

New pterosaur material from the Araripe Basin

Skull evolution, ontogeny and sexual dimorphism in Early Cretaceous pterosaurs from Brazil



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'There is nothing like geology; the pleasure of the first day's partridge shooting or first day's hunting cannot be compared to finding a fine group of fossil bones, which tell their story of former times with almost a living tongue.'

CHARLES DARWIN IN A LETTER TO HIS SISTER, 1834

Acknowledgments

Thomas Wolfe once wrote: "We are the sum of all the moments of our lives." This was true for him as it is for me. This thesis could not have existed were it not for specific moments and persons, one more special than the other.

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Finally I have to thank the one person who was always there for me, Sara. Sara encouraged me, supported me, helped me, discussed my ideas, criticized me (with good reason, though) and most importantly lived with me— and I have to congratulate her for this as I, the field expert, can confirm that this is not always easy. Without Sara this thesis was probably of a lesser standard if it had existed at all.

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Glossary, list of abbreviations and taxonomy

Centroid size: representative of size in geometric morphometric studies as it is uncorrelated with shape, hereby not interfering with the analyses. It is calculated by taking the square root of the summed squared distances of each landmark from the centroid of the landmark configuration.

Morphospace: representation of shape of one or more specimens. Each axis corresponds to one or more shape variables. By combining all axes the true shape of the specimen is found. In this thesis morphospace will be considered as one or more principal components of the RWA.

Type I landmark: landmark that is recognized by a biological distinguishable structure, e.g., the convergence of two sutures; also called true landmarks.

Type II landmark: landmark that is chosen on geometric ground, e.g., most anterior point; also called pseudo-landmarks.

Type III landmark: landmark of which the location is depended on the location of another landmark, e.g., the point perpendicular to the line between point x and point y; also called semi-landmarks.

ad:	adductor fossa
ar:	articular
fpc:	frontoparietal crest
fr:	frontal
gl:	glenoid
j:	jugal
l:	lacrimal
lf:	lacrimal foramen
lpj:	lacrimal process of the jugal
ltf:	lower temporal fenestra (fenestra infratemporalis)
md:	mandibula
mx:	maxilla
na:	nasal
naof:	nasoantorbital fenestra
ob:	orbit
par:	parietal
pe:	posterior extension
pm:	premaxilla
pmsc:	premaxillary sagittal crest
pt:	pterygoid
qa:	quadrate
qj:	quadratojugal
ra:	retroarticular process
sq:	squamosal
sym:	symphysis
tr:	transverse ridge
ver:	vertebra
LM:	Landmark
GLS:	General Least squares Procrustes Superimposition
PC:	Principle Component
PCA:	Principle Component Analysis
RWA:	Relative Weight Analysis

Table 1: The taxonomy of the Brazilian pterosaurs is difficult and several similar names are often mentioned throughout the text. To make things easier, and hopefully more clear, this table and accompanying reconstructions (figure A.15-A.21) are given. This first part of the table shows the different Ornithocheiridae while the part of the next page gives an overview of Tapejaridae.

Species	Maisey (1991)	Veldmeijer (2006)	Kellner (2006)	Wellnhofer (1985)	Veldmeijer (2006)/ Wellnhofer (1987)
<i>Anhanguera araripensis</i>		<i>Coloborhynchus araripensis</i>	<i>Anhanguera araripensis</i>	<i>Santanadactylus araripensis</i>	
<i>Anhanguera blittersdorffi</i>		<i>Coloborhynchus blittersdorffi</i>	<i>Anhanguera blittersdorffi</i>		
<i>Anhanguera piscator</i>		<i>Coloborhynchus piscator</i>	<i>Anhanguera piscator</i>		
<i>Anhanguera santanae</i>		<i>Coloborhynchus santanae</i>	<i>Anhanguera santanae</i>		
<i>Coloborhynchus spielbergi</i>			<i>Anhanguera spielbergi</i>		
<i>Tropeognathus mesembrinus</i>					<i>Criorhynchus mesembrinus</i>
<i>Brasilodactylus araripensis</i>	juvenile <i>Anhanguera</i>				
<i>Ludodactylus sibbicki</i>					
<i>Guidraco venator</i>					

Species	Family	Kellner & Campos (1985)	Unwin (2003)	Andres & Meyer (2013)
<i>Anhanguera araripensis</i>	Ornithocheiridae	Anhangueridae	Ornithocheiridae	Anhangueridae
<i>Anhanguera blittersdorffi</i>	Ornithocheiridae	Anhangueridae	Ornithocheiridae	Anhangueridae
<i>Anhanguera piscator</i>	Ornithocheiridae	Anhangueridae	Ornithocheiridae	Anhangueridae
<i>Anhanguera santanae</i>	Ornithocheiridae	Anhangueridae	Ornithocheiridae	Anhangueridae
<i>Coloborhynchus spielbergi</i>	Ornithocheiridae	Anhangueridae	Ornithocheiridae	Ornithocheiridae
<i>Tropeognathus mesembrinus</i>	Ornithocheiridae	Anhangueridae	Ornithocheiridae	Ornithocheiridae
<i>Brasilodactylus araripensis</i>	Ornithocheiridae			
<i>Ludodactylus sibbicki</i>	Ornithocheiridae			
<i>Guidraco venator</i>	Ornithocheiridae			

Species	Frey et al., 2003b	Kellner (2004)	Kellner & Campos (2007)	Unwin & Martill (2007)
<i>Thalassodromeus sethi</i>				
<i>Tupuxuara deliradamus</i>				
<i>Tupuxuara leonardii</i>				
<i>Tapejara welnhofferi</i>		<i>Tapejara welnhofferi</i>		
<i>Tupandactylus imperator</i>		<i>Tapejara imperator</i>	<i>Tupandactylus imperator</i>	<i>Ingridia imperator</i>
<i>Tupandactylus navigans</i>	<i>Tapejara navigans</i>			<i>Ingridia navigans</i>
Species	Subfamily	Family	Clade	
This thesis	This thesis/ Kellner (2007)	This thesis/ Kellner (2007)	Unwin (2005)/ Martill & Naish (2006)	Martill & Naish (2006)/ Andres & Myers (2013)
<i>Thalassodromeus sethi</i>	Thalassodrominae	Tapejaridae	Thalassodromidae	Neoazhdarchia
<i>Tupuxuara deliradamus</i>	Thalassodrominae	Tapejaridae	Thalassodromidae	Neoazhdarchia
<i>Tupuxuara leonardii</i>	Thalassodrominae	Tapejaridae	Thalassodromidae	Neoazhdarchia
<i>Tapejara welnhofferi</i>	Tapejarinae	Tapejaridae	Tapejaridae	Unnamed clade
<i>Tupandactylus imperator</i>	Tapejarinae	Tapejaridae	Tapejaridae	Unnamed clade
<i>Tupandactylus navigans</i>	Tapejarinae	Tapejaridae	Tapejaridae	Unnamed clade

Chapter 1

Introduction

In vertebrate paleontology, unlike other biological, or geological sciences, one cannot design an experiment, or organize a field excursion, to test a particular hypothesis. In a way it resembles the game of Cluedo: one knows that a crime has been committed but in this harder version one does not know what crime, who committed it or how he/she did it. The only thing a paleontologist knows when he receives new fossil material, is that, in Cluedo-talk, a crime has been committed. Typically he would start with describing the fossils. Then he would complete the game by constructing hypotheses, testing them and interpreting the results. But unlike in Cluedo, the game never really ends, and other researchers will have to complement his findings with new clues to come up with new hypotheses and insights. In this thesis the fossil material consists of cranial remains of Brazilian pterosaurs. Pterosaurs in general are mysterious: they were the first flying vertebrates, had several structures whose function still needs to be investigated (e.g. crests and hair-like structures called pycnofibers) and are found on every continent except for Antarctica. The specimens available belonged to two clades called Ornithocheiridae, and another called Tapejaridae.

Ludodactylus sibbicki, belonging to Ornithocheiridae, is a particularly interesting species as it has some peculiarities. It is one of the few, and the only Brazilian, Ornithocheiridae that lacks a premaxillary crest but has a large frontoparietal crest. Also, it highly resembles *Brasileodactylus*, which lacks a crest all together. *Ludodactylus* thus raises two questions. A first one is related to the meaning of the crest at the species-level. Is it a valid character to separate species or are *Ludodactylus* and *Brasileodactylus* just another case of sexual dimorphism? Second, does this crest have an evolutionary significance, and if so, which evolutionary driver was responsible for it? To answer the first question one should normally do a phylogenetic analysis. In the case of *Ludodactylus* and *Brasileodactylus* this does not produce unambiguous result based on distinct morphological characters that are used commonly in paleontological phylogenetic research. In modern day taxonomy, however, shape is often used as well. For example, in the first sentence of the description of the Goldeneye, *Bucephala clangula* : '**Compact** duck with **large, rounded** head like a knob on fairly short neck; crown **slightly peaked** and **shape of head triangular**' (Svensson,1999), with all characters related to shape are in bold typeface. However, quantitative descriptors of shape are rarely used in fossil taxonomy. Geometric morphometrics is an emerging

technique that is particularly promising because it allows to numerically compare shapes as defined by a (potentially large) collection of linear measurements (which on their own did not provide a useful dataset). In this thesis we will try, for the first time, to use this technique to look for evolutionary patterns within Ornithocheiridae. The sample size of vertebrate fossils, and pterosaurs in particular, is often too low to draw statistically significant conclusions. Also, the evolutionary forces in fossils are highly debated. We will, therefore, interpret the results from geometric morphometrics using literature, additional observations and additional tests, looking at the problem from as many angles as possible to compensate for the lack of statistical power.

We will use geometric morphometrics also to explore the highly disputed taxonomy of Tapejaridae (sensu Kellner, 2004). One of the available specimens belongs to the genus *Tupuxuara*, of which the phylogenetic position is uncertain both on the genus as well as on the family level. Although this specimen cannot be used in the geometric morphometric analysis due to its incomplete nature, it is of interest due to its small size. *Tupuxuara* consists of several species of which two, *T. deliradamus* and *T. leonardii*, have been considered as conspecific and sexual dimorphic. We will investigate whether the presence of juvenile–adult pairs may yield clues to confirm or reject this hypothesis. A final specimen belonged to *Tupandactylus*, which had an impressive crest, which, according to this new specimen, contained ‘hair’—pycnofibers in pterosaurs. As pycnofibers are usually not preserved in a condition as pristine as this specimen, discussing it in detail would not be possible in the limited space available.

Chapter 2

Literature review

2.1 Historical overview of pterosaur research

When *Pterodactylus antiquus*, the first pterosaur ever found, was discovered in the Solnhofen Limestone somewhere between 1767 and 1784, its position in the so called tree of life was questioned (Witton, 2013). It took more than 100 years until Pterosauria were considered a new and separate order. In those first 100 years Pterosauria were placed on many different branches of that tree of life.

Collini, who described the first pterosaur, placed *Pterodactylus antiquus* in Amphibia and reconstructed it with large flippers (Collini, 1784). When Cuvier (1801) studied the original illustration and description of the fossil, he managed to recognize the error of Collini and considered *Pterodactylus antiquus* to be a reptile. Soemmering (1812) considered pterosaurs as an animal not too different from bats (figure 1.1), but renamed the genus *Pterodactylus* to *Ornithocephalus*, ancient birdheads. This again highlights the taxonomic difficulties related to Pterosauria. The close resemblance with birds eventually lead Soemmering in 1825, to consider a new species of Pterosauria as 'Urvogel', ancient bird. The reconstruction he had in mind was a bird that resembled a gull (*Larus*) or a diver (*Gavia*) (Wellnhofer, 1991).

In 1831, Goldfuss, following Cuvier, placed Pterosauria within Reptilia although this was not accepted at the time. Until 1901 the pterosaurs would be considered as something between birds and mammals, a flying Marsupialia and even as the mythological Griffin (Newman, 1843; Soemmering, 1812; Wagler, 1830). Seeley (1901) published the first masterpiece on pterosaurs 'Dragons of the Air'. He considered Pterosauria, as well as Dinosauria, as something between birds and reptiles and called them Ornithosauria, or birdlizards. This proved wrong in the following years as pterosaurs are not as closely related as thought. More recent and extensive research seems to confirm the meticulous work of Cuvier, the founding father of modern comparative anatomy. Cuvier already noticed that the articulation of the quadrate with the mandibula is more reptile-like than mammal-like (Cuvier, 1801; Witton, 2013). Furthermore, the teeth of the toothed pterosaurs resemble these of reptiles in being simple and being constantly replaced. The two temporal fenestrae behind the eyes place Pterosauria within the diapsids, while the

mammals are all synapsids (Gower & Wilkinson, 1996; Witton, 2013).

Within these diapsids there are many taxonomical units to which Pterosauria could belong and a consensus about the exact location within the Reptilia is also absent. A first candidate is a place within the Protosaurs with as close relative the strange *Sharovipteryx* (Figure 2.2) (Peters, 2000). The comparison of *Sharovipteryx* with Pterosauria is clear. *Sharovipteryx* had a membrane between its legs that probably was used to glide from one tree to another, just as the hypothetical ancestor of the pterosaurs would have done. The location of the membrane responsible for the lifting power — between the legs — in *Sharovipteryx*, was, however, completely different from the pterosaurs. While pterosaurs also had a membrane between their legs, the uropatagium, it did not affect their lifting capability. The most impressive and most important membrane of pterosaurs was the brachioapatagium between the fourth digit and

the hip, or more likely, between the fourth digit and the ankles (Elgin *et al.*, 2011; Witton, 2013). This lead other authors to place the pterosaurs higher up the phylogenetic tree of the Reptilia. Nesbitt (2011) and Nesbitt & Hone (2010) among others do place the Pterosauria within the Archosauria, as a sistergroup of the Dinosauria. This classification is now used by most pterosaur-researchers (Witton, 2013). This new group within the Archosauria that combines the Dinosauria and the Pterosauria is called the Ornithodira. According to this widely used classification, birds are the most recent relatives of the Pterosauria, followed by the crocodiles. The most recent research (Bennett, 2013a) however places the Pterosauria between *Sharovipteryx* and the Archosauria, and considers them as basal Archosauriformes which are closely related to Archosauria, but the use of some characters is highly disputed (website 1).



Figure 2.1: The illustration of *Pterodactylus* as a bat by Edward Newman in 1843.

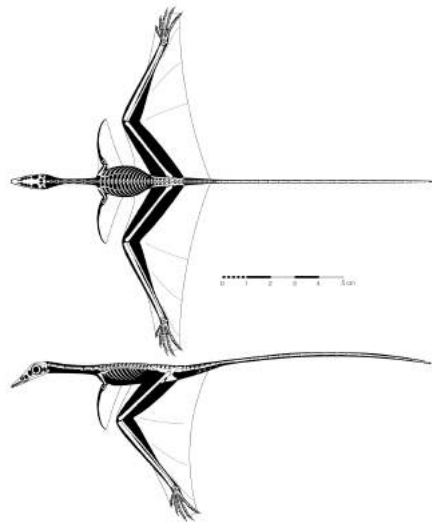


Figure 2.2: *Sharovipteryx* from the Madygen Formation (Upper Triassic) as drawn by John Conway. Notice that the membrane between the legs is the membrane sustaining flight.

2.2 Brazilian pterosaurs

2.2.1 Araripe basin

The Early Cretaceous was the summum of pterosaur diversity (Unwin, 2005). One of the areas that has yielded the highest number of pterosaur specimens is the Araripe Basin of north-east Brazil (figure 2.3). This basin contains several formations, of which two are of high importance to vertebrate paleontology. The Crato Formation, with its Nova Olinda Member, is a first one. This fossil site is best known from the outcrops near the village of Crato in the northern-central part of Chapada do Araripe. The Crato formation is between 50 and 60m thick but only the Nova Olinda Member, between 0 and 13m thick, contains fossils with exceptional conservation (Martill, 2007b). Most of the Nova Olinda Member is found between Nova Olinda, Santana do Cariri and Tatajuba (Martill & Frey, 1998; Frey *et al.*, 2003a). The Crato Formation is recognized as a Konservat Lagerstätten because of its remarkable preservation. The age of the Crato Formation is not well studied, but preliminary research suggests it to be of Late Aptian age. Some authors (Berthou *et al.*, 1994) suggest that the Formation depicts the border between Aptian and Albian. The Nova Olinda Member probably is of Late Aptian age with many authors assuming 112mya (Martill & Heimhofer, 2007) .

The depositional environment is still a point of discussion, ranging from fresh water to hypersaline waters, also covering the environments in between these extremes. The scientists who consider it as non-marine point out that it is one of the most diverse fossil assemblages of all known non-marine Cretaceous sites (Martill, 2007b). The marine setting is gaining more and more ground as both microfossils — marine foraminifera and dinoflagellates — as well as macrofossils — marine fish and turtles — suggest a saltwater environment (Martill, 2007b). The

Crato member also shows other geomorphological, stratigraphic and geochemical arguments for a strong marine influence (Arai, 2000). The relatively undisturbed laminae suggest a lagoon with a depth below the stormbase with an anoxic or highly saline environment (deeper than 50m) (Martill & Heimhofer, 2007). Certain ex-situ slabs, with a lamination typical for the Nova Olinda Member, show small wave structures that are probably damaged biofilms (Martill & Heimhofer, 2007). These bacteria could explain the pristine conservation, as known from other Lagerstätten (Narbonne, 2005). Carcasses would have floated some time on the water, disarticulating pieces of the skull, mandible and skeleton before sinking to the bottom. If this happened fast these pieces would be buried close to each other, articulated or disarticulated. The compression found in almost all fossils is from crushing of the sediment after burial. The depth of the lagoon or paleolake is also a point of dispute, with some authors suggesting a shallow lake while others consider it relatively deep (Martill & Heimhofer, 2007).

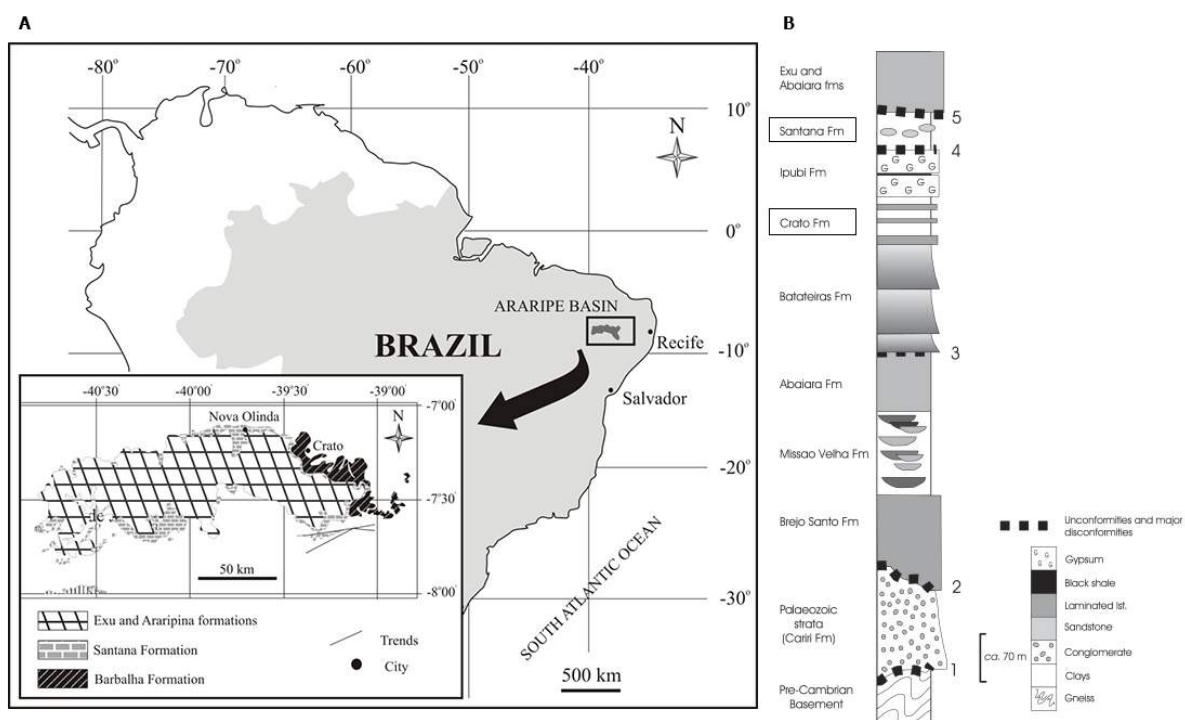


Figure 2.3: Location of the Chapada do Araripe in Brasil (A). The Araripe Basin is shown in detail with both the Crato Formation (Barballa Formation in this figure) and the Santana Formation (Ricardi-Branco *et al.*, 2013). Panel B shows the stratigraphic column of the Santana formation. The Crato formation is assumed to be the oldest of the two formations. (Martill, 2007a)

The second Konservat Lagerstätten of north-east Brazil was made famous by the exquisitely preserved fish, obtained by the Bavarian explorers Spix and Martius somewhere between 1817 and 1820 (Martill, 2007a). Especially the Romualdo member of the Santana Formation is extremely rich in superb fossils. The Romualdo Member consists of carbonate concretions, which contain uncrushed fossils in superior conservation that are often even preserved in three dimensions, in a matrix of silty shale (Martill, 2007). Outcrops can be found on the flanks of the Chapada do Araripe (figure 2.3). The top of the Santana Formation lies only tens of meters above the Nova Olinda member, and probably was about 10 mya younger than the Nova Olinda Member.

The Santana Formation was a non-marine or quasi-marine environment. Because of the absence of igneous rocks and fossils useable for high precision biostratigraphy, no reliable dating has been done yet. Estimates of the age of the Santana Formation range between Aptian and Cenomanian, but an age at the border of the Aptian and Albian is most likely (Martill, 2007a). The age of the Romualdo Member is estimated as 108mya (Website 2), but these estimates have a precision lower than 10 mya (Martill, 2007a) .

Many of the fossils of both the Crato Formation and the Santana Formation are found by workers in local quarries. The fossils are then sold to villagers who sell them again. It is a shame that most fossils only reach science through fossil trade, but further scrutiny shows that this fossil trade is vital for science. Without these workers most fossils would not leave the quarry, and if they would leave, they would leave as processed material. Quarries that prohibit the sale of fossils have 'trash piles' full of exceptional fossils (Martill, 2001).

2.2.2 Phylogeny of Brazilian pterosaurs

Although the first vertebrates were discovered in the early 1800's, it took scientists until the first half of the 20th century to describe the first tetrapod from the Santana Formation in Brazil. The first pterosaur, which are in general hard to find, *Araripesaurus castilhoi* was described by Price in 1971. In the following years more than 20 species were described (Table B.1).

The most recent phylogeny of Pterosauria is that of Andres (e.g. in Andres & Myers, 2013) (figure 2.4). All pterosaurs that will be discussed in this thesis belong to Monofenestrata as in all species the nasal and antorbital fenestra are fused into one nasoantorbital fenestra (NAOF). Within Monofenestrata all species in this thesis belong to Pterodactyloidea, a group with thin bone walls, elongated metacarpals and a tail and a fifth toe that are both reduced (Witton, 2013). Within Pterodactyloidea all Brazilian species belong to Ornithocheiroidea which typically have relatively large heads. Most specimens we investigated in this dissertation belong to Pteranodontia and within Pteranodontia the species like *Ludodactylus*, *Brasileodactylus*, *Tropeognathus*, *Anhanguera* and *Coloborhynchus* are positioned, highly debatable, in Ornithocheiridae, characterized by their teeth and crested (pre)maxillae.

Because of the extraordinary preservation of the pterosaurs of Brazil, many of these, and in particular, Ornithocheiridae (or Anhangueridae) were used for ecological and mechanical reconstructions (Costa, 2013; Habib, 2008; Witmer *et al.*, 2003). But although one of the best studied groups of pterosaurs, the definition of an anhanguerid is changing continuously. An overview in table form can be found in the front of this thesis. Veldmeijer (2006) considered all Anhangueridae as part of the genus *Coloborhynchus*. Rodrigues & Kellner (2008) studied these pterosaurs extensively and positioned *Coloborhynchus spielbergi* and all other anhanguerids in *Anhanguera*. They argue that *Anhanguera*, including *Coloborhynchus spielbergi*, have several distinctive features which distinguish them from the type species of *Coloborhynchus*, *Coloborhynchus clavirostris*. To complicate things even more, the taxon Anhangueridae (Campos & Kellner, 1985), appears to be invalid as Unwin stated that Ornithocheiridae (Seeley, 1870) have the same characters as defined for Anhangueridae and thus have a nomenclatural pri-

ority (Unwin, 2003; Witton, 2013). In the most recent phylogenies (Andres & Myers, 2013) Anhangueridae and Ornithocheiridae may represent two different clades instead of one. If this is the case the clade Anhangueridae would be valid once more. *Coloborhynchus spielbergi* is, however, not included in this analysis and the debate of its phylogenetic position remains open. In the same analysis *Ludodactylus sibbicki* is classified as a pteranodontoid rather than an ornithocheirid pteranodontoid (Andres & Myers, 2013). This new phylogeny has a topology that is clearly different from previous phylogenies so it is used with care (website 3). In this thesis we will use the term Ornithocheiridae as a group that includes both Anhangueridae and *Coloborhynchus spielbergi*.

The remaining pterosaurs, *Tupandactylus imperator* and *Tupuxuara deliradamus*, belong to Tapejaridae (sensu Kellner, 2003). An overview of the different taxonomic problems are presented in table form in the front of this thesis. Kellner (2003) considers Tapejaridae as the clade that clusters Tapejarinae (with *Tupandactylus*), Thalassodrominae (with *Tupuxuara*) and Chaoyangopterinae. This clade has been confirmed by Pinheiro *et al.* (2011). Martill & Naish (2006) considered Thalassodrominae as a separate clade within Neozhdarchia. This new clade, Thalassodromidae, is most closely related to the Azhdarchidae. This is the topology that is recovered in Andres & Myers (2013) as well (with the exception that the Chaoyangopteridae also moved together with the Thalassodrominae). Both *Tupandactylus* species were considered a member of *Tapejara* (Frey *et al.*, 2003b; Kellner, 2004). In 2007 both Unwin & Martill and Kellner & Campos realized that these two genera differ. Unwin & Martill (2007) called the new genus *Ingridia*, but the name *Tupandactylus* of Kellner & Campos (2007) got nomenclatural priority. These latter authors did, however, not include *Tupandactylus navigans* in their analysis.

Part of this thesis will explore the use and power of geometric morphometrics in the taxonomy of these two Brazilian clades that have been at the center of discussion for over a decade now.

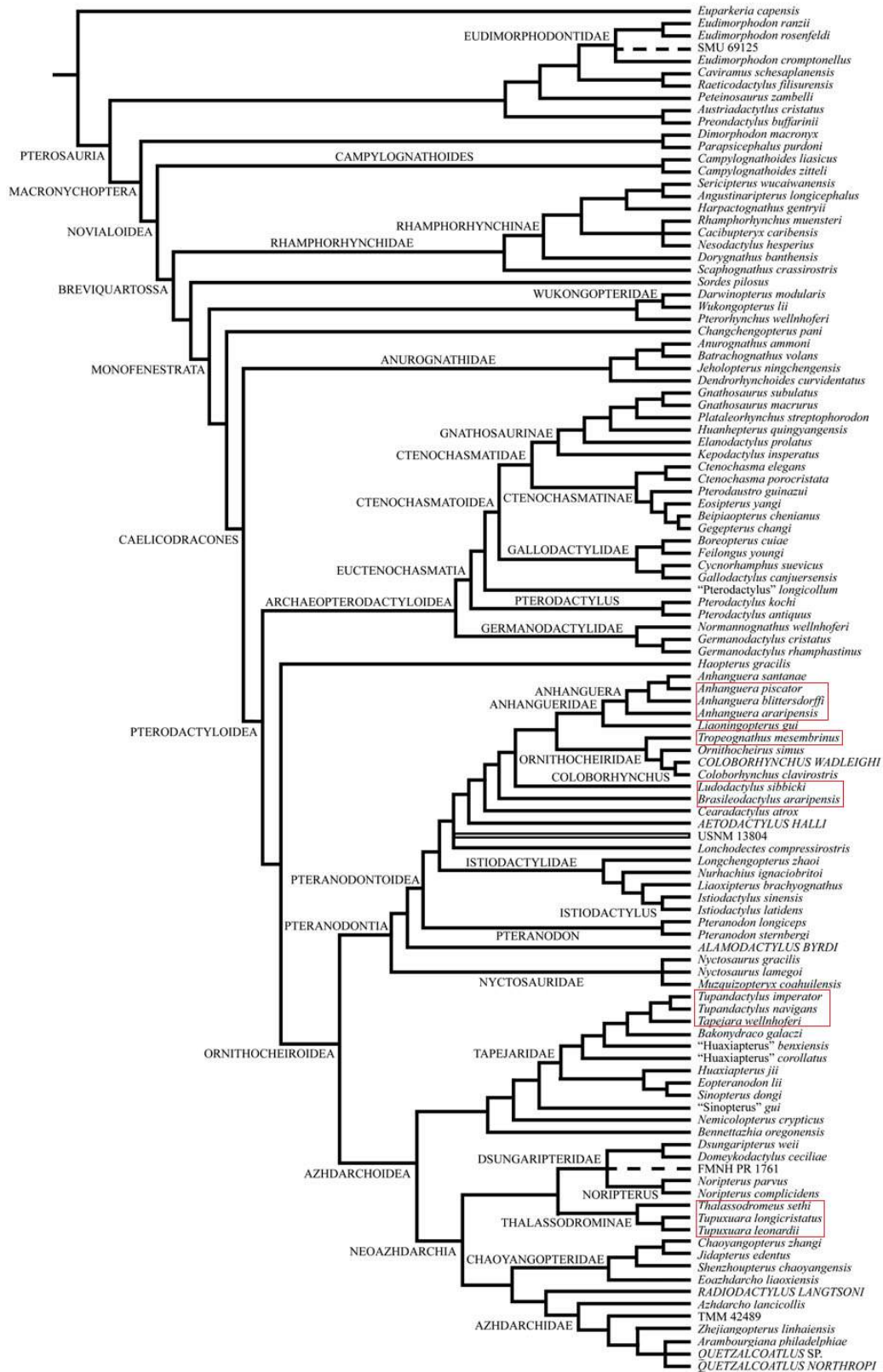


Figure 2.4: Cladogram depicting the phylogenetic relationships of the Pterosauria. Texas taxa are all capitalized as the article was focused on new Texan pterosaurs. Dashed lines represent the inferred position of taxa that can only be coded by a single character. The cladogram is an Adams consensus tree of 12 most parsimonious trees. Species used in this thesis, both as specimens and original descriptions used as comparison, are marked with a red box. Note that this tree suggests that Anhangueridae and Ornithocheiridae are not one clade. (Andres & Myers, 2013)

2.3 Ontogeny and sexual dimorphism in adult pterosaurs

2.3.1 Ontogeny

As in most organisms the shape and size of pterosaur changed during the course of their life. Although often compared with birds, ontogeny, among other life traits, of pterosaurs was different to that of birds (Witton, 2013).

Life of pterosaurs started, as in most archosaurs, as an embryo in an egg. This egg was not at all like those of birds or dinosaurs which had hard shells. Pterosaur eggs resembled modern reptiles in being soft and having a parchment-like texture (Ji *et al.*, 2004). This enabled water to enter the egg after it was laid. By laying permeable eggs the female pterosaur did not have to provide the egg with water provided that she lay the eggs in a moist environment. Contact-incubation, keeping the eggs warm by sitting on them, was not an option as the eggs would be easy to squash (Grellet-Tinner *et al.*, 2007).

The nest thus had to be a incubation chamber and probably was underground or a humid like nest as in modern lizards, crocodiles and megapode birds—which are an exception in Aves (Witton, 2013). Although parents could not incubate them, the association of one of the three known eggs with a large number of adult pterosaurs suggests that the parents at least stayed around as in other archosaurs like crocodiles (Chiappe *et al.*, 2004). When leaving the nest, the little pterosaurs probably were precocial and were independent of their parents starting from the moment they hatched (Lü *et al.*, 2011) (figure 2.5). Evidence for this is found in the embryos of which the bones are already well ossified, have similar proportions to adult pterosaurs and already have a fully developed set of membranes (Chiappe *et al.*, 2004; Wang & Zhou, 2004). This small pterosaur probably was able to fly within weeks. Being precocial had the important drawback that the small pterosaurs needed food not only to grow, but also to survive, regulate body temperature, avoiding predation, etc. (Witton, 2013). This way the pterosaurs did not grow as fast as altricial animals.

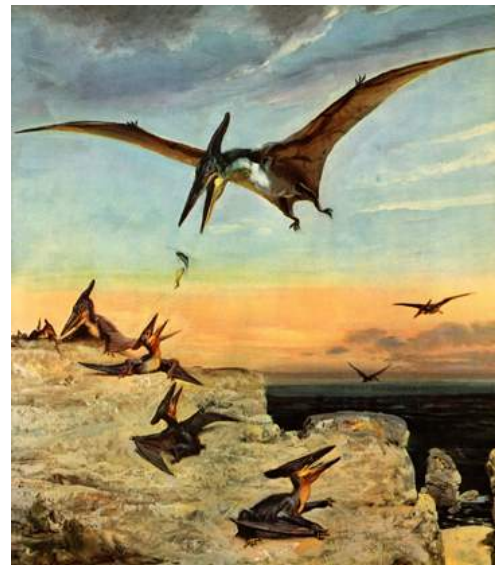


Figure 2.5: Pictures like these, showing a *Pteranodon* (?) bringing food to their helpless offspring are now considered wrong, as pterosaurs were probably highly precocial. Image by Zdenek Burian

Most of the growth of pterosaurs happened in early life. This phase of rapid juvenile growth ended when they reached about half their maximal size (Bennett, 1995; Chinsamy *et al.*, 2008; 2009) after which the growth slowed down probably due to becoming sexually mature at the costs of energy, normally invested in growth. Finally the pterosaurs would reach a phase of determinate growth in which they did not grow in size any more (figure 2.6). This diagram can be used to age the pterosaurs, as long as the size of the full adult is known.

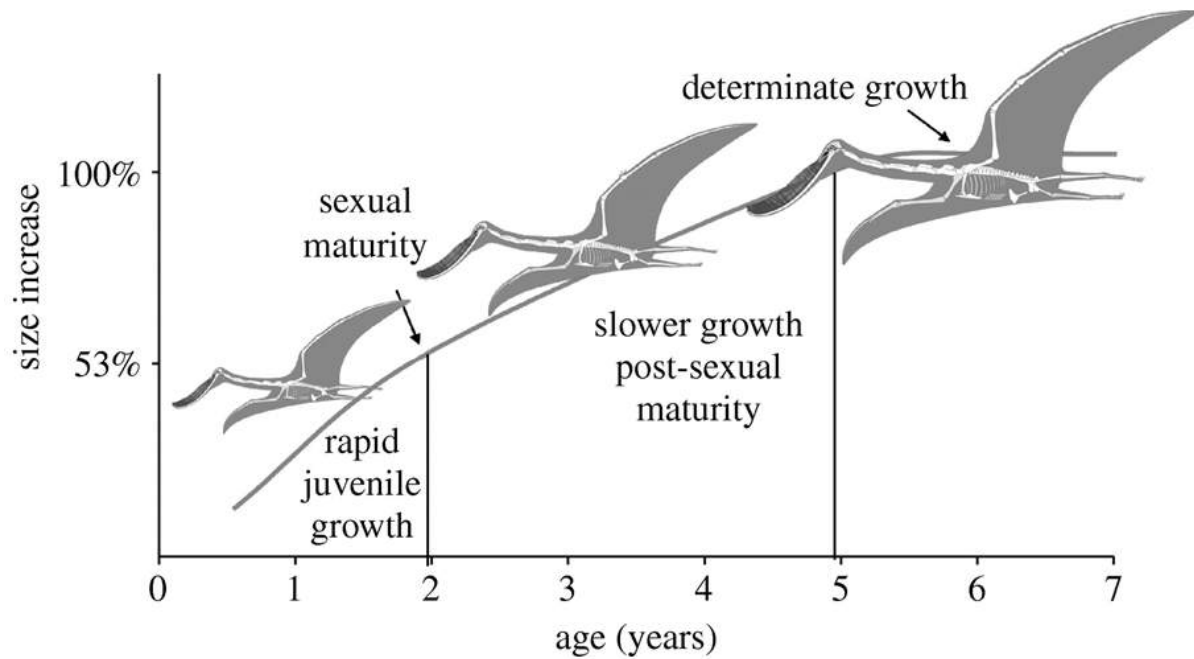


Figure 2.6: Growth strategies of *Pterosdaustro guinazui*. The growth in the first years of the pterosaur life is fast. After about 2 years they reached sexual maturity with a size of about 50%. When they reached sexual maturity the growth slowed down to finally come to a halt when they reached skeletal maturity. (Chinsamy *et al.*, 2008)

As in most animals, pterosaurs had different growth rates in different bones, a process called allometric growth (Witton, 2013). Although present in many bones concerning flight, it is most apparent in the cranial crests. These crest, consisting of bony or of soft tissue, are absent in all known juveniles of crested species and first appeared when the pterosaurs became the equivalent of human teenagers. The crests would reach their full extend in adult pterosaurs (Bennett, 1992, 2006; Martill & Naish, 2006; Witton, 2013). They could be larger than the rest of the skull together as in for example *Tupandactylus imperator*. Martill & Naish (2006) used this knowledge of allometric growth of the crest to reduce the number of species of *Tupuxuara*, and instead considered them as an ontogenetic sequence (figure A.14). They proposed that the *Tupuxuara longicristatus* specimen SMNK PAL 3858 was a sub-adult with the premaxillary crest ending anterior of the occiput. The *Tupuxuara leonardii* specimen IMCF 1052 in turn was an adult with the premaxillary crest posterior of the occiput. *Thalassodromeus sethi*, finally, was an old adult with a hypertrophied premaxillary crest that terminated far more posterior than the others (Martill & Naish, 2006). This was one of the first articles that reduced the taxonomic value of crests, and even completely excluded it in this case. Kellner & Campos, however, demonstrated that there were clear differences between the species of *Tupuxuara* (see Systematic Paleontology), and this was accepted by Martill & Naish (Witton, 2009). Although wrong, the suggestion that the taxonomic value of crests should be small is now getting more and more accepted (Hone *et al.*, 2011). Finally, Padian & Horner (2013a), pointed out that individuals may stop growing linearly, but the crests of these individuals may continue to grow, leading to different morphs, independent from the sex of this individual.

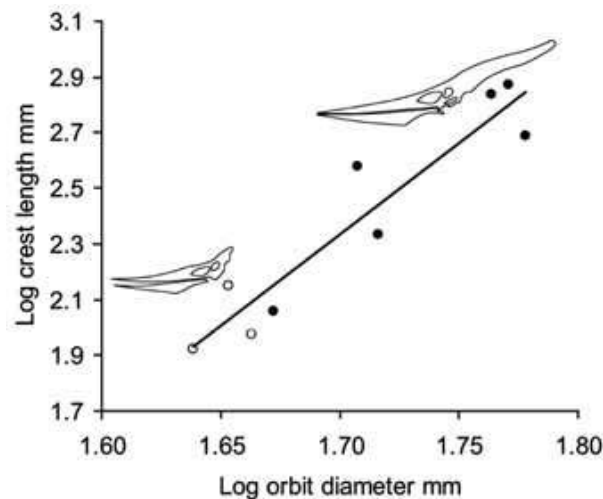


Figure 2.7: A bimodal distribution of *Pteranodon* fossils can be observed easily in a regression of orbit diameter versus crest length. The group with the large individuals has a large crest, the group with the small individuals has a small crest. These are male and female respectively (Bennett, 1992).

2.3.2 Sexual selection

Pterosaur crests

Some of the skulls of pterosaurs had crests that reached enormous sizes, others had small crests or were even entirely unornamented (Witton, 2013). Crests were present, either bony or as soft tissue, in most pterosaurs. Bony crests are present in the Ornithocheiroidea (e.g. *Ludodactylus*, *Pteranodon*,...), Ctenochasmatoidea, Dsungaripteroidea, Azhdarchoidea (e.g. *Tupuxuara*) and even in non-pterodactyls, thus in almost all groups of pterosaurs (Naish & Martill, 2006). Mechanical functions suggested include rudders and airbrakes (Bramwell & Whitfield, Stein, 1975), jaw stabilizers (Veldmeijer *et al.*, 2006; Wellnhofer, 1991) and thermoregulators (Kellner, 1989; Kellner & Campos 2002) among a plethora of other explanations, one more likely than the other. These hypotheses raise many unsolved questions: the most important being that if these crests are important mechanical and/or physiological structures, why do some individuals, and almost all juveniles, seem to be missing them, and even survived without them (Witton, 2013)? The crest is also small compared to the large surface area of the wings. These wings would thus be better at thermoregulation than a relatively small crest (Tomkins *et al.*, 2010; Unwin *et al.* 2011). As for rudders, airbrakes and jaw stabilizers, research has shown that these crests would have a negligible effect on flight efficiency (Elgin *et al.*, 2008; Humphries *et al.*, 2007). The weak nature of the thin bony or even soft tissue crests of pterosaurs, excludes the possibility of it being an interspecific character used to repel predators as suggested for dinosaurs. Furthermore, pterosaurs had a more effective anti-predator strategy: flying away (Hone *et al.*, 2011). All these hypotheses were examples of natural selection, but the hypothesis that is becoming more and more likely is that of sexual selection leading to crest forming. Another hypothesis is that of species recognition.

Sexual selection and species recognition

One of the first persons to realize that sexual selection might be at play was Bennett (1992). He noticed that only some *Pteranodon* specimens had large crests, and that these specimens were 50 percent larger than the small crested animals (figure 2.7). This was not because of immaturity as bones were fused and other osteological signs of adulthood were present. Furthermore the smaller individuals had larger pelvic canals, but were otherwise identical to the larger individuals (Bennett, 1992; Witton, 2013). The small individual with small crest and wider pelvic canal would represent a female in which the pelvic canal should be able to pass an egg. The large crested, larger individual would be a male, showing his strength and health with his large, and possibly colorful, crest. The fact that the crest is one of those bones that show a clear positive allometric growth, also suggest that this is only important after reaching sexual maturity (Knell *et al.*, 2013a,b; Tomkins *et al.*, 2010). Signs for sexual selection now have also been found in *Pterodactylus*, that also show a bimodal distribution of individuals and where a crest is also present but much less prominent than in *Pteranodon* (Bennett, 2013b) and *Darwinopterus modularis* (Lü *et al.*, 2011). Bimodal distributed, exaggerated structures are often associated with sexual selection, in which one sex of the species tries to convince the other sex to mate with him or her, by showing off their quality through these exaggerated structures.



Figure 2.8: A reconstruction of the sexual dimorphic *Darwinopterus* by Mark Witton. It shows a crestless female and a crested male. This species was the second species in which it could be indisputably shown that sexual dimorphism is present in pterosaurs (Lü *et al.*, 2011).

Sexual selection with males who had to show off their elaborate ornaments suggest that lekking, where males gather at certain locations to be checked out by females, may occurred. As sexual selection, and male ornamentation, is present in modern birds (and they are even famous for it!) and probably also in pterosaurs, it is likely that male ornamentation is deeply rooted deep in archosaur phylogeny and implies that dinosaurs also may have been sexual dimorphic, as already discussed by e.g. Hone *et al.*, 2011; Knell & Sampson, 2011; Knell *et al.*, 2013a; 2013b.

An argument that has often been used to counter the use of sexual selection is that in today's animals the ornament is not just present or absent, but often smaller but present in the female (e.g. the tusks in elephants, horns in goats, ...). These are however always mammals, and sexual dimorphism in birds and reptiles, the closely related extant animals, does happen in an absent/present fashion. For example the beautiful tail, color and dances of birds of paradise are present in males, but absent in females.

Padian & Horner (2011a), were more specific and stated that dimorphism in exaggerated skeletal structures is absent in Crocodylia, Squamata and rare in Aves and non-avian dinosaurs (note, however, that it is not completely absent in birds and these are, probably, the most closely related living taxum) . They use this argument to promote the concept of species recognition,

in which two different species develop these exaggerated structures to recognize members of their own species. This argument is incomplete as there are exaggerated skeletal structures in Squamata and Crocodilia and this skeletal structure may be even bimodal distributed among sexes. The Jackson's Chameleon, *Trioceros jacksonii*, has males with three horns, while the female has no horns. The male gharial has a bulbous nasal extension, while the female has a rather smooth upper jaw (Martin & Bellairs, 1977). In their article Padian & Horner (2011a) propose two tests to look for sexual selection or species recognition. The first states that in species recognition the direction in which the structure evolves is random, while it is directional in sexual selection (but see Knell & Sampson (2011) who contested this). The second test uses the geographic overlap as a condition for species recognition, but this condition is also necessary in sexual selection as two sexes have to be present at the same time and the same place for selection to take place.

Knell & Sampson (2011), do not completely agree with Padian & Horner (2011a) and propose a third and a fourth test. The third test follows Maynard Smith & Harper (2003), formulated species recognition as the process of evolution of structures whose main goal is to enable two members of a species to recognize each other to do some form of social behavior. As the interest of signaler and receiver are the same, dishonest signals should be absent. As the benefits are relatively low for the signaler, the costs should be low as well. Characters which are sexually selected on the other hand, have a clear benefit to the signaler and should be costly to maintain the honesty of the signal. Padian & Horner (2011b) argue that the model used by Knell & Sampson (2011) is too simple, and that costs often are a result of trade-offs, not visible in the fossil record. The final test proposed states that within species recognition the inter-individual variation should be limited, as small differences would lead to misidentification.

Sexual selection in pterosaurs, however, remains the most likely hypothesis because Knell *et al.* (2013) point out that: "Sexual selection is the most common selective force leading to the evolution of exaggerated traits in contemporary organisms and there is every reason to think that this was also the case in fossil organisms." Sexual selection explains why some individuals within the putative pterosaur species have crests whereas others are devoid of ornamentation, although it does not explain why a bimodal distribution is less clear in other taxa. The absence of a clear bimodal distribution of sexual traits, as often observed in pterosaurs, does not strictly exclude sexual selection. First the absence may be a taphonomic result. Certain sexes may be absent, especially when only a fistful of specimens are known — pterosaurs are often known from single specimens (Unwin, 2005). Second the presence of a male trait can be present in the female as well, often not too different from the male proportion of this trait. The absence of large numbers of specimens makes the required statistics to significantly discriminate the two clusters difficult. Finally sexual selection does not only act on males. Females, as well as both sexes at the same time, can be selected for as well. A rather new theory in paleontology called mutual selection explains this process (Hone *et al.*, 2011). Mutual sexual selection happens when both sexes select for the same ornaments (as known from birds like the Crested Auklet, *Aethla cristatella*, among other groups Hone *et al.*, 2011; Jones & Hunter, 1993). Studies have shown that this is likely to happen when both parents invest evenly to offspring care. As mentioned

earlier, pterosaurs probably did not care for their offspring. Both parents thus invested evenly in offspring care, possibly, completely absent. As a crest brings a significant cost with it, it is an honest signal. It is thus conceivable that both males and females selected for a character that showed off the health of the mate, leading to bigger crests in both sexes.

Although bimodal distributions of certain characters (like the pelvis and the crests) are convincing and other theories fail to explain the presence of these characters, there is no way to be certain of the sex of a fossil. Unless, of course, an egg would be found, not laid but still present in the (wider) pelvic canal. This is what happened with a *Darwinopterus* specimen and confirmed the believe that in this species the smaller individuals, with wide pelvic canals and without crest were females (Lü *et al.*, 2011).

Another method to look for different sexes is again based on birds as an analogue. In modern birds, and in dinosaurs, but not in crocodiles, there is a special type of bone, the medullary bone, that is laid down in bones in preparation of laying eggs. This bone however, has never (with one possible exception) been found in pterosaurs, and is most likely not present in the Pterosauria (Chinsamy *et al.* (2009), website 4). This method of sexing is thus, for now, not valid in pterosaurs.

2.4 Geometric Morphometrics

Conventional measurements focus on traits such as length, depth and width and combine series of measurements into large datasets. These datasets seem to give a vast amount of information but contain in fact less information as many measurements are correlated (Zelditch *et al.*, 2004). The main goal of geometric morphometrics is to study how shapes and their covariance are linked to other variables. Unlike other quantitative descriptions, e.g. linear morphometrics, they are also qualitative and interpretations do not vary among different scientists (Adrianes *et al.*, 2005). Geometric morphometrics also allows statistics, assuming that the dataset has enough samples.

Geometric morphometrics depends on landmarks, which are defined by the scientist based on simple rules. The number of landmarks vary but one should keep in mind that each landmark adds weight to the analysis. Three types of landmarks are used. Type I, true landmarks, are landmarks of which the location is defined by obvious biologically homologous structures e.g. an intersection of three bones (Zelditch *et al.*, 2004). These are hard to find in fossils since sutures are hard to distinguish. Type II landmarks, pseudo-landmarks, are defined by a point of obvious geometry and are thus relative locations, e.g. the point of highest curvature (Zelditch *et al.*, 2004). Type III landmarks, semi-landmarks, are defined as the location relative to other landmarks (Zelditch *et al.*, 2004), e.g. in the center of the line between the quadrate and the most anterior point of the premaxilla.

Geometric morphometrics is becoming a hot topic, and has been used increasingly during the last five years. Most studies using geometric morphometrics are used to investigated the disparity, the morphological diversity, of certain groups such as the crocodile-line of archosaurs (Stubbs

et al., 2013), theropods and basal saurischians (Foth & Rauhut, 2013) and even pterosaurs (Foth *et al.*, 2012). It has however been less used in taxonomy especially at species and genus levels. As geometric morphometrics can be used to compare different shape it is expected that it can detect differences in shapes (for example shape of the nasoantorbital fenestra) in different species. Recently Naish *et al.* (2014) used it to identify two cryptozoological big cats of the Peruvian Amazon while Maiorino *et al.* (2013), used it to distinguish several ceratopsid dinosaurs species, hereby confirming the contested (Scannella & Horner, 2010) taxonomic validity of *Torosaurus*. This same article used geometric morphometrics to look at the ontogeny of the analyzed ceratopsids. Other studies also used geometric morphometrics to look at heterochronic processes. Bhullar *et al.* (2012), clearly showed that adult birds resembled those of juvenile dinosaur skulls and thus were paedomorphic. Mitteroecker *et al.* (2005), also used geometric morphometrics to detect heterochrony in the cranial growth of *Pan paniscus* and *Pan troglodytes*. The use of these techniques in distant as well as in closely related groups, suggest that they can also be used in pterosaurs.

Chapter 3

Materials and methods

This chapter will start with the systematic description of the skulls of the new pterosaurs. As the main focus of this thesis is on pterosaur crania, additional descriptions of two new pterosaur mandibulae can be found in Appendix C. Following these descriptions the methods used in this thesis will be defined. Geometric morphometric analyses will be explained in detail.

3.1 Systematic paleontology

3.1.1 *Ludodactylus sibbicki*, Figure A.1

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

ORNITHOCHEIROIDEA Seeley, 1870

ORNITHOCHEIRIDAE Seeley, 1870

LUDODACTYLUS Frey *et al.*, 2003a

LUDODACTYLUS SIBBICKI Frey *et al.*, 2003a

Type locality and horizon: Nova Olinda Member of the Crato Formation. The fossil was found in the Chapada do Araripe region, but as in many pterosaurs from Brazil (Witton, 2008) this fossil was probably bought from a commercial dealer and no further details of its locality are known. This is the case for all further mentioned fossils from Brazil.

Diagnosis: Skull with several teeth which is typical for Ornithocheiridae. The combination of the posterior blade like crest and the absence of a premaxillary crest is typical for *Ludodactylus sibbicki*. Other diagnostic characters were absent due to taphonomic processes.

Description: The fossil consists of a well preserved, still articulated but laterally compressed and crushed cranium of an ornithocheirid. Parts of the skull look eroded or grinded. The

mandibula is absent. All bones are of a brownish colour, which is typical for Crato fossils of this type.

The large nasoantorbital fenestra is diagnostic for the pterodactyloid pterosaurs while the long snout with sharp, thin and slightly curved teeth that are still in their sockets, is diagnostic for Ornithocheiridae. These teeth can be used for determination as the pattern and size of different teeth seems to be species specific (Lü and Ji, 2005; Steel *et al.*, 2005; Unwin, 2001, 2003; Veldmeijer, 2006). In this specimen 9 teeth are present. This is not enough to use their pattern in the determination. Typical for this genus is the absence of a rounded premaxillary crest. The dorsal side of the rostrum is flat instead.

Although the basal part of the first tooth has been cut off — probably in processing it as building material or cement manufacture in the quarry (Martill & Bechly, 2007)— it is likely that it was present in the front of the maxilla, at an angle almost perpendicular to the long axis of the ventral side of the skull. The third tooth that is visible is the largest, while the fifth is the smallest. Starting from the fifth tooth, teeth increase in size with tooth seven reaching a new local maximum. Beyond tooth seven, only two teeth are visible, of which one is broken. After tooth three and nine, and on top of the premaxilla, three small replacement teeth are visible (figure A.1). The holotype of *Ludodactylus* has 23 pairs of teeth. Comparison of the teeth present in this specimen show that they had a similar pattern and shape (Frey *et al.*, 2003a). The teeth consist of premaxillary and maxillary teeth, but which are the premaxillary and which are maxillary teeth is not clear. The suture between the premaxillary and maxillary is obscured by the internal fragmentation of the fossil, but appears to be or somewhere between tooth three and four or somewhere between six and seven.

A blade-like frontoparietal crest, not too different from this of *Pteranodon ingens*, is complete for the first time. Within the Ornithocheiroidea this crest only known from *Ludodactylus sibbicki*, *Caulkicephalus trimicrodon* from the Lower Cretaceous of the Isle of Wight and possibly *Guidraco venator* and *Liaoningopterus gui* (Steel *et al.*, 2005; Wang, X.L. & Zhou, 2003; Wang *et al.*, 2012). This crest consists mostly of the parietal bones. The crest was thin as is visible in the broken parts of the crest. The distal end of the crest is hooked, something new in pterosaurs. It is not known if this is original or a relict from preparation or diagenesis.

In the original description a lacrimal foramen is present. It is rounded to triangular with one corner facing ventrally (Frey *et al.*, 2003a). Although present in this specimen the exact shape is not clear. As mentioned before the overall shape of the bones has been well preserved but it suffers from internal fractures. Some of these bone elements have filled up the lacrimal foramen, making its shape unclear. The lacrimal spine, visible in the holotype, is absent.

The nasoantorbital fenestra is elongated with straight sides while most ornithocheirids have concave sides. The orbit is rounded and confluent with the partly visible supratemporal fenestra. Above the orbit a groove is visible.

The fossiliferous slab also contains at least four fish, of which three are most likely *Dastilbe* and a fourth which consists of a skin impression. Finally the slab also contains an insect, possibly belonging to the Coleoptera or Heteroptera.

Notes: Posterial elements of *Ludodactylus* have never been found. One other post-cranial fossil, *Arthurdactylus conandoye*, with a size that resembles that of a reconstructed *Ludodactylus* (4m wingspan) has been found without a head. *Ludodactylus* thus might be a synonym of *Arthurdactylus conandoye*. It may also be synonymous with *Brasileodactylus araripensis*, which in turn has been suggested to be synonymous with *Anhanguera araripensis* (Maisey, 1991; Martill *et al.*, 2007).

3.1.2 *Coloborhynchus spielbergi*, Figure A.2

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

ORNITHOCHEIROIDEA Seeley, 1870

ORNITHOCHEIRIDAE Seeley, 1870

ANHANGUERINAE Campos & Kellner, 1985

COLOBORHYNCHUS Owen, 1874

COLOBORHYNCHUS SPIELBERGI Veldmeijer, 2003

Type locality and horizon: Romualdo member of the Santana Formation, Araripe Basin, Brazil.

Diagnosis: Large and elongated skull of pterosaur. The presence of alveoli suggests that it belonged to Ornithocheiridae. Although one of the more important taxonomic characters, the premaxillary crest is absent. The shape of the nasoantorbital fenestra resembles only that of *Coloborhynchus spielbergi*. This the only species of large Ornithocheiridae in which the posterior side of the nasoantorbital fenestra is almost straight. All other large ornithocheirids have a curving nasoantorbital fenestra.

Description: The specimen consists of a partially, but 3-dimensionally preserved cranium of a large pterosaur. The front part of premaxilla and maxilla are absent. This might be the result of processing in the quarry as in *Ludodactylus*. However, the skull was obviously elongated and slender. Because of this we cannot use the premaxillary crest (probably present in all known Ornithocheiridae of this size) for a conclusive determination. The skull was probably less than 8 cm wide, but more than 40 cm long, which is the preserved length in this specimen. Only one side is well preserved, the other side consists of sediment. After its discovery the cranium was treated with acid. The skull is laterally compressed, with the nasal, frontal, part of the parietal and even the orbit of both lateral sides visible in one plane. The two parietals are separated by a midline suture that forms a depression. The squamosal, quadrate, quadratojugal and the lower temporal fenestra are absent.

The nasoantorbital fenestra is subtriangular in shape with the two short sides of the triangular in an almost perpendicular angle. The posterior side of the triangle is straight, distinguishing

it from *Anhanguera piscator*, *Anhanguera blittersdorffi*, *Anhanguera santanae* and *Tropeognathus mesembrinus*, in which it is more rounded. This straight posterior side is also found in *Coloborhynchus spielbergi*. The ventral side of the nasoantorbital fenestra, consisting of the maxilla, is straight as in *C. spielbergi*. Due to the incomplete nature of the fossil, it is not possible to see the premaxillary crest, which is believed to have some taxonomic value as well (Veldmeijer, 2006); Martill & Naish (2006) suggest that it may be an ontogenetic signal rather than a phylogenetic signal.

The orbit, lying directly behind the nasoantorbital fenestra, is egg-shaped but tilted posteriorly. This differs from the orientation in the holotype of *C. spielbergi*, where its orientation is more straight. The dorsal side of the orbit is not much higher than the dorsal side of the nasoantorbital fenestra. In the holotype of *C. spielbergi*, nor in *Tropeognathus* or any other *Anhanguera*, this is not the case and the orbit extends another 50 percent of the height of the nasoantorbital beyond the nasoantorbital fenestra. In this new specimen the location of the orbit is probably shifted due to compression. An indication of this is found in the other bones and regions like the parietal and the orbit of the other side, which now lies in the horizontal plane of the previously described orbit. The lacrimal fossa is filled and cannot be used for comparison.

The left and right frontal which lie above the orbit, are separated by a suture ending in a small, slightly visible, parietofrontal crest. The lacrimal is relatively wide, which is consistent with *C. spielbergi*, and does seem to contain a lacrimal fossa. The jugal is present but broken. The quadrate, quadratojugal, lower temporal fenestra and squamosal are absent. The postorbital and parietal are present but difficult to recognize due to heavy twisting.

Underneath the cranium part of the mandibula is visible. Some alveoli are visible on the broken side, but these lack teeth.

The close resemblance with *C. spielbergi*, definitely places this specimen in the genus *Coloborhynchus* sensu Veldmeijer (2003). There are, however, differences. The orbit is placed lower in the skull and reaches its maximal height at approximately the same height as the nasoantorbital fenestra. The orbit is also more inclined posteriorly, while in the holotype the angle of anterior side of the orbit is more vertical. These differences either reflect the presence of a new species, or, more likely crushing during diagenesis.

Posteriorly a bony, yet porous structure is visible. This is not present in the holotype of *C. spielbergi*. This is probably a cervical vertebra as it appears to have three spines. An ellipse of different material is present, this was probably the neural canal.

Notes: *Coloborhynchus spielbergi* has often been placed in the genus *Anhanguera* and is thus often called *Anhanguera spielbergi* (Rodrigues & Kellner, 2008).

3.1.3 *Tupandactylus imperator*, Figure A.3

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

TAPEJARIDAE Kellner, 1989

TAPEJARINAE Kellner, 1989

TUPANDACTYLUS Kellner & Campos, 2007

TUPANDACTYLUS IMPERATOR (Affiliation uncertain) Campos & Kellner, 1997

Type locality and horizon: Nova Olinda Member of the Crato Formation.

Diagnosis: Part of the cranium of a crested pterosaur. This extremely large crest does resemble most reconstructions of *Tupandactylus imperator* crests, although no complete crest is known. The crest consists of soft-tissue arranged in parallel fibers curving caudally. The posterior extension, or occipital process, associated with the crest is only known from *Tupandactylus imperator*.

Description: This specimen consists of the posterior most region of the cranium, with parts of the orbit and the nasoantorbital fenestra still visible. Facing even further posterior a posterior extension forms the base of a soft-tissue crest with a surface of 0,25 m². The posterior extension is known only from *Tupandactylus imperator*. At least four other *T.imperator* crests are known, but this crest is the most complete *Tupandactylus imperator*(and *Tupandactylus* in general) crest known so far. This is interesting as the exact shape of the crest was not known before.

The crest of *Tupandactylus imperator* is different from Frey *et al.* (2003b)'s construction. Instead of being only partly composed of actinofibers, it appears that these actinofibers run all the way to the top of the crest at an angle of 45° to the posterior extension. The bony base is present, but does not extend as far as suggested. Furthermore these authors consider the crest of *Tupuxuara* is has a structure similar to the crest of *Tupandactylus*. This is not true as the crest from *Tupuxuara* is clearly made of bones, with no signs of actinofibers. The additional soft-tissue in the *Tupandactylus imperator* crest is absent as well.

Although the anterior part of the crest is absent, the anterior part that is present is different from the other known *T. imperator* specimens. Usually the anterior part of the crest consists of a bony bulge, but this appears to be absent in this specimen. Horizontal struts are, however, present at the base of the anterior part of the crest. These have a different structure from the actinofibers, and are also known from the holotype of *T. imperator* (Kellner, 2004) and *T. navigans* (Frey *et al.*, 2003). The function of these rods is still unknown but the placement suggest that they may have a support function.

On several locations on the posterior extension 'hair', or pycnofibers as they are called in pterosaurs, are visible. These are known from the mandibular ramus of *Tupandactylus*, but as these were loose here, close to the crest as well, it is possible that these were actually from the crest as in the new specimen (Kellner *et al.*, 2010; Pinheiro, 2011 *et al.*). In this new specimen these pycnofibers appear to be in situ. Two types of pycnofibers appear present. A first type which is long, up to 4cm, thin and lighter colored. A second type is thicker, short (less than 1 cm) and of a darker color, and resembles the hair of *Sordes pilosus* (Bakhurina & Unwin, 1995). It is possible that type II pycnofibers actually consists of several type I pycnofibers, but further, detailed microscopic study is necessary. It is interesting that different types of hair may

be present: thick hairs that appear similar to fur, and longer hair which may have had an other function (e.g. sexual selection?).

3.1.4 *Tupuxuara deliradamus*, Figure A.4–A.5

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

AZHDARCHOIDEA Nessov, 1984

TAPEJARIDAE Kellner, 1990

THALASSODROMINAE Kellner and Campos, 2007

TUPUXUARA Kellner & Campos, 1988

TUPUXUARA DELIRADAMUS Witton 2009

Type locality and horizon: Romualdo member of the Santana Formation.

Diagnosis: A toothless pterosaur skull with a posterior, rounded crest which is associated with *Tupuxuara*. The orbit is below the mid-height of the nasoantorbital fenestra. The angle between the quadrate and the maxillary part of the nasoantorbital fenestra is 150°. The angle between the maxillary part of the nasoantorbital fenestra and the jugal process is 120°. This is distinctive for *Tupuxuara deliradamus*. The small size and slender lacrimal is known from another, juvenile *Tupuxuara* specimen.

Description: This fossil consists of an almost complete mandible and partial cranium conserved in a nodule. The mandibula consists of two mandibular rami with a complete posterior region, including a complete articular region, but is broken just anterior of the symphysis. Most of the dorsal region of the cranium is missing. Anteriorly only part of the rostrum is preserved, while posteriorly only the posterior part of the ventral region is preserved. The absence of the anterior part of both the cranium and the mandible is possibly due to manipulation during excavation, weathering of bone outside the nodule or loss of bones before fossilization.

The presence of a large nasoantorbital fenestra is typical for Pterodactyloidea. The dorsal margin of the orbit lies below the dorsal margin of the nasoantorbital fenestra, which is a character of Azhdarchoidea (Unwin, 2003). Although the dorsal margin of the nasoantorbital fenestra is absent, extrapolation allows us to estimate the height of the nasoantorbital fenestra, which was somewhere between 4 and 5 cm. The distance between the dorsal margin of the orbit and the dorsal margin of the nasoantorbital fenestra appears relatively large, contrasting with Tapejaridae, in which this difference is marginal (Lü *et al.*, 2006). The straight, and non-downward projected rostrum is an additional character that separates it from Tapejaridae (Kellner, 2004).

The combination of a slender dorsal jugal process and an open ventral orbital region excludes it from Azhdarchidae, while the posterior end of the dorsal region of the nasoantro-

bital fenestra that is likely (but not visibly) to terminate before the jaw joint excludes it from Chaoyangopteridae (Lü *et al.*, 2008; Witton, 2009). Although the dorsal part of the crest is absent, the cranium has the overall shape of Thalassodromidae (*sensu* Witton, 2009). Due to the absence of the nasal, the absence of the nasal fenestra cannot be used to place it into the genus *Tupuxuara*. The overall shape, and the shape of the rostrum in particular, however, resembles that of *Tupuxuara*, while excluding it from *Thalassodromeus sethi* (Kellner & Campos, 2002). The relatively thin ventral side of the nasoantorbital fenestra (less than 1 cm) and the shape of the mandible and maxilla further exclude it from *Thalassodromeus sethi*, in which the mandibula and maxilla were bent near the end of the nasoantorbital fenestra, interlocking with each other (Figure A.4) (Kellner & Campos, 2002; Kellner & Campos, 2007). Within *Tupuxuara*, it can only be compared with *T. leonardii* (Kellner, 1994) and *T. deliradamus* (Witton, 2009) as the only known specimen of *T. longicristatus* (Kellner & Campos, 1988) consists of only a fragmentary rostrum. The shape of the rostrum near the nasoantorbital fenestra is the same in all *Tupuxuara* and the angle between the maxilla and the premaxilla is about 30°.

Although not complete, extrapolation of the lacrimal process of the jugal and the premaxilla shows that the nasoantorbital fenestra was high and subtriangular in shape with sides that were curved. The angle of the posterior and the ventral margin of the nasoantorbital fenestra is 120°. The posterior border of the nasoantorbital fenestra is not straight but slightly tilts posteriorly. This is seen in *Tupuxuara deliradamus* but not in *Tupuxuara leonardii*. The angle between the slender quadrate and the maxillary bar is about 150°, as in *Tupuxuara deliradamus*. This angle is 130° in the cranium of *Tupuxuara leonardii* (Witton, 2009). The articulation region of the quadrate, however, is not visible.

The crest consists of the premaxilla, frontals and parietals, of which only the frontal and parietal part of the crest is partially present in this specimen. This crest and the nasoantorbital fenestra form most to the cranium, reducing other bones to small and slender stick-like element (Witton, 2009). A sagittal suture between frontal and parietal is visible. Of the premaxilla, only the anterior most part is present, which is not part of the crest. A lateral suture between the premaxilla and the maxilla is visible in this part. In this region a palatal ridge, as shown by Kellner (2004) is visible. In the posterior region, the parietal, lacrimal and postorbital bones form a concave depression. On the back of the fossil a rounded occipital condyle is present. The squamosal stands out from the frontoparietal crest.

Two slender jugals are present but one of them is broken off, together with part of the maxilla and part of the parietal and is now laying on top of the mandibulae and premaxilla (figure A.3). These jugals are triradiate bone structures with slender processes. The lacrimal is also triradiate in morphology but is only represented by its ventral process. The dorsal region and the triradiate bone itself are absent. The lacrimal regions are not swollen, contrasting with other known specimens of *Tupuxuara*. This is known from one other, juvenile, specimen of *T. longicristatus* (Witton, 2009). No suture between the jugal and the lacrimal is visible. Posterior to the orbit, just above the lacrimal, the supratemporal fenestra is visible as a subtriangular fenestra (10 mm in the holotype, slightly smaller in this specimen).

The orbit was probably positioned below the mid height of the nasoantorbital fenestra, and close to the temporal fenestra (not visible due to insufficient preparation) and the quadrate. It is triangular in shape — probably due to preparation as most *Tupuxuara* have a tear shaped orbit. The orbit was probably smaller than half the size of the nasoantorbital fenestra. The orbit of this specimen is posteriorly inclined to the maxilla, resembling the orbit in *T. deliradamus*. The ventral border of the orbit is also more inclined than in *T. leonardii*.

The two mandibulae fuse together at the mandibular symphysis, which contains a groove, probably corresponding to a palatal ridge. Due to the absence of the anterior part of the mandibula, the cross section of the mandibula is visible. This is triangular but it progressively becomes rectangular posteriorly (Witton, 2009). Due to the destruction of the bone, trabeculae are visible as a honeycomb-structure. The retroarticular process of the mandibula is triangular in lateral view. Both mandibula and upper jaw lack teeth.

Notes: Comparison with other known *Tupuxuara* show that this specimen has all characters of *Tupuxuara deliradamus* but is relatively small (Martill & Naish, 2006; Witton, 2009). The ventral side of the nasoantorbital fenestra is about 14.2 cm, while the *Tupuxuara* in Kellner & Campos (2007) and Witton (2009) are both around 43 cm. The length of the nasoantorbital fenestra is about 55 % of the total length in *T. leonardii* (Kellner, 2004). This appears genus-specific as measurements of *T. deliradamus* give a 50 % ratio, with differences probably due to exact measurement methodology. Extrapolation of the length of the nasoantorbital fenestra of the new specimen gives a total length of 25 cm. This is only 30 % the size of an adult specimen.

3.2 Linear Measurements

Measurements of linear data like distances and angles were done using tpsDig v2.17. (Rohlf, 2005). Measurements used in Ornithocheiridae dataset were measured 3 times to reduce human error. In the dataset we used 2 extra codes. A '*' means that the measurement may not be exact due to boundaries that were not clear; a '**' means that the measurement was an estimate using similar specimens as the bone was not complete. Measurements taken were height of the skull at the quadrate, height of the orbit, width of the orbit, length of the nasoantorbital fenestra (NAOF), the distance between the anteriormost point and the NAOF, the height of the skull at the NAOF (=rostrum height), length of the mandibula (if present) and the height of the mandibula at the articular region (if present).

In the *Tupuxuara* specimen digital measurements was difficult because of the 3D preservation and the sediment still surrounding the specimen. In this case a caliper was used to measure height of the articular, height at the nasoantorbital fenestra, length of the nasoantorbital fenestra and the width of the orbit.

3.3 Geometric Morphometrics

3.3.1 Species used in geometric morphometric analyses

As many Brazilian Ornithocheiridae (sensu Unwin, 2001) as possible were included in this analysis (Figure A.2– A.3). One Asian Ornithocheirid, *Guidraco venator*, was used as an outgroup. *Anhanguera santanae* and a second *Anhanguera blittersdorffi* specimen were used in a separate analysis because they were not complete, lacking a premaxillary crest, one of the more important characters used in phylogenetic research. Foth *et al.* (2013), however, made an error by using the reconstruction of *Anhanguera santanae*, hereby including data that was actually absent. *Anhanguera robustus*, *Araripesaurus castilhoi*, *Araripedactylus dehmi*, *Arthurdactylus conandoyli*, *Barbosania gracilirostris*, *Cearadactylus atrox*, *Santanadactylus braziliensis*, *Santanadactylus pricei*, and *Santanadactylus spixi* were not included because they were either too incomplete or lacked a cranium altogether. *Liaoningopterus gui* from the Jiufotang Formation is interesting because it has both a premaxillary and a frontoparietal crest, was excluded because it is not complete enough.

A second part of the studies looked at the use of geometric morphometrics on Tapejaridae sensu Kellner (2004) versus Tapejaridae sensu Martill & Naish (2006), which does not include Thalassodrominae and see it as a separate clade within Azhdarchoidea, Thalassodromidae (as recovered in Figure 2.4). We will Tapejaridae sensu Kellner (2004) to denote this dataset as it includes both Thalassodrominae and Tapejarinae and this is easier to use. All Brazilian Tapejaridae with a fairly complete skull are used (Figure A.4). *Caupedactylus ybaka* and *Tupuxuara longicristatus* were excluded due to the absence of sufficient cranial material available.

At the beginning of this thesis these analyses were sufficient to include all Brazilian pterosaur families. Due to the description of *Banguela oberlii* a new pterosaur family, Dsungaripteridae, is known from the Araripe Basin (Headden & Campos, 2014). This species is only known from mandibular fragments and thus cannot be used in this thesis.

3.3.2 Landmarks

The landmarks chosen are the same as or a modification (*), correction (**), an extension (***) of the landmarks chosen in the pterosaur disparity article of Foth *et al.* (2012) (Figure A.12). Although this article was a good starting point, some landmarks were ill or wrongly defined.

1. Anterior corner of the premaxilla/skull. (*type 2 landmark*)
2. Anterior corner of the NAOF. (*type 2 landmark*)
3. Anteroventral most point of the orbit. (*type 2 landmark*)
4. Dorsal border of the skull constructed by a line at 90° to the midpoint between LM 1 and LM 2. (*type 3 landmark*)

5. Ventral border of the skull constructed by a line at 90° to the midpoint between LM 1 and LM 2. (*type 3 landmark*)
6. Dorsal border of the skull constructed by a line at 135° to the line constructed between LM 2 and LM 3 measured at LM 2. (*type 3 landmark*)
7. Ventral border of the skull constructed by a line at 135° to the line constructed between LM 2 and LM 3 measured at LM 2. (*type 3 landmark*)
8. Dorsal border of the skull constructed by a line at 90° to the midpoint between LM 2 and LM 3. (*type 3 landmark*)
9. Dorsal border of the NAOF constructed by a line 90° to the midpoint between LM 2 and LM 3. (*type 3 landmark*)
10. Ventral border of the NAOF constructed by a line 90° to the midpoint between LM 2 and LM 3. (*type 3 landmark*)
11. Ventral border of the skull constructed by a line 90° to the midpoint between LM 2 and LM 3. (*type 3 landmark*)
12. Posterodorsal border of the orbit constructed by a line at 45° to the line between LM 2 and LM 3 at LM 3. (*type 3 landmark*)
13. Posterior border of the orbit constructed by a line at 90° to the midpoint between LM 3 and LM 12. (*type 3 landmark*)*
14. Anterodorsal border of the orbit constructed by a line at 90° to the midpoint between LM 3 and LM 12. (*type 3 landmark*)*
15. Dorsal border of the orbit constructed by a line at 90° to the midpoint between LM 13 and LM 14. (*type 3 landmark*)*
16. Dorsal border of the skull constructed by a line at 90° to the midpoint between LM 3 and LM 12. (*type 3 landmark*)*
17. Posterodorsal border of the skull constructed by a line at 45° to the line between LM 2 and LM 3 and LM 3. (*type 3 landmark*)*
18. Dorsal border of the skull constructed by a line at 90° to the midpoint between LM 12 and LM 17. (*type 3 landmark*)*
19. Posterior border of the skull constructed by a line at 90° to the midpoint between LM 12 and LM 17. (*type 3 landmark*)*
20. Anteroventral corner of the NAOF. (*type 2 landmark*)**
21. Posterior border of NAOF, constructed by a line originating at LM 20 crossing the line between LM 2 and LM 3 at 90° (*type 3 landmark****)

22. Posteroventral corner of the quadrate. (*type 2 landmark*)***
23. Dorsal border of the skull constructed by a line at 90° to the line between LM 1 and LM 2, at a quarter of the length of the line between LM 1 and LM2. (*type 3 landmark*)***
24. Ventral border of the skull constructed by a line at 90° to the line between LM 1 and LM 2, at a quarter of the length of the line between LM 1 and LM2. (*type 3 landmark*)***
25. Dorsal border of the skull constructed by a line at 90° to the line between LM 1 and LM 2, at three quarter of the length of the line between LM 1 and LM2. (*type 3 landmark*)***
26. Ventral border of the skull constructed by a line at 90° to the line between LM 1 and LM 2, at three quarter of the length of the line between LM 1 and LM2. (*type 3 landmark*)***
27. Posterior most point of the skull. (only in Tapejaridae)(*type 2 landmark*)***
28. Dorsal border of the skull constructed by a line at 90° to LM 2. (only in Tapejaridae)(*type 3 landmark*)***

3.3.3 Geometric morphometrical analyses

As geometric morphometrics has become a technique on its own, the software uses a dedicated file format with a file extension '.tps' for morphometric studies. First, the different images (figure A.8-A.11) were converted and combined into one or two tps-files, depending on the analysis, using tpsUtil v1.58 (Rohlf, 2005). This tps-file contains the source of the image but no information about landmarks, or scale. To include this information tpsDig v2.17. (Rohlf, 2005) was used. Using this software, landmarks were placed in each image using a scheme as mentioned in the previous section. Subsequently, the according scale was added using the scaling function supplied by tpsDig v2.17. In order for the program to successfully add a scale to the different specimens some sort of scale already has to be available on the original image. By saving all this information in the tps-file the file now contained all the information needed to do the analysis.

The software tpsRelw v1.53. (Rohlf, 2005) was then used to standardize, called superimpose in geometric morphometric studies, the data. Superimposing data is necessary to match up shapes, and tpsRelw does this by placing the different landmark configurations on top of each other. Shape is defined as being independent of size and thus independent of affine transformations like translation, scaling and rotation and these are used by all superimposition methods. These methods use these transformations to eliminate all information unrelated to shape. The method used in this thesis is the Generalized Least Squares Procrustes superimposition (GLS). GLS minimizes the Procrustes distance, which is the summed squared distance between corresponding landmarks, by using only a few steps (Zelditch *et al.*, 2004).

In a first step the centroid —the mass point— of the configuration is calculated by calculating the point that consists of the average of the X- and Y- coordinates of every landmark. Next each landmark configuration is centered at the origin of an X-Y-plot by subtracting the coordinates

of the centroid from the coordinates of each landmarks, hereby translating the centroid of every configuration to the origin.

In a third step the landmark configuration is scaled to a unit, the centroid size. This centroid size is the square root of the sum of the squared distances of the landmarks from the centroid. The scaling is done by dividing every coordinate by the centroid size, and this for every configuration, using their own centroid size. In a last step one configuration is chosen as a reference and every other configuration will be rotated until the Procrustes distance between the two configurations that are being compared at that moment is as small as possible. When all are rotated to an optimal alignment, the average shape is calculated and all are, again, rotated around this average shape. Then the average shape is yet again recalculated and set as the new reference and the cycle restarts. This iteration stops when the newest reference is identical to the previous. This final configuration minimizes the average distance of shapes from the reference. Centroid size is not recalculated every step making this the partial Procrustes superimposition instead of the full Procrustes superimposition. The resulting reference shape, which can be looked at as an average shape, is called the consensus shape. All changes will be compared to this shape.

To analyze the data we used Morpho-J 1.05f. (Klingenberg, 2011). Morpho-J calculates partial warps using the thin-plate spline (tps), which are the eigenvectors of the bending energy matrix and they describe parts of the deformation pattern in the bending energy matrix. These partial warps thus decompose deformation into several components and then describe the contribution of each partial warp to the total deformation. The partial warp score is a vector that indicates the direction of the partial warp. This is all visualized on the bending energy function. Deformations along the X- and Y- axis are illustrated as deformations along the Z- axis. Steep bends represent closely spaced points that both change in opposite directions, as this requires more energy. Besides visualizing deformation, the great benefit of calculating these partial warps using tps lies in that they can be used in conventional statistics without having to worry about adjusting the degrees of freedom (Zelditch *et al.*, 2004).

3.3.4 Statistical analyses

To analyze the partial warp scores we did a relative warp analysis, RWA, in Morpho-J. This RWA is a weighted principal component analysis (PCA) of the partial warp scores that includes information provided by relative warp scores. We did several RWA's on Ornithocheiridae (with or without broken specimens), Tapejaridae and both datasets combined. MacLeod (2012) suggested that type III landmarks should be excluded in this analysis. Bookstein *et al.*, 1985, called the type III landmarks deficient and stated that their usage should be interpreted with care, if used at all. Working with fossils, however, does not give you type I landmarks, and our experience working with the software showed that more (type III) landmarks increased the accuracy, probably by better describing the actual shape. These extra landmarks were chosen based on characters used in their taxonomy (e.g. to include the presence of a premaxillary crest in Ornithocheiridae and the curvature of the premaxilla in Tapejaridae). Caution is still needed

as increasing the number of variables does increase the risk of overfitting.

All RWA analyses were accompanied by a Canonical Variate Analysis (CVA). While RWA combines variables into new variables that compare variation among individuals within a sample, CVA creates variables in order to minimize variation within groups (Zelditch et al., 2004). This type of analysis appeared to work only when using large sample sizes as in the combined dataset.

Regressions, with accompanying R^2 -values, between relative warps scores (called principal components by MorphoJ), centroid size and/or age of the specimen were calculated using SigmaPlot 11.0 from Systat Software (<http://www.systat.com/>). Ages were estimated based on articles by Martill (2007) and He *et al.* (2004). The age of the Romualdo member was based on references without actual peer-review (which were the only ones to 'stick' a number to it) (website 1). A separate analysis was, however, carried out by using the information that the Santana Formation as a whole (so not the Romualdo member in specific) is 10mya older than the Crato Formation. Note that Veldmeijer (2006) does not give information about the formation of the *Brasileodactylus* specimen used in these analyses. The age used for *Brasileodactylus* is the age of the oldest known member of that species (Sayao & Kellner, 2000). Although it is likely that the specimen used is actually younger —Veldmeijer (2006) explicitly refers to another specimen as the Crato specimen— using the oldest known occurrence is necessary when trying to resolve evolutionary trends throughout time.

Due to the low sample size, performing other statistical tests was not attempted. Normality could not be reached, no variances could be calculated and in most cases means would be constructed using only one specimen so that no standard errors were available and, hence, significance tests could not be carried out. While this is common when dealing with fossil records, in this case the results must be interpreted with the utmost care. All graphs were made using SigmaPlot 11.0 from Systat Software.

Chapter 4

Results

In this chapter we will present the results of the analyses described in the previous chapter. We will start with the (relatively simple) linear measurements of the Ornithocheiridae. Next the results of the geometric morphometric analyses will be presented. These last were used to investigate more intricate differences in shape between the skulls of different pterosaur species.

4.1 Linear measurements

4.1.1 *Tupuxuara*

Figure 4.1 shows the log-ratio of several measurements (Table B.3). The log-ratio is the logarithm of the difference of a measurements of the new specimen and the measurement of a standard (the adult *Tupuxuara deliradamus*) and is often used to compare different bones to each other in a relative way (Simpson *et al.*, 1960). A negative value indicates that the new specimens is smaller than the standard and vice versa. If all bones would grow at the same rate a horizontal line, between the several points, would be expected; if all bones would be half the size of the standard, we would get a line with at $\log(0.5)=-0.301$. As this is not the case, the different bones grew at different rates, with the highest growth rate in the length of the nasoantorbital fenestra, which is correlated with the total length of the animal. This yet again confirms that some parts of the pterosaur skull grew allometrically.

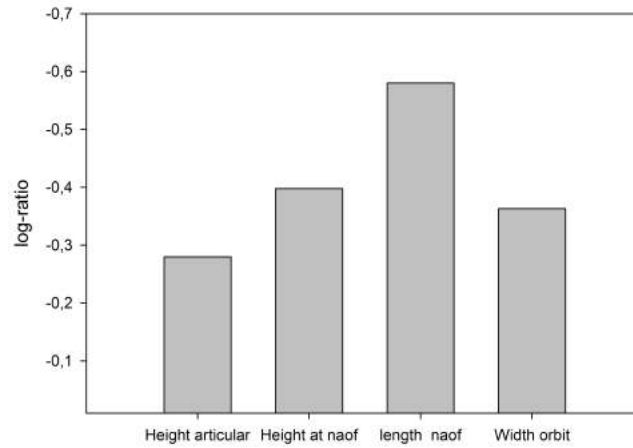


Figure 4.1: Log-ratio (logarithm of the difference) of the measurements of the skulls of both the adult and the putative juvenile *Tupuxuara deliradamus* specimen as shown in table B.3. The x-axis shows the character measured, while the y-axis shows the corresponding log-ratio value.

4.1.2 Ornithocheiridae

The linear measurements of the Brazilian Ornithocheiridae are shown in table B.2. Figure 4.2 shows the Nopcsa curves of the Brazilian Ornithocheiridae. These curves consist of connected points that represent logarithms of different measurements relative to the total length. The ratio of the measurements and the length were used to standardize between different measurements to the length. The logarithm of this ratio was used as this reduces the range of the values, hereby increasing the resolution. Bennett (2006) successfully used this method to distinguish *Germanodactylus* from *Pterodactylus* because similar species have similar Nopcsa curves. *Anhanguera* in darker blue often clusters together, as well as different shades of turquoise (*Ludodactylus sibbicki* and *Brasileodactylus araripensis*) but no real conclusions can be made, mainly due to low sample size.

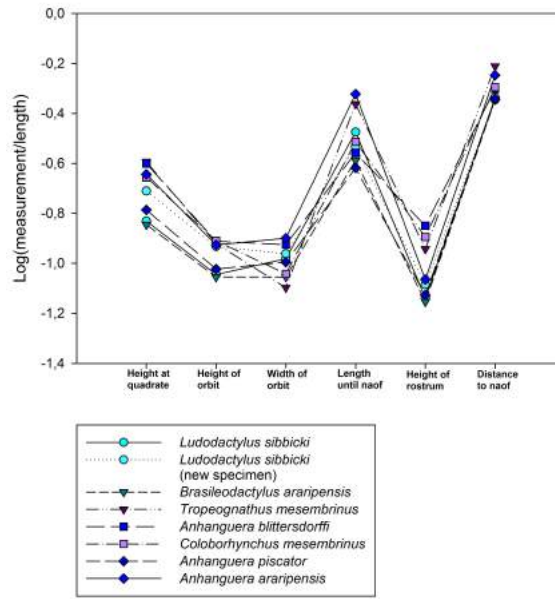


Figure 4.2: Linear measurements of Brazilian Anhangueridae presented as Nopcsa curves (as in Bennett, 2006). Different colors represent different genera, with different shades within a color corresponding with the relationship between different species.

4.2 Geometric morphometrics

4.2.1 All Brazilian pterosaur clades

Figure 4.3 shows the result of the RWA analysis using all Brazilian pterosaurs. Ornithocheiridae are easily recognized as one cluster. Tapejaridae sensu Kellner (2004) form separate, less defined, clusters with *Tapeja wellnhoferi* and especially *Thalassodromeus sethi* as main outliers. This is probably because these two have a more eccentric appearance.

Changes associated with the principal components are shown in figure 4.4. Changes in principal component 1 (PC1) mostly consist of changes in the height of the nasoantorbital fenestra, the height of the skull at the center part of the skull and the height, and shape of the rostrum. Changes in PC2 correspond to changes in the height and length of the frontoparietal crest corresponding to changes in the location of landmarks 17 and 16. Other changes that happen are changes in the location of landmarks 8 and 6, which are the height of the dorsal roof of the skull, which is made up by the premaxilla and is associated with the frontoparietal crest. Both principal components thus largely contain information of the dorsal side of the skull, while lacking much information about the ventral side. The percentage of the total variance that each principal component represents is shown in table B.4.

Figure 4.5 depicts the result of the CVA analysis of all the Brazilian pterosaurs. The geometric morphometric analysis appears to be able to pick up the different taxonomic groups. Although in figure 4.3 both Thalassodrominae and Tapejarinae appear to be close to each other, figure 4.5 shows that both have a distinctive morphospace that differs amongst each other as much as compared to Ornithocheiridae.

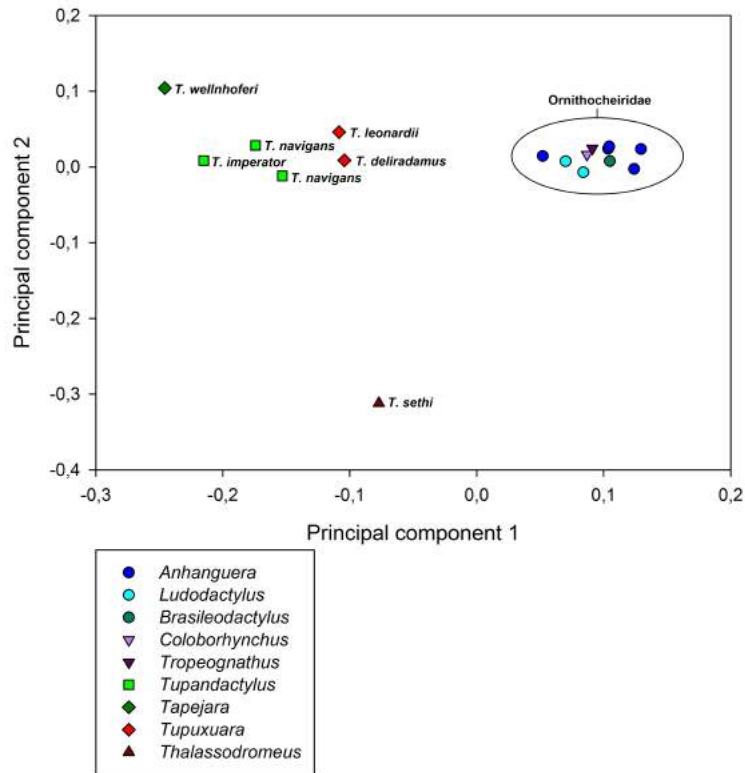


Figure 4.3: Morphospace of all available Brazilian pterosaurs skulls based on the first two principal components. Broken specimens were included to increase the sample size. These broken specimens all belonged to Ornithocheiridae and lacked a premaxillary crest. Different colors represent different families. The gradient within each color indicates the relationship between members of the family. Red = Thalassodrominae, Green = Tapejarinae & blue = Ornithocheiridae. Ornithocheiridae are not individually labeled as this would reduce the readability of the figure.

4.2.2 Ornithocheiridae

Figure 4.6 shows the first two (A) and first three (B) principal components of the RWA for Ornithocheiridae. Associated changes along the principal components are illustrated in figure 4.7. Changes in the score of along PC1 correspond with changes in both the parietofrontal crest and the premaxillary crest. Large values with respect to PC1 correspond to larger frontoparietal crest (seen in landmarks 16, 17 and 18) but in the meanwhile these large values correspond with a reduced height of the premaxillary crest (landmarks 4, 23 and 25). The changes in both the orbit and nasonatorbital fenestra appear to be minimal.

Changes in the values along PC2 correspond with major changes in the dorsal roof of the cranium (figure 4.7). An increase of both the premaxillary (landmarks 4 and 35) and the frontoparietal (landmarks 16 and 18) leads to a lower dorsal roof of the cranium and a much smaller nasoantorbital fenestra. PC3 provides similar information as PC1 as it also shows that an increase in height of premaxillary crest results in a lower height of frontoparietal crest while PC4 corresponds to an overall increase in size. The percentage of each principal component of the total variance is shown in table B.5.

The *Ludodactylus sibbicki*-cluster in figure 4.6(A) is surrounded with a 95% confidence ellipse. *Brasileodactylus araripensis* clearly falls within this range and shows that its morphology resembles more to *Ludodactylus sibbicki* than the two *Ludodactylus sibbicki* specimens resemble each other. A first *Anhanguera* 90 % confidence ellipse includes *Coloborhynchus*, while a second 95% confidence ellipse—which was made assuming that *Coloborhynchus* was an *Anhanguera*—shows that *Anhanguera piscator* is an outlier within the *Anhanguera*-cluster. Figure 4.6(A) illustrates that the Brazilian pterosaurs form one clade and the Chinese *Guidraco venator* does not resemble *Ludodactylus sibbicki* as much as previously thought. A linear trend appears to be present in the Brazilian pterosaur. When considering only PC1, a trend is not only visible in the Brazilian Ornithocheiridae, but it is extended up to *Guidraco venator*. The importance of this will be explained later.

The different relationships visible in figure 4.6(A) are less clear in figure 4.6(B), but still visible. By incorporating PC3, increasingly more details are used and the human error of placing the different landmarks, on sometimes obscure places (see material and methods), may become more important.

Figure 4.8 depicts the result of the CVA analysis. The different groups are not as clearly distinguishable as earlier. However, *Ludodactylus sibbicki*-like pterosaurs are positioned more to the right, the *Anhanguera*-like pterosaurs more to the left, and *Guidraco venator* and *Tropeognathus* are on the extremes of both sides. The reduced power is probably due to both low sample size and the lower taxonomic level, as we are now comparing within one family rather than between families. Within families the resemblance is much higher than between families. It is of course also possible that the clusters visible in the RWA are not real clusters.

To test if the pattern visible in figure 4.6(A) might be size related, a linear regression was attempted between principal component (PC) 1 and centroid size, which is a proxy for size. Figure 4.9(A) shows that there was no linear relation between centroid size and PC1. Figure 4.9(B) gave the same results but now for PC2. Statistical analysis confirmed this and gave adjusted R^2 -values of 0,3172 and 0,0000 (and p-values of 0,065 and 0,6077) respectively. Second order polynomial regressions yielded an adjusted R^2 -value of 0,245 (with corresponding p-value 0,087) for PC1 and a adjusted R^2 -value of 0,00524 (with corresponding p-value of 0,862) for PC2. For third order polynomial regressions an adjusted R^2 -value of 0,18 (and p-value of 0,2966) was found for PC1 and an adjusted R^2 -value of 0,5795 (and p-value of 0,065) was found for PC2. A multiple linear regression of PC1, PC2 and centroid size gave an adjusted R^2 -value of 0,256 and p-value 0,174.

As the pattern did not appear to be size-related, it was investigated whether it was age (and thus evolutionary) related. Figure 4.10(A–B) shows the regression between the first four principal components and the oldest age of the species. Statistical analyses were carried out and the adjusted R^2 -values shown are these of both a linear regression and a second order polynomial regression. For PC1, an adjusted R^2 of 0,739 (and p-values of 0,002 or below, for both the regression itself and all coefficients) was obtained with a linear regression, while for PC2 the second order polynomial regression resulted in an adjusted R^2 of 0,8979 (with p-values

of 0,0002 for all coefficients). Using 102 mya instead of 108 mya, to correct for the officious references of the latter by using the information that the Santana Formation as a whole was 10 mya younger than the Crato Formation , yielded similar results and even increased the R^2 -values to 0,741 and 0,9555 respectively. Either way these R^2 -values are high and must accordingly mean something. Finally a multiple linear regression gave an adjusted R^2 -value of 0,774 with corresponding p-values of 0,012.

In the previous analyses only complete specimens were used. Figure 4.11 depicts the result of the RWA including specimens with a broken premaxillary crest. The principal components contain the same landmarks as stored in the previous analyses. *Anhanguera blittersdorffi* specimen 2 falls within the range of the other *Anhanguera* specimens, but *Anhanguera santanae* is an outlier. Using these specimens reduced the separating power as can be seen in the equal frequency ellipses.

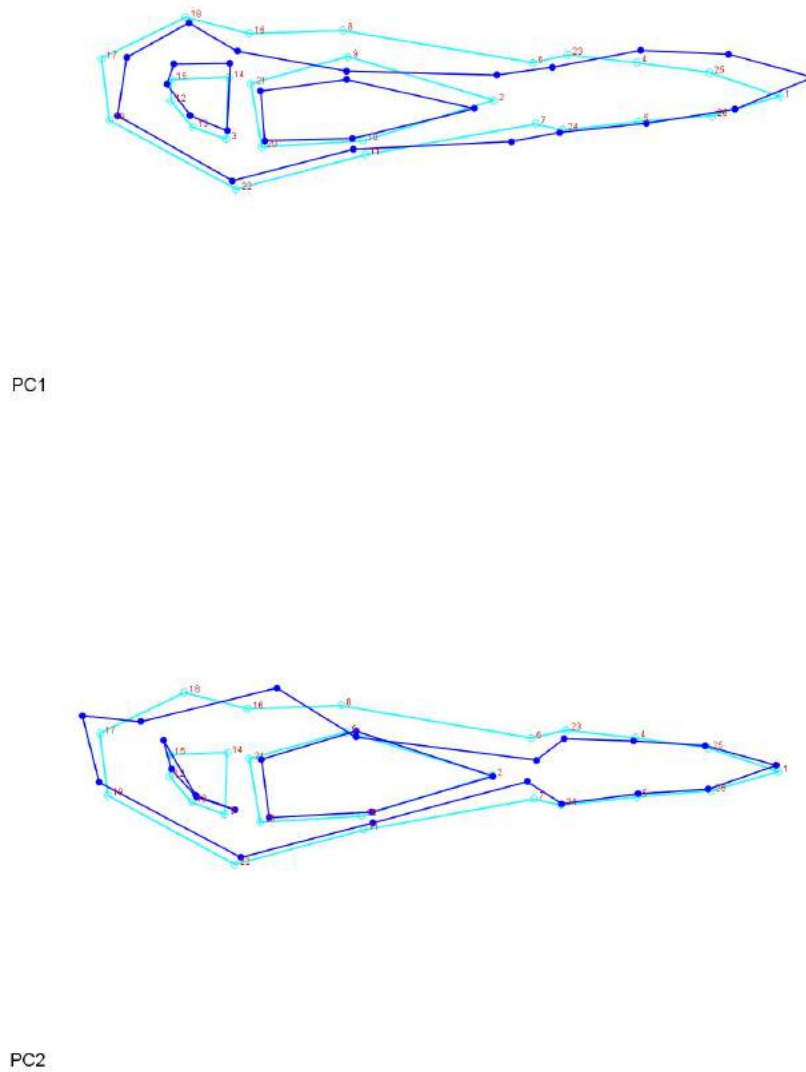


Figure 4.4: Morphological changes in the skull in the positive direction along the first (A) and second (B) principal component of the RWA with all Brazilian pterosaurs. Only the first two principal components are shown, as these explain the most of the variation. The consensus shape is shown in light blue while the actual change is visible in dark blue.

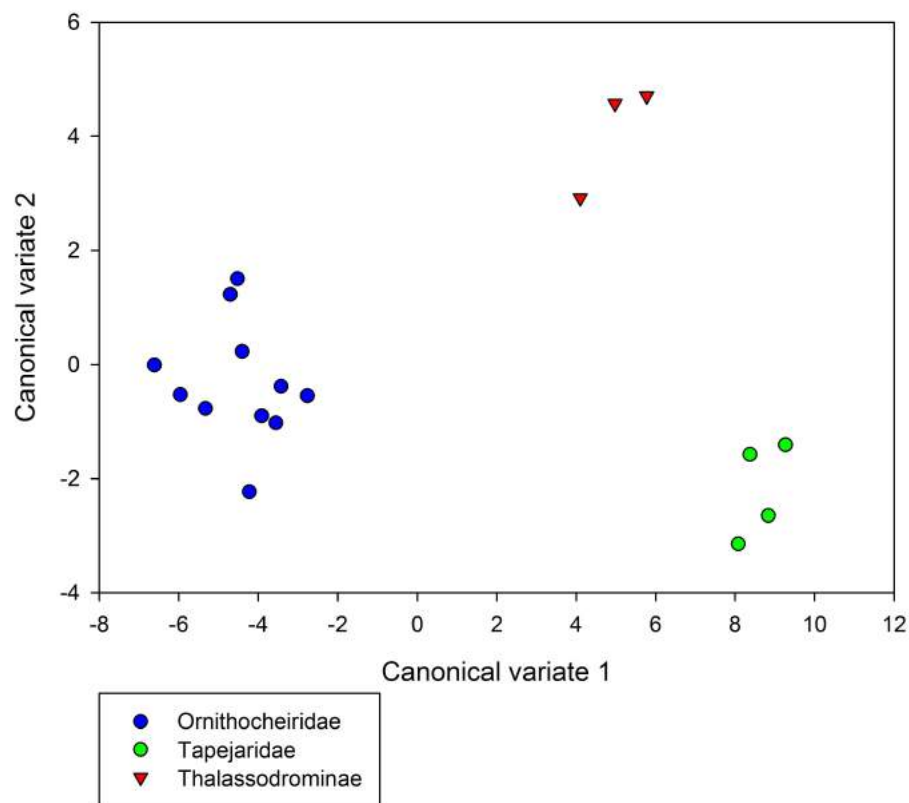


Figure 4.5: CVA plot of all available Brazilian pterosaurs skulls. CVA is used as a tool to how good the data fits the predefined groups. Different colors represent different families. Red = Thalassodrominae, Green = Tapejarinae & Blue = Ornithocheiridae.

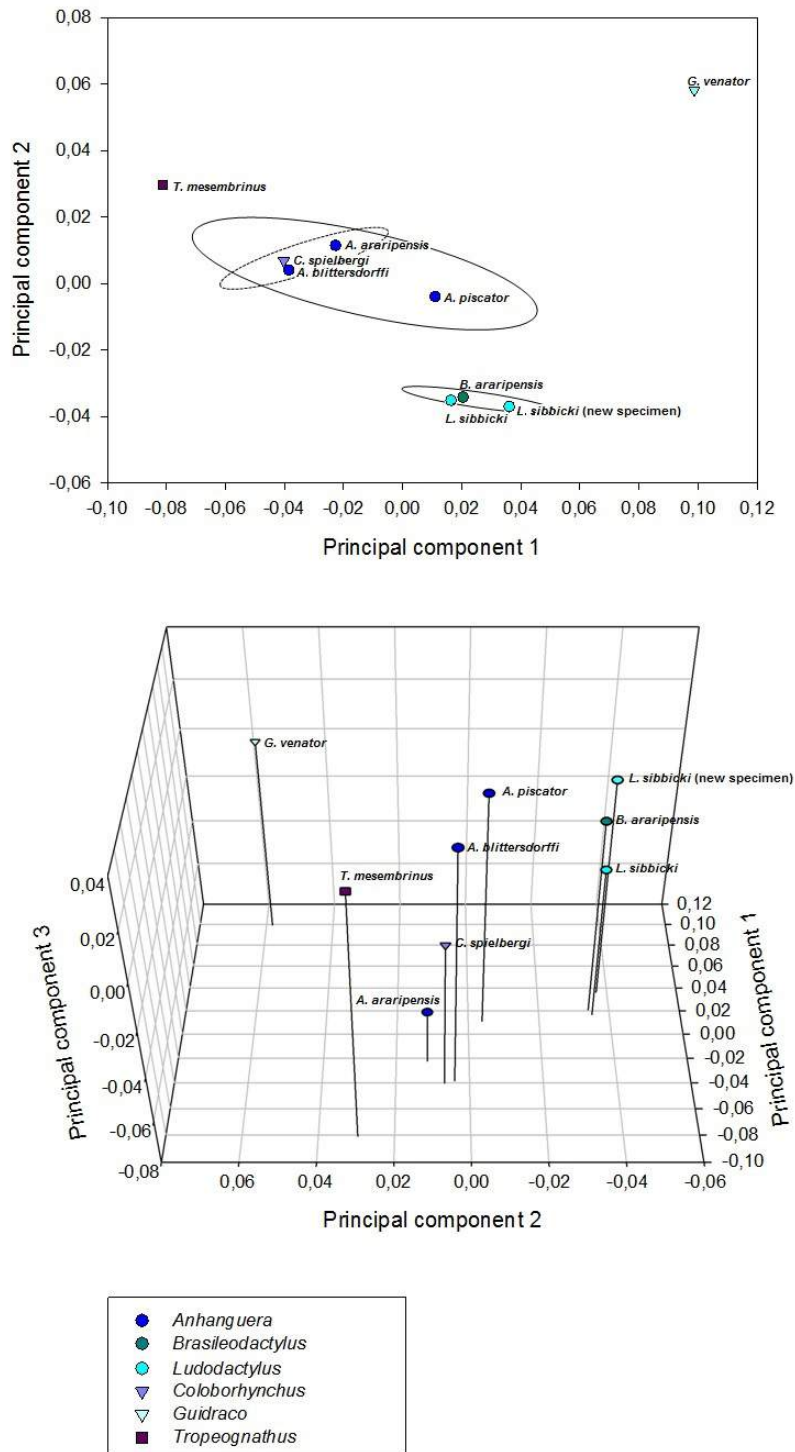


Figure 4.6: A: Morphospace of all (Brazilian + *Guidraco venator*) complete Ornithocheiridae skulls based on the first two principal components. Full ellipses represent 90 % equal frequency ellipses of the genus *Anhanguera* and *Brasileodactylus araripensis*, while the dotted ellipse is the 95 % equal frequency ellipses when *Coloborhynchus spielbergi* is considered as *Anhanguera spielbergi* as proposed by Kellner & Tomida (2000) and Veldmeijer (2006) — Veldmeijer considered all *Anhanguera* as *Coloborhynchus* — among others. B: Morphospace of all complete Brazilian Ornithocheiridae skulls based on the first three principal components. In both subfigures the gradient in the different shades of blue corresponds with the relationship between members of the family.

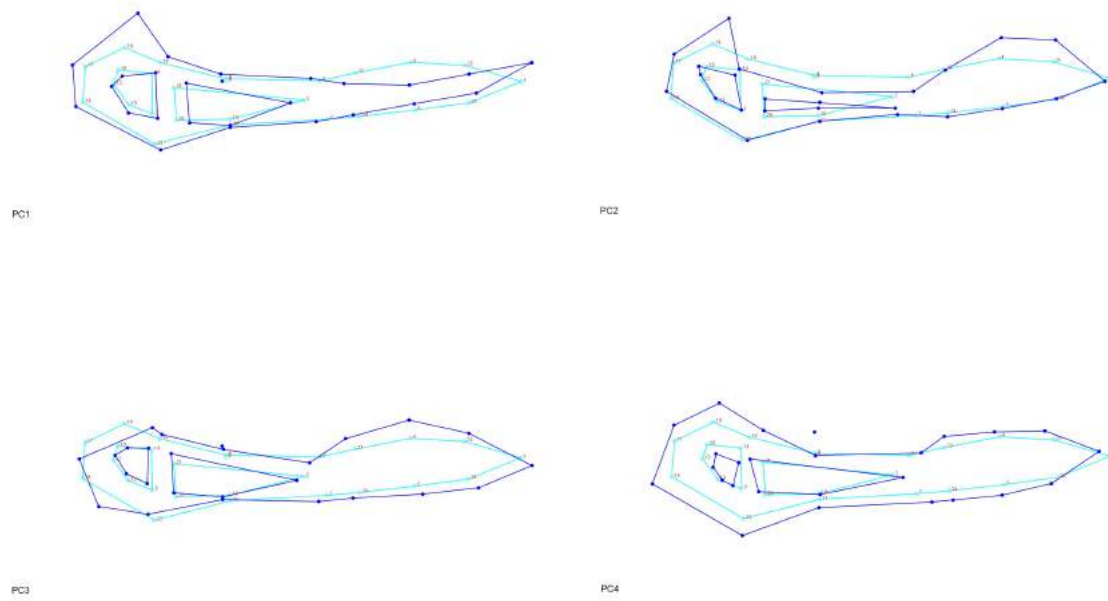


Figure 4.7: This figures shows the morphological changes in the skull in the positive direction along PC1 (A), PC2 (B), PC3 (C) and PC4 (D) principal component of the RWA using only ornithocheirids. The consensus shape is shown in light blue. Changes along the axis in the positive direction, up to the end of the axis results in the shape in dark blue.

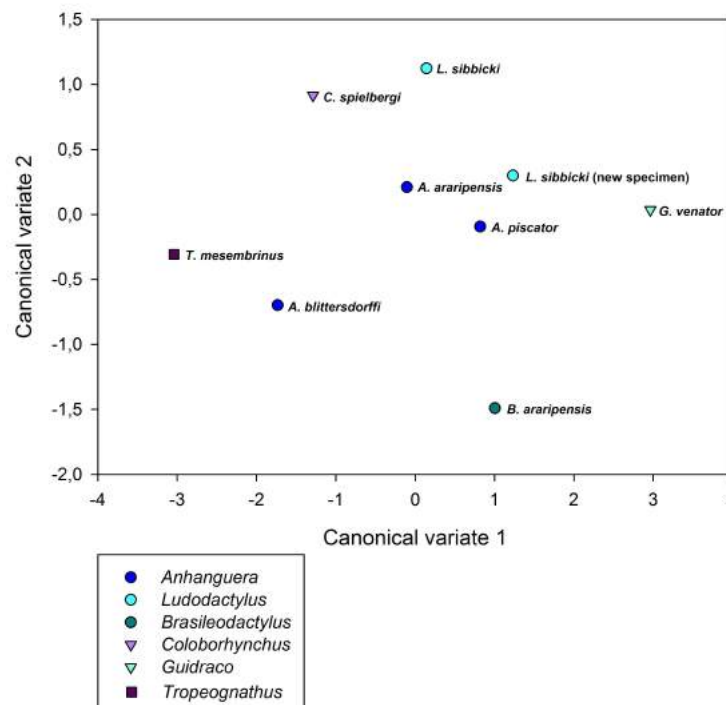


Figure 4.8: CVA plot of all (Brazilian + *Guidraco venator*) Ornithocheiridae skulls. CVA is used to show how good the data fits the predefined groups. The gradient in the different shades of blue corresponds with the relationship between members of the family.

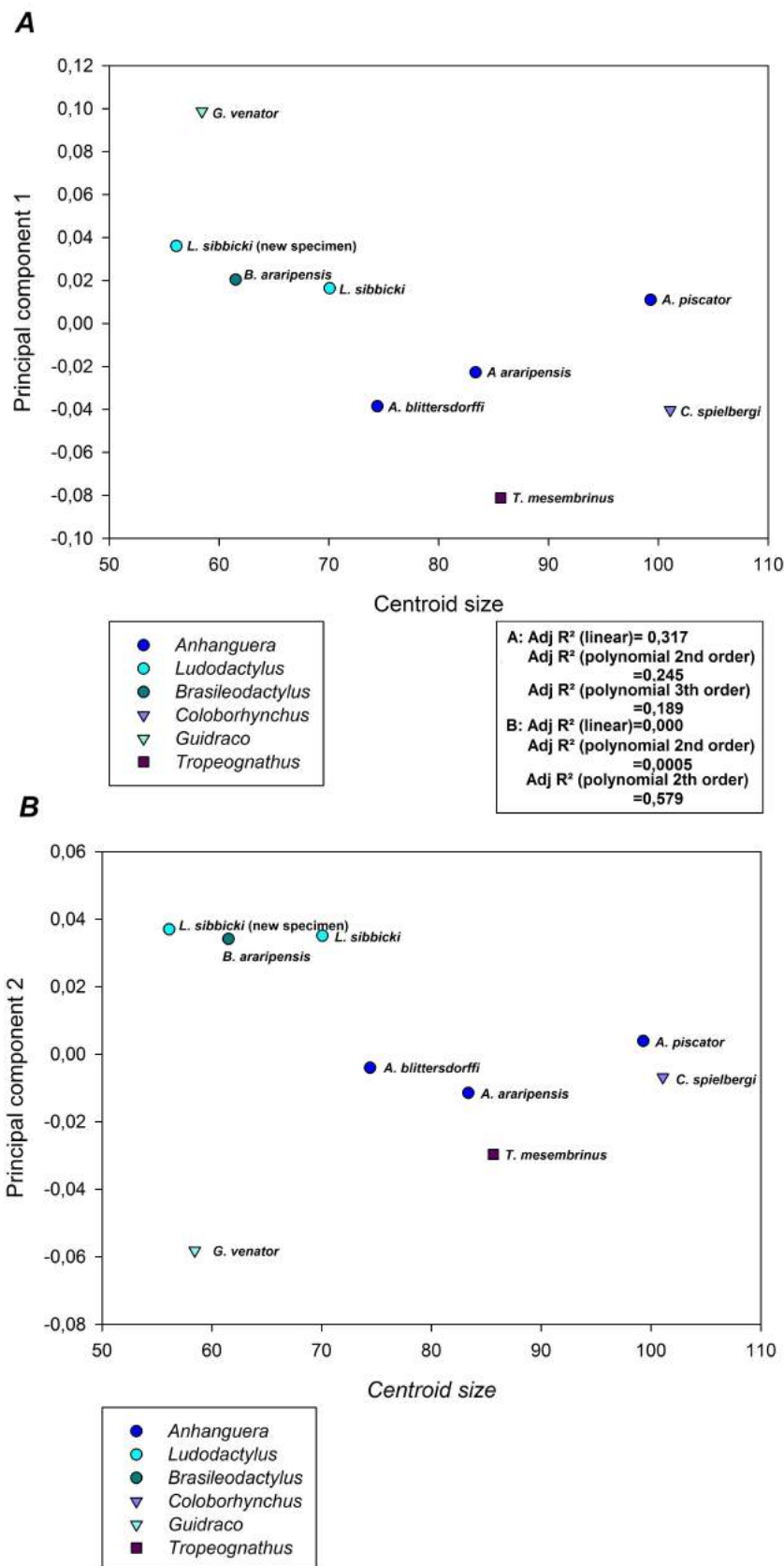


Figure 4.9: Regression of centroid size of all (Brazilian + *Guidraco venator*) complete Ornithocheiridae skulls versus their first (A) and second (B) principal component. In both subfigures the gradient in the different shades of blue corresponds with the relationship between members of the family. R^2 -values of

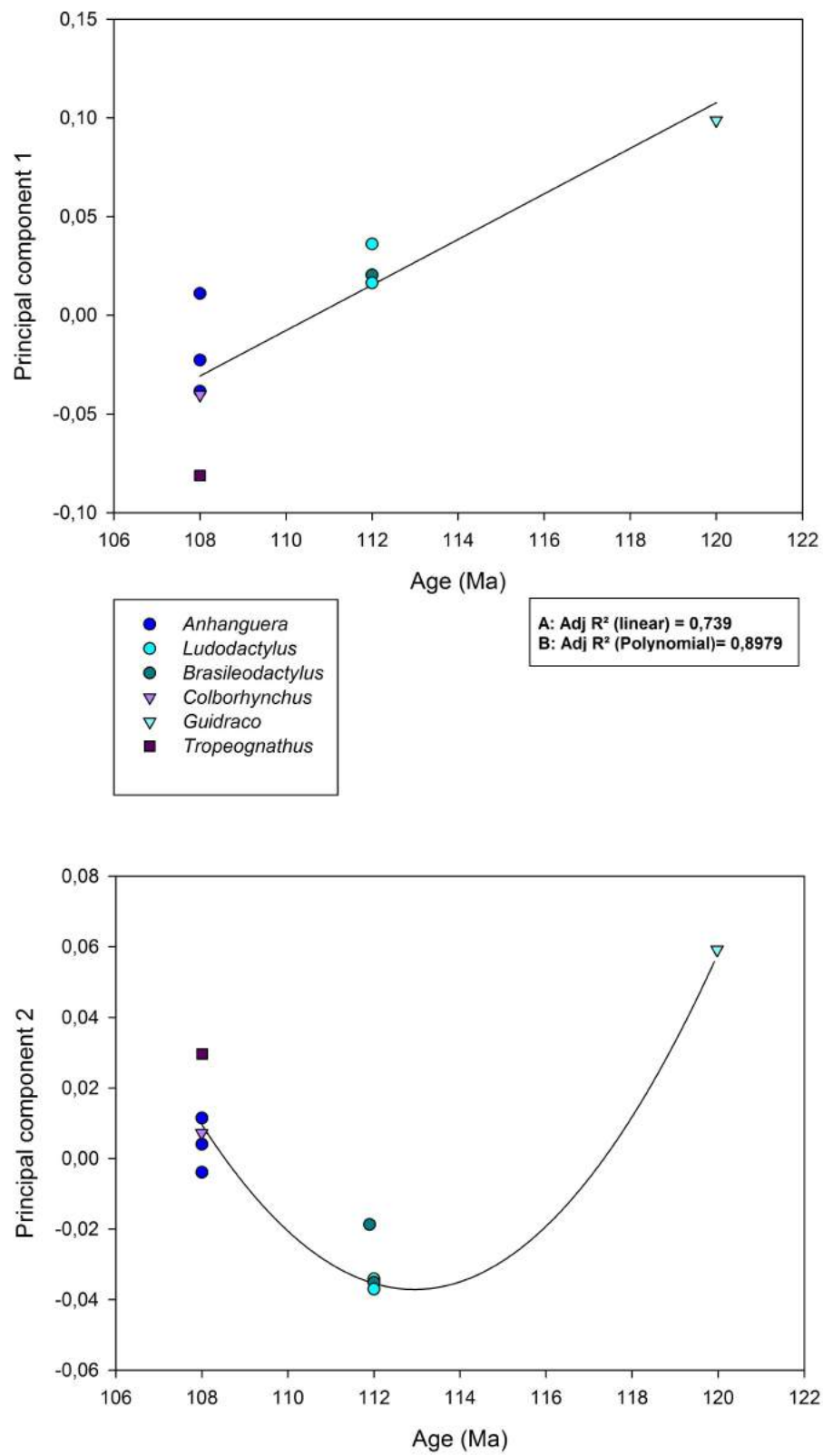


Figure 4.10: Regression of age million years ago (mya) versus principal component 1 (A) and principal component 2 (B) of the Ornithocheiridae. R^2 is always shown as well.

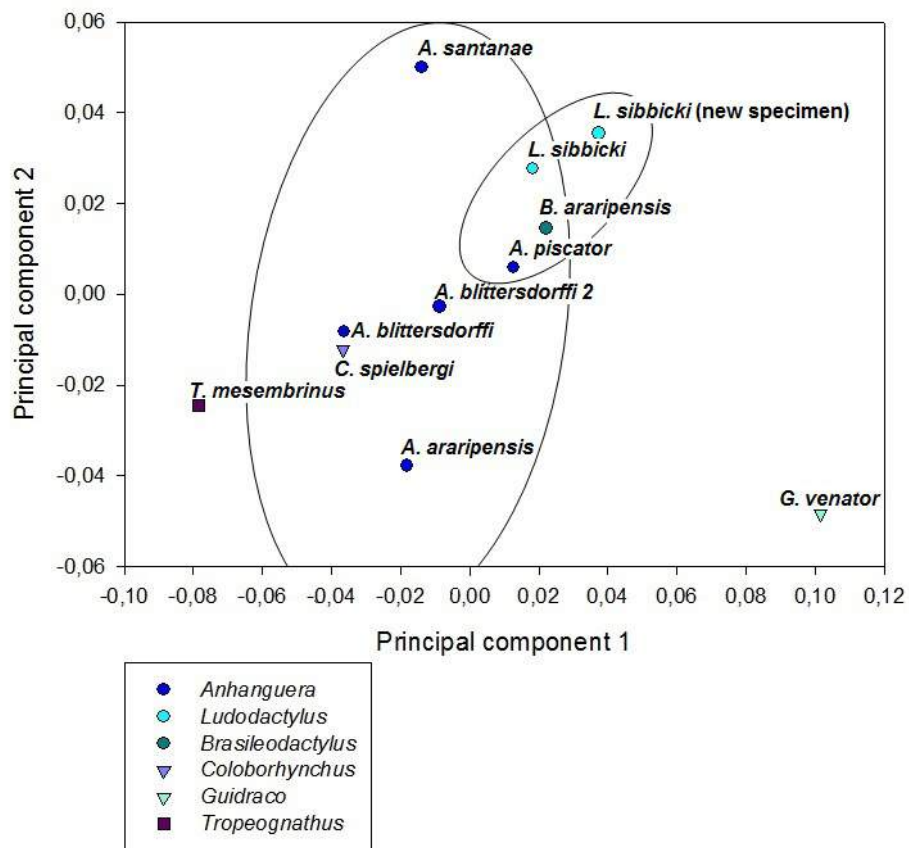


Figure 4.11: Morphospace of all (Brazilian + *Guidraco venator*) Ornithocheiridae skulls, including broken specimens, based on the first two principal components. Broken specimens (*A. blittersdorffi* 2 and *A. santanae*) were missing a premaxillary crest. Full ellipses represent 95 % equal frequency ellips of the genus *Anhanguera* and *Brasileodactylus araripensis*

4.2.3 Tapejaridae sensu Kellner (2004, 2007)

Figure 4.12 shows the result of the RWA analysis of Tapejaridae. Figure 4.13 shows the associated changes. A change in PC1 is most consistent with a change in the length of the parietofrontal crest of occipital spine as in *Tupandactylus imperator* (landmark 23). Further changes are apparent in the orbit which changes shape (landmark 14). Changes in PC2 correlate with changes in the height of the dorsal crest (landmark 28) and shape of the rostrum (landmarks 1, 4, 5, 26 and 27). PC3 incorporates similar information, with changes visible in the length of the parietofrontal crest, the height of the dorsal crest and the shape of the premaxilla. Note that with dorsal crest a parietofrontal crest is meant, that is erected dorsally of the nasoantorbital fenestra as in *Tupandactylus*, while the parietofrontal crest sensu stricto a posterior pointing parietofrontal crest as in *Tupuxuara* is meant. This to distinguish between the two types. PC4 adds details and is not associated with large changes. As in the previous analyses the dorsal side of the skull appears to be the most important factor changing. New is the importance of the premaxilla. This is not strange as the curvature of the rostrum is a taxonomic character often used in tapejarid taxonomy with a distinct curvature present in Tapejarinae but absent in *Tupuxuara* and something in between in *Thalassodromeus* (figure A.4). This is also visible on the y-axis of figure 4.12 where *Thalassodromeus* is somewhere between *Tupuxuara* and *Tupandactylus*. The percentage of variation explained by each principal component is shown in table B.6

Figure 4.12 also shows that both *Tupuxuara* species and *Tupandactylus navigans* are clustered together. *Tupandactylus imperator*, however, appears to differ from *Tupandactylus navigans*. *Thalassodromeus* is also an outlier with an exceptionally low PC1 score, indicating it had a long backwards pointing crest, but a low rostrum.

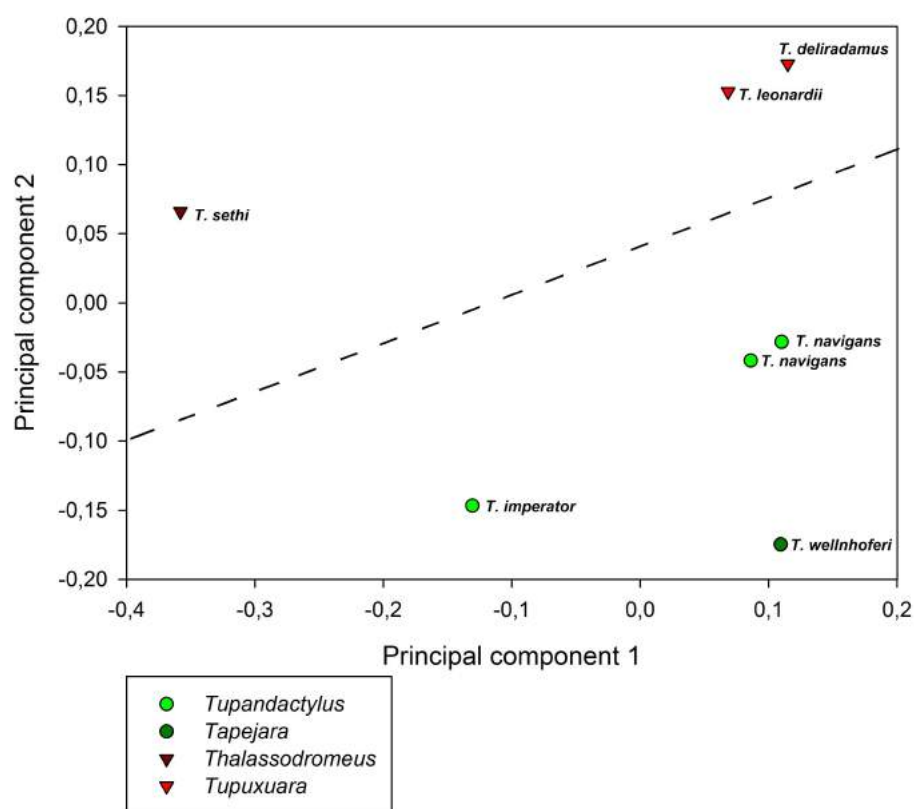


Figure 4.12: Morphospace of all Brazilian Tapejaridae (sensu Kellner (2004) which consists of Thalassodrominae and Tapejarinae). Different colors represent different families, while different shades of a color indicate relationships within a family. Red = Thalassodrominae, Green = Tapejarinae. A possible diagonal separation is shown as a broken line.

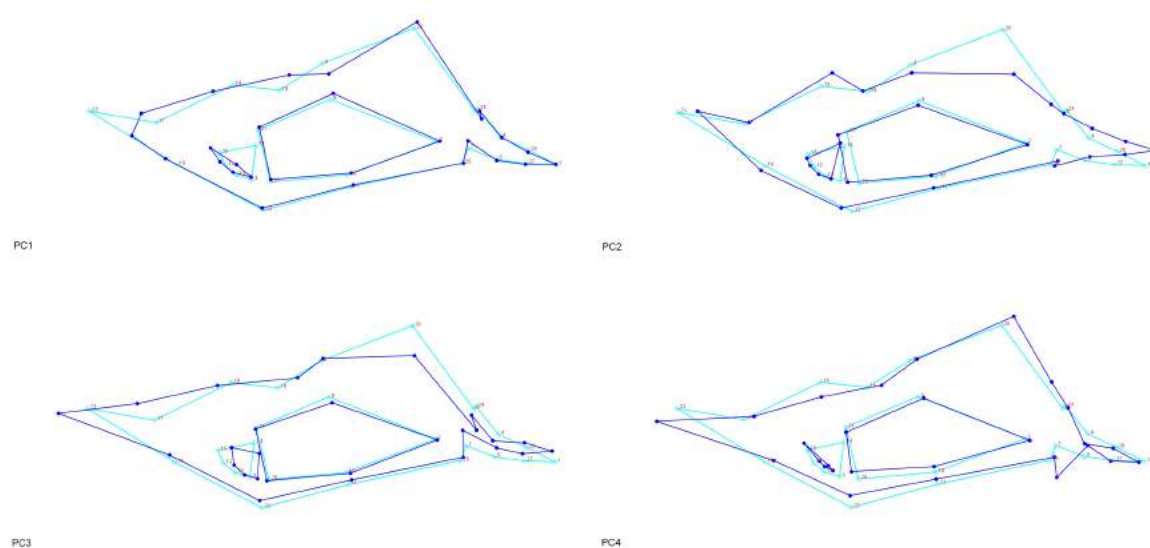


Figure 4.13: This figures shows the morphological changes in the skull in the positive direction along PC1 (A), PC2 (B), PC3 (C) and PC4 (D) principal component of the RWA using only Tapejaridae. The consensus shape is shown in light blue. Changes along the axis in the positive direction, up to the end of the axis results in the shape in dark blue.

Chapter 5

Discussion

In this chapter we will interpret the different results. First, we will evaluate the potential of geometric morphometrics on different taxonomic levels, ranging from family level down to the genus or even species level. Next, we will investigate the taxonomic value of the crest. A pattern in the morphospace created by the geometric morphometric analysis was discovered. This pattern was associated with changes in crest shape. It was thus investigated whether the differences in crests of the different Ornithocheiridae are due to ontogeny or evolution. While statistical analyses were used wherever possible, since the sample size was extremely low, in most cases it was not possible to draw statistically significant conclusions. We tried to compensate for the lack of statistics by applying several non-statistical tests. These test use circumstantial evidence to falsify, or promote certain hypotheses. Due to the fragmentary fossil record, this method is not uncommon in vertebrate paleontology.

5.1 The use of geometric morphometrics in taxonomy

5.1.1 Taxonomy of all Brazilian pterosaur families

To explore the taxonomic use of geometric morphometrics it was decided to discuss this from top to bottom, starting with higher taxonomic clades going down to the genus level. Figure 4.5 illustrates that the three main clades of the Araripe Basin can be separated using the canonical variate analysis (CVA) of geometric morphometrics. With the relative warp analysis (RWA), a weighted PCA, it was more difficult to separate Tapejarinae from Thalassodrominae (figure 4.3). The shape of *Tupandactylus* and *Tupuxuara* is similar. Both *Tupandactylus* species differ more from *Tapejara*, which belongs to the same clade, than from both *Tupuxuara* species. These in turn resemble more like the *Tupandactylus* species than *Thalassodromeus*, which belongs to the same clade of *Tupuxuara*. The difference between the two analyses is due to the mathematical background of these analyses. RWA describes the variation between individuals, while CVA describes the variation between groups. CVA will thus assign more value to certain characters in order to decrease the within group variation. Keeping this in mind, one would expect that groups that are clearly defined will also show up in the RWA, as the inter-individual variation

would be low. Note, however, that even the CVA acknowledges that Tapejaridae are closely related, as canonical variate (CV) 1, the most important axis, places the two subfamilies close to each other. These analyses thus show that these groups are very similar. They do not, however, tell us the taxonomic importance of this, but the results appear consistent with the presence of two, highly related, subfamilies.

The close relationship between Tapejaridae, but with strong outliers, is probably due to the low resolution used to look at the family level, created by the inclusion of a bad (too distant) outgroup family, Ornithocheiridae. The latter are completely different from Tapejaridae and are easily recognized by both analyses but the differences between the different putative subfamilies of Tapejaridae are too small for the RWA to recognize them as different subfamilies. When incorporating a grouping variable it is, however, possible to recognize the different groups. This illustrates the problem with Tapejaridae. They are very similar and different phylogenetic studies give different outcomes, some regarding Tapejaridae as one family, while considering Thalassodromidae as another, unrelated family (figure 2.4). Other studies consider them as two subfamilies: Tapejarinae and Thalassodrominae. This first analysis (RWA) appears to confirm the close relationship of Thalassodrominae and Tapejarinae and suggest that they may be closely related subfamilies, with similar shapes, as the outgroup, Ornithocheiridae is easily separated from the others. Further in this thesis we will try to increase the resolution by separating Tapejaridae and Ornithocheiridae. Although this would emphasize the differences between the two subfamilies of Tapejaridae, it also decreases the sample size.

Principal component (PC) 1 and 2 of figure 4.3 mainly consist of differences of the height of the skull above the orbit, nasoantorbital fenestra and premaxilla, and the length of the frontoparietal crest (figure 4.4). This is expected, as most characters used in the taxonomy of Tapejaridae are based on the shape and presence of a frontoparietal or premaxillary crest, and the shape of the rostrum as this is hooked in Tapejarinae, straight in Thalassodrominae and crested in Ornithocheiridae (figure A.8–A.11).

On the family scale geometric morphometrics appear helpful, especially in distant related families. The inclusion of an outgroup (Ornithocheiridae) that is not closely related reduces the resolution for closely related (sub)families. The strong separating power of the CVA is not unexpected, as the analysis yields an output that clusters families using information (figure 4.4) that is comparable with the information visible to paleontologist and these gave the same difficulties concerning Tapejaridae.

5.1.2 Taxonomy of Ornithocheiridae

Linear metrics are conventionally used to compare specimens. Using different measurements and plotting these measurements Nopcsa-curves are created. These Nopcsa curves were used by Bennett (2006, 2013) to distinguish several species of highly related *Pterodactylus* species by looking at the slopes between (and not the exact location of) different points. In this thesis we tried to use the same technique to investigate whether *Brasileodactylus araripensis* and *Ludodactylus sibbicki*, which are highly similar in shape, are conspecific and different from

Anhanguera (figure A.9). Due to the low sample sizes (opposed to Bennett (2006, 2013)) this approach is not very useful in our study (Figure 4.2), although some trends may be visible to the willing eye. *Ludodactylus sibbicki* and *Brasileodactylus araripensis*, for example, appear to follow the same trend. At some measurements clustering appears size related (e.g. length until naof). To increase the resolution two additional transformations were applied. A first one divided the measurement by the length of the skull in order to standardize it. Next, the logarithms of these standardized measurements were used, but the different Ornithocheiridae appear to be so similar that they are indistinguishable when using this low sample size. Future research may be aimed at comparing several *Ludodactylus* species, identifying a putative species specific pattern, and then compare this pattern to that of *Brasileodactylus araripensis*. If they would be similar, this common pattern could be compared to an *Anhanguera* specific pattern (if present), to find out whether their slope differ. If this would be the case this might indicate that *Brasileodactylus araripensis* and *Ludodactylus sibbicki* are highly related and differ significantly from *Anhanguera*. This is, however, not possible at this moment, and a different, more accurate, method was necessary.

Instead of using only linear measurements the dataset was now transformed in a new dataset that included information about shape, which is basically a dataset that contains all possible linear measurements. Although currently most paleontological phylogenies are based on morphological characters, e.g., the presence of structure 'X', it may be useful to use shape in lower levels of taxonomy. This is common practice in the taxonomy (of non-extinct taxa) at the species level, e.g., in birds where the curvature of a beak may be species specific. The largest drawback may be convergent evolution, but this is present in phylogenetic characters as well and no example in which two sympatric species look the same due to convergent evolution could be found in this thesis. Even species that appear almost the same, can always be distinguished. The dataset of all Brazilian pterosaurs were analyzed twice, one to explore the variation between individuals and another to explore the variation between groups. Figure 4.6, which considers variation between individuals, illustrates that the first three principal component, representing 75% of the total variation, creates two clusters, one including pterosaurs from the Crato Formation, *Ludodactylus sibbicki* and *Brasileodactylus araripensis*, and another with Brazilian pterosaurs from the Santana Formation. *Guidraco venator* and *Tropeognathus mesembrinus* form two out-groups. The significance of these clusters cannot be statistically verified due to low sample size. The equal frequency ellipses, which show where 90/95% (depending on the analysis) of the specimens would be expected, do confirm these clusters for the first two principal components (figure 4.6(A)). Such equal frequency ellipses have been used previously to separate nematode populations (Rau & Fassuliotis, 1970). The first cluster includes *Ludodactylus*–*Brasileodactylus* while the second cluster consists of the Anhangueridae. *Coloborhynchus spielbergi* falls in the *Anhanguera* cluster, which is not to suprising as both Veldmeijer (2003, 2006) and Rodrigues & Kellner (2008) consider the two congeneric. In a separate analysis *Coloborhynchus spielbergi* was considered as *Anhanguera spielbergi*. The equal frequency ellipse (the dotted line in figure 4.6(A)) narrowed and *Anhanguera piscator* is not included in the *Anhanguera* cluster but positioned somewhere in between the *Anhanguera* and the *Brasileodactylus* cluster. This

may appear strange, as *Anhanguera piscator* is definitely an *Anhanguera*, while the position of *Coloborhynchus* is still disputed. This may be explained by the fact that *Anhanguera piscator* is still a juvenile, which grew allometrically and thus may have had a skull that was not just a smaller version of an adult, but a smaller version with different proportions and thus a different shape compared with the adult skull. Finally, figure 4.11 also shows that *Anhanguera santanae* is different from *Brasileodactylus araripensis*, falsifying the hypothesis by Maisey (1991).

The fact that *Ludodactylus sibbicki* and *Brasileodactylus araripensis* are so closely located to each other suggest that they are highly related and probably congeneric or even conspecific as suggested before (Unwin & Martill, 2007), especially when compared to the inter-generic distance of *Anhanguera*. It is remarkable that the inter-individual variation between the two *Ludodactylus sibbicki* specimens is larger than the inter-individual variation between *Brasileodactylus araripensis* and the two *Ludodactylus sibbicki* specimens. Based on shape alone, the classical notion that *Guidraco venator* is the closest relative of *Ludodactylus sibbicki* does not seem likely. If this would be the case there should have been a lot of convergent evolution in shape (except for the crest) in *Ludodactylus sibbicki* and *Brasileodactylus araripensis* to explain their clustering, and this is just not likely as no example in present vertebrates is known. Even species that look almost identical (e.g. different species of tits) can be separated based on their skull morphology. It is our opinion that the suggestion of Unwin & Martill (2007) that *Ludodactylus sibbicki* and *Brasileodactylus araripensis* belong to the same species because of similar shape, is the most parsimonious solution.

Changes in shape associated with changes along the different principal component axes are mostly concerning the frontoparietal crest, the premaxillary crest and the general height of the skull. These are the same characters used by paleontologists in Ornithocheiridae taxonomy. This is interesting as paleontologists are inherently more subjective compared to a mathematical method as is geometric morphometrics and the latter may thus be a good addition to conventional taxonomy. It is also interesting that the crest present in *Ludodactylus sibbicki* does not interfere with the RWA. *Ludodactylus sibbicki* and the crestless *Brasileodactylus araripensis* appear rather similar in shape and are placed close to each other, despite of the fact that at least two landmarks, landmarks 17 and 18, are directly influenced by the crest. In fact, the higher cranium needed in *Ludodactylus sibbicki* to form a base for the crest is present in *Brasileodactylus araripensis*. Traditionally the crest has been used as a phylogenetic character. More and more studies argue against the use of the crest in phylogenetic analyses (Bennett, 1992; Martill & Naish, 2006). The results of the geometric morphometric studies in this thesis confirm this. This idea has been further elaborated by removing all crest related characters in the phylogeny by Andres & Myers (2013). This produced the same phylogeny as seen in figure 2.4, so no new phylogeny is shown. This crest was the only clear difference between *Ludodactylus sibbicki* and *Brasileodactylus araripensis* described by Frey *et al.* (2003a) (apart from a slightly more inflated mandibula, which Unwin & Martill (2007) suggest to be a taphonomic artifact). The lack of phylogenetic significance of the crest is again an indication that this may be only one species. Note, however, that only cranial characters are useable and the number of cranial characters are limited in the phylogenetic dataset. Further phylogenetic research could resolve this. Veldmeijer

(2006), suggested the use of characters concerning teeth. These are still not used in pterosaur phylogenies.

Other indications that this is yet another case of sexual dimorphism in pterosaurs, are found in the observation that *Ludodactylus sibbicki*, the proposed male, is larger than *Brasileodactylus araripensis*. The only counter intuitive feature is that the new *Ludodactylus sibbicki* specimen is smaller than the other two specimens. But as it also has a lower principal component 1 and 2 value with respect to the other specimens, it is possible that this specimen was a sub-adult, or just a smaller male. In this thesis, however, we lack the anatomical experience to confirm this using the morphology of the specimen. As the sample size is low no inter-sex ranges of size can be calculated neither.

The canonical variate analysis (figure 4.8) does not confirm the relationships that appear in figure 4.6. It should be kept in mind, however, that the low sample size (with almost no replicate) highly influences this, and any other, statistical analysis (Albrecht, 1992). Apart from this analysis, the geometric morphometric analysis does seem to be a robust way of doing taxonomy, considering that it does the same thing a paleontologist would do—looking at the fossil—but in a most objective way possible. Most results do converge with the taxonomies previously suggested. Regarding the CVA, a higher sample size would be especially interesting and could solve this conundrum.

5.1.3 Taxonomy of Tapejaridae

In this section only the toothless Brazilian pterosaurs were analyzed. First the results will be interpreted in function of a family or sub-family scale before moving on to the genus or species level. As the taxonomy is confusing it is suggested to use the table at the front of the thesis with the different taxonomic names.

Making a statement about the status of Thalassodrominae and Tapejarinae is difficult as we have no decent outgroup. As explained in the literature review, Thalassodrominae are considered to be a subfamily of Tapejaridae by some (Aires *et al.*, 2014; Kellner, 2007; Pinheiro *et al.*, 2011) while considered more closely related to the Azhdarchidae by others (Andres & Meyers, 2013; Headen & Campos, 2014; Martill & Naish, 2013). Both sub-families appear closely related (as in figure 4.3), with *Thalassodromeus sethi* differing a lot from both the other Thalassodrominae and Tapejarinae. It is unlikely that *Thalassodromeus sethi* is an ontogenetic stage of *Tupuxuara*, as its centroid size is similar to that of *Tupuxuara leonardii*. There appears to be a diagonal separation between Tapejarinae and Thalassodrominae in figure 4.12, but the importance of this is not known. This diagonal is present because PC1 is not able to distinguish *Tupandactylus* from *Tupuxuara*, while PC2 can. The result is that both species are separated by a diagonal. The sample size is too low to make a canonical variance analysis and thus no conclusions about the grouping can be made. Although the number of specimens used is the same as in the Ornithocheiridae dataset, in this dataset more subgroups were present. Furthermore, the status of *Tupandactylus* and Thalassodrominae are uncertain as is the relationship of *Tapejara* with

the other Tapejarinae. It is thus not clear how many groups would have to be used, and even if multiple groups would be used, most groups would contain only one member.

More samples and a good outgroup could clarify the affinities of Thalassodrominae. Good outgroups would be Azhdarchidae, which belong to the Neoazhdarchia, and Chaoyangopterinae, which belong to Tapejaridae (figure 2.4). Azhdarchidae skulls are rare and fragmentary (*Zhejiangopterus* has a fairly complete reconstruction, but it is not known what is constructed and what is not). The position of the Chaoyangopterinae is debated and complete skulls are rare as well. If these outgroups were added there would be two possible outcomes: a first in which Thalassodrominae are more closely related to Azhdarchidae and thus should be called Thalassodromidae, and a second case in which Thalassodrominae would be closer related to Tapejarinae and Chaoyangopterinae and would thus belong to Tapejaridae as Thalassodrominae.

Figure 4.12 further shows that geometric morphometrics are relatively stable up to the level of the genus. *Tupuxuara leonardii* and *Tupuxuara deliradamus* are placed together, as are both *Tupandactylus navigans* specimens. The distance between the two *Tupandactylus navigans* specimens is smaller than the distance between the two *Tupuxuara* species, reflecting their conspecific rather than just congeneric nature.

Within Tapejarinae the names of several species have been shifted considerably. Some of these deviations from the original description can be confirmed with the shape analysis. *Tupandactylus imperator* and *Tupandactylus navigans*, for example, were considered to belong to the genus *Tapejara* (Frey, 2003b; Kellner, 2004). Based on shape this classification of *Tupandactylus* as a member of the genus *Tapejara* appears to be incorrect as *Tapejara* is not placed near the *Tupandactylus* specimens.

Tupandactylus imperator is, however, not placed together with both *Tupandactylus navigans* specimens either. This is not unexpected as PC1 contains information about the posterior extension, which is large and rod-like in *Tupandactylus imperator*, while absent in *Tupandactylus navigans* (figure 4.13 and figure A.4). Kellner & Campos (2007) did not consider *Tupandactylus navigans* as part of their newly erected genus *Tupandactylus*, which is reflected here. In the original description of the genus, Kellner & Campos (2007) questioned whether or not *Tapejara navigans* should be included or not. Unwin & Martill (2007) did, however, include both *Tapejara imperator* and *Tapejara navigans* into their new genus *Ingridia*. Due to nomenclatural priority the name *Tupandactylus* remained, now with both species in it. As geometric morphometrics successfully differentiated *Anhanguera*, *Brasileodactylus* and *Tupuxuara*, the status of the genus *Tupandactylus* may have to be revised. The fact that both phylogenetic and morphological analyses suggest that *Tupandactylus navigans* and *Tupandactylus imperator* differ, implies that both may need their own genus. If *Brasileodactylus araripensis* and *Ludodactylus sibbicki*, which are placed together by the RWA, and which differ only in the presence or absence of a crest, it is even more likely that *Tupandactylus imperator* is separated from *Tupandactylus navigans* as they differ both in crest shape and the presence of a posterior extension. As *Ingridia* is still used by some authors to designate *Tupandactylus*, it may be interesting to use *Ingridia navigans* if further research confirms that this is indeed another genus.

Further phylogenetic research would be interesting as most phylogenetic analyses use only a limited set of cranial characters. Searching for more cranial characters, which appear to differ considerably between species, could improve the phylogeny. Shape is often considered a bad phylogenetic parameter as it is highly plastic, and convergent evolution due to similar ecological restraints often occurs. In the case of Tapejaridae, however, it can be useful in phylogenetic research. As previous phylogenetic analyses contradict each other (Kellner, 2004, 2007; Martill & Naish, 2006; Pinheiro *et al.*, 2011), conventional phylogenetic characters appear to be insufficient to give one consensus solution. Combining both phylogenetic and morphometric information could thus provide the solution.

5.2 Ontogeny or evolution in the crests of Ornithocheiridae?

Apart from the clustering, another, linear, trend is visible in the Brazilian Ornithocheiridae starting from *Ludodactylus sibbicki* up to *Tropeognathus mesembrinus* (figure 4.6). When considering only the first principal component this trend extends to *Guidraco venator*, and appears to be time related; however, as species near the outer extreme of PC1 are smaller species, could be size related as well. To test if there was a relationship with either one of these parameters, two types of bivariate regressions were made. A first one of centroid size versus the first two principal components and a second one of age versus the first two principal components — each principal component was considered separately.

5.2.1 Changes of crest size may be a consequence of ontogeny

Changes in size of several structures often can be explained by ontogeny, the development of an organism. In this thesis size was used as a parameter for growth stage as done by Maiorino *et al.* (2013). Figure 4.9 shows that there is no linear relation between the scores of PC1 or 2 and centroid size. Furthermore, even when taking in consideration that not all growth is linear, a polynomial fit of the second and third order was also not significant. As ontogeny is size related, it is not likely that the sequence visible is an ontogenetic sequence. There are, however, two outliers: *Anhanguera piscator* which is known to be an extremely large sub-adult or juvenile (Kellner & Tomida, 2000) and *Coloborhynchus spielbergi* which could be an older animal (Veldmeijer, 2006). To correct for these outliers centroid size would then better be replaced by ontogenetic stage to correct for the fact that *Anhanguera piscator* is a larger species; *Anhanguera piscator* would be placed together with *Brasileodactylus araripensis* and *Ludodactylus sibbicki* as their score with respect to PC1 is similar. If this sequence is interpreted as an ontogenetic sequence, *Brasileodactylus araripensis* and *Ludodactylus sibbicki* should be juveniles (suggested by Unwin, 2001 but later retracted) of an *Anhanguera* species, smaller than *Anhanguera piscator*. On the other side of the growth spectrum, this would imply that the crest would reach an optimal size in the adult members but would not increase in size when growing older, as *Coloborhynchus spielbergi* has a similar score with respect to PC1 value as the other *Anhanguera* species.

This all seems logical but there are several observations that do not make sense in this

context. As argued before, *Ludodactylus sibbicki* and *Brasileodactylus araripensis* are considered as an example of sexual dimorphism. (Secondary) sexual dimorphism, linked to sexual selection and mating, is not expected in juveniles. Furthermore, this sequence also fails to explain why the premaxillary crest is completely absent in *Ludodactylus sibbicki* and *Brasileodactylus araripensis*, while it is present in *Anhanguera piscator*, albeit in a smaller form. It is thus unlikely that this sequence is a result of size or ontogenetic changes. The lack of clear sutures in all specimens of *Ludodactylus sibbicki* and *Brasileodactylus araripensis* also suggests that these animals were fully grown adults, but in this thesis the author lacks the necessary experience with juvenile specimens to make an absolute statement. Finally, this ontogeny fails to explain the pattern in the regression of PC2 and centroid size. *Anhanguera piscator*, the sub-adult or juvenile, has a similar value as all other *Anhanguera* specimens, which all are of a higher ontogenetic stage. If the change in PC 2 was due to ontogenetic changes, one would expect that *Anhanguera piscator* had lower PC2 scores.

5.2.2 Evolution of crests in Ornithocheiridae

Figure 4.10 reveals that PC1, representing almost 50% of the variation, is, strongly correlated with the age of formation in which the fossil was found (which is assumed to be the age of the fossil), opposed to centroid size. PC2 does not show a linear correlation with age (figure 4.10) but a polynomial regression of the second order could be fitted with a very high R^2 and very low p-values —note, however, that this is influenced in part by *Guidraco venator* and the low sample size in general. The change in shape associated with PC1 is an increase in height of the posterior end of the skull and a decrease in the height of the premaxilla. Interestingly, this means that with time the frontoparietal crest reduced while the premaxillary crest (which is located right at landmark 4) grew larger. The odds that this pattern is random are small considering the low p-values, and the high goodness of fit (also compare for example with figure 4.3, where no pattern is visible). As ontogeny and size are already excluded, one possible explanation is evolution. Two ways of evolution most used to explain exaggerated structures (crests are considered exaggerated) are species recognition (advocated by Padian & Horner, 2011a) and selection, which is divided into natural and sexual selection as extensively discussed in the literature review.

To distinguish between the different hypotheses the proposed methods in both the article of Hone & Faulkes (2014), concerning behavior of extinct organisms in general, and those of Hone & Naish (2013), Hone *et al.* (2012), Knell & Sampson (2011), Knell *et al.* (2013a; 2013b), Padian & Horner (2011a; 2011b; 2013) and Tomkins *et al.* (2010) on sexual selection and species recognition, were used.

Species recognition versus selection

Padian & Horner (2011a) suggested two test to discriminate between selection and species recognition. Knell & Sampson (2011) extended this list by two additional tests. These tests focus on

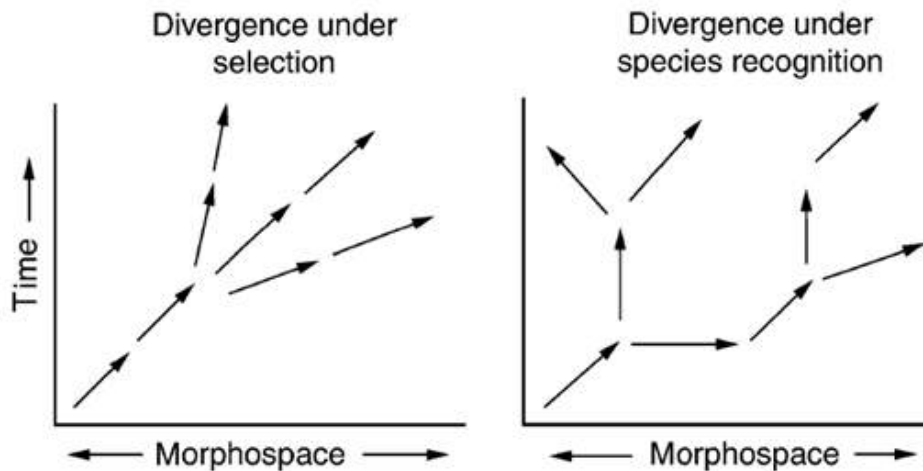


Figure 5.1: Evolution is the change of morphospace throughout time. Padian & Horner (2010) state that there are two possible macroevolutionary patterns of morphology when considering exaggerated structures. A first pattern explains selection, in which a global linear trend would be apparent, while under species recognition the trend would be more random, as the structure has no distinct function. Figure is from Main *et al.* (2005) as referred in Padian & Horner (2008).

the presence of sexual dimorphism.

The first test suggested by Padian & Horner (2011a) states that the overlap in both geological time and geography is typical for species recognition, as the divergent structures enabled several species, inhabiting, the same space to recognize each other. This test is, however, flawed as both species recognition as sexual selection expect overlap of species. If no overlap was present, no selection bias could occur, nor could there be mating. Sexual dimorphism also expects two species to overlap. Although we do not consider this a good test, overlap is present in the *Brasileodactylus araripensis* and the *Anhanguera* cluster. Remind that *Brasileodactylus araripensis* and *Ludodactylus sibbicki* are both known from the Crato Formation, but only *Brasileodactylus araripensis* is also known from the Santana Formation. The absence of *Ludodactylus sibbicki* in the latter formation can be a consequence of chance, as only small numbers of pterosaurs are found. *Brasileodactylus araripensis* thus inhabited the same area, in space and time, as *Anhanguera*, but this is consistent with both theories. Another problem with this test is that most fossils come from fossil traders, without exact stratigraphic information. Furthermore no exact stratigraphic is available in the first place.

The pattern of PC1 versus age, itself is an important observation contra species recognition. The second test of Padian & Horner (2011a; 2013), which are fierce opponents of selection in fossils, states that the pattern visible in morphospace associated with species recognition should be a random pattern. This is not the case. The pattern of morphospace through time (figure 4.10(A)) has a pattern that resembles figure 5.1(A), which is expected in the case of sexual or natural selection. It is not random as there is a clear linear, directional trend. Furthermore, one could argue that the arrows going away from the main arrow in 5.1(A) can be observed as well in the case of *Anhanguera piscator*, which has a higher PC1 score compared to the other *Anhanguera* specimens), and *Tropeognathus mesembrinus*, which has a lower PC1 score. In the

case of the first, a more plausible explanation is that this is an outlier due to it not being fully grown. In the case of the latter more specimens are needed to confirm this.

The third test assumes that the exaggerated structures should show minimal inter-individual variations in species recognition so that detection is possible. This is not testable as almost no referred specimens are available, and if they are present they are broken. One exception is *Anhanguera araripensis*, which shows little inter-individual variation but due to the absence of a scale on the image, no metrics can be used to verify this (Kellner & Tomida, 2000). Furthermore, a scenario of selection in which there would be little inter-individual variation of the exaggerated structure cannot be excluded. In an environment with high natural, or sexual, selection the selection pressure will be so high that the variation will be low as well. It is these cases, in which the inter-individual variation is low, that the real 'good' individuals (or males in the case of conventional sexual selection) would excel.

The final test states that sexual selection comes with a structure with a high cost, this to illustrate that they are fit enough to possess that trait. In these systems dishonest signals do come with a benefit, if able to deceive another. The proposed ornamental traits thus must come with a cost in order to maintain honesty (known as the handicap-principle, Zahavi (1975)). In species recognition both signaler and receiver lose when using dishonest signals. Models show that in these systems low cost signals do evolve (Knell & Sampson, 2011). It is not hard to imagine that crests, as for example in *Ludodactylus sibbicki* (and *Tupandactylus* to expand the topic to all crested pterosaurs), that these come with a cost. Apart from the energy spend in producing and maintaining one, additional muscles are needed to withstand the increased forces that comes with larger surfaces, especially in windy situations during flight. Naturally selected traits can come with a cost, but on the overall they do increase survival and thus have a net benefit on survival. This test suggests that species recognition is not likely as crests probably came with a cost and will be discussed in detail in the following section.

Furthermore, species recognition, in which the different types of crests would be used to recognize members of the same species, can be excluded on an even more basic ethological observation. Although it is not impossible that unknown behavior was present in extinct species but has been lost since, the odds of this are small. The fact that species recognition is considered virtually unknown, especially in vertebrates, thus limits the chances of species recognition explaining the pattern found (Knell & Sampson, 2011; Hone & Faulkes, 2014; Hone & Naish, 2013).

Although two out of four (test 1 and 3) test cannot be used, and appear to be flawed, test 2 and 4 suggest that species recognition is not likely. An additional observation further supports this. As both ontogeny and species recognition fail to completely explain the pattern visible, selection is the most likely evolutionary driver for the pattern visible. In the following section an attempt is made to distinguish between natural and sexual selection. Sexual selection consists of both intrasexual (between animals of the same sex) and intersexual (between animals of different sexes) selection. In the following section sexual selection is considered to be intrasexual selection, as it is unlikely that the crest was used in combat (Hone, *et al.* 2012).

Natural versus sexual selection

Horner & Padian (2011b) see sexual selection as a special case of natural selection, but in this thesis we follow Knell & Sampson (2011) and Knell *et al.* (2013b) and see these two as different evolutionary agents. Distinguishing one from the other is hard as we have no living males that we could observe from a hut while they perform their courtship display in order to attract the duller looking females. There are, however, some observations that could point in one direction and Knell *et al.* (2013a) have suggested that the indications that favor sexual selection are morphological disparity, sexual dimorphism, changes in growth rate during ontogeny, positive allometry and costliness. Furthermore one should try to falsify as much alternative hypotheses as possible. The following section will explore the presence, or absence, of these indications and will end with looking at the alternative hypotheses.

A first observation that, according to Knell *et al.* (2013a), corresponds with sexual selection is the presence of morphological disparity. This is the case because the crest has different positions — posterior (*Ludodactylus sibbicki*), in the middle of the rostrum (*Anhanguera*) and posterior (*Tropeognathus mesembrinus*). In this thesis, however, this is considered a weak test as it cannot completely exclude species recognition. Knell *et al.* (2013a) consider the highly divergent beetle horns and insect genitalia an example of this test. This can also be explained by using species recognition, in which it leads to higher mating success due to better recognition. Morphological disparity may even be a good indicator of species recognition as in species recognition species would benefit more from highly divergent characters, while this does not have to be the case in sexual selection. A second sign of sexual selection is sexual dimorphism. As stated before there are strong indications that *Brasileodactylus araripensis* and *Ludodactylus sibbicki* are one genus, and the high resemblance suggests that they may be one species (although this cannot be proven until more specimens are available). The presence or absence of a crest is then explained as sexual dimorphism, which favors that both frontoparietal and premaxillary crest are sexually selected. This sexual dimorphism is actually known from at least three species of pterosaur (Bennett, 1992; 1995), of which *Pteranodon* is considered the closest relatives of Ornithocheiridae. Using the crest in taxonomy should thus be done with care as stated before by Martill & Naish (2006). The sexual dimorphism present in the hypothetical *Brasileodactylus araripensis* (which is *Brasileodactylus*+*Ludodactylus*) appears absent in the Anhangueridae. Sexual dimorphism in the pelves is suggested by Bennett (1992) but contested by Kellner & Tomida (2000). There are several explanations for the apparent absence of sexual dimorphism. A first hypothesis is that sexual dimorphism is present but still has to be discovered. This is possible as often only two or less specimens are known. The chances of finding two males is as high as finding one male and one female. Another possibility is that females are just misidentified. Several specimens are known from lacking or having only small crests. The holotype of *Anhanguera araripensis*, BSP 1982 I 89, was not used in the original analysis as it lacked the premaxillary crest along with a complete cranium. *Anhanguera blittersdorffi*, n. 40 Pz-DBAV-UERJ, is a crestless specimen that is smaller than the holotype. *Anhanguera santanae* is only known from a crestless specimen and Veldmeijer (2006) suggests that it may have been crestless indeed (figure A.2 (D)).

To test whether these last two specimens with a cranium were crestless females, we made a RWA including these specimens (figure 4.11). If these were indeed two females there are two possible locations where we could expect them in morphospace. A first location, following the low taxonomic value of the crest in *Brasileodactylus araripensis*, expects them to appear nearby their putative male. In the case of sexual selection, *Anhanguera* and *Brasileodactylus araripensis* may have selected for different crests so the pattern may have been different. In the case that male and female would not plot together we would expect the females to plot as an outlier, but still together, as the possible male *Anhanguerae* also plot together. Looking at figure 4.11 it is visible that the two new specimens do not follow any of the expected patterns. *Anhanguera santanae* is an outlier and *Anhanguera blittersdorffi* is located near *Anhanguera piscator*, suggesting that a small (or absent) crest is a juvenile character.

Another mechanism by which sexual dimorphism is present, is that a female is already known: *Anhanguera piscator*. This is, however, not likely. First of all its bone structure suggests that it is a sub-adult (Kellner & Tomida, 2000), which would explain the small crest according to sexual selection or natural selection depending on its relative size (but this will be addressed later on in this section). Secondly it would be strange for a female to be the larger individual. This is only very seldom the case in current species (mostly predatory birds), and is known as sex role reversal. This has been suggested to be present in dinosaurs as well (Isles, 2009). Sex role reversal, however, would assume the female to have the largest crest and this is contradictory with the small crest. The most parsimonious solution is that the crests have indeed broken off and sexual dimorphism is either not discovered or possibly absent in Anhangueridae, which appears to be inconsistent with sexual selection.

The absence of sexual dimorphism does not necessarily exclude the possibility of sexual selection. Sexual selection without sexual dimorphism is possible and can be explained by an evolutionary process called mutual selection (Hone *et al.*, 2012). Somewhere in the evolution between *Brasileodactylus araripensis* and *Anhanguera* a low premaxillary crest may have evolved that was indeed an aerodynamical functional rudder (or another function that increased survival and was thus influenced by natural selection). Both males and females began selecting for this character, as they had a higher fitness, and thus better offspring. This then could have led to runaway selection in which both males and females chose mates that had larger premaxillary crest, and thus higher fitness, every generation until a species like *Tropeognathus mesembrinus* had evolved in which the crest would, hypothetically, be too large to function as a rudder. In even more extreme cases the preliminary crest would not have needed to be functional (for example, when a particular attractive color was present on the crest), but was found attractive by both sexes because it came with a cost and being able to carry a costly trait was a signal of their fitness.

Interestingly, *Anhanguera piscator* lies somewhere between the *Anhanguera* and *Brasileodactylus* clade on the regression. This could imply that the evolution of the premaxillary crest is a heterochrony, more specifically peramorphosis in which the period of growth is extended, of the premaxilla available in *Brasileodactylus araripensis*. The slope of the line between the adult *Anhanguera* specimens and *Anhanguera piscator* is the same as the slope of the line be-

tween the adult *Brasileodactylus araripensis* and the new, smaller *Ludodactylus sibbicki*. This again suggests that it may be a sub-adult specimen, and that this line represents the ontogenetic sequence. More specimens of different ontogenetic stages are interesting regarding this. The fact that sub-adults have a relatively small crest is interesting as this is consistent with two indications for sexual selection: changes in growth rate during ontogeny and positive allometry. Assuming that it would reach a similar size crest, the growth of the crest in the early stages of life up to the sub-adult stage was minimal, but extremely high in the adults.

As seen before, the actual function of the crest is not known yet, but just having them comes with a great cost. The aerodynamic function of a posterior crest of *Pteranodon*, with a crest similar to that of *Ludodactylus sibbicki* has been tested in a windtunnel. These tests showed that the overall aerodynamic effect is modest and suggested functions like airbrake, rudder or counterbalance to the beak are highly unlikely (Elgin *et al.*, 2008). They also concluded that it probably served as an ornamental structure which came with a cost. The premaxillary crest has been suggested to be a rudder as well, but now bringing hydrodynamical stability. Simple tests as in Veldmeijer *et al.* (2006) indicate that these crests improve the effectiveness of skim feeding. However, several assumptions may not be valid. First, the model that was used was a simple mathematical model that does not incorporate any factors of drag created for example by hair. This model predicts that a low angle between the jaw and the water minimizes the sinking of the jaw. Witmer *et al.* (2003), confirmed from the neuroanatomy that during flight the head was indeed kept at an angle with respect to its horizontal body. If a low angle was optimal, the premaxillary crest would never even touch the water, let alone function as a rudder. The model of Veldmeijer *et al.* (2006) thus only explains the use of a mandibular crest, but fails to explain the presence of a premaxillary crest. Different types of premaxillary crests are known. The crest of *Tropeognathus mesembrinus* started at the tip of the premaxilla, while the crest of *Anhanguera* started more posterior. The model of Veldmeijer *et al.* (2006) fails to explain these different types of premaxillary crests. Veldmeijer *et al.* (2006) mentioned this limitation of their model but did not account for it in their model. These rudders would be size depended as larger pterosaurs come with higher instabilities. Nonetheless there is no correlation between centroid size and PC1 score, which is linked to the size of the crest (figure 4.9). This is not consistent with linear growth. Figure 4.9 suggests that the PC1 scores reach a plateau, and older specimens like *Coloborhynchus spielbergi* have a similar value as adult animals. There is thus, a limit to the size of the keel. At a certain point the benefit of the rudder may have been too small to counteract the cost of maintaining the rudder.

An extension of this cost-benefit hypothesis can be tested by using the linear pattern visible in the scores of PC1. By extrapolating along this pattern a new pterosaur, with additional selection, for an ever larger premaxillary crest, could be imagined. It is interesting that evolution beyond *Tropeognathus mesembrinus* leads to the implosion of the the dorsal roof of the skull and brings the nasoantorbital fenestra on the brim of collapsing (figure 5.2). There thus appears to be a trade-off between cranial height and premaxillary height, and the optimal height and location was indeed reached in *Tropeognathus mesembrinus*. If this trade-off really was present, the height of the rudder would reach an optimal size and the growth pattern would reach a

plateau as in figure 4.9.

It is interesting that *Tropeognathus mesembrinus* is the final stadium in the Brazilian Ornithocheirids. Ornithocheirids from about the same time (or younger), but different location, e.g. *Ornithocheirus* from the Cambridge Greensand of England all have a premaxillary crest that, as in *Tropeognathus mesembrinus* starts anteriorly, instead of in the middle of the rostrum as in *Anhanguera*. Complete crania of younger Ornithocheirids could be used in future research to test if the premaxillary crest shape in *Tropeognathus mesembrinus* really was the evolutionary end of the line. If this would be the case, there is a strong indication that Ornithocheiridae evolved in Asia (e.g. *Guidraco venator*), reached Brazil where they evolved into species like *Tropeognathus mesembrinus*, which then dispersed (or even migrated) to Europe.

Finally, recent publications using both modeling (Humphries et al., 2007) and morphological comparison (Witton, 2012; Witton & Naish, 2008; Witton & Naish, 2014) conclude that skim-feeding was highly unlikely in pterosaurs. *Rhynchops*, the skimmer, has over 30 adaptations to its cranium and neck which enable it to skim feed. These are absent in pterosaurs and it would be highly unlikely that one or two rudders would compensate for that many adaptations (Humphries et al., 2007). Mechanical functions other than a rudder are also unlikely. Natural selection expects that the increase of certain structures comes with an increase in survival. Small individuals would thus have small crests, while large specimens would have large crests. *Anhanguera piscator* has almost no crest, although it is the largest Ornithocheirid known. If it had a strictly mechanical function, one would expect that the largest known Anhagueridae, even though it is a sub-adult, would have the largest crest.

The mechanical function of a crest appears to find little assistance from actual evidence. The plateau in figure 4.9 and the trade-off between the size of the crest and the height of the skull, may have been caused by something else. This all can be explained in the light of the sexual selection theory. It may have been that this was the optimal size as an ornament, with a larger crest to be too costly and not beneficial anymore. The pattern visible in figure 4.9 can also be observed in other permanently growing ornament structures like the tusk of narwhals, which is also sexually dimorphic and probably a case of sexually selection (figure A.13). Note, however, that narwhals are mammals, the tusk is a teeth and not a crest and that the curve is a von Bertalanffy curve. The latter is a widespread phenomenon in nature and thus may have low significance after all. It is likely that this pattern would change when more individuals would be added. The possibility that this pattern may change does not have to be a problem as it was tried to explain the pattern that is now visible (but may change in the future by adding specimens) as a consequence of both sexual and natural selection and not used as proof in favor for one or the other hypotheses.

The fact that there is no linear regression between PC2 and age is, at first sight, not consistent with evolution. Further scrutiny, however, offers a possible explanation. No linear regression is visible but a second degree polynomial regression is possible (although with high R^2 , one should keep in mind that the pattern is highly influenced by only point with high leverage, *Guidraco venator*) and this graph should be interpreted with care. PC2 contains even more information

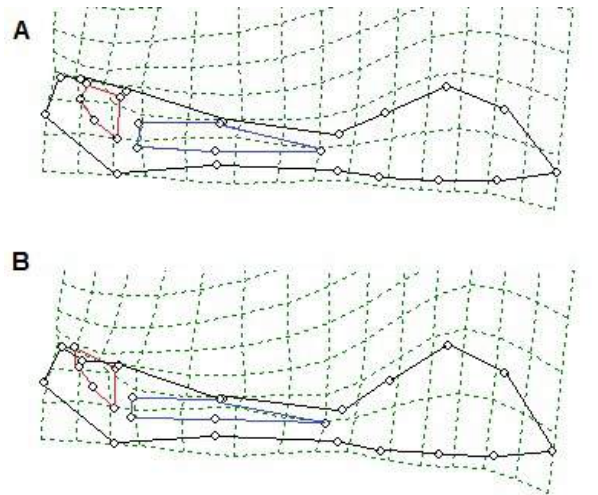


Figure 5.2: Using the pattern visible in the RWA extrapolation was used to create a hypothetical pterosaur (B) that evolved along this pattern, further than *Tropeognathus mesembrinus* (A). It also illustrates that *Tropeognathus mesembrinus* is the most extreme configuration that was possible as the orbit (red) of the hypothetical pterosaur is higher than the skull itself (black). The nasoantorbital fenestra (blue) of the hypothetical pterosaur is only just closed, and even further extrapolation would result in the collapse of this structure as well.

about the two crests compared to PC1. Apart from this, it also contains information about the height of the nasoantorbital fenestra. The dorsal side of this nasoantorbital fenestra consists of the premaxilla, the same bone that is part of the frontoparietal and premaxillary crest. It is thus not strange at all that the nasoantorbital fenestra is lowest in the intermediate variant where less bone is available as it is distributed to crests on both the anterior and the posterior side.

Although not always conclusive, most tests introduced by various authors in the past suggest that the change in crest shape may be driven by sexual selection. The influence of natural selection cannot, however, be excluded as sexual selection often starts with a character that was selected for by natural selection. Sexual selection would then drive the character beyond a point where it increased the direct benefit. This cost would be bearable only by the best individuals.

A possible evolutionary sequence is that females of *Guidraco venator*, as do their close relatives Pteranodontidae, were attracted by well-developed frontoparietal crests. Somewhere in their dispersion to the Araripe Basin they may have experience a shift in ecology that caused a premaxillary crest to become useful (e.g., as a stabilizing rudder when trawling through the water as known from *Ludodactylus sibbicki*). This crest grew larger until the point that it did not increase fitness. Now run-away selection may have favored it and it increased up to the point that no more bone was available and further extensions of the crest would lead to the implosion of the cranial roof. During this process the cost of two different crests probably became too high and the frontoparietal crest reduced somewhere between *Anhanguera* and *Brasileodactylus araripensis*. It is possible that the studs on the posterior side of the skull of all Anhanguerids are the base of a soft-tissue crest as known in other species (Bennett, 2013), or just a remnant of the larger crest in their predecessors. As a side note, it is mentioned that the neuroanatomy of pterosaurs suggests that these animals had highly developed visual systems. This does not

confirm sexual selection, but is needed for its evolution (Schmitz & Motani, 2011).

To conclude, Padian & Horner (2013) remarked that most studies lack the statistical rigor to make any conclusions. We do realise that the small number of fossils that were available did not allow for a detailed statistical analysis in this thesis. We did, however, try to support the possibility of sexual selection as much as possible based on suggestions made by Knell *et al.* (2013a). Furthermore Knell *et al.* (2013b) do point out that sexual selection is so common and so powerful as an evolutionary driving force that rejecting it in extinct organisms because statistical tests are not available, is an incorrect interpretation of the fossil record. Although Padian & Horner (2011b) warn for actualism, in this thesis we follow the statement of Knell *et al.* (2013b) which says that sexual selection is such a elementary selection force in extending organisms, that it must have been a strong evolutionary driver in the past as well. Further studies on the possible mechanical function of the premaxillary crest could solve this enigma for once and for all. One also has to keep in mind that sexual and natural selection are not mutually exclusive, and both can be used to explain the crests of Ornithocheiridae. Geometric morphometrics did not only confirm the relationship between the different *Anhanguera* species, it also suggested a close relationship between *Ludodactylus sibbicki* and *Brasileodactylus araripensis*. Even more surprisingly, it appears that geometric morphometrics could possibly be used in evolutionary research as well. All these results are exploratory and the inclusion of more specimens would increase the resolution. Incorporation of broken specimens, however, clearly reduced the resolution.

5.3 Striations with an unknown function on the crest of *Ludodactylus sibbicki*

Apart from the geometric morphometrics results, another morphological observation supports both the sexual selection and the natural selection theory. The new *Ludodactylus sibbicki* specimens shows striations that are almost parallel to each other, which end in a pit-like structure (figure 5.3). These pit-like structures appear to be lined up and are most apparent on the dorsal side of the skull. They are not likely to be remnants of preparation, but could be remnants of several physiological processes, some of which can be associated with natural selection, while others may have been associated with sexual selection.

5.3.1 Bloodvessels on pterosaur crests

A first possibility is that these striations were blood vessels as known from *Coloborhynchus spielbergi* and *Tropeognathus mesembrinus* (Kellner *et al.* 2013; Veldmeijer, 2006) but blood vessels appear more anastomosing. Kellner & Campos (2002), however, also mention small foramina and consider them as blood vessels or nerves. Hone *et al.* (2011) report vascularity in pterosaur skulls that resembles that of birds in shape and size. Close comparison with bird skulls show that these nutritional foramina are larger than the ones visible in *Ludodactylus sibbicki*.

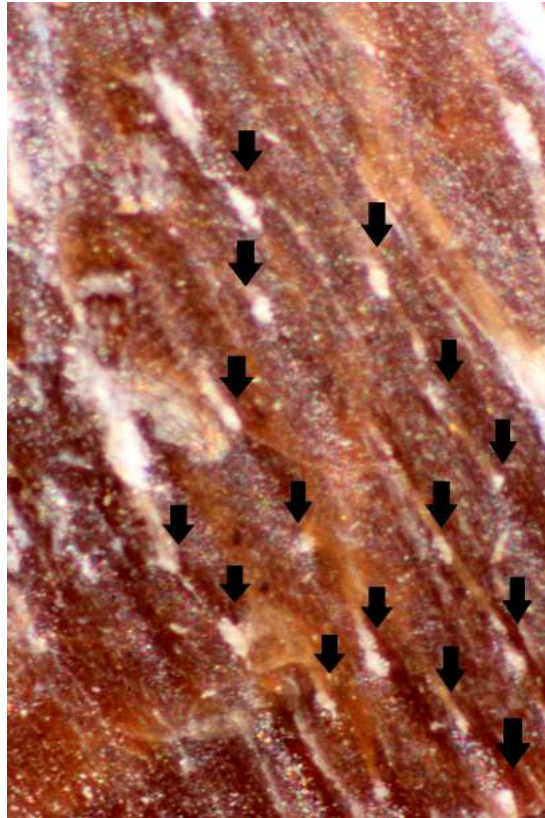


Figure 5.3: Striations followed by pit-like structures (black arrows) on the crest of *Ludodactylus sibbicki*. Scale not available due to the exploratory nature of the photographs.

Comparison with the foramina present in *Baconydraco galaczi* also shows that these were larger than the ones observed in this thesis (Ösi *et al.*, 2005).

Blood vessels are associated with rapid growth, and are known to be more present in juveniles, e.g., the plates of stegosaurs (Main *et al.*, 2005; Hone *et al.*, 2011). Assuming the possibility that the new *Ludodactylus sibbicki* specimen was a sub-adult — it is the smallest specimen so far — would imply that both areas associated with crest formation were associated with rapid growth. This further supports a sexual ornamentation function as characters under the influence of natural selection would have no need to grow exceptionally fast when becoming adult.

Thermoregulation has also been attributed to blood vessels in pterosaur crests (Kellner & Campos, 2002). This is not likely as the wings have a far more larger surface area than any crest, and are thus better at thermoregulation. The small crests, especially the premaxillary crests, would thus have a negligible effect.

Although most recent studies exclude the possibility of skim feeding, these plausible nutritional foramina may be an indication that this did happen. Accidents in *Rhynchops* are relatively common (Zusi, 1996) and to accommodate for this the ramphoteca is highly vascular which enables it to regenerate quickly. This ramphoteca is often associated with pit-like structures (personal observations on the available bird skulls) and may be an alternative explanation for the pit structures. This is, however, not likely as the ramphoteca, if present, was probably limited to the rostrum (and maybe the crest) but was not present on the dorsal roof of the

nasoantorbital fenestra, where these pits can be found as well.

These crest often broke off — it is broken in 1 out of 3 *Anhanguera* specimens! This implicates that it was one of the most fragile parts of the skull. It is not logical that the most fragile part, full of blood vessels (even if the striations are not blood vessels, blood vessels are present in other Anhangueridae), would have a structural function or a function that would be under constant stress like a rudder used in skim-feeding.

5.3.2 Sensory tracks on the pterosaur crest

The pit-like structures also resemble the morphology dentinal tubules of narwhals: a pit followed by a slit. All these slits are oriented in a similar direction. Although these dentinal tubules are in fact dental and of mammal origin, it is the shape of the orifices, and not the surrounding dentin, that is interesting. These orifices are of neural origin and the high resemblance suggests a similar origin and thus function. The dentinal tubules of narwhals are filled with interstitial fluid, and changes to this fluid are detected and processed as different stimuli. Stimuli that are detected include changes in temperature, pressure, percussion and proprioception (Nweeia *et al.*, 2014).

Sensory tracts have also been observed in birds, including Scolopacidae (sandpipers and snipes), Apterygidae (kiwi), and Threskiornithida (ibises, including spoonbills), but here they are mechanoreceptors, used for foraging in different substrates (Cunningham *et al.*, 2013). The morphology of these mechanoreceptors do, however, resemble the apertures visible in *Ludodactylus sibbicki* to a lesser extent.

The higher resemblance with the narwhals may suggest a similar function of the plausible sensory tracks in the cranium of *Ludodactylus sibbicki*. Different receptors have different morphology. This is consistent with the functions of the types two different sensory mechanisms (narwhal teeth versus bird bills). It is highly unlikely that Ornithocheirid pterosaurs dug in earth for their food. Interestingly, at least 3 of the stimuli that narwhal teeth detect in the water could serve a direct function in flight, with the only difference being the medium. Temperature and pressure could be used in thermal soaring or detecting prevailing winds, while proprioception could be used to aid precision flight. Diverse types of sensors could even calculate the speed of flight. The location, and even structure to some extent, resembles that of the pitot tube in airplanes used to measure velocity and flow stream. Furthermore, studies of the cranium of *Anhanguera* show that these pterosaurs had a exceptionally developed flocculi (Witmer *et al.*, 2003). This organ is used in present birds and mammals for proprioception (Witmer *et al.*, 2003). The large amount of possible sensors would imply that large amounts of stimuli must have been processed, which would be the work of the flocculi.

Facial bristles, or hair, as in various birds can be excluded as these are mostly found in the dermis and leave no marks on bones (Cunningham *et al.*, 2011), although reports of pit-like structures associated with hair are known (Wellnhofer, 1975). This source mentions these in one short sentence without further explaining. No images are known either, so comparison is

impossible.

The fact that these slots are concentrated on the frontoparietal crest and premaxilla (the location where the crest will evolve) of *Ludodactylus sibbicki* may indicate that the evolution of the crest may have been triggered by the function of these slits. In this case the evolutionary driver would be natural selection. Sexual selection can, however, as in the narwhals not be excluded. If the pits were sensors, they may have been used to track females that excreted pheromones, but this is unlikely as the vomeronasal organ which is used to detect pheromones is absent in birds and probably pterosaurs (although present in reptiles) (Witton, 2009). If these were blood vessels they may have fed a fast growing structure associated with ornamentation. As before too little is known to conclude anything. Further research could focus on the search for these structures on other Anhangueridae, and further comparison with known structures. It is expected that a sensory function is highly likely.

5.4 Ontogeny in *Tupuxuara deliradamus*

As mentioned in the description, the new *T. deliradamus* specimen was only 30 % the size of an adult specimen. Assuming that growth was analogue in *Pterodaustro* and *Tupuxuara* (a dangerous assumption, but illustrative nonetheless) it was calculated that this was an individual that was still in its rapid juvenile growth and was approximately one year old (figure A.5). Further histological research, if the bones permit it, could give a more precise estimate of the age but this is beyond the scope of this thesis, which is purely morphological. Besides the size of the animal, other observations support the juvenile hypothesis.

The absence of swollen lacrimal regions (figure A.3) is known from one other, probably juvenile, specimen of *Tupuxuara* (Witton, 2009). In modern archosaurs the lacrimal is associated with the nasal gland which is used in potassium or sodium regulation. This inflation of the lacrimal may thus indicate that larger *Tupuxuarae* needed more osmoregulation (Witton, 2009). The paleoecological reconstructions of pterosaurs, including *Tupuxuara*, often places them in a marine setting. Modern oceanic birds like the Procellariiformes have special adaptations to this salt water environment, for example the tubes near the nose to excrete salt. If pterosaurs did hover the oceans they must have had similar adaptations. The tubes present in modern Procellariiformes are, however, not present in pterosaur skulls, but maybe this swollen lacrimal may have had a similar function. The absence of swollen lacrimals in juveniles may indicate that they grew up in another environment, less saline compared to the adult environment. There seems to be a preservational filter in pterosaurs found in the Araripe Basin as no pterosaur larger than 1,5m has been found yet, and juveniles are rare. Other smaller animals are found so juveniles must have been rare, or just not present near the Araripe lagoon. This further supports the idea of separation in space of juveniles and adults. A possible explanation for this is that juveniles did not grow up near the lagoon itself. Finally, it should be noted that in modern squamates the lacrimal is also associated with the lacrimal gland and the vomerofactorial function of this gland. No vomerofactorial structures have been found in pterosaurs making this

hypothesis unlikely (Witton, 2009).

The dorsal roof of the cranium, including the premaxillary part of the crest are absent in this specimen (dark grey in figure A.13). The crest was probably extremely thin ($<2\text{mm}$) (Witton, 2009), which made it fragile. If this specimen was a juvenile, not all bones were fused. These non-fused bones break off easily, following sutures. During taphonomy these bones would then move around, get separated and finally lost from the fossil. This appears to be the case in this specimen. Other fossils are also broken, but in this specimen the fracture clearly follows the sutures.

The implications of a juvenile *T. deliradamus* are interesting. The presence of two *Tupuxuara* 'morphs', *T. deliradamus* and *T. leonardii*, with no intermediate variants previously suggest that these two morphs represent separate species. Sexual dimorphism was excluded because of the similar sizes in both skulls — sexual dimorphism almost always comes with size differences. The presence of a juvenile in both morphs, now confirms that these are indeed two species and not two morphs of one species as sexual selection, and thus secondary sexual dimorphism is normally not active in juveniles.

This new, more complete, description of a juvenile tupuxuarid also falsifies the theory provided by Martill & Naish (2006) (figure A.13). They suggested that the tupuxuarids were juvenile *Thalassodromeus*, hereby considering all *Tupuxuara* species as junior synonyms for *Thalassodromeus*. The presence of juvenile–adult couples of *Tupuxuara* proves that this theory is wrong and that *Tupuxuara* is a valid taxon. Further, the ontogenetic sequence suggested in figure A.14 is wrong because this younger specimen has a frontoparietal crest (light grey in figure A.13) similar to that of stage C. Also note that stage B is reconstructed using only the anterior part of a rostrum, which of course cannot be used to reconstruct the length of the frontoparietal crest.

Finally figure 4.1 shows that different bones grew at different rates. This complies with the hypothesis that pterosaurs, as most animals, grew allometrically. The articular region does not increase in size, the height of the nasoantorbital fenestra and the width of the orbit almost triple. The largest increase happens, however, in the length of the nasantorbital fenestra. Martill & Naish (2006) found out that this is closely related with the length of the skull, which in turn is related with the size of the crest. Juvenile *Tupuxuara* thus were short and blunt headed pterosaurs with relatively large eyes and high skulls.

Chapter 6

Conclusions and future research

6.1 Conclusions

New pterosaur material from the Araripe Basin was loaned to the museum. Most specimens consisted of pterosaur crania. These skulls were described and while describing these pterosaurs, it became clear that the taxonomy of these pterosaurs was highly debated ranging from family level up to species level. Traditional phylogenetic techniques gave contradicting results. In this thesis the value of shape in taxonomy was explored using geometric morphometrics.

First it was used for clarifying the taxonomy of two pterosaur families, Tapejaridae and Ornithocheiridae. When the sample size was large, CVA was able to discriminate between at least three subgroups. This confirmed that Tapejarinae and Thalassodrominae are different, but not to which degree. One of the most common hypothesis, that these are related subfamilies, is, however, consistent with this data. In a following test we only used Tapejaridae to investigate to which degree these two subfamilies differed. The sample size was too low to make absolute conclusions, but the fact that the differences were low may suggest that these are closely related.

Within Ornithocheiridae, geometric morphometric studies were used to investigate to which degree *Brasileodactylus araripensis* and *Ludodactylus sibbicki* differ, because visually they appear very similar, with the exception of a crest in the latter. These two species are almost identical in the geometric morphometric analysis, even though at least two landmarks explicitly incorporate information about the presence of a crest. A phylogenetic analysis confirmed that the crest had no phylogenetic value. These observations suggest that these belong to a same genus or species, especially when taking into account that the variance in the several *Anhanguera* species is larger than within this cluster.

The geometric morphometrics also showed a linear pattern of crest size, associated with PC1, through time. Ontogeny was excluded, and a thorough comparison between species recognition and selection, favored the latter. The distinction between natural and sexual selection was more difficult. There were, however, some observations that are more consistent with sexual selection. However, one must keep in mind that natural and sexual selection are often both acting on a certain structure, and these structures probably serve multiple functions.

Two new tapejarid specimens were interesting from a morphological point of view. A first one, *Tupuxuara deliradamus*, appears to be a juvenile, approximately one year old. Juveniles normally do not possess secondary sexual characters. At least two forms of *Tupuxuara* are described and a juvenile of one form was already known. The presence of this new specimen, a juvenile of the other form, thus confirmed that these forms were different species and thus at least two species of *Tupuxuara* were present in the Araripe Basin. A second Tapejaridae specimen, *Tupandactylus imperator*, was described and contained traces of pycnofibers, which resemble hair, but a thorough study is necessary in future.

6.2 Future research

As ornithocheirids were primarily investigated in this thesis, most of the hypotheses are based on this group. A first suggestion is therefore to increase the size of our sample. This would create higher confidence levels and in this case could allow for some statistics. More samples could lead to the discovery of a bimodal distribution in for example the premaxillary crests, which would suggest sexual dimorphism. More samples could also help to confirm the suggested lumping of the clades *Ludodactylus sibbicki* and *Brasileodactylus araripensis* and more samples would also allow for a higher resolution in the Tapejaridae dataset. Studies on different pterosaur groups could be interesting as well. Other pterosaurs like *Pteranodon*, *Pterodactylus* and others are known from numerous specimens, and are supposed to contain different ontogenetic stages and sexes. Comparison of the results of a geometric morphometric analysis may explain the pattern visible in these analyses.

With respect to the sexual selection hypothesis, further biomechanical researches are required. Using a windtunnel and the different Ornithocheiridae the aero- and hydrodynamical features may be tested. An alternative is the use of specific software (e.g., Computational Fluid Dynamics software). This software would allow the researcher to test the aerodynamical and hydrodynamical features of the different types of premaxillary crest. Additional factors like the presence of hair are expected to influence these results and the software can include these various parameters as well. As the best alternative hypothesis is the rudder, these tests are extremely interesting. The search for medullary bone could be interesting as well. Extensive search in dinosaurs has yielded the detection of possible medullary bone in several dinosaurs (Isles, 2009). The presence of medullary bone in pterosaurs would enable future researchers to make a distinction between male and female specimens, hereby improving the interpretation of the results. Finally, higher resolution stratigraphy would increase the accuracy of the analyses regarding time. It is especially interesting as *Tropeognathus mesembrinus* appears to be the end stage of the putative evolutionary sequence. A higher stratigraphic resolution could confirm if this species is indeed the youngest species.

In the new specimen of *Tupandactylus*, two types of pycnofiber are visible, and further use of high resolution microscopes could look if this is a result of taphonomy or if there really are two types of pycnofibers.

... Having shuffled the pieces around for a couple of centuries, the general outlines of the picture of the jigsaw puzzle have at last become visible. The task now is to try to fill in some of the big blank spaces that remain and, wherever possible, to improve the resolution of those bits of the puzzle that we already have. The picture will change: It will get bigger and sharper and more detailed and more complex, and as it does, so our wonder and fascination at the sheer extraordinariness of these animals will surely increase, too.

Yet, for all its glory, a picture is only a picture. Nothing will ever be quite like seeing a real, live, breathing pterosaur. An that's completely imposible, isn't it?

...Probably, but I live in hope.

DAVID M. UNWIN, THE PTEROSAURS FROM DEEP TIME, 2005

Chapter 7

Summary

* In this thesis several new cranial specimens of pterosaurs from the Araripe Basin were described. Several of these specimens belong to taxa that are highly debated. As phylogenetic analyses did not come to a consensus, the use of geometric morphometrics in taxonomy was explored. At the family scale this method appears to provide useful information, but at a lower scale, with fewer samples, it does not. Two clades were studied separately: Ornithocheiridae and Tapejaridae. Within the Ornithocheiridae *Ludodactylus* and *Brasileodactylus* are very similar, suggesting that they could be lumped together in a same genus or maybe even species. The resemblance between the different Tapejarinae and Thalassodrominae is so strong that the RWA cannot separate the two. This suggests a close relationship. The CVA, however, can separate the two. This suggests that the relationship is not as deep as suggested by the RWA. These results are consistent with the idea that these clades are two subfamilies. Apart from taxonomy, the geometric morphometric data was used to explore the evolution of several types of crests throughout time. The possibility of several evolutionary mechanisms, including species recognition, natural selection and sexual selection, were compared. Finally, one of the specimens studied, *Tupuxuara deliradamus*, appeared to be a juvenile specimen. Juveniles normally do not possess secondary sexual characters. Two forms of *Tupuxuara* are known and a juvenile of one form was already known. The presence of this new specimen, a juvenile of the other form, thus confirmed that these forms were different species and thus at least two species of *Tupuxuara* were present in the Araripe Basin.

Chapter 8

Samenvatting

* In deze thesis werden enkele nieuwe crania van pterosaurussen uit het Araripe-bekken beschreven. Veel van deze specimens behoren tot taxa die nog steeds controversieel zijn. Omdat fylogenetische analyses niet tot een consensus leidden, werd voor het eerst het potentieel van geometrische morfometrie in de taxonomie van deze specimens onderzocht. Wanneer grote aantallen specimens beschikbaar zijn, lijkt deze methode goede resultaten op te leveren, maar met een kleiner aantal specimens neemt de bruikbaarheid af. Twee clades, Ornithocheiridae en Tapejaridae, werden apart onderzocht. Binnen Ornithocheiridae tonen de analyses aan dat twee soorten, *Ludodactylus* en *Brasileodactylus*, zo gelijkaardig dat zij mogelijk behoren tot één genus, of zelfs soort. De gelijkenis tussen Tapejarinae en Thalassodrominae is ook groot, wat een nauwe verwantschap suggereert; een CVA toonde nochtans kleine verschillen aan. Dit is consistent met de hypothese dat deze twee subfamilies zijn van Tapejaridae. Naast taxonomie werden de geometrisch-morfometrische data ook gebruikt om de evolutie van verschillende kammen te bestuderen doorheen tijd. De aanwijzingen voor verschillende evolutionaire mechanismen zoals soortherkenning, seksuele selectie en natuurlijke selectie werden vergeleken. Tenslotte werd aangetoond dat een van de bestudeerde specimens, *Tupuxuara deliradamus*, waarschijnlijk een juveniel is. Juvenielen hebben normaal geen secundaire geslachtskenmerken. Twee *Tupuxuara* vormen zijn beschreven en van één van deze vormen is een juveniel gekend. De aanwezigheid van een juveniel van de tweede vorm bevestigt dat er tenminste twee soorten *Tupuxuara* aanwezig waren in het Araripe-bekken.

Chapter 9

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Appendix A

Figures

Front page

The figure on the frontpage is made by paleoartist Luis Rey. At the most left we see *Tropeognathus* just ahead of *Dsungaripterus* with the curved beak. *Tupuxuara* is shown with the rounded crest while *Tundandactylus imperator* is shown on top with the large red and black crest. On the bottom of the figure we see *Caulkicephalus* with teeth and crest (much what *Ludodactylus* would have looked like) and *Nyctosaurus*.

Material and methods



Figure A.1: The new specimen of *Ludodactylus sibbicki* (Crato Formation). Arrows represent replacement teeth. A: Skin impression of fish with tail-fin still present. B-C: Fish skeletons, possibly *Dastilbe*. D: Impression of bug, possibly Coleoptera or Heteroptera. fr: frontal, fpc: frontoparietal crest, j: jugal, l: lacimal, ltf: lower temporal fenestra, mx: maxilla, na: nasal, naof: nasoantorbital fenestra, ob: orbit, par: parietal, pm: premaxilla, pt: pterygoid, qa: quadratojugal, sq: squamosal. Scale is 5 cm.

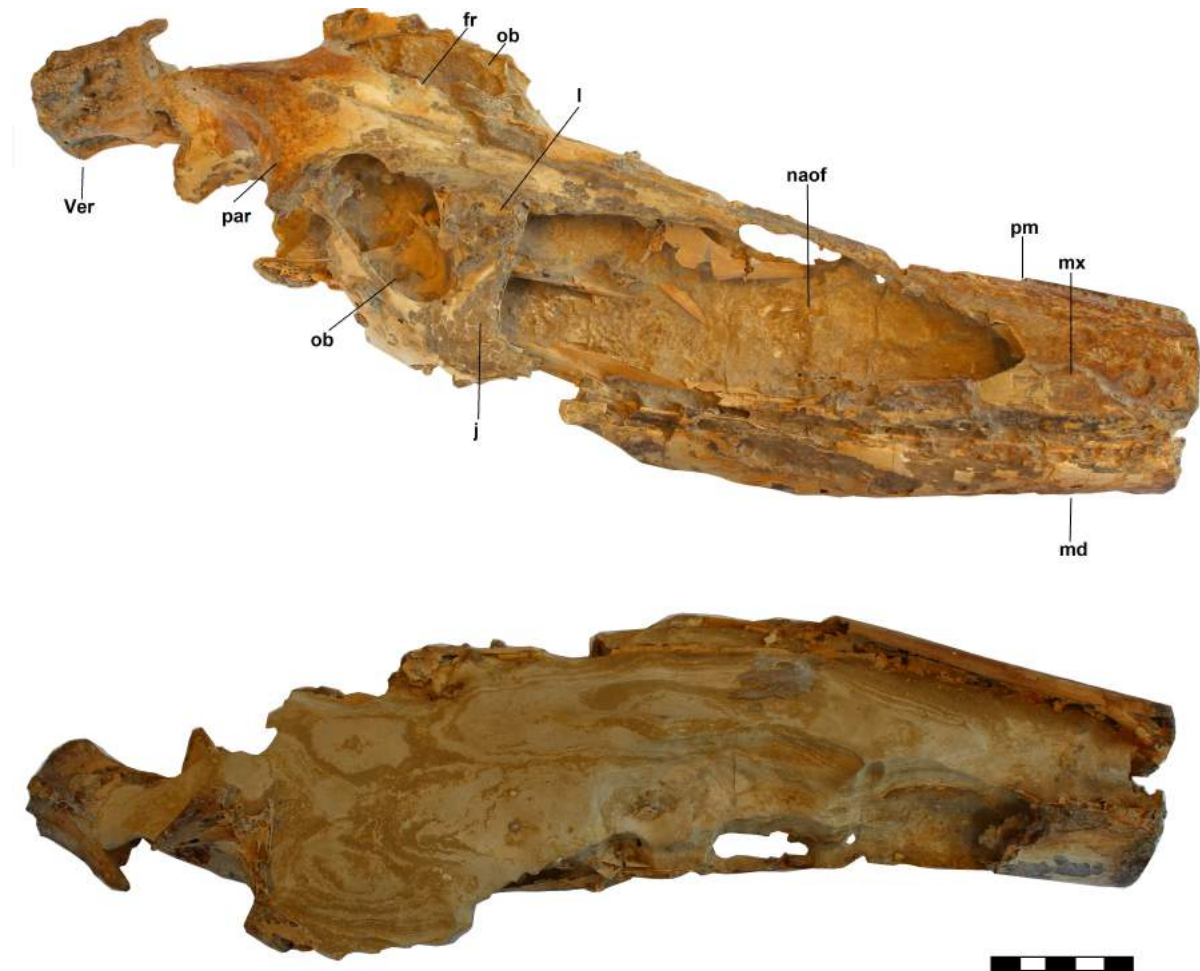


Figure A.2: New cranium specimen of *Coloborhynchus spielbergi* (Santana Formation). The first lateral side (upper figure) and the more eroded second lateral side (lower figure). fr: frontal, j: jugal, l: lacimal, md: mandibulla, mx: maxilla, na: nasal, naof: nasoantorbital fenestra, ob: orbit, par: parietal, pm: premaxilla, ver: vertebra. Scale is 5 cm.

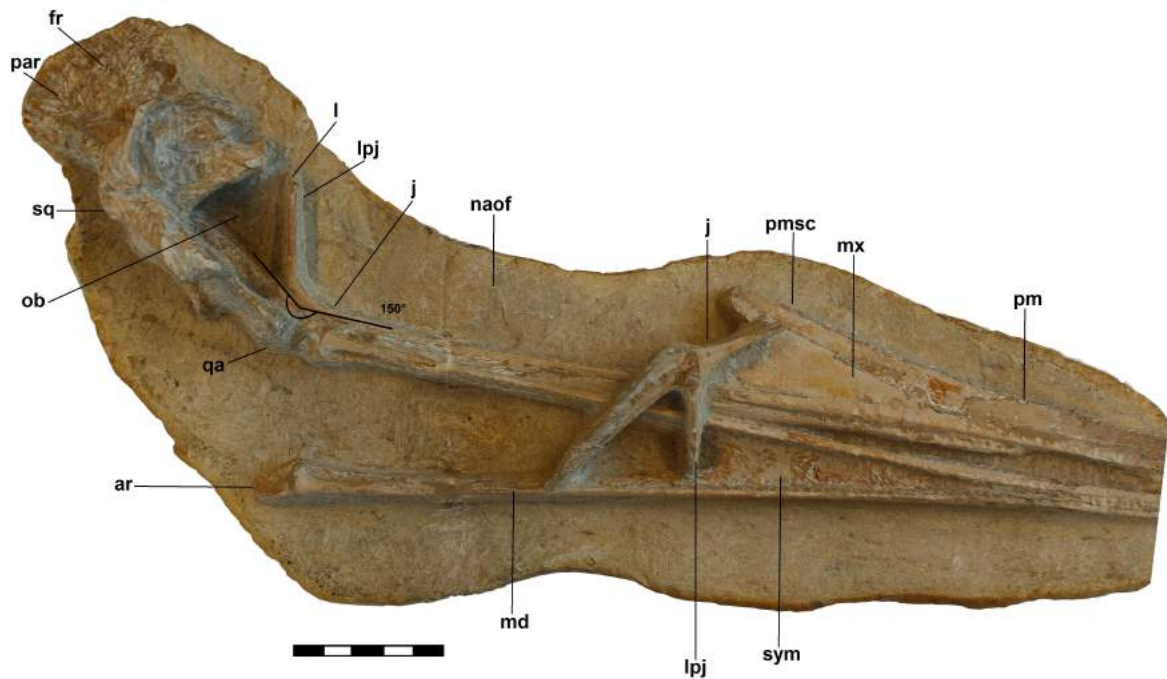


Figure A.3: Cranial region and mandible of a juvenile *Tupuxuara deliradamus* (Santana Formation). ar: articular, fr: frontal, j: jugal, l: lacimal, lpj: lacrimal process of the jugal, mx: maxilla, naof: nasoantorbital fenestra, ob: orbit, par: parietal, pm: premaxilla, pmsc: premaxillary sagittal crest, qa: quadrate, sq: squamosal, sym: symphysis. The angle between jugal and quadrate is of high taxonomic importance. Scale is 5 cm.

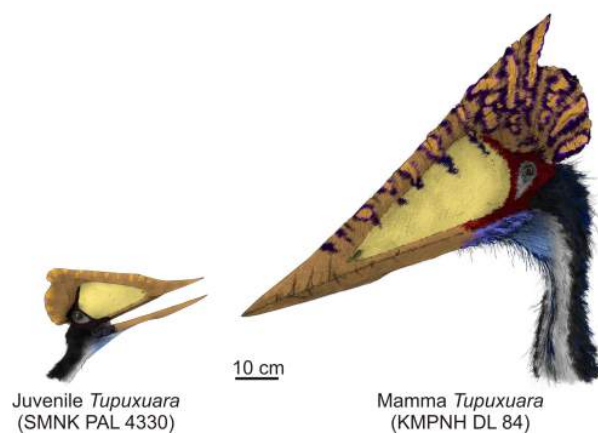


Figure A.4: This reconstruction by Mark Witton shows a juvenile and an adult *Tupuxuara leonardii*. Although another species the specimen described in this thesis would look a lot like the juvenile represented here.

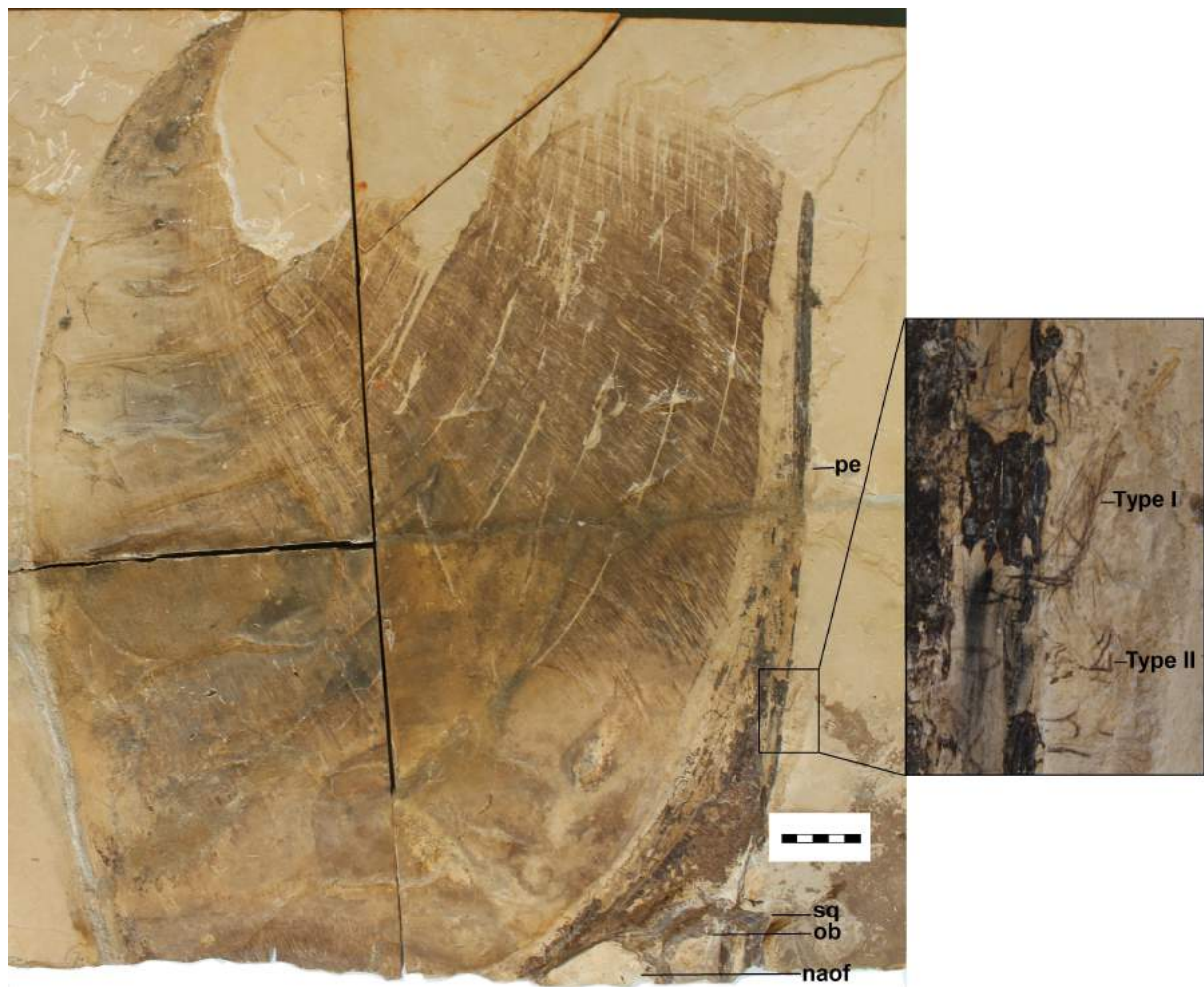


Figure A.5: Crest and posterior region of the cranium of a new *Tupandactylus imperator* specimen (Crato Formation). This is the most complete crest up to date. naof: nasoantorbital fenestra, ob:orbit, pe: posterior extension, sq: squamosal. Scale is 5 cm.

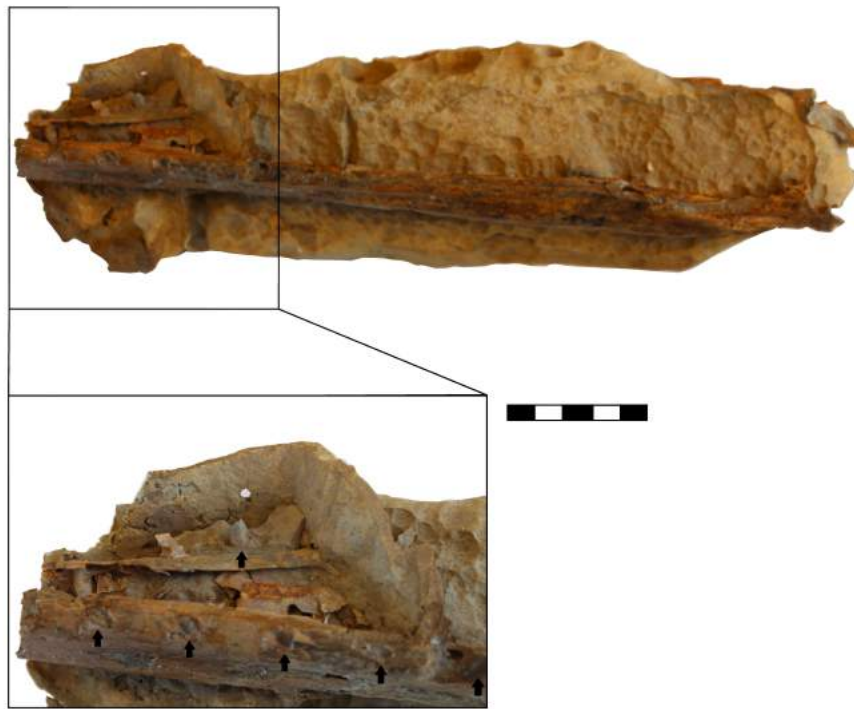


Figure A.6: Mandibula with symphysis of possible new specimen of *Brasileodactylus*. Teeth and alveoli are marked with arrows. Scale is 5 cm.



Figure A.7: Mandibular rami of possible new specimen of *Tropeognathus*. Lateral side (upper figure) and medial side (lower figure). af: adductor fossa, gl: glenoid, ra: retroarticular process, tr: transverse ridge. Scale is 5 cm.

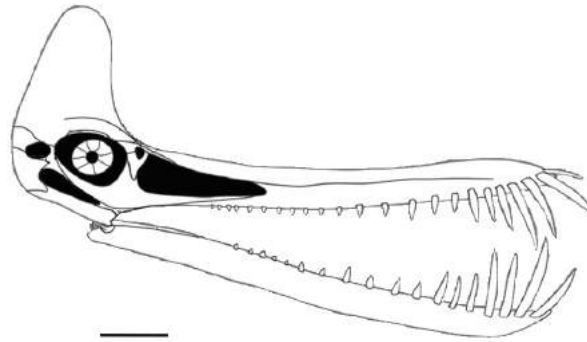


Figure A.8: *Guidraco venator*, holotype (IVPP V17083). Approximately 120 mya old. Scale bar is 50 mm (although Wang *et al.*, 2012, state that it is 5 mm). Drawing from Wang *et al.*, 2012

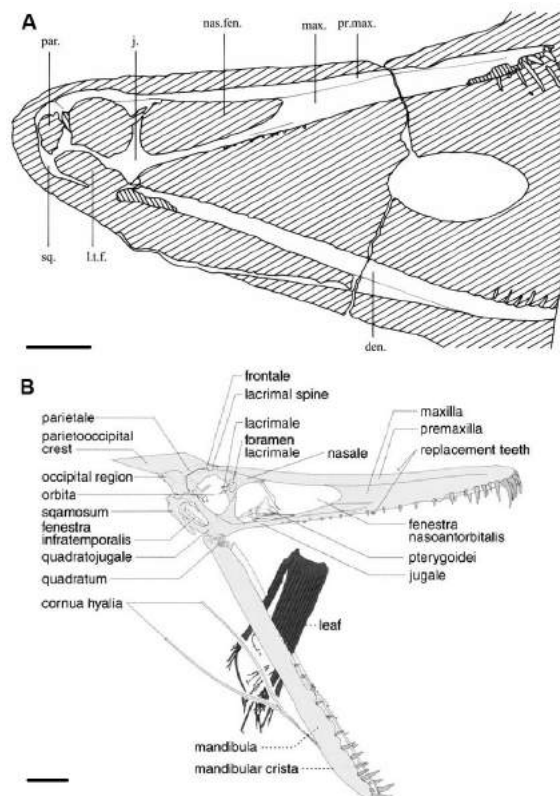


Figure A.9: Pterosaurs from the Crato Formation, approximately 112 mya old. A: *Brasileodactylus araripensis*, the New York specimen (AMNH 2444), drawing from Veldmeijer (2006). B: *Ludodactylus sibbicki*, holotype (SMNK PAL 3828), drawing from Frey *et al.* (2003a). Scale bar in both drawings is 50mm.

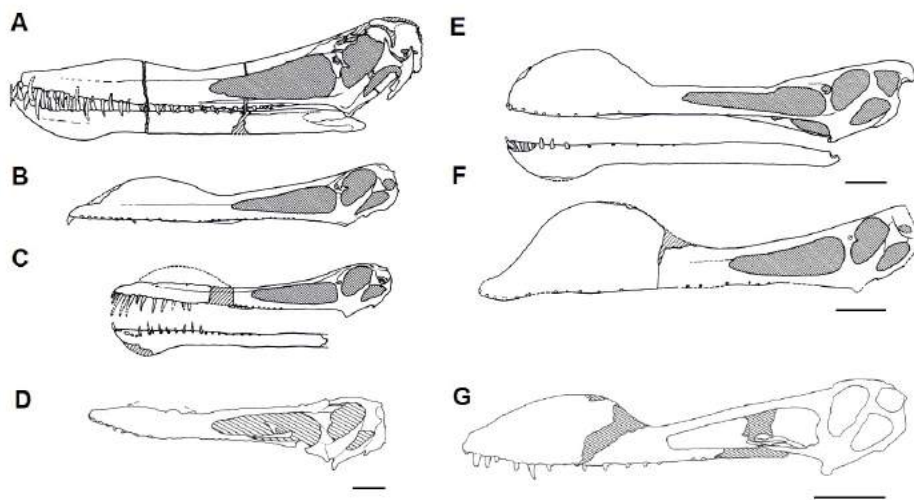


Figure A.10: Pterosaurs from the Santana Formation, approximately 108 mya old. A: *Anhanguera piscator*, holotype (NSM-PV 19892). B: *Anhanguera blittersdorffi*, holotype (CD-R-001), C: *Anhanguera blittersdorffi*, referred specimen (n. 40 Pz-DBAV-UERJ). D: *Anhanguera santanae*, referred specimen (AMMH 22555). E: *Tropeognathus mesembrinus*, holotype (BSP 1987 I 46). F: *Anhanguera araripensis*, referred specimen. (This is MN 4735-V which was not used as the original image was not clear, nor did this reconstruction contain a accurate scale. Instead SAO 16494 was used). G: *Coloborhynchus spielbergi*, holotype (RGM 401 880). Scale bar = 50 mm, except in G: scale bar = 100 mm. A-F from Kellner & Tomida (2000), G from Veldmeijer (2006).

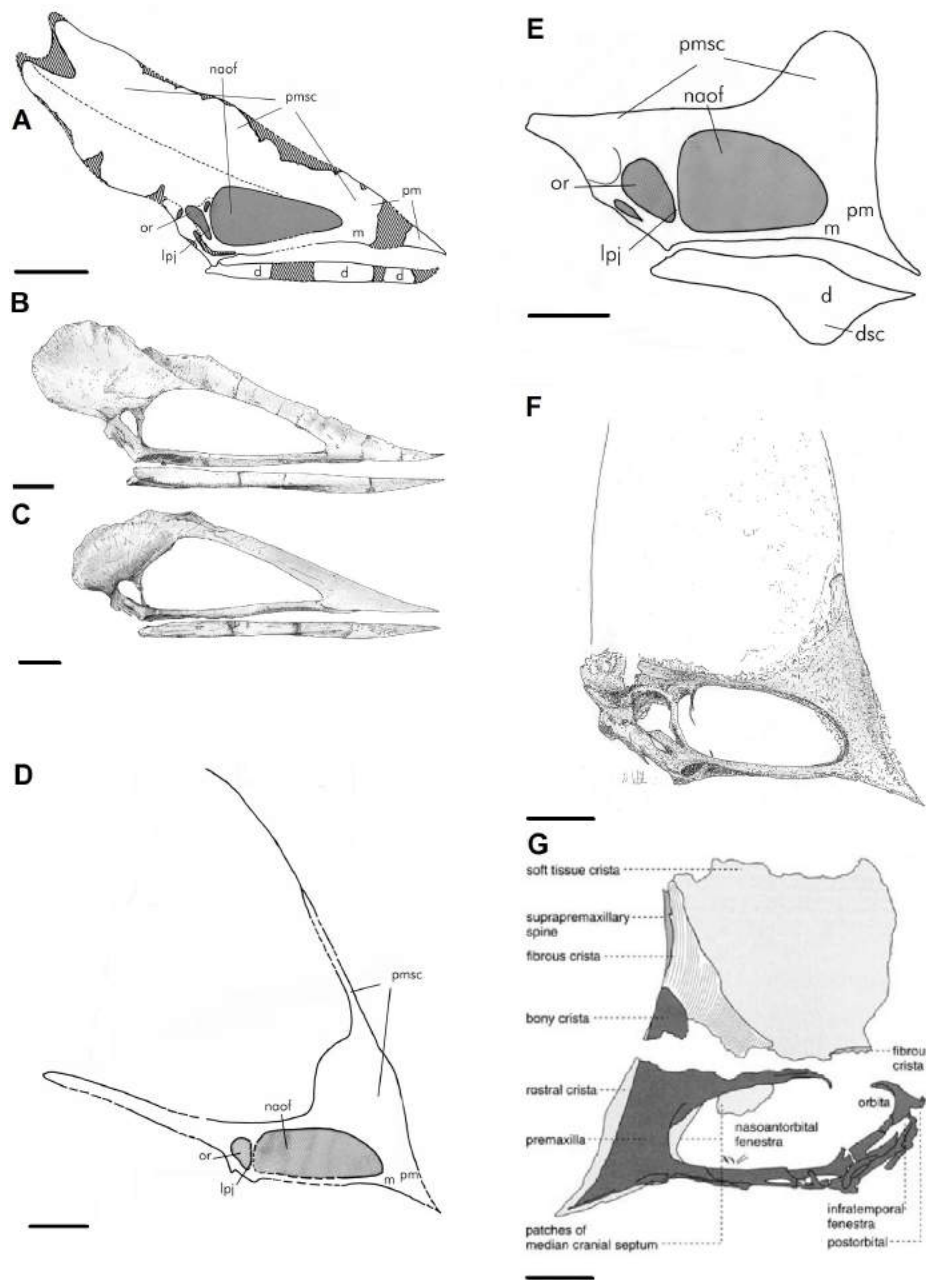


Figure A.11: A: *Thalassodromeus sethi*, holotype (DGM 1476-R). B: *Tupuxuara leonardii*, referred specimen (IMCF 1052). C: *Tupuxuara deliradamus*, referred specimen (KPMNH DL 84). D: *Tupandactylus imperator*, holotype (MCT 1622-R). E: *Tapejara wellnhoferi*, holotype (SMNK PAL 1137). F: *Tupandactylus navigans*, holotype (SMNK PAL 2344). G: *Tupandactylus navigans*, referred specimen (SMNK 2343). All species are from the Santana Formation, except both *Tupandactylus* species and *Thalassodromeus sethi*, which are from the Crato Formation. A: scale bar = 200 mm, B-C: scale bar = 100 mm, D-G: scale bar = 50 mm. A, D, E & G from Kellner (2004), B-C from Witton (2009), D from Witton (2013), F from Frey *et al.* (2003b)

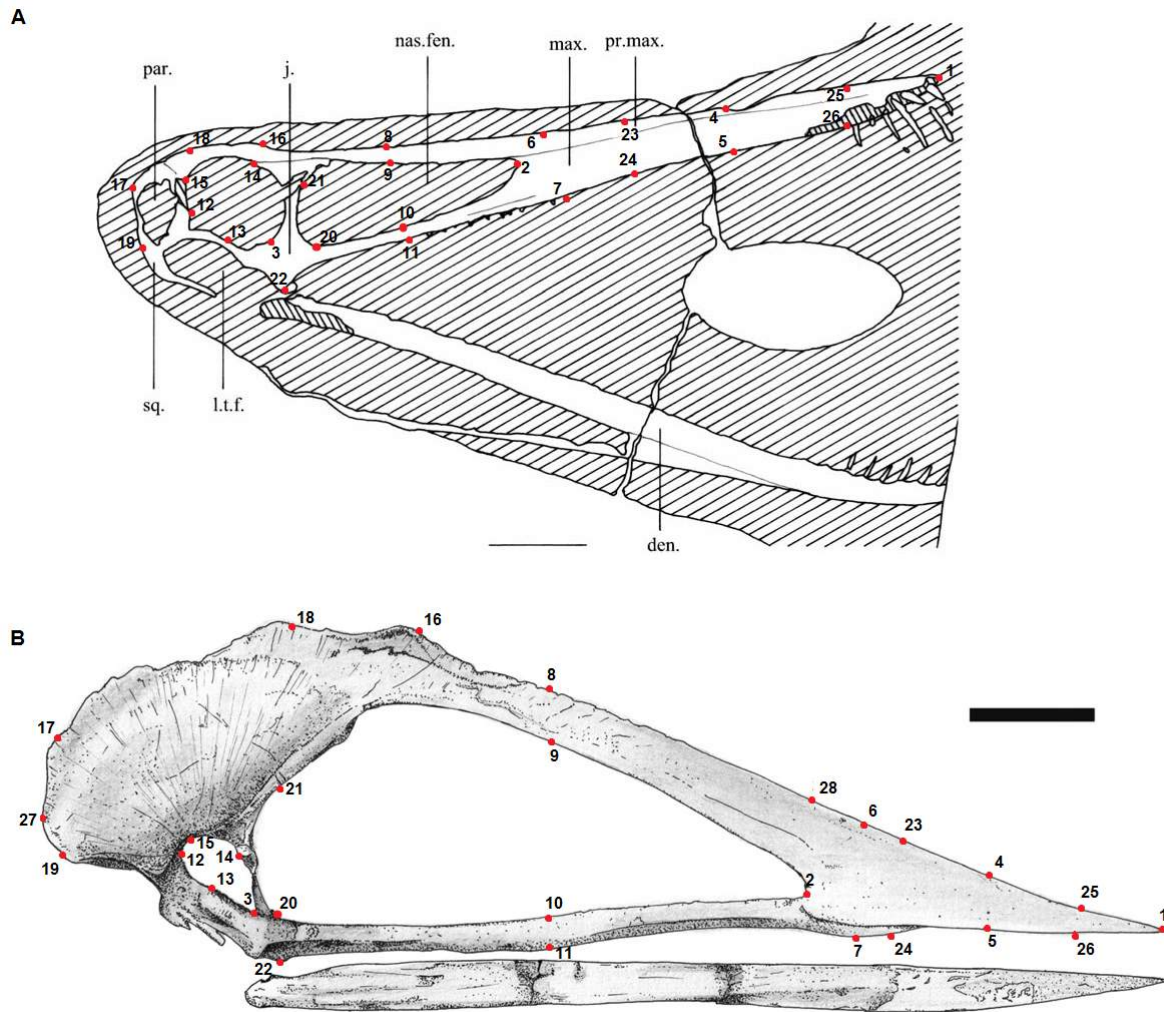


Figure A.12: Pterosaur skulls showing landmarks used in geometric morphometrics. A) *Brasileodactylus sibbicki* with 26 landmarks, B) *Tupuxuara deliradamus* with 28 landmarks. These two extra landmarks contain information about the crest, which is only useful in Tapejaridae (sensu Kellner, 2004).

Discussion

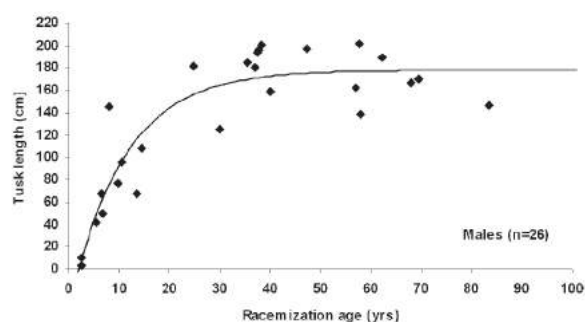


Figure A.13: Growth of tusks in male narwhals. Age estimates were based on the racemization of L-aspartic acid to D-aspartic acid in the nucleus of the eye lens (Garde et al., 2007).

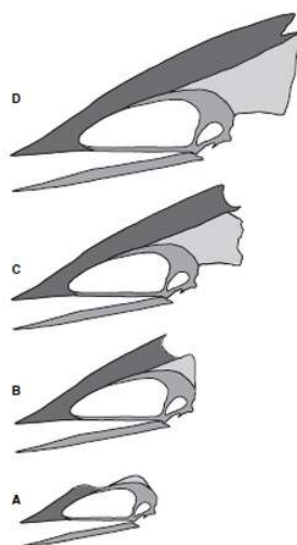


Figure A.14: Hypothetical ontogenetic sequence of the tupuxuarids as suggested by Martill & Naish (2006). A, shows the hypothetical juvenile stage. B, subadult stage corresponding to *Tupuxuara longicristatus*. C, adult stage based on *Tupuxuara leonardii*. D, old adult stage based on *Thalassodromeus sethi*. Dark grey corresponds with the premaxilla, lightest grey is the frontoparietal crest and the intermediate shade of grey corresponds with other cranial bones. Diagrams are not to scale.

Reconstructions

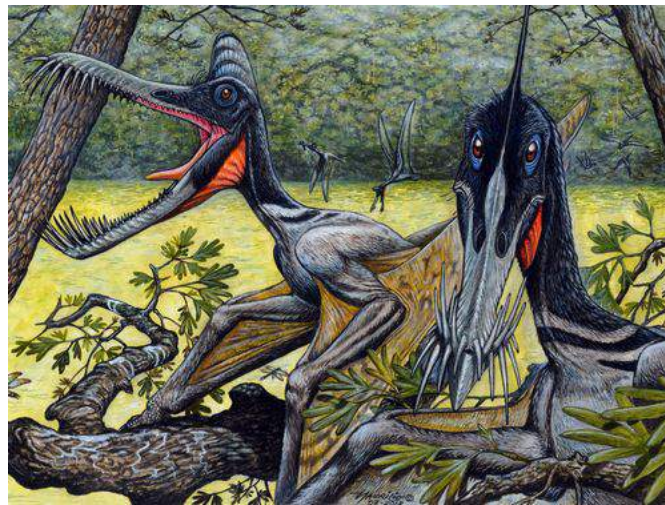


Figure A.15: Reconstruction of *Guidraco venator* (Jiufotang Formation) with a posterior crest. Image by Maurilio Oliveira.



Figure A.16: Reconstruction of *Ludodactylus sibbicki* (Crato Formation) with a posterior crest. No good reconstruction of *Brasileodactylus araripensis* is available, this would be similar but without a crest. Both species lack a premaxillary crest. Image by Sergey Krasovskiy.



Figure A.17: Reconstruction of *Anhanguera piscator* (Santana Formation). Note that the premaxillary crest is not completely at the front of the skull. Image by Mark Witton.



Figure A.18: Reconstruction of *Tropeognathus mesembrinus* (Santana Formation). Note that the premaxillary crest is located in the front of the skull. Image by Mark Witton



Figure A.19: Reconstruction of *Tupuxuara* (Santana Formation). Image by Mark Witton.



Figure A.20: Reconstruction of *Thalassodromeus sethi* (Crato Formation). Image by Mark Witton.

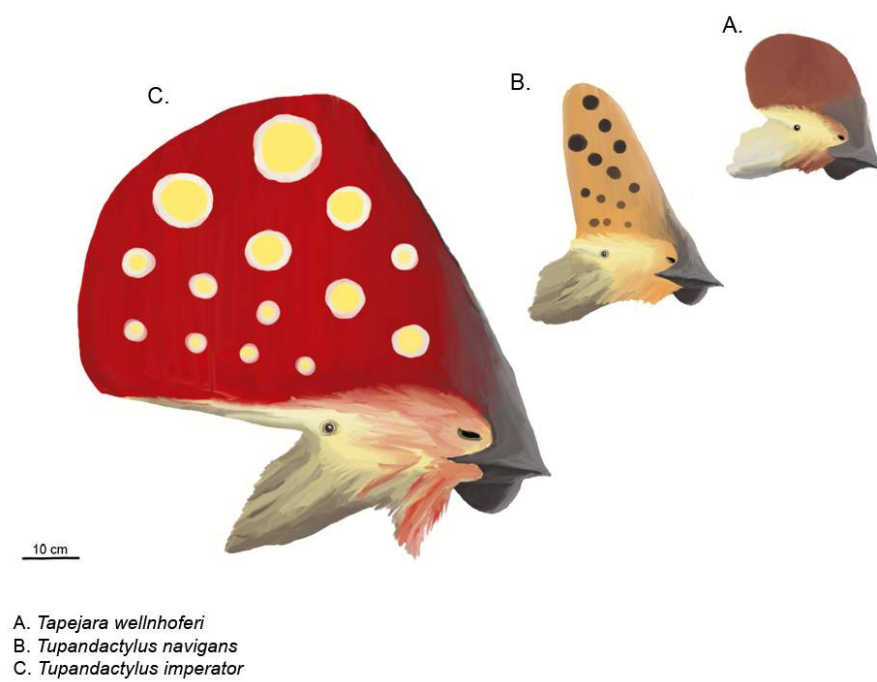


Figure A.21: Reconstruction of the different Tapejarinae. A: *Tapejara wellnhoferi* (Santana Formation), B: *Tupandactylus imperator* (Crato Formation) and C: *Tupandactylus navigans* (Crato Formation). Image by Matt Martyniuk.

Appendix B

Tables

Table B.1: Pterosaurs described from the Santana Formation, Brazil. These are listed alphabetically as there phylogenetic status is highly debated.

Genus	Species	Member	Reference
<i>Anhanguera</i>	<i>araripensis</i>	Romualdo	Wellnhofer, 1985
	<i>blittersdorffi</i>	Romualdo	Campos & Kellner, 1985
	<i>piscator</i>	Romualdo	Kellner & Tomida, 2000
	<i>robustus</i>	Romualdo	Wellnhofer, 1987
	<i>santanae</i>	Romualdo	Wellnhofer, 1985
<i>Araripesaurus</i>	<i>castilhoi</i>	Romualdo	Price, 1971
<i>Araripedactylus</i>	<i>dehmi</i>	Romualdo	Wellnhofer, 1977
<i>Arthurdactylus</i>	<i>conandoylei</i>	Nova Olinda	Frey & Martill, 1994
<i>Azhdarchid</i>	?	Nova Olinda	Martill & Frey, 1999
<i>Barbosania</i>	<i>gracilirostris</i>	Romualdo	Elgin & Frey, 2011
<i>Brasileodactylus</i>	<i>araripensis</i>	Nova Olinda & Romualdo	Kellner, 1984
<i>Caupedactylus</i>	<i>ybaka</i>	Romualdo	Kellner, 2013
<i>Cearadactylus</i>	<i>atrox</i>	Romualdo	Leonardi & Borgomanero, 1985;
	<i>?ligabuei</i>	Romualdo	Vila Nova <i>et al</i> , 2014
<i>Coloborhynchus</i>	<i>spielbergi</i>	Romualdo	Dalla Vecchia, 1993
<i>Lacusovagus</i>	<i>magnificens</i>	Nova Olinda	Veldmeijer, 2003
<i>Ludodactylus</i>	<i>sibbicki</i>	Nova Olinda	Witton, 2008; 2013
<i>Santandactylus</i>	<i>araripensis</i>	Nova Olinda	Frey <i>et al.</i> a, 2003
	<i>brasiliensis</i>	Romualdo	Wellnhofer, 1985
	<i>pricei</i>	Romualdo	de Buissonjé, 1980
	<i>spixi (Tupuxuara?)</i>	Romualdo	Wellnhofer, 1985
<i>Tapejara</i>	<i>wellnhoferi</i>	Romualdo	Wellnhofer, 1985
<i>Tropeognathus</i>	<i>mesembrinus</i>	Romualdo	Kellner, 1989
<i>Tupandactylus</i>	<i>imperator</i>	Nova Olinda	Wellnhofer, 1987
	<i>navigans</i>	Nova Olinda	Campos & Kellner, 1997
<i>Tupuxuara</i>	<i>deliradamus</i>	Nova Olinda	Frey <i>et al.</i> b, 2003
	<i>leonardii</i>	Romualdo	Witton, 2009
	<i>longicristatus</i>	Romualdo	Kellner & Campos, 1994
<i>Thalassodromeus</i>	<i>sethi</i>	Romualdo	Kellner & Campos, 1988
		Nova Olinda	Kellner & Campos, 2002

Table B.2: Measurements taken of different ornithocheirids. '*' means that parts of the skeleton were fragmented or obscured and that the measurements were taken using the obscured location. '**' means that the actual structure was absent but estimated using other specimens. Abbreviations used: qa=naso-orbit, NAOF=nasoantorbital fenestra, md=mandibula.

Genus	Species	Specimen	Height at qa (cm)	Height ob (cm)	Width ob (cm)	Length NAOF (cm)	Height rostrum (cm)
<i>Ludodactylus</i>	<i>sibbicki</i>	KBIN	9,026666667	4,412592593	4,273333333*	9,957592593	5,091944444
<i>Ludodactylus</i>	<i>sibbicki</i>	SMNK PAL 3828	10,63318777	5,934185901	4,374610106	14,77854024	6,154086089
<i>Brasileodactylus</i>	<i>araripensis</i>	AMNH24444	7,888696184	4,575086717	4,876555805	11,61038564	3,601305856
<i>Tropheognathus</i>	<i>mesembrinus</i>	SMNS 56994	\	\	\	\	\
<i>Tropheognathus</i>	<i>mesembrinus</i>	BSP 1987 I 46	9,463722397	4,941372537	5,254444914	19,83096244	3,595619308
<i>Anhanguera</i>	<i>blittersdorffi</i>	MN 4805-V	7,868832	4,808661331	5,556855587	17,85120357	3,869518416
<i>Coloborhynchus</i>	<i>spielbergi</i>	RGM 401 880	12,88557692	6,064423077	4,039423077	21,94423077	5,775961538
<i>Anhanguera</i>	<i>piscator</i>	NSM-PV 19892	12,95035971	7,769784173	7,267625899*	19,47266187	5,469784173
<i>Anhanguera</i>	<i>araripensis</i>	SAO 16494	8,949122807	5,527192982	5,528947368	16,18070175	4,4
<i>Anhanguera</i>	<i>robustus</i>	BSP 1987 I 47	\	\	\	\	\
Genus	Species	Specimen	Distance to NAOF	Length md	Length skull	Reference	
<i>Ludodactylus</i>	<i>sibbicki</i>	KBIN	17,93555556**		35,98592593**	First description	
<i>Ludodactylus</i>	<i>sibbicki</i>	SMNK PAL 3828	24,4198378	43,38739863	48,22520274*	Frey <i>et al.</i> , 2003	
<i>Brasileodactylus</i>	<i>araripensis</i>	AMNH24444	21,879208323	7,24489796**	41,69047133	Veldmeijer, 2003	
<i>Tropheognathus</i>	<i>mesembrinus</i>	SMNS 56994	\	40,90515	\	Veldmeijer, 2006	
<i>Tropheognathus</i>	<i>mesembrinus</i>	BSP 1987 I 46	23,59978573	44,47790333	53,2813523	Wellnhofer, 1987	
<i>Anhanguera</i>	<i>blittersdorffi</i>	MN 4805-V	24,5369027	\	50,54835338	Campos & Kellner 1985	
<i>Coloborhynchus</i>	<i>spielbergi</i>	RGM 401 880	31,06730769	\	66,53846154	Veldmeijer, 2003	
<i>Anhanguera</i>	<i>piscator</i>	NSM-PV 19892	30,02805755*	54,190681	62,6942446*	Kellner & Tomida, 2000	
<i>Anhanguera</i>	<i>araripensis</i>	SAO 16494	\	28,34035088	55	Veldmeijer, 2006	
<i>Anhanguera</i>	<i>robustus</i>	BSP 1987 I 47	\	57,27551497	\	Wellnhofer, 1987	

Table B.3: Measurements of the two known specimens of *Tupuzuara deliradamus*.

Species	Height articular	Height at NAOF	length NAOF	Width orbit
KPMNH DL 84	4 cm	10 cm	54 cm	6 cm
NEW SPECIMEN	2,1 cm	4 c m	14,2 cm	2,6 cm
Log ratio	0,279840697	0,397940009	0,580105415	0,363177902

Table B.4: Principal components of the analyses of all Brazilian pterosaurs, including broken specimens. Each principal component is shown with their eigenvalues, the variance and cumulative variance each of these principal components described.

Principal component	Eigenvalues	% Variance explained	Cumulative %
1.	0,01765582	54,322	54,322
2.	0,00673961	20,736	75,058
3.	0,00264983	8,153	83,211
4.	0,00175134	5,388	88,600
5.	0,00095003	2,923	91,523
6.	0,00078966	2,430	93,952
7.	0,00061768	1,900	95,853
8.	0,00035668	1,097	96,950
9.	0,00030638	0,943	97,893
10.	0,00016844	0,518	98,411
11.	0,00013652	0,420	98,831
12.	0,00011140	0,343	99,174
13.	0,00008933	0,275	99,449
14.	0,00007125	0,219	99,668
15.	0,00004227	0,130	99,798
16.	0,00003831	0,118	99,916
17.	0,00002735	0,084	100,000

Table B.5: Principal components of the analyses of all complete Ornithocheiridae. Each principal component is shown with their eigenvalues, the variance and cumulative variance each of these principal components described.

Principal component	Eigenvalues	% Variance explained	Cumulative %
1.	0,00273249	46,824	46,824
2.	0,00102096	17,495	64,319
3.	0,00065815	11,278	75,597
4.	0,00055627	9,532	85,129
5.	0,00033300	5,706	90,835
6.	0,00026347	4,515	95,350
7.	0,00018469	3,165	98,515
8.	0,00008668	1,485	100,000

Table B.6: Principal components of the analyses of all Tapejaridae sensu Kellner (2004). Each principal component is shown with their eigenvalues, the variance and cumulative variance each of these principal components described.

Principal component	Eigenvalues	% Variance explained	Cumulative %
1.	0,02634417	45,302	45,302
2.	0,01678880	28,871	74,173
3.	0,00719351	12,370	86,543
4.	0,00584456	10,051	96,594
5.	0,00156846	2,697	99,291
6.	0,00041234	0,709	100,000

Appendix C

Supplementary materials and methods

C.1 Systematic paleontology of pterosaur mandibulae

Brasileodactylus sp., Figure A.6

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

ORNITHOCHEIROIDEA Seeley, 1870

ORNITHOCHEIRIDAE Seeley, 1870

BRASILEODACTYLUS (Affinity uncertain) Kellner, 1984

Type locality and horizon: Santana Formation, Araripe basin, Brazil.

Diagnosis: Two, rather small, mandibular rami with elongated articular region, which is diagnostic for Ornithocheiridae. The presence of teeth further enhances this. No mandibular crest is present, which excludes several other Ornithocheiridae.

Description: The specimen consists of two smaller, toothed mandibular rami. At least 3 teeth in the right ramus and 1 tooth in the left ramus are still present in their socket. Only one of them, one of the right ramus, is relatively complete. The symphysis of the mandibula contains a groove. The mandibula still has two articular region and both are well preserved. The articular region contains two conus shaped cotyli, the lateral and the medial cotyle, separated by a ridge. The retroarticular process reaches far posteriorly and contains a pneumatic foramen. The elongated shape of the articular region is diagnostic for the Ornithocheiridae, as are the teeth.

Comparison with *Araripesaurus castilhoi*, *Araripedactylus dehmi*, *Santanadactylus brasiliensis*, *Santanadactylus pricei*, *Santanadactylus spixi*, *Anhanguera blittersdorffi* is impossible due to the lack of mandibulae in the previous. Comparison is possible, however, with *Anhanguera santanae*, *Anhanguera piscator*, *Coloborynchus spielbergi*, *Anhanguera araripensis*, *Cearadactylus atrox*, *Brasileodactylus araripensis*, *Ludodactylus sibbicki*, *Coloborhynchus robustus* and *Tropeognathus mesembrinus*.

The region just before the dorsal side of the articular has a convex bend as seen in *A. santanae*, *A. araripensis*, *B. araripensis*, *L. sibbicki* and other, larger species. This is not seen in *C. atrox*, where the mandibula is straight. *C. spielbergi*, *A. piscator*, *A. araripensis*, *T. mesembrinus* and *C. robustus* can be, however, excluded due to their large size.

The relatively small size — 30 cm, assuming that the distance to the mandibular rami is 2/3 of the total length as in most ornithocheirids — is comparable to the size of *A. blittersdorffi* and *A. santanae*. The slender symphysis is not seen in *A. santanae* and the absence of a mandibular crest excludes both *Anhanguera* species (considering that *A. blittersdorffi* as other *Anhanguera* species had a mandibular crest as their is no material to compare with).

By process of exclusion *Brasileodactylus araripensis* and *Ludodactylus sibbicki* remain as candidates. The slender nature of the is corresponding with *Brasileodactylus araripensis* or *Ludodactylus sibbicki*. No three dimensional conserved mandibula of *Ludodactylus sibbicki* is present, and differentiation between the two is hard even if it would be present (Martill *et al.*, 2007). This is of course if you consider the two as two different species. The articular region is only present in *Ludodactylus sibbicki* and this is comparable to this specimen with a straight ventral side.

The affinity remains uncertain as comparison was only possible using literature. Certain views are not available in the literature and further comparison with actual specimens could confirm the present determination.

***Tropeognathus mesembrinus* (Affinity uncertain), Figure A.7**

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

ORNITHOCHEIROIDEA Seeley, 1870

ORNITHOCHEIRIDAE Seeley, 1870

TROPEOGNATHUS Wellnhofer, 1987

TROPEOGNATHUS MESEMBRINUS (Affinity uncertain) Wellnhofer, 1987

Type locality and horizon: Santana Formation, Araripe basin, Brazil.

Diagnosis: Large mandibular rami with elongated articular region, which is diagnostic for Ornithocheiridae. The curvature of several regions of the articular excludes almost all other pterosaurs.

Description: This fossil consists of part of one acid prepared mandibular ramus that is three-dimensionally preserved. The adductor fossa is clearly visible. The cone shaped lateral cotyle is typical for pterosaurs, while the elongation is ornithocheirid in shape. The articular region consists of only one cotyle, the lateral cotyle. Here, the honeycombe structure of the bone is clearly visible. This implicates that it was really aerated. The pneumatic foramen and the retroarticular processus are absent.

Comparison with *Araripesaurus castilhoi*, *Araripedactylus dehmi*, *Santanadactylus brasiliensis*, *Santanadactylus pricei*, *Santanadactylus spixi*, *Anhanguera blittersdorffi* and *Anhanguera spielbergi* is impossible due to the lack of mandibulae in the previous. Comparison is possible, however, with *Anhanguera santanae*, *Anhanguera piscator*, *Coloborynchus spielbergi*, *Anhanguera araripensis*, *Cearadactylus atrox*, *Brasileodactylus araripensis*, *Ludodactylus sibbicki*, *Coloborhynchus robustus* and *Tropeognathus mesembrinus*.

As in the previous fossil, the dorsal region just anterior to the articular has a convex bend as seen in all *Anhanguera* species, *C. spielbergi*, *T. mesembrinus*, *C. robustus* and *A. araripensis*. This is not seen in *C. atrox*, where the mandibula is straight.

B. araripensis, *L. sibbicki*, *A. blittersdorffi* and *A. santanae* can be excluded due to their size. The large size resembles the size of *Anhanguera piscator*, but the ventral region of the articular in the latter seems to curve upwards in a lesser extent than that in this specimen. Although the retroarticular processus is not complete, extrapolation allows us to estimate the angle it will curve in, and this appears to be steeper than in *A. piscator*. *C. spielbergi* and *A. araripensis* also lack the upward curving retroarticular processus and can be excluded as well. Comparison of the mandibulae shown in Veldmeijer (2006) shows that this lack of upward curve is typical for *Anhanguera* mandibulae.

C. robustus can be excluded for the same reason as it also lacks the upward curve of the retroarticular processus and additionally has a higher articular region. *T. mesembrinus*, however, has this upward curve and appears to be of a comparable size. Furthermore both share the rather short (in comparison to that of *Anhanguera*) retroarticular if viewed at dorsally.

C.2 Risk analyses

Handling the specimens

Some specimens are located on high shelves. When taking these out it is suggested that a ladder is used and help should be asked if necessary. Not following these guidelines could lead to boxes falling on top of the person handling them, with injuries as a result. Other specimens are heavy and transporting them can result in neck- and backpain. This can be solved by using a correct

posture in which you bend through the knees to pick it up and walk with a straight back once picked up. Stress can be reduced by keeping the specimen close to the body. All these risks that come with handling are common but can easily be reduced following the guidelines.

Ergonomics

Most of the work is done while sitting behind a desk. The office should be well lit to reduce stress to the eyes. The monitor should be placed on a correct height, there should be enough space to sit comfortable and the chair should be adjustable as well. Applying these will reduce ergonomic stress. Ergonomic stress, however, happens very frequently even though these rules are followed, as even they do not protect if the reduced stress holds on a long time.

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