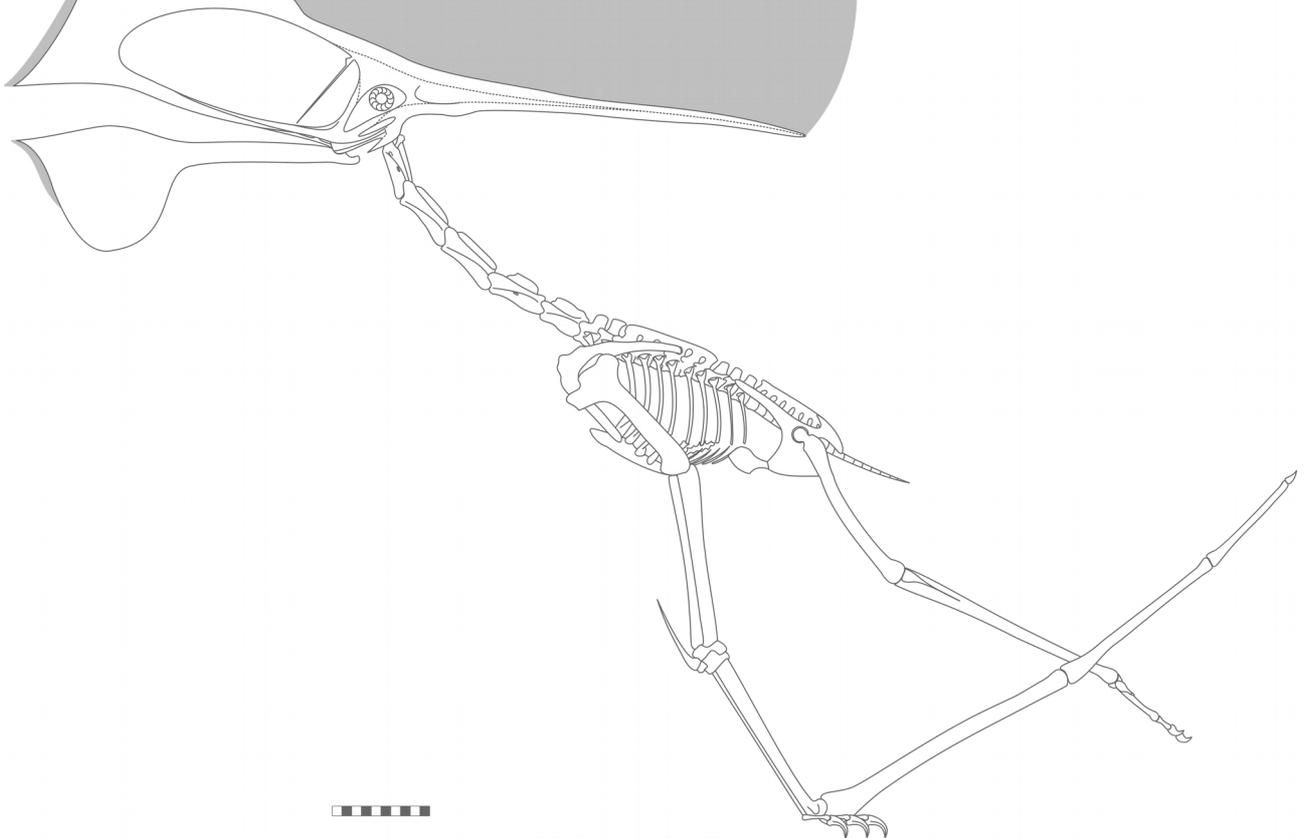


Lucas Piazzentin Costa

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SÃO PAULO – 2021

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A dissertation presented to the Instituto de
Biociências of the University of São Paulo, as
part of the requirements for obtaining the degree
of Master in Biological Sciences, Zoology.

Advisor: Prof. Dr. Hussam El Dine Zaher

Institution-Headquarters:

Museum of Zoology, University of São Paulo

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SÃO PAULO – 2021

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Prof. Dr. Hussam El-Dine Zaher

Orientador

EPIGRAPH

“To those who suffer:
Know that you are not alone.
Please ask for help”.

Atmos Games & Serenity Forge
Neversong (2020)

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This study is definitely not a work of my own. When I look back at these three last years, I see that it was only possible to finish it thanks to the help of many people. The help of many friends. A simple thank you does not express my total gratitude.

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INSTITUTIONAL ABBREVIATIONS

AMNH: American Museum of Natural History, New York, U.S.A.

BMMS: Bürgermeister-Müller-Museum, Solnhofen, Germany.

BPV: Beijing Museum of Natural History, Beijing, China.

BSP: Bayerische Staatssammlung für Paläontologie, Munich, Germany.

BXGM: Benxi Geological Museum, Benxi, China.

CP: Centro Paleontológico, Universidade do Contestado, Mafra, Santa Catarina, Brazil.

CPCA: Centro de Pesquisas Paleontológicas da Chapada do Araripe, Crato, Brazil.

D: Dalian Natural History Museum, Dalian, China.

FSAC: Faculté de Sciences, Laboratoire de Géosciences, Université Hassan II, Morocco.

GMN: Geological Museum of Nanjing, Nanjing, China.

GP: Paleontological Collection, Institute of Geosciences of the University of São Paulo, Brazil.

IGM: Institute of Geology, Mongolia.

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

IWCSM: Isle of Wight County Museum Service, Sandown, Isle of Wight, England.

JPM: Jinzhou Palaeontological Museum, Jinzhou City, Liaoning Province, China.

LPM: Liaoning Paleontological Museum, Liaoning, China.

MCCM-LH: Las Hoyas collection, Museo de las Ciencias de Castilla–La Mancha, Cuenca, Spain.

MCT: Museu de Ciências da Terra, Rio de Janeiro, Brazil.

MN: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

MOR: Museum of the Rockies, Bozeman, U.S.A.

MPSC: Museu de Paleontologia, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil.

MTM: Magyar Természettudományi Múzeum, Hungarian Natural History Museum, Hungary.

MZSP-PV: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

NHMUK: Natural History Museum, London, United Kingdom.

PMOL: Paleontological Museum of Liaoning, Liaoning, China.

SDUST: Vertebrate Paleontology, Shandong University of Science and Technology, China.

SMNK: Staatliches Museum für Naturkunde, Karlsruhe, Germany.

UEPG/DEGEO/MP: Departamento de Geologia, Universidade Estadual de Ponta Grossa, Brazil.

UFRJ-DG: Universidade Federal do Rio de Janeiro, Departamento de Geologia collection, Brazil.

USNM: National Museum of Natural History, Washington, D.C., U.S.A.

WDC: Wyoming Dinosaur Centre, Thermopolis, Wyoming, U.S.A.

XHPM: Dalian Xinghai Palaeontological Bio Expo Museum, Dalian, China.

ZMNH: Zhejiang Museum of Natural History, Zhejiang, China.

RESUMO

Pterossauros são arcosauros extintos especializados em vôo ativo. Pterodactilóides, um grupo monofilético de pterossauros, são especialmente conhecidos da Bacia do Araripe, no Brasil, mais especificamente das Formações Crato e Romualdo. Um grupo conhecido dessas Formações é dos Tapejaridae, com bicos desdentados e cristas altas e longas, que podem suportar uma grande crista de tecido mole. Dos tapejarídeos descritos para a Formação Crato, o mais fascinante é, sem dúvida, *Tupandactylus imperator* Campos & Kellner, 1997, conhecido por sua crista pré-maxilar, com um processo suprapremaxilar muito alto em forma de espinho dorsal, e uma longa crista occipital posterior, ambas ancorando uma membrana alta e longa de tecido mole. Embora muitos espécimens de tapejarídeos sejam conhecidos da Formação Crato, todas as espécies formalmente descritas são baseadas apenas em material craniano, incluindo *T. imperator*. O novo espécime aqui descrito, MZSP-PV 1249, possui um esqueleto pós-craniano quase completo, articulado com um crânio quase completo e uma mandíbula. É um dos primeiros materiais pós-cranianos que pode ser referido a uma espécie nomeada de tapejarídeo da Formação Crato, sendo o quinto espécime oficialmente referido à *T. imperator*. Este espécime, um subadulto, revelou que a curvatura palatal presente no rosto de tapejarídeos maduros pode ser uma característica alométrica, com espécimes adultos apresentando uma oclusão perfeita. *Tupandactylus imperator* compartilha com todos os tapejarídeos brasileiros um jugal tetraradiado, onde o processo quadratojugal é readquirido e direcionado postero-dorsalmente. *Tupandactylus*, *Sinopterus* e *Caiuajara* compartilham o processo suprapremaxilar, sendo sua morfologia única para cada gênero. As espécies de *Tupandactylus* compartilham o formato do processo suprapremaxilar, sendo sua inclinação única para cada espécie, e uma crista mandibular profunda. O processo retroarticular é alongado, algo único para *Tupandactylus* e *Sinopterus* dentre os tapejarídeos. O novo espécime revela que *T. imperator* possui um processo descendente do nasal fino e alongado, uma morfologia complexa da crista occipital posterior, com cada espécie de tapejarídeo apresentando uma morfologia única, e uma quarta falange vestigial do dígito alar. Todas as características axiais e apendiculares de *T. imperator* correspondem ao padrão conhecido para os tapejarídeos, incluindo a quarta e quinta cervicais medianas sendo as vértebras cervicais mais longas, a superfície ventral côncava das cervicais medianas e a segunda e terceira falanges da asa com uma crista ventral longitudinal. Há um quinto dígito pedal em *T. imperator*, com uma única falange vestigial, uma característica observada nos azdarcóides *Sinopterus* e *Jidapterus*. Duas análises filogenéticas preliminares foram realizadas, com resultados indicando que o clado Tapejaridae é suportado principalmente por caracteres mandibulares, e em sua composição interna foi recuperado uma relação mais próxima entre *Tupandactylus*, *Caiuajara* e *Sinopterus*.

ABSTRACT

Pterosaurs are extinct archosaurians specialized in active flight. Pterodactyloids, a monophyletic group of pterosaurs, are especially known from the Araripe Basin, in Brazil, more specifically from the Crato and Romualdo Formations. One group known from these Formations is the Tapejaridae, with toothless beaks and crests high and long, that may support a large soft tissue crest. Among the tapejarids described for the Crato Formation, the most fascinating is, undoubtedly, *Tupandactylus imperator* Campos & Kellner, 1997, known because of its premaxillary crest, with a very high suprapremaxillary process shaped as a dorsal spine, and a very long posterior occipital crest, both anchoring a high and long soft tissue membrane. Although many tapejarid specimens are known from the Crato Formation, all species formally described are based only on cranial material, including *T. imperator*. The new specimen described here, MZSP-PV 1249, has an almost complete postcranial skeleton, articulated with an almost complete skull and a lower jaw. It is one of the first postcranial material that can be referred to a named tapejarid species from the Crato Formation, being the fifth specimen officially referred to *T. imperator*. This specimen, a subadult, revealed that the palatal curvature present at the rostrum of mature tapejarids may be an allometric feature, with adult specimens presenting a perfect occlusion. *Tupandactylus imperator* shares with all Brazilian tapejarids a tetrarradiate jugal, where the quadratojugal process is reacquired and directed posterodorsally. *Tupandactylus*, *Sinopterus* and *Caiuajara* share a suprapremaxillary process, with its morphology being unique for each genus. *Tupandactylus* species share the suprapremaxillary process shape, with its inclination being unique for each species, and a deep mandibular crest. The retroarticular process is elongated, something unique for *Tupandactylus* and *Sinopterus* within tapejarids. The new specimen reveals that *T. imperator* has a thin and elongated nasal descending process, a complex morphology of the posterior occipital crest, with every tapejarid species presenting a unique morphology, and a vestigial fourth phalanx of the wing digit. All axial and appendicular features of *T. imperator* match the known pattern for the tapejarids, including the fourth and fifth mid-cervicals being the longest cervical vertebrae, the concave ventral surface of the mid-cervicals and the second and third wing phalanges with a longitudinal ventral ridge. There is a fifth pedal digit in *T. imperator*, with a single vestigial phalanx, a feature observed on the azhdarchoids *Sinopterus* and *Jidapterus*. Two preliminary phylogenetic analyses were performed, with results indicating that the clade Tapejaridae is supported mainly by lower jaw characters, and in its internal composition it was recovered a closer relationship between *Tupandactylus*, *Caiuajara* and *Sinopterus*.

1. INTRODUCTION

Pterosauria ("Winged Reptile", from the Greek "*Pteryx*", wing, and "*Sauria*", reptile) as a clade comprises extinct archosaurians specialized in active flight. Although flight appeared several times throughout metazoan evolutionary history, only four groups have specialized in active flight, with pterosaurs being the first vertebrates to experience such novelty (ALEXANDER, 2015). Their wings are highly modified forelimbs (Figure F1.1.01), with several adaptations to anchor wing structures, enhance resistance and, at the same time, provide lightness to the skeleton. These wings had their own unique arrangement (BENNETT, 2000), being composed by the fourth hypertrophied manual digit, also known as the wing digit, responsible for supporting a complex structure of skin membranes, muscles, blood vessels and nervous system network, reinforced by a fibers' network called actinofibrils (CHATTERJEE & TEMPLIN, 2004).

Pterosauria current definition (ANDRES, 2010) is apomorphy-based, that being the fourth hypertrophied wing digit. It is the first and most evident apomorphy inherited by *Pterodactylus antiquus* (SÖMMERRING, 1812), the internal specifier (Figure F1.1.02), and this definition not only is consistent with the current use but also with the historical use by Owen (1842), when Pterosauria was originally named in a precladistic sense. Although there is few to none consensus of relationships inside Pterosauria, the current definition includes all taxa regardless of tree topology and the name Pterosauria is firmly anchored in the notion of a diagnostic wing apomorphy.

Although many other characters have been defined as pterosaurian synapomorphies (WELLNHOFER, 1978; PADIAN, 1984a; SERENO, 1991; BENNETT, 1996b; KELLNER, 1996c; ANDRES, 2010), Romer (1956) diagnosis still applies, almost perfectly, to differentiate pterosaurs from all other amniotes. As a whole, pterosaurs have hollow pneumatic skeletons, with the smallest periosteum of all tetrapods. The skulls are long, being 50-90% of the torso length, with most taxa harboring correspondingly large external naris and antorbital fenestrae. On the other hand, the lower jaws are narrow and lack an external mandibular fenestra. The cervical vertebrae are larger and longer than the dorsal vertebrae, with extreme cases in azhdarchids where the mid-cervical V alone can reach the entire dorsal series length. The sternum is wide and expanded, with a prominent anterior projection analogous to the avian keel, called cristospine. The humerus has a bowed shaft, subequal in length with the femur, with a broad deltopectoral crest. The carpals are fused into two independent unities, at least in mature individuals, and there is one bone exclusive to pterosaurs, the pteroid bone. The manual digits I-III are small and thin, while digit IV is very elongated and robust

and digit V is absent. The manual phalangeal formula is 2-3-4-4-X, with the digit IV lacking an ungual. The ischium and pubis are thin and fused with a long prepubis. The femur is bowed with a hemispherical head offset from the shaft. The proximal tarsals are reduced to the astragalus and the calcaneum, with both elements fusing to the tibia in mature individuals. The pedal digit V has a twisted metatarsal and a simplified digit, presumably responsible for anchoring a membrane between the hindlimbs. Despite its entirely fossil record, pterosaurs have two soft tissue synapomorphies: a wing membrane, supported internally by a network of actinofibrils, and the presence of epidermal filaments called pycnofibers (KELLNER *et al.*, 2009). These pycnofibers, possibly present in all pterosaurs, indicates that they were endothermic. Yang *et al.* (2019; 2020) recently suggested that pycnofibers may be homologous and precursors of feathers, while Unwin and Martill (2020) viewed them as taphonomical artifacts, with pterosaurs possibly being covered by scales instead.

Since Huene (1914) the hypothesis of pterosaurs being highly modified diapsids has gained support, and since the beginning of the 20th century this relationship was no longer questioned. Even being highly modified, pterosaurs presents typical diapsid features, including two pairs of temporal fenestrae posterior to the orbits (OSBORN, 1903). The relationships between the diapsids are overall established, but some groups still have questionable relationships within Diapsida, with the pterosaurs being one such group because several distinct groups were proposed as pterosaurian relatives (WILD, 1978). Among these, three are worth mentioning, since they gained support recently. The primarily accepted hypothesis supports the clade Ornithodira, with Pterosauria and Dinosauria as sister groups (GAUTHIER, 1984; 1986; SERENO, 1991; HONE & BENTON, 2007; NESBITT, 2011; WITTON, 2015; EZCURRA *et al.*, 2020), while the other two hypothesis positions Pterosauria outside Archosauria, as the sister group of Archosauriformes (BENTON, 1982; 1984; 1985) or more closely related to Protosauria (WILD, 1978; 1983; 1984a; BENNETT, 1996b; 2013a).

Fossils attributed to pterosaurs are found throughout an extensive spatial and temporal record, being globally distributed in rocks from formations ranging from the Middle Triassic to the Late Cretaceous (BARRETT *et al.*, 2008). Throughout their evolution, they also presented great ecomorphological disparity, with internal clades being interpreted as evolving herbivory, omnivory, carnivory and even durophagy (ZHOU *et al.*, 2017). Despite their evolutionary success throughout the Mesozoic, pterosaurs disappeared entirely from the fossil record at the Cretaceous-Paleogene boundary. The causes of their extinction are a main topic of interest at least since the beginning of

the 21st century (BUTLER *et al.*, 2009; LONGRICH, MARTILL & ANDRES, 2018). Up to date, the group is composed of more than 140 species formally described (BARRETT *et al.*, 2008), with more than half of its diversity belonging to the Pterodactyloidea clade (WU, ZHOU & ANDRES, 2017; LONGRICH, MARTILL & ANDRES, 2018).

Pterodactyloids are specially known from the Araripe Basin in Brazil, and more specifically from the late Early Cretaceous Crato and Romualdo Formations. One of the main groups described for the Crato Formation is the Tapejaridae. This group is known from species such as *Tapejara* (KELLNER, 1989), evolving a lack teeth, replaced by a rhanphotheca, and having long limbs more adapted to life on land. Tapejarids are also known for their high premaxillary crest, together with a long posterior occipital crest, which may supported a large soft tissue crest. Regarding the tapejarids described for the Crato Formation, the most unusual is undoubtedly *Tupandactylus imperator* Campos & Kellner, 1997. Originally described as a *Tapejara* species, *T. imperator* is known from a relatively complete skull, which preserved a premaxillary crest with a very high dorsal spine, a very long posterior occipital crest, both being very thin, and dark spots on the matrix that are suggestive of soft tissue, indicating that these two bone crests anchored a high and long soft tissue crest. This crest composes 5/6 of the total lateral area of the skull, in addition to the nasoantorbital fenestra being equivalent to 50% or more of the total length of the skull (CAMPOS & KELLNER, 1997). "*Tapejara*" *imperator* was allocated to its own genus (KELLNER & CAMPOS, 2007), in addition to a second species, *Tupandactylus navigans* (FREY, MARTILL & BUCHY, 2003b). The two taxa described as *Tupandactylus* and the bizarre crest that they both present inspired biomechanical works such as Chatterjee and Templin (2012), which tested whether the crests would possibly hinder flying capabilities or make it impossible for tapejarids with high and long crests to fly.

Although many tapejarid specimens are known from the Crato Formation, all named species from this Formation are based only on cranial material. The species *T. imperator* has been described only from skulls and, although postcranial elements have been assigned to *Tupandactylus*, they have not been formally described. The only material, assigned to *T. imperator*, that is not only a skull and is of a reliable source is CPCA 3590, which has a lower jaw associated to a fragmentary skull. In this manner, a new specimen, MZSP-PV 1249, represents not only an almost complete postcranial skeleton, lacking few elements such as distal wing phalanges and pes digits, but it is also articulated with the skull and lower jaw, allowing its identification at specific level, being therefore one of the first reliable association of postcranial material to a tapejarid from the Crato Formation. This particular specimen allowed a detailed comparative study of *Tupandactylus* postcranial elements

with all other tapejarids, thus resulting in a diagnostic revision for the species and, possibly, the genus. The resulting morphological data allowed a more refined phylogenetic analysis for the genus and a reassessment of its phylogenetic positioning within Tapejaridae and Azhdarchoidea.

Considering that *T. imperator* does not have referred postcranial material up to date, this study aimed for the preparation and description of a new specimen of *T. imperator*, MZSP-PV 1249, with a skull and lower jaw associated with a virtually complete and articulated postcranial skeleton, thus the first specimen of *T. imperator* with information regarding the postcranial skeleton.

2. GOALS

This dissertation have the following goals:

- The preparation of MZSP-PV 1249, represented by a nearly complete specimen of *Tupandactylus imperator* Campos & Kellner, 1997, with a skull lacking only the posterior occipital crest and a postcranium with almost all the elements articulated, from the Early Cretaceous (Aptian) Crato Formation, Santana Group, Araripe Basin.
- The elaboration of a detailed osteological description of MZSP-PV 1249.
- A morphological comparative analysis with other specimens of Tapejaridae, described for Brazil and other countries, and available in the literature.
- The elaboration of a revised diagnosis for *T. imperator* and, possibly, the genus *Tupandactylus*, based on the new data available from this work.
- The elaboration of a character matrix that would allow testing the phylogenetic affinities of *T. imperator* with other members of Tapejaridae within the irradiation of Azhdarchoidea.

3. PTERODACTYLOID DIVERSITY

3.1. Pterodactyloidea

Following the description of the species *Pterodactylus antiquus* (SÖMMERRING, 1812), every new pterosaur species discovered was allocated in the genus *Pterodactylus* Rafinesque, 1815, making it a wastebasket taxon. After sixty years a distinct genus was recognized, *Rhamphorhynchus* Meyer, 1846, based on the separated external naris and antorbital fenestra, a long tail, a short metacarpal IV and a long pedal V digit. With more pterosaur species being described, both *Rhamphorhynchus* and *Pterodactylus* were used as a basis for a dichotomic separation, illustrating the possible morphologies for the external naris composition, the tail length, the metacarpal IV size and the pedal V digit proportion. Plieninger (1901) formalized this dichotomy (Figure F3.1.01), recognizing the superfamilies "Rhamphorhynchoidea" and Pterodactyloidea.

Traditionally, "Rhamphorhynchoidea" was composed by early diverging and, usually, more ancient taxa than Pterodactyloidea, since all representatives are exclusive from the late Triassic and Jurassic, whereas pterodactyloids are exclusive from the late Jurassic and Cretaceous. With the advent of Cladistics, Padian (1984a) analysis recovered "Rhamphorhynchoidea" paraphyletic relative to Pterodactyloidea, a hypothesis already discussed beforehand (WELLNHOFER, 1975; 1978). Since then, some "rhamphorhynchoids" monophyletic subgroups were recovered more closely related to pterodactyloids than any other early diverging lineages of "rhamphorhynchoids". Thus, all taxa formerly known as "Rhamphorhynchoidea" are either known as more early diverging lineages or non-pterodactyloid pterosaur. Pterodactyloidea, however, remains well supported.

The original definition by Plieninger (1901) listed two diagnostic features, a short tail and a long metacarpal IV, including four species in two groups. Tradition was to check these two characters to include new taxa in either Pterodactyloidea or "Rhamphorhynchoidea". A dilemma arose with the description of *Anurognathus* (DÖDERLEIN, 1923), a pterosaur with a short tail and a short metacarpal. Historical usage has emphasized metacarpal proportion as determinant for diagnosing pterodactyloids, with *Anurognathus* being defined as a non-pterodactyloid because it has a short metacarpal and a pedal digit V with two phalanges. Andres (2010) current definition follows this historical usage, defining the long metacarpal, as present in *Pterodactylus*, as a diagnostic apomorphy of the group, with *Pterodactylus* being considered the internal specifier. The definition is made by using the coding of Unwin (2003), where the metacarpal IV must be as long as 80% of

the humerus length. With this definition, taxa can be considered Pterodactyloidea regardless of topology, since it is an apomorphy-based definition. In addition, as Andres (2010) discussed, the metacarpal IV in pterosaurs is a very robust bone, with greater preservation potential than all other pterosaur bones and it is likely to preserve even in very fragmented specimens.

Additional synapomorphies used by Romer (1956), Kellner (2003) and Unwin (2003) to define Pterodactyloidea include: the basiptyergoids fused in an elongated medial bar, posteroventral orientation for the occipital condyles, deltopectoral crest proximally positioned without a proximal curvature, deltopectoral crest end attenuated and rounded, rather than expanded, and the fifth pedal digit reduced to a short metatarsal with no more than a single vestigial phalanx. Other characters have been used to diagnose Pterodactyloidea, but recent works associated them with major groups that include pterodactyloids. The external naris and antorbital fenestra fusing into a nasoantorbital fenestra is a character used by Kellner (2003) and Unwin (2003) to define Pterodactyloidea. Since the description of *Darwinopterus* (LÜ *et al.*, 2010), this character defines Monofenestrata, a clade that includes Pterodactyloidea. Another character used to define Pterodactyloidea is the shortening of the tail. In some topologies (ANDRES, 2010), Monofenestrata has Anurognathidae as a internal group. Anurognathids are non-pterodactyloids with a possible short tail (ANDRES, CLARK & XU, 2010). At least for topologies where anurognathids are recovered closely related to pterodactyloids, short tail may define Caelicodracones.

Pterodactyloidea is the best-known and better supported clade within Pterosauria. It contains more than eighty species, more than half of all pterosaurs, and its monophyly has never been seriously questioned. Phylogenetic analyses agree that Pterodactyloidea is composed mainly by three major clades (Figure F3.1.02). Ctenochasmatoidea, composed by mainly Jurassic filter feeding species, Pteranodontoidea, composed by entirely piscivorous Cretaceous taxa with long wings, and Azhdarchoidea, composed by mostly carnivorous Cretaceous taxa with short wings. Although phylogenetic analyses agree with their composition, interrelationships between these three major clades are still unsolved. Kellner (2003) supports the Ornithocheiroidea hypothesis, where Pteranodontoidea and Azhdarchoidea are sister groups, with Ctenochasmatoidea as a monophyletic subgroup of Archaeopterodactyloidea, representing the earliest divergence within pterodactyloids. Unwin (2003), on the other hand, supports the Lophocratia hypothesis, where Ctenochasmatoidea and Azhdarchoidea are sister groups, with Pteranodontoidea branching off as the earliest divergence within pterodactyloids. Most analyses up to date agree on overall Pterodactyloidea composition.

3.2. Azhdarchoidea

Azhdarchoidea, first recovered by Unwin (1992) as one of the three pterodactyloid major groups, never had its monophyly and main composition seriously questioned, although its full composition varies from topology to topology. Azhdarchoidea is attributed to Nesselmann (1984), but it was more clearly defined by Kellner (2003) and Unwin (2003), who gave the same node-based definition to the clade, with *Tapejara* and *Quetzalcoatlus* as internal specifiers.

There are two major conflicts regarding Azhdarchoidea. First, which major Pterodactyloidea clade is more closely related to it, if it is Ctenochasmatoidea, composing Lophocratia, or if it is Pteranodontoidea, composing Ornithocheiroidea. Azhdarchoidea are exclusively Cretaceous, being inferred as the last clade to appear in the fossil record, never been recovered as the earliest diverging pterodactyloids, which is why a closer relationship between ctenochasmatooids and pteranodontoids have never been proposed. Bennett (1989a; 1994) and Unwin (1992) recovered Lophocratia based on elongated and low cervical vertebrae. Kellner and Hasegawa (1993), Kellner (1995; 1996c) and Unwin (1995) analyzed shared apomorphies on the skull, present in tapejarids and azhdarchids, and proposed that the elongation of cervical vertebrae evolved independently in ctenochasmatooids and azhdarchids. Even Unwin (2003), recovering Lophocratia, supported the hypothesis of independent elongation of the cervicals, because both clades have early diverging taxa with relatively short cervicals. And second, although its internal composition remains stable, with Tapejaridae and Azhdarchidae as the main clades, its internal relationships are far from resolved.

Kellner (2003) and Unwin (2003) defined the same main synapomorphy for Azhdarchoidea simultaneously: the entire orbit positioned below the dorsal margin of the nasoantorbital fenestra, in lateral view (Figure F3.2.01). While in other pterosaurs the orbit is close to the dorsal margin of the skull, usually being higher than the dorsal margin of the antorbital or nasoantorbital fenestra, in azhdarchoids the orbit occupies a relatively low position. The azhdarchids presents an extreme condition, with the entire orbit positioned near the ventral margin of the skull. Kellner (1989) originally regarded the orbit position as a *Tapejara* autapomorphy, but more complete skulls of *Tupuxuara* (KELLNER & HASEGAWA, 1993) and *Quetzalcoatlus* (KELLNER & LANGSTON, 1996) revealed that this character is shared by a clade that includes the three taxa. Unwin (2003) hypothesized that this lateral position is related to a dorsal elevation of the posterior rostral region, together with a ventrolateral extension of the frontal. Regardless of character distribution within Pterodactyloidea, recent phylogenetic analyses of supermatrices recovered the same character state

as the main synapomorphy of Azhdarchoidea (ANDRES, CLARK & XU, 2014; WU, ZHOU & ANDRES, 2017; LONGRICH, MARTILL & ANDRES, 2018).

In addition to the diagnostic apomorphy cited above, many other characters defined by Unwin (1992; 1995), Kellner and Campos (1992), Kellner (1995; 2003), Kellner and Langston (1996), Unwin and Lü (1997) and Eck, Elgin and Frey (2011) were also recovered as synapomorphies for the group by Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017), Vidovic and Martill (2017) and Longrich, Martill & Andres (2018). These additional synapomorphies include: a longer nasoantorbital fenestra relative to the skull, premaxillary crest with the anterior margin subvertical, orbit relatively smaller, supraoccipital crest present, shorter subtemporal fenestra, toothless jaws, a deep flange on the ventral margin of the coracoid, responsible for the attachment of the *musculus supracoracoideus*, sternocoracoid articulations being anteroposteriorly instead of laterally, shorter humerus with a tall rectangular deltopectoral crest, ventral ulnar crest of the humerus, ventral distal tubercle of the ulna, radius with a distal cross-section subtriangular in shape with a large anterior process, proximal syncarpal as long as wide, a longer pteroid, a much longer metacarpal IV when compared to the humerus, the loss of contact between metacarpals II-III and the carpus, phalanges two, three and four of the manual digit IV reduced, in comparison with an elongated phalanx one, postacetabular process of the ilium with constricted shaft and hooked process at the apex and, finally, a longer femur with a pneumatic foramen between the greater trochanter and femoral collum and expanded distal epicondyles. Although Azhdarchoidea is supported by a variety of characters, most synapomorphies are not exclusive. Toothless jaws, for example, is also a synapomorphy for Pteranodontia. Depending on the topology, Dsungaripteridae is recovered inside Azhdarchoidea, a clade where all taxa have teeth.

Azhdarchoidea has always been recovered as a monophyletic group, composed by the clades Tapejaridae, Thalassodromidae, Chaoyangopteridae and Azhdarchidae. Although thalassodromids and chaoyangopterids were always recovered inside Azhdarchoidea, both have conflicting nomenclatures according to the topology (Figure F3.2.02). Thalassodromidae, recovered closely related to Tapejarinae by Kellner (2003) and Pinheiro *et al.* (2011), is named Thalassodrominae and considered a clade that defines Tapejaridae, a definition formalized by Kellner and Campos (2007). Pinheiro *et al.* (2011) also considered Chaoyangopteridae an internal clade of Tapejaridae, named Chaoyangopterinae, recovering it closer to Tapejaridae and Thalassodromidae than to Azhdarchidae. Vidovic and Martill (2017) recovered a group, named Azhdarchidae, composed of chaoyangopterids mixed with azhdarchids. There is a fifth clade that has conflicting relationships with azhdarchoids,

being the Dsungaripteridae. Andres, Clark and Xu (2014) recovered dsungaripterids inside Azhdarchoidea, closely related to Thalassodromidae and both composing Dsungaripteromorpha. Kellner (2003) did not recover dsungaripterids inside Azhdarchoidea, but it recovered closely related, with both composing Tapejaroidea. Unwin (2003) recovered Dsungaripteroidea, being composed by Dsungaripteridae and Germanodactylidae, and this clade formed a trichotomy with Ctenochasmatoidea and Azhdarchoidea, where this trichotomy was named Lophocratia. Pinheiro *et al.* (2011), using dsungaripterids as outgroup for the analysis, did not test its true relationship with Azhdarchoidea. Finally, Vidovic and Martill (2017) recovered a novel position for the group, as closely related of the Pteranodontoidea. Here, we will follow the Neoazhdarchia hypothesis provided by Unwin (2003), as recovered by Andres, Clark and Xu (2014).

Azhdarchoids are known entirely from the Cretaceous period, even when dsungaripterids are considered azhdarchoids, with only *Domeykodactylus* (MARTILL *et al.*, 2000) having a dubious age, possibly from the Latest Jurassic. While most fossils are restricted to Brazil and China (BARRETT *et al.*, 2008), azhdarchids are known to be geographically widespread, with fossils present in almost all continents bearing Cretaceous deposits. Of all groups recovered composing Pterodactyloidea, the azhdarchoids have the greatest ecomorphological disparity, with internal clades interpreted as being herbivorous, omnivorous, carnivorous and even durophagous when the dsungaripterids are considered belonging to the group (ZHOU *et al.*, 2017).

3.3. Tapejaridae

Of all clades described that composes Azhdarchoidea, Tapejaridae is so far one of the most intriguing. This group is known since the description of *Tapejara* (KELLNER, 1989), a Brazilian taxon that lacks teeth. Autapomorphies defined for *Tapejara* by Kellner (1989) are known today as synapomorphic for more inclusive clades, such as the orbit lateral position, with the skulls of *Tupuxuara* (KELLNER & HASEGAWA, 1993) and *Quetzalcoatlus* (KELLNER & LANGSTON, 1996) revealing it as synapomorphy for Azhdarchoidea, and the presence of crests together with the rostrum morphology, with more tapejarid skulls revealing it as a synapomorphy for Tapejaridae. Tapejarids have an average of 2m wingspan, being the smallest azhdarchoids in size, and Zhou *et al.* (2017) classified them as herbivores. According to Bestwick *et al.* (2018), herbivory consisting of leaves and fruits is generally the most accepted hypothesis (WELLNHOFER & KELLNER, 1991; MEIJER *et al.*, 2007; VULLO *et al.*, 2012), but durophagy of seeds and hard plants is also included with strong support (PINHEIRO, LIPARINI & SCHULTZ, 2014a; 2014b; HENDERSON, 2018). Other diets, such as carnivory, piscivory and insectivory have been proposed (UNWIN & MARTILL, 2007; WANG *et al.*, 2008a) but these hypotheses present few to none evidence. Although there are described taxa from different places such as Europe (VULLO *et al.*, 2012), there are two hotspot countries that concentrate most of the known tapejarid biodiversity (WU, ZHOU & ANDRES, 2017): China, since the description of *Sinopterus* (WANG & ZHOU, 2003a), and Brazil, since the description of *Tapejara* and *Tupandactylus*.

Kellner (1989) described tapejarids as toothless pterosaurs with a large sagittal crest, specifically a premaxillary crest, extending posteriorly, nasoantorbital fenestra occupying almost half of the skull lateral area and the rostrum inclined downwards. These synapomorphies were also listed as *Tapejara* autapomorphies, with the absence of a palatal ridge distinguishing it from *Tupuxuara*. Unwin (2003) also listed the mandibular symphysis inclined downwards, discussing that the presence and absence of ridges and depressions on the palate and symphysis dorsal surface may distinguish *Tapejara* from *Tupuxuara*. The rostral and mandibular characters remain as the main synapomorphies of Tapejaridae excluding Thalassodromidae. While pterosaurs have their upper and lower jaws both straight, as in *Pterodactylus* (SÖMMERRING, 1812), both upturned, as in *Pterodaustro* (BONAPARTE, 1970), or with variable morphologies and unique combinations, as in *Rhamphorhynchus* (MEYER, 1846), *Cycnorhamphus* (SEELEY, 1870) and *Thalassodromeus* (KELLNER & CAMPOS, 2002; PÊGAS, COSTA & KELLNER, 2018), only the tapejarids have both their rostrum and their symphysis downturned (Figure F3.3.01). Kellner (2003) and Unwin

(2003) recovered these characters as synapomorphies for the genus *Tapejara*, uniting *Tapejara wellnhoferi* with "*Tapejara*" *imperator*. There are two reasons why both the downturned rostrum and downturned symphysis are necessary to define the main synapomorphy of the tapejarids. First, some taxa lack preserved skulls but have preserved lower jaws with downturned symphysis, such as *Europejara* (VULLO *et al.*, 2012). Second, thalassodromids such as *Thalassodromeus* (KELLNER & CAMPOS, 2002; PÊGAS, COSTA & KELLNER, 2018), present a downturned rostrum, but the symphysis curved upwards. Interpretations regarding the evolution of the rostral and symphyseal configurations depends on the topology. If tapejarids and thalassodromids are recovered closely related, the downturned rostrum only can be considered a synapomorphy for the Tapejaridae as originally described by Kellner (1989). On the other hand, the Neoazhdarchia hypothesis indicates that it may be a homoplastic character with a rather complex evolution.

Other characters, originally described by Kellner (1989) and discussed by Kellner (2003) and Unwin (2003), were slightly modified but can still be considered synapomorphies for Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007). These and other synapomorphies defined by Wellnhofer and Kellner (1991), Frey, Buchy and Martill (2003), Kellner (2004c), Pinheiro *et al.* (2011), together with the recovered by Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018), include the following: rostrum and mandible with a middle lateral expansion, a large nasoantorbital fenestra occupying 45% or more of the skull lateral length, thin and subvertical lacrimal (dorsal or ascending) process of the jugal, small reversed pear-shaped orbit, square-shaped sternum with short and broad cristospine, scapula and coracoid both with large flanges on posterior surfaces, scapula longer than coracoid, making the glenoid fossa lateral position more ventrally, scapulocoracoid articulation perpendicular relative to the vertebral column, a broad and well-developed tubercle at the posteroventral margin of the coracoid, pneumatic foramina in both proximoventral and proximodorsal surface of the humerus, a shorter and more angled deltopectoral crest and a total of four crests, being a high premaxillary crest anteriorly positioned, with a posterior projection through the skull roof, short frontoparietal crest, posterior occipital crest of variable size and shape and a deep dentary crest not as large as the premaxillary crest. In *Tupandactylus* and quite possibly all tapejarids, the premaxillary, frontoparietal, and posterior occipital crests altogether support a large and thin sail-like crest of soft tissue. The notarium is inconclusive for tapejarids, with studies supporting its absence as a synapomorphy (UNWIN, 2003) while others suggest a notarium may be present but might not have been preserved (KELLNER, 2004c), since it appears in mature individuals and almost all tapejarids known so far with preserved postcranial material are juveniles.

Kellner (1989) originally defined Tapejaridae as a group including *Tupuxuara* and *Tapejara*, two taxa that would become representatives of Thalassodrominae and Tapejarinae, respectively, by Kellner and Campos (2007). Cladistic analysis (e. g. KELLNER, 2003) reinforced this hypothesis, recovering Tapejaridae composed by *Tupuxuara* and *Tapejara*. Unwin (2003), however, challenged this hypothesis, recovering Tapejarinae as sister group of Neoazhdarchia, where Thalassodrominae is more closely related with Azhdarchidae. The relationships between tapejarids, thalassodromids and azhdarchids are still uncertain (LONGRICH, MARTILL & ANDRES, 2018; PÊGAS, COSTA & KELLNER, 2018). Indeed, as discussed by Kellner (2004c), comparisons between these three clades are difficult to establish, since each one has its own pattern. Tapejarids have short skulls with downturned rostrum and dentary, large nasoantorbital fenestra and huge premaxillary crest with a posterior extension, with thin frontoparietal and posterior occipital crests. Thalassodromids have long skulls with a short rostrum, very large nasoantorbital fenestra, variable rostrum and dentary directions, small premaxillary crest connected with a big frontal crest and a huge parietal crest, with the posterior occipital crest as a posteroventral margin. Azhdarchids have long straight skulls with a long rostrum, short nasoantorbital fenestra and absence of crests. Here, we will follow the definition for Tapejaridae provided by Andres, Clark and Xu (2014), which is equivalent of Lü *et al.* (2006b) definition for Tapejaridae and Kellner and Campos (2007) definition for Tapejarinae (Appendix A).

3.4. The Genus *Tupandactylus*

Tapejarids, whether thalassodromids are included (KELLNER, 1989) or excluded (ANDRES, CLARK & XU, 2014), are known as the most strange of all pterosaurs, thanks to the morphology of their heads and crests. By far, the most fascinating of all tapejarids ever described, perhaps being the most bizarre of all pterosaurs, is *Tupandactylus*. Originally described as a species of *Tapejara*, *Tupandactylus* is known due to its enormous premaxillary crest, composed by both bone elements, which includes a very high but thin dorsal spine, and non-ossified soft tissues, in the shape of a high sail-like structure, which is remarkably preserved in all known specimens. Until today, two species are known and considered valid.

Tupandactylus Kellner & Campos, 2007.

Type Species: *Tupandactylus imperator* (CAMPOS & KELLNER, 1997).

Etymology: "Tupã Finger", from: Tupí-Guaraní "Tupã" or "Tupan", and Greek "Daktylos", finger. Kellner and Campos (2007) described "Tupã" or "Tupan" as the name of the Tupinambá god of thunder, highest deity in Tupinambá mythology, making *Tupandactylus* mean "God of Thunder Finger". According to Candido and Nunes (2012), "Tupã" was not exactly a god on its own terms, but rather a manifestation of god, in the form of thunder: that god would be "*Nhanderuvucu*" and it is credited by Lurker (2004) as the true Tupinambá supreme deity. In that sense, "*Tupana*", meaning roaring blow or thump, is mentioned by Cascudo (1954) as the original term for the phenomenon of thunder, caused by "*Nhanderuvucu*", described at different times as a messenger or a demon. Jesuit evangelizers at the time may have mistranslated "*Tupana*" as an actual deity and, as evidenced by Dooley (1998), perhaps due to the Guaraní indirect influence, "*Tupana*" originated the term "Tupã" for god of thunder, or simply god, in the Mbyá dialect. Cascudo (1954) discussed that "Tupã" is nothing more than a work of catechism adaptation, for a word that already existed in concept as the sound of thunder, an unknown and therefore feared phenomenon, for the South America indigenous people, both by the Tupinambá and the Guaraní. Thus, with "Tupã" or "Tupan" derivating from "*Tupana*", which means thunder, *Tupandactylus* would actually mean "Thunder Finger".

Diagnosis: According to Campos and Kellner (1997), Frey, Martill and Buchy (2003b), Kellner and Campos (2007) and Pinheiro *et al.* (2011): tapejarid with a very large nasoantorbital fenestra, comprising more than 45% of the skull preserved length, excluding cranial crests; premaxillomaxilla rostrum downturned or turned ventrally; huge and high cranial crest, composed by a subtriangular bone blade and extensive soft tissue area; premaxillary crest with anterodorsal and thin suprapremaxillary process; premaxilla posterior extension articulates with the nasal and

frontoparietal. Pinheiro *et al.* (2011) listed, as *T. imperator* autapomorphies, a very deep rounded mandibular crest with a steep anterior margin, forming an ~60° angle with the mandible, together with a small dorsal concavity at the symphysis turned ventrally. These characters could not be compared with *T. navigans*, since this taxon did not have preserved mandibles on the holotype or referred specimens. Since the discovery of specimen GP/2E 9266 (GIBNEY, 2014), these two characters can now be compared with *T. navigans*, being possible *Tupandactylus* synapomorphies.

Occurrence: Araripe Basin, Santana Group, Crato Formation, Brazil.

Lithology: Micritic laminated limestone.

Paleoenvironment: Shallow coastal lagoon with marine influences.

Period: Early Cretaceous.

Age: Aptian.

Comments: Both *Tupandactylus* species were originally described as two species in the genus *Tapejara*, with all three taxa presenting downturned upper jaws, nasoantorbital fenestra larger than half of the skull length and a high premaxillary crest, characters previously recognized as *Tapejara* synapomorphies. With the description of *Sinopterus* (WANG & ZHOU, 2003a), it was clear that most of *Tapejara* synapomorphies were actually synapomorphies of a more inclusive clade, including *Sinopterus* and all three supposed *Tapejara* species. This clade was labelled Tapejarinae by Kellner and Campos (2007), being defined as a stem-based clade with *Tapejara wellnhoferi* as an internal specifier and *Thalassodromeus sethi* as an external specifier. Andres, Clark and Xu (2014), performing a phylogenetic analysis, recovered a clade with the same composition being more early diverging than Neoazhdarchia, which included Thalassodromidae and Azhdarchidae. This clade was labelled Tapejaridae and defined as a node-based clade, with *Tapejara wellnhoferi* and *Sinopterus dongi* as internal specifiers. Although closely related to *Tapejara* and *Sinopterus*, not only both "*Tapejara*" *imperator* and "*Tapejara*" *navigans* present sufficient distinctions to be classified on distinct genera, but synapomorphies for both species indicate that they belong to the same genus (Figure F3.4.01). In 2007, two new genera were proposed to allocate "*Tapejara*" *imperator* and "*Tapejara*" *navigans*, with Kellner and Campos (2007) naming *Tupandactylus* and Unwin and Martill (2007) naming "*Ingridia*". *T. imperator* was erected as the type species for *Tupandactylus* and also "*Ingridia*", making them synonymous. Since Unwin and Martill (2007) is not a formal publication, being a book chapter, and also was published months after Kellner and Campos (2007), "*Ingridia*" became the junior synonym, thus, invalid.

Obviously the most outstanding feature about *Tupandactylus* is its cranial crest. Headcrests in pterosaurs are known and rather common, being valuable characters that have been defined as useful autapomorphies (BENNETT, 1994), although it has also resulted in species inflation

(BENNETT, 1994; WITTON, 2013; ZHANG *et al.*; 2019). Nevertheless, headcrests are vital for understanding both morphological and ecological specializations in pterosaurs. Headcrests are known since the very dawn of pterosaurs, with Triassic taxa such as *Austriadactylus* (DALLA VECCHIA *et al.*, 2002) and *Raeticodactylus* (STECHEER, 2008) preserving such structures. Since the first description of a *Tupandactylus* specimen (CAMPOS & KELLNER, 1997), concerns were raised regarding the exact function for a structure with such aberrant proportions. Campos and Kellner (1997) argued that counterbalance (BRAMWELL & WHITFIELD, 1974) and water stabilization (WELLNHOFER, 1987) seems unlikely, since the cranial crest begins at the most anterior limit of the skull. Campos and Kellner (1997) also argued that a long posterior occipital crest in *T. imperator* could be explained by a possible development of muscle attachment (EATON, 1910), but musculature anchoring alone could not explain why *T. imperator* has also a high crest. *Tupandactylus navigans* reinforces this conclusion, presenting a high crest without a posterior occipital crest, with a typical pterosaur occipital region. Pinheiro *et al.* (2011) suggested that *Tupandactylus* crests were important in social behavior, especially species recognition and sexual display. There is the possibility that these crests were multifunctional, similar to *Thalassodromeus* (KELLNER & CAMPOS, 2002; PÊGAS, COSTA & KELLNER, 2018), where in this taxon the crest also serves a thermoregulatory function. Finally, its sheer size indicates that these crests also resulted in aerodynamic interferences.

The most appealing function is species recognition and sexual display, as already suggested by Campos and Kellner (1997). *Tupandactylus* was the first taxon to suggest that other pterosaurs also have soft tissue crests with a similar function. As Pinheiro *et al.* (2011) suggested, headcrests in pterosaurs are rather common, with both morphologies and compositions being always variable between taxa, suggesting a link with a successful functional and/or reproductive strategy. Pterosaur neuroanatomy corroborates a sexual display function, since it indicates that pterosaurs were visually oriented (WITMER *et al.*, 2003). Sexual dimorphism has also corroborated this function, with *Pteranodon* (BENNETT, 1992) and *Hamipterus* (WANG *et al.*, 2014) presenting a possible crest in males, while females lack the structure or develop a smaller crest. Manzig *et al.* (2014) discussed, based on multiple specimens, that *Caiuajara* possibly had few to none crest variation between males and females, present in both sexes. However, as Pêgas, Costa and Kellner (2018) already pointed out, no complete specimens with crests were ever found, making it impossible to conclude if *Caiuajara* truly had perfectly equal crests for both males and females. Up to date, indeed, it is impossible to infer if any tapejarid is represented by males or females, including *Tupandactylus*. Considering that both males and females displayed headcrests, mutual sexual selection (KNELL *et*

al., 2013a) can be considered, aligned together with species recognition (MENDELSON & SHAW, 2012; PADIAN & HORNER, 2011). While the concept of species recognition is still a topic of interest under debate (PADIAN & HORNER, 2013; MENDELSON & SHAW, 2013; KNELL *et al.*, 2013b), all studies agree that discovering the function of such extravagant and specialized features, like headcrests, is challenging in view of the small and fragmentary sample size, normally available for studies with fossil taxa. Nevertheless, all studies regarding *Tupandactylus* agree that a headcrest this big is likely related to species recognition and sexual display.

Aside from any specific function, there seems to be little doubts about the aerodynamic nature and influence of the headcrests in *Tupandactylus*. Campos and Kellner (1997) discussed that the crests could have aerodynamic influence as a secondary function, improving maneuverability, but it was concluded that the crest usage as a rudder or airbrake is unknown and virtually impractical to test. Frey, Martill and Buchy (2003b) proposed that a self-adjustment rudder system was actually the main function for the crests, where turns of the head at low flight speeds would automatically readjust into the wind direction, similar to a weather vane. Experimental data corroborating this hypothesis, according to Pinheiro *et al.* (2011), are still unpublished. Chatterjee and Templin (2012), using a digital model of a *Tapejara* with a *T. imperator* soft tissue crest, performed simulations and concluded that tapejarids with a crest as large as *T. imperator* have indeed aerodynamic influence, as a rudder for fast turns or mediate flight control (Figure F3.4.02). Although a big headcrest in *Tupandactylus* and *Thalassodromeus* may result in aerodynamic interferences, considering that crests in pterosaurs, including *Tupandactylus* and *Thalassodromeus*, are rather diverse and more likely related to a sexual display, the use of crests as frontal rudders seems unlikely.

A third function, usually proposed for taxa with large crests, is thermoregulation. Kellner (1989) was the first to propose a thermoregulatory function for cranial crests, since the premaxillary crest in *Tapejara* preserved blood vessels scars. Kellner and Campos (2002) also suggested this function for *Thalassodromeus*, where the holotype preserved the impressions of a very complex vascularization network that could dissipate excessive heat. Tomkins *et al.* (2010) challenged this view, based on the allometric development of *Pteranodon*, while Pêgas, Costa and Kellner (2018) corroborated the thermoregulatory function, based on living analogues such as the ramphastids (TATTERSALL, ANDRADE & ABE, 2009), and agreed with Kellner and Campos (2002) that the crest of *Thalassodromeus* was most likely multifunctional. Thermoregulation is a possible function for the crest in *Tupandactylus*, since it presents a large surface area that, if irrigated with blood vessels, could absorb or dissipate heat. Pinheiro *et al.* (2011) argued, however, that even if huge

crests could actually work as a structure for dissipating heat, this function would probably be better performed by the patagia. Up to date, no specimen of *Tupandactylus* have preserved blood vessels grooves on the crests, but Pinheiro *et al.* (2011) also argued that this may be a preservational bias, because of the lateral compression and flattening of the skulls, typical in the fossils from the Crato Formation. Thus, thermoregulatory function in *Tupandactylus* remains unknown.

***Tupandactylus imperator* Campos & Kellner, 1997.**

Holotype: MCT 1622-R, a complete skull with soft tissue, with missing elements preserved in a cotype counterslab, which also preserves different soft tissue elements.

Referred Specimens: SMNK PAL 2839, labelled here the German specimen, a skull with soft tissue and posterior lower jaw; a complete skull with soft tissue housed in a private collection, labelled here the Private specimen; CPCA 3590, labelled here the Crato specimen, a skull with soft tissue, preserved on a slab and counterslab, together with a virtually complete lower jaw.

Etymology: "Thunder Finger Emperor", from: Latin "*Imperator*", emperor.

Diagnosis: According to Pinheiro *et al.* (2011), which is a emended diagnosis of Campos and Kellner (1997) and Kellner and Campos (2007): *Tupandactylus* species with a length to height ratio, measured from the premaxilla tip to the posterior squamosal margin and from the quadrate condyle to the premaxilla dorsal margin, dorsal to the orbits, about 3.6; premaxilla anteriorly projected, with anteriorly projecting convex blade; suprapremaxillary process with posterodorsal orientation, with soft tissue crest composed by parallel subvertical fibers with posterodorsal curvature; presence of a posterior occipital process, extending beyond the posterior margin of the skull and reaching about the skull length, measured from the premaxilla tip to the posterior squamosal margin.

Comments: *Tupandactylus imperator* was revealed and named as a species by Campos and Kellner (1997). Not only it was the first tapejarid from the Crato Formation, but also the second pterosaur specimen ever described for the Crato Formation, with the first being *Arthurdactylus* (FREY & MARTILL, 1994). The holotype, MCT 1622-R, preserved a remarkably huge skull crest, comprising approximately 5/6 of the total lateral area of the skull (Figure F3.4.03). Up to date, this crest is possibly the largest of these soft tissue structures in fossil and recent vertebrates, while *Thalassodromeus* presents an equally huge crest, being possibly the biggest bony cranial crest (KELLNER & CAMPOS, 2002; PÊGAS, COSTA & KELLNER, 2018). The nasoantorbital fenestra is equally huge, being almost 60% of the skull length. Campos and Kellner (1997) was already the first study to discuss the possible functions of the crest, concluding that it was primarily for sexual display. The holotype preserved not only thin and fragile elements of the huge crest, but also soft tissue, which revealed for the first time the potential of the Crato Formation as a *Lagerstätte*. The

presence of a soft tissue crest in *T. imperator* opened the possibility for more pterosaurs to present such structures, which was later proven true (CZERKAS & JI, 2002; FREY *et al.*, 2003). Campos and Kellner (1997) described the holotype as having few to none sutures and regarded it as an adult.

The specimen MCT 1622-R was broken in half, with most of the skull preserved on the slab, described by Campos and Kellner (1997) as the holotype. Some elements were also preserved on the counterslab, including soft tissue. More than twenty years later, Campos and Kischlat (2020) briefly described this counterslab material, defining it as cotype (Figure F3.4.04) and revealing new discoveries preserved on the cotype. The parietal and the occipital crests seems fused, composing the posterior occipital process. A rhamphotheca, known from other *Tupandactylus* specimens, is beautifully preserved on the cotype. Although the nasal septum is known from *T. navigans* (FREY *et al.*, 2003), the cotype of *T. imperator* preserved it complete. With the soft tissue crest being also divided and preserved on both the holotype and cotype, Campos and Kischlat (2020) argued that few colored points may be possible preserved melanosomes, concluding that it is expected from the Crato Formation *Lagerstätte*. The articulation between the posterior extension of the premaxilla with the nasal and frontoparietal was not observed on the cotype, a feature observed on *Tapejara* and *Sinopterus*, but not on the holotype of *T. imperator*. Regarding the suprapremaxillary process, it was concluded that it may be an ossified keratinous structure, rather than a premaxillary extension. Aside from this novel information, Campos and Kischlat (2020) also discussed rather controversial interpretations. The holotype and cotype of *T. imperator* was regarded as a sub-adult, based on soft tissue preservation and taphonomy, while Campos and Kellner (1997) originally regarded it as an adult. While Wellnhofer and Kellner (1991) and every study regarding tapejarid diet concluded that tapejarids were herbivorous (MEIJER *et al.*, 2007; VULLO *et al.* 2012; PINHEIRO, LIPARINI & SCHULTZ, 2014a; 2014b; ZHOU *et al.*, 2017; HENDERSON, 2018; BESTWICK *et al.*, 2018), Campos and Kischlat (2020) inferred a scavenging diet to *T. imperator*, based on the nasoantorbital fenestra being huge and possibly associated with well developed olfactory systems, something observed on scavenging predators. This hypothesis has no further evidence or support.

Six years later, a second specimen was attributed to *T. imperator* by Frey *et al.* (2003). This article focused on beautifully preserved specimens of pterosaurs, with new data about the anatomy of soft tissues in many aspects, such as the beak evolution, wing structure, hands and feet webbing and possible sexual structures, especially cranial crests. For example, for the first time an entirely soft tissue crest was reported on a new *Pterodactylus* specimen. Frey *et al.* (2003) discussed the preservation and structure of headcrests on the holotype and referred specimen of *T. navigans*. To

give an example of preserved mineralized fibers alongside bone crests, however, a new specimen of *T. imperator* never before seen was illustrated, with focus exclusively on its occipital crest. The specimen was identified as SMNK PAL 2839, but sometimes it is designated SMNK PAL 3829 and, here, it is labelled the German specimen (Figure F3.4.05). Frey *et al.* (2003) never cared to make a proper description and, up to date, this specimen was never fully described or even prepared, only figured. Both Frey *et al.* (2003) and Frey, Martill and Buchy (2003b) tested and concluded that the main function of the crest is related to a self-adjustment rudder system. Experimental data regarding these tests reported, according to Pinheiro *et al.* (2011), remain unpublished. SMNK PAL 2839 has not only the skull, but also the posterior mandibular rami preserved, possibly both, together with the hyoid apparatus disarticulated but closely associated. Yet, Frey *et al.* (2003) and Unwin and Martill (2007) insisted to report that no material other than skulls were known for *T. imperator*.

The third specimen attributed to *T. imperator* was revealed four years after the second, by Unwin and Martill (2007). This book chapter is one of a series that discussed the Crato Formation geology, stratigraphy, taphonomy and a list of known specimens and described species. This book focused on listing and illustrating the specimens housed in German Museum collections, especially the SMNK, or housed in private collections. Unwin and Martill (2007) figured the specimens at private collections and the SMNK almost exclusively, with few MN specimens reported. Many discussions also performed rather simple redescription comparisons between specimens, with the purpose of questioning the validity of named species. An example is Unwin and Martill (2007) regarding the holotype of *Ludodactylus* as being too similar with *Brasileodactylus*, concluding that both may be the same taxon. In one such redescription, the name "*Ingridia*" is proposed to allocate *T. imperator* and *T. navigans*, the two tapejarids from the Crato Formation previously described as *Tapejara*. To illustrate "*Ingridia*" *imperator*, Unwin and Martill (2007) figured the specimen housed in a private collection, revealing it as the third specimen of *T. imperator* (Figure F3.4.06). This specimen, without collection number or locality, is labelled here the Private specimen. Up to date, it is the biggest specimen of *T. imperator* ever reported, being also the specimen with the best preserved skull and crests, especially bone crests. While this specimen was never described nor figured, some angle curvatures were presented by Martill *et al.* (2020a).

Campos and Kellner (1997), naming *T. imperator*, performed only a preliminary description of MCT 1622-R, focusing its autapomorphic features. Frey *et al.* (2003) did not care to describe SMNK PAL 2839 in detail, aside from its soft tissue crest. Unwin and Martill (2007), even worse, did not bother to describe anything of the private collection specimen, concerned only in figuring

it to discuss the name "*Ingridia*". Four years after the reveal of the Private specimen, the fourth and, up to date, last published specimen attributed to *T. imperator* was described and illustrated, by Pinheiro *et al.* (2011). After its original description, it took 14 years for *T. imperator* to receive the detailed description and scientific attention it truly deserved. The fourth specimen, CPCA 3590, labelled here the Crato specimen, has the least amount of cranial elements preserved, but not only it is the first specimen to preserve a complete lower jaw with a mandibular crest, but also it is the specimen with the best preserved soft tissue elements, including the crest (Figure F3.4.07). It is also the specimen with the most complete information regarding its stratigraphic context, provenance, discovery and collection. The lower jaw is virtually complete and the skull was likely complete, but during collection the occipital and temporal regions were lost. This specimen has preserved rhamphotheca, both in the upper and lower jaws, being a direct evidence of a horny beak in a toothless pterosaur. CPCA 3590 also has thin structures preserved on the ventral margin of the lower jaw, being possible pycnofibers. As in all specimens, CPCA 3590 has the dorsal margin of the premaxilla vertically striated, indicating mineralization of the fibers composing the soft tissue crest that were dorsally close to the skull bones. This specimen revealed that the crest in *T. imperator* was not a concave sail-shaped structure, but rather had a convex rounded shape. Finally, for the first time in a study focused on *T. imperator*, it was performed a phylogenetic analysis to test the relationships of *T. imperator* and *Tupandactylus* within Azhdarchoidea. While *Tupandactylus* was recovered monophyletic and closely related to *Tapejara*, thalassodromids and chaoyangopterids were recovered inside Tapejaridae, creating a ghost lineage of ten million years for every major azhdarchoid group, with the extreme of 60 million years for Azhdarchidae. These results were likely due to a small sample of characters and taxons, with only 22 characters coded in only 19 taxa. Surprisingly, according to Pinheiro *et al.* (2011) in a personal communication with an English paleontologist, there are at least two more *T. imperator* specimens, never described nor figured, housed in private collections. While one is mainly cranial material, the other has associated lower jaws that were informed as being complete.

Pinheiro *et al.* (2011) focused on describing the osteology, crest shape and phylogenetic position of the fourth known specimen, also revealing it as the specimen where the soft tissue elements are best preserved, such as the rhamphotheca and the cranial crest. These mineralized soft tissues were further studied in two more articles, up to date, regarding the composition of the soft tissue crest in *T. imperator* at its molecular level. Pinheiro *et al.* (2012) reported presumed evidence of bacterial autolithification for the Crato Formation, associated with CPCA 3590, replacing the soft tissue headcrest. The phosphatization is regarded as a phenomenon induced by bacteria (BRIGGS

et al., 1993), with geochemical gradients created by microbial decay (SAGEMANN *et al.*, 1999), crucial for deposition of phosphate minerals, being usually apatite (BRIGGS, 2003). Preservation of fossil soft tissue by microbial influence are usually defined in two categories. Authigenic mineral deposition is when decay, made by bacteria, generate chemical gradients that replicate soft tissue with minerals, a process well known from the Romualdo Formation with phosphate (MARTILL, 1989; MARTILL & UNWIN 1989). Bacteria autolithification is when bacteria, decomposing the tissue, fossilize maintaining its shape (RAFF *et al.*, 2008), being uncommon and unknown for the Crato Formation (VINTHER *et al.*, 2008). Dispersive X-ray analysis, or EDS analysis, indicated that the presumed bacteria, preserved as many microscopic granules on the crest, were replaced by phosphate minerals, being very distinct from the mineralization of surrounding areas. The granules presented a morphology and organization pattern consistent with granules observed in modern and fossilized bacteria biofilms (STOODLEY *et al.*, 2002; TOPORSKI *et al.*, 2002) with few evidences of bacteria fossilized during the process of cell division. Pinheiro *et al.* (2012) concluded that these granules, lacking a highly organized pattern, could not be regarded as melanosomes, since they are randomly distributed, forming dense aggregations, and that would constitute the first evidence of bacteria autolithification in a fossil from the Crato Formation. This conclusion would later be disproven, however (PINHEIRO *et al.*, 2019). Since bacterial autolithification is most prevalent where extensive anaerobic decay occurred (BRIGGS & KEAR, 1993; SAGEMANN *et al.*, 1999), it could have played a key role on soft-tissue preservation of the Crato Formation *Lagerstätte*.

Pinheiro *et al.* (2019) was the second study made possible with the soft tissue of CPCA 3590, with color inference in extinct taxa being challenged by the structure of the preserved melanosomes. Melanosomes are organelles bearing melanin, rather common in fossils with excellent preservation (COLLEARY *et al.*, 2015; VINTHER, 2015). According to Vinther (2015), preserved melanin allows the chemical identification and color inference of fossil taxa, since the melanosomes on living taxa have correlated morphology with the specific pigment content in the structures with melanin. Pinheiro *et al.* (2019) argued, however, that these inferences are tentative, because few to none analyses integrate the morphology of the fossil melanosomes with the chemical identification of the pigments. Thus, Pinheiro *et al.* (2019) used alkaline hydrogen peroxide oxidation, followed by a high performance liquid chromatography, to chemically characterize the melanin content of the soft tissue headcrest in CPCA 3590. This study revealed the unequivocal presence of eumelanin in the crest of *T. imperator*, but scanning electron microscopy, followed by statistical analyses, also revealed that preserved melanosomes with eumelanin are undistinguishable from organelles bearing pheomelanin on living taxa. Pinheiro *et al.* (2019) concluded, based on morphological and chemical

analyses, that the microbodies once regarded as bacteria autolithification, by Pinheiro *et al.* (2012), are actually melanosomes. Li *et al.* (2014) demonstrated that feathers and hair present a very high diversity on the morphologies of the melanosomes, making the correlation between morphotypes, melanin contained and expressed color very clear. A similar predictive model cannot be extrapolated to other amniotes, since the shift of the patterns would have been driven by distinct physiological shifts, together with the loss of the chromatophore complex, superfluous for taxa with expressed colors in developed integumentary structures such as feathers and fur. According to Li *et al.* (2014) and Pinheiro *et al.* (2019), pterosaurs are not consistent with the feather or hair color patterns.

Tupandactylus imperator, nevertheless, can be considered a valid genus and a valid species, distinguished from any other known pterosaur, being a taxon supported by cranial autapomorphic characters and its validity never being questioned up to date (Figure F3.4.08).

***Tupandactylus navigans* Frey, Martill & Buchy, 2003b.**

Holotype: SMNK PAL 2344, a complete skull with soft tissue.

Referred Specimens: SMNK PAL 2343, labelled here the Eroded specimen, an incomplete skull with soft tissue; GP/2E 9266, labelled here the Recovered specimen, a complete skeleton with skull and lower jaw, articulated and with preserved soft tissues.

Etymology: "Thunder Finger Navigator", from Latin "*Navigans*", to sail or navigate.

Diagnosis: According to Pinheiro *et al.* (2011), which is a emended diagnosis of Frey, Martill and Buchy (2003b) and Kellner and Campos (2007): *Tupandactylus* species with a length to height ratio, measured from the premaxilla tip to the posterior squamosal margin and from the quadrate condyle to the premaxilla dorsal margin, dorsal to the orbits, about 2.3; premaxilla straight, without anteriorly projecting convex blade; suprapremaxillary process with subvertical orientation, with soft tissue crest composed by parallel subvertical fibers with anterodorsal curvature; absence of a posterior occipital process, with the posterior extension of all dorsal cranial crests reaching the very limit of the posterior margin of the skull.

Comments: Six years after *T. imperator* was officially described, another species of *Tapejara* was described, which would later be attributed as the second species of *Tupandactylus*. In the same single publication, Frey, Martill and Buchy (2003b) described both the holotype and the referred specimen, labelled here the Eroded specimen, of *T. navigans*, both housed at the SMNK museum (Figure F3.4.09). It was the second tapejarid described from the Crato Formation. Frey, Martill and Buchy (2003b) reported that these specimens were obtained with commercial fossil dealers from the region. Similar to *T. imperator*, both specimens preserved most of the skull bones, together with a

soft tissue crest associated with the premaxilla. Not only the headcrests, both specimens preserved their rhamphotheca, a direct evidence of a horny beak, and many soft tissue elements that were regarded as a nasal septum by Frey, Martill and Buchy (2003b) and Frey *et al.* (2003), all described in more detail by Frey *et al.* (2003). Frey, Martill and Buchy (2003b) concluded that *T. navigans* differed from *T. imperator*, by comparison, because of its cranial crest shape, with the vertical orientation of the dorsal crest and without a posterior process, and this difference could not be regarded as ontogenetic stages, since both holotypes seem to be the same semaphoront (HENNIG, 1966). By comparison, *T. navigans*, at the time described as *Tapejara*, was regarded as being more similar to *Tapejara wellnhoferi* than to *T. imperator*, at least in the general outline of the skull. Just like Campos and Kellner (1997) did with the description of *T. imperator*, Frey, Martill and Buchy (2003b) also discussed possible functions for the crest. Frey, Martill and Buchy (2003b) and Frey *et al.* (2003) concluded that the crest main function was related to a self-adjustment rudder system, comparable to a boat sail for headwinds, hence the etymology for the name *T. navigans*, informing that this conclusion was reached with a digital model testing. Experimental data regarding this testing, according to Pinheiro *et al.* (2011), remain unpublished. Sexual display was taken into account, but it was regarded as a secondary function to a crest that was primarily responsible for aerodynamic functions. Unwin and Martill (2007) agreed with Campos and Kellner (1997) and Pinheiro *et al.* (2011) that the crest in *T. navigans* was mainly for a sexual display and species recognition, but also insisted that aerodynamic would be a secondary function. Both specimens of *T. navigans* described by Frey, Martill and Buchy (2003b) were originally figured by Martill and Frey (1998), where a preliminary description was performed. Frey and Tischlinger (2000) and Frey *et al.* (2003) would later describe in detail the crest preservation and overall structure of these specimens. Kellner and Campos (2007) named *Tupandactylus* and reallocated only *T. imperator*, while Unwin and Martill (2007) reallocated both species within the genus "*Ingridia*", effectively making *T. navigans* the second known *Tupandactylus* species.

Since its description, *T. navigans* had its validity questioned in some publications. Kellner and Campos (2007), naming *Tupandactylus*, reallocated only *T. imperator* to the new genus, arguing that *T. navigans* could not be valid and its phylogenetic position depends on closer examination and re-evaluation of the specimens. It was concluded that the absence of a posterior occipital crest could not be regarded as a valid character, because the referred specimen had this region broken and eroded, while the holotype could not be regarded as perfectly preserved since it also shows signs of eroding. If these specimens indeed lack the occipital crest, then *T. navigans* could be considered a valid species. Kellner and Campos (2007) also commented that Martill and Naish (2006) recovered

Tapejara paraphyletic, with *Sinopterus* closer to *Tapejara wellnhoferi* than *T. navigans*. Sayão (2007), reviewing all valid taxa from the Crato Formation, discussed that the four autapomorphies originally proposed for *T. navigans*, Frey, Martill and Buchy (2003b), could not be regarded as valid or exclusive. First, the anterodorsal estriation on the premaxillary crest, is present in *T. imperator*, making it a *Tupandactylus* synapomorphy. This character was regarded as autapomorphic by Frey, Martill and Buchy (2003b) because the condition in *T. imperator* was unknown and could not be compared, since the preliminary description by Campos & Kellner (1997), did not provide sufficient biometric data. Second, the postorbital or posterodorsal process of jugal twice as broad when compared to other species of *Tapejara*, was not discussed. Third, the suprapremaxillary spine anterior to the soft tissue crest and vertically oriented, was regarded as also present in *T. imperator*, making it also a *Tupandactylus* synapomorphy. Finally, the fourth character, the posterior extension of the premaxilla fused with nasal and frontoparietal, is indeed absent in *Tapejara* but it is present in *T. imperator*, making it another *Tupandactylus* synapomorphy. While Sayão (2007) considered that these two specimens of *T. navigans* are indeed tapejarids, thanks to a downturned rostrum and nasoantorbital fenestra very large, they were regarded as *Tapejara* sp. *indet.*, because the absence of a parietal crest differentiated these specimens from *Tapejara wellnhoferi* and *T. imperator*. Frey, Martill and Buchy (2003b) warned that both specimens were partially prepared before they reached the museum, in which Sayão (2007) discussed that this may explain all differences between these specimens and *T. imperator*, aside from its proportions. The referred specimen is broken at the postorbital and lost almost all of its crest, while the holotype possibly had its crest carved out, together with the slab ending where it should be a parietal crest.

Pinheiro *et al.* (2011) focused on redescribing *T. imperator*, but also discussed that most of the skull of the holotype of *T. navigans* was preserved and included the neurocranium, together with the posterior portion of the skull, and that alone was sufficient to assume that *T. navigans* is a valid species that differs from *T. imperator* by its headcrest morphology, especially the posterior process. Pinheiro *et al.* (2011) agreed with Frey, Martill and Buchy (2003b) about the holotypes of both species of *Tupandactylus* being very close ontogenetic stages, which makes them comparable semaphoronts (HENNIG, 1966), thus they could not represent different ontogenetic stages of one single taxon, as in *Rhamphorhynchus* (BENNETT, 1995). However, Pinheiro *et al.* (2011) also questioned that, since all specimens attributed to *Tupandactylus* are only skulls, the possibility that they represent sexual dimorphism of a single species cannot be ruled out. That is because most characters that differ both species are restricted to the cranial crests, features presumed for sexual display and species recognition (BENNETT, 1992; CAMPOS & KELLNER, 1997; ELGIN *et al.*,

2008; KNELL *et al.*, 2013a; WANG *et al.*, 2014). Up to date, *T. navigans* can be redescribed in detail thanks to the latest find, the specimen GP/2E 9266, labelled here the Recovered specimen and attributed as the second referred specimen of *T. navigans* (Figure F3.4.10). While most specimens of *Tupandactylus* have their precedence unknown or uncertain, GP/2E 9266 has a long history, reported by Gibney (2014), regarding illegal fossil trade. This specimen, together with many others, was going to be scheduled for sale in another country if this scheme was not discovered in time. This case became an emblematic case for Brazil, with the fossils recovered and successfully dispatched to scientific institutions, including GP/2E 9266, the first and, up to date, only complete pterosaur from the Crato Formation ever reported. Now, it is currently under study and exposed at the museum of the Geosciences Institute, University of São Paulo, in a Araripe-based exposition.

There were few divergences regarding the phylogenetic position between both species of *Tupandactylus* relative to all other tapejarids. "*Tapejara*" *imperator* was coded and analyzed for the first time by Kellner (2003) and Unwin (2003), in the same volume where "*Tapejara*" *navigans* was officially described (FREY, MARTILL & BUCHY, 2003b; FREY *et al.*, 2003). Kellner (2003) recovered *Tapejara* monophyletic, with *Tapejara wellnhoferi* and "*Tapejara*" *imperator*, while Unwin (2003) coded both species as a single terminal. Since the description of *Darwinopterus* (LÜ *et al.*, 2010), *T. imperator* as *Tupandactylus* kept being recovered closely related with *Tapejara*. With the inclusion of *T. navigans*, phylogenetic analyses have been recovering *Tupandactylus* monophyletic (LONGRICH, MARTILL & ANDRES, 2018; PÊGAS, COSTA & KELLNER, 2018; LÜ *et al.*, 2017), with few exceptions. Usually, *Tapejara*, *Vectidraco*, *Bakonydraco* and *Europejara* are recovered closely related, composing Tapejarinae *sensu* Andres, Clark and Xu (2014). Andres (2010) and its updates always recovered *Tupandactylus* monophyletic, with only Andres (2010) naming it "*Ingridia*". Only three studies recovered *Tupandactylus* or *Tapejara* paraphyletic, being Martill and Naish (2006), with *Sinopterus* closer to *Tapejara wellnhoferi* than "*Tapejara*" *navigans*, Vidovic and Martill (2014), with *T. imperator* closer to *Tapejara* while *T. navigans* was closer to *Caupedactylus*, and Vidovic and Martill (2017), with *T. navigans* monophyletic with *Tapejara*. It is generally accepted that *Tupandactylus* is monophyletic, with two valid species, and both specimens GP/2E 9266 (Figure F3.4.11) and MZSP-PV 1249 may help elucidate this issue.

4. MATERIALS AND METHODS

4.1. Studied Material

The specimen studied and labelled here the São Paulo specimen is housed under the number MZSP-PV 1249 (Figure F4.1.01) at the Paleontology collection on the Museum of Zoology of the University of São Paulo, where it was also prepared and described. It consists of the osteological remains of a single *Tupandactylus imperator* specimen, with an almost complete skull and postcranial skeleton. The specimen was collected in calcareous sediments from the Crato Formation, Araripe Basin, southern portion of the state of Ceará, bordering the states of Pernambuco and Piauí, northeast Brazil, under documented approval and legal procedures. The specimen preserves a skull, mandible, axial series and both girdles with associated limbs, presenting enough information for osteological description, identification and phylogenetic positioning. Considering the specimen provenance, it represents an extinct species that originally existed at the Early Cretaceous period, specifically the Aptian age. The Crato Formation is considered of Latest Aptian age as a consensus (NEUMANN, 1999; HEIMHOFER & HOCHULI, 2010; SANTOS *et al.*, 2015; FABIN *et al.*, 2018; Melo *et al.*, 2020), but other studies suggested distinct ages such as a transitional age from the Aptian to the Albian (VALENÇA, NEUMANN & MABESOONE, 2003) or a Barremian age (Lúcio, Neto and Selby (2020). Nevertheless, the depositional environment that generated this fossil range from at least 130Ma to 110Ma.

4.2. Preparation and Description

For this study, only techniques of mechanical preparation were applied, where the sediment was removed manually. Preparation was performed with aircsribes, needles of different sizes and an abrasive air system, in addition to other tools for manual paleontological preparation. Since the specimen is buried within a limestone plate, the preparation occurred on one of the limestone sides. The specimen articulation suggests that many more details can be uncovered with a more extensive preparation on the reverse side of the limestone. Originally, this would be performed by immersing what is exposed of the specimen in CarboWax, a popular name for Polyethyleneglycol, and preparing the other side, cleaning completely the specimen from the rock matrix and leaving it on the new CarboWax matrix. A complex positioning and association of the bones, a risk of damages and, most of all, time constraints caused by the CoViD-19 outbreak hindered this next step and made it impossible to be performed. The protocols of preparation followed the methodologies for application and safety proposed by Chaney (1989), Sohl (1989), Palmer (1989) and May, Reser and Leiggi (1994). As a fossil consolidating to relocate any broken parts, we used a liquified adhesive based on cyanoacrylate Paraloid B-72, popularly known as acryloid. For the initial preparation, broken slabs were repaired back together with a stronger plastic resin. The set of tools and products for preparations are available at the Paleontology Laboratory of MZUSP, with preparations monitored by specialized technicians.

Once fully prepared, the specimen was subjected to a comparative morphological description, consulting other studies regarding pterosaurs formally published. The traditional terminology, or Romerian anatomical terminology, was used instead of the veterinary terms from the *Nomina Anatomica Veterinaria*, as proposed by Wilson (2006). For example, directional terms such as "anterior" and "posterior" were used instead of veterinary terms "cranial," "rostral," and "caudal". Measurements were taken with a digital caliper. For the comparative analysis and update of the morphological matrix, the specimen was photographed in detail with a Canon professional camera, model EOS 60D, with a tripod, a stand and external lighting. The camera was kept as far away as possible of the specimen, in order to avoid distortions related to the edges of the camera lens. The photos were taken with a scale, present on the figure unless otherwise noted. Exactly three photos were taken using a Macro lens, not on scale, due to structures in question being very small. Photos taken with a Macro lens are indicated. Figures were kept with a black background and the images were edited on the free software Krita v4.3.0.

4.3. Phylogenetic Analysis

Once MZSP-PV 1249 was fully described, an update of the codings for *Tupandactylus imperator* was performed, in the matrix of Longrich, Martill and Andres (2018). The updated matrix was then submitted to a phylogenetic analysis using the program TNT v1.5 (GOLOBOFF & CATALANO, 2016), in order to determine the phylogenetic relationships of *T. imperator* with other pterosaurs. Cladistics was applied as a methodology to test these relationships (HENNIG, 1966; NELSON & PLATNICK, 1991). Data was analyzed using the principle of parsimony (KLUGE & FARRIS, 1969; FARRIS, 1970) and the character states were polarized through comparisons with outgroups (FARRIS, 1982).

The original matrix of Longrich, Martill and Andres (2018) contains 271 morphological characters coded for 132 taxa, including 51 with continuous states and 220 with discrete states. In the modified version used here, whenever possible, continuous characters were rescored as discrete characters, following Garcia-Cruz and Sosa (2006), resulting in 356 characters with discrete states (Appendix B). 16 terminal taxa were added while 17 terminal taxa were excluded, resulting in 356 characters coded for 131 taxa (Appendix C). The matrix was edited with the program Mesquite v3.61 (MADDISON & MADDISON, 2019), being organized in twelve anatomical clusters of characters, grouped in three modules (Appendix B) for comparisons.

Taxa Selection

Four taxa were used as outgroups. The first taxon, used to root the analyses, is *Euparkeria*, a representative of the Pan-Archosauria. The following three taxa were also used as outgroups: *Ornithosuchus*, a representative of the Pan-Crocodylia, *Herrerasaurus*, a representative of the Pan-Aves, and *Scleromochlus*, a taxon recognized as a sister group of Pterosauria (PADIAN, 1984a; EZCURRA *et al.*, 2020). All remaining 111 taxa forming the internal group are valid species coded by Longrich, Martill and Andres (2018) and described as pterosaurs (Table T4.3.01). 16 terminal taxa were added, being valid species of pterosaurs, that were coded in the matrix of Wu, Zhou and Andres (2017), except for four taxa that were coded based on descriptions from the published literature, being *A. spielbergi*, *Aymberedactylus*, *Caupedactylus* and *Thalassodromeus oberlii*, in order to analyze the monophyly of *Anhanguera*, *Thalassodromeus* and the validity of *Aymberedactylus* and *Caupedactylus* as tapejarids (Table T4.3.02). 17 terminal taxa were excluded, because either their validity is questionable or no longer supported, such as *Piksi*, *Bennettazhia* and

both *A. santanae* and *A. araripensis*, or they represent indetermined specimens coded by Longrich, Martill and Andres (2018), such as Painten and the specimen OCP DEK-GE 716, or they represent valid species with very few characters coded, where preliminary analyses addind these taxa had no resolution, such as *Brasileodactylus*, *Vectidraco* and *Bakonydraco* (Table T4.3.03). Indetermined specimens coded by Wu, Zhou and Andres (2017) were not added. The exception to these rules is the terminal taxon *Sinopterus*, which was coded based on the coding provided by Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018), as well as information available from published literature, regarding *S. dongi*, "*S. gui*", "*S. jii*", *S. corollatus*, *S. benxiensis*, "*S. liui*", *S. lingyuanensis* and *S. atavismus*.

Some taxa had their coding revised, based on their original descriptions, indicating that Longrich, Martill and Andres (2018) coded them erroneously. For example, an absent notarium was coded for *A. piscator* Kellner and Tomida, 2000, even though Kellner and Tomida (2000) argued that this may be due to the holotype being a very young specimen and notaria being an ontogenetic character, fusing only on older specimens. In this case, the notarium was recoded as missing data. All revised coding were based on information reinterpreted from published literature, such as the postcranial characters being coded for *Tropeognathus* based on specimen MN 6594-V (KELLNER *et al.*, 2013). The exceptions to this rule were the three tapejarids where all characters were recoded based on direct observations of specimens attributed to these species, being: *Caiuajara*, reevaluated based on multiple specimens described by Manzig *et al.* (2014), *Tupandactylus imperator*, updated based on MZSP-PV 1249, the São Paulo specimen, and *Tupandactylus navigans*, updated based on GP/2E 9266, the Recovered specimen. Both specimens of *Tupandactylus* allowed the coding of postcranial characters for both taxa.

Character Argumentation

The structure for character states listing and coding follows the model proposed by Sereno (2007), which in turn was used by Andres (2010) to build a supermatrix with a sample of 182 characters. More characters were added along updates (ANDRES & MYERS, 2013; ANDRES, CLARK & XU, 2014; ZHOU *et al.*, 2017; WU, ZHOU & ANDRES, 2017), until Longrich, Martill and Andres (2018) updated the matrix to 271 characters. Multistate ordered characters, also known as additive coding, were used. Some discrete characters were not ordered, because these characters in particular do not present intermediate states in the coding. All ordered characters are indicated (Appendix B). Also, reductive coding was used, according to Maddison (1993), which is the same

of contingent coding (FOREY & KITCHING, 2000). The most common alternative for reductive or contingent characters is compound coding (STRONG & LIPSCOMB, 1999), however compound coding violates the character independence logic (COLLESS, 1985), the only necessary property of definition for characters (SERENO, 2007). For this reason, this coding was avoided.

One of the two main modifications on the matrix was adding new characters and taxa from other recently published analyses. After comparing Longrich, Martill and Andres (2018) matrix with the matrices of Pêgas, Costa and Kellner (2018), Lü *et al.* (2017) and Vidovic and Martill (2017), the four matrices were combined to create a new reference matrix for Pterosauria. All the overlapping characters present on all analyses were combined. New characters that were present on all matrices, but absent in Longrich, Martill and Andres (2018) were added to the revised matrix. Of all three analysis aside from Longrich, Martill and Andres (2018), Vidovic and Martill (2017) contributed the most with new characters for this combined matrix. Characters that needed reformulation were rewritten. Most of the changes were simply nomenclatural, but some had their coding revised and updated. Nomenclature modification and standardization proved necessary because each analysis used its particular nomenclature for the same structures or orientation. For example, "anterior" and "posterior" are used for orientation by Longrich, Martill and Andres (2018), while Pêgas, Costa and Kellner (2018) referred to as "cranial" and "caudal". Another example is the jugal process called "posterior" process by Longrich, Martill and Andres (2018) and "quadrate" process by Vidovic and Martill (2017). All ambiguous nomenclature was standardized with its synonyms on each and every character, using traditional or Romerian terms rather than the *Nomina Anatomica Veterinaria* terminology (WILSON, 2006). Finally, some new characters were deemed necessary to be created. That was because some characters on all analyses were vague. An example is teeth counting, a character that does not specify between upper and lower dentition, making it ambiguous and uniting taxa with different teeth counting on each jaws, but having the same total by combining upper and lower dentitions. When such characters were identified, they were decomposed into new characters.

Continuous Variation

The second main modification on the matrix was coding all linear morphometric characters as categoric qualitative characters. While phylogenetic analysis using parsimony relies on categoric characters that are qualitative in nature, quantitative characters are frequently used, being meristic, linear morphometrics or spatial landmarks (GOLOBOFF & CATALANO, 2016). Pterosauria have

been consistently defined by quantitative characters, for example Pterodactyloidea being defined as having the fourth metacarpal at least 80% as long as the humerus (ANDRES, 2010). Definitions like these made quantitative characters, especially continuous morphometric characters, crucial on pterosaur phylogenies and have been used frequently in cladistic analyses of the pterosaurs (KELLNER, 2003; UNWIN, 2003). Although continuous data are often disregarded or excluded, Goloboff, Mattoni and Quinteros (2006) and Wiens (2001) demonstrated that continuous characters, when coded and analyzed as such, present significant phylogenetic signal, strong enough that analyses with only continuous characters recovered trees similar to the ones with only qualitative characters. This coding avoids vague descriptions, such as "long" and "short", or coding such characters as categorical series, known as the arbitrary method of Garcia-Cruz and Sosa (2006), used by Kellner (2003), Unwin (2003) and their updates, where interval limits between character states were established, but with no succinct explanation for such demarcations. There is a risk of deleting informative variation within each state, which may not accurately reflect the magnitude of changes between series. Andres (2010) and all updates incorporated continuous variations as relative, quantitative continuous characters, with ratios between linear measurements. To reduce connectivity between characters, ratios were calculated comparing each bone, once, with elements with few or none relative variation in the same skeleton region, for example the humerus and the femur. This is consistent with previous analyses that used a similar coding. The advantage of such coding, besides eliminating subjectivity, is being able to use the same coding for meristic data, recovering very few trees and each and every node always having support. As of Longrich, Martill and Andres (2018), 51 characters were coded as continuous.

However, such coding also has its downsides. Andres (2010) and its updates never published the values of Consistency and Retention indexes, or even stability supports such as Bootstrap or Jackknife. When these are calculated, they reveal very low values and high instability, because of the continuous characters transforming in all and every node and taxa, hence the support on all nodes (pers. obs.). Some nodes and clades recovered based entirely on continuous data may also be suffering from allometric noise. Andres (2010), designing his main matrix, acknowledged studies that detected allometric variation within pterosaurs (BENNETT, 2001; JOUVE, 2001; CODORNIÚ & CHIAPPE, 2004). To solve this issue, Andres (2010) used the largest individual or a mean value of all individuals for coding. Three problems arise with this methodology. First, as Kellner and Tomida (2000) stated, the largest individual not necessarily is the oldest, but rather body growth is influenced by a number of non-ontogenetic variables, such as food availability, climate, competitions and individual variation, for example. In the same species, even in the same

population, it is possible to have smaller adults and larger juveniles, making it necessary to establish size-independent criteria for the recognition of the semaphoronts (HENNIG, 1966) in pterosaurs. Bennett (2001), for example, detected this variation on *Pteranodon*. Second, for the same reason, mean values may not be accurate, due to individual variation disturbing the data. Third and most important, many taxa are known solely from one or two semaphoronts only, such as the case of *A. piscator* Kellner & Tomida, 2000, a species known from a single juvenile specimen. Coding these taxa have only been possible by coding these specimens. With updates, such as Longrich, Martill and Andres (2018), more juvenile specimens were added with continuous characters, for example *Microtuban*, raising this allometric noise.

To avoid these issues, all 51 continuous characters were coded as qualitative data, following Garcia-Cruz and Sosa (2006). Works such as Goloboff, Mattoni and Quinteros (2006) and Wiens (2001) criticized this method for being arbitrary, indicating that this method is flawed and also not the best solution for continuous variation. Here, this method has been utilized because it establishes interval-determined spectres of variation. Mean values and standard deviations of quantitative data are coded inside each spectrum for each taxa. It is possible to code ranges of variation as continuous data, but dozens of specimens are necessary for such coding, virtually impossible for all taxa on a mainly fossil matrix. The logic behind each character coding was using the same interval for each state, while observing how each measure varies within pterosaurs, to make the so-called arbitrary coding choices as minimum as possible. Also, with this coding, these characters states maintain the same weight as all others. Although continuous characters coded and analyzed as such are the safest treatment for continuous data, it is only safe to apply them on extant taxa, so their use on matrices based entirely on fossil taxa must be discouraged.

Character Weighting

The dataset was analyzed with two distinct weighting parameters. The first analysis was with the characters equally weighted, with parameters being similar to those used by Longrich, Martill and Andres (2018), for a direct comparison. The second analysis was with a preliminary weighting against homoplasies, applying the implied weight principle proposed by Goloboff (1993), for direct comparison with the equally weighted analysis. Weighting against homoplasies, as discussed by many studies (FARRIS, 1983; CARPENTER, 1988; CARPENTER *et al.*, 1993; GOLOBOFF, 1993; CARPENTER, 1994; GOLOBOFF, 1997; GOLOBOFF *et al.*, 2008; GOLOBOFF, 2013), is when the characters have their weight estimated based on the data itself and during the analysis,

searching for the cladistic congruence, concordance or reliability between the character states and the most parsimonious trees. The higher the cladistic congruence, the higher the weight, while the higher the homoplasy degree, the lower the weight. Considering that some characters will always present convergence or reversal, even on an equally weighted analysis, an analysis with weighting against homoplasies will always favor the characters with higher cladistic congruence over characters with higher homoplasy degree. This is in agreement with the parsimony principle (GOLOBOFF, 1997), where the analysis seeks trees by minimizing homoplasies. Thus, weighting against homoplasies informs not only characters overall distribution on the trees, but also their cladistic congruence with said trees, an information that is disregarded on an equally weighted analysis. Also, while an equally weighted analysis imposes that all characters necessarily will have the same weight, weighting against homoplasies allows different characters to have different weights, allowing access of phylogenetic relevance for each character, making them have weights proportional to their respective levels of cladistic congruence.

The first attempt for implementing weighting against homoplasies in cladistics is from Farris (1969). Since then, methodologies have improved with discussions (FARRIS, 1983; CARPENTER, 1988; CARPENTER *et al.*, 1993; GOLOBOFF, 1993; CARPENTER, 1994; GOLOBOFF, 1997; GOLOBOFF *et al.*, 2008; GOLOBOFF, 2013) and while it has been criticized (MADDISON, DONOGHUE & MADDISON, 1984; SWOFFORD & OLSEN, 1990; KLUGE, 1997), all criticism was countered (FARRIS, 1983; CARPENTER, 1988; CARPENTER *et al.*, 1993; GOLOBOFF, 1993; CARPENTER, 1994; GOLOBOFF, 1997; GOLOBOFF *et al.*, 2008; GOLOBOFF, 2013). Up to date, weighting against homoplasies by implied weighting can be applied, on TNT v1.5 program (GOLOBOFF & CATALANO, 2016), by the command "piwe". With this command, a "k" constant value is applied for the analysis. Goloboff (1993) concluded that weighting with the constant value being equivalent to the Consistency index value, being one, is excessive. Goloboff, Torres and Arias (2017) in turn concluded that higher constant values tend to be the best suited for larger matrices, such as Longrich, Martill and Andres (2018), Vidovic and Martill (2017) and this study. Since there is no ideal "k" constant value established, multiple "k" constant values must be tested, followed by a sensibility analysis, which is a comparative analysis of the results, to find the ideal value for the specific matrix and analysis, as proposed by Wheeler (1995) and Prendini (2000). This method compares the results of many "k" constant values, allowing a more in-depth analysis of the stability and similarity of the clades obtained under different parameters. Since the implied weighting analysis performed here is preliminary, however, only one "k" constant value was applied, being one, the equivalent to the Consistency index value (GOLOBOFF, 1993). The implied weighted

analysis, with "k" constant value of one, was performed only for comparisons with the results of the equally weighted analysis made by Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017), Longrich, Martill and Andres (2018) and this study, thus finding the ideal "k" constant value was not the focus of this study.

Exhaustive searches

The matrix was submitted to a traditional parsimony analysis, through heuristic searches of Wagner Trees, in both equally weighted and implied weighted analysis. By applying the command "hold 50000", the program was able to save a total of 50.000 different most parsimonious trees. By applying the command "rseed 0", a value of zero was assigned to the random seed initial trees. In addition to assigning a random seed, the command "rseed [" made the insertions of the sequences in Wagner's Trees random. The analysis were configured with 5000 replications, saving up to 10 trees in each replication. If the analysis reached a value greater than 100 replicates where the most parsimonious solution was found, it could be concluded that the heuristic searches were sufficiently exhaustive. By applying the command "collapse auto", the program did not support branches with ambiguous support, thus all branches with a minimum length of zero were collapsed, automatically collapsing said branches, following Andres (2010). Once the most parsimonious trees were found, a strict consensus was applied using the command "nelsen". Then, a sequence of two commands were applied to execute the IterPCR algorithm, where unstable taxa are pruned and a reduced strict consensus is applied (POL & ESCAPA, 2009), being "pcr.>0" and "nelsen//{0}". The IterPCR algorithm reveals unstable taxa and all their possible positions.

Indexes And Stability

Three procedures were performed to calculate indexes and stability measures for the analysis. First, after each analysis, a script called "STATS.run" was applied. It makes the program calculate two indexes, the consistency and retention indexes (FARRIS, 1989), that measure the homoplasy degree of a matrix, a character or a tree. The indexes are specific to each matrix and indicate the characters congruence degree with the trees. The other two procedures apply two stability measures of similar branches, resample by Bootstrap (FELSENSTEIN, 1985) and Jackknife (FARRIS *et al.*, 1996). These analysis were performed by applying the command "resample boot rep 1000 freq", for the Bootstrap, and "resample jak rep 1000 freq", for the Jackknife. In both cases, a total of a thousand replicates have been defined for the analyses.

5. GEOLOGICAL SETTINGS

5.1. Araripe Basin and Crato Formation Lithology

In Brazil, most specimens of pterosaurs found, as well as species formally described, came from the Araripe Basin, although pterosaurs have been discovered in other formations, such as *Caiuajara*, known from the Goio-Erê Formation (MANZIG *et al.*, 2014). The Araripe Basin, quite possibly, is the most complex of all basins in Northeast Brazil (ASSINE, 1992). It extends through the states of Piauí, Pernambuco and almost the entire southern portion of Ceará. According to Assine (2007), the events associated with the opening of the Atlantic Ocean, resulting in the separation of the Gondwana into the continents of South America and Africa, acted in different ways in Northeast Brazil. The Araripe Basin, with many formations resulting from this event, is also the one with the most complex geological history in Northeast Brazil. Each sequence was formed during different paleogeographic contexts, integrated with all adjacent basins (Figure F5.1.01). The Araripe Basin has its geomorphology characterized by the Chapada do Araripe, a huge elongated plateau, limited by erosive and steep escarpments. Among the formations of the Araripe Basin that compose this plateau, the Cretaceous sequences range from the Aptian age, ~125 My, all the way up to the Cenomanian age, ~90 My, being mainly the post-rift sequences.

The Araripe Basin lithostratigraphy have been established since Beurlen (1962; 1963), while the identification of the units was performed since Small (1913), where 850 meters of sedimentary thickness were estimated in at least four, possibly five, sedimentary units that could be regarded as formations. Many studies, regarding stratigraphy proposals, suggested names and ranking for these units and subunits. Some publications proposed few, almost minimal, changes related to the nomenclature, with the Lower Cretaceous unit, regarded as Santana calcareous by Small (1913), being named the Santana Fomation (MORAES, BARROS & RAMOS, 1962; BARROS, 1963; GASPARY & ANJOS, 1964; BRAUN, 1966). Other works regarded some units as members of key formations, with the Lower Cretaceous unit presenting the Crato and Romualdo members of the Santana Fomation (SILVA-SANTOS & VALENÇA, 1968; BEURLEN, 1971; MABESOONE & TINOCO, 1973; MORAES, SANTOS & MASCARENHAS, 1976; LIMA, 1978; 1979). Most of the stratigraphy conceptions were outlined when the Araripe Basin was heavily researched, aimed at petroleum potential. For this reason, several conflicting nomenclatures were proposed for each sequence (SILVA, 1983; 1986a; 1986b; BERTHOU, 1990; BRITO-NEVES, 1990; ASSINE, 1990; PONTE & APPI, 1990; ASSINE, 1992; 1994; 2007). The majority of the studies were based only

on surface data. More recent nomenclatures regarded some units as formations of key groups, with the Lower Cretaceous unit presenting the Crato and Romualdo formations of the Santana Group (MARTILL & WILBY, 1993; NEUMANN & CABRERA, 1999; VALENÇA, NEUMANN & MABESOONE, 2003). Few studies proposed entirely new names and new rankings (BERTHOU, 1994; BERTHOU *et al.*, 1994), but these are rarely used. This lack of consensus on the hierarchy and nomenclature of the units reflects the complex structure of the basin. Here, it will be utilized the nomenclature proposed by Valença, Neumann and Mabesoone (2003), which is an update of Neumann and Cabrera (1999), where the units of Crato, Ipubi and Romualdo are regarded as formations of the Santana Group. Regardless of the nomenclature utilized, there is a consensus regarding how many sequences are recognized in the Araripe Basin as a whole, as well as which sequences and their overall compositions.

The Aptian-Albian sequence of the Araripe Basin records the beginning of the post-separation stage of the continents, resulting from a thermal flexural subsidence. Composed by the Rio Da Batateira, Crato, Ipubi and Romualdo formations, this sequence occurs all around the basalmost portion of the plateau. Although the Ipubi Formation is usually recognized, few works such as Assine (1992; 2007) questioned its validity and synonymized it as the Romualdo Inferior Member. The oldest formation of the Cretaceous sequence that composes the Santana Group is the Rio da Batateira Formation, named Barbalha Formation by Assine (1992; 2007), defined by sandstones interspersed with shales and fine conglomerate levels. The first lake system of the basin is marked by few layers of bituminous shales with carbonate sheets. A second fluvial sedimentary cycle overlaps these lake layers, forming an erosive contact with them (NEUMANN & CABRERA, 1999; ASSINE, 2007). The dark shales of the Rio da Batateira Formation presents an expressive amount of fossils (ASSINE, 1992). Over the Rio da Batateira Formation lies the micritic limestones of the Crato Formation, which form laminated and laterally discontinuous layers (ASSINE, 2007), interdigitated laterally with green shales (Figure F5.1.02). Fossiliferous association indicates that the sedimentation occurred on a lacustrine environment, with strong seasonal cycles under considerably hot and dry conditions. The upper-most top of the Crato Formation is marked by erosive discontinuity, characterizing discontinuous layers of gypsum, in association with green and black shales. This gypsum defines the Ipubi Formation, of primary laminated forms, with columnar crystals, and also secondary laminated forms, represented as alabaster or selenite. Heimhofer and Martill (2007) divided the Crato Formation into four distinct members. The lower-most is named the Nova Olinda Member, characterized by thick packs of laminated biomicritic limestone. Above it is defined as the Caldas Member, formed by silt and clay, fine to medium sandstones and thin sheets

of limestone. The Jamaru Member would be similar to the Nova Olinda Member, while the uppermost unit is formed by black shales and sandstones, intercalated with clay. This unit was called the Casa De Pedra Member by Heimhofer and Martill (2007). The depositional environment proposed for the Crato Formation would be of calm waters, with such inference based on laminated meters without signs of disturbances, such as wave marks or evidences indicating currents or water flows (MABESOONE & TINOCO, 1973). The absence of bioturbation signs, such as scavenging scars on fossils of partially eaten bones, are strong indications that deeper waters were anoxic, while the presence of halite pseudomorphs serve as evidence of hypersalinity episodes (HEIMHOFER & MARTILL, 2007). Such conditions were crucial for preservation of articulated vertebrate remains, common in these laminated limestones, since it is not a favorable environment for scavengers.

For the fossils discovered from the Crato Formation, the mechanical preparation is usually enough for a complete preparation and elimination of the rock matrix with precision and safety. Different preparation techniques have been proposed and used to remove the rock matrix that surrounds fossil specimens. This is due to different rocks presenting varied lithological structures and constitutions, for example each proposed member of the Crato Formation (HEIMHOFER & MARTILL, 2007). Also, each fossil has its unique composition, resulting in multiple preparation techniques for every particular scenario. While some cases present a matrix too hard for purely mechanical preparation (RIXON, 1976), for example the limestone concretions from the Romualdo Formation, the Crato Formation laminated limestones are usually not as rigid.

Although the Santana Group is regarded as a Lower Cretaceous sequence, from the Aptian up to the Albian, another lack of consensus is regarding the specific age for each unit. The consensus is the Crato Formation being regarded as Latest Aptian (HEIMHOFER & HOCHULI, 2010), while the Romualdo Formation is regarded as Early Albian and the Ipubi Formation, being the very limit of the Aptian and the Albian, considered a transitional moment (NEUMANN, 1999; SANTOS *et al.*, 2015; FABIN *et al.*, 2018). Valença, Neumann and Mabesoone (2003) is an example of study that pushes up these ages, with the Crato Formation being the transitional moment and both the Ipubi and Romualdo formations encompassed at the Albian. More recently, Melo *et al.* (2020) became an example of study that challenged these ages, using biostratigraphic and palaeoecological data of foraminifera, ostracods and microfacies, to pull down these ages, with both Crato and Ipubi formations encompassed at the Aptian and the Romualdo Formation being the transitional moment, or at least portions of the Romualdo Formation, occurring at the Alagoas Stage locality, being constrained at the Aptian. Lúcio, Neto and Selby (2020) pulled even further, with the Ipubi

Formation being regarded as a transitional moment, but from the Barremian to the Aptian. These exact ages being far from resolved is one of the many reasons, as discussed by Cheng *et al.* (2020), for putative dispersion events of the tapejarids being tentative, together with taxa absence bias in Africa and Europe (WELLNHOFER & BUFFETAUT, 1999; VULLO *et al.*, 2012; MARTILL *et al.*, 2020a) and the relationships of the Tapejaridae also being far from resolved (KELLNER *et al.*, 2019). Nevertheless, it is safe to assume that most tapejarids existed during the Early Cretaceous.

The lacustrine systems that originated the Crato Formation, and influenced on the creation of all other formations of the Santana Group, represents the marine transgression on the Albian, facilitated by the subsidence continuity and the global rise of the sea levels, all reaching the interior of Northeast Brazil. Paleogeographic reconstructions of this temporal interval are controversial, as discussed by Assine (2007), since marine inflows have already been suggested from the basins of Sergipe-Alagoas, Potiguar and Parnaíba. Based on the assumption that the river paleocurrents of the Rio Da Batateira and Marizal formations indicate a continental paleodrainage to the south and southeast, the most natural path for incursion would be exactly in the opposite direction to the paleodrainage, therefore, from the south and southeast to the north and northwest. Thus, the Aptian-Albian sequence reveals a transgressive-regressive cycle, reflecting the thermal subsidence and the global eustatic events of rising sea levels, which created an accommodation space for deposition and preservation of marine deposits in the interior of Northeast Brazil. It is an almost complete cycle, truncated at the top, because it is lacking the alluvial rocks resulting from the offshore systems at the end of the cycle.

5.2. Crato Formation Biota

The fossils discovered at the Araripe Basin have excellent preservation degree not only for pterosaurs, but for several groups (MAISEY, 1991). While some have relatively low diversity, such as dinosaurs, others have enormous diversity, in addition to pterosaurs, such as insects and bony fishes. The vast majority of the discovered specimens are from the Crato and Romualdo formations, where the preservation degrees differs radically. The fossils from the Crato Formation are usually compressed, in laminated micritic limestones, preserving hard elements and soft tissue alike, as in *Tupandactylus*, while the fossils from the Romualdo Formation are usually tridimensional and uncrushed, in carbonate concretions, preserving bone or hard mineralized elements, as in *Tapejara*, although specimens with soft tissue are known (CAMPOS, LIGABUE & TAQUET, 1984).

According to Maisey (1991), the first time, in history, that fossils were reported from the Araripe Basin, at least in a formal publication, dates back to Spix and Martius (1823-1831). In 1817, the King of Bavaria arranged for the two members of the Munich Sciences Academy, von Spix and von Martius, to accompany Brazilian philosophers and natural historians in an Austrian delegation for studies all over Brazil (MAISEY, 1991). In addition to the reports of the limestone formations at the Araripe Basin, Spix and Martius (1828) reported the presence of multiple fossil fishes, many of them well preserved. Their work presented an illustration of a *Rhacolepis* in a limestone concretion (SPIX & MARTIUS, 1831), the very first illustration of a fossil from Brazil (Figure F5.2.01). The very first report, however, dates back to a letter sent from João da Silva Feijó, in 1800, regarding fish specimens sent to Portugal and remaining there, in scientific collections, up to date (PINHEIRO & FERNANDES-FERREIRA, 2014). Alongside fish records, Spix and Martius (1823-1831) reported that few elements poorly preserved may represent a fossil snake, which sparked discussion and started searches for fossils in the Araripe Basin, especially for possible squamate specimens from the Mesozoic (MAISEY, 1991).

The presence of pterosaurs in sedimentary basins from Brazil were announced many years later. The first alleged reports are from Woodward (1891a, 1891b, 1896), with the description of quadrates recovered from the Recôncavo Basin, Bahia. Attributed to pterosaurs, they were regarded as the largest pterosaurs ever described. Mawson and Woodward (1907), Price (1953) and Rodrigues and Kellner (2010) reevaluated these quadrates, based on new taxa from Brazil, and reallocated to *Mawsonia*, a taxon of Coelacanthiformes. Mawson and Woodward (1907), however, also briefly reported a single tooth from the Recôncavo Basin. Price (1953) claimed that if this tooth

was indeed from a pterosaur, it would have been thoughtfully described. Rodrigues and Kellner (2010), also reevaluating this tooth, concluded that it indeed belongs to a Ornithocheirae pterosaur, a typical clade from the Early Cretaceous, confirming that this tooth is the first pterosaur material recovered from Brazil, South America and all countries from the entire Southern Hemisphere. While this single tooth was the first specimen, Price (1953; 1971) named the first species. The first named pterosaur species for Brazil and South America was *Nyctosaurus lamegoi*, by Price (1953), based on a single humerus from the Gramame Formation, Paraíba (Figure F5.2.02). This species, up to date, is considered valid and has shown many similarities with some recently described Morocco specimens (LONGRICH, MARTILL & ANDRES, 2018). Almost 20 years after that, Price (1971) described a limestone concretion with elements from a wing, recovered from the Romualdo Formation, and named "*Araripesaurus castilhoi*". Even though this species is not currently valid since Kellner and Tomida (2000), it still remains as the very first pterosaur specimen recovered from the Araripe Basin that was formally published.

After these discoveries, countless fossils of pterosaurs were discovered in Brazilian deposits from the Cretaceous, the vast majority coming from sediments of the Santana Group. Since Price (1971), the Romualdo Formation has been, historically, the main formation of the Santana Group studied for its fossiliferous potential. Over the years, many specimens were discovered and species described. Descriptions listed, but not limited to, as follows: "*Araripedactylus*" (WELLNHOFER, 1977), "*Santanadactylus*" (BUISONJÉ, 1980), *Brasileodactylus* (KELLNER, 1984), the first soft tissue preserved in a pterosaur from the Santana Group (CAMPOS, LIGABUE & TAQUET, 1984), *Anhanguera blittersdorffi* and the proposition of Anhangueridae (CAMPOS & KELLNER, 1985), *Cearadactylus* (LEONARDI & BORGOMANERO, 1985), the entire osteology of the Anhangueria described in detail, based on multiple specimens (WELLNHOFER, 1985; 1991), *Tropeognathus* (WELLNHOFER, 1987), many reallocations for "*Santanadactylus*" (BENNETT, 1989a; 1994; KELLNER, 1995), hindlimb bones with a pelvis (BENNETT, 1990), "*Cearadactylus*" *ligabuei* (DALLA VECCHIA, 1993), the braincases of both *Anhanguera* and *Tapejara* (KELLNER, 1996a), *Anhanguera piscator* and the revision of Anhangueria *sensu* Rodrigues and Kellner (2013), as well as propositions for ontogeny and pathology (KELLNER & TOMIDA, 2000), a toothed rostrum (FASTNACHT, 2001), lists of specimens housed in museums (VELDMEIJER, 2002), *Anhanguera spielbergi* (VELDMEIJER, 2003), tarsal bones of *Anhanguera* and *Tapejara* (KELLNER, 2004b), lower jaw fragments of *Anhanguera* and *Thalassodromeus* (VELDMEIJER, SIGNORE & MEIJER, 2005), possible specimens of *Brasileodactylus* (VELDMEIJER, MEIJER & SIGNORE, 2009), the redescription of *Cearadactylus* (VILA NOVA, KELLNER & SAYÃO, 2010; VILA NOVA *et al.*,

2014), wing elements discovered in a controlled excavation (VILA NOVA *et al.*, 2011), possibly the largest Gondwana pterosaur (KELLNER *et al.*, 2013), *Maaradactylus* (BANTIM *et al.*, 2014), the redescription of *Anhanguera* (PINHEIRO & RODRIGUES, 2017) and many, many more. There were also specimens and species of non-Anhangueria pterosaurs described, including the following: *Tupuxuara longicristatus* (KELLNER & CAMPOS, 1988), *Tapejara* and the original proposition of Tapejaridae (KELLNER, 1989), a whole skull of *Tapejara* described with new referred specimens (WELLNHOFER & KELLNER, 1991), *Tupuxuara leonardii* (KELLNER & CAMPOS, 1994), the original description of *Thalassodromeus* (KELLNER & CAMPOS, 2002), a fragmentary skull of *Tupuxuara* (MARTILL & WITTON, 2008), *Lacusovagus* (WITTON, 2008), "*Tupuxuara deliradamus*" (WITTON, 2009), *Caupedactylus* (KELLNER, 2013), an indetermined cervical series (LEAL *et al.*, 2017), the redescription of *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018) and many others. Countless studies were published regarding the fossil specimens from the Araripe Basin, regarding not only pterosaurs, but many other groups (MAISEY, 1991).

Studies with pterosaurs worldwide were heavily influenced by the specimens from the Araripe Basin, especially the Romualdo Formation. Examples as follows: Wellnhofer (1988) was one of the first studies regarding biomechanics in pterosaurs, with an anhanguerid pelvis. Martill and Unwin (1989) performed one of the first histological studies, with all its conclusions refuted by Kellner (1996b). Hazlehurst and Rayner (1992) performed equivocal tests of biomechanics and concluded that "*Santanadactylus*" could not perform powered fly. Frey, Buchy and Martill (2003) analyzed the pectoral girdle articulation of tapejarids. Sayão (2003) performed histological analyses in specimens of both Romualdo and Crato formations. Witmer *et al.* (2003) used a braincase of an *Anhanguera* for paleoneurological studies of the pterosaurs. Chatterjee and Templin (2004) included species from the Romualdo Formation in a major biomechanical study. Martill and Naish (2006) revised *Tupuxuara*, with all its conclusions refuted by Kellner and Campos (2007). Wilkinson, Unwin and Ellington (2006) used *Anhanguera* as a model to discuss the pteroid function. Fastnacht (2007) studied patterns of dental substitution using an anhanguerid fossil from the Romualdo Formation. Humphries *et al.* (2007) performed biomechanical studies to refute the proposal of Kellner and Campos (2002) that *Thalassodromeus* was adapted to skimming. Claessens, O'Connor and Unwin (2009) modeled air sacs position using specimens of *Anhanguera*. Vila Nova and Sayão (2012) delimited wing disparity and size patterns between the two main groups of pterosaurs from the Santana Group, anhanguerids and tapejarids. Costa, Rocha-Barbosa and Kellner (2013) reanalyzed gait and posture on land, using complete specimens of *Anhanguera* for a biomechanical study of the optimal stance. Bantim, Saraiva and Sayão (2014) re-evaluated the variation and shapes of the skull

and premaxillary crest growth in anhanguerids. Eleutério *et al.* (2015) analyze growth patterns of pterosaurs with histological studies, including specimens from the Santana Group. Direct evidence of paleoecology has been found in the Romualdo Formation, with Buffetaut, Martill and Escuillié (2004) reporting three articulated cervical vertebrae, of an anhanguerid, with the first vertebra pierced by a spinosaurid tooth (Figure F5.2.03). While Buffetaut, Martill and Escuillié (2004) interpreted this specimen as a scavenging event, Kellner (2004a) discussed that the teeth represents clear evidence of a predation event, where the specimen offered resistance prior to death.

The fossiliferous potential of the Crato Formation applies not only to animals, but to any group that has even the slightest possibility for fossilization. That means plants, microscopic or macroscopic, extant and extinct, are not uncommon. Batten (2007) reported well over 150 spore and pollen taxa, recorded in the literature, from the Crato Formation and other formations of the Araripe Basin, vital for implications about their geological age and palaeoenvironment. While Mabesoone and Tinoco (1973) listed several palynomorphs found especially at the Romualdo Formation, Batten (2007) discussed in better details about the finds from the Crato Formation. Together with pollen fossils, macrofossils of vascular plants are frequent. Mohr, Bernardes-de-Oliveira and Loveridge (2007) discussed that these macrofossils are remarkable, not only because of their preservation and completeness, but also because of their scientific value, being representatives of the rise and the adaptative radiation of the angiosperms, also known as KTC, the Cretaceous Terrestrial Revolution (LLOYD *et al.*, 2008), a key moment in the evolution of the seed plants. Many specimens are the entire organism preserved, to the point that it is relatively common findings with its roots, stems, leaves, sporangia and even flowering structures attached. Few, remarkable examples preserved even some palaeosoil attached with the specimen. The most common finds are dispersed reproductive organs, from plants that remains unknown until complete specimens are found or attribution with living or extinct taxa can be recognized (Figure F5.2.04). While the palaeoflora from the Crato Formation is known to be relatively diverse (LIMA, SARAIVA & SAYÃO, 2012), it has not been fully described, with new descriptions being published recurrently (LIMA *et al.*, 2014). The flora from the Crato Formation also allows paleoecological studies, such as environment elucidation of the Crato Formation (SILVA *et al.*, 2013), interactions between plants and insects (FILHO *et al.*, 2017) and episodic palaeo-wildfires (LIMA *et al.*, 2019).

Several non-vertebrate metazoans were recovered from the Araripe Basin, with most from the Crato Formation and few reports from the Romualdo Formation (MAISEY, 1991). As Menon and Martill (2007) discussed, the fossil assemblage of the Crato Formation is highly dominated by the

arthropods, especially insects, in numerical abundance and taxonomic diversity. However, there are three recurrent groups that are not insects. One such group is the Chilopoda (MARTILL, 2007a), known by its rather soft, unmineralized exoskeleton, consequently being rare in the fossil record as a whole. At the Crato Formation, however, few but almost perfectly preserved specimens were recovered, represented by scolopendrids and scutigerids. The other group is Arachnida (DUNLOP, MENON & SELDEN, 2007), better represented and more diverse, with spiders, scorpions, mites and ticks, camel spiders, whip spiders and even whip scorpions (Figure F5.2.05). For arachnids, specifically, the Crato Formation is one of the most important fossil localities from the Mesozoic, if not the most important, being the sole formation up to date where unambiguous Mesozoic arachnids were described. The third and far less represented group is Crustacea (SCHWEIGERT, MARTILL & WILLIAMS, 2007), with few decapods and ostracods. Despite being an aquatic deposit, typical aquatic crustaceans, being decapods and ostracods, are very rare in the Crato Formation. A similar unusual pattern can be recognized for the insects (MENON & MARTILL, 2007).

Hexapoda, especially the insects, are the most diverse animal group of all time, with the most diverse groups being the Hemiptera, Coleoptera, Diptera, Hymenoptera and Lepidoptera (BECHLY, 2007a). In the fossil record, insects are also the most abundant fossils from the Crato Formation, as discussed by Menon and Martill (2007), in numerical abundance, preservation and also taxonomic diversity. Almost all groups of Insecta are represented in the Crato Formation, such as Apterygota (STANICZEK & BECHLY, 2007), Ephemeroptera (STANICZEK, 2007) and its related stem-group (WILLMANN, 2007), Odonata (BECHLY, 2007b), Dermaptera (HAAS, 2007), Mantodea (GRIMALDI, 2007), Blattodea (BECHLY, 2007c) including Termitoidae (BECHLY, 2007d), the enigmatic and extinct Chresmododea (BECHLY, 2007e), Orthopterida (HEADS & MARTINS-NETO, 2007), Cicadomorpha (MENON, HEADS & SZWEDO, 2007), Fulgoromorpha (SZWEDO, 2007), Coleorrhyncha (BECHLY & SZWEDO, 2007), Heteroptera (POPOV & BECHLY, 2007), Neuropterida (MARTINS-NETO, HEADS & BECHLY, 2007), mainly Neuroptera (Figure F5.2.06), Coleoptera (WOLF-SCHWENNINGER & SCHAWALLER, 2007), Hymenoptera (OSTEN, 2007), Mecoptera (BECHLY, 2007f), Diptera (WILLKOMMEN & GRIMALDI, 2007), Trichoptera and Lepidoptera (BECHLY, 2007g), totaling more than seventy families and almost one hundred distinct taxa. The taxonomic diversity of the insects from the Crato Formation differs from other aquatic deposits, notably, by the abundance and diversity of terrestrial adults of the groups Orthopterida, Hemiptera, Ephemeroptera and Odonata, whereas Coleoptera, often highly abundant in Cretaceous assemblages, are relatively scarce in the Crato Formation (MENON & MARTILL, 2007).

More than twenty fish taxa have been described from the Araripe Basin, both from the Crato and Romualdo formations. Chondrichthyes, rare in the fossil record, are known from the Romualdo Formation, such as *Tribodus* and *Rhinobatos* (MAISEY, 1991). Actinopterygii, on the other hand, is represented in both formations by an enormous diversity, a huge number of fossils and many with an excellent preservational state. According to Brito (2007), examples of non-Teleostei ray-finned fishes are the Semionotiformes *Lepidotes* and *Araripelepidotes*, Amiiformes akin to *Calamopleurus* and Ionoscopiformes *Placidichthys*. The teleosts from the Crato Formation are better represented by the Aspidorhynchidae *Vinctifer*, the Cladocyclidae *Cladocyclus* and the Chanidae *Dastilbe*, as well as *Santanichthys*, an Othophysini *incertae sedis*. Some of these taxa, such as *Rhacolepis* from the Romualdo Formation, *Dastilbe* (Figure F5.2.07) from the Crato Formation and *Vinctifer* from both formations, are known from an immeasurable amount of recovered specimens, with many in an excellent state of preservation. Several non-Tetrapoda Sarcopterygii taxa have also been described, represented specially by the group Actinistia. Mawsoniidae is the main group of coelacanths (BATISTA *et al.*, 2019), with *Mawsonia* at the Romualdo Formation (MAISEY, 1991) and *Axelrodichthys* at the Crato Formation (BRITO, 2007).

Tetrapoda, excluding Amniota, are represented by frogs from the Crato Formation (LEAL, MARTILL & BRITO, 2007). True frogs are scarce in the Mesozoic, becoming common and diverse only in the Cenozoic, according to Leal, Martill and Brito (2007). The Anura group as a whole achieved their basic body plan far back, at least at the Early Jurassic, persisting without significant modification for at least 200Ma. More than 30 extant clades are recognized, with five having fossil record extending back to the Mesozoic: the Leiopelmatidae, Discoglossidae, Pipoidea, Pelobatidae and Leptodactylidae. Of these groups, Leptodactylidae and Pipoidea are represented in the Crato Formation (Figure F5.2.08). As recorded by Leal, Martill and Brito (2007), there is a sixth group, Palaeobatrachidae, exclusively Mesozoic but it does not occur in Gondwana.

Turtles are highly distinctive and well represented in the Cretaceous fossil record, but from the Crato Formation only few specimens are known (NAISH, 2007). Isolated, broken elements of the carapace are among the typical fossil elements, however the Crato Formation has provided specimens that, according to Naish (2007), are complete and articulated. The fossil record for turtles of the Crato Formation highly contrasts with the record of the Romualdo Formation, which has a considerable diversity and at least one taxon, *Araripemys*, being known from multiple specimens. All specimens from the Crato Formation and all but very few fossils from the Romualdo Formation are attributed to Pleurodira (NAISH, 2007). In this manner, *Araripemys* (Figure F5.2.09) not only is

the most well-represented taxon from the Romualdo Formation, but also makes up the majority of the turtle fossils from the Crato Formation, aside from few *Pleurodira indet.* specimens.

As Maisey (1991) reported, the descriptions provided by Spix and Martius (1823-1831) for the fossils from the Araripe Basin, handed for study, included some elements that were attributed to a fossil snake, which encouraged searches for possible specimens of Squamata at the Araripe Basin. Martill (2007b) reported that, eventually, few but almost complete and articulated specimens were found and described. Martill (2007b) reports the description of two taxa, *Tijubina* (BONFIM Jr. & MARQUES, 1997) and *Olindalacerta* (EVANS & YABUMOTO, 1998), with more taxa being described over the years, such as *Calanguban* (SIMÕES, CALDWELL & KELLNER, 2014) and *Tetrapodophis* (MARTILL, TISCHLINGER & LONGRICH, 2015). It has been proved that the Crato Formation is also a source of key taxa, vital and revolutionary for studying the evolution of some distinct groups, resolving old issues and intense debate. *Tetrapodophis* is, perhaps, the best example of this clarification (Figure F5.2.10). The highly modified snake anatomy has generated decades of uncertainty about the origin of Serpentes, if it was aquatic or fossorial, and which group would be the closest relative, Mosasauria or Varanoidea. Martill, Tischlinger and Longrich (2015), describing *Tetrapodophis*, raised strong evidences for the hypothesis of fossorial origin and closest relationship with the Varanoidea, evidences tentatively questioned (LEE *et al.*, 2016). Christakou (2015) reported that one unclarified controversy about *Tetrapodophis* is the holotype provenance.

Pseudosuchia, specifically the Crocodylomorpha, is by far the most diverse and the most numerous amniotes from the Mesozoic of Brazil (RIFF *et al.*, 2012), with a huge taxa diversity and ecomorphological disparity. A less expressive, but still comparable, diversity from the Cenozoic can be observed, but very few taxa remained extant in Brazil (CIDADE, FORTIER & HSIU, 2018). This enormous group is better represented at the Bauru Basin, with the clade as a whole, especially Notosuchia, presenting greater preservational bias than any other archosaur (BANDEIRA *et al.*, 2018). At the Araripe Basin, however, crocodiles are poorly represented, with few and somewhat fragmentary specimens. Maisey (1991) reported the presence of *Itasuchus* and *Araripesuchus* at the Romualdo Formation. The diminutive taxon *Susisuchus* (SALISBURY *et al.*, 2003) and few specimens akin to *Araripesuchus* (FREY & SALISBURY, 2007) have been described from the Crato Formation. *Susisuchus* specimens are few and, usually, fragmentary, but some were preserved with enough information for an analysis regarding their growth pattern (Figure F5.2.11), based on paleohistological data (SAYÃO *et al.*, 2016).

Perhaps the most famous archosaurs are the dinosaurs (PISANI *et al.*, 2002). As a whole, the dinosaurs presented an unmatched diversity and ecomorphological disparity, in the whole planet, throughout the Mesozoic. However, after the K-Pg extinction, only the theropod group Aves persisted (LE LOEUFF, 2012). Of the main major clades of Dinosauria, according to Bittencourt and Langer (2011), Ornithischia is not represented in Brazil, aside from tentative, very fragmentary specimens, although there are studies saying otherwise (FERIGOLO & LANGER, 2007; LANGER & FERIGOLO, 2013; CABREIRA *et al.*, 2016; MÜLLER & GARCIA, 2020). The remaining two groups, being Sauropodomorpha, including Sauropoda, and Theropoda, including Aves, are well represented in Brazil, having early diverging forms from the basins of the Triassic and a large diversity reported throughout the whole Cretaceous (BITTENCOURT & LANGER, 2011). Sauropods are widely represented by titanosaurs, dinosaurs exclusive from the Cretaceous, better known from the Bauru Basin and with key taxa such as *Tapuiasaurus* (ZAHER *et al.*, 2011; WILSON *et al.*, 2016). However, sauropods are absent from the Araripe Basin. The only dinosaurs present at the Araripe Basin are the theropods (BITTENCOURT & LANGER, 2011). By itself, Theropoda is a huge clade with many representatives, specially at the Bauru Basin (BRUSATTE, CANDEIRO & SIMBRAS, 2017), such as Carcharodontosauridae (DELCOURT *et al.*, 2020) and Abelisauridae (DELCOURT, BRILHANTE & RICARDI-BRANCO, 2020) to name a few. At the Araripe Basin, theropod remains are rare and a little more diverse in the Romualdo Formation, mainly because of fragmentary elements of spinosaurids and taxa such as *Angaturama* and *Irritator* (BITTENCOURT & LANGER, 2011). Theropods are also represented with *Mirischia* (NAISH, MARTILL & FREY, 2004), *Santanaraptor* (KELLNER, 1999) and *Aratasaurus* (SAYÃO *et al.*, 2020). Dinosaur fossils at the Crato Formation are mostly isolated feathers (Figure F5.2.12). It is known that representatives of Eumaniraptora have inhabited the Crato Formation since the very first feather from the Crato Formation have been described, as reported and figured by Maisey (1991). As more feathers were eventually described (PRADO *et al.*, 2016), it became a matter of debate whether these feathers belonged to dromeosaurids, birds or something in between (SAYÃO, SARAIVA & UEJIMA, 2011). Indeed, as Bittencourt and Langer (2011) discussed, the occurrence of birds in the Crato Formation is expected, both chronostratigraphically and biogeographically, as the clade Aves is known since the Late Jurassic and it is already widespread in the Early Cretaceous. Naish, Martill and Merrick (2007) reported, aside from feathers, possible bird bones, based on specimens at private collections or museums without informed precedence. Carvalho *et al.* (2015) and Smyth *et al.* (2020) described two theropods from the Crato Formation, the Enantiornithes *Cratoavis* and the Compsognathidae *Ubirajara*, both based on articulated skeletons with feathers. Miranda (2020) reported that, similar to *Tetrapodophis*, one unclarified controversy about *Ubirajara* is the holotype provenance.

The pterosaurs from the Crato Formation are not limited to *Tupandactylus* (CAMPOS & KELLNER, 1997; FREY, MARTILL & BUCHY, 2003b) and *Aymberedactylus* (PÊGAS, LEAL & KELLNER, 2016). The first pterosaur described for the Crato Formation was *Arthurdactylus*, by Frey and Martill (1994). It was based on an almost complete but disarticulated skeleton, lacking the skull, cervical vertebrae, sternum and caudal vertebrae. In this same article, other specimens of pterosaurs from the Crato Formation were reported, including the anterior portion of a rostrum associated with a lower jaw and fragments of wings partially disarticulated. The second species described for the Crato Formation was "*Tapejara*" *imperator*, now *Tupandactylus imperator*. The description of *Tupandactylus navigans* came after the publication of two toothed taxa. First, Sayão and Kellner (2000) described a partial rostrum, previously reported by Frey and Martill (1994) but without a detailed description. Sayão and Kellner (2000) assigned this material to *Brasileodactylus* sp., based on the absence of premaxillary and dentary crests, the relative distance between alveoli and the presence of a long groove in the dorsal surface of the mandibular symphysis, starting at the anterior tip. It is worth mentioning that this material cannot be compared with *Arthurdactylus* since both specimens lack preserved elements that are comparable. If this specimen is indeed attributed to *Brasileodactylus*, then the presence of this taxon in both Crato and Romualdo formations would show that there are faunistic similarities between these two stratigraphic units, something already well documented for most of the aquatic fauna (BRITO, 2007). Second, in the same volume where *T. navigans* was named (FREY, MARTILL & BUCHY, 2003b) and several specimens from the Araripe Basin were figured, including a specimen attributed to *T. imperator* (FREY *et al.*, 2003), Frey, Martill and Buchy (2003a) described a complete skull, missing only the distal portion of the parieto-occipital crest, and named it *Ludodactylus* (Figure F5.2.13). It has been defined as a *Pteranodon*-like taxon with anhanguerid jaws and teeth, similar to typical misunderstood toys. An interesting aspect about this specimen is a leaf stuck between the mandibular rami. Frey, Martill and Buchy (2003a) speculated that the leaf would have been mistaken for food by the specimen and, after being stuck in the mouth, it would have prevented feeding and caused its demise, but this hypothesis has already been disproven (PÊGAS *et al.*, 2018). Unwin and Martill (2007) questioned the similarities between the holotypes of *Ludodactylus* and *Brasileodactylus*, concluding that both may represent the same species. In this manner, Unwin and Martill (2007) inferred that, quite possibly, *Arthurdactylus* may represent this same species, but cannot be compared to either *Ludodactylus* or *Brasileodactylus* due to the lack of comparable bone elements. Unwin and Martill (2007) also figured possible thalassodromids that were on sale online, without authorization for photographic evidence. Aside from *Aymberedactylus* and many unnamed fragmentary specimens,

such as the ones described by Sayão and Kellner (2006) and Cheng *et al.* (2018), one more species was named, up to date, from the Crato Formation. Based on a fragmentary and smashed anterior half of the skull, Witton (2008) named *Lacusovagus* and assigned it to the Chaoyangopteridae, while Wu, Zhou and Andres (2017) recovered it closely related to *Tupuxuara*.

Last, but not least, the limestone sediments of the Crato Formation preserved many elements that are regarded as biological in origin, but unknown or rather dubious in nature. Martill (2007c) reported that the most common elements, more common than the fossils themselves, are the small pellet-like structures that cover bedding surfaces, usually interpreted as faecal pellets of *Dastilbe*, but few to no studies have focused on analyzing such elements. Other objects listed by Martill (2007c) are mucous membranes, phosphatic coprolites, amorphous brown patches, few pieces of amber and a few more mysterious elements.

5.3. Preservational Status

The specimen MZSP-PV 1249, here labelled the São Paulo specimen, is a typical example of a fossil from the Crato Formation, both for the articulation of the elements and the damage degree (Figure F5.3.01). It is mainly comprised by a nearly complete and articulated skeleton, with a skull, mandible, most of the associated crests, virtually all cervical vertebrae, most dorsal series, the sternum plate, the left shoulder girdle exposed, few pelvic girdle elements and most bones of both forelimbs and hindlimbs (Figure F5.3.02). This skeleton is almost entirely articulated. The skull is articulated with the mandible and the cervical series, disconnected but associated with the dorsal vertebrae. Limbs and girdles, if not articulated, are closely associated, being very close to their natural positions alongside the vertebral column. This articulation degree reveals that this skeleton represents one single specimen. When compared to the fossils from the Romualdo Formation, which are typically tridimensional and uncrushed, each element of this specimen is badly crushed. For each bone, this damage occurred in different ways and degrees, according to a number of diagenetic factors. Thus, some characteristics and exact morphology are impossible to determine in some views. When such identification is possible, the elements are either slightly damaged, with weathering and few twists, or severely damaged, with vital and diagnostic structures completely broken and lost. Originally discovered in five pieces, the specimen is now embedded within two large laminated limestones, being one half mainly for the skull and lower jaws while the other half is mostly for the postcranial skeleton. The postcranial matrix is composed by four broken pieces that were rejoined with plastic resin prior to preparation.

The skull is mostly complete, exposed in right lateral view and in natural association with the lower jaw, which is articulated in occlusion with the upper jaw and it is also visible in right lateral view. While buried within the matrix, the left lateral side for both the skull and the lower jaws have been preserved. The premaxillary and dentary crests have been extensively crushed, with many lost pieces, but their overall shapes are preserved. The dorsal and ventral borders of the nasoantorbital fenestra, as well as the dentary ramus, have few and minimal damage, with the most apparent damage caused during collection (Figure F5.3.03). Inside the fenestra, there is a nasal process that is thin, long and extensively crushed, but overall preserved. While most ventral bones at the temporal and occipital regions of the skull, such as the quadrate and quadratojugal, have minimal damage and are preserved in natural position, the neurocranium and bones dorsal to it have been badly crushed, so few to none bones regarding the braincase are recognizable. Even heavily damaged, however, it is possible to identify that most, if not all, neurocranium bones were preserved deep within the

matrix, being visible at the very contact area between the two limestone slabs (Figure F5.3.04). During the collection, both the posterior occipital crest and most of the area of the soft tissue crest were lost. Likely the crests of the specimen were complete at the time when it was found. What was preserved of the posterior occipital crest is also extensively crushed, similar to the premaxillary and dentary crests. The frontoparietal crest is preserved, mostly as bone scars on the matrix, similar to the dorsal limits of the premaxillary crest. The preserved dorsal spine of the premaxillary crest is hardly recognizable. What can be identified as the soft tissue crest are possible scars on the matrix. The posterior articular portions of the mandibular rami are preserved and exposed, with the right ramus in right lateral view and the left ramus in left medial view. Although present, what can be assumed as the rhamphotheca is badly preserved and hardly recognizable, with similar weathering as the suprapremaxillary process.

The entire cervical column is virtually complete. The atlas-axis complex, which are the first two cervicals, are badly crushed and partially covered by the skull or embedded in sediment, being visible only the posterior condyle of the axis. This condyle, apparently, is in ventral to ventrolateral view. The mid-cervicals, which are cervicals III to VII, are better preserved and exposed in ventral view. They are all articulated with each other and the third cervical is articulated with the atlas-axis complex. All mid-cervicals are slightly rotated in left ventrolateral view, but since they are dorsoventrally flattened, their lateral aspects were crushed and most information were lost, except for the mid-cervicals III, VI and VII. Almost all mid-cervicals have shallow grooves on their surfaces, similar to the grooves on the skull, the mandible rami and the left humerus, caused during collection (Figure F5.3.05). While disarticulated from cervicals VIII and IX, all cervical vertebrae remain close to their natural position. Cervical VIII is visible in ventral view and the last cervical, together with the anterior-most dorsal vertebrae, are covered by many crushed bones. Cervical VIII is perhaps the best preserved cervical, since it appears to maintain some of its tridimensional shape. Although not the anterior-most dorsals, some of the anterior and middle dorsal vertebrae can be observed, preserved posterior to the crushed bones that covered the anterior-most dorsals and the last cervical. The dorsal vertebrae are preserved in dorsal view and are in natural articulation with each other. While most of the dorsals lost their neural spines, at least three exposed and articulated dorsals have their neural spines intact, slightly distorted to the left. Most dorsals have preserved both of their transverse processes, visible in dorsal view, but the crushed neural spines makes the right transverse processes appear to have the double of the left processes length. It is possible to identify at least five left and eight right dorsal ribs, all articulated with their respective vertebrae. They are all crushed to several degrees and most left ribs are displaced posteriorly. The sternum

plate is displaced from its natural position, lying posterior to the dorsal vertebrae. It is complete, but it is crushed and broken into several pieces. Its limits are covered by many bones, so its overall shape is hard to recognize, although it has preserved its contact with possible sternal ribs. Both the sacral and the caudal series, unfortunately, should be located on the region where the limestone is most weathered, so either these series are badly crushed by all other bones on this region or, more likely, these vertebrae eroded and are lost.

Both scapulae and coracoids are preserved close to their natural positions. The left scapula is the best preserved bone, almost entirely exposed. It is articulated with its respective coracoid, while its respective humerus lies very close to its natural position. The lateral half of the left coracoid is visible, associated with its respective scapula, but the rest of the bone is covered by other crushed bones, mainly the seventh cervical vertebra. The right scapula is badly crushed, covering many elements, such as the anterior-most dorsal vertebrae, and it is also covered by other crushed bones, such as the sixth and seventh cervical vertebrae. The right coracoid is nowhere to be seen, likely buried under the cervical series. Most of the bone elements from both wings have disarticulated, remaining very close to their natural positions. While some bones kept their contacts intact, such as the articulations between the phalanges of digits I-III and even few bones of the wing finger, other bones disarticulated completely and have been displaced by different degrees, from a low degree, for the contact between the right humerus with the right radius+ulna, to a high degree, for the contact between the left humerus with the left radius+ulna.

The right humerus is displaced from the right scapulocoracoid but lies close to it, parallel to the dorsal series, with its head covered by the fifth and sixth cervical vertebrae. Exposed in anterior view, it is badly crushed inside itself, partially covered by the left digits I-III. Only part of the distal condyles can be described in detail. The proximal half of the right radius+ulna is covered by the sternal plate, with some bone surfaces recognizable where the sternum is broken. It is also covered by the left femur and few crushed bones, remnants of a pelvic girdle. Only the distal third of both bones are truly exposed, together with the carpal series, in dorsal view. In this manner, the radius can be distinguished from the ulna, since both bones are close to each other. The carpal series is partially covered by sediment, so the identification of each element is difficult to establish. The position of the right pteroid bone is unknown, likely buried and also crushed under the right forelimb bones. All right metacarpals remain very close to each other, but disarticulated and far from the carpal series. The right metacarpals I-III are exposed, next to each other and adjacent to their respective digits. There is a long thin bone, partially covered by the wing metacarpal, that

possibly is the proximal half of the right metacarpal I. The first phalanx of the three right digits, as well as the second phalanx of digit III, are crushed and covered by the right tibia. Only the second phalanx of digit II can be recognized, because the second phalanx of digit III is crushed and the third has eroded and is lost, remaining only the proximal tip and fragments of the distal tip. The three right unguals are preserved and exposed. Unguals I and II are intact, with the second ungual articulated with its respective phalanx. The third ungual is damaged, with most of the bone eroded, preserving only both ends, being the claw tip and the articular surface, as well as a natural mould of the ungual diaphysis in the matrix. The right fourth metacarpal, also known as the wing metacarpal, is almost entirely covered by the right first wing phalanx. The only surface exposed is the distal roller-joint condyles, disarticulated from the wing phalanx but closely associated, in posterior view. All four right wing phalanges are preserved and exposed. The first phalanx is almost entirely exposed in ventral view. The distal end, except the tip, is mostly buried in few layers of matrix under the carpal series, but some portions are also exposed and can be compared with the left phalanx. The second phalanx is disarticulated but lies next to the first phalanx, in an oblique view where both dorsal and ventral views can be seen. While the distal end is next to the first phalanx diaphysis, the proximal lies distant, next to the left humerus. The diaphysis is covered by the right radius+ulna and associated carpal series, with some eroded surface where the matrix originally eroded. The third phalanx, being exposed in ventral view, lost its proximal third with the proximal end entirely, but most of its diaphysis is preserved, together with the distal end, disarticulated but closely associated with the fourth phalanx. The fourth phalanx rotated its shaft $\sim 85^\circ$ from the third phalanx shaft. While the fourth wing phalanx lost few pieces of its distal tip, it is overall preserved and exposed, so it can be described in detail.

The left humerus lies very close to its natural position and it is visible in anterodorsal view. Its head is overall preserved, except the deltopectoral crest, which is crushed beneath the right second wing phalanx. The diaphysis of the left humerus is progressively crushed inside itself all the way up to the distal condyles, that are heavily crushed and eroded, thus virtually lost. The left radius+ulna, as well as the rest of the left wing, lies separated from the left humerus, standing at the right side of the dorsal series. Almost all elements are disarticulated. The proximal ends of the left radius+ulna are exposed in anterodorsal view. In this manner, the radius can be distinguished from the ulna, since it is lying entirely over the ulna. As for the diaphysis and distal end, it is crushed under and inside the skull, with only the distal end of the radius being visible inside the orbit. The left ulna is heavily crushed inside itself. The proximal end of the left radius is completely crushed, making descriptions impossible. The proximal end of the left ulna is less crushed, but it is partially covered

by the radius and a possible epiphysis, which in turn are slightly disarticulated from it. There is only one left carpal exposed, inside the orbit, and its identification is difficult to establish. The right carpal series seems better preserved than the left carpal series. The left pteroid is nowhere to be seen, likely buried and also crushed under the left forelimb bones. The left metacarpals I-III remain very close to each other, but disarticulated and far from the carpal series. These metacarpals are heavily crushed, covered by the cervicals four and five and, partially, by the first left wing phalanx. Even with the distal halves exposed, it is difficult to establish which metacarpal articulates with each left digit. The phalanges of digits I-III are heavily eroded. The first phalanx of digit I is perhaps the left phalanx that is best preserved, being entirely exposed but, still, mostly eroded. While the second phalanx of digit II is exposed but broken in half, the first is covered by crushed pieces of phalanges. Digit II is the only left digit that all its phalanges and ungual are not in full articulation, with the first phalanx possibly being disarticulated from the second. Digit III has all its phalanges exposed and articulated, similar to the digit I, but they are all broken and eroded in several associated pieces. Nevertheless, it is possible to compare the elements of the right digits with left digits, since what is almost lost in the left digits are preserved on the right digits and what is almost lost in the right digits are preserved on the left digits. The three left unguals, just like the three right unguals, are preserved and exposed. While the right ungual III is the most damaged of the right unguals, the left ungual III is the best preserved of the left unguals, being complete and exposed with minimal to no signs of damage. Unguals I and II lost their tip and, while the proximal articulation surface of the second ungual is covered by most of the first ungual, the proximal articulation surface of the first ungual is damaged and eroded, together with the first phalanx. The left fourth metacarpal, also known as the wing metacarpal, is crushed and buried under the left radius+ulna. The only surface exposed is part of its diaphysis and a heavily crushed condyle, possibly from the the distal roller-joint condyles. The first wing phalanx is disarticulated but closely associated with the fourth metacarpal, partially covering it. The proximal articulation tip is covered by the left metacarpals and first phalanges of digits I-III, while the diaphysis is covered in different regions by the left radius+ulna, the possible associated epiphysis of the left ulna, the right femur and the left tibia+fibula. Nevertheless, this phalanx is mostly exposed and its overall shape can be recognized. The second phalanx is disarticulated from the first, but remains closely associated, which its shaft rotated $\sim 65^\circ$ from the first phalanx shaft. The proximal end and diaphysis of the second phalanx is preserved and exposed, but the diaphysis has been damaged in three distinct ways. First, it has been broken and eroded where the matrix originally divided. Second, it is crushed where it was covered by the left tibia+fibula. Third, it was cut in half during collection. Even with all this damaged, it is overall preserved. The distal half of the second phalanx, as well as the third and fourth phalanges,

are possibly preserved and complete, but are buried in few layers of matrix under the mandibular crest, thus cannot be recognized.

The majority of the pelvic girdle has been lost, breaking and eroding where the matrix originally broke, or being crushed by many other bones, thus becoming impossible to identify. What is preserved and exposed are remnants of the posterodorsal portion of the right plate, composed by the dorsal-most third of the ischiopubic plate, together with the acetabulum, the diaphysis of the ilium, dorsal to the acetabulum, and its postacetabular process. The ilium is damaged and eroded in several degrees, with the postacetabular process being divided, but some of its shape has been preserved in dorsolateral view. Half of the acetabulum is preserved and exposed, with few signs of damage, but the other half eroded and is lost. The ischium has mainly its posterior region preserved, although broken and without its tips, while the rest, together with the pubis, are broken in small fragments ventral to what is preserved of the acetabulum. Aside from this plate, there is one bone tip crushed and far from the remains of the pelvic girdle, next to a dorsal vertebra and over the sternum plate, standing on the same horizontal line of the preserved right ilium. Possibly, this element is the anterior tip of the preacetabular process. For the left side, there is one long bone parallel to the dorsal vertebrae and the left femur. This bone may be the left preacetabular process of the ilium, but since it is extensively crushed and partially covered by the femur, its identification is tentative. Both hindlimbs are almost complete and articulated or closely associated, but all bones are largely crushed and eroded. Nevertheless, their morphology are overall preserved and exposed.

The right hindlimb is perhaps the best hindlimb preserved, with most elements exposed. The right femur is complete and in anterolateral view. The femoral head and femur has disarticulated from the acetabulum, but it lies very close to the pelvic girdle. The region of the greater trochanter is partially covered by sediment. The femoral head and the greater trochanter preserved some of its tridimensional shape. The femur diaphysis at the proximal third is mostly broken and eroded, so the proximal elements lie more in anterior view while the rest of the femur lie more in lateral view. The distal condyles are disarticulated but closely associated with the tibia+fibula, with their shaft rotated $\sim 135^\circ$ from the femoral shaft. While the right tibia is complete, mostly in anterolateral view, the fibula is nowhere to be seen, likely buried under the tibia or eroded. The right tibia covers many bones, such as the second left wing phalanx and almost all phalanges of the right manus digits, and its diaphysis also has one single point, in the middle, that is covered by the left tibia. This middle point was also cut in half during collection. Distal to this middle point, it also has one eroded crack at the diaphysis, where the matrix originally broke. Nevertheless, the right tibia is overall preserved

aside from all this damage. The right tarsals are preserved and articulated with the tibia and the metatarsals, showing very few eroded surfaces. The same is true for all five metatarsals, complete and articulated, where the right metatarsal IV shows more signs of weathering. Metatarsal V is the only metatarsal that is disarticulated, remaining over the metatarsal I. All phalanges of the right pes digits are disarticulated but closely associated with each other and the metatarsals, making precise identification impossible. As for most of the distal phalanges and all unguals, they were lost during collection. Likely the specimen pes was complete at the time when it was found, similar to what happened with the posterior occipital crest and the soft tissue crest. The only exception is the single, vestigial fifth digit phalanx, close to its metatarsal articulation. Although eroded, the distal end of the tibia, all the tarsals, metatarsals and phalanges kept their tridimensional shape.

The left femur is almost complete and in anterolateral view. It is entirely crushed and broken, mainly inside itself, with only its overall shape preserved. While covering some dorsal vertebrae, the left femoral head and greater trochanter eroded and are lost, being positioned where the matrix was originally divided. There is still some remnants of the femoral head, eroded and with its inner structure exposed. The diaphysis also eroded at the proximal third, where it would cover the right radius+ulna and the sternal plate, and almost in the same anatomic region where the right femur also broke and eroded. The left femur and the left tibia+fibula maintained its natural articulation. These bones are also badly preserved, being crushed and with a large eroded area, at the diaphysis, where the matrix naturally broke and where they would cover the first left wing phalanx, which is eroded as well. The left tibia was cut in half during collection, where it covers the right tibia, but nevertheless it is overall preserved and its shape can be recognized. The left fibula eroded in the same area, losing most of its shaft. It is impossible to measure its length. The proximal head of the left fibula, however, is preserved, covering the tibia. The distal third of the tibia, as well as the tarsals, metatarsals and all left digits phalanges, are possibly preserved and complete, but are buried in few layers of matrix under the mandibular crest, thus cannot be recognized. There is one long thin bone, exposed inside the fragments of the mandibular crest, that possibly is a left metatarsal. It seems there is another similar bone exposed, parallel to it, that can be another metatarsal. However, it remains in a position where other buried bones could be located, so this identification is tentative.

When the specimen was discovered, most of the remains of the postcranial skeleton were preserved in four broken and eroded pieces of limestone. These pieces, arriving at the Paleontology Laboratory in the Museum of Zoology of the University of São Paulo (MZSP-PV), were joined back together in a single slab, being repaired with plastic resin. Then, the skeleton underwent

mechanical preparation at the same laboratory. The articulation and preservational state of the skeleton suggests that many more details could be uncovered with a more extensive preparation from the reverse side of the limestone. That was planned by immersing what is exposed of the specimen in CarboWax, a popular name for Polyethyleneglycol, and preparing the other side, cleaning completely the specimen from the rock matrix. However, a complex positioning and association of the bones, a risk of damages and, most of all, time constraints prevented this next step from occurring. During preparation, three associated materials were recovered in the limestone with the postcranial elements. Next to the second right wing phalanx, there is a complete, but poorly preserved, specimen of *Dastilbe*, with many skull and postcranial elements preserved entirely or as a natural mould. There were also two wood fossils discovered. One wood was kept in the limestone, between the cervical series and the left metacarpal IV, covered by the left radius+ulna. Some of this wood is also covered. The other was disassociated after preparation. It was found between the right wing phalanges 3 and 4 and the long thin bone that, presumably, is the right metacarpal I.

6. RESULTS

6.1. Systematic Paleontology

Pterosauria Kaup, 1834 *sensu* Owen, 1842 and Padian, 2004.

Macronychoptera Unwin, 2003.

Novialoidea Kellner, 2003.

Breviquartossa Unwin, 2003.

Monofenestrata Lü *et al.*, 2010.

Caelicodracones Unwin, 2003 *sensu* Andres, Clark & Xu, 2014.

Pterodactyloidea Plieninger, 1901 *sensu* Padian, 2004.

Lophocratia Unwin, 2003

Eupterodactyloidea Bennett, 1994.

Ornithocheiroidea Seeley, 1891 *sensu* Bennett, 1994 and Kellner, 2003.

Azhdarchoidea Nesso, 1984 *sensu* Unwin, 1995, Kellner, 2003 and Unwin, 2003.

Tapejaridae Kellner, 1989 *sensu* Lü *et al.*, 2006b and Andres, Clark & Xu, 2014.

Tupandactylus Kellner & Campos, 2007.

Type species: "***Tapejara***" ***imperator*** Campos & Kellner, 1997.

Tupandactylus imperator (CAMPOS & KELLNER, 1997).

Holotype: MCT 1622-R, slab, with counterslab defined as cotype.

Referred Specimens: SMNK PAL 2839, the Private Collection specimen, CPCA 3590.

New Referred Specimen: MZSP-PV 1274, an almost complete and articulated skeleton, which includes the skull, mandible, cervical and dorsal vertebrae, remnants of shoulder and pelvic girdles and most elements of both forelimbs and hindlimbs.

6.2. Cranial Skeleton

The skull is almost complete (Figure F6.2.01). It is overall laterally compressed. Exclusive of cranial crests, it is very long, being longer than the entire dorsal, sacral and caudal series combined (Table T6.2.01). The lateral surface area is mostly occupied by the cranial crests and the huge nasoantorbital fenestra. Inside the nasoantorbital fenestra, there is a long and thin nasal process. The skull is lacking the posterior occipital crest and most of the soft tissue crest, but few of these are preserved, indicating that they were present but not preserved, rather than possibly absent. Together with these crests, the specimen also has a long frontoparietal crest and a large premaxillary crest, with a long and thin suprapremaxillary process. The skull is in natural association with the lower jaw, being articulated in occlusion with the upper jaw. It is long and thin, with a long symphysis. At the anteroventral surface of the symphysis, there is a large and rounded mandibular crest. Thus, this specimen bears a total of five cranial crests, being four bony crests. Hardly recognizable, there are some remnants of a rhamphotheca in front of what can be assumed as the beak of the specimen.

6.2.1. Anterodorsal

This section refers to the anterior half of the skull, with the rostrum and dorsal cranial crests. It covers the morphology of most of the cranial crests and bones related to the rostrum and upper jaw, highly variable within pterosaurs and associated with feeding strategies (ZHOU *et al.*, 2017). The palate is related to the next section, together with the remaining bones of the skull.

Premaxillomaxilla

The premaxillomaxilla is quite possibly the largest bone in the skull, and skeleton entirely, of *T. imperator*, thanks to the premaxillary crest. There are no visible sutures between the premaxilla and the maxilla, a common feature among pterosaurs previously reported in tapejarids (KELLNER, 1989; LÜ & YUAN, 2005). Both bones, together, constitute almost all of the upper jaw, as well as most of the margins of the nasoantorbital fenestra. Anteriorly, the premaxillomaxilla is shaped in a sharp, pointed rostrum. The rostrum here is regarded as the region anterior to the anterior margin of the nasoantorbital fenestra. The rostral value, which is the length of the premaxillary rostrum relative to the height of the anterior-most point of the external naris or nasoantorbital fenestra, measured perpendicularly from the ventral margin of the skull (KELLNER, 2010), is ~2. Likewise, the rostral index, which is the full height of the rostrum at the anterior-most point of the external naris or

nasoantorbital fenestra, including potential premaxillary crests, relative to the length of the prenarial rostrum (MARTILL & NAISH, 2006) is ~ 2.8 . Both values indicate that *T. imperator* has a relatively short rostrum, as in all tapejarids and thalassodromids (MARTILL & NAISH, 2006).

This beaked rostrum is inclined ventrally, at an angle of $\sim 15^\circ$, relative to the posterior process of the maxilla. Below the anterior margin of the nasoantorbital fenestra, in a region anterior to the jugal and at the posterior limit of the prenarial rostrum, the upper jaw and palate have an arched configuration. In a lateral aspect from a posterior-to-anterior perspective, the rostrum first incline upwards before it bend downwards. The dorsal aspect of the lower jaw has a corresponding configuration, so both jaws perform a perfect occlusion. When the deflection angle is measured from this region, the rostrum is inclined at an angle of $\sim 25^\circ$. This feature is not unknown to *T. imperator*, since the cotype also presents a similar morphology on the skull (CAMPOS & KISCHLAT, 2020). This is also known for other tapejarids, because it can be observed in some specimens of *Sinopterus*, specifically a specimen that can be regarded as ontogenetically mature (LÜ *et al.*, 2007). Although attenuated, all specimens of *T. navigans* shows a similar configuration (FREY, MARTILL & BUCHY, 2003b; pers. obs.). This configuration cannot be safely determined for *Caiuajara*, since all available specimens lack a complete and articulated upper jaw (MANZIG *et al.*, 2014; pers. obs.). For *T. imperator* specifically, the São Paulo specimen has a deflection angle of $\sim 15^\circ$ relative to the posterior margin, similar to the Crato specimen, and of $\sim 25^\circ$ relative to the arched margin, similar to the Private specimen. The cotype has a similar pattern (CAMPOS & KISCHLAT, 2020). The only possible exception seems to be *Tapejara*, with both Wellnhofer and Kellner (1991) and Eck, Elgin and Frey (2011) describing specimens that, at the region of the skull below the anterior margin of the nasoantorbital fenestra, the palate is pointed convex and the lateral aspect of the skull is straight, while the palate is concave only anterior to this region, where the rostrum is downturned. However, there is one specimen, still not described but illustrated by Elgin and Campos (2012) and figured both by Witton (2013), at the page 222, and Veldmeijer (2006), at the page 219, that seems to present an attenuated arched-and-downturned configuration.

The rostrum anteriorly has sharpened occlusal margins. Along the rami of the maxillae, the sharp ridges of the occlusal margins become progressively lower until they disappear, right under the middle of the nasoantorbital fenestra. The occlusal margins posteriorly, where the maxilla articulates with the jugal, are broader and rounded. The dorsal element of the premaxilla forms the bony premaxillary crest, as well as most of the anterodorsal margin of the nasoantorbital fenestra. Exclusive of the cranial crest, the internasal (dorsal) process of the premaxilla is very slender, being

thinner than the anteroventral margin of the nasoantorbital fenestra, where the premaxilla and the maxilla possibly contact. At the skull roof, it is impossible to determine the exact total extent of the premaxilla. The premaxillae in other pterosaurs, such as *Pteranodon* (BENNETT, 2001), extends posteriorly over the nasals and contacts the frontals. Campos and Kischlat (2020), however, argued that the posterior margin of the premaxilla in *T. imperator* extends posterior to the occipital region, in a similar fashion to *Sinopterus* (LÜ *et al.*, 2007) or even *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018), two taxa where the frontoparietal crest is overlapped by the premaxillary crest. In this manner, the entire crest of soft tissue would be anchored on the skull solely by a complex premaxillary crest that is both anteriorly high and posteriorly long. Indeed, in many tapejarids such as *Tapejara* (WELLNHOFER & KELLNER, 1991) the posterior process of the premaxilla extends all the way up to the parietal. For *T. imperator*, unfortunately, nothing can be concluded for certain, because all specimens attributed to *T. imperator* have their sutures between these bones obliterated or too damaged. Campos and Kischlat (2020), describing the cotype, could not distinguish if the elongated dorsal bone was truly a posterior extension of the premaxillary crest, a frontoparietal crest or a fusion of both. Here, the high crest that is triangular and anteriorly placed will be regarded as the premaxillary crest, the long and low crest at the skull roof will be regarded as the frontoparietal crest, with participation of the extended premaxilla dorsally, and the long crest beyond the occipital region will be regarded as the posterior occipital crest, where part of its composition is also the extended posterior process of the premaxilla.

Premaxillary Crest

The premaxillary crest is the highest and largest crest in the skull of *T. imperator*. The crest is triangular in shape, with a height that is posteriorly decreasing. The anterior margin of the crest begins posterior to the tip of the rostrum, raising with a subvertical anterior margin. Like all skulls attributed to *T. imperator*, the anterior margin of the crest projects anteriorly, as a plate-like element, with a convex blade projecting anteriorly. This blade has a subrounded margin. Dorsal to it, there is a spine-like process that is long, thin and extends well beyond the dorsal limits of the premaxillary crest. This is the suprapremaxillary process, a typical character of *Tupandactylus*, and it supports most of the soft tissue crest in height. Beginning at the anterior blade, it extends posterodorsal to the premaxillary crest at an angle of $\sim 15^\circ$. The anterior blade is what causes the change in direction of the suprapremaxillary process, from a subvertical to a posterodorsal orientation. The preservation of the dorsal spine indicates that it may not be composed of bone. Campos and Kischlat (2020), describing the cotype, discussed that this process may be composed by keratinous component that

forms the rhamphotheca, concluding that it represents merely an extension of the beak in *Tupandactylus*. While the suprapremaxillary process indeed looks more keratinous than bone, at least in the São Paulo specimen, it also begins dorsal to the anterior blade, while the beak seems to end ventral to the same blade (Figure F6.2.02). Here, the suprapremaxillary process is considered a keratinous component of the premaxillary crest. The posterodorsal margin of the premaxillary crest is more rounded. This margin is strongly striated, with undefined limits and deeply connected with the possible remnants of the soft tissue crest (Figure F6.2.03). Frey *et al.* (2003) and Pinheiro *et al.* (2011) discussed that, in this region, originates the parallel fibers composing the soft tissue crest, with the fibers penetrating the bone. Campos and Kischlat (2020) considered this posterior margin a secondary ossification for the crest, with the original premaxillary crest being a dorsal blade high and triangular, the basis for the anterior convex blade and the suprapremaxillary process. This conclusion was based on observation only, lacking histological analyses. The São Paulo specimen presents a morphology that resembles this proposed morphology. The crest have a triangular blade that is thicker and anterodorsal to the posterior margin, more striated and seemingly more damaged during preservation. The posterior margin ends over the nasoantorbital fenestra, beyond two thirds of the fenestra, but the striation caused by the fibers extends posterior to the premaxillary crest.

Nasoantorbital Fenestra

The naris and antorbital fenestra in *Tupandactylus imperator* are confluent, as for any other monofenestratan. The nasoantorbital fenestra is huge, bounded by the premaxillomaxilla, jugal, lacrimal and nasal. It is rounded and elongated. The anteroventral margin is rounded and have a curvature, together with the ventrolateral sinuosity on the skull, accompanying the arched-and-downturned configuration of the upper jaw. The posterior margin is concave and slightly reclined, with the posterodorsal margin of the fenestra posterior to the posteroventral margin, but still anterior to the orbit. This condition is typical for *T. imperator*, as observed on the cotype and the German specimen (FREY *et al.*, 2003; CAMPOS & KISCHLAT, 2020), with the three specimens exhibiting a $\sim 65^\circ$ reclination angle relative to the posterior process of the maxilla. Truly the largest fenestra in *T. imperator*, the nasoantorbital fenestra represents $\sim 60\%$ of the total length of the skull, excluding the posterior occipital crest. Inside the nasoantorbital fenestra, at the anterior margin, there is a long and very thin bone, possibly a hyoid (Figure F6.2.04), but this identification is merely tentative. It is rod-like in shape and appears to be elongated.

Nasal

The nasal bones are preserved and are possibly triangular in shape, with a anterior process sharp and long. While the nasal can be identified at the posterodorsal margin of the nasoantorbital fenestra, most of its limits cannot be determined because all sutures are obliterated. Possibly, as Bennett (2001) described for *Pteranodon*, they meet at the dorsal midline of the skull, overlapped by the premaxillae and articulate with the frontal, posteriorly, and the lacrimal, ventrally. The Crato specimen (PINHEIRO *et al.*, 2011) has a preserved anterior process of the nasal articulating with the overlapping premaxilla, the normal condition in all pterosaurs. Possible foramina cannot be identified. Contrary to the condition observed in all other specimens attributed to *T. imperator*, the nasal in the São Paulo specimen has a very long descending process, identified for the first time in *T. imperator* but not for *Tupandactylus*. It is entirely thin and rod-like, with a triangular base articulated by its posterior tip with the main body of the nasal. While the process tapers from the ventral tip of the triangular base, the anterior tip is projected anteriorly. Due to preservation, it is slightly disarticulated, revealing that both processes are lateral on the skull but directed medially, meeting at the middle point and fusing into a single and thin medial process for half of its length. The process has a anteroventral orientation and is very elongated, reaching the ventral limit of the nasoantorbital fenestra but not articulating with it. Being very thin, any pneumatic foramina are absent. This shape for the descending process has never been documented in any other pterosaur, but it resembles the process in *T. navigans* where the holotype and one referred specimen presents such processes (FREY, MARTILL & BUCHY, 2003b; pers. obs.). This process is preserved in at least one specimen of *Tapejara* (WELLNHOFER & KELLNER, 1991).

Jugal

In Pterodactyloidea (PÊGAS, COSTA & KELLNER, 2018), the jugal is a triradiate bone that contacts four bones: the maxilla, through the maxillary (anterior) process; the lacrimal, through the lacrimal (dorsal or ascending) process; the postorbital, through the postorbital (posterodorsal) process; and, finally, the quadratojugal. Non-pterodactyloids have tetra-radiate jugals, with the quadratojugal articulating with the quadratojugal (posterior) process. In monofenestrates, the process is lost and the contact is made directly on the main body of the jugal (BENNETT, 2001). However, Pêgas, Costa and Kellner (2018) and Zhang *et al.* (2019) reported that there is a reversion of this condition on tapejarids from Brazil, with *Tapejara* (WELLNHOFER & KELLNER, 1991), *T. navigans* (FREY, MARTILL & BUCHY, 2003b; FREY *et al.*, 2003) and also *Caiuajara* (MANZIG *et al.*, 2014) all presenting an elongated quadratojugal (posterior) process, thus

tetraradiate jugals. The posteroventral margin of the nasoantorbital fenestra is formed by the maxillary (anterior) and the lacrimal (dorsal or ascending) processes. The ventral margin of the orbit is composed by the lacrimal (dorsal or ascending) and the postorbital (posterodorsal) processes. Finally, the ventral margin of the lower temporal fenestra is defined by the quadrate, quadratojugal and postorbital (posterodorsal) process, but in pterosaurs with tetraradiated jugals, it is delimited by the postorbital (posterodorsal) and quadratojugal (posterior) processes of the jugal. The ventral margin of the jugal also composes part of the margin of the upper jaw, anterior to the articulation. In *T. imperator*, the ventral margin of the jugal is concave. The maxillary (anterior) process is slender and elongated. As observed on the Crato specimen (PINHEIRO *et al.*, 2011), it reaches half of the length of the nasoantorbital fenestra. There is a long scar on the upper jaw that represents the suture between the maxilla and the jugal (Figure F6.2.05). As typical for any pterosaur (BENNETT, 2001), the maxillary (anterior) process laps laterally over the maxilla. The lacrimal (dorsal or ascending) process is thin and directed vertically. Its contact with the lacrimal is obliterated and also broken, thus impossible to identify. However, the location where the bones were fused can be identified, being located dorsal to the midline of the orbit. The anteroventral margin of the lacrimal (dorsal or ascending) process of the jugal has a deep concavity, being the nasoantorbital fossa on the jugal, a feature observed on the holotype of *T. navigans* (FREY, MARTILL & BUCHY, 2003b), a referred specimen of *Tapejara* (WELLNHOFER & KELLNER, 1991), specimens of *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.) and the holotype of *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018), but not in *Tupuxuara* (KELLNER & HASEGAWA, 1993). The postorbital (posterodorsal) process, like the other processes, is thin and flat. This process was divided in half during collection, but few fragments of the bone remained, indicating its shape. Its contact with the postorbital is damaged and cannot be described, but it is possible to locate the region of the contact, showing that the bar between the orbit and the lower temporal fenestra is composed mainly by this process. Finally, different from most pterodactyls and similar to tapejarids from Brazil, *T. imperator* has a tetraradiate jugal, with a thin and elongated quadratojugal (posterior) process. It is posterodorsal in orientation, a feature exclusive to the tapejarids with tetraradiate jugals. It composes most of the posterior bar of the lower temporal fenestra, together with the quadratojugal and quadrate.

Orbit

The orbit is bounded ventrally by the jugal, with the lacrimal (dorsal or ascending) and the postorbital (posterodorsal) processes. Dorsally, it is bounded by the lacrimal, postorbital and, quite possibly, the prefrontal and postfrontal, however the presence and morphology of these bones in

pterosaurs are highly questionable (BENNETT, 2001). The orbit in *T. imperator* is large, rounded and overall resembles an inverted triangle in outline, ovate to piriform, which is typical for all tapejarids. It is located right over the jaw articulation, with the center of the orbit posterior to it. The lateral position of the orbit on the skull of *T. imperator* is low, with the entire orbit below the dorsal margin of the nasoantorbital fenestra. Like all other tapejarids and thalassodromids, *T. imperator* has the main synapomorphy of the Azhdarchoidea (KELLNER, 2003; UNWIN, 2003).

Lacrimal

The lacrimal is usually a small bone that is roughly triangular and forms the posterodorsal corner of the nasoantorbital fenestra, as well as the anterior margin of the orbit (BENNETT, 2001). For *T. imperator*, specifically the São Paulo specimen, this morphology and its sutures with other bones cannot be recognized, since this region is broken in the middle, with one half raised above the other half. Other specimens, specially the cotype and the German specimen (FREY *et al.*, 2003; CAMPOS & KISCHLAT, 2020) revealed that it is a small and flat bone, with no orbital process and with a single and large lacrimal foramen, in contrast to *Tapejara* (WELLNHOFER & KELLNER, 1991) that presents a highly fenestrated lacrimal, with multiple tiny lacrimal foramina.

6.2.2. Posteroventral

This section refers to the posterior half of the skull, with the occiput and palate. It covers most of the morphology of the bones that composes the braincase, the posterior cranial crests and the palate, a structure highly variable in pterosaurs with the homology of some elements still uncertain (ÓSI *et al.*, 2010; PINHEIRO & SCHULTZ, 2012).

Frontoparietal

The frontoparietal is quite a long bone in the skull of *T. imperator*. There are no visible sutures between the frontal and the parietal, a common feature among pterosaurs which is also reported in tapejarids (KELLNER, 1989). Both bones constitute almost all of the skull roof over the orbits and braincase. Due to the preservation of this specimen, it is impossible to identify sutures between these two bones and other bones of the skull, such as the nasal and the premaxillomaxilla. Indeed, as elucidated by Campos and Kischlat (2020), it is impossible to conclude if the dorsal process of the skull roof is the frontoparietal or an elongated posterior process of the premaxilla that

is fused with the frontoparietal. Nevertheless, the frontoparietal can be described as a smooth bone that begins anterior to the preorbital bar and, together with the premaxillomaxilla exclusive of crests, makes the dorsal margin of the skull have a convex aspect. Posteriorly, its contact with the postorbital, supraoccipital and squamosal are obliterated, making it impossible to determine its extent posteriorly. Its shape as the margin of the upper temporal fenestra cannot be recognized. It is possible to identify that the skull roof is entirely articulated with the premaxilla, a feature present on the holotype of *T. imperator* (CAMPOS & KELLNER, 1997). Campos and Kischlat (2020) briefly reported that the cotype do not present this connection, similar to *Tapejara* and *Sinopterus*.

Frontoparietal Crest

As discussed above, the long and low crest at the skull roof, posterior to the triangular and high premaxillary crest, will be regarded as the frontoparietal crest with participation of the extended premaxilla dorsally. In this manner, the entire dorsal surface of the frontoparietal forms the frontoparietal crest. It is overall low and elongated, but not as long as any other crest in any specimen of *T. imperator*. While the São Paulo specimen lack sutures between most bones of the skull, it is expected that the frontoparietal and its crest begins posterodorsal to the nasal bones, which in turn are anterodorsal to the preorbital bar. That means some portion of the crest, possibly the dorsal-most region, is indeed the internasal (dorsal) process of the premaxilla, but the limits between the premaxilla and the frontoparietal cannot be established. This crest is striated, with undefined limits dorsally and deep connections with the possible remnants of the soft tissue crest. This crest is less striated than the premaxillary crest, but it still striated entirely through its dorsal margin. Anteriorly, it seems more ossified, while posteriorly it shows more possible remnants of the soft tissue than bone, which may be a preservational bias (Figure F6.2.06). Frey *et al.* (2003) and Pinheiro *et al.* (2011) discussed that this region is where the parallel fibers of the soft tissue crest connect with the skull, with the fibers penetrating the bones. All parallel fibers have a subvertical orientation, with a posterodorsal curvature. Quite possibly, the crest of soft tissue connects entirely with the premaxilla, without participation of the frontoparietal.

Temporal Fenestrae

Pterosaurs, as observed in *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018), have at least three pairs of temporal fenestrae, a symplesiomorphic condition for the diapsids (OSBORN, 1903). The dorsal pair, being the supratemporal or upper temporal fenestrae at the skull roof, and

the ventral pair, being the subtemporal fenestrae posterior to the palate, cannot be described in any specimen attributed to *T. imperator*, up to date, due to the preservation of all specimens in lateral view. Some taxa may have more fenestrae, specific for each group, as observed in thalassodromids like *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018), but this also cannot be verified for *T. imperator*, since extra pairs of temporal fenestrae usually occurs at the palate. What can be assumed for the supratemporal fenestrae, in some specimens including the São Paulo specimen, is that its ventral margin lies above the middle line of the orbit. The lateral pair, posterior to the orbit, are the infratemporal or lower temporal fenestrae, being the only fenestrae overall preserved that can be described in detail. It is bounded by the squamosal, the jugal by the postorbital (posterodorsal) and quadratojugal (posterior) processes and, possibly, the postorbital. It has a elliptical and elongated shape, a length approximately the height of the orbit, an inclined orientation and a position, relative to the orbit, posterior to it but with the ventral half of the inclined fenestra reaching under the orbit.

Squamosal

The squamosal forms the posterodorsal margin of the infratemporal fenestra and, as observed in *Pteranodon* (BENNETT, 2001), part of the lateral margin of the supratemporal fenestra. The contact of the squamosal with the postorbital and parietal are impossible to determine, with sutures badly preserved. Due to preservation, any information regarding this bone in posterior view, at the occiput, has been lost. It is possible to recognize the squamosal in *T. imperator* as an unexpanded bone, with its processes thinner than the base. In a horizontal line, it is located above the base of the lacrimal (dorsal or ascending) process of the jugal. At ventral limits of the the squamosal, it is possible to identify its sutures with the quadratojugal, the quadrate and, quite possibly, with the quadratojugal (posterior) processs of the jugal, but the region where the squamosal and the jugal would contact is damaged. Ventral to the suture, there is a process that is sharp pointed and extends below the surface of the quadrate, in an anteroventral direction. This is a large and conspicuous otic process, which according to Bennett (2001) produces a narrow notch that may have supported the tympanic region of the ear. According to Vidovic and Martill (2017), this condition is prevalent among pterosaurs from the Cretaceous.

Quadratojugal

The quadratojugal is a thin and long bone, lying posteroventral to the jugal and anterolateral to the quadrate. Ventrally, it thickens and forms the lateral surface of the condyloid process for the

articulation of the jaws. As in all tapejarids from Brazil, the quadratojugal in *T. imperator* articulates with the quadratojugal (posterior) process of the jugal, composing the lower temporal bar. At its posteroventral surface, it laps onto the ascending process of the quadrate. Being very thin and as long as the quadrate, the quadratojugal does not separate the quadrate and the jugal completely, with the quadrate contacting the jugal at the medial surface of the latter. The jugal, quadratojugal and quadrate are in close contact with each other, but sutures between these three bones are clear and visible, anterodorsal to the otic process (Figure F6.2.07) and running parallel to the temporal bar.

Quadrate

The quadrate is elongated and robust. It contacts the quadratojugal throughout all its length, while the contact with the squamosal is at the posterodorsal limit. The medial surface of the jugal also contacts the quadrate. As Bennett (2001) described for *Pteranodon*, other possible contacts are with the pterygoid and the lateral surface of the braincase, but this cannot be observed in the São Paulo specimen or any other specimen attributed to *T. imperator* due to preservational bias. The anteroventral surface forms the condyloid process for the articulation of the jaws, with the lateral surface composed by the quadratojugal. This subcylindrical process articulates with the concave glenoid fossa of the lower jaw, formed by the articular and surangular. The jaw articulation is placed ventral to the level of the palate. Although covered by sediment and other bones, it is possible to identify the shape of the quadrate, being a wide and rectangular bone with two distinct condyles (Figure F6.2.08). The orientation of the condyles, relative to the skull, cannot be determined since they are partially broken and displaced from the skull. The overall size of the condyles, relative to each other, cannot be measured since they are both partially buried under the matrix. As for the mandibular articulation, relative to the ventral margin of the skull, it has a posterior inclination of $\sim 120^\circ$, being positioned below the orbit, but anterior to the center of the orbit.

Postorbital And Others

The postorbital is dorsal and lateral to the neurocranium, forming the posterior margin of the orbit. Its ventral surface contacts both the jugal and the squamosal, possibly bounding both the supratemporal and infratemporal fenestrae. Although the postorbital is preserved in most specimens of *T. imperator*, including the São Paulo specimen, it cannot be described since it is always heavily crushed and badly preserved. This also applies to the prefrontal and postfrontal, if these bones are indeed present in *Tupandactylus* as observed in *Pteranodon* (BENNETT, 2001). The postorbital has

been cut in half during collection, where it contacts the jugal. The morphology and contact between these bones remains unknown.

Occiput Elements

All bones located at the posterior surface of the skull constitute the occiput elements. The occiput is responsible for connecting the skull with the rest of the skeleton, but these bones are also responsible for bounding the braincase (BENNETT, 2001). In tapejarids, the occiput and braincase are better known from three specimens attributed to *Tapejara*. The first, described by Wellnhofer and Kellner (1991), have all the occiput and quite possibly the braincase intact, but they remain undescribed up to date because they are covered by few layers of matrix, cervical vertebrae and hyoid bones. The second, described by Kellner (1996a), have the braincase and occiput virtually complete, tridimensional and exposed, allowing its full description. The third, described by Eck, Elgin and Frey (2011), have mostly the dorsal half of the occiput and braincase preserved, but it is uncrushed and allowed a silicone cast of the brain of *Tapejara* to be made (ECK, ELGIN & FREY, 2011). As for all other tapejarids, all specimens attributed to *Sinopterus* (ZHANG *et al.*, 2019), *Europejara* (VULLO *et al.*, 2012) and *Tupandactylus* (FREY, MARTILL & BUCHY, 2003b; PINHEIRO *et al.*, 2011), including the São Paulo specimen, are known from skulls that are preserved in lateral view, with the braincases badly preserved. *Afrotapejara* (MARTILL *et al.*, 2020a) is known only from pieces of fragmentary beaks. *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), although not described, has most of the occiput and braincase preserved on the holotype. The occiput and the braincase are also known from the thalassodromids, allowing comparisons with the tapejarids, such as *Caupedactylus* (KELLNER, 2013) and *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018). Nevertheless, the occiput elements in *T. imperator* cannot be described up to date, including the shape and contact of the supraoccipital, paraoccipital, exoccipitals, opisthotics, basioccipital, the associated occipital condyle, prootics, basisphenoid with associated basipterygoid processes and laterosphenoid. The same is true for possible pneumatic foramina and posttemporal fenestrae, along with other posterior openings of the skull. The angle of the basipterygoid processes cannot be measured. According to Bennett (2001) for *Pteranodon* and quite possibly all pterosaurs, the prootic extent, as well as the presence of the presphenoid and parasphenoid, cannot be identified due to a complete fusion of all these elements, with obliterated sutures.

What can be described about the occiput in *T. imperator* is its shape in lateral view, preserved in most specimens including the São Paulo specimen. The supraoccipital bounds the dorsal margin

of the foramen magnum and quite possibly contacts the frontoparietals and squamosals. Posteriorly, it is projected as a supraoccipital crest. The occiput is reclined, with a posteroventral orientation. Bennett (2001) provided a methodology to measure the angle of the occiput relative to the palate, to verify how reclined the occiput was in *Pteranodon*. In the São Paulo specimen, it was measured the angle of the line formed between the condyloid process and the squamosal tuberosity, relative to the line formed by the margin of the upper jaw below the nasoantorbital fenestra, which is the posterior process of the maxilla articulated with the maxillary (anterior) process of the jugal. The angle measured is $\sim 40^\circ$, an angle similar or at least very close to the angle measured in the holotype and cotype of *T. imperator*, possibly being the pattern for the species. According to Bennett (2001) for *Pteranodon*, some of the measured angle may be an artifact of crushing. However, even when this crushing effect is considered, the range of variation seems smaller than $\sim 5^\circ$, which seems to be the typical variation within a species. A range of variation between $\sim 35^\circ$ and $\sim 40^\circ$ is also the pattern present in *T. navigans* (FREY, MARTILL & BUCHY, 2003b; pers. obs.), indicating a consistent variation within *Tupandactylus*. The paraoccipital processes, or exoccipitals, do not appear to be expanded, or at least their distal ends, while expanded exoccipitals can be observed in *Tapejara* (WELLNHOFER & KELLNER, 1991) and in *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018). The São Paulo specimen preserved the braincase entirely, but extensively crushed inside many layers of matrix. The endocranial cavity can possibly be described with a CT-Scan.

Posterior Occipital Crest

During collection, the skull lost most of its posterior occipital crest, but the base of the crest is still preserved in the São Paulo specimen, indicating that it was present and likely complete when it was discovered. As discussed above, the long crest beyond the occipital region will be regarded as the posterior occipital crest, where part of its composition is also the extended posterior process of the premaxilla. In this manner, this crest begins at the posterodorsal limit of the skull and extends way beyond the occiput. Since only its base is preserved, its extent cannot be measured, but it can be estimated based on other specimens attributed to *T. imperator*, possibly reaching about the length of the skull, measured from the tip of the premaxilla to the posterior margin of the squamosal. Although its shape is simple and elongated, at least three different layers of bones can be identified composing this complex crest (Figure F6.2.09), as in all specimens attributed to *T. imperator* except the Crato specimen. The ventral layer is a robust and elongated process, being the supraoccipital crest. The dorsal layer is also a robust and elongated process, but its true nature cannot be identified in the São Paulo specimen. It is possibly the elongated internasal (dorsal) process of the premaxilla,

which also composes the premaxillary crest, as in *Tapejara* (WELLNHOFER & KELLNER, 1991), *Sinopterus* (ZHANG *et al.*, 2019) and *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018). However, it can also be the frontoparietal crest or a fusion of both crests in *T. imperator*. This can only be described with specimens where the skull is better preserved with this crest. The processes extend posteriorly until they meet in a single, elongated unit, but how and where they fuse can only be described in complete specimens. Finally, the middle layer is a thin bone sheet that is vertically elongated, connecting the ventral and dorsal processes. The nature of this middle layer also cannot be determined. It can be a posterior extension of the parietal, a posterodorsal extension of the supraoccipital that is dorsal to the posteroventral crest, or a fusion of both bones as a blade-like unit. A very similar morphology can be observed on *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), where the holotype has a horizontal supraoccipital crest supporting dorsally a vertical posterodorsal crest. *Sinopterus* (ZHANG *et al.*, 2019) also have a similar morphology, but in this case the dorsal and ventral processes are entirely fused without a middle connective element.

Palatal Complex

All bones located at the ventral surface of the skull constitute the palatal complex. With a variable morphology, their evolution carried trends (BENNETT, 2001), even with the homology of some elements highly questionable within pterosaurs (ŐSI *et al.*, 2010; PINHEIRO & SCHULTZ, 2012). In tapejarids, these bones can be better observed on two specimens attributed to *Tapejara* (WELLNHOFER & KELLNER, 1991; WITTON, 2013) and on the holotype of *T. navigans* (FREY, MARTILL & BUCHY, 2003b), but they remain undescribed and not figured. As for related taxa, the palate of thalassodromids have been described in detail, such as *Tupuxuara* (PINHEIRO & SCHULTZ, 2012), *Caupedactylus* (KELLNER, 2013) and *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018). For *T. imperator*, the cotype (CAMPOS & KISCHLAT, 2020) and the German specimen (FREY *et al.*, 2003) revealed that the palate is convex, ventral to the ventral margin of the jugal, forming what Vidovic and Martill (2017) called the suspensorium, a condition prevalent among the pterosaurs from the Cretaceous, present in *T. navigans* (FREY, MARTILL & BUCHY, 2003b; PINHEIRO *et al.*, 2011), *Tapejara* (WELLNHOFER & KELLNER, 1991) and possibly in *Caiuajara* (MANZIG *et al.*, 2014). The palatal complex of the São Paulo specimen of *T. imperator*, however, cannot be described in detail, due to this region being covered by matrix and the lower jaw. In this manner, the shape and the contact of the pterygoids, palatines, ectopterygoids and parasphenoids are unknown. Internal naris or choanae, subtemporal fenestrae and interpterygoid opening cannot be described. The presence of palatal ridges and vomers are inaccessible.

6.2.3. Mandible

This section refers to the lower jaw, including possible crests (Figure F6.2.10). It covers the morphology of the bones related to the lower jaw, including the shape of the mandibular crest, if present (Table T6.2.02). Lower jaws in pterosaurs are highly variable, with this diversity associated with feeding strategies and quite possible sexual selection (NAVARRO, MARTIN-SILVERSTONE & STUBBS, 2018), especially on taxa with mandibular crests.

Dentary

Both dentaries, together, constitute almost all of the lower jaw in *T. imperator*, excluding the medial and posterior surfaces. As Bennett (2001) discussed, this elongation is synapomorphic for pterosaurs, with taxa from the Triassic such as *Preondactylus* and *Eudimorphodon* exhibiting lower jaws where two thirds of the jaws are exclusively the dentaries. With a developed mandibular crest, *T. imperator* reveals that the dentaries fuse anteriorly into a symphysis. Considering that the crest alone is approximately half the length of the mandible, it is safe to assume that the symphysis occupy between half and two thirds of the total length of the lower jaw, a trait observed in all pterosaurs including *Pteranodon* (BENNETT, 2001), except the most early diverging taxa from the Triassic, such as *Peteinosaurus* and *Eudimorphodon*. Bennett (2001) discussed that a shorter symphysis was the primitive condition and its elongation, together with the elongation of the dentaries at the rami, likely vary with the feeding specializations and may not help for phylogenetic reconstructions. Similar to the configuration of the skull, the dentaries, as well as the whole lower jaw, are laterally compressed. The lower jaw in *T. imperator*, overall, is similar to the observed in all tapejarids, such as *T. navigans* (GIBNEY, 2014; pers. obs.), *Tapejara* (WELLNHOFER & KELLNER, 1991; ECK, ELGIN & FREY, 2011; ELGIN & CAMPOS, 2012), *Sinopterus* (ZHANG *et al.*, 2019), *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), *Europejara* (VULLO *et al.*, 2012) and, to a lesser extent, *Caupedactylus* (KELLNER, 2013; PÊGAS, LEAL & KELLNER, 2016) and *Aymberedactylus* (PÊGAS, LEAL & KELLNER, 2016). The anterior margin is a sharp tip that extends anterior to the dentary crest, making it shaped like a prow. Similar to the premaxillomaxilla, the anterior end of the lower jaw is downturned, a typical trait of the tapejarids. Posterior to the downturned tip, the dorsal surface raises dorsally, relative to the mandibular rami, into a low distinct eminence. In a lateral aspect from a posterior-to-anterior perspective, the lower jaw first incline upwards before it bend downwards. This low eminence with the downturned tip makes the dorsal

aspect of the lower jaw have a convex-and-downturned configuration, thus performing a perfect occlusion with the upper jaw. Even with this dorsal morphology, the mandibular symphysis is subparallel to the mandibular rami. In lateral view, the mandibular rami, mostly composed by the dentaries, are straight with a convex dorsal margin, but without a dorsal eminence. Since the lower jaws of *T. imperator* are preserved in lateral view, both in the São Paulo specimen and the Crato specimen (PINHEIRO *et al.*, 2011), it is impossible to describe its dorsal, ventral and medial views. The Meckelian fossa cannot be described and overall mid-depth measurements are inaccessible.

Dentary Crest

Tupandactylus imperator has a mandibular crest that is composed solely by the dentaries, unified into a symphysis. It is located at the anteroventral portion of the lower jaw, ventral to the entire symphysis. The length of the crest is almost half the length of the mandible. With a rounded shape, it is massive and deep. The ratio of the height of the dentary crest relative to the height of the mandibular ramus is ~ 5.5 , while Vullo *et al.* (2012) registered a range of ~ 1.5 to ~ 3 for tapejarids, except *Europejara*, with a value of ~ 4 . A ratio higher than 5 can be observed on the Recovered specimen of *T. navigans* as well. This would make *Tupandactylus* the genus with the deepest mandibular crest of all pterosaurs. It begins posterior to the rostrum, in a steep and convex angle relative to the mandibular rami, ending posteriorly at the posterior limit of the symphysis, also in a steep angle relative to the rami. Broken and eroded portions of this crest reveals that the mandibular crest, similar to the premaxillary crest, is a vertical blade that is very thin. The anterior and posterior margins of the crest are asymmetrically convex, as in the Crato specimen (PINHEIRO *et al.*, 2011). However, differing from the Crato specimen, both margins are very steep and the posterior margin is steeper than the anterior margin. The anterior margin, relative to the mandibular rami, forms an angle of $\sim 65^\circ$. The posterior margin, relative to the mandibular rami, briefly forms an angle of $\sim 50^\circ$, bending to an angle of $\sim 75^\circ$ until it reaches the ventral margin. Due to preservational bias, both in the Crato and the São Paulo specimens, it is impossible to verify the texture of the crest, as well as if there are scars of blood vessels or similar structures on the dentary crest. Different from the Crato specimen as well (PINHEIRO *et al.*, 2011), where the ventral limit of the crest lies more anteriorly than posteriorly, the ventral limit in the São Paulo specimen is virtually on the middle line of the crest, with the anterior and posterior halves of the crest almost mirroring each other. These slightly differences on the shape of the crest and the relative position of the ventral limits are caused by the steep angles of the posterior margin.

Retroarticular Process

The posterior portion of the mandibular rami are mainly composed by the surangular, angular and articular. The surangular is the posterodorsal element, the angular is the posteroventral element and the articular is the posterior-most element. The surangular and articular compose the concave glenoid fossa of the lower jaw, which articulates with the condyloid process of the upper jaw. The articular and angular compose the retroarticular process, posteroventral to the glenoid fossa. In lateral view, it is possible to identify the suture between the dentary and the surangular on the right ramus (Figure F6.2.11). That means the dentary in *T. imperator* is very elongated and effectively separate the angular and the surangular. All other sutures are too damaged to be safely identified. The left ramus is exposed in medial view, but it is crushed and none of the three bones can be identified, thus their morphology and contact with other bones are inaccessible in medial view. There is a dorsal element raised on the right ramus that may be the dorsal surface of the surangular, but this identification is tentative. The morphology of the glenoid fossa cannot be described because it is covered in both rami, by the skull for the right ramus and by sediment for the left ramus. Both retroarticular processes are preserved and exposed, in right lateral view and left medial view. The processes are relatively short, relative to the mandibular rami. They are subhorizontal, relative with the mandibular rami, forms a right angle with the articular facet and have a continuous axis without a constricted posterior expansion. The Crato specimen has both retroarticular processes damaged (PINHEIRO *et al.*, 2011), giving the impression that they have a triangular shape, as in *Tapejara* (WELLNHOFER & KELLNER, 1991; ECK, ELGIN & FREY, 2011; ELGIN & CAMPOS, 2012), *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), possibly *Europejara* (VULLO *et al.*, 2012) and, to a lesser extent, *Aymberedactylus* (PÊGAS, LEAL & KELLNER, 2016). These taxa have triangular retroarticular processes, with the posterior-most tip located posteroventral. *Aymberedactylus* takes this to an extreme, presenting an elongated extra process at the triangular tip, thus the retroarticular process is unusually elongated, a feature regarded as autapomorphic (PÊGAS, LEAL & KELLNER, 2016). The São Paulo specimen reveals that the retroarticular processes on *T. imperator* are similar to *T. navigans* (pers. obs.) and *Sinopterus* (ZHANG *et al.*, 2019), as in the specimen described by Lü *et al.* (2007), where the ventral margin is convex and the dorsal margin is concave, shaping the process into a rounded and elongated hook, slightly directed posterodorsal. While tapejarids with triangular processes have angular sharp tips pointed posteroventral, the tapejarids with elongated processes have rounded tips pointed posterodorsal.

Medial Morphology

The medial view of the lower jaw on the São Paulo specimen is visible on what is exposed of the posterior half of the left ramus. However, it is badly preserved and extensively crushed, so no bone can be identified and described. Medial on the lower jaw, pterosaurs have the prearticular and the splenial, together with the medial surfaces of the surangular, angular, articular and, posterior to the symphysis, the medial surface of the dentary. It is also impossible to describe the Meckelian fossa, the adductor fossa and the possible presence of a concavity, at the medial surface of the retroarticular process, that ends in a pneumatic foramen, as in *Pteranodon* (BENNETT, 2001) and *Anhanguera* (KELLNER & TOMIDA, 2000).

6.2.4. Soft Tissue Elements

T. imperator, like all tapejarids and closely related groups, is edentulous. As Bennett (2001) and Pinheiro *et al.* (2011) discussed, edentulous pterosaurs usually present a horny sheath covering the anterior surface of both jaws. Bennett (2001) could not find direct and indirect evidence of a rhamphotheca on *Pteranodon*, while Pinheiro *et al.* (2011) identified a preserved rhamphotheca on both jaws of the Crato specimen. Such structure have also been identified on the cotype (CAMPOS & KISCHLAT, 2020) and all three specimens of *T. navigans* (FREY, MARTILL & BUCHY, 2003b; GIBNEY, 2014; pers. obs.). The rhamphotheca is not made of bone, instead being composed of soft tissue. Especially for *Tupandactylus*, another important structure that is preserved in all specimens is the high and long crest of soft tissue. This section will refer to the two elements of soft tissue identified in specimens attributed to *T. imperator*, the rhamphotheca and the crest of soft tissue. The sclerotic ring, another structure present on pterosaurs, have been observed on only one specimen of *Tapejara* (WELLNHOFER & KELLNER, 1991), few scleral plates on *Europejara* (VULLO *et al.*, 2012) and, quite possibly, one or two elements on the German specimen (FREY *et al.*, 2003).

Rhamphotheca

In the São Paulo specimen, there are some linear structures, preserved on the matrix, that here are considered pieces of the rhamphotheca. Campos and Kischlat (2020) applied for *T. imperator* the nomenclature provided by O'Malley (2005) for the rhamphotheca on birds, based on association of the beak with the jaws. Thus, the element of the upper jaw, being the superior rhamphotheca or the keratinous shield for the premaxillomaxillae, was named rhinotheca, while the element of the lower jaw, being the inferior rhamphotheca or the keratinous shield for the dentaries, was named

gnathotheca. Overall, the rhamphotheca in the São Paulo specimen is badly preserved and hardly recognizable, with a preservation very similar to the observed for the suprapremaxillary process. It is lighter than the fossil bones, with a similar color of the matrix, and its appearance is chipped and damaged, where only remnants can be recognizable. The rhamphotheca is located anteriorly to both jaws, delimiting what would be the beak of the specimen. It resembles pairs of smooth lines running parallel to the surface of the bones. The rhinotheca begins ventral to the anteriorly projecting blade and it does not contact the suprapremaxillary process (Figure F6.2.12). Its ventral limits cannot be determined, but it appears that it composes a pointed beak right anteriorly to the beaked rostrum of the premaxillomaxilla. The dorsal limit of the gnathotheca cannot be safely determined as well, but it may also compose the beak in front of the tip of the symphysis. Its ventral limit runs parallel to the dentary crest until they merge, at the horizontal middle line of the crest (Figure F6.2.13). Aside from keratinous elements, taxa that may present rhamphotheca also present few slit-like foramina, positioned in a row, at the ventrolateral limit of the rostrum or the dorsolateral limit of the mandible. This can be seen on *Tapejara* (KELLNER, 1989; WELLNHOFER & KELLNER, 1991), *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018) and *Alanqa* (IBRAHIM *et al.*, 2010). Due to the preservation in lateral view of all specimens attributed to *T. imperator*, such foramina cannot be identified. However, since elements of beaks have been described, proving its presence, it is safe to assume that *T. imperator* has such foramina.

Soft Tissue Crest

Dorsal to the frontoparietal crest, there are dark marks on the sediment that may be the very few remnants of the crest, but this identification is tentative. The dorsal surface of both the premaxillary crest and frontoparietal crest are striated, being the parallel fibers of the soft tissue crest penetrating the bones, as concluded by Frey *et al.* (2003) and Pinheiro *et al.* (2011). Aside from these evidences, there are strange channel marks on the matrix, on the dorsal-most region of the crest without bones (Figure F6.2.14). These channel scars and the matrix surrounding them are very smooth, in contrast to the laminated or rugose surface of the whole matrix surrounding the specimen. While this smooth surface with channels can be considered the mould of the soft tissue crest, there is no evidence of preserved soft tissue on the São Paulo specimen, as observed in the holotype (CAMPOS & KELLNER, 1997), cotype (CAMPOS & KISCHLAT, 2020) and the Crato specimen (PINHEIRO *et al.*, 2011). Thus, the pattern of the fibers at the middle surface of the crest cannot be identified and any mould preserved at this region is dubious. Nevertheless, these moulds can be indeed moulds of the soft tissue crest, so they were not prepared and were left untouched.

6.3. Axial Skeleton

What was preserved of the vertebral column suggests that, as Bennett (2001) discussed, most vertebrae in *T. imperator* are procoelous, a trend observed in *Pteranodon* and non-pterodactyloids, being a conserved pattern in pterosaurs. Bennett (2001) delimited that the usual vertebral count in pterosaurs is 7-9 cervicals, 12-14 dorsals, at least 3-5 sacrals and variable caudals. The cervical series is virtually complete and articulated, except cervical IX which is covered by other bones. The atlas-axis complex is associated with the skull and mid-cervicals, while the last cervical is closely associated with the mid-cervicals and dorsal series. The cervical series are large and relatively long, while the remaining vertebrae are compact and short. Cervical vertebrae are especially large and robust, displaying anterior cotyles broad and oval and posterior condyles elongated. There are three accessory articular processes, being a long hypapophysis, at the anteroventral limit of the cotyle, and a pair of postexpapophyses, ventrolateral to the condyle. Some dorsal vertebrae are preserved, but they are covered by crushed bones and sediment. They exhibit extensive fusion that strengthens and stiffens the whole series. The exposed dorsal vertebrae suggest the presence of a notarium partially developed. Sacral and caudal vertebrae are not preserved.

6.3.1. Cervical Series

This section refers to the neck vertebrae, being all vertebrae posterior to the skull and anterior to the shoulder girdle (Figure F6.3.01). It covers the morphology of all possible nine cervicals, being the two united atlas-axis complex, five mid-cervicals and two posterior vertebrae, although cervical IX is not exposed (Table T6.3.01). According to Bennett (2001), cervicals VIII and IX are cervicalized dorsals that provide a stronger connection between the cervical series and the skeleton, thus there was no reduction in the number of cervical and dorsal vertebrae since pterodactyloids appeared on the fossil record.

Atlas-Axis Complex

Although preserved, the atlas-axis complex is almost entirely covered by the skull, sediment and the third cervical. Quite possibly, both vertebrae fuse on adults on a single unit, as observed by Bennett (2001) for *Pteranodon* and pterodactyloids. What is exposed is the posteroventral surface of the condyle of the axis. It indicates that the oval condyle is wider than the anterior half of the vertebra. Ventrolateral to the condyle there are both postexpapophyses, with one entirely exposed and

the other partially covered by the skull and damaged (Figure F6.3.02). They are broad, rounded and directed laterally at an angle of $\sim 35^\circ$ from the axis of the centrum. The posteroventral surfaces of the postexapophyses are marked by shallow muscle scars. The ventral surface of the condyle, between the postexapophyses, is concave. What is exposed for *T. imperator* is similar to many ornithocheiroids listed by Bennett (2001), such as *Pteranodon*, *Nyctosaurus*, *Dsungaripterus*, *Azhdarcho*, *Quetzalcoatlus* and *Ornithocheirus*. Most of the differences that were listed for the archaeoptero-dactyloid *Pterodactylus* are, however, related to the morphology and fusion of the atlas, inaccessible in *T. imperator* so far.

Mid-Cervicals

The mid-cervicals in *T. imperator* present a morphology quite similar to the observed in *Pteranodon* that Bennett (2001) defined as a pterodactyloid pattern. All vertebrae are very similar in shape. These vertebrae are the longest and largest in pterodactyloids, considerably bigger than the dorsal vertebrae. Specifically for *T. imperator*, in comparison, each single mid-cervical is longer than five articulated dorsals. Their lengths are variable, with the third cervical increasing in length until it reaches the longest fourth and fifth vertebrae, and then decrease in length for the sixth, seventh and eighth vertebrae. Cervical VIII is the shortest exposed cervical, but quite possibly cervical IX is the true shortest cervical. This pattern is the same described by Kellner (1995) and Vila Nova *et al.* (2015) for tapejarids, where both cervicals IV and V are the longest and subequal in length. It differs slightly from what was described by Bennett (2001) for *Pteranodon* and Vila Nova *et al.* (2015) for *Azhdarcho*, azhdarchids and pterodactyloids with shorter cervicals, where the fifth cervical is the longest. Also, the length of each mid-cervical is longer than twice the mid-width, a pattern described by Vila Nova *et al.* (2015) that differentiate tapejarids from the extreme case in azhdarchids, where the length is longer than thrice the mid-width, and thalassodromids, with shorter cervicals that the length is longer than the mid-width, but shorter than twice the mid-width.

The mid-cervicals have expanded prezygapophyses, laterally diverging at an angle of $\sim 30^\circ$ from the axis of the centrum. Following their natural curvature, they are confluent with a lateral constriction of the centrum that is gradual, slightly more posterior until the middle line of the vertebra. After the middle line, where the maximum constriction occurs, the vertebra expands on the postzygapophyses, laterally diverging at an angle of $\sim 40^\circ$ from the axis of the centrum. Being all mid-cervicals procoelous, they have anterior cotyles that are broad, oval and are delimited by the prezygapophyses, while the posterior condyles are elongated, robust and extend posterior to the

postzygapophyses. Mid-cervicals in *T. imperator* also have three accessory articular processes, being the anterior hypapophysis, located at the middle ventral point and directed anteriorly, and the posterior postexapophyses, ventrolateral to the condyle and directed laterally at an angle of $\sim 30^\circ$ relative to the axis of the condyle, except for cervical VII, which diverges at a $\sim 35^\circ$ angle. Postexapophyses are observed in all tapejarids, azhdarchoids, ornithocheiroids and almost all pterodactyloids, with very few exceptions of archaeopterygoids, coded by Longrich, Martill and Andres (2018). Mid-cervicals in *T. imperator*, in lateral view, have a concave ventral surface. While most vertebrae are broken perpendicular to their axis, distorting such morphology, it is possible to observe such shape in all mid-cervicals, especially cervical VII, where the damage is the minimum possible, clearly showing this concave ventral surface (Figure F6.3.03). Vila Nova *et al.* (2015) observed that the ventral configuration of the mid-cervicals, in lateral view, follows a pattern for thalassodromids and tapejarids. In *T. imperator*, similar to the tapejarids, the surface is concave and differs from the oblique and straight surface of the thalassodromids. Vila Nova *et al.* (2015) discussed that, while both groups have well developed ventral processes, thalassodromids have shallower hypapophyses and broader postexapophyses, marking the oblique straight shape. In tapejarids, the hypapophyses are pronounced, even with the postexapophyses being the ventral-most processes, marking the concave surface. Pronounced hypapophyses occur in *T. imperator* and, similar to the tapejarid described by Vila Nova *et al.* (2015), they increase in size towards the posterior mid-cervicals and reaches the largest size, for mid-cervicals, at cervical VII. This can be observed even though some hypapophyses are a little eroded. Bennett (2001) and Vila Nova *et al.* (2015) discussed that both exapophyseal and hypapophyseal articulations, together, complement the zygapophyseal articulations. The combination of condylar-cotyler, zygapophyseal and exapophyseal articulations would prohibit longitudinal rotation and prevent downward bending, relative to the axis of the vertebrae. Bennett (2001) reported that this is possibly the pattern for pterodactyloids, because while postexapophyses occur in ornithocheiroids, *Pterodactylus* has the condylar-cotyler articulation broad and oval, severely limiting, if not prohibiting, rotation. The three articulations combined would limit movement to flexion and extension in the vertical plane, with very few lateral flexion. Although a little eroded, the hypapophyses are moderately rugose, possibly for anchoring hypaxial muscles. Postexapophyses, however, are markedly scarred by shallow muscle scars on their ventral surfaces, in all mid-cervicals (Figure F6.3.04). Laterally, the margin of the ventral surface curves smoothly up onto the centrum sides.

Since all mid-cervicals are articulated, the morphology in anterior and posterior views cannot be observed, including the surfaces for zygapophyseal articulation, the surface of pre-exapophyseal

articulation and the neural canal. Also, since all cervical vertebrae are preserved mostly in ventral view, the dorsal view, neural spine and neural arch cannot be described. Quite possibly, the dorsal view in all vertebrae are crushed and have been lost, because all vertebrae were preserved covering other bones, such as the left scapulocoracoid, the right humerus and the left metacarpals. As for the lateral surface, cervicals III and VI are a little rotated, exposing few of their lateral sides, with both vertebrae revealing that the mid-cervicals in *T. imperator* have small and elongated pneumatic foramina. As Vila Nova *et al.* (2015) discussed, the presence and number of pneumatic foramina, at the lateral surfaces of the centrum, distinguishes tapejarids, thalassodromids and azhdarchids. These foramina are absent in azhdarchids, while tapejarids have a single pair on each vertebrae and thalassodromids have two pairs, with few specific exceptions presenting up to three pairs. There is an odd pattern in *T. imperator*, where cervical III have a pair of foramina, with one at the base of the prezygapophysis and the other in the middle of the lateral side of the centrum, while cervical VI has a single and much narrower foramen located at the middle of the lateral side of the centrum (Figure F6.3.05). A variation in position was reported for *Pteranodon* (BENNETT, 2001), where few specimens present vertebrae with a pneumatic foramen at the base of the prezygapophysis and the centrum without foramina. Pneumatic foramina at the lateral side of the centrum were described for all tapejarids, except *Sinopterus dongi* (WANG & ZHOU, 2003a), however this absence only on the holotype, a young juvenile, may be an artefact of dorsoventral crushing, according to Vila Nova *et al.* (2015). As far as observations allow, there are no longitudinal sulcus at the prezygapophyses, as observed on the Chinese tapejarid described by Liu *et al.* (2014). Mid-cervicals in *T. imperator* are defined by the absence of transverse processes, thus virtually absent cervical ribs, a feature of the pterodactyloids with some exceptions of archaeoptero-dactyloids, as coded by Longrich, Martill and Andres (2018). Although covered by their own centra, sediment and articulated vertebrae, the prezygapophyses in *T. imperator* can be observed, being robust, elongated and curved, while the postzygapophyses are less pronounced and straight, a pattern similar to *Tapejara* (ECK, ELGIN & FREY, 2011; ELGIN & CAMPOS, 2012), *Sinopterus* (ZHANG *et al.*, 2019) and *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), which differs from the simple and relatively smaller pattern in *Pteranodon* (BENNETT, 2001) and thalassodromids (VILA NOVA *et al.*, 2015).

Posterior Cervicals

The posterior cervicals, which according to Bennett (2001) are cervicalized dorsals, resembles an intermediate between the mid-cervicals and dorsals. Cervical VIII and, possibly, cervical IX are similar with the mid-cervicals in presenting broad cotyles, oval condyles, a medial hypapophysis, a

pair of postexapophyses and exapophyseal articulations, while they mirror the dorsals by having their lengths shorter than their mid-widths and transverse processes with associated cervical ribs. Cervicalized dorsals are a possible feature of the ornithocheiroids, because Bennett (2001) reported two posterior cervical vertebrae in *Pteranodon*, *Quetzalcoatlus*, *Nyctosaurus* and *Anhanguera*, while *Pterodactylus* has two extra anterior dorsals and no cervicalized dorsals. Compared with the 8 cervicals and 15 dorsals from *Rhamphorhynchus*, Bennett (2001) concluded that there was no reduction in the number of cervical and dorsal vertebrae on the pterodactyloids. Bennett (2001) also concluded that cervicalized dorsals are associated with the formation of a notarium. Both structures are observed in *Pteranodon*. *Quetzalcoatlus*, another taxon with developed notarium, have cervicals VIII and IX with hypapophyses that not only are shaped like their corresponding vertebrae in *Pteranodon*, but also the muscle scars have the same shapes and positions. *Nyctosaurus*, another taxon with notarium, was described by Williston (1903) as possessing posterior cervicals that are functional cervicals but structural dorsals. Finally, both structures can be observed on the holotype of *Anhanguera spielbergi*, represented by an ontogenetic old specimen (VELDMEIJER, 2003). Quite possibly, the two vertebrae provided a firm and strong articulation between the cervical series and the notarium. Eventually, they developed condylar-cotyler and exapophyseal articulations, like the mid-cervical vertebrae, and some groups may even incorporate cervical IX into the notarium (AIRES *et al.*, 2020). Thus, the presence of cervicalized dorsals in the São Paulo specimen is an indicative for the presence of a notarium in *T. imperator*, an ontogenetic feature.

The centrum of the cervical VIII is broad, low and very short when compared to the centra of the mid-cervicals. The anterior surface has a oval cotyle. There is a huge hypapophysis at the anteroventral end of the centrum. This hypapophysis is larger than the one in mid-cervical VII, being the biggest cervical hypapophysis. This was reported by Bennett (2001) in *Pteranodon*, with the hypapophysis of cervical IX being small and residual. The size of the hypapophysis of cervical IX in *T. imperator* remains unknown. Since the hypapophysis is damaged, muscle scars cannot be identified. There are large parapophyses projecting ventrolateral from the centrum that have part of the pre-exapophyseal articular surfaces on their ventral sides, with the remainder of the articulation occurring on the centrum (Figure F6.3.06). Exapophyseal articular surfaces are continuous with the articular surface of the cotyle. In ventral view, the centrum has a constriction between the large parapophyses and the slightly smaller postexapophyses. The centrum of the cervical VIII is not pierced by pneumatic foramina. The posterior end of the centrum has a oval condyle and a pair of postexapophyses. The articular surface of the condyle extends ventrally, below the middle of the condyle and close to the posterior line between the postexapophyses, possibly articulating with the

hypapophysis of cervical IX. On the ventral surface, at the base of each postexapophysis, there is an elongated and triangular muscle scar for the insertion of hypaxial muscles (Figure F6.3.07). This contrasts with the condition of the mid-cervicals, where the muscle scars are large and on the end of the postexapophyses, below their articular surfaces. The posterior limits of the condyle and the postexapophyses are separated by a groove, since the three elements are convex in ventral view. Cervical VIII is preserved in ventral view, so the anterodorsal and posterodorsal views remain covered in sediment. The neural spine, neural arch and the zygapophyses cannot be described. Prezygapophyses are preserved and partially exposed, but heavily crushed so it may be possible to describe it with a complete preparation and disarticulation or a CT-Scan. It is possible to observe that the prezygapophyses are dorsal to the parapophyses. Cervical VIII ribs are articulated to their respective transverse processes, fused with no sutures. They are bicapitate or dicephalous, lacking a shaft. Each head has a distal process, so the rib overall has the shape of an angular hourglass. The ribs articulated make the transverse processes and parapophyses appear to have connected distal ends that are fan shaped, with expanded tips. These distal processes are probably related with lateral muscles of the neck. Lastly, cervical IX is nowhere to be seen, likely buried under mid-cervical VII and the left scapulocoracoid. There is a rib next to the cervical VIII, but it is too thin for a rib of cervical IX. Posterior cervical ribs, nonetheless, do not articulate with the sternum.

6.3.2. Dorsal Series

This section refers to the back vertebrae, being all vertebrae posterior to the cervical vertebrae and anterior to the synsacrum (Figure F6.3.08). It covers the morphology of the twelve or possibly more dorsals, separated in possibly five notariums, five free mid-dorsals in average and at least two synsacrals (Table T6.3.02). Bennett (2001) reported for *Pteranodon* and *Nyctosaurus* a total of 12 dorsals, the same value described for the holotype of *Anhanguera spielbergi* (VELDMEIJER, 2003), which has a notarium, and this value was also defined by Cheng *et al.* (2020) for the two specimens of axial skeleton of tapejarids from the Crato Formation. This possibly is the pattern for the ornithocheiroids, however some specimens attributed to *Sinopterus* casts doubt on this dorsal count. Nevertheless, quite possibly, *T. imperator* had 12 dorsals.

Dorsal Vertebrae

For ornithocheiroids, Bennett (2001) reported for *Pteranodon*, *Quetzalcoatlus*, *Nyctosaurus* and *Anhanguera* that the dorsal vertebrae can be further distinguished into three groups, being the

notarials, which are the anterior-most vertebrae that fuse into a notarium, the free dorsals, which are the middle vertebrae that present few to none fusion, and the synsacrals, which are the posterior-most vertebrae that are incorporated into the synsacrum. A similar pattern has been observed for the tapejarids from the Crato Formation (SAYÃO & KELLNER, 2006; CHENG *et al.*, 2020). How many vertebrae are incorporated on both the notarium and the synsacrum is expected to be variable, since it is an ontogenetic feature (KELLNER & TOMIDA, 2000; BENNETT, 2001; SAYÃO & KELLNER, 2006; CHENG *et al.*, 2020). For the dorsal vertebrae preserved in *T. imperator*, the synsacral vertebrae are presumably lost, because the region in the matrix where the pelvic girdle would be located is the most damaged and eroded. Also, what can be identified as posterior dorsals have no extensive fusion ongoing. The dorsals preserved and exposed on the São Paulo specimen are regarded as posterior notarials and free dorsals. The notarials are preserved, but most of them are crushed beneath other bones such as the right scapulocoracoid and cervical VII, with respective ribs preserved and exposed, revealing their position on the specimen even when the associated transverse processes relative to some ribs were eroded. According to Bennett (2001), all dorsals have a similar shape, except the anterior-most notarials and the last synsacral. Indeed, all preserved dorsals in *T. imperator* have the same morphology. The three vertebrae exposed with neural spines can be considered the dorsal V, or the last notarial, and free dorsals VI and VII.

The notarium is a rigid axial structure formed by the fusion of cervical IX and dorsals I to V, considered the notarials I to VI. It is generally related to an extra articulation between the scapulae and the dorsal vertebrae. As noted by Bennett (2001), it occurs mainly in ornithocheiroids, such as *Dsungaripterus*, *Nyctosaurus*, *Santanadactylus*, *Azhdarcho* and *Quetzalcoatlus*. Sayão and Kellner (2006) and Cheng *et al.* (2020) reported notaria for two specimens of tapejarids from the Crato Formation, while Aires *et al.* (2020) reported notaria for *Istiodactylus*, *Anhanguera*, *Tropeognathus*, *Tupuxuara*, an indetermined thalassodromin and azhdarchids, but homology is also questionable because the notaria is also present in archaeoptero-dactyloids *Germanodactylus* and *Ardeadactylus*, yet apparently absent in *Sinopterus*, *Chaoyangopterus* and *Shenzhoupterus*, three azhdarchoids. Aires *et al.* (2020) described a total of seven stages for the formation of notaria on pterosaurs, based on birds and direct observation. Different ontogenetic stages present different levels of fusion of the elements composing the notaria, including centra, neural spines, transverse processes, ventral processes and ossification of the tendons, all occurring at different paces for different notarials. In *T. imperator*, unfortunately, this region was entirely crushed and covered by other bones, such as both scapulae, so a notarium cannot be observed with certainty.

However, the notarium can be considered present for a number of indirect evidences. First, both scapulae are preserved in a position that suggests articulation with the dorsals, a feature that is exclusive to taxa with notarium. Aires *et al.* (2020), specifically, described that scapulae articulates with the dorsal IV, or notarial V. Second, and most important, two of the three dorsals preserved and exposed with neural spines, adjacent to the scapulae and considered here dorsals V to VI, suggest that they were in process of fusion. The distance between the neural spines of dorsals VI and VII is longer than the distance between dorsals V and VI, suggesting a progressive proximity for the anterior dorsals. Although a little covered, the dorsal surface of the neural spines suggest that they are in contact (Figure F6.3.09). This agrees with the fusion for the posterior notariales described by Aires *et al.* (2020) and Cheng *et al.* (2020), where the fusion occur from the anterior to posterior vertebrae, starting from the neural spines and the ossification of tendons dorsal to the spines. These dorsals are posterior to the ruined vertebra where the scapulae are located, possibly dorsal IV. Being the dorsals V and VI, these are the last notarial and the first free dorsal. Aires *et al.* (2020) described that the dorsal V is the last notarial to be incorporated into the notarium, but dorsal VI is also connected by the ossified tendon, a pattern observed in *T. imperator*. Third, the seven preserved transverse processes follow a pattern of decreasing distance from posterior to anterior, with dorsals IV, V and VI having articulated transverse processes, although suture lines can be identified. Transverse processes being fused on the notarium were observed by Bennett (2001) for *Pteranodon*, *Nyctosaurus* and *Dsungaripterus*, where the notaria in these taxa are connected at the transverse processes by longitudinal ossifications, these being possible ossified tendons. Finally, an ossified structure, identified here as an ossified tendon, can be seen where the transverse processes of the anterior dorsals would be located, articulated ventrally with dorsal ribs II, III and IV. With all this evidence, *T. imperator* can be considered a taxon where the notarium was present.

As for the morphology of the dorsals, the vertebrae preserved and exposed are quite similar in shape. Neural spines are quadrangular in shape and their height is approximately the length of the transverse processes, however this can be a preservational bias. Both neural spines and transverse processes are robust bone plates, similar to the tapejarids described by Sayão and Kellner (2006), Eck, Elgin and Frey (2011) and Cheng *et al.* (2020), while the pattern in *Pteranodon* (BENNETT, 2001) is of elements anteroposteriorly narrow. The transverse processes are extended laterally, perpendicular to the vertebrae, and quite possibly dorsal as well, but this cannot be identified due to these elements being crushed. Both proximal and distal ends of the transverse processes are elongated anteroposteriorly, giving the impression that they have constricted shafts. There are four left and at least seven right transverse processes visible, but the two right posterior-most are heavily

damaged. Both transverse processes of dorsal VIII, one vertebra without preserved neural spine, lost their contact with their respective ribs, revealing that the distal tip has a concave articular facet for their ribs (Figure F6.3.10). Bennett (2001) reported, as a pattern for pterosaurs, that the capitular facet moves progressively dorsal on the vertebrae, becoming a single articular facet with the tubercular facet, starting from dorsal IV or notarial V to the remaining dorsal vertebrae. Due to preservation, it is not possible to determine if the facet at the tip of the transverse processes in *T. imperator* represents a confluent diapophysis and parapophysis, as in other taxa. Preserved in dorsal view and articulated, the anterior, posterior and ventral views of the dorsals cannot be described, including the centra, the neural canal and ventral sides of the transverse processes, which would include the parapophyses. Zygapophyses are preserved and mostly exposed, but they cannot be described in detail due to crushing and sediment partially covering most of them. Nevertheless, they are quite simple in shape. Aside from the middle series, there is a single notarial vertebra exposed, amalgamated with other crushed bones. Judging from its position, it is presumed that this is the dorsal II or notarial III, but this identification is tentative. Nothing can be identified for this vertebra, except the broken base of its neural spine, revealing it to be relatively thick and robust.

Dorsal Ribs

Although heavily crushed and misplaced, most right ribs preserved have their corresponding left pair preserved and in close position. The posterior-most dorsals, the only dorsals that could potentially have naturally absent ribs, are eroded and lost, so the number of pairs of ribs cannot be identified, or if *T. imperator* have nine pairs of ribs, as in *Pteranodon* (BENNETT, 2001). For the preserved dorsals with preserved ribs, it is clear that the first pair is the biggest and most robust, becoming progressively slender posteriorly until the ribs of dorsal VII, which are very slender. Putting in comparison, the first ribs are twice the thickness of the seventh ribs. Preserved in dorsal view, no pneumatic foramina can be identified, which usually occur in the posterior surface. Also, since the capitulum is a ventral and proximal process, it can be observed on few ribs. Dorsal pairs of ribs I and II are heavily crushed, with the right ribs directed laterally and the left ribs directed posteriorly, so their morphology cannot be described except for their thickness and overall curved axis. The first pair appear to have an elongated groove through their axis, but this may be an artefact of crushing. Only the right third rib is preserved, with both the capitulum and corresponding transverse process eroded. Its tuberculum is huge, rounded and almost as thick as the diaphysis of the rib. It then tapers distally through its curved diaphysis, but its distal end is covered by the right humerus. Dorsal pair of ribs IV is perhaps the best pair preserved, with both ribs laterally directed

and showing most damage at their diaphysis. Even crushed, it is possible to describe their proximal head, which are bicapitate or dicephalous. The capitulum and the tuberculum are virtually the same size, although the tuberculum has a broader base and the capitulum is shaped as a cylindrical process. Both heads fuse at the proximal thick end of the rib, gradually tapering at its axis. Both ribs also have their distal tips covered. The pairs of ribs V and VI are preserved, with the right ribs directed laterally and left ribs directed posteriorly. The left rib V suggests that the posterior ribs are still bicapitate or dicephalous, but it is way too damaged to be safely assumed as two headed. Nevertheless, posterior ribs are regarded as functionally single-headed (BENNETT, 2001). The right rib VII is perhaps the most complete exposed rib. It is very elongated and curved, seemingly single-headed and, even being very slender, it slightly tapers until its distal end, which is a sharp tip. Only the right rib VII has the same overall thickness of its preceding rib. This differs from the condition observed in *Pteranodon* (BENNETT, 2001), where the posterior ribs reach the same slender thickness starting from the pair IV. Where the distal tip of the right rib VII is located, there are disarticulated distal tips of unknown ribs, possibly associated with the disarticulated sternum. It is impossible to distinguish if these are the distal tips of dorsal ribs or sternal ribs. If the ribs fuses with their corresponding vertebrae in *T. imperator* remains unknown.

6.3.3. Sacral and Caudal Series

Pterosaurs usually present three sacrals, possibly more, and the eventual fusion with the last dorsals and first caudal into a synsacrum. They fuse at the centra and zygapophyses, with the neural spines fusing into a supraneural plate, and they also fuse with their respective sacral ribs at the transverse processes, becoming a single and robust unit with the contact and fusion with the pelvic girdles. Also, early diverging pterosaurs had numerous and very elongated caudals, with elongated connecting processes and stiffening of the tail, a similar evolutionary trend with arboreal theropods (PERSONS IV & CURRIE, 2012). However, a pterodactyloid trend was the shortening of the tail (ANDRES, CLARK & XU, 2010), reaching an extreme case in *Pteranodon* and *Nyctosaurus* (BENNETT, 2001). For *T. imperator*, the region where the synsacrum and tail would be located is the most damaged and eroded, so there are no sacral or caudal vertebrae preserved. Nothing regarding the synsacrum and tail of *T. imperator* can be described. There are two regions where sacral elements are possibly preserved (Figure F6.3.11), but this identification is tentative because these bones are heavily crushed and eroded. Even if any vertebral element was preserved, it remains crushed and buried, with few to none information preserved, but it may be possible to expose it with a CT-Scan. Until then, it is safe to assume that the sacral and caudal series are virtually lost.

6.4. Appendicular Skeleton

The pectoral girdle and forelimbs in *T. imperator* are, as in all pterosaurs, highly modified for flight. As Bennett (2001) elaborated, this includes the scapulocoracoid articulating with the sternum and, through the notarium, with the dorsal vertebrae, glenoid fossa facing posterolaterally, a robust humerus with a large head and a long deltopectoral crest, the carpals modified through fusion into the proximal and distal syncarpals, a preaxial carpal with the pteroid bone for the control of the propatagium and manus consisting of three short digits, bearing strong claws, and the fourth digit greatly enlarged and hyperelongated to support a brachiopatagium. Together with the notarium and articulation of the scapulae with the vertebral column, other features that *T. imperator* has that are exclusive to pterodactyloids are an extremely elongated metacarpal IV and the virtually atrophied metacarpals I-III. The prepubis is nowhere to be seen. The pelvic girdle, even badly preserved, present the typical pattern of azhdarchoids, including a possible elongated ilium, a deep ischiopubic plate and a pelvis entirely fused with each side and the synsacrum. The imperforated acetabulum is directed laterally and, similar to *Pteranodon* (BENNETT, 2001), is entirely emarginated, allowing extreme free movement of the femur. The hindlimb is composed by a bowed femur, with a hemispherical head set on a distinct neck, elongated tibia, reduced fibula quite that possibly fused with the tibia, a mesotarsal ankle with astragalus and calcaneum fused to the tibia, forming a tibiotarsus, two distal tarsals and a pes consisting of four elongated metatarsals, bearing moderately long and unspecialized digits, and a metatarsal V reduced and stout, with a vestigial phalanx.

6.4.1. Shoulder Girdle

This section refers to the shoulder and thorax region, with its connection with axial elements (Figure F6.4.01). It covers the morphology of both scapulae and coracoids, as well as their contact with each other and any other bones (Table T6.4.01), including the sternum, an axial element that bears a robust articulation with the coracoids, a typical feature in all pterosaurs (BENNETT, 2001), making it a vital element on the connection between the forelimbs and the rest of the skeleton.

Scapula

The scapula and coracoid are co-ossified, composing a stout V-shaped scapulocoracoid that articulates with the notarium dorsomedially, the sternum ventromedially and the humerus laterally. On the left scapulocoracoid, a suture between both bones can be identified. The scapula is the bone

that articulates with the notarium, making the scapulocoracoid laterally rotated relative to the dorsal series. It is an elongated bone, medially curved and very thin, thanks to a lateral compression that begins after the scapular process and remains homogeneous until its dorsal end, with no evidence of expansions at the tip, related to the scapulonorarial articulation. A oval scapular expansion has been observed in *Pteranodon*, *Dsungaripterus* and *Quetzalcoatlus* (BENNETT, 2001). The pointed scapular process makes the shaft seems wider and some of its shape is partially covered by the left humerus. The scapula has a concavity on its shaft, between the pointed scapular process and the elongated supraglenoid process. Its lateral surface, including the supraglenoid process, composes the dorsal half of the glenoid fossa, being expanded when compared to the thin shaft. The scapula being longer than the coracoid is a typical feature of the tapejarids (ECK, ELGIN & FREY, 2011), as for any pterosaur except the pteranodontoids (AIRES *et al.*, 2014) and possibly is the condition in *T. imperator*, but this identification is tentative due to both coracoids being covered by other crushed bones. Due to crushing, a possible post-glenoid strut, also known as the scapulocoracoid pneumatic foramen, and any muscle scars cannot be observed. However, the dorsal tip and some of the surface of the shaft are heavily scarred (Figure F6.4.02). Bennett (2001) described a similar pattern for *Pteranodon*, as scars of the surface for the attachment of tendons or ligaments, related to the articulation of the scapula with a notarium. Thus, this rugose surface is yet another indirect evidence for the presence of the notarium in *T. imperator*.

Coracoid

Only the left coracoid can be described, but its ventral half is covered by the cervical VII, so its length compared to the scapula cannot be verified. Quite possibly the scapula is longer, as in every other tapejarid (ECK, ELGIN & FREY, 2011) and non-pteranodontoid pterosaur (AIRES *et al.*, 2014). It is a long bone, gently curved and its lateral surface, including the infraglenoid process, composes the ventral half of the glenoid fossa, which is expanded compared to the narrow shaft of the coracoid. The glenoid fossa is crushed and few of its shape can be described, being squared concave and laterally directed. It possibly performed a near perfect joint with the humeral head, while also providing extra space for limited flexion. The fossa is delimited dorsally by the broad supraglenoid process, of the scapula, and ventrally by the infraglenoid process, of the coracoid, also known as coracoidal process. There is another process, ventral to the coracoidal process, that is heavily crushed. Here, this ventral process is regarded as the ventral tubercle, coracoidal flange or *musculus supracoracoideus* attachment crest, defined by Kellner (2004c) as a synapomorphy of the tapejarids, but observed in azhdarchids such as *Quetzalcoatlus* and chaoyangopterids such as

Chaoyangopterus (LIU *et al.*, 2014). The crest has a variation in shape, being more of a tubercle in *Tapejara* and thalassodromids (AIRES *et al.*, 2014) and more of a flange in *Chaoyangopterus*, *Quetzalcoatlus* and *Sinopterus* (LIU *et al.*, 2014). The shape and size of this crest, relative to the coracoid, cannot be safely determined for *T. imperator*. The *supracoracoideus* crest and both the glenoid processes are mostly rugose (Figure F6.4.03), related to scars of muscle or ligaments. Due to preservational bias, it is impossible to measure the lateral angle of the scapulocoracoid relative to the axial series. The mid-cervical VII covered most of the shaft and ventral end of the left coracoid, so the shape of its tip and sternocoracoidal articulations cannot be seen.

Sternum

The sternum in *T. imperator*, an axial element that performs a robust articulation with the coracoids, is preserved and mostly complete. However, it is badly preserved and heavily crushed (Figure F6.4.04). The sternal plate is exposed, broken in half where the matrix originally broke, but all its limits are covered by crushed bones, such as the dorsal series, ribs, remnants of the pelvic girdle, both femora and a wing phalanx. Thus, the sternal plate and cristospine cannot be described. There is only one area, below the remnants of the pelvic girdle, where a portion of the sternum is exposed, with at least three elongated bone elements directly articulated with the sternal plate, here interpreted as sternal ribs, but this identification is tentative. If those elements are anterior sternal ribs, related to the notariums, posterior sternal ribs, related to the free dorsals, or anterior gastralia articulated with the posterior surface of the sternum, remains unknown. The sternum is apparently complete, so it may be possible to expose it and describe its shape and elements with a CT-Scan. However, since it is heavily crushed and eroded, it may have lost most information, if not all. Aside from these elements, disarticulated sternal ribs and gastralia are nowhere to be seen.

6.4.2. Fore Limbs

This section refers to the arms and wings, being the anterior limbs. It covers the morphology of the humerus, radius and ulna, carpals, metacarpals, phalanges with unguals, the wing metacarpal and the wing phalanges (Table T6.4.02). The description will regard the anatomical positions of the forelimb as extended laterally in flight, following Wellnhofer (1985; 1991) and Bennett (2001). Therefore, the directions given are anterior, posterior, dorsal, ventral, proximal and distal. Compared with the homology of all other tetrapods, the medial and lateral are, respectively, anterior and posterior, for the humerus, and dorsal and ventral, for the radius+ulna, while the rotated or

folded elements of the metacarpal makes the medial surface of the tetrapods homologous with the dorsal of the metacarpals I-III and the ventral of the metacarpal IV.

Humerus

The humerus is a large and robust bone, with a rounded head, a long deltopectoral crest and a distal end that is expanded, bearing two condyles for the articulation with the radius+ulna at the elbow (Figure F6.4.05). The left humerus has the proximal half better preserved, while the right humerus has the distal half better preserved. Even so, descriptions are limited to what is exposed. Both humeri, together with all other appendicular bones from the forelimbs and hindlimbs, have a very thin cortex and a wide lumen, as observed in all regions where the bones are crushed, such as the shaft of the humeri. The humeral head has the shape of a crescent moon, in proximal view (Figure F6.4.06), and it is distinct to the point that it seems flared out from the diaphysis. The way that both humeri are preserved, no region where pneumatic foramina occur is exposed. Usually, tapejarids such as *Tapejara* (ECK, ELGIN & FREY, 2011) and *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.) have two pneumatic foramina, one on ventral view, next to the anterior limit of the deltopectoral crest, and one on dorsal view, next to the ulnar crest. Both ulnar crests or posterior tuberosities are covered and cannot be described, by sediment for the left humerus and by mid-cervicals for the right humerus. Overall, the humerus has a smooth texture. The humeral head in proximal view has a granulated surface, suggestive of cartilage from the articular surface with the glenoid fossa. The shaft immediately distal to the head and next to the deltopectoral crest has a weakly rugose surface, probably a muscle scar. However, the study of Bennett (2008) regarding the myology of the wing had no muscle anchored at this area, so it may be scars of ligaments. At the middle of this area, there is a shallow groove with a thin and very small nutrient foramen. The deltopectoral crest has a proximal position, relative to the shaft, and lies adjacent to the humeral head. The base of the crest is elongated, extending through ~30% of the humeral shaft, with the axis of the crest parallel to the axis of the humerus, showing no evidence of a distal curvature. Distal curvatures are observed mostly on pteranodontoids, such as *Pteranodon* and *Anhanguera*, but not in *Nyctosaurus*, while crests parallel to the shaft are the main pattern in pterosaurs and the nyctosaurids, such as *Nyctosaurus* (BENNETT, 2001). The crest is very thin and, due to extensive crushing, its shape is hard to recognize. The proximal margin of the crest diverges from the humeral head in an almost straight line, while the distal margin is angular, near perpendicular with the humeral shaft. The deltopectoral crest of the left humerus is entirely crushed, but broken fragments of the crest lie associated to their original positions, under the second wing phalanx, suggesting that

T. imperator had a tall and elongated rectangular crest, with its length as long as the width of the humeral head. Tall and rectangular deltopectoral crest is a typical pattern of the azhdarchoids, as observed in *Tapejara* (ECK, ELGIN & FREY, 2011), *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), *Sinopterus* (ZHANG *et al.*, 2019), *Caupedactylus* (KELLNER, 2013), thalassodromids (AIRES *et al.*, 2014; BUCHMANN *et al.*, 2017), *Eopteranodon* (LÜ *et al.*, 2006a), *Montanazhdarcho* (McGOWEN *et al.*, 2002), *Tupuxuara* and *Quetzalcoatlus* (WITTON, MARTILL & GREEN 2009).

Both humeri suggests that their entire shafts in *T. imperator* are subcircular in cross-section and virtually straight, with a very small and subtle curvature. The curvature visible on the left humerus may be an artefact of crushing. No muscle scars can be identified on both shafts. The distal end of the humerus consists of a large trochlea, a much larger capitulum and the distal epicondyles, being the entepicondyle and ectepicondyle, all related to the articulation between the humerus and the radius+ulna (BENNETT, 2001). At the right humerus, the capitulum and ectepicondyle are exposed, while the trochlea is heavily crushed but with the outline preserved and the entepicondyle is covered by the crushed trochlea and sediment (Figure F6.4.07). Epicondyles are overall rounded, separated by a groove. With the trochlea and entepicondyle mostly covered, the shape and the relative size of the distal aspect and condyles are difficult to determine. It may be possible to expose it with a complete preparation and disarticulation or a CT-Scan. Similar to the proximal half of the left humerus, no region where pneumatic foramina occur at the distal end is exposed or preserved. What is preserved and exposed of the distal end of the right humerus has a shallow scar of muscles and collateral ligaments, at the surface of the shaft of the ectepicondyle, and a granulated surface at the distal end, suggestive of cartilage for articulation between the humerus and the radius+ulna. There are no visible isolated epiphysis, possibly because they are already fused with the humeri.

Radius+Ulna

The radius and ulna are moderately long and robust bones, with straight shafts and expanded ends (Figure F6.4.08). They are heavily and extensively crushed, so very few of their morphology can be described. Diameters cannot be measured, due to artefact of crushing. The right radius and ulna are entirely covered by the sternal plate, left femur, the carpals and more crushed bones, with only their diaphysis partially exposed, including inside the major cracks on the sternal plate. The left radius and ulna are better preserved and almost entirely exposed. Both ends and tips of the left ulna are buried under sediment, the skull and the supposed ulnar epiphysis, so their morphology cannot be described. Both ulnae can be exposed and described with a CT-Scan. Nevertheless, their

shafts are heavily crushed, so possible ridges cannot be identified. What can be described for the ulnae is that their diameters are virtually the double of the diameters for the radii, with the width of both ends being almost the double of the width of their diaphysis. The ulnae may be slightly longer than the radii, but this cannot be safely verified because only the left radius is entirely exposed, with its proximal end covering the ulna and its distal end being inside the orbit. The proximal end of the left radius is crushed and eroded, so most of its shape is lost. There are remnants of a proximal tubercle, a feature present in *Tapejara* but absent in *Caiuajara* and *Sinopterus*, as coded by Vidovic and Martill (2017). The distal end of the left radius is inside the orbit, with its shape preserved but covered by sediment and the skull. For what is exposed, there is a large anterior process, which makes the cross-section of the distal end have a subtriangular shape. Perhaps more information can be uncovered and described with a CT-Scan. What is exposed have few shallow scars for the attachment of muscles or ligaments (Figure F6.4.09). Finally, there is a bone that is heavily crushed, adjacent to the proximal end of the left ulna, that is regarded here as a proximal epiphysis. This identification is tentative, however, because in all other bones the epiphysis appear to be fused.

Carpals

The carpals are very complex bones. According to Bennett (2001), in pterosaurs, the carpal series are composed by two proximal carpals, with the anterior element named radiale and the posterior element named ulnare, five distal carpals, named according to their anatomic position, being the anterior, posterior, dorsal, distal and preaxial elements, the pteroid, which is a element unique for the pterosaurs, and usually up to three sesamoids. In specimens that are ontogenetically mature or old, the carpals fuse, with the two proximal carpals fusing into the proximal syncarpal and four distal carpals fusing into the distal syncarpal. The holotype of *A. piscator* is a juvenile with all carpals preserved and unfused (KELLNER & TOMIDA, 2000), being the first study to identify the small distal element of the distal carpals, the first to fuse during ontogeny. The fifth distal carpal, which in mature specimens remains unfused, articulates with both the distal syncarpal and the pteroid, which also holds an extensor tendon far away from the axis of the limb. Commonly referred as the lateral carpal, but sometimes also called the medial carpal, Bennett (2001) termed this bone the preaxial carpal, to avoid further confusions. Thus, the carpus of a mature pterosaur is composed by proximal and distal syncarpals, the preaxial carpal, the pteroid and the sesamoids. In *T. imperator*, the right carpus is preserved, but covered in sediment and crushed (Figure F6.4.10). A complete preparation and disarticulation might expose all preserved elements, with some having a tridimensional shape. However, the position of the right ulna is an indicative that some elements

were lost. The element that is better preserved and exposed is the radiale, articulated with the right radius, and has its characteristic anterior process. There is a distal concavity for articulation with the distal syncarpal. No pneumatic foramina can be identified. Any other carpal elements are nowhere to be seen. For the left carpus, there is one element partially exposed inside the orbit, with no indicative of pneumatic foramina. Distal carpals usually have less foramina, but it is impossible to tell which element is this carpal. A CT-Scan can elucidate this issue. Both pteroids and all possible six sesamoids were not found, probably buried into the matrix, under other bones or not preserved.

Metacarpals I-III

The metacarpus in *T. imperator*, as in all pterosaurs, consists of a large and hyperelongated metacarpal IV and the relatively small metacarpals I-III. Compared with the wing metacarpal, the metacarpals I-III are considerably shorter and thinner, with their proximal ends tapered into sharp points and, in some cases such as *Pteranodon* (BENNETT, 2001), they may not articulate with the carpus. Lying on the side of the wing metacarpal, in those extreme cases the proximal tips articulate only with the shaft of the wing metacarpal. However, in some cases such as *Sinopterus* (LÜ & YUAN 2005; ZHANG *et al.*, 2019), the metacarpal I is thin, like the metacarpals II and III, but also elongated and articulated with the carpus, like the wing metacarpal. By contrast, early diverging taxa have all four metacarpals articulated with the carpus (BENNETT, 2001). The metacarpals in *T. imperator* have an overall similar shape, being long and very thin rods with proximal tips tapering in a pointed end, when compared with the wing metacarpal. As in *Sinopterus* (LÜ & YUAN 2005; ZHANG *et al.*, 2019), the metacarpal I is elongated and articulates with the carpus (Figure F6.4.11). The proximal tip of the metacarpal I is not tapered, with a rounded cross-section throughout all of its length. It is worth mentioning, however, that the right metacarpal I is partially buried under the right wing metacarpal and first wing phalanx. Only a complete preparation from the matrix opposite side or a CT-Scan can confirm if the elongated thin bone, continuous to the right metacarpalia, is truly the metacarpal I. That is because some studies like Bennett (2001), Kellner (2003) and Lü and Yuan (2005) concluded that the metacarpal III is the elongated metacarpal. If there is a variation between taxa, regarding the elongated metacarpal, or erroneous identification can only be clarified with a complete preparation of *T. imperator* and a major comparative study. Nevertheless, its shape is similar to the first metacarpal in *Sinopterus* (ZHANG *et al.*, 2019). The distal tips have enlarged ends that support the functional clawed digits. They differ significantly in shape, with the distal end of the metacarpal I being entirely rounded and robust, while the distal ends of metacarpals II and III are large and slightly curved blades, being blunt, anteroposteriorly compressed and flat. This distal

morphology seems similar to *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), but it differs from the condition in *Tapejara* (ECK, ELGIN & FREY, 2011), where all three metacarpals have bladed and flat distal ends. Phylogenetic and biomechanical influences regarding this variation in morphology remains to be seen. The metacarpals I-III are usually preserved side by side, but in *T. imperator* they remained separated from the wing metacarpal in both manus. Quite possibly, the three articulated with the wing metacarpal, where the metacarpal I is the dorsal-most and metacarpal III is the ventral-most, as in *Pteranodon* (BENNETT, 2001). The distal ends of all four metacarpalia are approximate and this can be observed in both manus. The left manus is exposed, but it is heavily crushed by mid-cervicals IV and V (Figure F6.4.12). Their morphology matches the morphology of the right manus. Proximal tips are buried under the mid-cervicals, so their exact length cannot be determined. No pneumatic foramina can be identified. The articular surfaces for the digits are smooth and oval, at the rounded tip of metacarpal I and at the distal-most tip of the flanges on the metacarpals II and III. This can be better seen at the right manus, because this region on the left manus is heavily crushed and eroded and the digits of the right manus are disarticulated, but closely associated. Considering that both metacarpals I and IV articulate with the carpus, what is exposed of the right metacarpal I suggests that it was at least as long as the left humerus, so the wing metacarpal is at least as long as the humerus, a typical pterodactyloid apomorphy (PLIENINGER, 1901; KELLNER, 2003; UNWIN, 2003; PADIAN, 2004; ANDRES, 2010).

Wing Metacarpal

The metacarpal IV, also known as the wing metacarpal, is highly modified and hypertrophied, together with the digit IV, being the exclusive synapomorphy that defines the pterosaurs (OWEN, 1842; ANDRES, 2010). In *T. imperator*, both wing metacarpals are partially buried under matrix, making a complete description impossible. The proximal end of the left metacarpal is buried under the left radius+ulna. Its shaft is exposed, but heavily crushed. The cross-section of the shaft is unknown, but its surface is entirely smooth. The distal end is crushed and eroded. While a condyle can be identified, possibly ventral, it is too damaged to be described. The right metacarpal is entirely buried under the first wing phalanx. Only its distal tip is preserved and exposed. While the shaft before the tip is crushed, the tip itself kept most of its tridimensional shape. The distal end of the wing metacarpal has two condyles for articulation with the first wing phalanx. Both condyles are angled, so the posterior surface is directed dorsally and slightly offset from the shaft. Both the condyles have a rounded shape with a virtually constant radius (Figure F6.4.13), extending over the anterior and the posterior surfaces of the shaft in the form of rounded tubercles. The dorsal condyle

is comparatively wider, being flared out from the metacarpal diaphysis dorsally, in posterior view, and its dorsal surface is concave, filled with sediment. Usually, the dorsal condyle is flat at the anterodistal limit, but this region is buried and cannot be observed. Between the condyles, the distal end is flat, with no evidence of any median ridge, as observed in *A. piscator* (KELLNER & TOMIDA, 2000). For both wing metacarpals, a complete preparation and disarticulation from the opposite side of the matrix or a CT-Scan may expose them entirely, allowing full description. No scars of foramina can be seen. As a pterodactyloid, what is exposed of the left wing metacarpal suggests it was at least as long as the left humerus in *T. imperator*.

Digits I-III

The clawed digits are large, relative to the body size, but are all dwarfed by the wing finger. The digit I is the shortest and the digit III is the longest, and this size is related to their phalangeal formula, which is 2-3-4 for the digits I-II-III, respectively, including the strongly curved unguals (Figure F6.4.14). All phalanges of the digits, excluding the unguals, have approximately the same length with very few variation in size, except the second phalanx of digit III, which is much shorter than half of any other phalanx. Even heavily crushed in both manus, this can be seen in both manus. The proximal articular facet of the first phalanx in all digits differ considerably, being a concave oval facet for digit I, a concave and elongated subtriangular facet for digit III and an intermediate between these two morphologies for digit II. This can only be verified at the right manus, where the digits are disarticulated from the metacarpals and exposed (Figure F6.4.15). This variation in morphology, as described by Bennett (2001) for *Pteranodon*, may have biomechanical influences, allowing different types of movement for each digit. The left manus is so heavily crushed that it is impossible to safely associate each and every digit to its respective metacarpal. However, overall shape of the phalanges can be better observed on the left manus (Figure F6.4.16), because they are all exposed and kept most of their tridimensional shape, while only the second phalanges of digits II and III of the right manus are preserved and entirely exposed. All phalanges are straight, with a rounded cross-section and expanded ends, except the unguals, with their specific shape, and the second phalanx of digit III, which is atrophied and virtually vestigial. The first phalanx of digit III is more similar to the phalanx of *Sinopterus* (ZHANG *et al.*, 2019), with a straight shaft, instead of a shaft with a proximal bend as in *Tapejara* (ECK, ELGIN & FREY, 2011). However, the same phalanx is similar to the phalanx of *Tapejara* (ECK, ELGIN & FREY, 2011) in having a proximal expansion, absent in *Sinopterus* (ZHANG *et al.*, 2019). To make matters more complicated, the thickness of this same phalanx is greater, relative to any other phalanx, being almost the double of

the thickness of the other phalanges, whereas all phalanges have overall the same thickness in both *Tapejara* (ECK, ELGIN & FREY, 2011) and *Sinopterus* (ZHANG *et al.*, 2019). The interphalangeal joints are all ginglymoid, which means a freely moving joint with a very firm articulation that allows extensive movement in one single plane. This includes the joints between the penultimate phalanges and the unguals, better preserved at the right manus, with the articulation between the unguinal and the second phalanx of digit II entirely preserved and exposed. The exception to this rule is the articulation between the second and third phalanges of digit III, seemingly a more complex ginglymoid with more limitation to movement. *Sinopterus* (ZHANG *et al.*, 2019) has a similar morphology, as most pterosaurs, but *Tapejara* (ECK, ELGIN & FREY, 2011) has a radically different morphology, where only the first digit have a ginglymoid interphalangeal joint with condyles, while the rest of the digits have a simple concave and convex joints, including unguals that are more simplified in consequence. For the phalanges except the unguals, no foramina can be identified. Most of the phalanges kept their tridimensional shape, thus a complete preparation and disarticulation or a CT-Scan may reveal at least some foramina on some phalanges.

All six manual unguals have the same shape, being much larger than the other phalanges, with a moderately lateral compression and being curved, tapering into a very sharp distal tip. They all have a huge ventral flexor tubercle. For comparison, flexor tubercles in *Pteranodon* (BENNETT, 2001) are comparably long, but still shorter than the articular facets of the unguals. In *T. imperator*, the flexor tubercles are as long as the articular facets, with the tubercle on the unguinal of digit II being longer than the facet. There is also a shallow groove on each side of each unguinal, starting between the articular facet and the flexor tubercle and extending parallel to the curvature of the unguinal until the tip. This overall morphology may be related to grasping abilities. A pneumatic foramen can be observed on the tubercle of the unguals, more ventrally placed than the foramina observed in *Pteranodon* (BENNETT, 2001). All unguals have an approximate size, with minimum to no variation, differing from the condition in *Tapejara* (ECK, ELGIN & FREY, 2011) where the unguinal of digit III is significantly smaller. All the variation in size and shape indicates that *Tapejara* may have a different lifestyle than all other tapejarids. A comparative biomechanical study may help elucidate this issue and remains to be seen.

Wing Phalanges

As a pterosaur, *T. imperator* have a digit IV, also known as the wing digit, consisting of four hyperelongated phalanges. The wing digit lacks a unguinal and, as a pterosaur, *T. imperator* lacks a

digit V. The first three phalanges are straight or slightly curved. As an azhdarchoid, the first wing phalanx of *T. imperator* is both the largest and the longest phalanx (Figure F6.4.17), being one of the longest bones in *T. imperator*. The shaft of the first phalanx suggests it was oval to subtriangular in cross-section, with a subhorizontal axis. Interphalangeal joints are mildly expanded and flexed, giving the wing finger an overall curvature. The first wing phalanx is the exception to this rule, because of the proximal end being greatly expanded. Shaped as two huge and rounded cotyles for the articulation with the wing metacarpal, the proximal tip has a small and complex element firmly fused, known as an ossified extensor tendon process. The extensor tendon process is responsible for most of the ventral cotyle, through its posterior surface, together with few of the surface of the phalanx. The extensor tendon process is complex and saddle-shaped, with a distal facet fused with the phalanx and a proximal facet pointed and rounded, both separated by a deep proximal groove. The process develops from a secondary center of ossification and, although it is firmly fused with the phalanx, a suture line can be identified. This is a strong evidence that this specimen is not a juvenile, but also not an adult. The dorsal cotyle is at least twice as large as the ventral cotyle, positioned more posteriorly and being composed entirely by the wing phalanx. The dorsal cotyle extends beyond the shaft of the phalanx, through the posterior process. Even infilled with sediment, it is possible to observe the proximal ridge that distinguish both cotyles. There is a small ventral process on the phalanx, near the posterior end of the ventral cotyle. Bennett (2001) concluded that this was responsible for collateral ligaments, but it might also helped in preventing any dislocation of the joints. Very few scars of muscles or collateral ligaments can be identified. It is possible to identify some structures on the proximal end of the left first wing phalanx, but they are all heavily crushed and covered by left metacarpalia, while also covering the wing metacarpal. A pneumatic foramen can be identified, at the ventral surface immediately posterior to the ventral cotyle, distal to the ventral process. It is rather small, compared with the large foramina in *Pteranodon* (BENNETT, 2001) and *Tapejara* (ECK, ELGIN & FREY, 2011), a possible artefact of crushing. Other two foramina are present at the extensor tendon process, on the surface of the ventral cotyle, similar to the foramina identified by Bennett (2001) in *Pteranodon*, being the proximal-most pneumatic and the distal-most, in contact with the phalanx, nutrient. The diaphysis is simple and rounded, and the diameter is constant until the distal tip, which is buried in the right phalanx and, although a little eroded, better exposed at the left phalanx. The distal end is slightly expanded and flat to convex, with rugose scars for collateral ligaments and the joint capsule.

The remainder phalanges have a simpler shape and kept most of their tridimensional shapes. The second wing phalanx is thinner than the first, being an elongated bone with slightly expanded

tips and a long, suboval diaphysis with a constant diameter (Figure F6.4.18). The proximal articulation is flat to concave, for a rather simple articulation with the first phalanx, and also have rugose scars for collateral ligaments and the joint capsule. The right phalanx is exposed almost entirely, while the left phalanx is partially buried under the mandibular crest. The right phalanx reveals that there are rugose scars of ligaments in both tips of the phalanx. There are no pneumatic foramina in both phalanges, as observed in *Pteranodon* (BENNETT, 2001). The interphalangeal joints between the second and third phalanges are expected to be rather similar to the phalangeal joints between the first and second, and also to the joints between the third and the fourth. The simple and weakly convex-concave interphalangeal joints, according to Bennett (2001), allow very little freedom of movement and functions only to absorb shock and prevent fractures and damages. The third wing phalanx, as other azhdarchoids, is much more slender than the second, presenting almost the same thickness of the phalanges of digits I-III (Figure F6.4.19). The proximal tip is broken and lost, so its full length is unknown. It is expected that it is much shorter than the second wing phalanx. This third phalanx has a cross-section T-shaped, with a longitudinal ventral ridge, and this shape can be better seen at the broken tip (Figure F6.4.20). This is the ventral ridge that Martill and Frey (1999) considered an apomorphy of the Azhdarchidae, observed in *Azhdarcho* and *Quetzalcoatlus* (BENNETT, 2001), but it was later regarded as a feature of the azhdarchoids (SAYÃO & KELLNER, 2006) which includes the tapejarids. Indeed, *T. imperator*, which is a tapejarid, has the same ventral ridge, so it is safe to conclude that this ridge is apomorphic for the more inclusive Azhdarchoidea and, thus, pterosaurs from the Crato Formation preserving phalanges with T-shaped cross-sections are not necessarily azhdarchids. Martill and Frey (1999) reported that the ventral ridge occurs on the second phalanx as well, and this can only be partially seen in the São Paulo specimen of *T. imperator*. The right second wing phalanx has the same ventral ridge, starting as a ventrally shallow process that elongates and develops through its shaft, but since the shaft is broken and buried, few of this ridge can be seen. Nevertheless, the shaft between both phalanges are overall straight. The interphalangeal joint between the third and fourth phalanges is crushed, but it still maintain some of its tridimensional shape, being simple, flat and weakly convex-concave.

The fourth and last wing phalanx differs considerably in shape from the other wing phalanges. The proximal end of this phalanx has an articular facet expanded and flat to subcircular, with scars for collateral ligament and no visible pneumatic foramen, but this may be a preservational bias of missing broken pieces. The shaft is markedly curved with a subcircular cross-section. Lacking a distal articulation, the fourth phalanx tapers into a terminal distal end that is pointed. The fourth wing phalanx is expected to be the shortest in pterodactyloids, and azhdarchoids usually have very

short terminal phalanges. *Tupandactylus imperator*, however, takes this to an extreme, with the phalanx being shorter even relative to the phalanges of digits I-III, thus it is virtually vestigial. This extreme shortening of the fourth wing phalanx was observed on two azhdarchoids (KELLNER & LANGSTON, 1996; ELGIN & FREY, 2011). This can only be observed on the right phalanges, because the left phalanges, although preserved, are buried under the mandibular crest. A CT-Scan may expose them, allowing their full description and comparison with the exposed right phalanges.

6.4.3. Pelvic Girdle

This section refers to the pelvis and hip region, with its connection with the sacral elements (Figure F6.4.21). It covers the morphology of both ilia, ischia and pubis, as well as their contact with each other and any other bones (Table T6.4.03), including the prepubis, an axial element that bears a robust articulation with the ischiopubic plate, a feature that is observed in all pterosaurs (BENNETT, 2001) and may have been a vital element regarding lung ventilation (CLAESSENS, O'CONNOR & UNWIN, 2009).

Ischiopubic Plate

Most elements of the pelvic girdle, together with both prepubis, are missing, possibly eroded and lost. Prepubis of tapejarids are known from Sayão and Kellner (2006) and Cheng *et al.* (2020), with two specimens presenting prepubis that are fan-shaped and articulated medially with each other, posteriorly with the pubis and anteriorly with the posterior-most gastralia. The pubis is also heavily crushed, eroded and lost, with only few pieces composing the acetabulum and preserved anteroventral remnants. The shape of both the pubis and ischium and how they contact each other is unknown, together with the presence and position of a obturator foramen, as in *Tapejara* (ECK, ELGIN & FREY, 2011). The ischium is heavily crushed and eroded, with most of its morphology lost. What is preserved is the posterodorsal margin, which forms the sciatic notch, a sulcus in which the sciatic nerve and other soft tissues are situated, together with the postacetabular process of the ilium. As in *Sinopterus* (ZHANG *et al.*, 2019), the sciatic notch has approximately the same height or depth as the depth of the acetabulum (Figure F6.4.22). Since most of the posterior margin is not preserved, it is impossible to tell its shape in lateral view, if it is angular, as in *Tapejara* (ECK, ELGIN & FREY, 2011), or rounded, as in *Sinopterus* (ZHANG *et al.*, 2019). The ischiopubic plate in dorsal view is certainly longer than wide.

Acetabulum

The main lateral feature of the ischiopubic plate is the acetabulum, being very large, deep and directed laterally, with a slight posterior orientation. The acetabulum is formed by all three bones of the pelvic girdle, but in *T. imperator* a third of the acetabulum, composed by the pubis, is eroded and lost. Shaped as a rounded concavity nearly hemispherical, it is imperforated as in all pterosaurs (BENNETT, 2001). The acetabulum, preserved where the matrix suffered most of the taphonomical damage, is mostly tridimensional, revealing that it is very robust and deep, thanks to a peripheral emargination around the whole cotyle, which may have guaranteed that the acetabulum resisted better to damage, relative to the remainder of the pelvic girdle. Nevertheless, foramina and scars of muscles were not preserved due to extensive crushing and eroding. The surface of the cotyle inside the emargination is rugose, being possibly scars from ligaments with the femur.

Ilium

The ilium is a long and slender bone that composes the dorsal third of the acetabulum, with this region being a landmark for delimiting the preacetabular and postacetabular processes. For the left side, an elongated but heavily crushed bone may be the left preacetabular process, but this identification is tentative. For the right side, there is a small bone over the sternum that is rounded, eroded and it remains on the same horizontal plane of the right ilium. It possibly is the anterior tip of the preacetabular process, as in *Tapejara* (ECK, ELGIN & FREY, 2011), *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.) and *Sinopterus* (ZHANG *et al.*, 2019), but this identification is tentative as well. The remainder diaphysis of the ilium is long and straight, being very thin and plate-like. The postacetabular process extends posterodorsal, delimiting the dorsal-most limit of the posterior margin of the pelvis and, ventrally, the sciatic notch with the ischium. Although possibly shorter than the preacetabular process, the postacetabular process is at least twice as long as the length of the acetabulum, as observed in *Tapejara* (ECK, ELGIN & FREY, 2011). It is divided in half, but its overall shape is preserved, being a process with a constricted shaft, expanded posterior end and a pointed hook process directed anteriorly, at the dorsal surface, making the postacetabular process have a fan shape in lateral view. If this hooked process fuses with the sacral supraneural plate, as in *Pteranodon* (BENNETT, 2001) and the specimens of tapejarids described by Sayão and Kellner (2006) and Cheng *et al.* (2020), remains unknown. The medial surface is entirely buried in the matrix. Scars and foramina cannot be identified due to preservational bias.

6.4.4. Hind Limbs

This section refers to the legs and feet, being the posterior limbs. It covers the morphology of the femur, tibia and fibula, tarsals, metatarsals, phalanges with unguals, the fifth metatarsal and the fifth digit, if present (Table T6.4.04). Following Bennett (2001), even if the hindlimb is abducted during flight, it is described lying in a parasagittal plane for terrestrial locomotion. Therefore, the orientation terms such as medial and lateral correspond and are homologous with other tetrapods.

Femur

Both femora, overall, are elongated relative to the skeleton, as with all the elements of the hindlimbs (Figure F6.4.23). The femora are long, slender and straight to slightly bowed. The right femur is better preserved than the left femur, but its proximal end is damaged and somewhat rotated, making it appear more strongly bowed as an artefact of crushing. The left femur, even heavily crushed, kept its overall shape of the shaft, although its distal half is also partially angled as an artefact of crushing. The femoral head is distinct, rounded hemispherical and would perform a perfect and tight fit articulation with the acetabulum. Scars of muscles and ligaments are visible on the femoral head and neck. Posterior to the femoral head, the femoral neck with a subcircular cross-section is constricted in approximately half the diameter of the head. This narrow neck is angled $\sim 130^\circ$ anteromedial, relative to the axis of the femur. As Bennett (2001) observed on *Pteranodon*, a femur with a rounded head and slender neck, articulated in an acetabulum entirely emarginated, would allow enormous freedom of movement for the hindlimb. This can be better seen at the right femur, because the left femur lost almost all of its head. However, what has been preserved also shows the expanded head, constricted neck and an anteromedial inclination. In proximal view, the eroded bone also shows that it had few to none pneumatization (Figure F6.4.24). This may be an artefact of crushing, however Bennett (2001) also noted for *Pteranodon* that the hindlimb does not appear to have been pneumatic, because all foramina are quite small and resembles more nutrient foramina. The only pneumatic foramen at the hindlimb of *Pteranodon* is at the proximal portion of the femur, between the femoral neck and the great trochanter. The presence of this foramen, inside the intertrochanteric fossa, cannot be observed in *T. imperator*, since the left femur lost this region entirely and the right femur, although preserved, has this region crushed and buried. Lateral to the region where the femoral neck joins the shaft, there is a large and rugose process that is regarded as the greater trochanter, which according to Bennett (2001) is responsible for the insertion of the *musculus iliofemoralis* (Figure F6.4.25). The lesser trochanter is represented by a small and eroded

process, immediately distal to the greater trochanter on the shaft, however this region is the most damaged on the right femur so most of its shape and scars are crushed and eroded. Since the posterior view is buried, the internal trochanter cannot be observed, but a complete preparation or a CT-Scan may expose this region entirely.

The shaft of the femur is slightly bowed in anterolateral view. The cross-section of the shaft is not known for the proximal third, since it is entirely crushed, but for the remainder of the shaft it is elongated and suboval. The right femur resisted crushing and preserved most of the tridimensional shape of the shaft, but it did not preserve any visible muscle scars on the shaft. The posteromedial view is mostly covered, so the fourth trochanter cannot be seen, only with a complete preparation or a CT-Scan. The distal end is laterally expanded, with large distal condyles for the articulation with the tibiotarsus. Both medial and lateral condyles on both femora are crushed, so it is impossible to distinguish each other, but on both femora the condyles are huge, developed and flared out of the diaphysis. The condyles are usually separated by a posterior and shallow intercondylar sulcus, being buried on both femora. The condyles are angled slightly posteriorly, extending onto the posterior surface. Bennett (2001) discussed that the angled condyles suggest a maximum angle of extension, between the femur and the tibiotarsus, of $\sim 140^\circ$, while the condyles flared out onto the posterior surface suggests that considerable flexion was possible, as observed in one specimen of *Pteranodon* with a preserved knee articulated and flexed. Biomechanical studies testing the limits of flexion and extension, however, remains to be seen. The lateral epicondyle, presumably as well as the medial epicondyle, is large and rugose, possibly of collateral ligaments. The size of the lateral epicondyle relative to the medial epicondyle, as well as for the medial condyle relative to the lateral condyle, cannot be verified because one condyle and epicondyle is buried on each femur.

Tibia+Fibula

The atrophied fibula and the proximal tarsals, being the astragalus and calcaneum, are fused to the large tibia forming the tibiotarsus (Figure F6.4.26). The tibia itself is a long and slender bone with a straight shaft. The proximal articular surface is flat, slightly concave, with rugose scars of collateral ligaments. This can be better seen on the right tibiotarsus. The proximal cnemial crest of the tibia, as well as any scars of muscle or ligament, are hard to identify due to preservational bias, aside from the proximal scars of collateral ligaments. Both tibiae are extensively crushed, so their cross-sections are unknown, but the shafts are mostly preserved. The diameter is almost constant, tapering slightly from the proximal quarter to the distal quarter. At the distal end, the tibia has an

apparent lateral expansion, in the shape of two condyles, being the exposed lateral and the buried medial condyles, but these elements are actually the fused tarsals. Aside from the condyles, there is a lateral epicondyle that is exposed, proximal to the lateral condyle, and it is small and pointed. The left tibiotarsus is rotated, so the posterior view is exposed. There are some remnants of a fibula preserved, apparently fused but crushed and eroded. The proximal end of the fibula is robust and elongated, but dwarfed by the tibia. It has a proximal cotyle for the articulation with the femur and an overall triangular shape, with a dramatic decrease in diameter to a very thin and slender bone. Its true length is unknown because its distal half is eroded and lost, but it possibly was half to a third of the length of the tibia, as in *Tapejara* (ECK, ELGIN & FREY, 2011) and *Pteranodon* (BENNETT, 2001). The proximal end of the fibula is fused to the proximal end of the tibia and quite possibly both bones were entirely fused, as observed in ontogenetically older and mature specimens of *Pteranodon* (BENNETT, 2001), but not in a juvenile specimen of *Tapejara* (ECK, ELGIN & FREY, 2011). The distal end of the left tibia is buried under the mandibular crest.

Tarsals

The tarsals, as well as the metatarsals and pedal digits, are only visible for the right pes, since the left is buried under the mandibular crest (Figure F6.4.27). All elements kept their tridimensional shape, no matter how extensively they were damaged. Tarsals are composed by a pair of proximal tarsals, being the astragalus and the calcaneum, and a pair of distal tarsals. Some specimens, such as one attributed to *Rhamphorhynchus* (BENNETT, 2001) and one attributed to *Sinopterus* (ZHANG *et al.*, 2019), revealed that there may be three distal tarsals, with two fusing ontogenetically into one. If no tarsals fuse with each other or if indeed a third distal tarsal fuse with another distal tarsal remains to be carefully studied. Both the proximal tarsals are fused with the tibia into a tibiotarsus, composing the two distal condyles, but suture lines can be identified. The lateral condyle is exposed in anterolateral view, while the medial condyle is buried within the matrix. As Kellner (2004b) described for the morphology of the proximal tarsals in *Tapejara*, the calcaneum composes the anterior half of the lateral condyle, while the broader astragalus composes the medial condyle entirely and the posterior half of the lateral condyle. The lateral condyle has a middle linear suture, possibly from the contact between the proximal tarsals (Figure F6.4.28), that runs adjacent to the suture between the tibia and the tarsals, immediately distal to the small and pointed lateral epicondyle of the tibia. The proximal tarsals are overall subequal in size, relative to the distal tarsals. In lateral view, the lateral condyle is subcircular, flared out of the diaphysis of the tibia and forming a convex $\sim 290^\circ$ angle, being convex in anterior view. With the medial condyle buried, its

size and the intercondylar sulcus cannot be observed. The distal tarsals are much more complex in shape, and only some of their morphology can be described, since both are partially buried. The exposed surface of the medial tarsal is elongated and concave, presumably for the articulation with the medial condyle. The lateral tarsal is more exposed and has a more complex shape, with one medial facet concave, associated with the medial tarsal, a distal squared concavity, associated with the fourth metatarsal, and both connected by a convex surface, presumably for the articulation with the fifth metatarsal. The proximal surface is shaped into two distinct cotyles for the distal condyles of the tibiotarsus, with the posterolateral cotyle larger than the anteromedial cotyle. Lying in close association, almost in articulation, the dorsolateral corner of the medial distal tarsal and the medial corner of the lateral distal tarsal fit together, as a proximomedial process, that would articulate into the intercondylar sulcus of the tibiotarsus. How this articulation occur is unknown, since the sulcus is covered with sediment. Both proximal and distal lateral tarsals are a little eroded on their surface, including the contact surface of the distal tarsal for the fifth metatarsal, revealing their internal structure that apparently is pneumatic. Anteriorly, the lateral distal tarsal tapers into a small point, posteroventral to the larger proximal concavity. Bennett (2001) described something similar to *Pteranodon*, concluding that it probably anchored ligaments relative to the flexion of the pes.

Metatarsals

The pes in *T. imperator* are composed by the metatarsals I-IV, which are long and slender, and a metatarsal V robust and short. Metatarsals I-IV differ very little in size, being virtually the same length and thickness. Although with a minimal variance, the metatarsal III is longer than all others. The cross-section of all four metatarsals is rounded. The four proximal ends are slightly expanded and subtriangular, with a proximal concavity for articulation with the tarsals. This is better seen for the metatarsal IV, the most exposed metatarsal, showing that there are at least two articulation surfaces for, quite possibly, both distal tarsals. Also, metatarsals I-IV appear to articulate with each other laterally, at their proximal ends, forming a single articulation unit with the tarsals. These long metatarsals have little to no curvature, being virtually straight. There are no visible scars of muscles or ligaments, possibly buried or covered. A complete preparation may allow the disarticulation of each bone, exposing possible scars. The distal ends have little to almost no expansion, being convex in shape. There are a pair of distinct, but shallow distal condyles, better seen at metatarsals I and III, suggestive of a ginglymoid articulation with the digits. The four distal ends are associated with each other, but do not seem to be articulated. As the most damaged metatarsal, there seems to be no pneumaticity on metatarsal IV, however there is one possible nutrient foramen on the proximal end.

The metatarsal V is dwarfed by the other four metatarsals, with a length as long as a third of the lengths of metatarsals I-IV. It is triangular and hook-shaped, with a proximal width much wider than the distal width and a medial process that articulates with the lateral distal tarsal laterally. The metatarsal V is disarticulated from the lateral distal tarsal, so the contact surface between these bones are exposed. The articular surface is rugose, remnants of collateral ligaments, and its shape is rather complex but matches perfectly the tarsal region where it would articulate. The metatarsal has a bend at the midsection, where the medial process is located, with the concave side directed anterolaterally and the convex side directed posteromedially. This morphology makes the proximal half located more anteriorly, relative to the metatarsals I-IV, but the distal half remains in line with the metatarsals I-IV. Foramina cannot be identified, possibly buried or covered by the metatarsal I. The lateral surface is buried and cannot be described. The distal end tapers into a cylindrical process with a flat convex tip. As for the proximal tip, although it does not articulate with any other bone, it is a rounded square in shape. The left metatarsals are buried under the mandibular crest, but are certainly preserved. There is one elongated bone exposed inside the cracks of the crest that matches the morphology of the right metatarsals I-IV (Figure F6.4.29), with a similar element associated with it. It may also be the left wing phalanges, but most probably these are left metatarsals. That reinforces the necessity of a complete preparation and disarticulation of the opposite side of the matrix or a CT-Scan to expose the buried left pes.

Pedal Phalanges

All four digits are disarticulated and mixed with each other, together with the distal phalanges and all unguals being lost during collection. Thus, no preserved phalanx can be associated with a specific digit. Overall, they have an approximate length, are subcircular in cross-section with a slender diaphysis and have ginglymoid interphalangeal joints, with proximal cotyles and two distal rounded condyles. The only phalanges that differ in morphology are the second phalanx of digit III and both the second and third phalanges of digit IV, which are very short in taxa such as *Pteranodon* (BENNETT, 2001), but these cannot be recognized in *T. imperator*. The digit V have a rather peculiar evolutionary pattern in pterosaurs. As coded by Longrich, Martill and Andres (2018), early diverging taxa have two elongated and straight phalanges on the digit V, supporting a patagium (DALLA VECCHIA, 2003). There is some variation on its morphology, as observed in other taxa (LÜ *et al.*, 2010), but overall they have the same basic pattern. However, this pattern changed for pterodactyloids, to a single and vestigial phalanx with no visible functions, as observed

in archaeopteroxyloids (LÜ, 2003). A presumed synapomorphy for the ornithocheiroids is the entire loss of the digit V, as observed in *Pteranodon* (BENNETT, 2001), *Anhanguera* (KELLNER & TOMIDA, 2000) and *Tapejara* (ECK, ELGIN & FREY, 2011). A residual phalanx has been reported for the chaoyangopterids, as observed in *Jidapterus* (WU, ZHOU & ANDRES, 2017), that could be a synapomorphy for a more inclusive clade inside Chaoyangopteridae. However, *Sinopterus* was coded by Longrich, Martill and Andres (2018) without a digit V, possibly because the presence of the phalanx in *S. dongi* (WANG & ZHOU, 2003a) was reinterpreted as an erroneous identification. The reappearance of the digit V in *Sinopterus* was confirmed by Zhang *et al.* (2019), where the specimen described had one vestigial phalanx perfectly preserved in both pes. The evolution of the pedal digit V for the azhdarchoidea can be interpreted in three different ways: first, Chaoyangopteridae may indeed be inside Tapejaridae, as recovered by Pinheiro *et al.* (2011), and closely related to *Sinopterus*, with these taxa sharing the reappearance of the digit V. Second, the evolution of this character may have been more complex than previously thought, reappearing and disappearing more than once inside Ornithocheiroidea. Third, the digit V may not have disappeared at all in some clades, such as Azhdarchoidea, and its presumed absence in taxa such as *Tapejara* (ECK, ELGIN & FREY, 2011) may be a preservational bias. *T. imperator*, just like *Sinopterus*, have a present and exposed pedal digit V, disarticulated from the metatarsal V but closely associated (Figure F6.4.30), confirming that this digit is present in more than one species of tapejarid. Similar to all pterodactyloids with a digit V, such as *Sinopterus* (ZHANG *et al.*, 2019), it is composed by a single vestigial phalanx, being the smallest of all bones in the skeleton of *T. imperator*. Although not formally described and referred to a taxon, the tapejarid from Brazil originally considered an azhdarchid by Frey *et al.* (2003) also has a vestigial digit V. The pes of this specimen is better figured by Witton (2013), at the page 048. The evolution of the digit V in Azhdarchoidea remains a mystery and further researches are more than necessary.

6.5. Phylogenetic Analyses

The new São Paulo specimen of *T. imperator*, together with previously described remains attributed to *Tupandactylus*, allows a case study of the phylogenetic relationships and position of *T. imperator* within Tapejaridae, Azhdarchoidea and Pterosauria, with a comprehensive cladistic analysis. The dataset is a modified version of the character list (Appendix B) and taxon matrix (Appendix C) by Longrich, Martill and Andres (2018), where multistate characters, ordering and reductive coding were used and the characters were polarized based on four outgroup taxa, with *Euparkeria* as the main outgroup, followed by *Ornithosuchus*, *Herrerasaurus* and *Scleromochlus*.

6.5.1. Equally Weighted Analysis

The dataset was first analyzed with the characters equally weighted, with similar parameters as used by Longrich, Martill and Andres (2018), for a direct comparison. This analysis resulted in an overflow of most parsimonious trees, reaching the maximum 50.000 designated space for trees on the analysis and indicating there were more trees that overflowed. Although not all trees have been saved, the maximum value saved represents a safe sample for discussion. Exploratory analyses using New Technology searches (GOLOBOFF & CATALANO, 2016) recovered a very similar result. These 50.000 trees have a best score of 2964 steps, consistency index of 0.208 and retention index of 0.659. Overall, the strict consensus kept a similar structure recovered by Wu, Zhou and Andres (2017), but with differences and five unstable positions revealed by the IterPCR algorithm.

Equally Weighted Tree

For non-pterodactyls, the main difference is a paraphyletic Eopterosauria (Figure F6.5.01). Most taxa from the Triassic were recovered as a grade to Macronychoptera. *Arcticodactylus* was the first taxon on this grade, followed by *Preondactylus* and *Austriadactylus*, thus Preondactylia was also recovered paraphyletic. A trichotomy follows up, being composed by the Macronychoptera, *Peteinosaurus* and Eudimorphodontoidea as recovered by Andres, Clark and Xu (2014), excluding *Arcticodactylus*. Macronychoptera and Novialoidea kept the exact same composition from Wu, Zhou and Andres (2017), with Dimorphodontia and *Campylognathoides* remaining unchanged. Breviquartossa presented a novel composition, with *Scaphognathus* and *Orientognathus* outside of Rhamphorhynchidae, as a grade towards Pterodactylomorpha. This Rhamphorhynchidae recovered *Fenghuangopterus* associated with *Qinglongopterus*, while *Dorygnathus* was recovered as a sister

group to Rhamphorhynchini. Here is where the first instability is located, with two possible positions for Angustinaripterini excluding *Qinglongopterus*: as sister group to *Dorygnathus* and Rhamphorhynchini or as sister group to the clade with *Fenghuangopterus* and *Qinglongopterus*. It was recovered the same composition of Pterodactylomorpha, Monofenestrata, Darwinoptera and Wukongopteridae from Wu, Zhou and Andres (2017), except Wukongopteridae presented another internal resolution. *Darwinopterus* was not recovered monophyletic, because *Kungpengopterus* and *Changchengopterus* were recovered inside the genus. Also, *D. linglongtaensis* was the second instability, recovered in three different positions: as sister group to *D. robustodens*, as sister group to the clade with *Kungpengopterus* and *Changchengopterus* or as sister group to *Changchengopterus*. As for Anurognathidae, a grade was recovered inside this clade, made by *Luopterus*, *Anurognathus* and *Batrachognathus* all the way up to *Dendrorhynchoides* and *Jeholopterus*.

For Pterodactyloidea, *Kryptodrakon* was recovered as the most early diverging taxon, maintaining its position as the earliest pterodactyloid and as the sister group of Lophocratia, which is the remaining pterodactyloids (Figure F6.5.02). Archaeopterodactyloidea was recovered as a trichotomy, composed by *Cuspicephalus*, Euctenochasmata and a clade where *Germanodactylus* is closely related to *Altmuehlopterus* and *Kepodactylus*, thus *Kepodactylus* was recovered outside of Ctenochasmata. Euctenochasmata is composed by *Pterodactylus* and Ctenochasmatoidea. Both clades composing Ctenochasmatoidea resembles the clades in Wu, Zhou and Andres (2017) in many ways. One such clade is a trichotomy of *Normannognathus*, *Cycnorhamphus* and *Aurorazhdarcho*, closely related to *Ardeadactylus*. The other is Ctenochasmata, with small differences compared to Wu, Zhou and Andres (2017). Ctenochasmatinae remained as the earliest internal clade, but composed by *Liaodactylus* as sister group to a clade with two dichotomies, being *Ctenochasma* with *Pterodaustro* and *Gegepterus* with *Beipiaopterus*. Ctenochasmatinae was recovered as sister group to a clade composed by Moganopterinae and Gnathosaurinae, with their internal composition unchanged when compared to Andres, Clark and Xu (2014). As for Eupterodactyloidea, *Haopterus* was recovered outside Ornithocheiroidea, as of Wu, Zhou and Andres (2017), which is composed by Pteranodontoidea and Azhdarchoidea. Pteranodontoidea was recovered composed by two unnamed groups, with one group composed by Lonchodectidae and Boreopteridae and the other composed by *Hongshanopterus* with Pteranodontia and Lanceodontia. Although *Hongshanopterus* was recovered closer to pteranodontians than to lanceodontians, it remained an early diverging taxon inside Pteranodontoidea, but with Lonchodectidae and Boreopteridae being the earliest clades, thus Ornithocheiromorpha was recovered invalid. For Pteranodontia, Pteranodontidae had the same composition of Wu, Zhou and Andres (2017), while Nyctosauridae had a very similar

composition of Longrich, Martill and Andres (2018), with changes being *Muzquizopteryx* having a closer relationship with *Alcione* and *Simurghia* and this clade is closely related to a trichotomy, with a paraphyletic *Barbaridactylus* and a monophyletic *Nyctosaurus*. For Lanceodontia, Istiodactylidae remained unchanged from Wu, Zhou and Andres (2017) and related to a clade with a monophyletic *Cimoliopterus* and Anhangueria. Anhangueria had drastic changes, thanks to the third instability on the trees. It is composed by a trichotomy of *Cearadactylus*, *Tropeognathus* and the remaining taxa, roughly resembling the Anhangueridae of Wu, Zhou and Andres (2017). However, *Liaoningopterus* is related to another trichotomy, composed by *A. blittersdorffi*, *A. spielbergi* and a clade including *A. piscator* and *Ludodactylus* with *Guidraco*, effectively making *Anhanguera* paraphyletic. To make matters worse, the third instability is caused by a clade where *Ornithocheirus* is related to a trichotomy of *Siroccopteryx* and both *Coloborhynchus*, so this clade resembles the Ornithocheiridae of Wu, Zhou and Andres (2017). The positions this clade recovered where as sister group to *Ludodactylus* and *Guidraco*, inside *Anhanguera*, and as the earliest diverging clade in Anhangueria.

As for Azhdarchoidea, major clades kept a very similar composition, but there are significant differences (Figure F6.5.03). Azhdarchoidea was recovered composed by two major clades. One is Neopterodactyloidea with a worse resolution, composed by a trichotomy of *Eoazhdarcho*, another trichotomy of the chaoyangopterids, with *Shenzhoupterus*, *Chaoyangopterus* and *Jidapterus*, and the Azhdarchidae. Although monophyletic, Azhdarchidae is the clade with the worst resolution, where *Montanazhdarcho* was recovered as sister group to a polytomy of eight taxa, including *Azhdarcho*, *Zhejiangopterus*, *Phosphatodraco*, *Aralazhdarcho*, *Eurazhdarcho*, *Arambourgiania*, *Quetzalcoatlus* and *Hatzegopteryx*. On the other clade that composes Azhdarchoidea, it is also composed by a dichotomy. One of the clades of this dichotomy is Dsungaripteromorpha, with Dsungaripteridae and Thalassodromidae. Dsungaripteridae had the exact same composition as of Andres, Clark and Xu (2014). Thalassodromidae have *Tupuxuara* monophyletic and the earliest diverging clade, followed by *Caupedactylus*, which is recovered closer to the thalassodromids instead of the tapejarids. *Caupedactylus* was recovered as sister group to *Thalassodromeus*, which is monophyletic. A variation in this clade occurred because of the fourth instability, the clade including *Alanqa* and *Aerotitan*, recovered as the earliest thalassodromids or as the sister group to *Caupedactylus* and *Thalassodromeus*. The other clade of this dichotomy is the Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014). This Tapejaridae was recovered based on the length of the mandible, being longer than one fourth of the width, and the presence of a mandibular crest. These are the characters scored 126, from 0 to 1, and 137, from 0 to 1. This Tapejaridae has *Aymberedactylus* as the earliest tapejarid, which is recovered closer to the tapejarids instead of the

thalassodromids, and a polytomy of seven taxa: *Tapejara*, *Europejara*, *Caiuajara*, *Sinopterus*, *T. imperator*, *T. navigans* and *Eopteranodon*. This polytomy is united by a downturned symphysis, a step-like and distinct dorsal eminence on the symphysis and a symphyseal middle expansion, characters coded 109, from 1 to 2, 112, from 0 to 1, and 124, from 0 to 1. When the IterPCR algorithm is applied, the fifth and final instability is detected, which is *Europejara* being recovered as sister group to either *Tapejara* and *Caiuajara*. When *Europejara* is removed, this internal node becomes better resolved, with *Tapejara* and *Eopteranodon* closely related and as sister group to the four taxa that is recovered bearing a suppremaxillary process. In this clade, *Sinopterus* is the earliest diverging taxon, followed by *T. navigans* up to *T. imperator* closely related to *Caiuajara*, making *Tupandactylus* paraphyletic with respect to *Caiuajara*.

Equally Weighted Stability Measures

Two alternative stability measures were performed to measure the frequency of the nodes in the 50.000 most parsimonious trees. These measures, resampling by Bootstrap (Figure F6.5.04) and Jackknife (Figure F6.5.05), were made with 1000 replicates, using heuristic searches.

As a result, all trees from the Bootstrap and Jackknife had a huge polytomy, indicating that many of the internal clades of Pterosauria are not recovered in at least half of the trees. Most of these same clades, when recovered by the group contradicted frequencies, indicate that they have very low values. Some clades always maintained stability, regardless of the analysis, such as *Pteranodon*, *Thalassodromeus* and *Tupuxuara*, which always had more than a 50% frequency, Anurognathidae with more than 80% in all trees, all up to *Campylognathoides* and Istiodactylidae, which had more than 95% frequencies, to name a few. While some clades had variable frequencies, such as Anhangueria ranging from 44% to 58%, other groups were never recovered on the 50% cut trees and had very low measures of frequencies on the 0% cut tree, such as Azhdarchidae, where 28% was the highest value on a internal node only, Nyctosauridae, where the group had up to 42% of frequency but the internal nodes had lower values, and all Ctenochasmatidae, where the highest frequency was 37%, except for the internal nodes of Gnathosaurinae, with more than 60%, and Moganopterinae, with more than 90%. As for Tapejaridae, both 50% cut trees did not recover *Aymberedactylus* with the tapejarids, while the remaining taxa were recovered as a polytomy with 63% of frequency for the Bootstrap and 76% for the Jackknife. This indicates that at least the internal node of Tapejaridae has a good frequency. For the 0% cut trees, except for this same node, all nodes had very low values, with 20% being the highest value on a clade uniting *Caiuajara* with

Europejara, on the Bootstrap tree, while this clade had 13% on the Jackknife tree. *Tupandactylus* was recovered monophyletic only on the 0% cut Bootstrap tree, with a frequency value of 6%.

6.5.2. Preliminary Implied Weighted Analysis

The dataset was then analyzed with weighted characters, applying an implied weight principle as proposed by Goloboff (1993), for a direct comparison with the equally weighted analysis. Since the analysis performed is preliminary, only one "k" constant value was applied, being one, instead of testing multiple "k" constant values and performing a sensibility analysis to find the ideal value, as proposed by Wheeler (1995) and Prendini (2000). Here, the implied weighted analysis, with "k" constant value of one, was performed only for comparisons with the results of the equally weighted analysis made by Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017), Longrich, Martill and Andres (2018) and this study. This analysis resulted in a fixed number of 918 most parsimonious trees, with a best score of 378.06372 highest total fit, consistency index of 0.212 and retention index of 0.666. Overall, the strict consensus presented relationships and structure more similar to the ones recovered by Wu, Zhou and Andres (2017) than the equally weighted analysis, but also with notable particular differences. This analysis had two unstable positions revealed by the IterPCR algorithm.

Implied Weighted Tree

Regarding non-Pterodactyloidea, most groups that composes Eopterosauria were recovered monophyletic, however Eopterosauria remained paraphyletic (Figure F6.5.06). Preondactylia was recovered as the earliest diverging clade of Pterosauria, followed by Eudimorphodontoidea and then *Peteinosaurus*, with the two clades having the same compositions of Wu, Zhou and Andres (2017). An interesting aspect of this result is that *Eudimorphodon* could be considered monophyletic if, similar to Wu, Zhou and Andres (2017), *Arcticodactylus* and *Carniadactylus* were considered two species of *Eudimorphodon*. The Macronychoptera and Novialoidea also kept the same composition recovered by Wu, Zhou and Andres (2017), so Dimorphodontia and *Campylognathoides* remained unchanged. Breviquartossa presented a novel composition, with Rhamphorhynchidae rearranged yet again. In this analysis, *Orientognathus* was recovered as the earliest divergence than other taxa, while *Fenghuangopterus* and *Scaphognathus* remained outside of the Rhamphorhynchidae as a grade towards Pterodactylomorpha. Rhamphorhynchinae had the same relationships as Wu, Zhou and Andres (2017), with *Dorygnathus*, Rhamphorhynchini and Angustinaripterini unchanged. Pterodactylomorpha remained unchanged, but Monofenestrata had variations. *Pterorhynchus* was

recovered as sister group to a clade including Wukongopteridae and Caelicodracones, effectively making Darwinoptera paraphyletic. Wukongopteridae kept a similar composition, when compared to Wu, Zhou and Andres (2017), except for *Changchengopterus* recovered closely related to *Kungpengopterus*. *Darwinopterus* was recovered monophyletic and with the same arrangement observed on Wu, Zhou and Andres (2017). Since *Changchengopterus* was recovered as a Wukongopteridae, Pterodactyliformes was recovered invalid. Caelicodracones remained valid and composed by Anurognathidae and Pterodactyloidea. As for Anurognathidae, it is composed by two groups, one with *Luopterus* and *Dendrorhynchoidea*, the other with *Anurognathus* related to *Batrachognathus* and *Jeholopterus*. An interesting aspect of this result, quite similar to the taxa on Eudimorphodontidae, is that *Dendrorhynchoidea* can be considered monophyletic if, similar to Wu, Zhou and Andres (2017), *Luopterus* was considered a species of *Dendrorhynchoidea*.

For Pterodactyloidea, *Kryptodrakon* was recovered again as the most early diverging taxon, maintaining its position as the earliest pterodactyloid and as the sister group of Lophocratia, which in Wu, Zhou and Andres (2017) represents the remaining pterodactyloids (Figure F6.5.07). The Archaeopterodactyloidea was recovered monophyletic, composed by Euctenochasmatia and a clade with *Cuspicephalus*, *Germanodactylus* and *Altmuehlopterus*, not unlike the composition in Wu, Zhou and Andres (2017). An interesting aspect of this result, quite similar to *Eudimorphodon* and *Dendrorhynchoidea*, is that *Germanodactylus* could be considered monophyletic if, similar to Wu, Zhou and Andres (2017), *Altmuehlopterus* was considered another species of *Germanodactylus*. Euctenochasmatia composed by *Pterodactylus* and Ctenochasmatoidea, together with both clades composing Ctenochasmatoidea, resembles Wu, Zhou and Andres (2017) in many ways. The first clade have *Ardeadactylus* as sister group to a polytomy of four taxa, with *Normannognathus*, *Cycnorhamphus*, *Aurorazhdarcho* and also *Kepodactylus*, thus *Kepodactylus* was recovered again outside of Ctenochasmatidae. The other clade is Ctenochasmatidae, with small differences when compared to Wu, Zhou and Andres (2017). Moganopterinae remained the earliest diverging clade and sister group to a paraphyletic Gnathosaurinae, thanks to Ctenochasmatinae being recovered inside it. Thus, this second clade has a grade composed by *Huanhepterus*, *Plataleorhynchus*, *Gnathosaurus* as a monophyletic genus, all the way up to *Liaodactylus* as sister group to a clade with two dichotomies, being *Ctenochasma* with *Pterodaustro* and *Gegepterus* with *Beipiaopterus*. Eupterodactyloidea had *Haopterus* again recovered outside Ornithocheiroidea, as in Wu, Zhou and Andres (2017), which is composed by Pteranodontoidea and Azhdarchoidea. Pteranodontoidea had a very similar result to the equally weighted analysis. There are two unnamed groups, being one composed by the Lonchodectidae and Boreopteridae and the other composed by *Hongshanopterus*

with Pteranodontia and Lanceodontia. *Hongshanopterus* was recovered closer to pteranodontians than to lanceodontians again, but it remained an early diverging taxon inside Pteranodontoidea. With the position of Lonchodectidae and Boreopteridae, Ornithocheiromorpha was yet again recovered invalid. For Pteranodontia, the Pteranodontidae had the same composition of Wu, Zhou and Andres (2017), while Nyctosauridae had few to no resolution. *Alamodactylus* was recovered as the earliest nyctosaurid, followed by *Cretornis* and a polytomy, composed by *Muzquizopteryx*, both *Barbaridactylus* and another polytomy of four taxa, with *Alcione*, *Simurghia* and both *Nyctosaurus*. This time, both *Nyctosaurus* and *Barbaridactylus* were not recovered monophyletic, instead of only *Barbaridactylus* as in the equally weighted analysis. The four species were recovered related on the equally weighted analysis, more similar to Longrich, Martill and Andres (2018), while the implied weighted analysis recovered few to no resolution and relationships between these taxa. As for Lanceodontia, Istiodactylidae again remained unchanged from Wu, Zhou and Andres (2017) and related to a clade with a monophyletic *Cimoliopterus* and Anhangueria. Anhangueria had interesting changes, thanks to the first instability on the trees. It is composed by a clade with *Cearadactylus* and *Tropeognathus* as sister group to a group including Anhangueridae and *Ludodactylus* with *Guidraco*. *Liaoningopterus* is recovered related to a monophyletic *Anhanguera* in Anhangueridae, and *A. blittersdorffi* is more closely related to *A. piscator* than to *A. spielbergi*. The instability here is caused by a clade where *Ornithocheirus* is related to a trichotomy of *Siroccoptyx* and both *Coloborhynchus*, so this clade resembles the Ornithocheiridae of Wu, Zhou and Andres (2017), the same observed on the equally weighted analysis. This clade is recovered as sister group to the clade of *Ludodactylus* with *Guidraco*, or as sister group to *Cearadactylus* with *Tropeognathus*.

As for Azhdarchoidea, major clades kept the same composition as in Wu, Zhou and Andres (2017), with interesting differences (Figure F6.5.08). Azhdarchoidea was recovered composed by two major clades, being Neoazhdarchia and Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014). Neoazhdarchia is composed by the Neopterodactyloidea and Dsungaripteromorpha, as in Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018). Dsungaripteromorpha was recovered composed by Dsungaripteridae, which had the exact same composition as of Andres, Clark and Xu (2014), and Thalassodromidae, with *Tupuxuara* monophyletic. *Tupuxuara* forms a sister group with a trichotomy of *Caupedactylus*, a monophyletic *Thalassodromeus* and *Alanqa* with *Aerotitan*. *Caupedactylus* was again recovered closely related to the thalassodromids instead of the tapejarids, but this result must be interpreted with caution. Neopterodactyloidea is formed by Chaoyangopteridae, with *Shenzhoupterus*, *Chaoyangopterus* and *Jidapterus*, and similar to Longrich, Martill and Andres (2018), *Eoazhdarcho* was recovered closer

to Azhdarchidae. Again the clade with the worst resolution, Azhdarchidae had the same composition as the equally weighted analysis, where *Montanazhdarcho* forms a sister group to a polytomy of eight taxa, being *Azhdarcho*, *Zhejiangopterus*, *Phosphatodraco*, *Aralazhdarcho*, *Eurazhdarcho*, *Arambourgia*, *Quetzalcoatlus* and *Hatzegopteryx*. Here lies the second instability, where *Phosphatodraco* and *Aralazhdarcho* are recovered as a group, similar to Longrich, Martill and Andres (2018), but only if all other taxa except *Azhdarcho* are removed.

Finally, Tapejaridae on this analysis was recovered based on a single character, being the presence of a mandibular crest, scored 137, from 0 to 1. *Aymberedactylus* is again the earliest tapejarid, closely related to the tapejarids instead of the thalassodromids, and is the sister group of a clade united by a downturned symphysis, a step-like and distinct dorsal eminence on the symphysis and a symphyseal middle expansion, characters coded 109, from 1 to 2, 112, from 0 to 1, and 124, from 0 to 1. This clade, in turn, is composed by *Eopteranodon* and a group united by a shorter mandible, the reacquisition of the quadratojugal (posterior) process of the jugal, parasagittal condyles of the mandibular articulation, shallow fossa on the anterodorsal surface of the symphysis and a relatively shorter first wing phalanx, characters coded 002, from 2 to 3, 060, from 1 to 0, 088, from 1 to 0, 119, from 1 to 0, and 295, from 5 to 4. This group has *Tapejara* as sister group to a clade that is united by the presence of the suprapremaxillary process, quadrate articulated with medial surface of the jugal, a relatively longer wing metacarpal and shorter fourth wing phalanx, characters scored 022, from 0 to 1, 084, from 0 to 1, 278, from 3 to 4, and 303, from 1 to 0. This clade of taxa with a suprapremaxillary process and tetradial jugals has two monophyletic groups. One has *Europejara* grouped with *Caiuajara*, united only by a shorter symphysis, character 117 coded, from 4 or 5 to 3. The other has *Sinopterus* closely related to *Tupandactylus*, with the three taxa grouped by the retroarticular process being an elongated and rounded hook, a longer mandibular crest, five synsacral vertebrae at least and a strongly bowed fourth wing phalanx, characters scored 133, from 0 to 2, 138, from 1 to 2, 202, from 4 to 3, and 304, from 0 to 1. Finally, *Tupandactylus* was recovered monophyletic, on the implied weighted analysis, based on an striated premaxillary crest, thanks to its connection with a high soft tissue crest, the posterior margin of the nasoantorbital fenestra being reclined, where the dorsal margin of the fenestra is posterior to the ventral margin, and the tip of the symphysis being elongated and shaped like a prow, being the characters 025, from 1 to 0, 038, from 1 to 0, and 108, from 1 to 2.

Implied Weighted Stability Measures

Two alternative stability measures were performed to measure the frequency of the nodes in the 918 most parsimonious trees. These measures, resampling by Bootstrap (Figure F6.5.09) and Jackknife (Figure F6.5.10), were also made with 1000 replicates, using heuristic searches.

As a result, not unlike the equally weighted analysis, all trees from the Bootstrap and Jackknife had a huge polytomy, indicating that many of the internal clades of Pterosauria are not recovered in at least half of the trees. When these same clades are recovered by group contradicted frequencies, it is indicated that they have very low values. Similar to resamples performed for the equally weighted analysis, some clades always maintained stability, regardless of the analysis, such as *Thalassodromeus* and *Tupuxuara*, with more than 50% frequency on trees of group frequencies and 48% or more on the trees of group contradicted frequencies, Boreopteridae and *Pteranodon*, which always had more than 60%, all up to Anurognathidae and *Campylognathoides*, which had more than 90%, to name a few. While some clades had variable frequencies, such as Anhangueria ranging from 11% up to 24%, other groups were never recovered on the 50% cut trees and had very low measures of frequencies on the 0% cut tree, such as Azhdarchidae, where the clade was recovered with 1% to 8% values, with higher values of 28% on internal nodes only, Nyctosauridae, where the group had 28% to 31% support, and Ctenochasmatidae, where the clade had 7% and 17% support, while internal nodes had better support, such as Moganopterinae, with more than 90%. As for Tapejaridae, both 50% cut trees did not recover *Aymberedactylus* with the tapejarids, similar to the equally weighted analysis. The remaining taxa were recovered with 78% for the Bootstrap and 79% for the Jackknife. This indicates that at least the internal node of Tapejaridae has a good frequency, similar to the equally weighted analysis. Another internal node recovered was the tapejarids united by the tetra- and jugals, with 71% for the Bootstrap and 75% for the Jackknife. Finally, a relationship between *Sinopterus* and *Tupandactylus* was also recovered as a trichotomy, presenting 55% for the Bootstrap and 59% for the Jackknife. For the 0% cut trees, an interesting result was *Caupedactylus* closely related to the tapejarids instead of the thalassodromids. These supports have very low values and only happened because Thalassodromidae was recovered paraphyletic on both cases. The highest value uniting *Caupedactylus* and *Aymberedactylus* with all other tapejarids was 15%. The remaining tapejarids were united in both cases with more than 70% support. The group sharing tetra- and jugals had 64% for the Bootstrap and 70% for the Jackknife. Internal nodes had low values, however, with the highest frequency being 17% for the clade with *Tapejara*, *Europejara* and *Caiuajara*. *Sinopterus* with *Tupandactylus* had 31% for the Bootstrap and 37% for the Jackknife and, lastly, *Tupandactylus* monophyletic was recovered in 26% frequency for the Bootstrap and 24% for the Jackknife.

7. DISCUSSION

7.1. Tapejaridae Taxonomy

The cranial material of the new specimen corroborates with characters already described for *T. imperator* and overall tapejarids, but it also provides new information regarding the morphology and the ontogeny of *Tupandactylus* and closely related taxa.

7.1.1. *Tupandactylus imperator* Autapomorphies

The São Paulo specimen presents all synapomorphies that distinguish *Tupandactylus*, as defined by Pinheiro *et al.* (2011), and can be safely referred to this genus. It has a very large nasoantorbital fenestra, comprising more than 45% of the preserved length of the skull, excluding cranial crests. Recurrent in all specimens, including the São Paulo specimen, the nasoantorbital fenestra represents ~60% of the length of the skull. This makes the preorbital rostrum very long in *Tupandactylus*, but also makes the prenasal rostrum very short, something expected for tapejarids and thalassodromids (MARTILL & NAISH, 2006). This is highlighted with the rostral value and the rostral index of the São Paulo specimen, respectively ~2 and ~2.8. The rostral index, however, is closer to the values of the thalassodromids *Tupuxuara* and *Thalassodromeus* than to the values of the tapejarids *Tapejara* and *T. navigans*, presented by Martill and Naish (2006). Curiously, *Tapejara* and *T. imperator* were plotted erroneously on the scale of rostral indexes provided by Martill and Naish (2006), where *Tapejara* has an index of 0.5 and was plotted as higher than 2, while no value was informed for *T. imperator* and it was plotted together with *T. navigans*. The prenasal rostrum of the premaxillomaxilla and the anterior tip of the dentary symphysis, regardless of curvatures, are downturned or turned ventrally in a linear configuration. This condition is typical for tapejarids and it differs from *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018), which has a rostrum downturned in an arched configuration, being related to its rostral autapomorphies. The premaxillary crest is huge, with a bone blade high and subtriangular supporting an extensive area of soft tissue. While the soft tissue crest is badly preserved, maybe not preserved at all, the presence of said crest is confirmed thanks to the striated surface at the premaxillary and frontoparietal crests, being the parallel fibers of the crest penetrating the bones, as considered by Frey *et al.* (2003) and Pinheiro *et al.* (2011). Although hardly recognizable, the premaxillary crest has an anterodorsal suprapremaxillary process very high and thin, at the dorsal limit of the crest. Finally, the posterior extension of the premaxilla articulates with the nasal and the frontoparietal. The posterior margin of

the internasal (dorsal) process of the premaxilla cannot be identified in the São Paulo specimen, but the frontoparietal and its dorsal crest, together with the premaxilla, merge into a single long unit, with no disassociation between the long crest and the skull. Thus, there is a contact between the premaxilla, the nasal and the frontoparietal. This last character regards the skull configuration of *Tupandactylus* in comparison to *Tapejara* (WELLNHOFER & KELLNER, 1991) and *Sinopterus* (ZHANG *et al.*, 2019), where the posterior extension of the premaxilla is disarticulated but parallel to the skull roof. Pinheiro *et al.* (2011) already discussed that this may be an ontogenetic feature.

Regarding *Tupandactylus*, Pinheiro *et al.* (2011) defined a total of four autapomorphies for *T. imperator*, providing also four autapomorphies for *T. navigans* that differentiate these two species apart. First, the ratio of skull length to height, being the length from the tip of the premaxilla to the posterior margin of the squamosal, relative to the height from the quadrate condyle to the dorsal margin of the premaxilla, dorsal to the orbits and exclusive of crests, is about 3.6. This reflects that *T. imperator* has a very long skull, much longer than *T. navigans*, with the nasoantorbital fenestra, premaxillary crest and upper jaw composing more than half of this length. The São Paulo specimen does present a very close value to ~ 3.6 . Second, the premaxilla is anteriorly projected, with a convex blade anteriorly projected. This character reflects the anterior process at the premaxillary crest, absent in *T. navigans* and present in the São Paulo specimen. Third, the suprapremaxillary process has a posterodorsal orientation, with the parallel fibers of the soft tissue crest subvertical with a posterodorsal curvature. This character is influenced by the anterior projection, because the anterior blade occurs at the ventral limit of the suprapremaxillary process, being responsible for its change of direction. In *T. navigans*, without the process, the parallel fibers and suprapremaxillary process have a subvertical orientation with an anterodorsal curvature. The São Paulo specimen has the suprapremaxillary process with a posterodorsal direction, as expected, and this change of direction is indeed caused by the anterior blade. Even with the São Paulo specimen virtually not preserving the soft tissue crest, it is possible to identify that most of the striated surface of the bony crests have a very gentle posterodorsal curvature. Finally, the main autapomorphy distinguishing these two taxa is the posterior occipital process, as long as the skull, extending beyond the posterior margin of the skull. This long process is present in *T. imperator* and absent in *T. navigans*. Unfortunately, this region was lost during collection, so the size of the process cannot be observed. However, the base of this process is preserved, posterodorsal to the occiput, confirming its existence in the São Paulo specimen. Thus, the São Paulo specimen exhibits all autapomorphies, as defined by Pinheiro *et al.* (2011), assigned to *T. imperator*, being safely referred to this species.

It is worth mentioning that the posterior occipital process in *T. imperator* is more complex than previously thought, being composed by the supraoccipital crest and two more crests that unite into a long bifurcated process. Here, the three elements of the crest will be regarded following Lü *et al.* (2007) for *Sinopterus* and Wellnhofer and Kellner (1991) for *Tapejara* as the main morphology for the tapejarids, where the posterior process of the premaxilla extends beyond or until the parietal, respectively. Thus, the posterior occipital process in *T. imperator* is composed by three elements: the dorsal process being the premaxillary internasal process, elongated posterior to the occiput, the ventral process being the elongated supraoccipital crest and the middle element, a thin and vertical bone blade connecting the two processes, being the parietal crest. Other hypothesis regarding the identity of these elements, however, cannot be ruled out. The frontoparietal crest may compose the dorsal process, other bones may participate on this posterior crest, as well as where and how the two processes meet are few of the many questions that remains to be answered in light of complete and better preserved skulls with this complex crest. Nevertheless, the main autapomorphy distinguishing *T. imperator* from all other tapejarids must refer not only to its size, not preserved on the Crato and São Paulo specimens, but also to its overall shape, not preserved only on the Crato specimen.

7.1.2. *T. navigans* and *Tupandactylus* Synapomorphies

According to Pinheiro *et al.* (2011), as characters defined for *T. imperator*, *T. navigans* also has four autapomorphies that distinguish it as a separated species. First, the length to height ratio in *T. navigans* is about 2.3, against the ratio of 3.6 in *T. imperator*. Second, the premaxilla is straight, without the anteriorly projecting convex blade as seen in *T. imperator*. Third, the suprapremaxillary process, since there is no anterior blade, has a subvertical orientation, with the parallel fibers of the soft tissue crest directed subvertical with an anterodorsal curvature, while in *T. imperator* both the process and fibers have a posterodorsal curvature. Finally, the main autapomorphy for each species of *Tupandactylus*, the posterior occipital process is absent in *T. navigans*, where the posterior extension of all cranial crests reaches the very limit of the posterior margin of the skull. Here, both *T. imperator* and *T. navigans* are considered valid species within the same genus, in agreement with Pinheiro *et al.* (2011). While the possibility of sexual dimorphism cannot be ruled out (PINHEIRO *et al.*, 2011), it is more likely that they represent two species with different crests (CHENG *et al.*, 2017). This issue can only be solved in light of more complete specimens, however.

A new character, described for the first time for *T. imperator*, is the presence of a descending process of the nasal. The specimen designated as the holotype, by Campos and Kellner (1997), and

cotype, by Campos and Kischlat (2020), did not preserve this structure, indicating that it possibly was absent on this taxon. Frey *et al.* (2003) and Unwin and Martill (2007) never cared to performed a complete description of the German and Private specimens, nor to illustrate the skull in detail or even to complete preparations to testify if the process is indeed absent in these specimens. Finally, the Crato specimen described by Pinheiro *et al.* (2011) does not have the posterior half of the skull preserved. This apparent absence of a descending process of the nasal became dubious with the holotype of *T. navigans* (FREY, MARTILL & BUCHY, 2003b), where a partially eroded process is present. Here, the São Paulo specimen reveals that not only the descending process is present, but it has a shape never before seen in any pterosaur. The descending process of the nasal is thin and triangular, with the posterior tip articulated with the main body of the nasal, the anterior tip being projected anteriorly and the ventral tip elongated into a thin rod-like process. It is a lateral process directed medially and anteroventrally, meeting at the middle point and fusing into a single medial process. Finally, it is long, reaching the ventral limit of the nasoantorbital fenestra but it does not articulate with it. Elongated and free descending processes of the nasal are known in many taxa, for example *Ludodactylus* from the Crato Formation (FREY, MARTILL & BUCHY, 2003a), but all taxa that have free descending processes have a different shape. In the example of *Ludodactylus*, the process is also triangular but tapers entirely to a middle point, then expands again until it tapers to a sharp tip close to the ventral limit of the nasoantorbital fenestra. Other taxa, such as *Pterodactylus* and *Germanodactylus*, usually have a simple process, with a tapered base that is firmly articulated with the main body of the nasal and an elongated tip, beyond half of the nasoantorbital fenestra (WELLNHOFER, 1970), but in such cases none actually reach its ventral limit, as in the São Paulo specimen of *T. imperator*. It is safe to assume that this morphology for the descending process is a new apomorphy. There is one consideration that must be taken into account, that is the condition in *T. navigans*. The holotype present remnants indicating that the descending process also reaches the ventral limit of the nasoantorbital fenestra, not articulating with it as well. Since it is fragmentary, however, its shape cannot be observed, whether it has a triangular base or an unique shape. If a new specimen reveals that *T. navigans* actually presents the exact same configuration for the descending process, then this character can be entirely considered a *Tupandactylus* synapomorphy instead. Until then, presence, length and orientation of the descending process can be considered synapomorphies for *Tupandactylus*, while the overall shape can be considered a new autapomorphy for *T. imperator*.

It is worth mentioning that the posterior occipital process is not only the main autapomorphy distinguishing *T. imperator* from all other tapejarids, but its presence and shape is one of the main characters that distinguishes each and every species of tapejarid with a skull. In *T. imperator*, as

discussed, there is a very long, straight and complex posterior process, composed possibly by the premaxilla, as a dorsal process, the supraoccipital, as a ventral process, and the parietal, as a thin vertical blade connecting both processes. In *T. navigans*, the posterior process is absent, a condition exclusive to this species. In *Tapejara* (WELLNHOFER & KELLNER, 1991; ECK, ELGIN & FREY, 2011), the process is mainly formed by the frontoparietals with a ventral contribution of the supraoccipital, being straight, shorter than in *T. imperator* and elliptic in cross-section. In *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), what is preserved on the holotype is a horizontal supraoccipital crest with a vertical parietal crest, but the posterodorsal limits are eroded. Nevertheless, it has a posterodorsal bend on the middle of what is preserved, with straight outlines aside from this bend. In *Sinopterus* (LÜ *et al.*, 2007; ZHANG *et al.*, 2019), both the premaxilla and the parietal, possibly with ventral contribution of the supraoccipital, composes a long process curved dorsally, with dorsal and ventral processes running parallel to each other in close association, without a connecting blade. In this manner, this specific variation is true even when Tapejaridae *sensu* Kellner (1989) is used, because *Tupuxuara* (KELLNER & CAMPOS, 2007) and *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018) also have their own unique configurations for the posterior process. A similar condition has been observed for the wukongopterids (CHENG *et al.*, 2017) and this may be true to all tapejarids and thalassodromids described, but without complete skulls this remains unknown.

Pinheiro *et al.* (2011) also listed, as two more autapomorphies for *T. imperator*, a very deep and rounded mandibular crest with a steep anterior margin, forming an angle of $\sim 60^\circ$ with the mandible, and a small dorsal concavity at the downturned anterior region of the symphysis. These characters were determined for *T. imperator* in basis of the Crato specimen, the first with a lower jaw preserved that was described. Until then, no lower jaws attributed to *T. navigans* were known. The discovery of the Recovered specimen (GIBNEY, 2014; pers. obs.), a complete specimen of *T. navigans* which includes a complete lower jaw, allows comparison between the morphologies of the lower jaws in *T. imperator* and *T. navigans*. In the lower jaw of the Recovered specimen, there is a very deep and rounded mandibular crest, bigger than any tapejarid except *T. imperator*. Due to its size, it also has a steep anterior margin with an angle of $\sim 60^\circ$ to $\sim 65^\circ$ with the mandibular rami. It also has a small and long dorsal concavity at the anterior region of the symphysis, where the jaw is downturned. These two characters can be observed in *T. navigans*, making them synapomorphies for *Tupandactylus*. The Recovered specimen also has a steep posterior margin for the crest, similar to the São Paulo specimen but different from the Crato specimen. The difference in the size of the crest and the angle of the posterior margin, between the Crato and São Paulo specimens, may be due to ontogenetic variation, as in *Anhanguera* (PINHEIRO & RODRIGUES, 2017). *T. navigans*

differs from *T. imperator* by having a comparatively shorter crest, while *T. imperator* has a longer crest, together with the convex dorsal margin being higher and more angular, while in *T. imperator* it is more attenuated and rounded, both relative to their mandibular rami.

Another character of the lower jaw that is worth mentioning is the shape of the retroarticular process. Tapejarids have, as a pattern, triangular retroarticular processes. The triangular process is comparatively short, except in *Aymberedactylus* (PÊGAS, LEAL & KELLNER, 2016), presenting a subhorizontal ventral margin, a descending dorsal margin and the posterior tip is sharp and directed posteroventral. Both the São Paulo specimen, for *T. imperator*, and the Recovered specimen, for *T. navigans*, have a retroarticular process comparatively elongated, with a convex ventral margin, a concave dorsal margin and the posterior tip is a rounded eminence directed posterodorsal, shaped like a rounded elongated hook. The Crato specimen did not present this morphology (PINHEIRO *et al.*, 2011) due to both rami having this area heavily damaged. The right retroarticular process was cut in half during collection and was not preserved, while the left process is eroded and also close to the same cut line made during collection. Pinheiro *et al.* (2011) concluded that the retroarticular process in *T. imperator* was triangular and similar to all other tapejarids, although smaller, because of this preservational bias. With both processes preserved and complete in the São Paulo specimen, as well as the left process exposed in the Recovered specimen (GIBNEY, 2014; pers. obs.), it is safe to assume this character as synapomorphic for *Tupandactylus*, the third synapomorphy of the lower jaw for the genus. Another interesting aspect is this synapomorphy being not exclusive, because it is shared with some specimens of *Sinopterus* (LÜ *et al.*, 2007; ZHANG *et al.*, 2019).

7.1.3. Comparisons and *Aymberedactylus* Validity

Regarding the pterosaurs described from the Crato Formation, *Tupandactylus* differ from all toothed pterosaurs, like *Brasileodactylus* (SAYÃO & KELLNER, 2000) and *Ludodactylus* (FREY, MARTILL & BUCHY, 2003a), by the lack of teeth and the presence of a rhamphotheca in place of the teeth. *Arthurdactylus* cannot be compared with *Tupandactylus* due to a lack of preserved skulls on the former, but Frey and Martill (1994) already pointed out characters, such as a triangular and warped deltopectoral crest, that indicates the close relationship of this taxon with the anhanguerids, instead of the azhdarchoids, so it is safe to assume that they do not represent the same taxon. As for the toothless pterosaurs from the Crato Formation, *Tupandactylus* can be distinguished from both *Lacusovagus* (WITTON, 2008) and the thalassodromid illustrated by Unwin and Martill (2007) by the presence of a downturned rostrum and a high premaxillary crest. The only remaining pterosaur

from the Crato Formation to compare is *Aymberedactylus*, a tapejarid without a skull, based solely on a lower jaw. As Pêgas, Leal and Kellner (2016) pointed out, *Aymberedactylus* can be considered a valid species thanks to the unusual morphology of the retroarticular process. The retroarticular process in *Tupandactylus* is elongated and similar to *Sinopterus* (LÜ *et al.*, 2007; ZHANG *et al.*, 2019), while in all other tapejarids, including *Aymberedactylus*, it is triangular. *Aymberedactylus* differ from all tapejarids with a triangular process by presenting an extra posterior process at the triangular tip, shaping it as an unusually triangular and elongated retroarticular process. When compared to *Tupandactylus*, *Aymberedactylus* can also be safely regarded as a different and valid taxon, due to a dorsal concavity throughout the entire extent of the mandibular symphysis and a shallow mandibular crest, while in *Tupandactylus* there is a dorsal convex eminence, together with an anterodorsal concavity, and a deep mandibular crest. Since it has never been documented that the shape of the retroarticular process changes during ontogeny in pterosaurs, it is safe to conclude that *Aymberedactylus* and *Tupandactylus* do not represent distinct ontogenetic stages of a single taxon. Other autapomorphies of *Aymberedactylus* cannot be compared with *Tupandactylus*, up to date, due to preservational bias.

7.1.4. Crest Variation in *Sinopterus*

Sinopterus, as a genus, had up to eight species described, four originally *Sinopterus* and four originally "*Huaxiapterus*", synonymized with *Sinopterus* as of Zhang *et al.* (2019). Including the holotypes of these taxa, there are at least three more specimens formally described and assigned to the genus (LÜ *et al.*, 2006c; LIU *et al.*, 2014; ZHANG *et al.*, 2019), with almost all of them being complete skeletons with skulls. Three species have already been considered invalid, being "*S. gui*" (LI, LÜ & ZHANG, 2003), synonymized with *S. dongi* as of Kellner and Campos (2007), "*S. jii*" (LÜ & YUAN, 2005), synonymized with *S. dongi* as of Zhang *et al.* (2019) and "*S. liui*" (MENG, 2008), which was never valid to begin with, because it was named on a Masters Degree dissertation, making it a *nomen nudum*. Thus, since Zhang *et al.* (2019), there are five valid species attributed to *Sinopterus*. Witton (2013) already suggested that all species described for *Sinopterus* are, quite possibly, the same species, *S. dongi*, represented by all ontogenetic stages. A similar pattern for descriptions already happened for virtually all Solnhofen pterosaurs, such as *Rhamphorhynchus* (BENNETT, 1995), *Pterodactylus* (BENNETT, 1996a) and *Germanodactylus* (BENNETT, 2006), but also happened for the pteranodontoids *Pteranodon* (BENNETT, 1994) and *Anhanguera* (PINHEIRO & RODRIGUES, 2017). Indeed, in all these examples, different species were named based on few morphometric data, for example the size of the orbit relative to the skull, together with

the presence and size of the cranial crests, characters with an ontogenetic variation (PINHEIRO & RODRIGUES, 2017) or simply sexually selected (WANG *et al.*, 2014). A similar pattern can be observed on overall descriptions of the species of *Sinopterus*.

Zhang *et al.* (2019), redescribing *S. atavismus* based on a new specimen, defined the presence of a pointed process, in the middle of the dorsal margin of the premaxillary crest but not a part of it, as its sole autapomorphy. This process made the crest of the specimen shaped as a distinct squared crest, similar to *S. corollatus*, however Zhang *et al.* (2019) concluded that this process is not part of the crest since there is a line between the process and the pointed crest, different from *S. corollatus*. Unfortunately, Zhang *et al.* (2019) never attempted to identify the nature of this process and how it is related on other taxa. Here, it is concluded that the pointed process is, in fact, a suprapremaxillary process, being possibly homologous with the process in *Tupandactylus*. Considering the process as a keratinous component of the premaxillary crest, the small process would indeed be part of the premaxillary crest, effectively making the specimen have a squared crest. Another possibility is that the pointed process is nothing more than a preservational bias, where the crest broke in half. In both cases, nevertheless, the specimen would have a squared crest with no autapomorphic distinctions. Henceforth, there are no characters distinguishing *S. atavismus* from *S. corollatus*, making it invalid and synonymous. The reason why the short crests would be distinct between "*S. atavismus*" and *S. corollatus* is here interpreted as an ontogenetic character, where a secondary ossification on the suprapremaxillary process fuses the process on the crest as a single unit, being incomplete on "*S. atavismus*" and complete on *S. corollatus*. For the hypothesis of preservational bias, the damage on the originally squared crest highlighted an erroneous difference. Since both specimens are juveniles, however, an artefact of crushing may be more plausible to explain the crest of "*S. atavismus*".

"*S. jii*", originally described as a new taxon based on its premaxillary crest, revealed with its synonymy that *S. dongi* developed a premaxillary crest during ontogeny. Also, the holotype of *S. dongi* revealed that the posterior process of the premaxilla is developed beyond the occipital region, in parallel with a parietal spine. Both processes, associated, becomes curved posterodorsal. All these crests and their overall morphology, but larger and longer, are regarded as autapomorphies for *S. benxiensis*, especially the posterior occipital crest being longer and more curved. There seems to be little doubt that these characters are ontogenetic variations, as observed in *Anhanguera* (PINHEIRO & RODRIGUES, 2017). Aside from size and morphology of the crests, the remaining character that distinguishes *S. benxiensis* as a valid taxon is a shallow fossa at the anterodorsal surface of the symphysis, anterior to the distinct dorsal eminence of the symphysis. In fact, this fossa is also

observed on *Tapejara* (WELLNHOFER & KELLNER, 1991) and *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.). Henceforth, there are no characters distinguishing *S. benxiensis* from *S. dongi*, making it invalid and synonymous. The apparent absence of a shallow fossa on the symphysis of most specimens attributed to *Sinopterus*, aside from "*S. benxiensis*", may be an artefact of crushing or even an ontogenetic character, where the anterodorsal surface of the symphysis would become deeper during ontogeny. Since most specimens are laterally flattened, however, a preservational bias may be more plausible to explain a lack of fossa on other specimens of *Sinopterus*.

Aside from the variations of the size and shape of the premaxillary crest being affected by ontogeny (PINHEIRO & RODRIGUES, 2017), there seems to be little doubt that the morphology of the crest in all specimens of *Sinopterus* overlap, particularly the morphologies in *S. corollatus*, "*S. benxiensis*" and "*S. atavismus*". Lü *et al.* (2006b) listed, as autapomorphies for *S. corollatus*, a distinct squared crest that is located above the anterodorsal margin of the nasoantorbital fenestra, extending anterodorsally and its short axis is perpendicular to the margin of the fenestra. All these characters match perfectly the anterior crest on both "*S. benxiensis*" and "*S. atavismus*". As Lü *et al.* (2007) already elucidated when describing "*S. benxiensis*", the small crest has a perpendicular axis, relative to the anterodorsal margin of the nasoantorbital fenestra, that is not well preserved and quite similar to the crest observed on *S. corollatus*, with the only difference being a longer and narrower crest in "*S. benxiensis*". Henceforth, there are no characters distinguishing *S. corollatus* from "*S. benxiensis*", which is a synonym of *S. dongi*, making it invalid and synonymous. Lü *et al.* (2007) disregarded "*S. benxiensis*" as synonymous with "*S. jii*" or "*S. corollatus*" solely on the size of the posterior occipital crest, even though this region was not preserved on "*S. jii*" and "*S. corollatus*", something explicitly reported by Lü *et al.* (2007). Apparently, these specimens had a tendency for a shorter posterior process of the premaxilla that would not reach beyond the occiput, or at least not as long as in "*S. benxiensis*", which may actually be an ontogenetic signal. Thus, *Sinopterus* can indeed be considered a taxon where the growth series are rather complete, comprising hatchlings and very young juveniles all the way up to fully grown adults. The hatchlings would be represented by "*Nemicolopterus*", here considered invalid following Witton (2013), because its autapomorphies are more likely ontogenetic variation or preservational bias.

Thus, every specimen with a preserved skull that could potentially represent a semaphoront for *S. dongi* ended up described as a new taxon, resulting in *Sinopterus* suffering from an oversplit (KELLNER, 2004c; WANG & ZHOU 2006; KELLNER & CAMPOS, 2007) that is similar to the complex taxonomic histories of *Pteranodon* (BENNETT, 1994), *Rhamphorhynchus* (BENNETT,

1995), *Pterodactylus* (BENNETT, 1996a), *Germanodactylus* (BENNETT, 2006) and *Anhanguera* (PINHEIRO & RODRIGUES, 2017). Inside this growth series, *S. lingyuanensis* quite possibly can be included as another invalid taxon, because the two autapomorphies setting it apart from other species of *Sinopterus* are relative ratios. Linear and relative ratios are safe characters of taxonomic significance for defining major groups of pterosaurs, as used by Kellner (2003) and Unwin (2003), and they remained as crucial characters in recent matrices, such as Lü *et al.* (2017), Vidovic and Martill (2017), Longrich, Martill and Andres (2018) and Pêgas, Costa and Kellner (2018). However, these characters proved to be useful for determining major groups, not for distinguishing species apart. It is particularly problematic for *Sinopterus*, since Zhang *et al.* (2019) followed previous descriptions (WANG & ZHOU, 2003a; LI, LÜ & ZHANG, 2003; LÜ & YUAN, 2005; LÜ *et al.*, 2006b; LÜ *et al.*, 2007; MENG, 2008; LÜ *et al.*, 2016) and associated exact values of relative ratios as autapomorphies for every single species of *Sinopterus*. For example, "*S. atavismus*" differentiate from *S. dongi* by having the metatarsal II as the longest metatarsal, while the longest metatarsal in *S. dongi* would be the metatarsal I. The difference in size between metatarsals, in all specimens of *Sinopterus*, ranged on the scale of tenths of millimeters, a variation quite possibly inside the range of individual variations within a single taxon. In the same example, the second metatarsal of "*S. atavismus*" was longer because it measured 35.61mm on the left pes and 36.36mm on the right pes, while the first metatarsal measured 35.36mm on the left pes and 36.18mm on the right pes, thus a difference of exactly 0.25mm for the left pes and 0.18mm for the right pes. With the difference in size falling inside a range of a quarter of millimeter, it is unlikely that they do not represent an individual variation for this specimen. Here, it is concluded that the exact values of relative ratios are not useful for distinguishing species apart within closely related taxa, since they can reflect an individual variation within groups, and should be discouraged. The exceptions for this conclusion would be ranges of ratios that define major groups or aberrant, disproportional ratios never before seen in most, if not all, pterosaurs within a same group. Until autapomorphies that are not based on relative ratios are described, all species attributed to *Sinopterus* should be regarded as dubious or invalid, synonymized with *S. dongi*, including "*S. lingyuanensis*".

7.2. Ontogeny

The holotype of *T. imperator* was considered an adult specimen by Campos and Kellner (1997), since most sutures of the skull were obliterated by fusion. Pinheiro *et al.* (2011), describing the Crato specimen, also observed sparse evidence of sutures between bones, concluding it was also an adult animal, together with the size of the skull being close to the size in all other specimens, although the Crato specimen is slightly smaller and the Private specimen is much bigger. Campos and Kischlat (2020) challenged these inferences, concluding without a microscopic analysis that the posterodorsal margin of the premaxillary crest would be a radial fibrolamellar tissue, because it is strongly striated. Bantim (2017) analyzed a similar fibrous tissue on *Maaradactylus* (BANTIM *et al.*, 2014), concluding that it is a support tissue of fast developing that is focused on guaranteeing support against mechanical stress, thus growing and developing earlier than skeletal maturity. This would explain why so many juvenile specimens of pterosaurs, or subadults as in *Maaradactylus*, already developed complex and elaborated cranial crests. Campos and Kischlat (2020) extrapolated these results for *T. imperator*, inferring that the holotype and cotype actually represents a subadult individual. It is imperative to notice, however, that Campos and Kischlat (2020) failed to recognize any sutures between bones on the cotype. Ontogenetic status of the German and Private specimens is unknown, because Frey *et al.* (2003) and Unwin and Martill (2007) never cared to describe them. Pinheiro *et al.* (2011) stated that the Private specimen is the biggest *T. imperator* so far.

7.2.1. Ontogeny of the São Paulo Specimen

As Kellner and Tomida (2000) already elucidated, one of the main issues in studies regarding fossil systematics is recognizing the ontogenetic stage of the specimen and, with it, if its particular characters reflect a phylogenetic history or a mere ontogenetic signal. Because of this, it is crucial to identify and distinguish young, juvenile and mature specimens apart whenever a taxon is described. This is particularly tricky for pterosaurs, since there are no living descendants that allow extensive studies of ontogeny. Although it is expected that older specimens are bigger than the younger ones, Kellner and Tomida (2000) already reported from studies with neontological tetrapods that size alone cannot predict maturity, since growth and body size are affected by numeral variables: food supplies, climate alterations, competitions, among others. This may result in the juvenile specimens being larger than their adults counterparts, even in the same population. An emblematic example of this issue in pterosaurs is *Anhanguera piscator*, which Kellner and Tomida (2000) concluded it was a juvenile, a very young specimen, but its wingspan was already longer than the wingspans of other

anhanguerids, making it one of the largest anhanguerid ever described for the Santana Group. It is imperative that size-independent criteria are established to identify semaphoronts (HENNIG, 1966).

Some examples of studies that established such criteria are Johnson (1977), for ichthyosaurs, and Galton (1982), for stegosaurs, both defining the ossification degree, the texture and the fusion of bones as criteria. Brochu (1966) observed the closure of the neurocentral suture as criterion for living crocodyles and its implications for fossil archosaurs, and Kellner and Tomida (2000) pointed out that the ossification degree in carpals, tarsals and phalanges are particularly useful as criteria for mesosaurids. As for pterosaurs, Wellnhofer (1970) employed the ratios of the skull length relative to the diameter of the orbit and the ossification degree of the phalanges of pedal digits III and IV to identify juveniles in *Pterodactylus*. Wellnhofer (1975) also used the fusion degree of pectoral and pelvic girdles, together with presence of caudal tendons, to identify juveniles of *Rhamphorhynchus*. Mateer (1976) employed a multivariate analysis on the measurements of Wellnhofer (1970). Finally, Bennett (1993) established three criteria to determine relative age of *Pteranodon*, being the fusion of bones, degree of epiphyseal ossification in limb bones and the grain surface at the bone. These studies focused on distinguishing juveniles from adults, discussing little about the sequence of the fusions. Wellnhofer (1975) observed that almost all bones fuse early on juveniles, but girdles fused only on adults. Bennett (1993) observed that the fusion of the atlas-axis complex, humerus with its epiphysis and development of notarium usually happened earlier, while the fusion of the extensor tendon process with the first wing phalanx would begin only shortly before the skeletal maturity was achieved. Comparing the very young juvenile of *A. piscator* with many specimens of the Santana Group, Kellner and Tomida (2000) attempted to define the sequence of fusions of the bones and ossification of elements during ontogeny for *A. piscator*, extrapolating to all pterosaurs.

In the São Paulo specimen, almost all of the bones that fuse completely in older specimens are indeed fused, but suture lines can be identified. The jugal is firmly connected with the maxilla, the lacrimal, the postorbital and the quadratojugal, with the quadratojugal also almost fused with the quadrate. As Kellner and Tomida (2000) listed, the premaxillomaxilla, mandibular symphysis and frontoparietal are the first cranial bones to fuse, leaving no evidences of sutures, while the jugal is one of the last bones to develop fusions. The jugal was in process of fusion with all other bones and is seemingly fused with the maxilla, so it is evident that the São Paulo specimen does not represent a juvenile. However, sutures between the contacts of the jugal with the maxilla, quadratojugal and quadrate can be easily identified, which indicates that they were still in process of complete fusion. Thus, the São Paulo specimen is not a old, mature specimen as well. Fusion between the nasal and

lacrima cannot be observed due to preservational bias. The carpal series and the epiphyses on both humeri and ulnae cannot be safely identified, so their fusion status is unknown. It seems that the left scapulocoracoid is fused with suture lines visible, but since these bones are extensively crushed, this identification cannot be accepted as unambiguous. What is preserved of the acetabulum shows that there are no evident sutures distinguishing the few recognizable remnants of the right pelvic girdle, but this observation is also ambiguous. Of the fused elements, it is worth highlighting the extensor tendon process. As Bennett (1993) and Kellner and Tomida (2000) concluded, the fusion between the ossified extensor tendon process with the first wing phalanx happens only at the final stages of skeletal maturity, which clearly is the case of the São Paulo specimen. Thus, it is safe to assume that the São Paulo specimen is not a juvenile. However, a truly mature, adult and old specimen shows no sign of sutures between these bones, as in the holotype of *Caupedactylus* (KELLNER, 2013), which is not the case in the São Paulo specimen, presenting a clear suture line. Mature specimens usually have the tibiotarsus completely fused as well. While the proximal tarsals are indeed fused with the tibia, sutures between the tibia and tarsals are clear and exposed, being possible to distinguish the astragalus, the calcaneum and the lateral epicondyle of the tibia as different unities. Henceforth, it is safe to assume that the ontogenetic stage of the São Paulo specimen is that of a subadult, very close to full maturity at the time of death. On the preliminary classification of the six ontogenetic states by Kellner (2015), the São Paulo specimen would fall into the category of the Ontogenetic Stage 5, or OS5, where the main proxy of this stage is the extensor tendon process fused with the first wing phalanx. The OS6 would represent an adult, quite possibly the case for the Private specimen.

7.2.2. Rostral Curvature

Specifically for tapejarids, ontogenetic status can also be inferred based on the morphology of the rostrum. With the downturned rostrum and symphysis being the main feature of the tapejarids (KELLNER, 2003; UNWIN, 2003), Martill *et al.* (2020a) observed in *Sinopterus* (ZHANG *et al.*, 2019) and *Caiuajara* (MANZIG *et al.*, 2014) that there is a variation in the rostral deflection angle, as both taxonomic and ontogenetic features, possibly being sexually dimorphic as well (BENNETT, 1992). Older specimens of these taxa would have a higher deflection angle when compared to the younger specimens, indicating that the rostrum keeps bending ventrally during ontogeny. A feature that here is identified as an ontogenetic signal is the curvature posterior to the deflected rostrum. Older and virtually mature specimens of tapejarids exhibit an arched curvature, posterior to the downturned rostrum, making the rostrum have an arched-and-downturned configuration, in a lateral aspect from a posterior-to-anterior perspective. This has been identified in specimens considered

subadults or mature adults, such as the cotype of *T. imperator* (CAMPOS & KISCHLAT, 2020), the Crato (PINHEIRO *et al.*, 2011) and the São Paulo specimens, *Sinopterus* (LÜ *et al.*, 2007), all specimens attributed to *T. navigans* (FREY, MARTILL & BUCHY, 2003b; pers. obs.) and, quite possibly, *Tapejara* (VELDMEIJER, 2006; ELGIN & CAMPOS, 2012; WITTON, 2013). Here, the presence of this curvature is regarded as a feature exclusive to mature and older tapejarids, being a landmark to distinguish juveniles from subadults. From morphological observations, the São Paulo specimen indicates that the arched-and-downturned rostrum matches the convex-and-downturned symphysis, caused by the dorsal eminence and downturned tip of the symphysis, performing a perfect occlusion of the jaws, contrary to the occlusal gap proposed for *Tapejara* by Wellnhofer and Kellner (1991). The dorsal eminence of the lower jaw would develop much earlier than the rostral curvature on the upper jaw, making only juveniles have a occlusal gap, as observed in the specimen of *Tapejara* described by Wellnhofer and Kellner (1991). This indicate that the lower jaw eminence plays a key role in feeding habits for tapejarids and the delayed development of the rostral curvature is more affected by allometry and, possibly, cranial integration, as in psittaciforms that are hard seed eaters (BRIGHT *et al.*, 2019). The tapejarids resembles the most the Palm Cockatoo, *Probosciger aterrimus* (GMELIN, 1788), a taxon characterized by a relatively short and high skull (PECSICS *et al.*, 2020), a curved beak with a powerful bite force and a median process on the beak that helps cracking hard seeds (TAYLOR, 2000). The Palm Cockatoo is also a great living analogue because it presents a feathered crest both high and long, not unlike the crest of soft tissue of the tapejarids (Figure F7.2.01). The function and development timing of the dorsal eminence of the lower jaw in tapejarids, however, can only be confirmed with studies regarding biomechanics, phylogenetics and geometric morphometrics. The same is true for the rostral curvature.

Aside from an ontogenetic signal and possible feeding influences, this rostral curvature can bias how the deflection angle is measured. While some works specified that the angle was measured relative to the posterior process of the maxilla, for example the $\sim 15^\circ$ for *T. imperator* (PINHEIRO *et al.*, 2011) and the $\sim 25^\circ$ for *Tapejara* (WELLNHOFER & KELLNER, 1991), this was not the case for Martill *et al.* (2020a) and all angles measured for *Afrotapejara* and other tapejarids. Martill *et al.* (2020a) measured the deflection angle in many specimens that are incomplete, like all specimens attributed to *Afrotapejara*, to *Caiuajara* and the Private specimen of *T. imperator*, all broken at the anterior margin of the nasoantorbital fenestra. For these specimens, the deflection angles may be overestimated because they were measured from the region that could be arched, as observed in the São Paulo specimen, with cases such as *Caiuajara* presenting an extreme measured angle of $\sim 40^\circ$. Although the variation is real, the rostral curvature indicates that the deflection angles must be

measured with caution and, for the measures provided by Martill *et al.* (2020a), the angles may have a smaller spectrum depending on the ontogenetic stage of the specimen. This is certainly true for the Private specimen of *T. imperator*, the biggest specimen so far. This can also be especially tricky for *Afrotapejara*, because if the holotype is not a juvenile, but an adult with the curvature already developed, then the deflection angle relative to the posterior process of the maxilla is close to zero. This can only be resolved with more and complete specimens. With the cotype and both Crato and São Paulo specimens presenting the arched rostrum, it is safe to assume that these three specimens are at least subadults. Since the German and Private specimens are as big or bigger than these three specimens, then all specimens attributed to *T. imperator* are at least subadults.

This curvature puts in check the identity of the specimen described by Ósi, Buffetaut and Prondvai (2011) as a referred specimen of *Bakonydraco*, whether it truly represents a tapejarid. As originally described by Ósi, Weishampel and Jianu (2005), *Bakonydraco* was classified, based on characters present in most azhdarchoids, as an azhdarchid with tapejarid convergences, with the holotype, a lower jaw, being very similar to *Tapejara* and *Sinopterus*. By referring a long and straight rostrum to this taxon, with a distinct dorsal eminence on the symphysis, Ósi, Buffetaut and Prondvai (2011) concluded that the occlusion of the jaws on *Bakonydraco* would be a composite of lower tapejarid-like and upper azhdarchid-like, still being similar to *Tapejara* and *Sinopterus* due to the morphology of the rhamphotheca, which was not preserved. Without both the curvature and the downturned rostrum on this specimen, apparently a mature adult, it is safe to conclude that this referred specimen is not a tapejarid. This can lead to two interpretations. First and most likely, the holotype and referred specimen of *Bakonydraco* represents two distinct taxa, where *Bakonydraco* is possibly a tapejarid and the referred specimen is another kind of azhdarchoid. Although described as an azhdarchid, *Bakonydraco* has been repeatedly recovered as the youngest tapejarid of the fossil record (ANDRES & MYERS, 2013; ANDRES, CLARK & XU, 2014; WU, ZHOU & ANDRES, 2017; LONGRICH, MARTILL & ANDRES, 2018), especially when only the holotype is coded on a phylogenetic analysis for *Bakonydraco*. Second, the rostrum indeed represents the upper jaw of a *Bakonydraco* and this taxon is not a tapejarid. Recently described taxa, such as *Alanqa* (IBRAHIM *et al.*, 2010) and *Mistralazhdarcho* (VULLO *et al.*, 2018), reveal that both taxa, being azhdarchids, have long and straight upper jaws and a dorsal eminence on the lower jaws. The difference is that the eminence in these two taxa is more of a median keel, not an entire dorsal eminence as in the tapejarids and *Bakonydraco*. This can be tested with a phylogenetic analysis including all three taxa, verifying their positions relative to the tapejarids and the azhdarchoids.

7.3. Wingspan

For pterosaurs, the most efficient method to evaluate the size of a specimen is by calculating its wingspan. As Kellner *et al.* (2013) already elucidated, establishing the wingspan of a specimen of pterosaur is always complex and can become more tricky when the specimen is fragmentary. Other highly debated issue is how to deal with natural flexures of several regions on the wing, such as between the scapulocoracoid with the humerus, the humerus with the radius+ulna, the carpals with the radius+ulna and metacarpals and the phalanges of the wing finger with themselves. The degree of natural bending on a wing, during flight, may influence the calculated value of wingspan. Thus, Kellner *et al.* (2013) suggested two values for calculating the wingspan in pterosaurs, being the Maximized Wingspan (MaxWs) and the Normalized Wingspan (NorWs). Maximized Wingspan is essentially the sum of the maximum length of all elements composing the wing, including carpals and the scapula or coracoid, always the smaller of the bones composing the scapulocoracoid. It is a straightforward measure and offers a good basis for comparisons, regarding size, between different taxa or specimens, since it has less subjectivity other than the estimatives of incomplete bones. Then, a Normalized Wingspan is calculated by multiplying the Maximized Wingspan by a reducing factor, the latter reflecting a dorsoventral bending and the natural flexures between different bones on each region of the wing. Proportions of the wing bones vary among clades, so this reduction is likely to change depending on the clade. For pteranodontoids, Kellner *et al.* (2013) suggested that this reducing factor is 5%, and here the same reducing factor will be used. It should be noted that studies focused on calculating the reducing factor on each and every major group of pterosaurs is more than necessary, since the wing patterns of the azhdarchoids and tapejarids is clearly different from the pattern in pteranodontoids and anhanguerids (KELLNER *et al.*, 2013). Nevertheless, 5% can be considered an acceptable standarsized value for the reducing factor in tapejarids.

To use the methodology presented by Aureliano *et al.* (2014), which is the method proposed by Bennett (2001) and refined by Kellner *et al.* (2013), the lenghts of some bones were estimated for the São Paulo specimen of *T. imperator*. Quite possibly, all bones of both the forelimbs are at least partially preserved on the São Paulo specimen, however some are eroded or buried. The right coracoid, both wing metacarpals and the left third wing phalanx are buried under sediment and other bones, while the left coracoid is only partially exposed and the proximal tip of the right third wing phalanx has been lost. Based on comparisons with *Tapejara*, *Caiuajara* and *Sinopterus*, as coded by Wu, Zhou and Andres (2017), the lenghts of the coracoid, wing metacarpal and the third wing phalanx were estimated (Table T7.3.01). Since the ratios have variations for each of the three

taxa, a mean value for the wingspans was also calculated for a direct comparison. Based on the comparisons with these three taxa, the Maximized Wingspan of the São Paulo specimen resulted in 3.12 meters, while the Normalized Wingspan of the São Paulo specimen resulted in 2.96 meters. Thus, the São Paulo specimen reached a wingspan of 3m (Table T7.3.02).

This agrees well with what was already proposed for *T. imperator*. Describing the holotype, Campos and Kellner (1997) suggested a wingspan of 3m, arguing that this distinguishes from the estimated wingspan of 1.5m for *Tapejara*. Pinheiro *et al.* (2011) also suggested that *T. imperator* likely could reach wingspans from 3m up to an extrapolated 4m, however the absence of any attributed specimens with postcranial remains associated made these estimatives merely tentative. Since the São Paulo specimen is a subadult very close to maturity, reaching at least the stage of OS5 as defined by Kellner (2015), quite possibly a wingspan of 3m is a standard value for wingspans of mature specimens attributed to *T. imperator*, including those that would have reached OS6. The Private specimen, up to date the biggest and probably the only specimen reaching OS6 so far, quite possibly could reach a wingspan of 3.5m, but would not reach a wingspan of 4m. This makes *T. imperator* the largest species of Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007), as Campos and Kischlat (2020) already concluded. Considering how big the crest of soft tissue is on *T. imperator*, biomechanical studies regarding the influence of the crest on the flying capabilities of a taxon with a wingspan of 3m remains to be seen. Nevertheless, the morphology of the bones from the forelimbs suggest that *T. imperator* was a volant creature and, as far as evidences reveal, a competent flyer (Figure F7.3.01).

7.4. Specimens Scale of *T. imperator*

All known specimens of *T. imperator* have virtually the same size. Being all subadults close to maturity, if not already mature individuals, it is expected that they at least almost reached their maximum size. The only variation between each specimen seems to be the size and precise shape of the crests. Pinheiro *et al.* (2011) observed that the Crato specimen is slightly smaller than the holotype, possibly being the smallest and youngest of all known specimens of *T. imperator*, even though it can be considered a subadult. Comparing the lower jaw of both Crato and São Paulo specimens, specifically the dentary crest, it is clear that the Crato specimen has a smaller and slightly shallower crest of 93mm, with this measure including the mandibular symphysis, with a steeper anterior margin and the ventral-most tip being more anterior than posterior. The crest of the São Paulo specimen is much deeper, up to 134mm in height including the symphysis, both of the margins of the crest are steep, with the posterior being steeper, and the ventral-most tip is more centralized thanks to the steep angle posteriorly. It is safe to assume that the Crato specimen falls into an earlier ontogenetic stage than the São Paulo specimen. The few possible comparisons between the holotype, the cotype and the Crato specimen indicate that the Crato specimen is slightly smaller, with a lower premaxillary crest. Thus, the Crato specimen can be considered the youngest subadult on the scale and, on the preliminary classification of the six ontogenetic states by Kellner (2015), it would possibly fall into the category of the Ontogenetic Stage 4, or OS4, if not in OS5.

Comparisons between the holotype, cotype and São Paulo specimen indicate that they have a very close size, but the São Paulo specimen is slightly bigger. Campos and Kellner (1997) reported a total of 420mm for the length of the skull, from the tip of the rostrum to the posterior end of the squamosal, together with a length of the nasoantorbital fenestra of 250mm. The São Paulo specimen has very close values but slightly longer, with a 427mm length of the skull and a 261mm length of the nasoantorbital fenestra. Both holotype and cotype are smaller than the São Paulo specimen, but they can be considered the same ontogenetic stage nonetheless, being OS5. Since Frey *et al.* (2003) and Unwin and Martill (2007) never cared to describe or figurate in detail the German and Private specimens, ontogenetic comparisons are limited. As far as comparisons allow, the Private specimen is indeed the biggest one, being the only certain specimen within OS6, and the German specimen is slightly larger than the holotype. That can be observed comparing the size of the soft tissue crest and its anchoring with the suprapremaxillary process and posterior occipital crest. The holotype, German and Private specimens preserved enough of the soft tissue crest and both dorsal and posterior anchoring sites, revealing that the posterior crest on the holotype is more dorsally oriented,

while the suprapremaxillary process is more posteriorly oriented, compared to the almost horizontal posterior crest and more dorsally raised suprapremaxillary process of the Private specimen. Inside this spectrum, the German specimen appears to fall into an intermediate between the holotype and the Private specimen. Finally, it is impossible to compare the German and São Paulo specimens up to date, due to Frey *et al.* (2003) never caring to describe the German specimen, figurating it in detail or even informing if it was entirely prepared. Here it will be assumed that both fall on the same ontogenetic stage, with the German specimen also falling into the OS5.

Thus, a scale regarding the size of the specimens attributed to *T. imperator* can be tentatively traced. The Crato specimen, a subadult, would be the smallest known specimen, possibly the only specimen classified as OS4 or an intermediate between OS4 and OS5. The holotype and cotype, next, would already be within OS5. Next is the São Paulo and the German specimens, since precise comparisons are impossible. Finally, the Private specimen, an adult, is the oldest and biggest known specimen, possibly the only specimen that reached OS6. Simplified, this tentative scale would be: Crato < Holotype + Cotype < São Paulo ~ German < Private. If this scale indeed represent their ontogenetic stages, then another ontogenetic signal for *T. imperator* is revealed, being the soft tissue crest becoming slightly bigger as the specimen grows older. The suprapremaxillary process, with a posterodorsal direction on earlier stages, becomes more dorsally oriented during ontogeny, while the posterior occipital crest, also directed posterodorsal, becomes more ventrally placed, until both reach the condition seen on the Private specimen, with a soft tissue crest slightly taller and longer than other specimens. A similar pattern is also observed on the mandibular dentary crest. The Crato specimen indicates that the crest starts developing from an anterior to a posterior perspective, intimately associated with the gnathotheca, making the ventral-most tip more anteriorly placed. The posterior half deepens while the specimen grows older and the crest keeps growing, as seen in the São Paulo specimen, until the deepest tip moves to a centralized region. It is worth pointing out that the specimen here considered the youngest, the Crato specimen, is nevertheless a subadult, falling at least on the OS4 of Kellner (2015), meaning that no juveniles of *T. imperator* are known up to date. The timing of development for the crests on both the skull and the symphysis remains to be seen in light of new specimens. This tentative scale of sizes is lacking known specimens, because they were never described nor figurated, only mentioned (PINHEIRO *et al.*, 2011) as specimens comprised by skulls with at least one preserving a lower jaw.

Finally, a similar pattern for the growth of the crest can also be tentatively recognized for *T. navigans* (FREY, MARTILL & BUCHY, 2003b). The holotype would represent the youngest of the

three known specimens, with a suprapremaxillary process directed more posterodorsal. Following up would be the Eroded specimen, with a anteroventral to subhorizontal orientation, all the way to the Recovered specimen (GIBNEY, 2014; pers. obs.), with a suprapremaxillary process presenting an anterodorsal orientation, even though the process is mostly straight. In this manner, a tentative scale of the sizes for the specimens of *T. navigans* would be: Holotype < Eroded < Recovered. A complete redescription of the species based on the Recovered specimen may help elucidating this issue. At least for *T. navigans*, the stages of all specimens on the preliminary classification of the six ontogenetic states by Kellner (2015) remains unknown. What can be truly concluded is that none of the known specimens would fall into the categories OS1, OS2 and OS3, appearing to be at least old juveniles or young subadults. The Recovered specimen (pers. obs.) possibly falls into the OS6, but this identification is also tentative and only its complete description can elucidate this issue.

7.5. Cranial Shared Characters

The new São Paulo specimen also provides insights regarding the evolution of characters and apomorphies for all tapejarids, especially the Brazilian tapejarids, but to a lesser extent the species from all over the world.

7.5.1. Premaxillary Connection with the Skull Roof

The São Paulo specimen has the premaxillomaxilla firmly fused, dorsal to the skull roof, with the nasal and the frontoparietal, with no clear signs of sutures, similar to all specimens attributed to *T. imperator*. This contrasts with the condition in *Tapejara* (WELLNHOFER & KELLNER, 1991) and *Sinopterus* (ZHANG *et al.*, 2019), where the internasal (dorsal) process of the premaxilla seems to only run parallel to the skull roof. Pinheiro *et al.* (2011) considered it a synapomorphy for both species of *Tupandactylus*. Campos and Kischlat (2020) reported that the premaxillomaxilla seemed unfused on the cotype, but this observation has no further support and quite possibly is an artefact of crushing or an erroneous interpretation. Pinheiro *et al.* (2011) discussed with the Crato specimen that this fusion can be an ontogenetic feature. Up to date, it is impossible to conclude the nature or even the timing for the formation of this contact, because all known specimens of *T. imperator* are at least subadults. In light of new juvenile specimens of *T. imperator*, this issue may be addressed, as well as how complex this contact is. A CT-Scan of all specimens of *T. imperator* may also help elucidate this issue. Although the evolution of this character in tapejarids is still in need of more researches, including its biomechanical implications, the fusion between the premaxillomaxilla and the skull roof can maintain its status as a synapomorphy for *Tupandactylus*.

7.5.2. Suprapremaxillary Process

All specimens attributed to *T. imperator* have the suprapremaxillary process at least partially preserved. It is a character defined by Pinheiro *et al.* (2011) as a synapomorphy for *Tupandactylus*, with the main difference between *T. imperator* and *T. navigans* being the presence of an anterior blade that changes the direction of the process. However, as coded by Vidovic and Martill (2017), Longrich, Martill and Andres (2018) and Pêgas, Costa and Kellner (2018), the high crest observed on *Caiuajara* is interpreted as possessing a suprapremaxillary process as well. In this manner, the synapomorphy defined for *Tupandactylus* is that the suprapremaxillary process is a thin and high dorsal spine, while the condition in *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.) would be the

process shaped as a dorsal blade with a short posterior process. Longrich, Martill and Andres (2018) coded the presence of the suprapremaxillary process in *Caiuajara* and recovered it as sister group to a monophyletic *Tupandactylus*, with the three taxa closely related to *Tapejara*, to *Vectidraco* and to *Europejara*. Although the condition in "*S. atavismus*" (ZHANG *et al.*, 2019) may quite possibly be an artefact of crushing, here it is interpreted that a suprapremaxillary process is present on the premaxillary crest of this specimen and in *Sinopterus*, shaped as a reduced triangular or trapezoidal element that potentially fuses with the crest in older individuals, giving the crest a squared crest. In this manner, the evolution of the process would be more complex than previously thought, because it would indicate that *Sinopterus* may be closely related to *Tupandactylus* and *Caiuajara*. How these crests evolved in tapejarids remains to be carefully studied, especially in a chronostratigraphic and biogeographic context. That is because some studies concluded that the tapejarids from China and Europe could be considered geologically older than their Brazilian counterparts (VULLO *et al.*, 2012), but this conclusion can be considered tentative because the age of the Crato Formation have conflicting hypothesis (NEUMANN, 1999; VALENÇA, NEUMANN & MABESOONE, 2003; HEIMHOFER & HOCHULI, 2010; SANTOS *et al.*, 2015; FABIN *et al.*, 2018; LÚCIO, NETO & SELBY, 2020; MELO *et al.*, 2020) that potentially change interpretations regarding their evolution.

7.5.3. Descending Process of the Nasal

The descending process of the nasal also appears to have a complex evolution. *T. imperator* does present a nasal process that is long and quite similar to the process in *T. navigans* (FREY, MARTILL & BUCHY, 2003b). Its morphology is unique, being considered a new autapomorphy, although many characteristics regarding this process is synapomorphic for *Tupandactylus*. This process is also present in *Sinopterus* (ZHANG *et al.*, 2019) and *Tapejara* (WELLNHOFER & KELLNER, 1991). Tapejarids with this process have them directed anteriorly. The presence of this process can be recovered as a synapomorphy uniting Tapejaridae *sensu* Kellner (1989), because it is present in thalassodromids such as *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018). In this case, however, the process is triangular and much reduced, contrary to the elongated condition observed in *Tupandactylus*.

7.5.4. Tetraradiated Jugal

Pêgas, Costa and Kellner (2018) discussed that the ramii of the jugal have a very complex evolutionary history in pterosaurs. Non-pterosaurs have triradiated jugals, with the lacrimal (dorsal

or ascending), postorbital (posterodorsal) and quadratojugal (posterior) processes. The jugals of the pterosaurs develop a fourth process, the maxillary (anterior) process, making the jugal tetra radiated. The jugal becomes tri radiated again with the monofenestrates, with the loss of the quadratojugal (posterior) process. However, Pêgas, Costa and Kellner (2018) and Zhang *et al.* (2019) reported that some Brazilian tapejarids present a reversion of this condition, developing again tetra radiated jugals with the quadratojugal (posterior) process. This was observed first on *Tapejara* (WELLNHOFER & KELLNER, 1991), then in *T. navigans* (FREY, MARTILL & BUCHY, 2003b; FREY *et al.*, 2003) and finally in *Caiuajara* (MANZIG *et al.*, 2014). Both the holotype (CAMPOS & KELLNER, 1997) and the cotype (CAMPOS & KISCHLAT, 2020) of *T. imperator* poorly preserved this region, while the Crato specimen (PINHEIRO *et al.*, 2011) did not preserve this region at all and both Frey *et al.* (2003) and Unwin and Martill (2007) never cared to describe in detail the German and Private specimens. Thus, the condition in *T. imperator* was unknown. With the São Paulo specimen, it is confirmed that *T. imperator* also have a tetra radiate jugal, with the quadratojugal (posterior) process reacquired. Henceforth, the reacquisition of tetra radiated jugals can be considered a synapomorphy exclusive to Brazilian tapejarids, especially because the quadratojugal (posterior) process is directed posterodorsal, a trait that is exclusive to the Brazilian tapejarids. As Zhang *et al.* (2019) reported, no specimens attributed to *Sinopterus* appear to have tetra radiate jugals, but all specimens have this region poorly preserved. The morphology of the jugals in *Sinopterus* remains to be seen in light of new specimens better preserved. The condition of the jugal in thalassodromids is also unknown, because as Pêgas, Costa and Kellner (2018) concluded at least for the holotype of *Thalassodromeus*, the sutures between the jugal and all bones contacting it are obliterated. This, at least, reveals that the holotype of *Thalassodromeus* is a mature specimen falling into OS6 of Kellner (2015).

7.5.5. Occlusal Gap of the Jaws

Wellnhofer and Kellner (1991), redescribing *Tapejara*, concluded that its jaws would have a occlusal gap, since the dorsal eminence of the lower jaw would not fit within the upper jaw. Here, this character is disregarded as a taxonomic feature and reinterpreted as an ontogenetic signal of the rostrum, indicating that juveniles and young subadults of tapejarids have occlusal gaps. Mature and older specimens, at least subadults falling into the OS5 of Kellner (2015), develop a curvature on the rostrum that allows a perfect occlusion of the jaws. The occlusal gap occur thanks to the dorsal eminence of the lower jaw developing earlier than the rostral concavity of the upper jaw, indicating that such eminence plays a key role in feeding habits and the delayed development of the rostral curvature has another explanation, possibly allometry and integration between bones of the skull, as

observed mainly for parrots that are hard seed eaters (BRIGHT *et al.*, 2019). Studies regarding the biomechanics, phylogenetics and geometric morphometrics of this delayed development are more than necessary. Nevertheless, considering that the perfect occlusion is an ontogenetic signal and not a taxonomic character matches well the conclusion for *Caupedactylus* by Kellner (2013), where the holotype was considered an adult specimen but it differed from most tapejarids by having a perfect occlusion and not a occlusal gap. Here, this character is no longer considered a taxonomic character for *Caupedactylus*, but reinforces its identity as an adult specimen, possibly OS6 of Kellner (2015).

7.5.6. Deep Mandibular Crest

The Recovered specimen of *T. navigans* (GIBNEY, 2014; pers. obs.) revealed that a deep and massive mandibular crest is present on both species of *Tupandactylus*. Mandibular crests are present in all tapejarids and anhanguerids, as coded by Longrich, Martill and Andres (2018), but not on the thalassodromids. For tapejarids, Vullo *et al.* (2012) calculated the ratio of the height of the dentary crest relative to the height of the mandibular ramus and observed that the crests in tapejarids would fall into a range of ~ 1.5 to ~ 3 . The exception would be *Europejara*, registering a value of ~ 4 , which indicates that this taxon would have the deepest crest of all pterosaurs. A high ratio was defined as an autapomorphy for *Europejara*, based on the value of 4. For *Tupandactylus*, it was registered the value of 3, based on the Crato specimen, being the highest limit of the tapejarid spectrum, but only *Europejara* would fall outside this range. Here, the São Paulo specimen registered a ratio of ~ 5.5 , much higher than the ratio of *Europejara*. The Recovered specimen of *T. navigans* also register a ratio higher than 5. These ratios reveal that the mandibular crest in both species of *Tupandactylus* is bigger than previously thought, and not only *Europejara* falls outside the range of the tapejarids. A range higher than 5 can be considered a new synapomorphy for *Tupandactylus* and, most important, *Tupandactylus* can officially be considered as the genus with the deepest mandibular crest of all pterosaurs. This ratio also reinforces the identity of the São Paulo specimen as ontogenetically older than the Crato specimen, where the mandibular crest in the latter was still in process of growth.

7.5.7. Elongated Retroarticular Process

The retroarticular process in tapejarids is triangular, as it was first observed in all specimens attributed to *Tapejara* (WELLNHOFER & KELLNER, 1991; ECK, ELGIN & FREY, 2011; ELGIN & CAMPOS, 2012). It is comparatively short, with the ventral margin subhorizontal, dorsal margin inclined and descending and the posterior tip being angular and sharp, directed posteriorly or

posteroventrally. *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.) also presented such shape and, as far as comparisons are possible, *Europejara* (VULLO *et al.*, 2012) have a similar condition. For the Tapejaridae *sensu* Kellner (1989), a triangular retroarticular process remains a pattern, being present in *Tupuxuara* (KELLNER & HASEGAWA, 1993) and in *Thalassodromeus* (PÊGAS, COSTA & KELLNER, 2018). The first taxon with a different shape was *Sinopterus* (ZHANG *et al.*, 2019), specifically with a specimen where this region is better preserved (LÜ *et al.*, 2007). In *Sinopterus*, the process is elongated, with a ventral margin convex and a dorsal margin concave, shaping the process into a rounded hook, with a rounded tip directed posterodorsal, instead of the angular tip. As Pinheiro *et al.* (2011) described for the Crato specimen, *T. imperator* would present the same triangular process as in other tapejarids. However, both retroarticular processes on this specimen were cut in half or eroded, thus they were damaged enough to distort its shape. Both the São Paulo specimen, for *T. imperator*, and the Recovered specimen, for *T. navigans* (pers. obs.), revealed that the process in *Tupandactylus* is actually elongated, as in *Sinopterus* (LÜ *et al.*, 2007). This indicates a closer relationship or a convergence, between *Sinopterus* and *Tupandactylus*, that remains to be carefully studied. A phylogenetic analysis coding these morphologies can test how the retroarticular process evolved inside Tapejaridae. The only exception to these rules is *Aymberedactylus*, that has a triangular retroarticular process with an extra unusual elongated process, autapomorphic for this taxon (PÊGAS, LEAL & KELLNER, 2016).

7.6. Axial Shared Characters

Tupandactylus imperator presents no axial autapomorphies, with the overall morphology of the vertebrae following typical patterns of more inclusive clades. This is expected, because the axial series in pterosaurs is highly conservative and very few exceptions present axial autapomorphies at any vertebral series, especially in the cervical vertebrae (PEREDA-SUBERBIOLA *et al.*, 2003). As a pattern defined by Bennett (2001) for pterosaurs, *T. imperator* have procoelous cervicals, which may be the same configuration for all vertebrae, and capitular facets of the dorsal ribs progressively moving dorsally, making the ribs functionally single-headed at the ribs of the posterior dorsals. Liu *et al.* (2014) described for a specimen of tapejarid, likely a *Sinopterus*, an isolated dorsal with a biconcave centrum, while Bennett (2001) described procoelous dorsals for *Pteranodon*. Further researches are necessary to elucidate the evolution of dorsal centra in pterosaurs. Agreeing with Bennett (2001), Sayão and Kellner (2006), Vila Nova *et al.* (2015), Aires *et al.* (2020) and Cheng *et al.* (2020), *T. imperator* have the typical cervical morphology for the pterodactyloids, with absent transverse processes and ribs, presenting eight exposed cervicals but quite possibly having up to nine cervicals. The pattern in cervicals and preserved dorsals indicate that *T. imperator* may have 12 dorsals, as in every other pterodactyloid. Cheng *et al.* (2020) pointed out possible exceptions to this rule, with few specimens attributed to *Sinopterus* with 13 or 14 dorsals, arguing that the pattern in tapejarids may be loss of extra dorsals until it reached 12. If this pattern is exclusive to tapejarids, to Chinese taxa such as *Sinopterus* or even an artefact of crushing remains unknown and further examinations of these specimens of *Sinopterus* are required to elaborate this issue. Nevertheless, almost all pterodactyloids have a fixed total of 21 pre-sacral vertebrae. Bennett (2001) concluded that the rigid, powerful cervical series is another trend in pterodactyloids, since *Pterodactylus* has a condylar-cotylar articulation broad and oval, almost prohibiting rotation. Ornithocheiroids takes this to an extreme, presenting large and developed postexapophyses, also present in *T. imperator*. This morphology puts in check the conclusions of Frey, Martill and Buchy (2003b), Frey *et al.* (2003), Unwin and Martill (2007) and Chatterjee and Templin (2012) of the cranial crest in *Tupandactylus* being used as a self-adjustment rudder system. To be used as a rudder, *Tupandactylus* would need to turn the head to readjust into the wind direction, fast turns or mediate flight control. However, all of the morphology of the cervical vertebrae indicates that lateral turns of the head were impractical, if not impossible, because as Bennett (2001) observed for *Pteranodon* and defined as a pattern for the pterodactyloids, the combination of condylar-cotylar, zygapophyseal and exapophyseal articulations would severely limit lateral flexions. Thus, here it is concluded that *Tupandactylus* would not use its headcrest for an aerodynamic function, based on the morphology of the cervicals.

Ornithocheiroids are also known for the presence of cervicalized dorsals, which are present in *T. imperator*, and the notarium, with indirect evidences showing that it was present in *T. imperator*. Aires *et al.* (2020) questioned the homology of the notarium, being absent in *Sinopterus* and chaoyangopterids. The absence of notaria in *Tapejara* and *Anhanguera piscator* is because these taxa are represented by immature specimens, so their condition is actually unknown. Quite possibly, both taxa had notaria. This supposedly cannot be assumed for *Sinopterus* and chaoyangopterids. Lü *et al.* (2006c), for *Sinopterus*, and Lü *et al.* (2008), for *Shenzhoupterus*, indicated that the specimens described were close to maturity and lacked a notarium, seemingly a trend in azhdarchoids from China. Further studies are more than necessary to elucidate this issue, especially because Lü *et al.* (2006c) concluded that *Sinopterus* lacks a notarium based on a specimen with all potential notarial vertebrae covered by other bones, so its condition is actually unclear. Notaria are also present in *Germanodactylus* and *Ardeadactylus*, as reported by Aires *et al.* (2020), proving that the evolution of notaria is more complex than previously thought. The only taxa with morphologically distinct notaria are the pteranodontians *Pteranodon*, where the dorsal ossified tendon is hypertrophied with a scapular articulation, mostly over the dorsal IV, and *Nyctosaurus*, where the neural spines and scapulae are articulated without direct contact, through ossified tendons lateral to the neural spines, with the neural spines on the notaria of *Nyctosaurus* being T-shaped in anterior and posterior views.

As for the patterns of the tapejarids, *T. imperator* is in agreement with Kellner (1995) and Vila Nova *et al.* (2015) by having a relative cervical length formula of $III < IV = V > VI > VII > VIII$. As Vila Nova *et al.* (2015) concluded, the size differences from cervical IV to V, relative to the typical formula of the azhdarchoids where the fifth is the longest, can be related to phylogeny or mere stochastic variation. This issue still remains uncertain, but the presence of this same pattern in *T. imperator* suggests that it may truly be a pattern of the tapejarids. The evolution of the lengths of cervical vertebrae in azhdarchoids remains to be carefully studied, because the chaoyangopterids also deviates from the typical pattern where the fifth is the longest. As Wu, Zhou and Andres (2017) elaborated, *Jidapterus* would be unusual by having the fourth cervical as the longest, while both *Chaoyangopterus* and *Shenzhoupterus* have virtually no distinction in the size of the cervicals and the fourth to seventh cervicals have almost the same length. Quite possibly, each internal clade of Azhdarchoidea have its own unique pattern, with few exclusive exceptions such as *Jidapterus*. Although the postexapophyses are indeed the ventral-most cervical processes in *T. imperator*, the hypapophyses are also very pronounced, giving the mid-cervicals a concave ventral surface in lateral view. Thus, *T. imperator* exhibit the tapejarid pattern that differs from the straight pattern in

thalassodromids, as concluded by Vila Nova *et al.* (2015). The hypapophyses increase in overall size towards the posterior cervicals, until they reach maximum size at cervical VIII. This pattern is observed in the tapejarid described by Vila Nova *et al.* (2015) and *Pteranodon* (BENNETT, 2001), so this may be a feature of the ornithocheiroids. The tapejarid described by Cheng *et al.* (2020) has a pair of pre-exapophyses and a bifurcated hypapophysis, features never before seen in pterosaurs. If this is a pattern in tapejarids or an autapomorphic feature of a new taxon remains unknown. Prezygapophyses and postzygapophyses are very similar to the tapejarid described by Vila Nova *et al.* (2015) and differs from the condition in *Pteranodon* (BENNETT, 2001) and thalassodromids (VILA NOVA *et al.*, 2015). The morphology of the zygapophyses may be another pattern for the tapejarids, but this can only be confirmed with further studies comparing the cervicals of tapejarids with all azhdarchoids. Mid-cervicals in *T. imperator* are very similar to the cervicals described by Liu *et al.* (2014), except by lacking a longitudinal sulcus at the prezygapophyses, present on the Chinese tapejarid. This may be an artefact of crushing or a pattern for Chinese tapejarids, which reinforces the need of a study regarding a comparative morphology of cervicals in azhdarchoids. A similar study is necessary for the dorsals, since the robust neural spines and transverse processes in *T. imperator* differ from the thin and constricted condition in *Pteranodon* (BENNETT, 2001) and resembles more the dorsals with a robust square shape, described by Sayão and Kellner (2006), Eck, Elgin and Frey (2011) and Cheng *et al.* (2020). Comparisons with the dorsals of thalassodromids and azhdarchids are necessary.

Finally, the cervical III in *T. imperator* have two small and elongated pneumatic foramina, while cervical VI has only one. A single foramen at the lateral side of the centrum was described by Vila Nova *et al.* (2015) as a pattern for the tapejarids, while thalassodromids have two pairs and the azhdarchids have no foramina. A pair of foramina is observed in all specimens attributed to the Tapejaridae and, as Vila Nova *et al.* (2015) questioned, the few specimens attributed to *Sinopterus* where such foramina are apparently absent not only are juveniles, but also this region is heavily crushed, so the supposedly absence of these foramina may be an artefact of crushing. However, as already elucidated by Buchmann and Rodrigues (2019), presence and evolution of the pneumatic foramina in the vertebrae of pterosaurs, especially cervicals, are way more complex than originally thought and further studies are more than necessary. Vila Nova *et al.* (2015), as an example for azhdarchoids, reported that only mid-cervical V in a specimen of thalassodromid had up to three pneumatic foramina, and only on the left side, while the right side had the typical pattern of two foramina. This specimen is not the only exception to the patterns established. A single cervical in a specimen attributed to *Tapejara* (ELGIN & CAMPOS, 2012) have two foramina and only on one

side, a pattern of the thalassodromids even though it is a tapejarid. At least in one referred specimen of *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.), there is a single cervical with up to three foramina on the right side. As for the São Paulo specimen of *T. imperator*, cervical III have two foramina, a feature of the thalassodromids, however one foramen is located at the base of the prezygapophysis, a feature observed on *Pteranodon* (BENNETT, 2001). It is possible that each and every mid-cervical have their own unique pattern of fenestration, but it is also possible that extra pneumatic foramina, besides the defined patterns, are specific traits of specific individuals. Further researches are more than necessary to address the issue of this complex evolution of fenestration.

7.7. Appendicular Characters

The appendicular morphology of *Tupandactylus imperator* also matches the typical patterns of the pterosaurs. Similar to the axial series, this is expected, because the specializations for active flight happen quickly, with multiple characters modifying all at once, and these apomorphies remain unchanged and highly conservative while the taxa keep occupying flying niches (ALEXANDER, 2015). This has been observed as pattern in all flying vertebrates, being the pterosaurs, bats and even the birds, where intermediates flightless and poor flyers are known and the character evolution is more widespread (ALEXANDER, 2015). Nevertheless, there are characters variable enough that configured autapomorphies for many taxa (ANDRES & MYERS, 2013).

7.7.1. Shared Characters

T. imperator have the typical characters of the pterosaurs, such as a robust humerus with a large head and long deltopectoral crest and the fourth digit greatly enlarged and hyperelongated to support the wing. As for the characters of the pterodactyloids, all indirect evidences suggest that *T. imperator* has a notarium, but other characters are certainly present, such as the articulation between the scapulocoracoid with the dorsal vertebrae and extremely elongated metacarpal IV, as long as the humerus. Two metacarpals lost articulation with the carpus, but the evolution of such metacarpals remains to be carefully studied. An acetabulum entirely emarginated may be at least a feature of the ornithocheiroids, since it occurs in *Pteranodon* (BENNETT, 2001), but it may be more widespread within pterodactyloids. As an azhdarchoid, *T. imperator* has a rectangular deltopectoral crest that is tall and elongated, together with the first wing phalanx being the largest and the longest phalanx, dwarfing even the other wing phalanges. The coracoid of *T. imperator* have a ventral process that is similar to the deep flange, typical for the azhdarchoids, and the broad tubercle that is defined as a character of the tapejarids. Liu *et al.* (2014) already concluded that such structures are homologous, thus it may not distinguish tapejarids from other azhdarchoids. However, Liu *et al.* (2014) also showed that the morphology of the process is similar to a flange in chaoyangopterids, azhdarchids and Chinese tapejarids, while a tubercle is more characteristic of thalassodromids and Brazilian tapejarids (AIRES *et al.*, 2014). This structure is also present in *Pteranodon* (BENNETT, 2001). Thus, how complex the evolution of this character is within azhdarchoids and ornithocheiroids remains to be thoughtfully studied. The same is true for the fifth pedal digit, which is present in few azhdarchoids but it is recovered absent in ornithocheiroids by Longrich, Martill and Andres (2018).

T. imperator presents a ventral longitudinal ridge on the second and third wing phalanges, another character of the azhdarchoids. This character was observed by Martill and Frey (1999) on an indetermined specimen from the Crato Formation, concluding it was an azhdarchid thanks to this character. Sayão and Kellner (2006), however, observed the same ridge in specimens preserving postcranial remains without skulls, identified as tapejarids, and concluded that the ridges are a feature of the azhdarchoids. With *T. imperator* presenting the same ridge and being a tapejarid with an associated skull, it is safe to conclude that this ridge is synapomorphic for Azhdarchoidea. Thus, specimens from the Crato Formation with T-shaped cross-sections of the wing phalanges are not necessarily azhdarchids, but possibly tapejarids or thalassodromids. Finally, the evolution of the pedal unguals is another feature that remains to be carefully studied. In *Sinopterus*, as Zhang *et al.* (2019) described, manual and pedal unguals have the same size on specimens described by Wang and Zhou (2003a), Lü *et al.* (2016) and Zhang *et al.* (2019), but not on specimens described by Lü *et al.* (2006c) and Lü *et al.* (2007), with these specimens of *Sinopterus* seemingly being older and more mature. Thus, quite possibly this is an ontogenetic character ruled by allometry, where the manual unguals actually grow faster than the pedal unguals. More studies are necessary to observe if it is an allometric character and which groups present this variation.

7.7.2. *Tupandactylus imperator* Last Wing Phalanx

The fourth wing phalanx in *T. imperator* is the sole postcranial bone that, relative to the rest of the wing, has a unique character never before seen in all but two pterosaurs. The last wing phalanx is always expected to be the shortest in pterodactyloids. Specifically in azhdarchoids, the last wing phalanx is very short, as in *Tapejara* (ECK, ELGIN & FREY, 2011), *Caiuajara* (MANZIG *et al.*, 2014; pers. obs.) and *Sinopterus* (LÜ *et al.*, 2006c). In few taxa, being *Anurognathus* (BENNETT, 2007) and *Nyctosaurus* (BENNETT, 2001), the fourth wing phalanx is lost, being an autapomorphy for both taxa that occurred independently. Aside from these two taxa, the morphology and the length of the fourth wing phalanx remains constant for major clades within Pterosauria and no other taxa has autapomorphies referred to the length of said phalanx, except *Microtuban* (ELGIN & FREY, 2011). The shape of the phalanx in *T. imperator* is similar to the observed in other azhdarchoids, but its size relative to the other phalanges is something worth discussing here. The shortening of the last wing phalanx was taken to an extreme, with the phalanx being virtually vestigial. This phalanx in *T. imperator* is the smallest manual phalanx, disconsidering the atrophied second phalanx of digit III. Putting in perspective, the ratio between the length of the fourth wing phalanx, relative to the length of the first wing phalanx, is only 0.055, or ~5%. In comparison, as coded by Longrich, Martill and

Andres (2018), this same ratio ranges from ~20% to ~28% in *Sinopterus* (ZHANG *et al.*, 2019), ~29% in *Caiuajara* (MANZIG *et al.*, 2014) and up to ~43% in *Tapejara* (ECK, ELGIN & FREY, 2011). This extreme shortening of the fourth wing phalanx, making it smaller than the other manual phalanges of all digits, is regarded here as a new autapomorphy for *T. imperator*.

There are three considerations that must be taken into account regarding this autapomorphy. First, there are two other azhdarchoids that registered a very similar extreme shortening of this phalanx. Elgin and Frey (2011) defined two autapomorphies for *Microtuban*, being a high ratio for the length of the second wing phalanx relative to the length of the first phalanx, which is 85%, and an extreme shortening of the fourth wing phalanx, quite similar to *T. imperator*, with the phalanx representing only 1.1% of the total length of the wing finger. For the ratio between the length of the fourth phalanx relative to the length of the first phalanx, *Microtuban* registered a value of 0.026, or ~3%, shorter even than in *T. imperator*. Here, it is concluded that the extreme shortening of the fourth wing phalanx can be regarded as autapomorphic for *T. imperator* and for *Microtuban*, being acquired independently. However, there is the possibility that this extreme shortening of the phalanx is not an autapomorphic feature for *T. imperator* or even for *Microtuban*, because it can be a more widespread character within the azhdarchoids. That is because Elgin and Frey (2011) pointed out another azhdarchoid with this extreme shortening, being the specimen attributed to *Quetzalcoatlus* described by Kellner and Langston (1996). While the focus was the description of the skull bones of *Quetzalcoatlus*, one of the described specimens was entirely illustrated by Kellner and Langston (1996), including the preserved postcranial bones such as the articulated wing phalanges. In this case, the fourth wing phalanx also is extremely reduced and virtually vestigial. A comparative study regarding the evolution of the fourth wing phalanx is more than necessary. It is worth mentioning that the relationships of *Microtuban* are still uncertain (ELGIN & FREY, 2011; LONGRICH, MARTILL & ANDRES, 2018) and a complete redescription in light of more comparisons with more azhdarchoids is more than necessary to address this issue. Second, the condition of the fourth phalanx in *T. navigans* is unknown. If *T. navigans* also has the same vestigial phalanx, then this character could be regarded as a synapomorphy for *Tupandactylus* instead. Third and lastly, this condition was only observed on the right fourth wing phalanx, which is a little damaged although preserved. The left phalanx is possibly preserved, but it remains buried under the mandibular crest. A CT-Scan may expose it entirely, allowing the full description and comparison with the already exposed right phalanx. Quite possibly, both the third and fourth phalanges are preserved, allowing comparisons with the incomplete third phalanx as well.

7.8. Phylogenetics of the Pterosauria

The stability and instability recovered on different nodes, regarding both the equally weighted analysis and the implied weighted analysis, provides insights about the evolution of characters and clades related to the Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), as well as all other groups of pterosaurs.

7.8.1. Eopterosauria

Andres (2010) was the first study to ever recover Eopterosauria monophyletic, followed up by its updates (ANDRES & MYERS, 2013; ANDRES, CLARK & XU, 2014; ZHOU *et al.*, 2017; WU, ZHOU & ANDRES, 2017; LONGRICH, MARTILL & ANDRES, 2018). This monophyletic group of pterosaurs from the Triassic was never recovered in any other phylogenetic analysis. Contrary to these studies, however, here Eopterosauria was also not recovered monophyletic. Both analyses of this study were based on a modified version of the matrices that did recover Eopterosauria, so this result raises questions about the existence of this group. The Triassic taxa kept their position as the earliest pterosaurs, but with variable rearrangements. The implied weighted analysis recovered two clades that compose Eopterosauria, being Preondactylia and Eudimorphodontoidea, but as a grade towards Macronychoptera. An interesting result of the equally weighted analysis was having a structure that, overall, is more similar to Britt *et al.* (2018), where *Arcticodactylus* is more early diverging than *Preondactylus* and *Austriadactylus*, followed up by Eudimorphodontidae *sensu* Britt *et al.* (2018), which in turn is the same as Eudimorphodontoidea *sensu* Andres, Clark and Xu (2014) without *Arcticodactylus*. The difference is that Dimorphodontidae in Britt *et al.* (2018) is more early diverging than Eudimorphodontidae, while in Andres, Clark and Xu (2014) and this study it is the opposite, with Eudimorphodontoidea more early diverging than Macronychoptera, which in turn has Dimorphodontia. More studies are necessary to address the conformations of the pterosaurs from the Triassic, but the most probable hypothesis is that Eopterosauria is not valid and the reason it was recovered monophyletic may be because of long branch attraction, caused by continuous characters as coded by Andres (2010). This hypothesis needs to be thoughtfully tested, however.

7.8.2. Dimorphodontia and *Campylognathoides*

Macronychoptera, Dimorphodontia, Novialoidea and *Campylognathoides* had no variations on both analyses when compared to Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017) and

Longrich, Martill and Andres (2018). This indicates that these taxa have overall a strong stability on their position and relationships. This is also true when compared to other analysis such as Britt *et al.* (2018), with a very similar composition except the equivalent of Dimorphodontia, being more early diverging than the equivalent of Eudimorphodontoidea. More studies are welcomed to challenge these results, but it is unlikely that these taxa will present major variations on their positions.

7.8.3. Rhamphorhynchidae

Comparing the equally weighted and implied weighted trees with published analyses reveal that Rhamphorhynchidae needs to be thoughtfully reanalyzed. Rhamphorhynchidae as in Wu, Zhou and Andres (2017) was not recovered, thanks to a whole rearrangement of taxa. Only taxa closely related to *Rhamphorhynchus* were recovered as a monophyletic group. Taxa like *Orientognathus*, *Scaphognathus* and *Fenghuangopterus* had variable positions, usually as a grade relative to variable clades such as Monofenestrata or the equivalent of Rhamphorhynchidae. Scaphognathinae, as proposed by some descriptions of rhamphorhynchids (LÜ, FUCHA & CHEN, 2010), was never recovered here or on Andres (2010) and updates (ANDRES & MYERS, 2013; ANDRES, CLARK & XU, 2014; ZHOU *et al.*, 2017; WU, ZHOU & ANDRES, 2017; LONGRICH, MARTILL & ANDRES, 2018), raising questions about its validity. A major study regarding the comparative morphology and the phylogeny of all rhamphorhynchids is more than necessary to address this issue. A study of this magnitude can be performed because most taxa are known from complete specimens, in many cases more than one complete specimen.

7.8.4. Darwinoptera and Wukongopteridae

Monofenestrata was recovered as in Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018), but Darwinoptera and Wukongopteridae also need a careful re-evaluation. Almost all taxa had variable positions, to the point that the implied weighted analysis did not recover Darwinoptera because *Pterorhynchus* was recovered outside of this clade. *Kungpengopterus*, *Changchengopterus* and *D. linglongtaensis* had variable positions as well and *Darwinopterus* was recovered paraphyletic at least on the equally weighted analysis. It is quite possible that all these taxa indeed represent a monophyletic group, however this instability indicates that redescriptions and comparative studies are more than welcome, which is also possible because almost all species attributed to wukongopterids are known from complete specimens.

7.8.5. Anurognathidae

Andres (2010) and updates (ANDRES & MYERS, 2013; ANDRES, CLARK & XU, 2014; ZHOU *et al.*, 2017; WU, ZHOU & ANDRES, 2017; LONGRICH, MARTILL & ANDRES, 2018), as well as the analyses of this study, always recovered Anurognathidae monophyletic, being safe to conclude that these taxa indeed forms a natural group. Issues regarding anurognathids are related to their position on Pterosauria. Kellner (2003) and updates such as Pêgas, Costa and Kellner (2018) recovered Anurognathidae as the earliest pterosaurs. Unwin (2003) and updates such as Lü *et al.* (2017) recovered Anurognathidae as one of the earliest pterosaurs, if not the earliest, which is not unlike Kellner (2003). Andres (2010) and updates such as Longrich, Martill and Andres (2018) recovered Anurognathidae as sister group to Pterodactyloidea, a result recovered on this study using a similar matrix. Other positions have already been proposed, such as Britt *et al.* (2018) recovering Anurognathidae as sister group to Breviquartossa. Aside from positions within Pterosauria, internal relationships also shows variation, with Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017), Longrich, Martill and Andres (2018), the equally weighted and the implied weighted trees all having their own unique internal configuration, to the point that a comparative strict consensus between these five analysis would have no resolution in a polytomy of five taxa. This also indicates that reviews and phylogenetic studies focusing anurognathids are crucial to elaborate this issue. Up to date, reviews regarding the morphology and taxonomy of the anurognathids have been performed (HONE, 2020), while the description of *Sinomacrops* (WEI *et al.*, 2021) provided a much needed revision of the phylogenetic studies, character evolution and testing of the position of anurognathids within Pterosauria, with a brand new revised supermatrix.

7.8.6. Archaeopterodactyloidea

Pterodactyloidea remained monophyletic, with *Kryptodrakon* as the earliest pterodactyloid, being considered here a safe result. Lophocratia was recovered valid as of Andres, Clark and Xu (2014), composed by Archaeopterodactyloidea and Eupterodactyloidea. A variation from this study, when compared to Wu, Zhou and Andres (2017), was *Kepodactylus* recovered outside of the Ctenochasmatidae, recovered as one of the earliest archaeopterodactyloids with *Cuspicephalus*, *Germanodactylus* and *Altmuehlopterus* on the equally weighted analysis and closely related to *Normannognathus*, *Cycnorhamphus* and *Aurorazhdarcho* on the implied weighted analysis. This may indicate that this taxon need a careful revision. As for the remaining taxa, overall relationships kept a similar conformation, with *Pterodactylus*, a clade with *Cycnorhamphus* and *Ardeadactylus* as

sister group to Ctenochasmatidae and the ctenochasmatids within three identifiable clades, being the Ctenochasmatinae, Moganopterinae and Gnathosaurinae. Relationships between these groups are a little controversial, since Ctenochasmatinae was recovered inside Gnathosaurinae on the implied weighted analysis, but overall structures were similar to Wu, Zhou and Andres (2017), except for the taxa recovered outside Ctenochasmatidae, such as *Kepodactylus* and *Ardeadactylus*, and the internal relationships of Ctenochasmatinae, which were the same on the equally weighted and implied weighted trees, but slightly different from Wu, Zhou and Andres (2017). Although stable, more studies regarding the redescriptions and re-evaluations of phylogenetic positions are welcome, especially for taxa such as *Kepodactylus*.

7.8.7. Pteranodontoidea

Eupterodactyloidea and Ornithocheiroidea kept a similar composition, remaining as stable major groups. For Pteranodontoidea, Lonchodectidae and Boreopteridae as a monophyletic group were recovered as the earliest pteranodontoids, while *Hongshanopterus* was recovered being the earliest pteranodontian. Wu, Zhou and Andres (2017) recovered pteranodontians as the earliest pteranodontoids, followed by *Hongshanopterus* and Lonchodectidae with Boreopteridae all up to Lanceodontia. Although there is variation between these relationships, an observable trend is both *Hongshanopterus* and the clade with Lonchodectidae and Boreopteridae being earlier divergences within the pteranodontoids. As for Pteranodontia, it remained monophyletic with a Pteranodontidae stable, where *Pteranodon* was always monophyletic, and a highly variable Nyctosauridae. Only *Alamodactylus* and *Cretornis* kept a stable position, comparing the equally weighted tree with the implied weighted tree and Longrich, Martill and Andres (2018). *Alcione* and *Simurghia* were always closely related, but on the implied weighted analysis both fell on a polytomy with both species of *Nyctosaurus*, being the only tree where *Nyctosaurus* was not recovered monophyletic. This resulted in variation of the position of *Muzquizopteryx* relative to *Nyctosaurus*. Longrich, Martill and Andres (2018) recovered *Muzquizopteryx* with *Barbaridactylus* and *Nyctosaurus*, the equally weighted tree recovered closely related to *Alcione* and *Simurghia* and the implied weighted tree recovered on a polytomy with both *Barbaridactylus* and the clade with *Alcione*, *Simurghia* and both *Nyctosaurus*. *Barbaridactylus* monophyletic was recovered only with Longrich, Martill and Andres (2018). These results indicate that pteranodontids are more or less stable, although the taxonomic complex is far from resolved (KELLNER, 2010; MARTIN-SILVERSTONE *et al.*, 2017; KELLNER, 2017; ACORN *et al.*, 2017), but nyctosaurids needs a careful re-evaluation and redescription, including for all taxa described by Longrich, Martill and Andres (2018).

The equally weighted and implied weighted analyses both had Lanceodontia as sister group to Pteranodontia. In both cases, Istiodactylidae was the earliest lanceodontian, with the same stable composition, followed up by a monophyletic *Cimoliopterus*. These results indicate that the earliest divergences of the lanceodontians have few to none variation, being quite similar to Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018). This is not the case for Anhangueria, the single clade where the IterPCR algorithm detected rogue taxa on both equally weighted and implied weighted analyses. In this manner, *Ornithocheirus*, *Siroccoptyx* and *Coloborhynchus*, composing a clade that resembles the Ornithocheiridae of Wu, Zhou and Andres (2017), had few resolution on Anhangueria and always had more than one possible position, being close to *Cearadactylus* and *Tropeognathus* or close to *Ludodactylus* and *Guidraco*. *Ludodactylus* and *Guidraco*, always as a monophyletic group, also had variations, where in Wu, Zhou and Andres (2017) it was the earliest anhanguerians, in the implied weighted tree it was sister group to Anhangueridae and in the equally weighted tree it was inside *Anhanguera*, thus effectively making the genus paraphyletic. These results, aligned with the high diversity of this group, reveals that morphological and phylogenetic re-evaluations of the anhanguerids are more than necessary, not unlike the studies of Rodrigues and Kellner (2013) and Holgado and Pêgas (2020), two studies focused on reviewing samples of the sheer diversity of anhanguerids and the closely related taxa of the anhanguerians.

7.8.8. Azhdarchoidea non-Tapejaridae

Azhdarchoidea kept a stable internal composition, in many ways similar to Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018). Thus the equally weighted and implied weighted analysis recovered Dsungaripteridae inside Azhdarchoidea, a result that must be interpreted with caution because the dsungaripterids, similar to anurognathids, present a variable position on different analysis. Andres (2010) and updates recovered the dsungaripterids inside Azhdarchoidea. Kellner (2003) and updates such as Pêgas, Costa and Kellner (2018) have the dsungaripterids as sister group to the azhdarchoids, composing Tapejaroidea. Unwin (2003) and all its updates such as Lü *et al.* (2017) have dsungaripterids, ctenochasmatooids and azhdarchoids composing Lophocratia. Vidovic and Martill (2017) recovered closely related to pteranodontoids. All these results indicate that a careful re-evaluation of all dsungaripterids, as well as a refined and revised phylogenetic analysis to test their relationships with all other pterodactyloids, are more than necessary. Nevertheless, a pattern observed is that all studies indicate that the dsungaripterids are among the earliest ornithocheiroids, while at least most studies indicate a closer relationship with

the azhdarchoids. The monophyly of the Dsungaripteridae with *Dsungaripterus*, *Domeykodactylus* and *Noripterus* have never been seriously questioned, with only Unwin (2003) and updates such as Lü *et al.* (2017) questioning if taxa like *Germanodactylus* and *Altmuehlopterus* composes this clade.

A revision of the dsungaripterids is also imperative for a comparative analysis with the thalassodromids, a group that also presented variable positions and some analyses suggest a closer relationship between the thalassodromids and the dsungaripterids. Andres (2010), all its updates and the implied weighted analysis recovered thalassodromids with dsungaripterids, both composing Neoazhdarchia. Unwin (2003) and updates such as Lü *et al.* (2017) recovered Neoazhdarchia, but without Dsungaripteridae. Kellner (2003) and all updates, such as Pêgas, Costa and Kellner (2018), recovered Tapejaridae *sensu* Kellner (1989), where thalassodromids and tapejarids forms a clade sister group to Neopterodactyloidea. Here, the equally weighted analysis recovered an equivalent composition, where tapejarids and thalassodromids are united on a clade that is sister group to Neopterodactyloidea. However if this clade is considered Tapejaridae *sensu* Kellner (1989), then the dsungaripterids can be considered effectively inside this Tapejaridae, since it was recovered as sister group to the thalassodromids and this Dsungaripteromorpha was sister group to Tapejaridae. While this indicates that the dsungaripterids and thalassodromids need careful revisions, an interesting aspect of this result is that it closely resembles Andres and Ji (2008) the most. Andres and Ji (2008), describing *Elanodactylus*, recovered a Dsungaripteridae sister group to a Tapejaridae *sensu* Kellner (1989), while this clade was recovered as sister group to Neopterodactyloidea. The results of Andres and Ji (2008) reinforces that the dsungaripterids deserve complete redescrptions with phylogenetic analyses, but it also reinforces the conclusion of dsungaripterids representing one of the earliest ornithocheiroids, with a closer relationship with the azhdarchoids. As for Thalassodromidae, both *Tupuxuara* and *Thalassodromeus* were recovered monophyletic, as observed in Pêgas, Costa and Kellner (2018), and these results are considered stable. *Alanqa* and *Aerotitan* with thalassodromids was also recovered by Longrich, Martill and Andres (2018), which concluded that both are known from very fragmentary specimens and this result is not supported, because a complete redescription of these two taxa based on more complete remains are more than necessary. Here, *Caupedactylus* was recovered closer to the thalassodromids and this result is also not supported, since it represents a tapejarid with features of the thalassodromids, as Kellner (2013) proposed. Its relationships with all other azhdarchoids need to be elaborated in light of a complete morphological re-evaluation of the thalassodromids, because if a Tapejaridae *sensu* Kellner (1989) is recovered with *Caupedactylus* being the earliest divergence, it may indeed represent a mosaic of the characters that evolved within the tapejarids and the thalassodromids. Further researches are required to elaborate this issue.

With the sole exception of Pinheiro *et al.* (2011), most of the phylogenetic analyses recovered Neopterodactyloidea or, in cases such as Vidovic and Martill (2017), an equivalent of this clade. The equally weighted and implied weighted analyses recovered Neopterodactyloidea, here considered stable. However, its internal composition had few to none stability. *Eoazhdarcho* had an unstable and variable position, inside the Chaoyangopteridae on Wu, Zhou and Andres (2017) and closely related to azhdarchids on Longrich, Martill and Andres (2018). Here, the equally weighted analysis recovered a trichotomy with Azhdarchidae, Chaoyangopteridae and *Eoazhdarcho*, while the implied weighted analysis had *Eoazhdarcho* closer to the azhdarchids, as of Longrich, Martill and Andres (2018). Both Chaoyangopteridae and Azhdarchidae were recovered monophyletic, a result here considered stable, but with few to none resolution. Chaoyangopteridae, being better resolved, had *Chaoyangopterus* as sister group to *Shenzhoupterus*, instead of *Jidapterus*, on the implied weighted analysis, while the equally weighted analysis had the three taxa on a trichotomy. Wu, Zhou and Andres (2017), as all updates of Andres (2010), had *Chaoyangopterus* as sister group to *Jidapterus*. Since Wu, Zhou and Andres (2017) focused on redescribing *Jidapterus*, these results indicate that the remaining chaoyangopterids need a similar redescription and phylogenetic re-evaluation. As for the azhdarchids, only *Montanazhdarcho* as the earliest azhdarchid was a stable result. The huge polytomy on both analyses of this study reflects that most taxa are known from very fragmentary material, with few to none comparisons possible between each taxa. Only mid-cervicals are known from all taxa, to the extreme of *Phosphatodraco* and *Arambourgia* being known solely from the mid-cervicals. A complete morphological redescription and comparative anatomy, together with phylogenetic studies, regarding all known azhdarchids and possible taxa related to azhdarchids are more than necessary to elucidate this issue.

7.8.9. Tapejaridae Relationships

In both equally weighted and implied weighted analyses, Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014) was recovered monophyletic and based mostly on characters of the lower jaw. This is expected, because most named tapejarids are known from lower jaws, with *Europejara* having more lower jaw elements preserved than skull elements, and *Aymberedactylus* is known solely from a single lower jaw. *Aymberedactylus* was recovered as the earliest tapejarid, something recovered by Pêgas, Leal and Kellner (2016). Regarding these mandibular characters, the presence of a mandibular crest appears to be one of the main characters that set tapejarids apart from other azhdarchoids. A similar trend is observed on the node inside Tapejaridae, with characters

of the lower jaw that are not present in *Aymberedactylus*. Tapejarids excluding *Aymberedactylus* can be distinguished from azhdarchoids by a downturned symphysis, a step-like dorsal eminence and a symphyseal middle expansion. These characters were regarded as synapomorphies of the tapejarids by Wellnhofer and Kellner (1991), Kellner (2003), Unwin (2003), Frey, Buchy and Martill (2003), Kellner (2004c) and Pinheiro *et al.* (2011). Coded and analyzed by Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018), the same characters were indeed recovered as unique apomorphies of the tapejarids. Here, the four characters are considered synapomorphic for the tapejarids and distinguish them from all other azhdarchoids, with only the mandibular crest not being exclusive. The curvature on the upper jaw could also be considered a trait exclusive to most tapejarids, if not all, however this character seems more like an ontogenetic signal related to the dorsal concavity of the lower jaw, and its evolution appears to be more affected by allometry and cranial integration, as in parrots that are hard seed eaters (BRIGHT *et al.*, 2019). As the implied weighted analysis recovered, tetra-radiated jugal is indeed a synapomorphic character for Brazilian tapejarids, however *Sinopterus* and *Europejara* were also recovered inside this group. The condition in *Europejara* is unknown due to the holotype poorly preserving this region. As far as comparisons are possible, *Sinopterus* indeed have tri-radiated jugals and no quadratojugal (posterior) process of the jugal. However, as Zhang *et al.* (2019) reported, no specimen attributed to *Sinopterus* preserved this region in good enough condition for an unambiguous conclusion. The morphology of the jugal in *Sinopterus* remains to be confirmed in light of new specimens better preserved. The clade that excludes *Eopteranodon* is recovered based on a shallow fossa at the anterodorsal surface of the symphysis. It is worth mentioning that both characters, on the jugal and lower jaw, cannot be safely determined for *Eopteranodon*. Thus, it can be concluded that the condition of both characters are unknown in *Eopteranodon* and remains to be seen in light of new specimens or redescrptions of both specimens attributed to this taxon.

The equally weighted analysis, through a reduced strict consensus, and the implied weighted analysis recovered a monophyletic group composed by *Sinopterus*, *Tupandactylus* and *Caiuajara*, united by the presence of the suppremaxillary process at the dorsal tip of the premaxillary crest. If the coding is correct and the crests of *Sinopterus* and *Caiuajara* indeed present the process, the this would indicate that the process is indeed synapomorphic for these taxa. However, the hypothesis of the process on the crest in *Sinopterus* being actually an artefact of crushing cannot be ruled out. The condition in *Caiuajara* also needs to be carefully re-evaluated and redescrbed. *Europejara* was also recovered inside this group, as sister group to *Caiuajara* on the implied weighted analysis and having *Caiuajara* as one of the possible sister groups on the reduced strict consensus of the equally

weighted analysis. The premaxillary crest of *Europejara* is unknown, so the process on this taxon cannot be observed, remaining to be confirmed in light of new specimens better preserved. Only on the implied weighted analysis a monophyletic *Tupandactylus* with *Sinopterus* was recovered, based on the morphology of the retroarticular process, a longer mandibular crest and a strongly bowed fourth wing phalanx. This could indicate that the retroarticular process as a long, rounded hook is indeed a synapomorphic feature of the three taxa, but the equally weighted analysis recovered *Caiuajara* as a sister group to *T. imperator*, making *Tupandactylus* paraphyletic. In this case, the process would be synapomorphic for the group with a reversal on *Caiuajara*. The same can be noted for the length of the dentary crest and the curvature of the fourth wing phalanx. The evolution of such features can be tested in light of more specimens, however it is safe to assume that they indeed are shared by *Sinopterus* and both *Tupandactylus*, regardless of *Caiuajara* being recovered closely related. Finally, at least for the implied weighted analysis, *Tupandactylus* was recovered monophyletic. All three characters that united *T. imperator* with *T. navigans* indeed are exclusive to them, considered here synapomorphies that distinguish *Tupandactylus* from any other azhdarchoid. First, the premaxillary crest is striated, which is related to the dorsal surface anchoring the crest of soft tissue. As Frey *et al.* (2003) and Pinheiro *et al.* (2011) elucidated, this striated morphology is caused by the parallel fibers of the crest of soft tissue penetrating the bones, causing a stiffening for extra support of the crest. Second, although all tapejarids presents an overall rounded nasoantorbital fenestra, *Tupandactylus* presents a reclined posterior margin, with the dorsal margin being posterior to the ventral margin. In any other tapejarid, such as *Sinopterus* (ZHANG *et al.*, 2019), the nasoantorbital fenestra is subangular, almost perpendicular with the ventral margin of the skull. Third, the anterior tip of the symphysis is sharp and elongated, shaped like a prow. Although these characters may not be exclusive of *Tupandactylus*, such as the configuration of the nasoantorbital fenestra, here it is concluded that these characters can be included as useful autapomorphies on the list of characters that defines *Tupandactylus*. It is worth mentioning that the equally weighted analysis recovered *Caiuajara* inside *Tupandactylus*, indicating that these taxa may have more in common than previously thought. More studies regarding the overall morphology and a complete redescription of *Caiuajara* are necessary to elucidate this result.

8. CONCLUSIONS

This study described a new specimen of *Tupandactylus imperator* (CAMPOS & KELLNER, 1997), housed at the Paleontology collection on the Museum of Zoology of the University of São Paulo, under the number MZSP-PV 1249. Labelled here the São Paulo specimen, it is the fifth specimen formally described and figured for the taxon. Being a nearly complete and articulated skeleton, including a skull, mandible, most crests, cervical and dorsal vertebrae, the sternum plate, one visible shoulder girdle, remnants of the pelvic girdle and most elements of both forelimbs and hindlimbs, this new specimen complements previous descriptions for this taxon and the genus *Tupandactylus*. Two preliminary phylogenetic analyses were performed to assess the position and relationships of the species within the irradiation of pterosaurs, in particular the tapejarids. An updated classification can be established for this taxon from the Araripe Basin.

New information has been uncovered for Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), which is the same as Tapejarinae *sensu* Kellner and Campos (2007):

→ The ontogenetic status of the tapejarids can be inferred based on the morphology of the rostrum. Rostrum and symphysis both downturned are the main feature of the tapejarids (KELLNER, 2003; UNWIN, 2003), where Martill *et al.* (2020a) observed variation in the rostral deflection angle, as a taxonomic and ontogenetic feature, possibly sexually dimorphic as well. An extra feature identified as an ontogenetic signal is the arched curvature posterior to the deflected rostrum, where mature specimens of tapejarids exhibit a rostrum with an arched-and-downturned configuration, in a lateral aspect from a posterior-to-anterior perspective, a feature exclusive to mature and older tapejarids that would fall into the categories OS5 and OS6, possibly on the OS4 as well, of Kellner (2015). The arched-and-downturned rostrum matches the convex-and-downturned symphysis, caused by the dorsal eminence and downturned tip of the symphysis, performing a perfect occlusion of the jaws, while juveniles present a occlusal gap. The dorsal eminence of the lower jaw develops earlier than the rostral curvature of the upper jaw, indicating that such eminence plays a key role in feeding habits for tapejarids and the delayed development of the rostral curvature is more affected by allometry and, quite possibly, cranial integration, as in parrots specialized in hard seeds (BRIGHT *et al.*, 2019). The function and development of the dorsal eminence on the lower jaw, however, can only be confirmed with biomechanical, phylogenetic and geometric morphometric studies. Rostral deflection angles must be measured with caution, because the rostral curvature may overestimate the angles, as in Martill *et al.* (2020a) for *Afrotapejara* and the Private specimen of *T. imperator*.

→ Agreeing with Pêgas, Costa and Kellner (2018) and Zhang *et al.* (2019), Brazilian tapejarids present tetra radiated jugals, with a quadratojugal (posterior) process. This process is not exclusive to tapejarids, but its reappearance within a group of pterosaurs with triradiated jugals can be considered exclusive to Brazilian tapejarids. A trait that is exclusive is the quadratojugal (posterior) processes being directed posterodorsal. The condition in Chinese tapejarids such as *Sinopterus* is dubious, and in thalassodromids such as *Thalassodromeus* is unknown, so the evolution of the jugal within these groups remains to be seen. The evolution of the jugal in azhdarchoids may be even more complex than previously thought.

→ The shape and size of the posterior occipital process is the main autapomorphy distinguishing *T. imperator* from other tapejarids, but the presence, shape and size of this process is also a valuable character that distinguish each and every species of tapejarid with skulls, thus the diagnosis of all tapejarids should incorporate these attributes of the posterior occipital process as an autapomorphy. This is true even considering the definition of Tapejaridae *sensu* Kellner (1989), since *Tupuxuara* and *Thalassodromeus* also have unique configurations for the posterior occipital process.

→ Downturned symphysis, step-like dorsal eminence and symphyseal middle expansion are three characters that can be considered unique and exclusive to the Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007). These are the same characters discussed by Wellnhofer and Kellner (1991), Kellner (2003), Unwin (2003), Frey, Buchy and Martill (2003), Kellner (2004c), Pinheiro *et al.* (2011), and also coded and recovered as unique traits of tapejarids by Andres, Clark and Xu (2014), Wu, Zhou and Andres (2017) and Longrich, Martill and Andres (2018). This indicates that most characters valuable to distinguish the tapejarids are related to the lower jaw.

→ While the presence of a mandibular crest is not exclusive to the tapejarids, it surely can be used to distinguish Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007) from all other azhdarchoids. Ranges of the ratio regarding the height of the crest, relative to the height of the mandibular ramus, may distinguish major groups.

An emended diagnosis can be elaborated for the genus *Tupandactylus*, being the species of tapejarid with a wingspan of 3m defined by the following shared characters:

→ Prenarial rostrum of the premaxillomaxilla and the anterior region of the dentary symphysis both downturned, in a linear configuration. This character is not exclusive to *Tupandactylus*, since it is synapomorphic for all of the Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007).

- Huge and high cranial crest, composed by a subtriangular bone blade and extensive area of soft tissue. A premaxillary crest shaped as a high bone blade is also observed on *Caiuajara*, however in *Tupandactylus* it is subtriangular with a posterior margin subrounded, whereas in *Caiuajara* it is a high blade and no soft tissue elements are known up to date. The soft tissue crest makes the premaxillary crest striated, a character present in many pterosaurs, but it distinguishes *Tupandactylus* from all other Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007).
- Premaxillary crest with anterodorsal, thin and spine-like suprapremaxillary process. This process is exclusive to *Tupandactylus*. The presence of a similar process might occur in *Sinopterus* and *Caiuajara* and, if they indeed present such process, in *Tupandactylus* the suprapremaxillary process is shaped as a thin and long spine, whereas in *Sinopterus* it would be very short and triangular and in *Caiuajara* it would be shaped as a large blade with a posterior process.
- Posterior margin of the internasal process of the premaxilla articulating with the nasal and the frontoparietal. This character contrasts with the condition observed in *Tapejara* (WELLNHOFER & KELLNER, 1991) and *Sinopterus* (ZHANG *et al.*, 2019), but other features regarding this contact, or the absence of this contact in other taxa, such as ontogenetic developments and biomechanical influences, remains to be carefully studied.
- Nasoantorbital fenestra very large and long, comprising ~60% of the preserved length of the skull, exclusive of cranial crests. This character is exclusive to *Tupandactylus*.
- Posterior margin of the nasoantorbital fenestra slightly reclined, with the posterodorsal margin of the fenestra posterior to the posteroventral margin, but still anterior to the orbit. While this condition occurs in many pterosaurs, it distinguishes *Tupandactylus* from all other Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007).
- Descending process of the nasal elongated, reaching the ventral limit of the nasoantorbital fenestra but not articulating with it. This character is exclusive to *Tupandactylus*. In *T. navigans*, although crushed and eroded, remnants on the holotype reveal that it is also elongated.
- Anterior tip of the mandibular symphysis sharp and elongated, shaped like a prow. This character is exclusive to *Tupandactylus*.
- Very deep and rounded mandibular crest, with a steep anterior margin, forming an angle of ~60° with the mandible. This character is exclusive to *Tupandactylus* with differences in the size of the crest, position of the ventral-most limit of the crest and angle of the posterior margin reflecting ontogenetic variations between different specimens.
- The ratio of the height of the dentary crest, relative to the height of the mandibular ramus, being higher than 5, at least in mature specimens. Vullo *et al.* (2012) registered for *Europejara* a value of

~4, while all other tapejarids ranged from ~1.5 to ~3 and the Crato specimen of *T. imperator* had a value of ~3. This character can be observed on mature specimens of *Tupandactylus*, or specimens close to maturity. *Tupandactylus* is officially the genus with the deepest mandibular crest of all pterosaurs. This ratio also reinforces the identity of the São Paulo specimen as ontogenetically older than the Crato specimen, where the mandibular crest in the latter was still in process of growth.

→ Small dorsal concavity at the anterior region turned ventrally of the symphysis. This character is not exclusive to *Tupandactylus*, since it is synapomorphic for the Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007).

→ Retroarticular process elongated, with a convex ventral margin, a concave dorsal margin and the posterior tip as a rounded eminence directed posterodorsal, shaped like a rounded elongated hook. This character is not exclusive to *Tupandactylus*, since it is also shared with *Sinopterus*, however it distinguishes *Tupandactylus* and *Sinopterus* from all other Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), or Tapejarinae *sensu* Kellner and Campos (2007).

Both species of *Tupandactylus* can be considered valid species. Pinheiro *et al.* (2011) pointed out that both taxa may represent a single taxon that is sexually dimorphic, but the variation on the cranial crests, specifically the posterior occipital process, indicates that this seems unlikely. Some characters suggest a close relationship between *Tupandactylus* and *Sinopterus*, such as the shape of the retroarticular process, the length of the metacarpal I and a vestigial pedal digit V, as well as a possible suppremaxillary process in *Sinopterus*. *Tupandactylus* shares exclusive characters with the Brazilian tapejarids, such as tetraradiate jugals, a feature that remains to be seen in *Sinopterus*. *Caiuajara*, possibly presenting a suppremaxillary process, may share a closer relationship with *Tupandactylus* and also with *Sinopterus*. A preliminary phylogenetic analysis has recovered a closer relationship between *Tupandactylus*, *Caiuajara* and *Sinopterus*, but this result must be interpreted with caution, because the feature that unites the three taxa is the presence of a suppremaxillary process. More studies are necessary to evaluate if the crest in both *Sinopterus* and *Caiuajara* indeed present such process, or if the crest on each taxon has a unique composition.

An emended diagnosis can also be elaborated for the species *Tupandactylus imperator*, being the species of *Tupandactylus* defined by the following characters:

→ A length to height ratio, measured from the tip of the premaxilla to the posterior margin of the squamosal and from the quadrate condyle to the dorsal margin of the premaxilla, dorsal to the orbit, about 3.6. The skull of *T. navigans* is overall shorter, with a length to height ratio about 2.3.

- Premaxilla anteriorly projected, with anteriorly projecting convex blade. In *T. navigans*, there is no such blade, so the premaxilla is anteriorly subvertical.
- Suprapremaxillary process with posterodorsal orientation, with soft tissue of the cranial crest composed by parallel subvertical fibers with posterodorsal curvature. *T. navigans* do not present a convex blade anteriorly projected, so the suprapremaxillary process have a subvertical orientation, with the fibers of the soft tissue crest having an anterodorsal curvature.
- Descending process of the nasal with a thin triangular shape, with the posterior tip articulated with the main body of the nasal, the anterior tip projected anteriorly and the ventral tip elongated into a thin rod-like process. Although listed here as a new autapomorphy for *T. imperator*, the condition in *T. navigans* remains unknown due to the process in *T. navigans* being poorly preserved. Possibly it is the same morphology and this character is possibly a synapomorphy of *Tupandactylus*.
- Descending process of the nasal positioned laterally, directed medially and anteroventrally, meeting at the middle point and fusing into a single medial process. Although listed here as a new autapomorphy for *T. imperator*, the condition in *T. navigans* remains unknown due to an artefact of crushing, so it is unknown if the processes meet medially. Possibly it is the same morphology and this character is possibly a synapomorphy of *Tupandactylus*.
- Posterior occipital process composed by three elongated components, with the dorsal process being the premaxillary internasal process, the ventral process being the supraoccipital crest and the middle element being a thin and vertical parietal crest connecting the two processes. The homology of these three elements are still uncertain, but this morphology is exclusive to *T. imperator*, whereas in *T. navigans* there is no posterior occipital process, a condition that is also exclusive to this taxon within the tapejarids.
- Posterior occipital process extending beyond the posterior margin of the skull and reaching about the length of the skull, measured from the tip of the premaxilla to the posterior margin of the squamosal. This character is exclusive to *T. imperator*, whereas in *T. navigans* there is no posterior occipital process, a condition that is also exclusive to this taxon within the tapejarids.
- Fourth wing phalanx vestigial, smaller than the manual phalanges except the second phalanx of the digit III, where the ratio between the length of the fourth wing phalanx, relative to the length of the first wing phalanx, is only 0.055, or ~5%. This feature is not exclusive to *T. imperator*, because a similar character is observed on *Microtuban*. Here it is concluded that the extreme shortening of the phalanx was acquired independently, but it can be a more widespread character within the azhdarchoids, since it is present on a specimen attributed to *Quetzalcoatlus*. The condition in *T. navigans* remains unknown and comparative studies are more than necessary.

A rostral value and a rostral index of ~ 2 and ~ 2.8 , respectively, reveal that the São Paulo specimen has the prenarial rostrum very short, as in all tapejarids and thalassodromids, however the rostral index presented a value closer to the values of the thalassodromids, instead of the tapejarids. No specimen attributed to *T. imperator* can be regarded as a juvenile, while at least one specimen, the Private specimen, can be considered a fully grown adult. The São Paulo specimen reveals that all specimens are at least subadults very close to maturity, falling into the category OS5 of Kellner (2015), while the Private specimen would be the only specimen that reached OS6 and the Crato specimen being the only specimen that possibly falls into OS4 or an intermediate between OS4 and OS5. Simplified, the tentative scale of overall sizes between specimens attributed to *T. imperator* is Crato < Holotype < São Paulo \sim German < Private. If the scale size is true, it would reveal other ontogenetic signal for *T. imperator*, that is the crest of soft tissue becoming slightly bigger as the specimen grows older. During ontogeny, the posterior occipital crest would become more ventrally directed, while the suprapremaxillary process would become more dorsally directed, making the crest slightly taller and longer in older specimens. A similar pattern can also be observed on the mandibular crest, where the crest develops from an anterior to a posterior perspective, intimately associated with the gnathotheca, making the ventral-most tip more anteriorly placed. The posterior half deepens and the crest keeps growing, until the deepest tip moves to a centralized region. The timing of development of the crests on both the skull and the symphysis remains to be seen in light of new specimens. A similar pattern for crest growth can be tentatively recognized for *T. navigans* (FREY, MARTILL & BUCHY, 2003b), with the suprapremaxillary process having a posterodorsal direction, becoming subhorizontal all the way to a anterodorsal process in an older specimen. Thus, a tentative size scale of the specimens of *T. navigans* would be Holotype < Eroded < Recovered. A complete redescription, based on the Recovered specimen, may help elucidate this issue. The São Paulo specimen reveals that the soft tissue crest in *T. imperator* may have blood vessels, but this identification is merely tentative and further researches are necessary.

As for the axial and the appendicular skeleton, *T. imperator* reveals that the patterns of the pterodactyloids, azhdarchoids and tapejarids maintained stable for this taxon. The notarium cannot be observed directly on the São Paulo specimen, but indirect evidences reveal that it was present on *T. imperator*, indicating that the tapejarids indeed may present this structure, unknown from taxa represented only by juveniles or the case of *Sinopterus*, where the lack of a notarium may be an erroneous identification, while both specimens that preserved a notarium (SAYÃO & KELLNER, 2006; CHENG *et al.*, 2020) are unidentified. *T. imperator* has a relative formula for the length of the cervicals of III < IV = V > VI > VII > VIII, with concave ventral surfaces in lateral view. The

new specimen of *T. imperator* reinforces the need for further studies regarding the presence and evolution of pneumatic foramina in pterosaur vertebrae, especially cervicals, indicating that they are way more complex than originally thought. The morphology of the cervicals puts in check the conclusions of Frey, Martill and Buchy (2003b), Frey *et al.* (2003), Unwin and Martill (2007) and Chatterjee and Templin (2012) of the cranial crest in *Tupandactylus* working as a self-adjustment rudder system. The cervical vertebrae indicates that lateral turns of the head were impractical, if not impossible, with severe limitations to lateral flexions. Thus, here it is concluded that *Tupandactylus* would not use its headcrest for an aerodynamic function. Not only the notarium, the new specimen also reveals that the dorsal ribs have a decreasing thickness and both scapulae articulate with the vertebral column in older specimens. The wing phalanges have a decreasing size, with the first wing phalanx being the longest and thickest. The second and third phalanges have a cross-section T-shaped, with a longitudinal ventral ridge, a character previously believed to be a feature of the azhdarchids, but with *T. imperator* it is confirmed as a apomorphic for the azhdarchoids. The acetabulum is hemispherical rounded and imperforated, being very robust thanks to a peripheral emargination around the whole cotyle, while the femur has a rounded head with a slender neck, which together would allow enormous freedom of movement. As far as observations allowed, more information can be revealed with a complete preparation or a CT-Scan of the São Paulo specimen, such as the braincase, the morphology of the covered vertebrae, the sternal plate, both radii and ulnae, the wing metacarpals, the distal wing phalanges, all trochanters of the femora, fibula and the pes digits. Biomechanical influences regarding the interference of the cranial crest on the flying capabilities of a taxon with a wingspan of 3m, virtually presenting three wings, remains to be carefully tested. The morphology of the wings indicate that *T. imperator* was a competent flyer.

Sinopterus here is regarded as presenting a small suprapremaxillary process that fuse with the premaxillary crest in adults. An artefact of crushing on the specimen that potentially present this process cannot be ruled out, but in both cases the crest would have a conformation similar to the observed on other specimens. Thus, there are no characters that distinguishes species apart, aside from exact relative limb proportions, as presented by Zhang *et al.* (2019), that appears to fall into a individual variation within a single taxon. All the species formely described as valid species for *Sinopterus*, being "*S. atavismus*", "*S. benxiensis*", "*S. corollatus*" and "*S. lingyuanensis*", are here synonymized with the species *S. dongi*, all representing different ontogenetic stages of *S. dongi*. Agreeing with Witton (2013), here "*Nemicolopterus*" is also considered invalid and synonymous with *S. dongi*, because its autapomorphies are likely ontogenetic variation or preservational bias. *Sinopterus* can be considered a genus with a single species, where the growth series are rather

complete comprising hatchlings and very young juveniles all the way up to fully grown adults. Exact relative ratios are not useful for distinguishing species apart within a same genus or closely related taxa, since they can reflect individual variation within groups, and should be discouraged. The exceptions to this rule are using relative ratios to define major groups of pterosaurs or aberrant, disproportional ratios never before seen in closely related taxa, where only the taxon falls outside a known spectrum. Until true autapomorphies that are not based on relative ratios or ontogenetic features are described, all species of *Sinopterus* aside from *S. dongi* should be regarded as dubious or invalid, synonymized with the type species *S. dongi*.

Pterosaurs from Brazil are of paramount importance, both for preservation of the osteological elements as well as providing new information regarding the irradiation and evolution of the pterodactyloids. Here it is concluded that further researches are more than necessary to elucidate the evolution of specific traits within pterosaurs, including the dorsals centra, cervicals lengths in azhdarchoids, a comparative morphology in cervicals and dorsals of azhdarchoids, the evolution of the ventral coracoidal tubercle, coracoidal flange or *musculus supracoracoideus* attachment crest in azhdarchoids and ornithocheiroids, the phylogenetic and biomechanical influences regarding the morphological variation of the articulation between the three metacarpalia and the manual digits, if there are different movement types for each digit and how this influenced the shortening of the metacarpalia in pterodactyloids, biomechanical comparative studies regarding the manual and pedal digits of *Tapejara*, since they differ significantly from all other tapejarids and may indicate that this taxon occupied a unique niche and, lastly, how the fifth pedal digit evolved in azhdarchoids, pterodactyloids and all pterosaurs. As for the phylogenetic aspects, this study agrees with most phylogenetic analysis that Eopterosauria may not form a monophyletic group, contrary to Andres (2010) and updates. Certain stability have been recovered in some clades, such as Dimorphodontia, *Campylognathoides*, overall Archaeopterodactyloidea and internal groups, overall Pteranodontia and the internal groups, overall Lanceodontia and internal groups, Istiodactylidae, Azhdarchoidea *sensu* Andres, Clark and Xu (2014), internal composition and relationships of the Dsungaripteridae, Neopterodactyloidea as a clade and Tapejaridae *sensu* Lü *et al.* (2006b) and Andres, Clark and Xu (2014), being the same as Tapejarinae *sensu* Kellner and Campos (2007). Others had instability internally or even externally, such as Rhamphorhynchidae, Darwinoptera, Anurognathidae, internal relationships on groups inside the Archaeopterodactyloidea, Pteranodontia and Lanceodontia, the relationships of Dsungaripteridae with all other azhdarchoids and the internal relationships of Neopterodactyloidea. Anhangueria had no stability, indicating that even more morphological and phylogenetic re-evaluations similar to Rodrigues and Kellner (2013) and Holgado and Pêgas (2020)

are necessary. Similar studies are necessary for the Azhdarchidae, with no resolution whatsoever. Dsungaripteridae recovered inside Azhdarchoidea is a result that must be interpreted with caution, with a careful re-evaluation of taxa and a phylogenetic analysis of the Dsungaripteridae being more than necessary. The same is true for the relationships of Thalassodromidae within Azhdarchoidea, because the Tapejaridae *sensu* Kellner (1989) or Neoazhdarchia *sensu* Unwin (2003), excluding Dsungaripteridae, or recovered as of Andres (2010), including Dsungaripteridae, is a matter far from resolved. As for Tapejaridae, the clade was recovered based mostly on lower jaw characters, reflecting that most named taxa presents more lower jaw elements preserved than any other anatomical region. Finally, *Caiuajara* being closely related to *Tupandactylus* shows that a complete redescription of *Caiuajara* is more than necessary to elucidate this possible relationship. All Bootstrap and Jackknife trees had a huge polytomy, indicating that more phylogenetic studies regarding internal relationships of Azhdarchoidea, Pterodactyloidea and Pterosauria are necessary.

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