



## PALEONTOLOGY

# A taxonomic approach on diagnostic characters used to define new pterosaur taxa and an estimation of pterosaur diversity

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**Abstract:** Diagnostic characters from 227 pterosaur species were listed, separated into cranial or post-cranial elements and counted. From 21 post-cranial and 23 cranial elements, most diagnostic characters were related to phalanges (15%) and rostrum. Post-cranial characters comprise 44.23%, and cranial characters 55.77% of all characters used in pterosaur diagnoses. The highest correlation between diagnostic features occurs between the coracoid and the scapula. 25.11% and 28.63% of sampled taxa were diagnosed with 3-4 and 5-6 characters, respectively. The mean number of 6.79 characters was found in specimens with both cranial and post-cranial elements, and 4.86 and 4.17 in those with just cranial or post-cranial elements, respectively. 31 from 227 species (13.7%) were erected based on single elements, which are most frequently complete or partial mandibles (n=18). We estimate that 23.4% of the total pterosaur genera are currently known, with 90% of this diversity to be unveiled up to 2145. As the requirements of broad and cautious revision of genus/group must be undertaken, and some deposits will provide mostly fragmented and incomplete material, the assignment of fairly incomplete specimens to the most inclusive taxonomic level is feasible. Tracing this scenario can guide future works on the description of new pterosaur taxa.

**Key words:** Morphology-based species, Pterosauria, Systematic Biology, Taxonomy

## INTRODUCTION

Delineating species and their taxonomy has been traditionally a matter of recognizing morphological characters (Schwentner et al. 2011) as structural attributes of organisms that are primarily recognized as different from any other. For centuries, Morphology has been the primary or sole source of data for delimiting species (Cook et al. 2010). Under the requirement of a species being unique and identifiable following a specific code, each name has to be linked to a type specimen, and this identification is associated to a species concept (Cook et al. 2010). That of Mayr's (1996) defining species as "a morphological kind that is different

from other such kinds" particularly restricts data to morphological characters (Cook et al. 2010). Despite data defining morphology-based species have been currently complemented by other data source such as DNA sequence data, which has fomented plenty of debate on the sufficiency of morphological data alone to define species (e.g., Ebach & Carvalho 2005a, b, Packer et al. 2009), this cannot be applied to some areas that usually can count solely on structure (Morphology), such as the case of Paleontology. Indeed, recognition of paleontological species relies almost exclusively on their morphological differences, which is hampered by the often fragmentary and isolated nature of fossils (Forey et al. 2004). This explains the differences

between the nature of elements that are used to define new taxa, ranging from cranial to post-cranial elements or both, and from complete to fairly incomplete material.

When it comes to pterosaurs the number of characters raised as diagnostic to define a new species varies from one (e.g., *Azhdarcho lancicollis* Nessov, 1984, *Bennettazhia oregonensis* (Gilmore, 1928), *Domeykodactylus ceciliae* Martill, Frey, Diaz & Bell, 2000, *Gnathosaurus subulatus* Meyer, 1833, “*Huaxiapterus*” *corollatus* Lü, Jin, Unwin, Zhao, Azuma & Ji, 2006, *Nyctosaurus lamegoi* Price, 1953, *Rhamphorhynchus etchesi* O’Sullivan & Martill, 2015 and *Tupuxuara longicristatus* Kellner & Campos, 1988) to up to 29 features (*Eudimorphodon ranzii* Zambelli, 1973), which could be related to the completeness degree of material (the more complete the specimen, the higher number of osteological features to be eventually pointed as diagnostic). When it comes to the type of characters (i.e., autapomorphic or synapomorphic), there is also a noticeable variation in this number of diagnostic features that could be assigned to methodological bias whether in complete specimens or not. For instance, *Mythunga camara* Molnar & Thulborn, 2007 is an Early Cretaceous pterodactyloid pterosaur described based on 10 original features of an incomplete snout and mandible, but only two of them were identified as autapomorphic. On the other hand, the abovementioned and much more complete Chinese tapejarid “*Huaxiapterus*” *corollatus*, a partial skeleton and skull, is defined by a single supposed autapomorphy (a distinctive hatched-shaped process on the cranial crest). There are also taxa (e.g., species of the genus *Anhanguera* Campos & Kellner, 1985, Pinheiro & Rodrigues 2017) largely diagnosed by subtle differences in cranial anatomy based particularly on the morphology and position of structures as crests,

which may presumably be sexual dimorphisms or ontogenetic variations (Bennett 1992, Manzig et al. 2014). However, neither dimorphic or ontogenetic aspects, nor the type of characters termed as diagnostic are here considered, and such discussion is beyond the scope of this paper.

The systematic biology, as it is known, is based on the description of an organism that supports taxonomic recognition, and the diagnosis of new or revised taxa has long been considered part of systematic accounts (Cifelli & Kielan-Jaworowska 2005). The International Code of Zoological Nomenclature (ICZN) provides definitions and a set of rules on how to name newly described organisms, assuring the stability of the zoological nomenclature. However, it does not set a norm on the amount (from 1-29 features in pterosaurs) or nature of the diagnostic characters used to define new taxa, which is widely variable among researchers and depends on the nature of studied organisms. The character-based species, as defined by Nixon & Wheeler (1990) as “the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)”, has the number of diagnostic traits to be considered to define a species as one of its major practical difficulties (Willmann & Meier 2000). Thus, as a matter of debate and also to try to delineate a pattern regarding the most used structures for diagnosing pterosaur species, we have delineated three main aims to this study: to determine (1) the nature of elements from which the osteological characters that diagnose new species are defined, (2) the average number of characters used to diagnose pterosaur species, and (3) to make a projection concerning the rate of future pterosaur discoveries to predict these discoveries as to guide future works on the description of new pterosaur species.

### Institutional abbreviations

IVPP - Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MN - Museu Nacional, Rio de Janeiro, Brazil; NHMUK - The Natural History Museum, London, UK; PIMUZ - Paläontologisches Institut und Museum, Universität Zürich, Switzerland; UJA - University of Jordan, Amman, Jordan.

### MATERIALS AND METHODS

Data on diagnostic characters from all taxonomically diagnosable pterosaur species ever described up to August 2020 ( $n = 227$ ) were compiled from *The Paleobiology Database* (PaleoDB: [www.paleobiodb.org](http://www.paleobiodb.org)) and published literature. Diagnostic characters are here interpreted as differential character states (i.e., uniquely shared by all members of a taxon but not by non-members) or a unique and differential combination of characters used to define a taxon. The former is here termed as autapomorphic (as a unique apomorphy to a taxon or a group of organisms), as discriminated by Dubois (2017). Here we refrain from differing the type of characters in the sense of separating autapomorphic from synapomorphic ones (i.e., whether unique from a single taxon or shared with other taxa). All of them are termed as diagnostic and considered according to their nature (cranial or post-cranial).

The final dataset comprises (for each listed species) nature of preserved skeletal material (cranial, post-cranial or both), the number of characters used to diagnose each pterosaur species, completeness degree (i.e., complete or partial skeletons, and which parts are preserved in incomplete material), year of description, period, locality and country (see the supplementary DataSet by Fernandes et al. 2021 at [doi:10.17632/w7thrrs9dh.1](https://doi.org/10.17632/w7thrrs9dh.1)).

As to provide the most updated compilation of diagnosable pterosaur species so far, we have checked along for synonyms and *nomina dubia* (not considered). Despite the fact that other pterosaur species compilations have been provided previously (e.g., Andres 2010, Butler et al. 2013, Dean et al. 2016), our purpose differs by focusing on the number and nature of characters used in the original diagnoses of pterosaur species, as well as predicting the rate of future pterosaur discoveries. It is worth mentioning that once we have considered the elements that have historically been used as original diagnostic features, we disregarded whether the characters are currently valid or not. Neither aspects of pterosaur diversity nor the quality of fossil record has been evaluated or discussed herein.

Once fossil species are mainly diagnosed on the basis of osteological characters, cranial and post-cranial elements used to define these characters in each species were determined. These elements were then individually counted regarding the number of times they were used when diagnosing species that comprised only cranial and both cranial and post-cranial material (cranial elements), and only post-cranial and both cranial and post-cranial material (post-cranial elements). Osteological elements were only considered once per diagnosis (e.g., if a taxon was diagnosed using two distinct phalangeal features, it was counted as “phalangeal elements” - 1). Moreover, when these elements were combined with others to term a single diagnostic character, they were counted separately (e.g., if a taxon was diagnosed by the hypothetical diagnostic character “wing metacarpal shorter than ulna and first wing phalanx, with a pronounced posterior curvature”, it was counted as “phalangeal elements” - 1, “metacarpal elements” - 1, and “ulnar elements” - 1). Subsequently the frequency (%) of these

(cranial and post-cranial) elements related to diagnostic characters was determined in order to indicate which elements would have been most used in the diagnosis of new species.

Mean, median and mode were calculated from the number of characters used to diagnose each pterosaur species. The frequency (%) of the amount of characters (ranging from the min-max values of 2 - 31) that diagnosed new pterosaur species was calculated, as well as the frequency of each cranial and post-cranial element used to diagnose these species.

A Principal Component Analysis (PCA) was applied to analyze similarity patterns of characters frequency between diagnoses due to the very large dataset (Jolliffe & Cadima 2016). PCA is an orthogonal linear transformation of the data for a new coordinate system, reducing the dimensionality of such datasets, increasing interpretability and minimizing information loss (Jolliffe 2002). In this analysis, the greatest variance for any projection of data is along the first coordinate (Principal Component 1 - PC1) and the second greatest variance is along the second coordinate (Principal Component 2 - PC2), and so on, being the number of principal components less than or equal to the number of original variables (Jolliffe 2002). The Hierarchical Cluster Analysis was performed as a complement with the linkage criterion of UPGMA (unweighted pair group method with arithmetic mean) and applying a correlation similarity index to find out which any given pair of characters join together in the tree diagram (Sokal 1958, Krebs 1999, Nielsen 2016). The goal is to build a tree diagram where the characters that were more used in the same diagnosis are placed on branches that are close together.

To estimate pterosaur diversity and to make a projection concerning the rate of future pterosaur discoveries, the number of specimens assigned to each genus was taken from the

PaleoDB (Alroy 2013) downloaded on August 16<sup>th</sup>, 2019. From this date up to August 2020 new genera were sourced from the literature. Here we applied the Abundance-based Coverage Estimator (ACE) (Chao & Lee 1992, Chao & Yang 1993) as a statistical method to consider the incompleteness of the fossil record (following Wang & Dodson 2006). The ACE model estimates the number of discoverable genera also comprising future discoveries, and only takes into account genera considered scarce (i.e., those with ten or less individuals assigned to a genus), which avoid inaccuracies (e.g., those motivated by difficulties in estimating the exact number of material available for abundant genera, such as *Pteranodon*, with more than a thousand individuals known so far (Bennett 2000)). The diversity was estimated with the following equation:

$$\text{Estimated Diversity} = D_{\text{abun}} + \frac{D_{\text{rare}}}{C_{\text{rare}}} + \frac{f_1}{C_{\text{rare}}} \gamma_{\text{rare}}^2$$

Where

$$\gamma_{\text{rare}}^2 = \max[\max(\frac{D_{\text{rare}} \sum i(i-1)f_i}{C_{\text{rare}}(\sum if_i)^2} - 1, 0)(1 + \frac{1 - C_{\text{rare}} \sum i(i-1)f_i}{C_{\text{rare}} \sum if_i - 1}), 0]$$

and

$$C_{\text{rare}} = 1 - \frac{f_1}{n_{\text{rare}}}$$

$D_{\text{abun}}$  is the number of abundant genera ( $n > 10$ ),  $D_{\text{rare}}$  is the number of rare genera ( $n < 10$ ),  $n_{\text{rare}}$  is the number of individuals among rare genera, and  $f_i$  is the number of individuals known from exactly  $i$  individuals. All calculations were made using the LibreOffice® Calc software and Past4.3 was used to generate the dendrogram.

It is worth mentioning that specimens not assigned to a specific genus (e.g., IVPP V 17959, a wukongopterid; Cheng et al. 2016) were not considered in the estimation using the ACE model, neither ichnotaxa nor species without a valid diagnosis. Here we have accounted for the “discoverable” and “assignable” pterosaur genera with current technology and taxonomic

methods, and thus provided a lower estimate of the ever existed diversity (Wang & Dodson 2006) since the original diversity cannot be recovered.

Other data related to each species, such as year of the species' description and the number of assigned specimens to a species, were also used to predict future pterosaur discoveries and to produce statistics for estimating pterosaur diversity, respectively. The prediction of future discoveries was performed by fitting a logistic accumulation curve of the form  $y=807/(1+806*e^{(-0,026026*t)})$  to the cumulative counts of known genera throughout the years using the estimation of pterosaur diversity as the point where the curve becomes an asymptote.

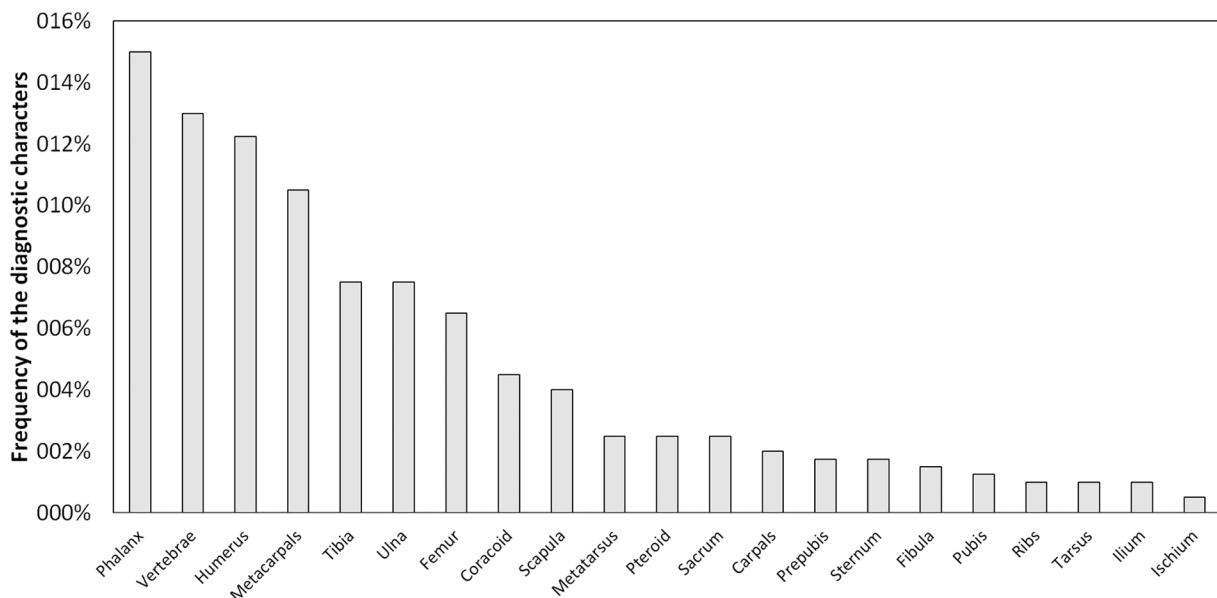
## RESULTS AND DISCUSSION

### Which osteological elements are the most employed to diagnose new pterosaur species?

From 21 post-cranial elements, most diagnostic characters were related to phalanges (15%), followed by humeri (13%) and vertebrae (12.25%)

(Figure 1), and from 23 cranial elements the most used cranial-related characters regard those of the rostrum, as follows: teeth (16.20%), mandible (12.93%) and premaxilla (10.44%) (Figure 2). Post-cranial characters comprise 44.49%, and cranial characters 55.51% of all characters used in pterosaur diagnoses. If species with both cranial and post-cranial elements are considered, teeth (9.99%) account for the majority of characters, followed by mandible (7.64%), phalanges (6.61%) and humeri (5.43%) (Figure 3).

In PCA analysis, it was found that the first two components (PC1 and PC2) correspond to 32.28% of all variance. and the other two (PC3 and PC4) to 6.50% and 5.34%, respectively. The scatterplot of PC1-PC4 scores are shown in Figure 4 but, as explained before, the representation of the variance is low in PC3 and PC4. Thus, we have limited our approach to the first two components. The reduced space of the first two components (Figure 5) show that PC1 has a positive correlation especially with the frequency of cranial elements, while PC2 mostly has positive correlation with the



**Figure 1.** Frequency of post-cranial elements diagnosing new pterosaur taxa.

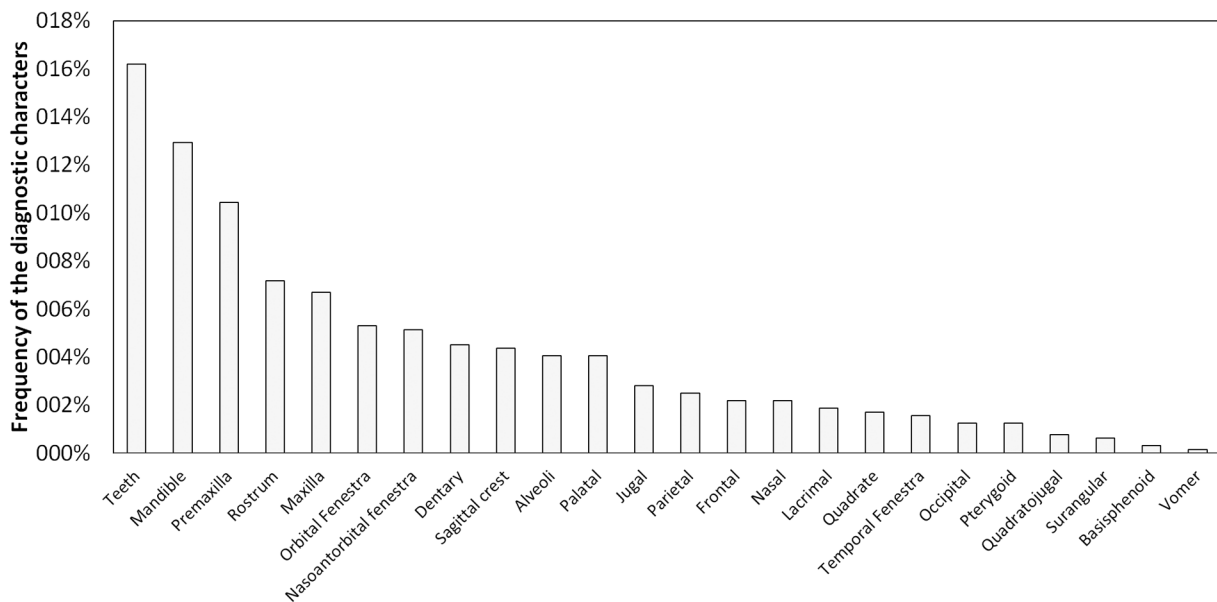
frequency of post-cranial elements. The scatter plot groups in the negative side of both axes the features that have low frequency in diagnosis and that are mostly used to diagnose the most complete specimens with both cranial and post-cranial elements. Factor loadings are presented in Figure 6. When considering the axes alone, it can be seen that taxa diagnosed with only cranial elements are influencing PC1, with *Austriadactylus cristatus* Dalla Vecchia, Wild, Hopf & Reitner, 2002, *Istiodactylus sinensis* Andres & Qiang, 2006, *Maaradactylus spielbergi* Veldmeijer, 2003, *Haopterus gracilis* Wang & Lü, 2001, and *Cearadactylus atrox* Leonardi & Borgomanero, 1985, respectively, with major descendant contribution. PC2 is being influenced by taxa with only post-cranial elements, with *Ningchengopterus liuae* Lü, 2009, *Changchengopterus pani* Lü, 2009, *Vesperopterylus lamadongensis* Lü, Meng, Wang, Liu, Shen & Zhang, 2017, *Orientognathus chaoyngensis* Lü, Pu, Xu, Wei, Chang & Kundrát, 2015, and *Carniadactylus rosenfeldi* Dalla Vecchia, 1995, respectively, with major descendant contribution. Taxa diagnosed with both cranial and post-cranial elements influence both axes,

depending on how many characters used in the diagnosis are cranial or post-cranial (Figure 6).

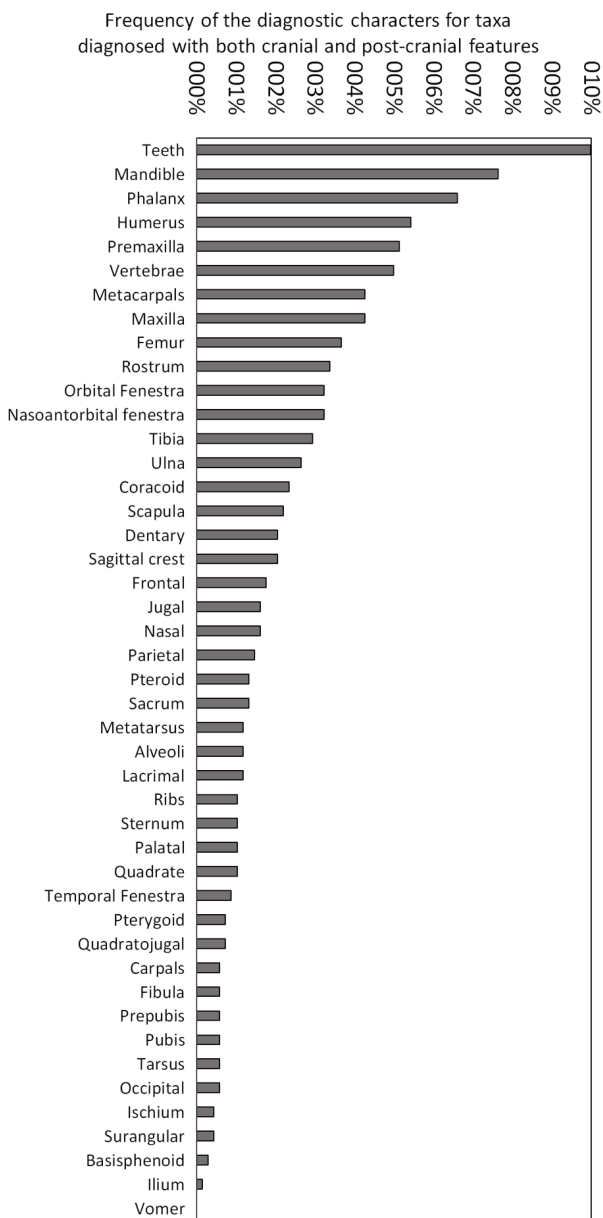
The Hierarchical Cluster Analysis shows a dendrogram in which osteological elements are frequently used together to erect new taxa, which is organized in eight main clusters (Figure 7). Most clusters group features that are often found together due to being anatomically near to each other, but it is not always the case because of the low frequency of some of the features (e.g., a cluster grouping the ischium with the occipital bone). The highest correlation between diagnostic features occurs between the coracoid and the scapula. Other features often used together for diagnostic purposes include both nasoantorbital and orbital fenestrae; fibula and tarsus; and femur and tibia. Features that do not often occur with other specific features are pteroid, lacrimal, and dentary.

### How many characters on average are used to diagnose pterosaur taxa?

Mode and median were 5.0, with mean of 5.6. There was also a strong negative correlation between the number of diagnostic features and the percentage of taxa (-0.77), which



**Figure 2.** Frequency of cranial elements diagnosing new pterosaur taxa.



**Figure 3.** Frequency of cranial and post-cranial elements diagnosing new pterosaur taxa.

means that less taxa are diagnosed with more characters. 25.11% and 28.63% of pterosaur taxa were diagnosed with 3-4 and 5-6 characters (Figure 8). Despite this pattern, some taxa are outstandingly out of the normal curve as quite complete specimens being diagnosed within the range of 13-29 characters (e.g., *Eudimorphodon ranzii* and *Vesperopterylus lamadongensis* Lu, Meng, Wang, Liu, Shen & Zhang, 2017, with 31 and 15 cranial and post-cranial diagnostic characters, respectively).

There is a quite obvious tendency of having more diagnostic characters in more complete specimens, which is numerically substantiated by a mean of 6.79 characters in specimens with both cranial and post-cranial elements, and 4.86 and 4.17 in those with just cranial or post-cranial elements, respectively. Notwithstanding, there are fairly complete specimens with a sole diagnostic feature, such as the case of "*Huaxiapterus*" *corollatus* diagnosed by a hatchet-shaped process on the cranial crest, as well as "*Huaxiapterus*" *atavismus* Lü, Teng, Sun, Shen, Li, Gao & Liu, 2016 and "*Huaxiapterus*" *benxiensis* Lü, Gao, Xing, Li & Sun, 2007, with only two diagnostic elements (Lü et al. 2006, 2007, 2016). *Caviramus shesaplanensis* Frösbisch & Frösbisch, 2006 (PIMUZ A/III 1225), on the other hand, consists of an incomplete mandible and is diagnosed by 10 characters, such as the case of *Cretornis hlavaci* Fric, 1881 (an incomplete left wing) with 14 diagnostic features (Averianov & Ekrt 2015).

### What are the problems in taxonomy of fossil taxa anyway?

Theoretical and practical problems concerning the erection of higher taxa are currently being addressed and hamper the efficiency and transparency of the taxonomical work (Komarek & Beutel 2006). If taxonomy of extant taxa can benefit from molecular studies

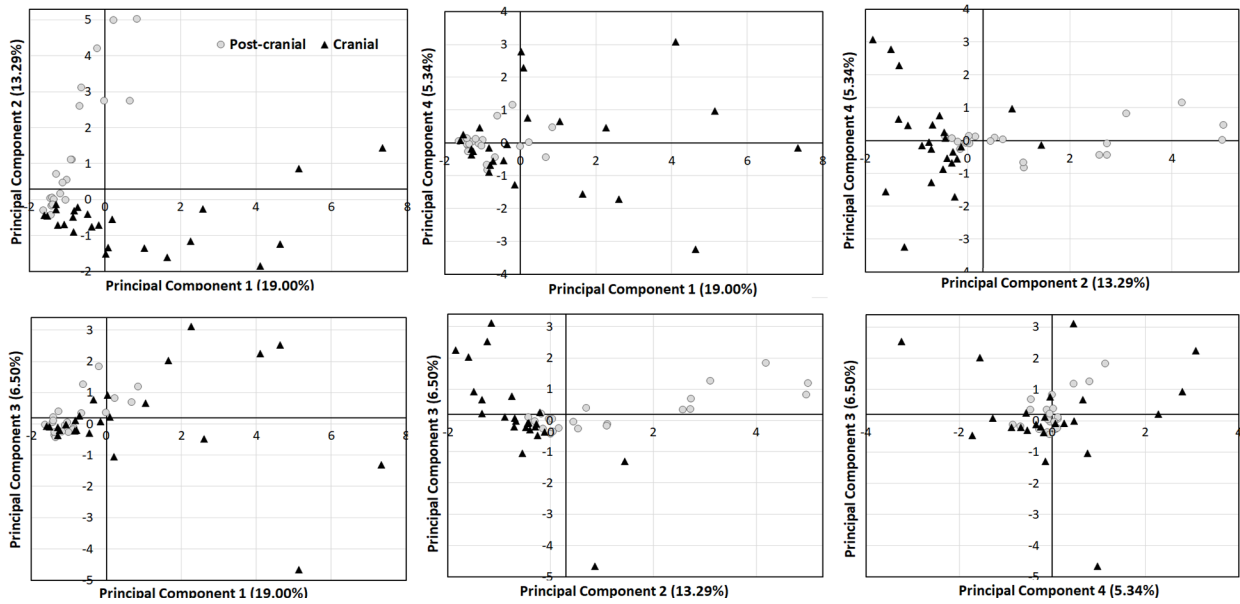


Figure 4. The six possible PCA scatter plot combinations for PC1 to PC4 of post-cranial (circle) and cranial (triangle) osteological features.

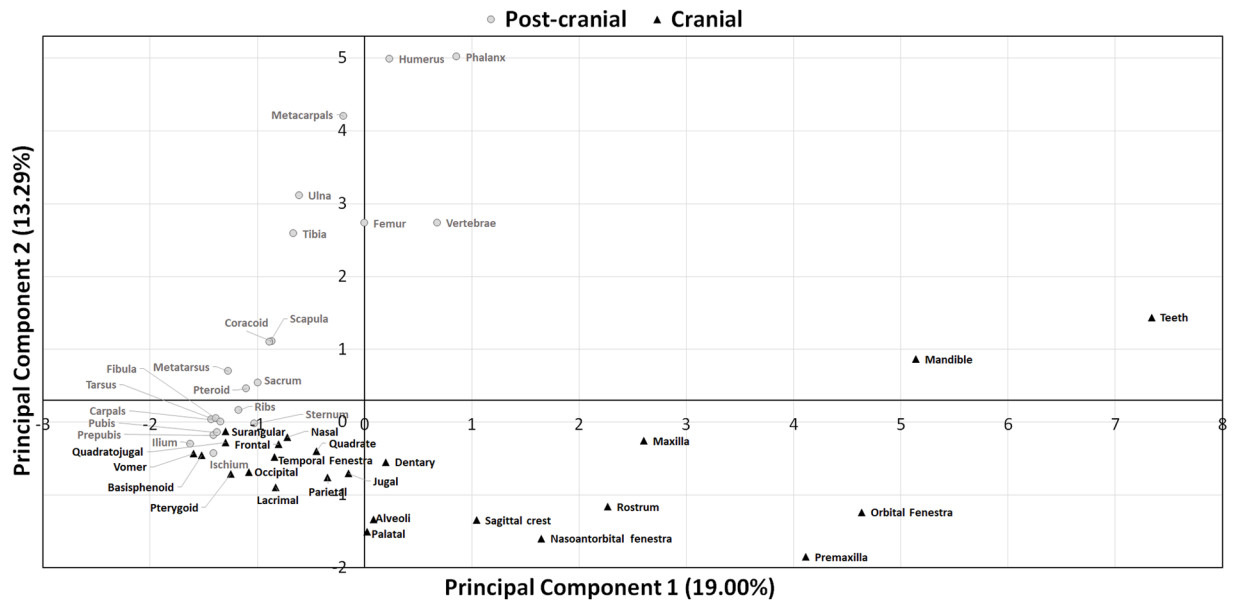
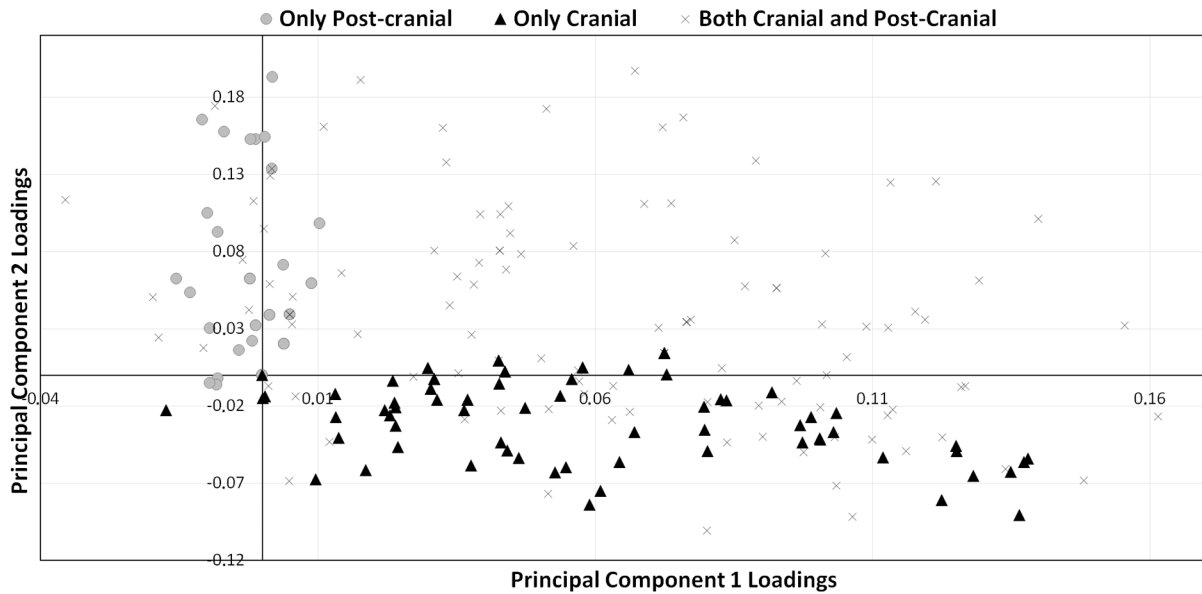


Figure 5. PCA scatter plot (PC1 and PC2) of the diagnostic signal of post-cranial (circle) and cranial (triangle) osteological features.



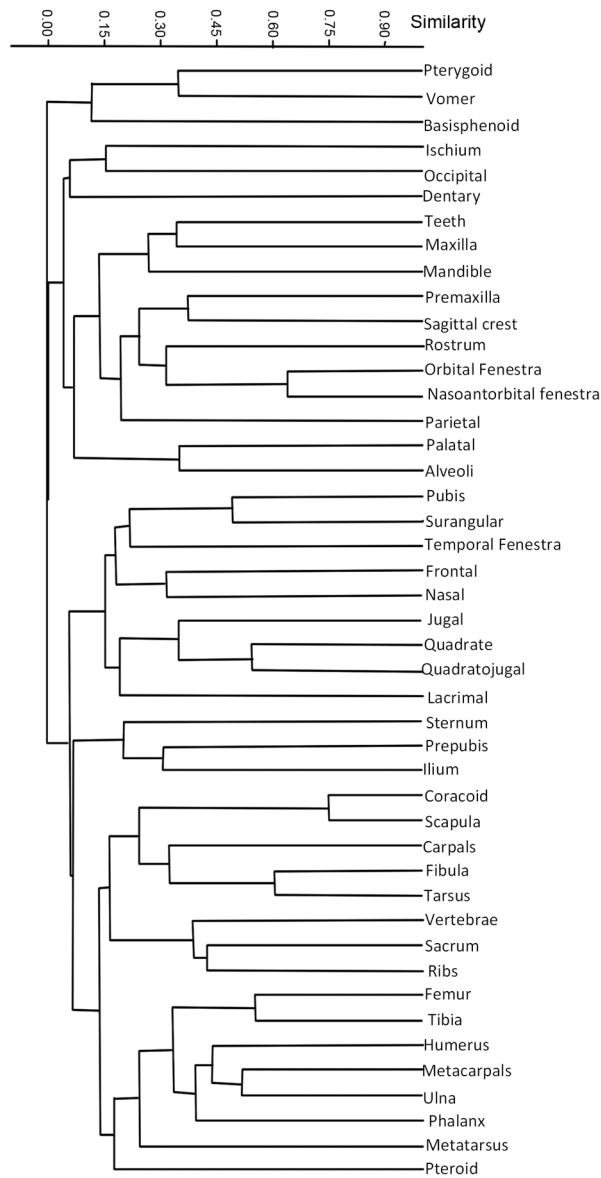


**Figure 6.** PCA factor loadings (PC1 and PC2) of taxa described with only post-cranial (circle), cranial (triangle) and both cranial and post-cranial (cross) osteological features.

using conservative and fast evolving genes for phylogenetic reconstructions on both high and lower levels, respectively (Komarek & Beutel 2006), extinct taxa can basically count, as already mentioned, solely on morphology itself. This increases the concern about making (good) choices of suitable characters as a crucial stage of appropriate taxonomic work (Komarek & Beutel 2006). Thus, if we mainly deal with combination of morphological characters to advocate species recognition (not considering here the discussion on chronospecies and stratospecies, which is beyond the scope of this paper), our selection of characters relies on how deep is our taxonomic approach. This directs towards an easily detectable issue as we are dealing with species recognition based solely on morphological differences of specimens that are usually fragmentary and highly incomplete: the level of taxonomic identification depends on which parts of the morphology is preserved, and how complete they are. It is obviously different to describe individual parts as separate species or a fairly complete skeleton, and depending

on the amount of parts we have (i.e., a single element, a bunch of cranial or/and post-cranial elements), we can turn to even fine details on the morphological investigation of perceptible differences (i.e., deepen the taxonomic level of investigation).

However, how deep we go on this task is constantly a matter of debate, with some advocating against (and even strongly refusing to) the erection of new taxa based on single elements (specially fragmentary ones) as it could bring excessive noise to phylogenetic analysis (e.g., less resolved consensus trees and increased numbers of EMPTs; Huelsenbeck 1991, Wiens and Reeder 1995, Wiens 2003), or even create systematic problems to be further solved on late reassessments of these taxa when insufficient study of types or taxa have created synonyms. This can happen when the authors do not consider reviewing all species of a group under consideration, which creates an insufficient background to substantiate the introduction of a new species, tending to produce synonyms (Komarek & Beutel 2006). The lack of



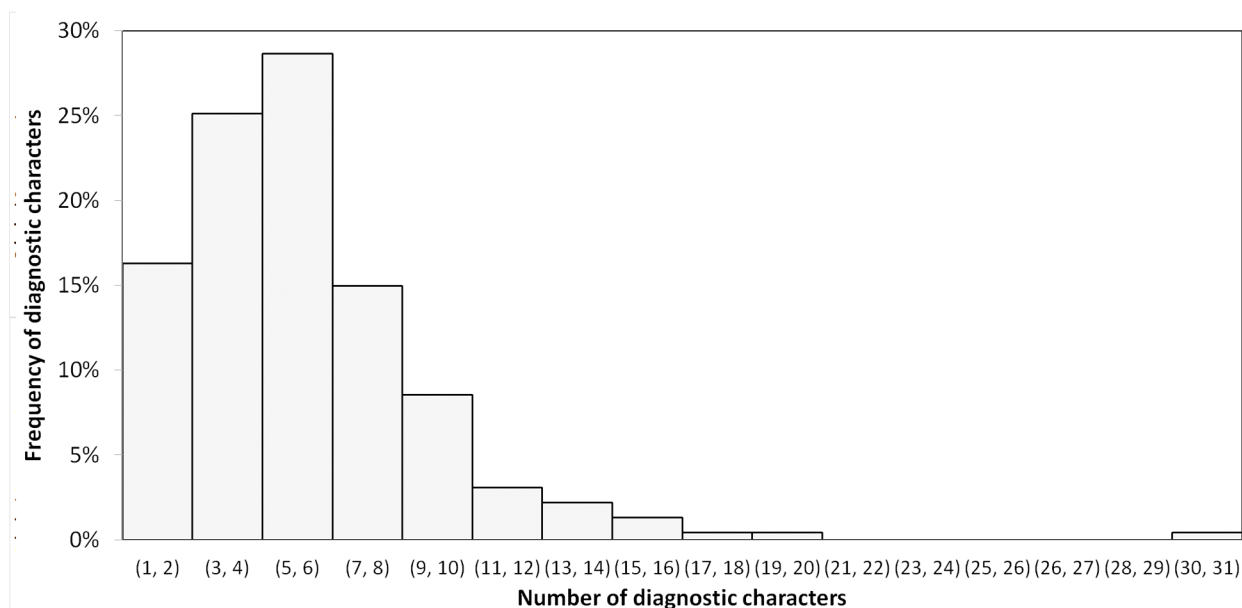
**Figure 7. Dendrogram showing the co-occurrence of diagnostic features.**

this critical approach to erect new taxa without sufficient comparison with other species and/or an extensive review may lead to inadequate taxonomic results. A recent example is the case of *Thalassodromeus oberlii* (Headen & Campos 2014), formerly "*Banguela*" *oberlii* described as a new species of dsungaripterid pterosaur based on an incomplete mandible from the Romualdo Formation (Santana Group, northeastern Brazil)

(Pêgas et al. 2018). This synonymization has been proposed as none of the four autapomorphies erected for "*Banguela*" *oberlii* could distinguish it from *Thalassodromeus sethi* Kellner & Campos, 2002, and the recognition of a second species of *Thalassodromeus* Kellner & Campos, 2002 would in turn reflect the speciose nature of some pterosaur taxa from this formation (Pêgas et al. 2018). Nonetheless, if requirements of a broad revision of genus/group are properly undertaken, we can walk the path to assign these fairly incomplete specimens to the most inclusive taxonomic level.

Another abovementioned topic that can be debated is that the correct identification of fragmented fossils has proven to be difficult, and because of this reaching a more inclusive taxonomic level to erect a new species can raise doubts on the validity of this species. The severity of this issue is directly proportional to the degree of fragmentation displayed by specimens. A single piece of element demands a deepened analysis on its morphological features that can be potentially diagnostic. This varies depending on the nature of this element (e.g., a plain bone diaphysis or a piece of vertebra). The holotype of the monotypic species *Araripedactylus dehmi* Wellnhofer, 1977, for instance, consists of a single first phalanx embedded in a limestone concretion that was originally allocated into the Pterodactyloidea, and lately considered to belong to the Ornothocheiroidea (*sensu* Kellner) based on its provenance by Kellner & Tomida (2000), who was not able to confirm none of its autapomorphies (even though seven were erected).

Indeed, few features can be taken from pterosaur phalanges themselves, particularly if their extremities are lacking/damaged (such as the case of *A. dehmi*). Notwithstanding, the case of other elements such as mandible is fairly different, but it depends on the completeness



**Figure 8.** Frequency of characters used to diagnosis new pterosaur taxa.

level of the specimen that is being described. If we take as an example the ventral shape (concave) of the mandibular symphysis that diagnoses the only element of the dsungaripteroid *Tendaguripterus recki* Unwin & Heinrich, 1999, which is the best known taxon from the Upper Jurassic Tendaguru Beds of Tanzania (Kellner et al. 2007), a mapping on the diagnostic characters of all the analyzed species in this study shows that the shape of dorsal/ventral margins of the mandibular symphysis can be found also diagnosing *Argentadraco barrealensis* Kellner & Calvo, 2017 (mandibular symphysis with marked concave ventral margin in lateral view), *Aussiedraco molnari* Kellner, Rodrigues & Costa, 2011 (dorsal margin of mandibular symphysis markedly convex, ventral margin of the symphysis straight), *Aymberedactylus cearensis* Pêgas, Leal & Kellner, 2016 (dorsally concave mandibular symphysis throughout entire extent) and *Caupedactylus ybaka* Kellner, 2013 (posterior half of the ventral margin of the mandibular symphysis forming a slight convex surface). It is interesting to notice that all of the listed taxa, apart from *C. ybaka*, are only known

from a (complete or partially complete) lower jaw, such as the case of *T. recki*. Thus, this level of analysis regarding the shape of a specific portion of the lower jaw, or any specific bone structure from other bones, are more likely to be identified when the taxonomist can rely on (very) fragmented specimens. This seems to be quite obvious since we are “forced” to perceive the details of more incomplete material to try to reach the more inclusive taxonomic level as possible.

Another well-known problem concerning the erection of new species regards the limited sample size of fossils, which was recently addressed by Massare & Lomax (2018) for *Ichthyosaurus*. Aquatic reptiles, as pterosaurs, bear unique morphological characters and did not have living representatives or suitable analogs. The authors have evaluated if different hindfin morphology in *Ichthyosaurus* was of taxonomic utility in the sense of erecting new species, and argued that the sample size has “implications for identifying unique diagnostic characters (autapomorphies) based on limited fossil material”. In the case of *Ichthyosaurus*,

if just fewer specimens would have been available, variation in hindfin morphology could have appeared less variable and more distinct. This shows that the more reduced sample size, the less variation will be recognized, which hampers morphotypes identification (Massare & Lomax 2018). As morphotypes are defined as different types of individuals that belong to the same species (morph), recognition of morphotypes relies upon many quite complete specimens of a species, otherwise intermediate morphologies could not be identified. Thus, unique morphologies can only be stated as such if numerous specimens can more confidently show that these are indeed taxonomically distinct characters and not a grade form within the variation. Massare & Lomax (2018) also call the attention for the case of isolated elements that seem to bear these particular morphologies. As these elements seem to be slightly different from other known species, and in the lack of more elements that could provide a better comparison to these same elements in different species, they are usually erected as new species.

Regarding pterosaurs, most species are erected based on one or few specimens and, as usual for fossil material, relies primarily upon morphology (although anatomical information is frequently missing). A worth mentioning case is the *Pteranodon*-complex, which comprises the best known pterosaurs so far and was a subject of investigation by many researchers concerning the identification of different species. This much-debated complex has been lately addressed by Kellner (2010) who re-evaluated the genus *Pteranodon* and erected two new species (*Geosternbergia maiseyi* Kellner, 2010 and *Dawndraco kanzai* Kellner, 2010). The author also discussed other problems besides the reduced number of specimens to define new species, such as the incompleteness of fossil material, taphonomy and the absence

of modern representatives or suitable analogs. However, as abovementioned, the major issue to be considered for taxonomy in fossils is morphology, but as form and structure can vary depending on ontogeny, gender, individual differences and taphonomy (Kellner 2010), the lack of a considerable number of specimens hampers the recognition of variation as a result of one of these factors or taxonomically distinct characters. In the case of the *Pteranodon*-complex, although different ontogenetic stages have already been recognized by Bennett (1993) for *Pteranodon*, a total of 14 species have been described, 11 of which referred to *Pteranodon* but considered as inflated by some reviewers (Kellner 2010). Thus, fossil taxonomy can possibly be failing to reflect the real diversity and consequently biasing our view over the paleobiology of extinct taxa.

### **But what would be the impact in pterosaur systematics if fairly fragmented fossils are erected as new taxa?**

As morphological information is essential to taxonomic studies but is constantly incomplete in fossils, which are subjected to many taphonomic and diagenetic processes (Lautenschlager 2016), some pterosaur taxonomists refrain from erecting new taxa from single pieces of bone elements. However, 31 from 227 species (13.7%) are erected based on single elements: 1-5 characters are used to diagnose 24 species, 6-9 to 6 species and up to 10 characters to 1 species. From the nature of these elements, they are mostly complete or partial mandibles (n=18), and others consist of maxillae (n=4), cervical vertebrae and snout fragments (n=3 for both), humeri (n=1), premaxillae (n=1) and phalanx (n=1). The taxonomic validity of *Arambourgiana philadelphiae* Arambourg, 1954 (holotype UJA VF-1, cervical V lacking its posterior end), one of these species, has been questioned by Witton

et al. (2010) who have proposed to synonymize it with *Hatzegopteryx thambema* Vremir, 2010. Indeed the misinterpretation over the mid-cervical vertebra of *Arambourgiana* Nesov & Jarkov, 1989 (originally described as a wing metacarpal by Arambourg (1954, 1959)) may have been induced by the difficulties in identifying a single 620 mm cylindrical cervical vertebra at the time azhdarchids were not known (and consequently neither giant pterosaurs that could have bear such elongated necks) and the lack of fully developed vertebral processes that could give an easier clue about its nature. Thus, it is understandable that a piece of bone with a circular cross-section could be attributed to a limb bone diaphysis instead of being considered an axial element.

As already mentioned, *A. dehmi* consists of a single first phalanx and was originally allocated into the Pterodactyloidea (and lately considered as an ornothocheiroid *sensu* Kellner). The extreme thickness of this phalanx pointed out by the original description of Wellnhofer (1977) (not lately confirmed by Kellner & Tomida (2000)), together with the damaged condition of its distal end, would have imposed difficulties in the identification of a plain piece of bone in the late 70's. Also, *Bogolubovia orientallis* (Bogolubov 1914) described in the early XX century, was originally assigned to the genus "*Ornithostoma*" Seeley, 1871 and belonging to pteranodontids before having its own genus erected (Nesov & Yarkov 1989). The specimen, which consisted of a fragment of the posterior portion of a cervical vertebra, was lately regarded as a *nomen dubium* by Bakhurina and Unwin (1995), who have questioned the possibility of identification of its type material. This potential taxonomical invalidity was then refuted by Averianov et al. (2005) based on the species being considerably different from other known cervical vertebrae of azhdarchids in which concerns the position

of the spinal canal, the low condyle and well developed postexapophyses (Averianov et al. 2005).

Taxonomic discordances have also comprised *Brasileodactylus* Kellner, 1984 (holotype MN4804-V, proximal part of a mandible) firstly assigned to the Ornothocheiridae by Kellner (1984) before being more contentiously allocated in the Pterodactyloidea *incertae sedis* (Kellner 1991), then to have affinities to the Anhangueridae (Kellner & Tomida, 2000) and even considered to be a species of *Coloborhynchus* Owen, 1874 (Frey et al. 2003). However, a dentary sagittal groove bearing small sub-grooves and the extremely elongated mandibular symphysis when compared with that of *Anhanguera*, *Criorhynchus* Owen, 1974 and *Coloborhynchus* seem to be apomorphic features of *Brasileodactylus* (Veldmeijer et al. 2005). The anterior portion of the rostrum (partial mandible) of the holotype (NHMUK PV 39409) of *Cimoliopterus cuvieri* (Bowerbank, 1851), formerly *Pterodactylus cuvieri*, was lately reassigned to the genus *Ornithocheirus* and *Coloborhynchus* until Rodrigues & Kellner (2013) have placed it in a new monotypic genus. Also, *Coloborhynchus clavirostris* Owen, 1874 (holotype NHMUK PV R 1822), a fragment of premaxilla and maxilla, has been synonymized with *Ornithocheirus simus* [= *Criorhynchus simus*] by Hooley (1914), Kuhn (1967) and Wellnhofer (1978) until being revalidated by Lee (1994) whose position was corroborated by Unwin (2001) and Rodrigues & Kellner (2013). On the contrary, *Lonchodectes compressirostris* (formerly attributed to the genera *Pterodactylus* Cuvier, 1809 and *Ornithocheirus*), a partial maxilla also referred by Hooley (1914) who re-introduced the genus *Lonchodectes* Hooley, 1914 and considered *Lonchodectes compressirostris* (Owen, 1851) one of the nine *Lonchodectes* species, was considered a valid species by Unwin (2001) and

lately a *nomen dubium* by Rodrigues & Kellner (2013). *Uktenadactylus wadleighi* (Lee, 1994), former *Coloborhynchus wadleighi*, consists of a partial snout that was reassigned to a new genus in 2009 by Kellner & Rodrigues, who had restricted the genus *Coloborhynchus* to the single species *C. clavirostris*. Another *Lonchodectes* species, *Lonchodectes sagittirostris* (Owen, 1874), consisting of a pair of lower jaws (formerly allocated to the *Ornithocheirus* genus), was also considered a *nomen dubium* by Rodrigues and Kellner (2013) and then reassigned to the genus *Serradraco* by Rigal *et al.* (2017). Indeed, the exceedingly fragmentary nature of the Cambridge Greensand pterosaurs made their systematic a constantly disputed taxonomic question over a decade until Rodrigues and Kellner (2013) have extensively reviewed the *Ornithocheirus* complex and discussed many ornithocheirids in the light of the revised taxonomy.

Even *Siroccopteryx moroccensis* Mader & Kellner, 1999, only known from the front portion of the mandible, had its genus considered as a junior synonym of *Coloborhynchus* by Unwin (2001) by the resemblance of this genus to a specimen of *Coloborhynchus* described by Lee (1994) and closely related to *Anhanguera* by Fastnacht (2001). Rodrigues & Kellner (2009) have then considered *Siroccopteryx* a distinct genus.

As abovementioned, 13.7% of all pterosaur species were erected based on single elements. According to Massare & Lomax (2018), isolated or fragmentary elements lack plentiful information to justify the erection of new taxon, and in the absence of several specimens it is not possible to properly identify whether what appear to be unique morphologies are indeed taxonomically distinct characters or intermediate forms within the variation. Therefore, it is not possible to know if the erection of these species is justified, especially in the lack of a more deepened and

detailed taxonomic study, until other studies challenge these nominations by critically re-examining these species. This frequently poses a major problem concerning the discard of previously accepted taxonomic names by synonymization or the proposal of *nomina dubia*. This current procedure makes an effort to minimize taxonomic inflation (i.e., inflation of species names) when individual parts being described as separate species are shown to be problematic. As above exemplified, this is also a major concern when it comes to pterosaurs, with several species being constantly challenged.

Another problem of increasing species-level taxa based on limited fossils is the increased diversity bias. Taxonomic inflation is more critical when taxa have a fragmentary and sparse fossil record (Uhen & Pyenson 2007). However, it is noteworthy that sometimes the description of new taxa based solely on complete specimens may also bias diversity, but differently from what is expected when dealing with incomplete specimens (Donovan 2001). Thus, if diversity bias can occur even when complete specimens are described, this cannot be an argument to prevent limited specimens to be erected as new taxa.

Notwithstanding, although numerous problems are related to naming species based on incomplete and fragmentary material, many type specimens are incomplete but diagnostic in vertebrate paleontology (Uhen & Pyenson 2007). We thus refrain from advocating against this practice despite these potential problems, but suggest being particularly cautious when species-level taxa are erected based on limited and/or isolated material. In the case of pterosaurs, as already mentioned, potential taxonomic problems could be avoided if diagnostic features are mapped with cautious by a broad and deep taxonomic study also based on as many comparisons with other material

as possible. Along with that, current research practices can help, such as reproducing high-resolution photographs in descriptive research articles and publishing informative figures, which enables better anatomical comparisons to be done.

### **How many pterosaur genera are still unknown?**

One of the major substantial challenges in Paleontology is to quantify the diversity of animal groups (Alroy et al. 2001), and despite some punctual efforts on quantifying some of these groups (e.g., the diversity of dinosaurs; Dodson 1990, Russell 1995, Wang & Dodson 2006), studies of this kind are still scarce. The well-known incompleteness of the fossil record, as well as taxonomic difficulties, indeed hampers the diversity estimation of fossil groups (Wang & Dodson 2006). Research on particularly estimating the pterosaur diversity also follows this pattern, with few studies having been performed so far (e.g., Butler et al. 2009, 2012, 2013).

There are 189 valid pterosaur genera up to now. Although a deep analysis on pterosaur diversity using different approaches is beyond the scope of this paper, we have estimated it by using the ACE model to reach a result for the generic pterosaur diversity of 807, which means that 23.4% of the pterosaur genera are currently known. Because of the small sample sizes from the Late Triassic to the Mid Jurassic, estimation for these periods are very unreliable (Table 1). These data allowed us to predict the rate of future pterosaur discoveries by fitting a logistic accumulation curve to the cumulative counts of known genera throughout the years using the estimation of pterosaur diversity as the point where the curve becomes an asymptote. This curve indicates that near 2060 about half of the pterosaur diversity will be known, and predicts

that 90% of this diversity will have been unveiled up to 2145 (Figure 9).

From 2000 to 2019, 116 genera were described, which means that in those two decades on average 6.11 new genera are described per year. The prediction that 90% of the generic richness will be known in 2145 requires 5.5 new genera to be described per year, or that in a bit more than a century, 540 new genera need to be described.

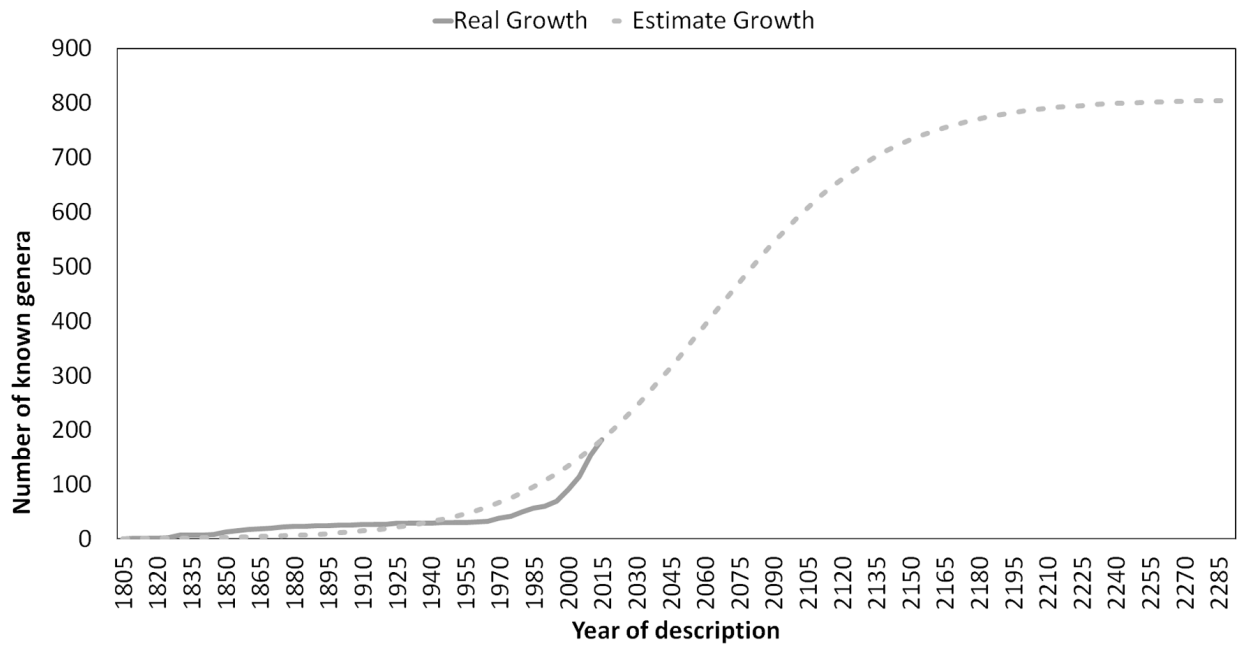
The number of 807 genera is especially low for the entire Mesozoic when compared to the current diversity of flying vertebrates, and to the diversity of land vertebrates of the time. Neornithes, a group that includes all living birds, is presently the most diverse clade of present-day vertebrates that is widespread to roughly all ecological niches (Gill 2007), and bats (order Chiroptera) account for ~20% of mammal diversity, which make these modern flying vertebrates one of the largest monophyletic mammalian clades (Lei & Dong 2016). It is estimated that 88% of bats that ever existed did not enter the fossil record (Eiting & Gunnell 2009), and the similarity of Character Completeness Metric (CCM) records for pterosaurs, extinct chiropterans and birds are probably due to similar taphonomic bias related to their resembling ecologies (Dean et al. 2016, Brocklehurst et al. 2012, Brown et al. 2019). Thus, a low percentage of the pterosaurs that ever existed is also expected.

## **CONCLUSIONS**

The level of taxonomic identification relies on which parts of the morphology are preserved, and how complete they are. Analyzed data showed that 31 from 227 pterosaur species (13.7%) are erected based on single elements that are mostly complete or partial mandibles (n=18). Selection of characters relies on how deep is our taxonomic approach as we mainly deal

**Table I. Generic diversity (richness) estimated for each Mesozoic periods and the entire Mesozoic. Since some genera are found in the interface of two epochs, the sum of the richness of these subperiods do not add up to the richness of the entire Mesozoic.**

Period	Known diversity	Estimated diversity	Percentage known
Entire Mesozoic	189	807	23.4%
Late Triassic	13	25	52.0%
Early Jurassic	5	6	89.3%
Mid Jurassic	15	35	42.5%
Late Jurassic	38	141	27.0%
Early Cretaceous	82	396	20.7%
Late Cretaceous	43	196	22.0%



**Figure 9. Rate of future pterosaur discoveries using a logistic accumulation curve of the form  $y=807/(1+806*e^{(-0,026026*t)})$ . The dotted line represents the estimated curve, and the solid line corresponds to the known growth.**

with combination of morphological characters to advocate species recognition, but the lack of a critical approach to erect new taxa without sufficient comparison with other species and/or an extensive review may lead to inadequate taxonomic results. The fragmentary nature of some fossils can also raise doubts on the validity of the erected species and could be avoided by a more deepened and detailed taxonomic

study. Finally the limited sample size of fossils hampers the recognition of morphotypes and thus intermediate morphologies could not be identified. Despite all these problems, we refrain from advocating against the erection of new taxa based on limited and/or isolated material, but suggest being particularly cautious when species-level taxa are erected. Moreover, since some deposits will provide mostly fragmented



and incomplete fossil material (as many type specimens are incomplete but diagnostic in vertebrate paleontology), as far as the requirements of a broad and cautious revision of genus/group are properly undertaken, the assignment of these fairly incomplete specimens to the most inclusive taxonomic level is feasible.

We still have much more than half of the estimated pterosaur genera to discover (more specifically, 77.9% is yet to be discovered), which justify the continuous effort of unveiling this diversity by describing new taxa, even though if we account for single, very fragmented material (together with deepening the taxonomic level of investigation). As this statistical survey regarding the nature and number of the osteological structures that use to define new pterosaur taxa has never been made before, tracing this scenario has the potential to guide future works on the description of new pterosaur taxa.

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#### Author contributions

FRC and IN conceived and designed the study; DLF collected all data; FRC, DLF and IN wrote the paper. All authors have discussed and reviewed the manuscript.

