapejaridae

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A new specimen of *Tupandactylus imperator*, comprising an incomplete skull with associated lower jaw, is described. The material is the best preserved specimen of this species known so far and provides new information on the anatomy of this pterodactyloid pterosaur, especially with respect to the morphology of the lower jaw, the first one formally described for the species. Also, the new specimen shows an extensive preservation of soft tissues such as the soft-tissue component of the headcrest, ramphoteca associated with the premaxillae and lower jaw, as well as probable pycnofibres. A phylogenetic analysis was performed in order to test the relationships of the taxon within Tapejaridae. The results of the analysis support Tapejaridae, as well as monophyly of Tapejarinae and Thalassodrominae.

Key words: Pterosauria, Tapejaridae, *Tupandactylus imperator*, phylogeny, Crato Formation, Brazil.

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Introduction

The pterosaur assemblage from the Romualdo and Crato formations (Araripe Basin, northeastern Brazil) has attracted the attention of researchers primarily due to the exceptional preservation and diversity of its taxa. On some rare occasions, however, what actually claims most attention is the anatomical extremism of some species. One of the best examples is the pterosaur *Tupandactylus imperator* (Campos and Kellner, 1997). When it was first described (referred, at the time, to the genus *Tapejara*), this bizarre pterosaur was enigmatic for the huge size of its cranial median crest which comprised approximately 5/6 of the total lateral area of the skull (Campos and Kellner 1997).

Campos and Kellner (1997) placed *T. imperator* within Tapejaridae, a clade of pterodactyloid pterosaurs supported by five synapomorphies: (1) comparatively large nasoantorbital fenestra, forming 45% or more of the skull length; (2) long median crest, formed mostly by the premaxillae, arising from the rostral terminus of the skull and extending posteriorly; (3) thin subvertical lacrimal process of the jugal; (4) small reverse pear-shaped orbit; and (5) a broad and well-developed tubercle at the ventro-posterior margin of the coracoid (Kellner 2004). Monophyly of the Tapejaridae sensu Kellner has been recently questioned (Unwin and Lü 1997; Unwin 2003; Martill and Naish 2006; Lü et al. 2006).

After the first description of *T. imperator*, further cranial remains have been referred to this taxon (Fig. 1). Frey et al. (2003) documented an incomplete skull housed at the collection of the Staatliches Museum für Naturkunde, Karlsruhe, Germany (SMNK PAL 2839) (Fig. 1C). The proximal portion of the lower jaw is preserved, though this was not mentioned in the description. Unwin and Martill (2007) illustrated a more complete, well-preserved specimen without lower jaw, presently housed in a private collection (Fig. 1D). At least two more, hitherto undescribed specimens are housed in private collections. Only one of them has associated lower jaws (David Martill, personal communication 2010).

All the fossil remains attributed to *T. imperator* are restricted to the biomicritic laminated limestone of the Crato

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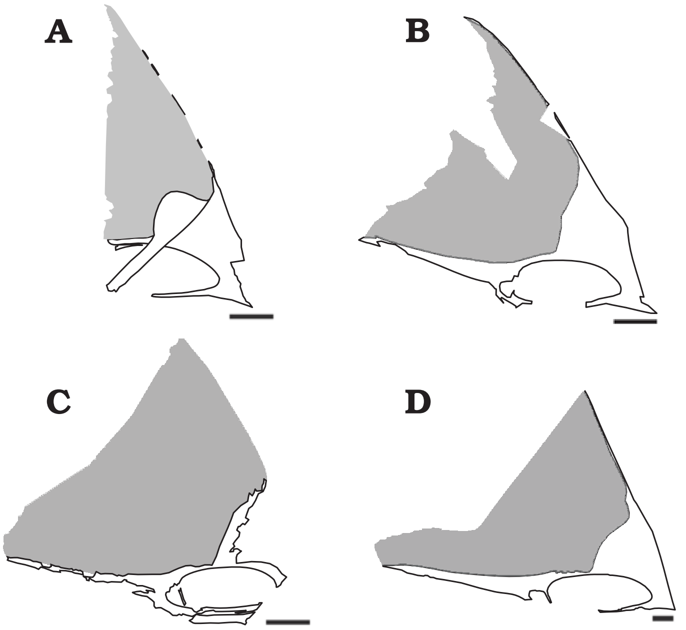

Fig. 1. The four known specimens of tapejarinid pterosaur *Tupandactylus imperator* (Campos and Kellner, 1997) from the Crato Formation of the Araripe Basin, Brazil. **A**. CPCA 3590, the specimen described herein. **B**. MCT 1622-R, the holotype, described by Campos and Kellner (1997). **C**. SMNK PAL 2839, illustrated by Frey et al. (2003). **D**. The specimen housed at a private collection, illustrated by Unwin and Martill (2007). Scale bars 10 cm.

Formation (?Aptian) in the Araripe Basin (Campos and Kellner 1997; Frey et al. 2003; Unwin and Martill 2007). This stratigraphic unit, interpreted as deposited in a low-energy lacustrine environment, is known for its abundant and diversified fossil biota which is composed by plant remains, arthropods, fishes, anurans, lizards, crocodylomorphs, pterosaurs, and birds (Neumann and Cabrera 1999; Viana and Neumann 2002; Heimhofer and Martill 2007).

The laminated limestone of Crato Formation is intensely exploited and, usually, new fossils are discovered during commercial prospecting (Andrade 2007). Thus, the specimens lack their stratigraphic context and are often damaged. In the year 2009, at the Mina Triunfo quarry (city of Nova Olinda, Ceará province, UTM 24M-0423025E/9212692N) (Fig. 2), a pterosaur skull and lower jaw were found. The new specimen is here identified as *T. imperator* based on the presence of a spine-like dorso-posteriorly oriented process and an anteriorly projecting convex blade on the premaxillae (see below). Likely the specimen was complete at the time of the finding. Due to the activities of quarry workers, however, the occipital and temporal portions of the skull were lost. This new material, although incomplete, is the best-preserved *T. imperator* known so far. It allows, as well, a better comprehension of its phylogenetic relationships and the possibility of testing the position of this species within Tapejaridae.

Institutional abbreviations.—CPCA, Centro de Pesquisas Paleontológicas da Chapada do Araripe (Departamento Nacional de Produção Mineral, Crato, Brazil); MCT, Museu de Ciências da Terra (Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil); SMNK, Staatliches Museum für Naturkunde (Karlsruhe, Germany).

Systematic paleontology

Pterodactyloidea Plieninger, 1901

Tapejaridae Kellner, 1989

Tapejarinae Kellner and Campos, 2007

Genus *Tupandactylus* Kellner and Campos, 2007

Type species: *Tupandactylus imperator* (Campos and Kellner, 1997).

Tupandactylus imperator (Campos and Kellner, 1997)

Figs. 1, 3, 4.

Holotype: MCT 1622-R.

Material.—CPCA 3590, an incomplete skull and lower jaw with associated soft tissues.

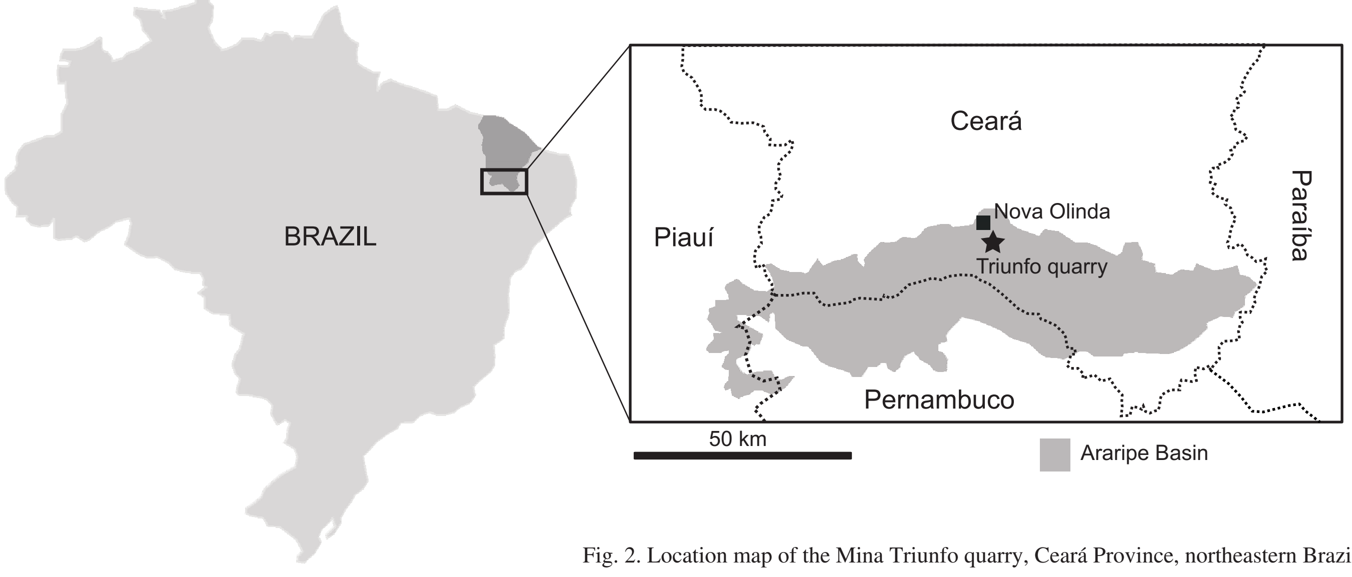

Fig. 2. Location map of the Mina Triunfo quarry, Ceará Province, northeastern Brazil.

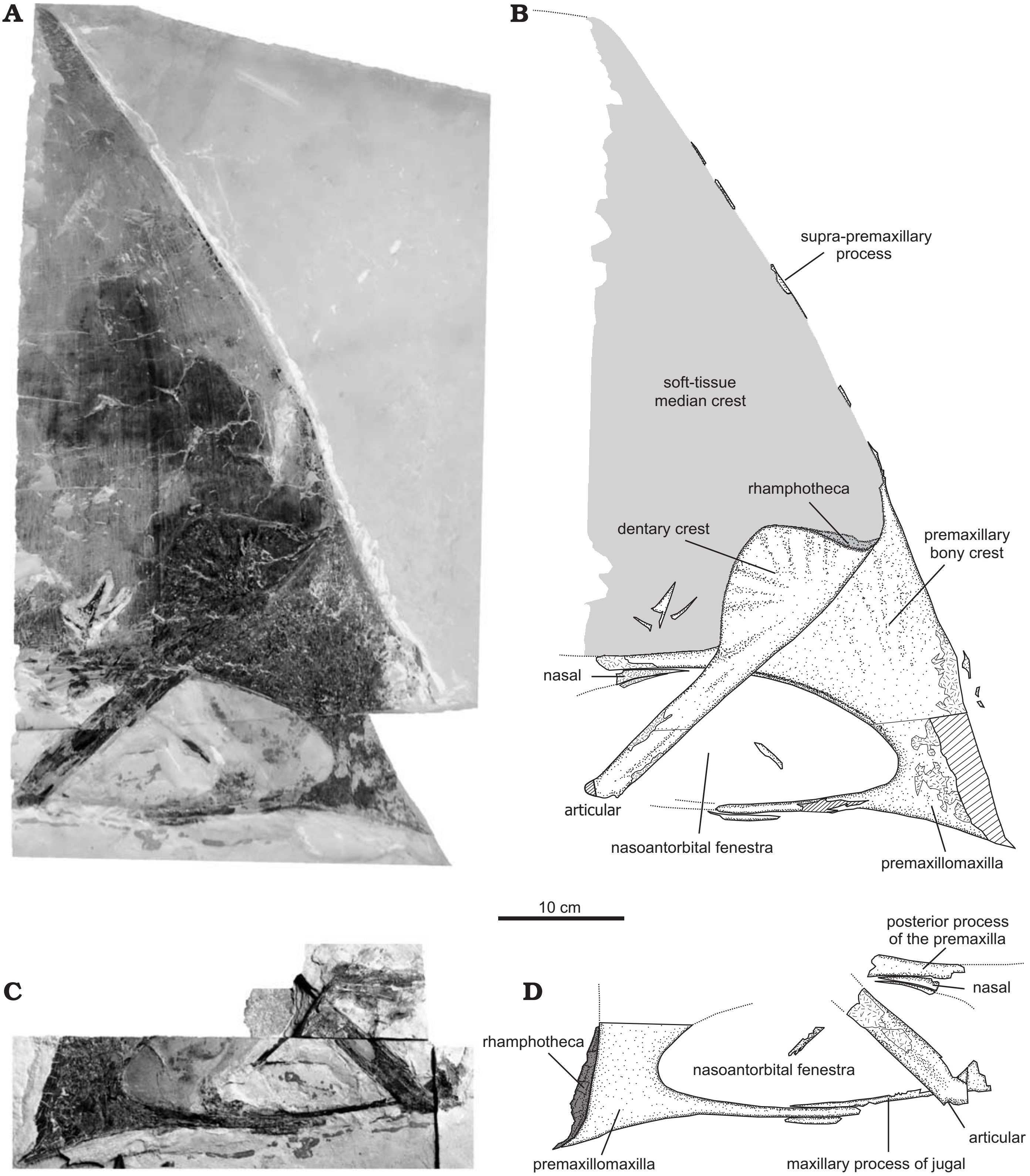

Fig. 3. Tapejarinid pterosaur *Tupandactylus imperator* (Campos and Kellner, 1997), specimen CPCA 3590 from the Crato Formation (?Aptian), Brazil. **A**. Specimen in right lateral aspect. **C**. Counterpart of the specimen. Photographs (A, C) and drawings (B, D).

Emended diagnosis.—Tapejarid pterosaur with an occipital process that reaches about the length of the rest of the skull (measured from the tip of the premaxillae to the squamosals); an extremely large soft-tissue median cranial crest supported anteriorly by a spine-like, caudally inclined suprapremaxillary process; soft-tissue component of the cranial crest composed

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of parallel fibers curving in caudal direction; an anteriorly projecting convex blade on the premaxillae and a lower jaw bearing a very deep rounded median mandibular crest with a steep rostral margin forming an angle of approximately 60° with the mandible.

Description.—Specimen CPCA 3590 is preserved in four limestone slabs. When the slabs were split the skull was divided along a sagittal plane with considerable bone substance in both slab and counterslab. Here we consider the slabs with bones preserved in internal view as counterslab. The counterslabs contains only a restricted portion of the antorbital part of the cranium (premaxilla, maxilla, anterior process of the jugal, nasal and the proximal extremity of the lower jaw; Fig. 3C, D). The two remaining slabs preserve, in addition to the structures mentioned above, both bony and soft-tissue components of the median crest, as well as the dorsal margin of the nasoantorbital fenestra and the distal portion of the lower jaw (Fig. 3A, B). The rostral margin of the premaxilla is exposed in internal view only in the counterslab. The skull is seen in a right lateral aspect and all the bones of the counterslabs are actually remains of the right side of the skull in internal view. The lower jaw is dislocated from its original position, now lying diagonally across the skull covering the middle part of the nasoantorbital fenestra. The rostral tip of the mandible lies adjacent to the anterior bony component of the median cranial crest. The mandible is arranged with its ventral margin placed upwards. Therefore, this structure is preserved in left lateral aspect.

The temporal and occipital portion of the specimen was cut off, probably by quarrymen, and the region posterior to the nasoantorbital fenestra as well as a considerable portion of the soft-tissue cranial crest are therefore missing. The skull has preserved length of 333 mm and is 670 mm high. The lower jaw has a total length of 305 mm. There is only sparse evidence of sutures between bones. The size of the skull, when compared with other specimens referred to *T. imperator,* is compatible with the hypothesis that the specimen represents a mature individual, although CPCA 3590 is slightly smaller than the holotype of *T. imperator* (MCT 1622-R; Fig. 1B; Campos and Kellner 1997) and the specimen illustrated by Unwin and Martill (2007) is the biggest known so far. It is likely that *T. imperator* could reach 3–4 m of wingspan, though the absence of postcranial remains associated with this species makes any estimative merely tentative.

Premaxillomaxilla.—The premaxillomaxilla is almost completely preserved but the rostral end of the premaxilla is intact only in the counterslab of the specimen. There is no visible suture between premaxilla and maxilla, which is common among most pterosaurs, even in presumably juvenile specimens, and was previously reported in Tapejaridae (Kellner 1989; Lü and Yuan 2005). Ontogenetic studies reveal that the fusion between the premaxilla and the maxilla occurs very early in the ontogeny of pterodactyloid pterosaurs (Kellner and Tomida 2000). The anterior margin of the premaxillary bony crest is badly preserved. In this region the bone is broken, with numerous fragments scattered adjacent to the skull. It is likely that fragmentation occurred before burial. The rostral end of the beak is inclined ventrally at an angle of about 15° against the posterior process of the maxilla. The dorsal element of the premaxilla forms the bony component of the median cranial crest as well as a considerable portion of the anterodorsal margin of the nasoantorbital fenestra. In CPCA 3590, and in other skulls referred to *T. imperator*, the cranial median bony crest rises anteriorly as a plate-like element with an anteriorly projecting convex blade that marks a well-distinguished change in the direction of the anterior margin of the premaxilla, from a sub-vertical to a more dorso-posterior orientation (at an angle of about 15°). The dorsal-most portion of the premaxillae forms a spine-like dorso-posteriorly oriented process that supports the huge soft-tissue element of the cranial crest. The premaxilla has a very slender posterior process that forms the anterior part of the dorsal margin of the nasoantorbital fenestra. The dorsal margin of the posterior process of the premaxilla is strongly striated. Here, the parallel fibers that compose the soft-tissue median crest originated, with the fibers penetrating the bone, as was observed by Frey et al. (2003) for SMNK PAL 2839.

At the rostral end of the premaxilla there is a dark structure with a smooth appearance when compared with the rough bony surface. This structure is identified as a remnant of a rhamphotheca (Fig. 4C).

Nasals.—In CPCA 3590, the right nasal is preserved in internal view in the counterslab of the specimen and has a triangular outline, with a sharp anterior process. The bone is dorsally articulated with the posterior process of the premaxilla and ventrally forms the dorsoposterior margin of the nasoantorbital fenestra. The frontonasal and the lacrimonasal sutures are not preserved.

Jugal.—Only the slender maxillary process of the jugal is preserved. Together with the posterior process of the maxilla, the maxillary process of the jugal forms the ventral margin of the nasoantorbital fenestra. In CPCA 3590 these bones are partially dislocated in a region close to the mid-line of the total longitudinal extension of the opening. In CPCA 3590 the lacrimal and most of the jugal are broken and the posterior region of the skull, including the frontoparietal and the caudally-orientated parietal process, are missing.

Lower jaw.—The edentulous lower jaw has a total length of 305 mm and does not preserve any sign of sutures. Although the dorsal margin of the dentary part of the mandible is badly preserved, a depression is discernible, following the ventrally turned premaxillomaxilla. The mandibular symphysis extends into a deep ventral bony crest that reaches a maximum height of 93 mm and occupies approximately the anterior half (51%) of the mandible. The margin of the crest is asymmetrically convex with the anterior margin being steeper than the caudal one, almost reaching the rostral symphyseal extremity of the dentary, which has a sharp, very discrete anterior projection.

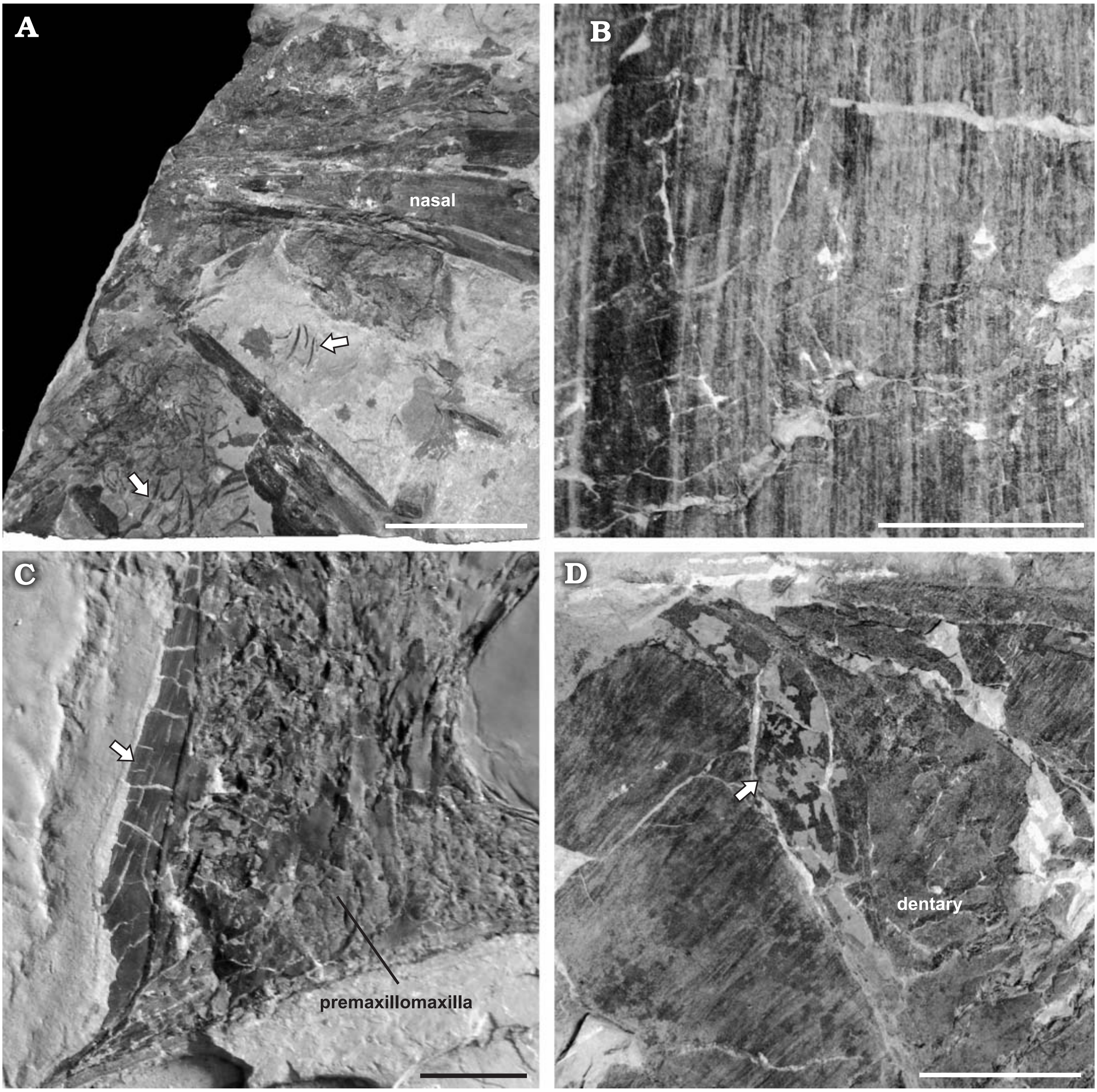

Fig. 4. Tapejarinid pterosaur *Tupandactylus imperator* (Campos and Kellner, 1997), Crato Formation (?Aptian), Brazil. Soft-tissue preservation in CPCA 3590. **A**. Probable pycnofibres associated with the left mandibular ramus (indicated by the arrows). **B**. Pattern of subvertical parallel fibers that compose the soft-tissue component of the cranial crest. **C**. Probable rhamphotheca associated with the tip of the premaxillae (indicated by the arrow). **D**. Probable rhamphotheca associated with the anterior end of the dentary (indicated by the arrow). Scale bars 20 cm.

The mandibular rami are longitudinally slender and bear a small retroarticular process. Similar to the upper jaw, the anterior extremity of the mandibles is covered by a smooth unossified structure, likely a remnant of a keratinous rhamphotheca (Fig. 4D). At the middle of the left mandibular ramus there are small filamentous structures of uncertain affinities. Most of the filaments are curved, the biggest ones reaching 8 mm and 0.8 mm thick (Fig. 4A).

Soft-tissue median crest.—The soft-tissue component of the cranial median crest in CPCA 3590 is exceptionally well-preserved and shows a pattern of sub-vertical fibers that begins at the dorsal margin of the premaxilla and extends to the dorsal extremity of the crest (Fig. 4B). At the posterior-most preserved portion of the crest the fibers are vertically arranged for most of their extension, describing a slight caudally directed curvature at the top of the crest. Toward the an-

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terior part of the skull, the fibers become more dorso-posteriorly orientated, the most anterior ones almost reaching the inclination of the supra-premaxillary process. The fibers run parallel to each other with no sign of cross-over. The dorsal margin of the premaxilla is vertically striated, indicating that the fibers mineralize at that spot.

Geographic and stratigraphic range.—The specimen comes from the laminated limestone of the Crato Formation, (Araripe Basin, northeastern Brazil) and was collected by quarrymen at Mina Trinfo (Nova Olinda city, Ceará Province, UTM 24M-0423025E/9212692N). Although the precise stratigraphic horizon from where the specimen was collected remains unknown, the light gray color of the sediment and its style of lithification are compatible with the basal layers of the biomicritic limestone package of the Crato Formation, which is usually interpreted as Aptian (Pons et al. 1990; Assine 2007).

Discussion and comparisons

CPCA 3590 is referred to *Tupandactylus imperator* based on the presence of the following diagnostic anatomical features: (i) a very large nasoantorbital fenestra, comprising most of the preserved length of the skull; (ii) rostral end of premaxillomaxilla turned ventrally; (iii) cranial crest supported anteriorly by a spine-like and slightly caudally-inclined supra-premaxillary process; and (iv) premaxillae bearing an anteriorly projecting convex blade. The two latter features are exclusive for *T. imperator*. The main autapomorphy distinguishing *T. imperator* from other tapejarids is a caudally orientated occipital process that reaches nearly the size of the rest of the skull measured from the anterior tip of the premaxilla to the posterior extremity of squamosals (Campos and Kellner 1997; Kellner and Campos 2007). This feature, however, is not preserved in CPCA 3590. *Tapejara wellnhoferi* also has an occipital process, mainly formed by the frontoparietals with the contribution of the supraoccipital ventrally (Wellnhofer and Kellner 1991). Although the real extension of this process cannot be inferred from the known specimens of *T. wellnhoferi*, it is unlikely that it reached the dimensions observed in *T. imperator*, which may reflect ontogenetic differences among specimens. An occipital process also occurs in the Chinese tapejarids from the Jiufotang assemblage (Aptian, western Liaoning province). *Sinopterus dongi* has a short frontoparietal posterior process that differs from *T. imperator* both in size and morphology; in *S. dongi* the structure is curved dorsally (Wang and Zhou 2003). The conditions for *Sinopterus jii* and "*Huaxiapterus*" *corollatus* remain unknown (Lü and Yuan 2005; Lü et al. 2006). "*Huaxiapterus*" *benxiensis* has a long occipital process that, like in *S. dongi,* curves dorsally (Lü et al. 2007).

As observed in other *T. imperator* specimens and in SMNK PAL2344 (the best-preserved *Tupandactylus navigans* known so far), in CPCA 3510, the posterior extension of the premaxillae articulates with nasals and frontoparietals. This contrasts with the condition observed in other tapejarinid pterosaurs such as *T. wellnhoferi* and *S. dongi*, where there is a short space between these bones and the posterior extension of the premaxilla runs parallel to, but not in direct contact with, nasals and frontoparietal (Wellnhofer and Kellner 1991; Wang and Zhou 2003). It remains unclear whether or not this condition is due to the ontogenetic stage of the specimens, since adult individuals of *T. wellnhoferi* and *S. dongi* remain unknown.

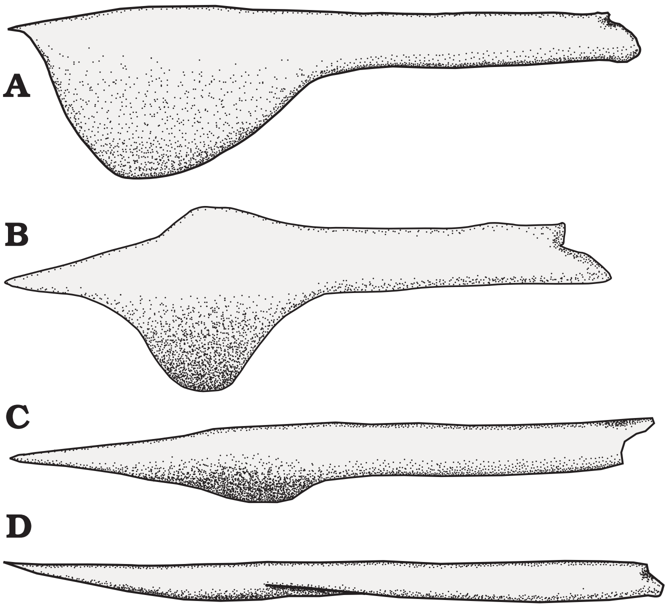

Fig. 5. Variation of mandibular morphology in Tapejaridae. **A**. *Tupandactylus imperator* (Campos and Kellner, 1997). **B**. *Tapejara wellnhoferi* Kellner, 1989. **C**. *Sinopterus dongi* Wang and Zhou, 2002. **D**. *Tupuxuara leonardii* Kellner and Campos, 1994. Not to scale.

Following Frey and Martill (2003), the main differences between *T. navigans* and *T. imperator* are the lack of an occipital spine in the former and the inclination of the leading edge of the soft-tissue crest, which stands vertical to the long axis of the skull in *T. navigans* whereas in *T. imperator* it is inclined caudally. This difference in the inclination of the supra-premaxillary process is well marked in *T. imperator* by an anteriorly projecting convex blade on the premaxilla. This projection is, therefore, diagnostic of *T. imperator.* It is also noteworthy that the skull of *T. imperator* is more flat than that of *T. navigans,* with a length-height ratio of about 3.6 for *T. imperator* and 2.3 for *T. navigans* (whereby the length is measured from the tip of the premaxilla to the caudal margin of the squamosal and the height from the quadrate condyle to the dorsal margin of the premaxilla dorsal to the orbits). Provided the holotype of *T. navigans* completely preserves the occipital region, the presence or absence of an occipital process is sufficient to distinguish these two species. However, the referred specimen of *T. navigans* (SMNK PAL 2343) is abraded in occiput and in the holotype (SMNK PAL 2344) the posterior extension of the frontoparietals, where the occipital spine would be presumably located, is eroded. The integrity of the holotype of *T. navigans* has been previously questioned by Kellner (2007). Although it is improbable that the differences between the two taxa could be interpreted as ontogenetic variation (Frey and Martill 2003), we do not discard the possibility of sexual dimorphism, considering the fact that most of the differences between the two species are associated with the cranial median crest, a structure probably related to sexual display and, therefore, most likely to be sexual dimorphic (Elgin et al. 2008). The hypothesis that sexual dimorphism in Pterosauria is associated with cranial crests has been proposed previously by Bennet (1992). Nevertheless, it was later questioned by Kellner and Tomida (2000). In the specific case here discussed, the issue can be only solved in the light of new specimens.

CPCA 3590 is the first known specimen of *T. imperator* that preserves a nearly complete mandible. There is sparse information about one other specimen with a complete mandible which is presently housed in a private collection (David Martill, personal communication 2010). Specimen SMNK PAL 2839 preserves a fragmentary but yet undescribed lower jaw and a pair of hyoids. Although not much can be said about the lower jaw of CPCA 3590 due to the lack of sutures between bones, its structure is similar to that of *T. wellnhoferi* in the presence of a very deep ventral median crest in the symphyseal area. In CPCA 3590, however, the crest is deeper and more asymmetrically rounded than that of *T. wellnhoferi* (Fig. 5B). Furthermore, the deepest part of the mandibular crest in CPCA 3590 lies more anteriorly when compared with *T. wellnhoferi*, which has a pointed set-off symphyseal beak anterior to the crest (Wellnhofer and Kellner 1991). Jiuofutang Formation tapejarids such as *S. dongi*, *Sinopterus jii*, “*H*”. *corollatus,* and “*H*”. *benxiensis* all show a low, blade-like crest comparatively longer than that of CPCA 3590 and *T. wellnhoferi* with respect to the mandibular length (Wang and Zhou 2003; Lü and Yuan 2005; Lü et al. 2006, 2007; Fig. 5). In this respect, the lower jaws of the Chinese tapejarids are more comparable with the ones of some azdharchoid pterosaurs such as *Bakonidraco galaczi* Ösi, Weishampel, and Jianu, 2005. In CPCA 3590 the dorsal margin of the mandible has a gentle anterior concavity following the ventrally turned rostral portion of premaxillomaxilla. This concavity is better developed in *T. wellnhoferi* (Wellnhofer and Kellner 1991). The lower jaw of CPCA 3590 bears a ventrally sloping retroarticular process similar to the one of *T. wellnhoferi*, although smaller.

The filamentous structures associated with the left mandibular ramus resemble the pycnofibres described by Kellner et al. (2010). Pycnofibres are hair-like structures that covered most of the pterosaur body. The composition of these fibers is unknown but is likely that they were mostly composed by keratin (Kellner et al. 2010). Pycnofibres associated with the mandibular rami could suggest that, in *T. imperator*, the rhamphotheca was restricted to the symphyseal region of the lower jaw.

Structure and morphology of the cranial crest

A soft-tissue cranial crest showing a pattern of sub-parallel vertical fibers has been already reported for *Tupandactylus navigans*. In this pterosaur, however, these fibers gently curve rostrally (Frey and Martill 2003), while in CPCA 3590 they curve caudally.

In the holotype of *Tupandactylus imperator* (MCT 1622-R) the soft tissue crest is preserved as an impression of a triangular patch dorsal to the bony crest (Campos and Kellner 1997). For that reason *T. imperator* has been repeatedly de-

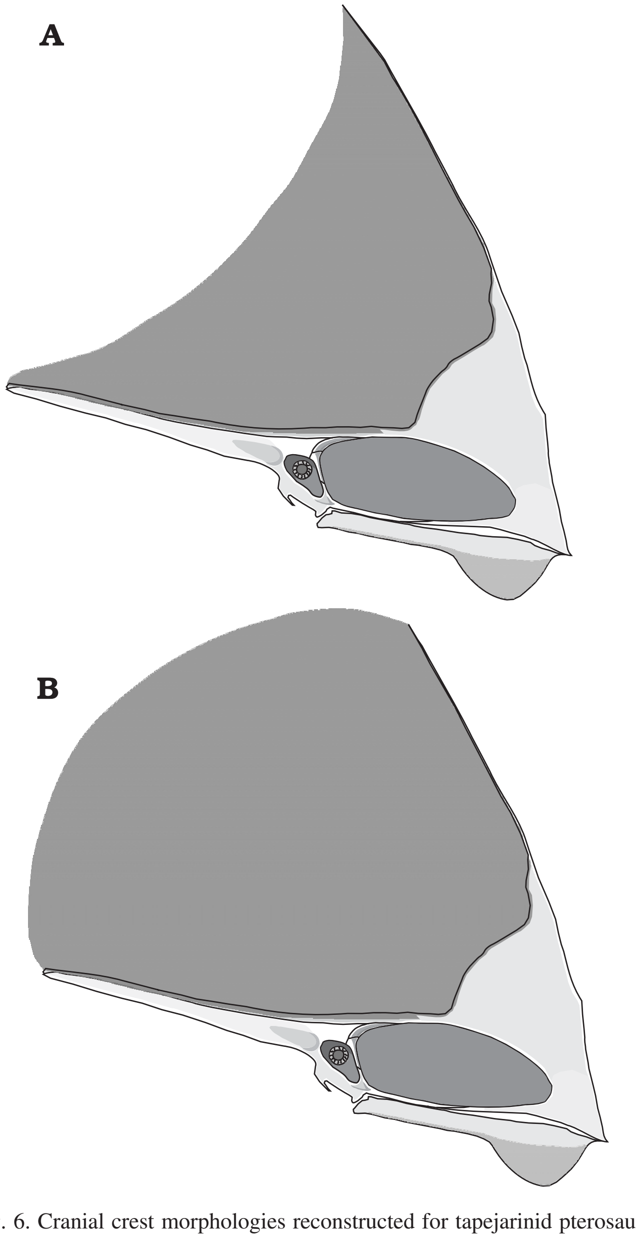

Fig. 6. Cranial crest morphologies reconstructed for tapejarinid pterosaur *Tupandactylus imperator* (Campos and Kellner, 1997). **A**. “Sail-shaped” morphology, suggested by the holotype (MCT 1622-R). **B**. Rounded morphology, suggested by CPCA 3590 and the specimen stored in a private collection.

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picted with a "sail-shaped" median crest with a deeply concave caudal margin. However, considering the bad preservation of MCT 1622-R, it is unlikely that the crest morphology as preserved represents its actual shape in life. Although incomplete, the cranial crest of CPCA 3590 (the best-preserved known so far) shows a dorsal margin posterior to the suprapremaxillary ossification describing a curvature that suggests that the dorsoposterior contour of the crest must have been convex rather than concave (Fig. 6). This convex margin of the cranial crest is consistent with the condition observed in the specimen illustrated by Unwin and Martill (2007: fig. 17.9; at time of publication stored in a private collection) as well as with the morphology proposed by Frey et al. (2003: fig. 10). A fibrous crest supporting a soft-tissue element, both anchored in the bony premaxillary crest, as illustrated by Frey et al. (2003) could not be observed in CPCA 3590. Here, the fibers of the soft-tissue crest remain uniform throughout the extension of this structure. Some differences in the color pattern in different portions of the crest are likely a result of differential oxidation. Because only the anterior part of the crest is preserved, nothing can be said about density variations in the posterior part of this structure.

It was proposed that the function of the cranial crest of *T. imperator* was related to a self-adjustment rudder system (Frey and Martill 2003). Turns of the head at low flight speeds would result in an automatic readjustment into the wind direction, like a weather vane. However, experimental data corroborating this hypothesis are still unpublished. Cranial sagittal crests are extremely frequent among Pterodactyloidea and, as recent finds suggest, were also present in a considerable number of long-tailed pterosaurs (Czerkas and Ji 2002; Dalla Vecchia et al. 2002; Carpenter et al. 2003; Stecher 2008). The great variety and distribution of cranial crests between pterosaur clades, culminating in the huge bony crest showed by *Thalassodromeus sethi* (Kellner and Campos 2002), suggest that they were linked to either a successful functional or reproductive strategy such as specific recognition or sexual display. Pterosaur neuroanatomy indicates that these animals were mostly visual-based (Witmer et al. 2003), a fact that also corroborates a sexual display function for the headcrests. A thermoregulatory function was proposed for the cranial crests of *Tapejara wellnhoferi* (Kellner 1989) and *T. sethi* (Kellner and Campos 2002). This was mostly based on branching channels on the bony surface of the crests, interpreted by these authors as indicative of the presence of blood vessels. Though the huge bony crest of *T. sethi* could actually work as a heat-dissipation structure, this function would probably be better performed by the patagia, the same being valid for *T. wellnhoferi*. There is no sign of similar channels in CPCA 3590 but this could be influenced by the laterally compressed preservation of this specimen.

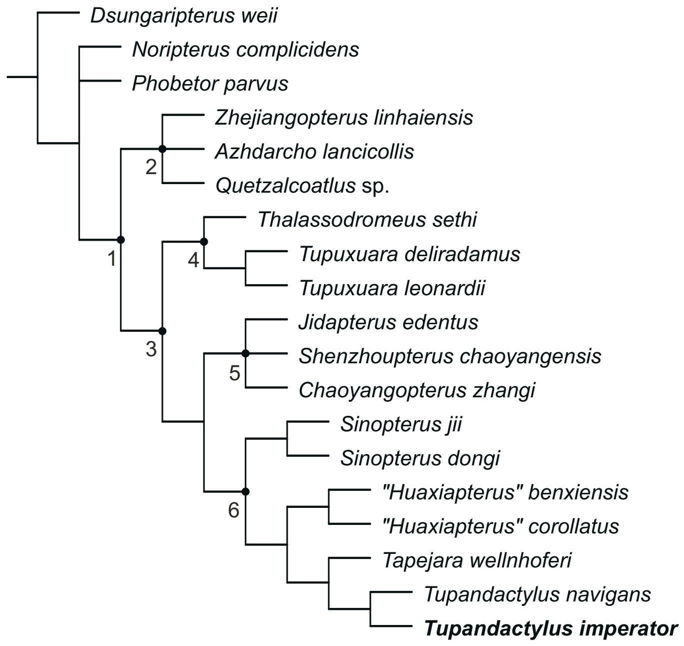

Fig. 7. Most parsimonious tree of 37 steps recovered in the cladistic analysis. 1, Azhdarchoidea; 2, Azhdarchidae; 3, Tapejaridae; 4, Thalassodrominae; 5, Chaoyangopterinae; 6, Tapejarinae.

Phylogenetic relationships of *Tupandactylus imperator*

The completeness of the new specimen of *Tupandactylus imperator* described here, together with previously described remains, allow testing the phylogenetic relationships of *Tupandactylus imperator* through a comprehensive cladistic analysis.

Kellner (2003) was the first to include *Tupandactylus imperator* in a phylogenetic analysis (*Tapejara imperator* at that time), recovering a close relationship among *Tapejara*, *Tupandactylus*, and *Tupuxuara*. However, this work and further analyses (e.g., Kellner 2004; Wang et al. 2005, 2008; Martill and Naish 2006; Lü et al. 2010) used a reduced taxa sampling of Tapejaridae. The analysis presented here includes all described species of Tapejaridae sensu Kellner and Campos (2007), except *Tupuxuara longicristatus* Kellner and Campos, 1998, due to its incompleteness. It also includes three species that comprise the Chaoyangopteridae sensu Lü et al. (2008). The analysis has the objective to test the monophyly of Tapejaridae and the relationships of tapejarid taxa.

The dataset is based on 19 taxa and 22 characters. Three Dsungapteridae taxa were selected as successive outgroups, and the ingroup includes Azhdarchidae, Tapejaridae sensu Kellner and Campos (2007) and Chaoyangopteridae sensu Lü et al. (2008) taxa (see Appendix 3). Characters are from Kellner (2003), Martill and Naish (2006), Lü et al. (2008) and some are new (see Appendix 2).

This phylogenetic dataset was analyzed with equally weighted parsimony using TNT v. 1.1 (Goloboff et al. 2003). The low number of taxa allowed us to perform an exact search strategy using the "implicit enumeration" option. This analysis resulted in only one most parsimonious tree (Fig. 7) of 37 steps (CI = 0.83, RI = 0.9).

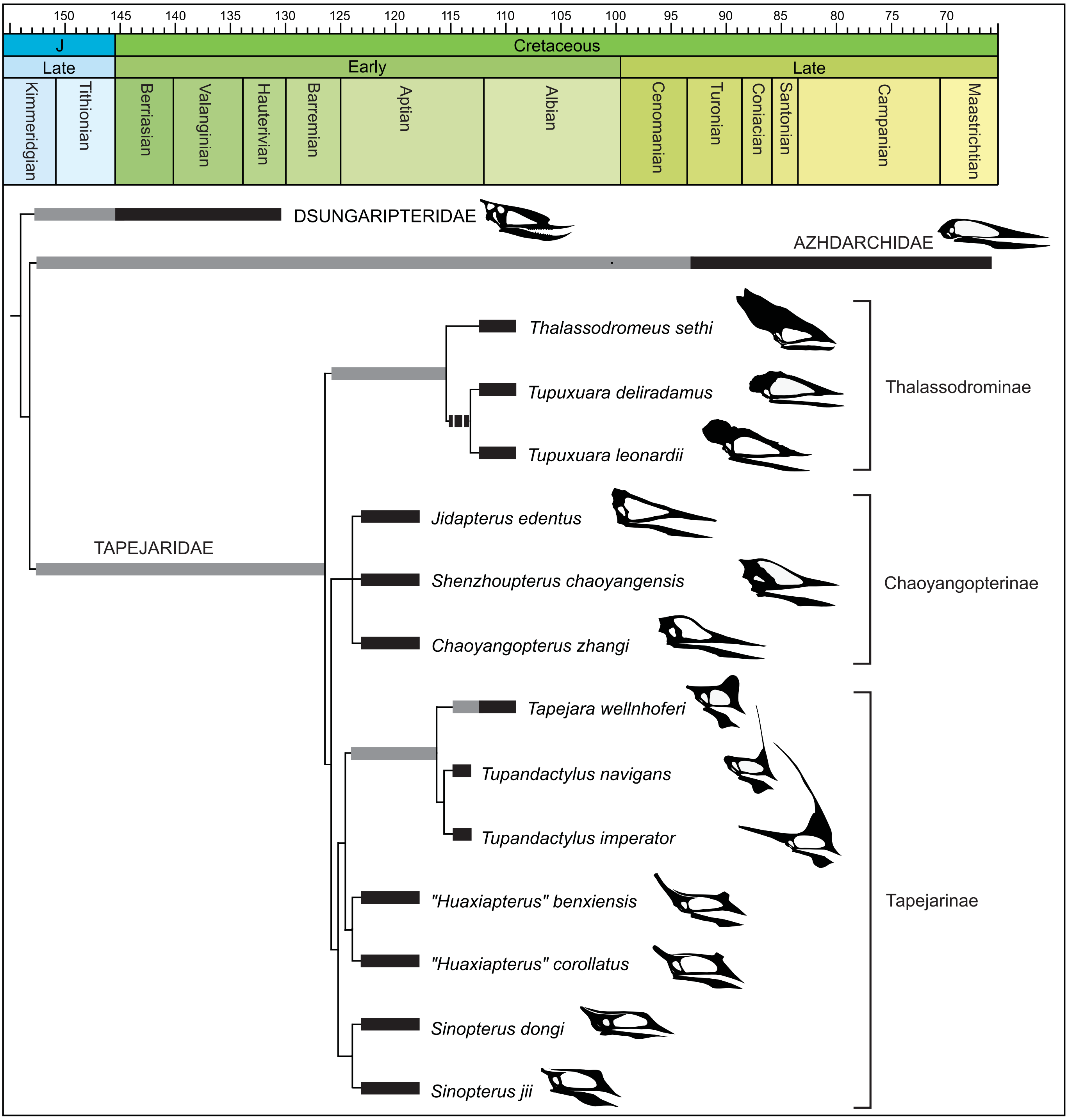

Fig. 8. Biochronology of Azhdarchoidea, based on the most parsimonious tree recovered by our analysis and recorded temporal range.

The most parsimonious tree of this analysis depicts Tapejaridae as a monophyletic group, supported by three synapomorphies (see Appendix 4 for list of apomorphies), in agreement with previous works (Kellner 2004; Wang et al. 2005, 2008, 2009; Andres and Ji 2008). Also, Thalassodrominae Kellner and Campos, 2007 (*Thalassodromeus sethi* and *Tupuxuara*) and Tapejarinae (*Tapejara wellnhoferi*, *Tupandactylus*, "*Huaxiapterus*", and *Sinopterus*) were recovered as monophyletic groups (Fig. 8).

Andres and Ji (2008) recovered a monophyletic clade composed by the Chaoyangopteridae sensu Lü et al. (2008). In the analysis proposed by the authors, this clade has a sister-group relationship with the Azhdarchidae.

According to our analysis, the Chaoyangopteridae sensu Lü et al. (2008) (*Chaoyangopterus* Wang and Zhou, 2006, *Jidapterus* Dong, Sun, and Wu, 2005, and *Shenzhoupterus* Lü, Unwin, Xu, and Zhang, 2008) are a clade within Tapejaridae and form a sister-group relationship with Tapejarinae. To

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avoid nomenclatural incoherence, we suggest name change to Chaoyangopteridae, being henceforth called Chaoyangopterinae (Lü et al. 2008), a clade defined as all pterosaurs more closely related to *Chaoyangopterus zhangi* than to *Tapejara wellnhoferi*. In our analysis, the clade is supported by a dorsal margin of nasoantorbital opening bounded by a slender bar (character 8). *Eopteranodon* lacks a more accurate description and illustration in order to provide a precise attribution to Chaoyangopterinae. The position of *Eoazhdarcho* remains dubious because cranial remains referred to this species are still unknown. It is noteworthy that, mainly due to the limited anatomical information provided at the original descriptions of most Chaoyangopteridae (sensu Lü et al. 2008) taxa, the phylogenetic relationships of these enigmatic pterosaurs are still controversial.

It is noteworthy that our analysis is congruent with the proposition of Kellner and Campos (2007) that "*Huaxiapterus*" *jii* should be renamed to *Sinopterus jii*. Therefore, as "*H*". *jii* is the type species of the genus *Huaxiapterus*, "*Huaxiapterus*" *corollatus*, and "*Huaxiapterus*" *benxiensis* still need a new generic name (Kellner and Campos 2007).

Lü et al. (2010) also recovered a monophyletic Tapejarinae, but all taxa laid in a polytomy. The analysis presented here recovered a monophyletic Tapejarinae, positioned as the sister group of Chaoyangopterinae. The Brazilian tapejarines form a monophyletic group, whilst the Chinese tapejarines form a paraphyletic group. It suggests that the Tapejarinae originated in China and then dispersed to South America.

The monophyly of Tapejaridae

When Kellner (1989) described *Tapejara wellnhoferi*, this new pterosaur species was, together with *Tupuxuara longicristatus* (a taxon named one year before: Kellner and Campos 1988), placed in a new clade of pterodactyloid pterosaurs: the Tapejaridae Kellner, 1989. Some years later, some other pterosaur species such as *Tupandactylus imperator*, *Tupandactylus navigans*, *Thalassodromeus sethi*, *Tupuxuara leonardii*, as well as a series of toothless pterosaurs from the Jiufotang Formation (China) were positioned within this clade. According to Kellner (2004), the Tapejaridae clade is supported by five synapomorphies (listed in the introduction of the present paper).

Unwin (2003) proposed a new taxon (Neoazhdarchia) including *Tupuxuara longicristatus*, *Quetzacoatlus northropi*, their most recent common ancestor and all its descendents. This clade was supported by the presence of a notarium and the loss of contact between metacarpals I–III and the syncarpal. After Unwin (2003), a notarium is reported for azhdarchids and *Tupuxuara* but is absent in *Tapejara*. According Unwin (2003), in *Tapejara* at least one of these metacarpals retains the contact with the syncarpal. An additional character supporting Neoazhdarchia would be a long rostrum, measured from the anterior margin of the orbit to the anterior end of the premaxillae, with more than 88% of the total skull length, contrasting with *Tapejara* which, after Unwin (2003), has a rostrum of only 70% of the total skull length. Therefore, following Unwin and Lü (1997) and Unwin (2003), the Tapejaridae sensu Kellner would be paraphyletic with respect to Azhdarchidae. This was further supported by Martill and Naish (2006) and Lü et al. (2006).

The analyses of Kellner (2003, 2004), Wang et al. (2005, 2008, 2009) and Andres (2008) supported monophyly of the Tapejaridae sensu Kellner and Campos, 2007. According to Kellner and Campos (2007) the loss of contact of metacarpals I–III with the syncarpal is not conclusive for *Tupuxuara* due to the fact that these structures are not completely preserved in any known specimen of this taxon. Kellner (2004) argued that the presence of a notarium is a dubious feature because this structure is only observed in ontogenetically mature individuals. With respect to the comparative length of the rostrum, Kellner (2004) argued that, although there is a difference between the taxa, the basic configuration and proportions of the skull in *Tupuxuara* and azhdarchids are distinct, with *Tupuxuara* having a larger nasoantorbital fenestra and a shorter rostrum (anterior to the nasoantorbital fenestra) in respect to the total length of the skull. This configuration is also observed in *Thalassodromeus*.

It is also noteworthy that in most of the Brazilian tapejarines postcranial elements are missing (e.g., *Tupandactylus imperator* and *Tupandactylus navigans*) or are only known from immature individuals (e.g., *Tapejara wellnhoferi*; Wellnhofer and Kellner 1991; Kellner 2004). Some of the Chinese Tapejarinae are also known only from juveniles (Kellner and Campos 2007). Therefore, the absence of structures such as a notarium could be biased by ontogenetic factors. Besides this, the condition of the contact between metacarpals I–III and the syncarpus cannot be accessed. According to Lü et al. (2003) "*Sinopterus gui*" has a notarium. However, Kellner and Campos (2007) stated that in "*S. gui*" a notarium is in fact absent and, based also on other anatomical and biometrical features such as the proportions between femur and tibia, synonymized this species with *Sinopterus dongi*.

In our phylogenetic analysis the Tapejaridae sensu Kellner is supported by three synapomorphies: (1) nasoantorbital fenestra forming 45% or more of the skull length measured from the tip of premaxilla to the caudal terminus of the squamosal (2) orbit reverse pear-shaped and (3) very thin sub-vertically orientated lacrimal process of the jugal.

It is noteworthy that a "long sagittal crest made mostly by the premaxillae that starts at the rostral end of the skull and extends posteriorly", advocated by Kellner (2003, 2004) and Kellner and Campos (2007) as a synapomorphy of Tapejaridae, is broad enough to agglutinate two very distinct morphologies: In Tapejarinae, the premaxillary crest has a constriction dorsal to the nasoantorbital fenestra, whereas in thalassodrominids this structure remains high dorsal to the nasoantorbital fenestra and extends posteriorly together with the frontoparietals forming a high laterally compressed post-occipital crest.

Although it is possible that a broad tubercle situated at the ventroposterior margin of the coracoid is indeed a synapomorphy of Tapejaridae, as was proposed by Kellner (2003, 2004) this character was so far observed only in *T. wellnhoferi* and *T. leonardii*. The presence of a coracoid tubercle among the Chinese tapejarids could be only confirmed through a closer examination of the specimens.

Conclusions

CPCA 3590 has sufficient diagnostic features that allow its accurate identification as *Tupandactylus imperator*. The specimen constitutes the best-preserved *T. imperator* known so far. It preserves associated soft tissues such as a soft-tissue headcrest, a ramphotheca and, probably, pycnofibres. Probably the most interesting feature of the new specimen is the associated lower jaw, which has a morphology similar to the one observed for *Tapejara wellnhoferi*. A revised diagnosis is proposed for the species, with new characteristics related to the lower jaw and the sagittal cranial crest.

The cladistic analysis showed that *Tupandactylus imperator*, together with *Tupandactylus navigans*, *Tapejara wellnhoferi, Sinopterus* and "*Huaxiapterus*" forms a monophyletic group, the Tapejarinae, in agreement with Kellner (2007). Thalassodrominae and Tapejaridae are also considered monophyletic taxa.

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Appendix 1

Measurements of CPCA 3590.

Maximum height of the nasoantorbital fenestra: 101.31 mm

Mandibular length: 304.72 mm

Dentary sagittal crest height (maximum height between the dorsal and ventral margins of the deepest part of the mandible): 92.75 mm

Maximum preserved length: 333.48 mm

Total height (measured from the ventra-lmost extremity of the premaxillae to the dorsal extremity of the soft-tissue median crest): 599.25 mm

Appendix 2

List of characters employed in the phylogenetic analysis.

Twenty-two characters were used, some based on Kellner (2003), Martill and Naish (2006), and Lü et al. (2008), and some are new. The characters are listed here (arranged per anatomical region) and their respective sources are cited along with the character number of the original publication. All characters were set as non-additive.

Skull

Character 1 (Kellner 2003: character 4): Rostral end of premaxillae/maxillae downturned: absent (0), or present (1).

Character 2 (modified from Kellner 2003: character 8): Naris and antorbital fenestra: confluent, shorter than 45% of the skull length (0), or confluent, longer than 45% of the skull length (1).

Character 3 (Kellner 2004: character 10): Orbit pear-shaped: absent (0), or present (1).

Character 4 (modified from Kellner 2003: character 10): Position of the orbit relative to the nasoantorbital fenestra (naris + antorbital fenestra): same level or higher (0), orbit slightly lower than the dorsal level of the nasoantorbital fenestra (1) or orbit leveled with the ventral half of the nasoantorbital fenestra (2).

Character 5 (modified from Kellner 2003: character 12): Premaxillary sagittal crest: high, displaced backward, near the anterior margin of the nasoantorbital fenestra, reaching the skull roof above the orbit, and extending backwards (0), starting at the anterior portion of the skull and extended posteriorly above the occipital region without constriction above the nasoantorbital fenestra (1), starting at the anterior portion of the skull and extended posteriorly above the occipital region with a constriction above the nasoantorbital fenestra (2), starting at the posterior half of the nasoantorbital fenestra (3), or absent (4).

Character 6 (modified from Martill and Naish 2006: character 2): Suprapremaxillary spine-like process: absent (0), or present (1).

Character 7 (NEW): Anterior portion of the premaxillary crest (anterior to the nasoantorbital fenestra): low (0), or high, above the dorsal margin of the premaxillae (above the nasoantorbital fenestra) (1).

Character 8 (Lü et al. 2008: character 8): Dorsal margin of nasoantorbital opening bounded by slender bar: absent (0); present (1).

Character 9 (NEW): Rectangular protuberance at the premaxillary crest: absent (0), or present (1).

Character 10 (modified from Kellner 2004: character 18): Lacrimal process: broad (0), or thin, subvertical (1).

Character 11 (modified from Kellner 2004: character 20): Bony parietal crest: present, “finger-like” without dorsal curvature (0), present, “finger-like” with accentuated dorsal curvature (1), present, constituting the base of a posterior element of the premaxillary crest (2), or present, short, flange-like (3).

Character 12 (modified from Kellner 2003: character 27): Palatal ridge: discrete, tapering anteriorly (0), strong, confined to the posterior portion of the palate (1), or absent (2).

Character 13 (NEW): Palate: flat/bearing a concavity (0), or strongly convex (1)

Character 14 (modified from Kellner 2003: character 33): Dentary bony sagittal crest: absent (0), blade-like and shallow (1), or massive and deep (2).

Character 15 (modified from Kellner 2003: character 34): Teeth present (0), or absent (1).

Axial skeleton

Character 16 (modified from Kellner 2003: character 41): Notarium: present (0), or absent (1).

Character 17 (modified from Kellner 2003: character 44): Lateral pneumatic foramen on the centrum of the cervical vertebrae: present (0), or absent (1).

Character 18 (modified from Kellner 2003: character 45): Midcervical vertebrae: short, subequal in length (0), elongated (1), or extremely elongated (2).

Character 19 (modified from Kellner 2003: character 47): Neural spines of the midcervical vertebrae: tall, blade-like (0) or extremely reduced or absent (1).

Appendicular skeleton

Character 20 (Kellner 2004: character 56): Deep coracoidal flange: absent (0), or present (1).

Character 21 (Kellner 2003: character 56): Proportional length of the humerus plus ulna relative to the femur plus tibia (hu+ul/fe+ti): humerus plus ulna about 80% or less of femur plus tibia length (hu+ul/fe+ti<0.80) (0), or humerus plus ulna larger than 80% of femur plus tibia length (hu+ul/fe+ti>0.80) (1).

Character 22 (Kellner 2003: character 55): Proportional length of the humerus relative to the femur (hu/fe): hu/fe ≤0.80 (0) or 1.4 > hu/fe >0.80 (1).

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Appendix 3

List of character scores.

Character scores for the taxa used in this work. Nineteen taxa were used in this analysis, coded for 22 characters. Three Dsungaripteridae (*Dsungaripterus weii*, *Phobetus parvus*, and *Noripterus complicidens*) were used as successive outgroups. 16 ingroup taxa include three Azhdarchidae (*Quetzalcoatlus* sp., *Azhdarcho lancicollis*, and *Zhejiangopterus linhaiensis*) and 14 Tapejaridae (see below).

Dsungaripterus weii	`00000 00000 00000 00000 00`
Phobetor parvus	`00000 00000 1?000 ????? ??`
Noripterus complicidens	`???0? 0000? ????0 ?000? 00`
Quetzalcoatlus sp.	`00023 00000 ?2001 01211 00`
Azhdarcho lancicollis	`???2? 00?0? ????1 0121? ??`
Zhejiangopterus linhaiensis	`00024 00000 ???01 0?211 00`
Tupuxuara leonardii	`01121 00001 21101 00000 00`
Tupuxuara deliradamus	`01121 00001 21101 ????? ??`
Thalassodromeus sethi	`01121 00001 21001 ????? ??`
Tapejara wellnhoferi	`11112 01001 02021 10000 00`
Tupandactylus imperator	`11112 11001 0??21 ????? ??`
Tupandactylus navigans	`11112 11001 ????1 ????? ??`
Sinopterus dongi	`11?12 0000? 1??11 1?1?0 10`
Sinopterus jii	`1???2 0000? ???11 1?1?? 10`
"*Huaxiapterus*" *corollatus*	`11??2 0101? ???11 1?1?1 01`
"*Huaxiapterus*" *benxiensis*	`11?12 01011 1??11 1?11? 00`
Chaoyangopterus zhangi	`0???? 0010? ???11 1?1?? 00`
Shenzhoupterus chaoyangensis	`01124 0010? 3??11 1?1?1 00`
Jidapterus edentus	`0???? 0010? ????1 ??1?? 01`

Appendix 4

List of unambiguous apomorphies.

The apomorphy list here is provided only for the ingroup and its internal nodes. The relationships of Dsungaripteridae and Azhdarchidae were not tested in this work.

Azhdarchidae + Tapejaridae: 4(1), 5(4), 15(1)
Azhdarchidae: 17(1), 18(2), 19(1), 20(1)
Tapejaridae: 2(1), 3(1), 10(1)
Thalassodrominae: 5(1), 11(2), 12(1)
Thalassodromeus sethi: no autapomorphies
Tupuxuara: 13(1)
Tupuxuara leonardi: no autapomorphies
Tupuxuara deliradamus: no autapomorphies
Chaoyangopterinae: 8(1)
Chaoyangopterus: no autapomorphies
Shenzhoupterus: no autapomorphies
Jidapterus: no autapomorphies
Tapejarinae: 1(1), 5(2)
"*Huaxiapterus*" + (*Tapejara* + *Tupandactylus*): 7(1)
Tapejara + *Tupandactylus*: 11(0), 14(2)
Tapejara wellnhoferi: no autapomorphies
Tupandactylus: 6(1)
Tupandactylus imperator: no autapomorphies
Tupandactylus navigans: no autapomorphies
"Huaxiapterus": 9(1)
"Huaxiapterus" benxiensis: no autapomorphies
"Huaxiapterus" corollatus: no autapomorphies
Sinopterus: 21(1)
Sinopterus dongi: no autapomorphies
Sinopterus jii: no autapomorphies