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MEMOIR ARTICLE

PHYLOGENETIC SYSTEMATICS OF *QUETZALCOATLUS* LAWSON 1975 (PTERODACTYLOIDEA: AZHDARCHOIDEA)

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ABSTRACT—The Azhdarchidae have come to be known as the most diverse clade of Late Cretaceous pterosaurs and the largest flying creatures in existence. Since the erection of the taxon nearly four decades ago, many partial specimens have been referred to it from the Early Cretaceous and Late Jurassic, but none of these identifications can be confirmed. The most comprehensive phylogenetic analysis and taxonomy of Pterosauria is presented, and the evolutionary history of the Azhdarchidae is reviewed. As currently known, azhdarchids are restricted to the Late Cretaceous (Turonian–Maastrichtian). Fourteen species are currently included in the Azhdarchidae: *Quetzalcoatlus northropi* and *Q. lawsoni* are recovered as sister taxa in a monophyletic *Quetzalcoatlus*, with *Arambourgiania philadelphiae*, *Hatzegopteryx thambema*, a trichotomy with *Cryodrakon boreas* and *Wellnhopterus brevirostris*, *Zhejiangopterus linhaiensis*, *Eurazhdarcho langendorfensis*, a *Phosphatodraco mauritanicus* + *Aralazhdarcho bostobensis* sister group, as well as an *Azhdarcho lancicollis* + *Albadraco tharmisensis* + *Aerotitan sudamericanus* + *Mistralazhdarcho maggii* clade are recovered as successive outgroups to *Quetzalcoatlus* in the Azhdarchidae. The previous azhdarchid species *Montanazhdarcho minor* and *Radiodactylus langstoni* are recovered as non-azhdarchid azhdarchiforms; *Alanqa saharica* and *Argentinadraco barrealensis* are thalassodromines; *Cretornis hlavaci* and *Volgadraco bogolubovi* are pteranodontians; and *Bakonydraco galaczi* is a tapejarine. Up to a dozen pterosaur lineages persist into the latest Cretaceous (Maastrichtian Age) including azhdarchids, pteranodontids, and nyctosauromorphs. In the Late Cretaceous, an ornithocheirid, cimoliopterids, a lonchodrachonid, a lonchodectid, pteranodontians, tapejarines, thalassodromines, a chaoyangopterine, and azhdarchiforms are present. The pterosaurs did not have a terminal decline in diversity and were increasing in species number at the end of the Cretaceous Period.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The giant pterosaur *Quetzalcoatlus* has been invoked in almost 40 years of pterosaur systematics. It is used in the phylogenetic definitions of 15 pterosaur clades (Andres et al., 2014)—more than any other taxon—and it is the basis of the taxon Azhdarchidae, all without a clear delineation and description of its component species. To this end, a comprehensive phylogenetic analysis is presented here of the Pterosauria with *Quetzalcoatlus northropi* Lawson, 1975, *Quetzalcoatlus lawsoni* Andres and Langston, 2021, *Wellnhopterus brevirostris* Andres and Langston, 2021, the putative species of the Azhdarchidae, and Late Cretaceous pterosaurs. At stake is our understanding of pterosaur evolution. *Quetzalcoatlus* figures into discussion of the quality of the pterosaur fossil record as well as the evolution and extinction of the last pterosaurs.

That *Quetzalcoatlus* is a member of the Azhdarchidae is unquestioned. It was incorporated in the first iteration of the Azhdarchidae (Nesov, 1984) and every subsequent one, becoming codified into first phylogenetic definitions for the clade in the same journal and issue (Kellner, 2003; Unwin, 2003). However, the taxonomic content of the Azhdarchidae has varied greatly. Hundreds of specimens over almost 90 million years of geological time have been referred to the Azhdarchidae (see Averianov, 2014, for a review). More specimens have been referred to the Azhdarchidae than to any other specific pterosaur taxon, with the possible exception of *Pteranodon* (Bennett, 1991:table 27, 1994).

Although azhdarchid species have traditionally been found in Late Cretaceous deposits, specimens dating back to the Late Jurassic have been referred to the Azhdarchidae. The oldest of these were dated from the Kimmeridgian–Tithonian ages (Sayão and Kellner, 2001; Kellner et al., 2007; Costa et al., 2013, 2015), making them contemporaneous with the oldest of the pterodactyloid pterosaurs known at the time. This would imply a ghost lineage (Norell, 1992) of up to 65 million years between the oldest referred specimens and the traditionally recognized species of the Azhdarchidae. Considering that the azhdarchids are both the youngest and least basal pterodactyloids known, this ghost lineage would extend all the major groups of the Pterodactyloidea back into the Jurassic Period and would imply a undocumented explosive radiation in that period (Andres and Ji, 2008). This would in turn indicate a massive amount of unsampled time along those lineages, as well as a high amount of stratigraphic incongruence between the fossil record and phylogeny. Such stratigraphic incongruence is possible. It could be the result of specimen misidentification, poor sampling, misdating of the fossil record, erroneous phylogenetic results, or a combination thereof. There is broad agreement between phylogenetic

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analyses for the position of the Azhdarchidae within the Pterosauria, and all recover this taxon as the highest nested or one of the highest nested pterosaur clades (Kellner, 2003; Unwin, 2003; Andres and Ji, 2008). Evidence of misdated specimens is lacking, and so a poorly sampled fossil record of the pterosaurs (Butler et al., 2009, 2013) might be assumed to be the cause of these putative ghost lineages. All things being equal, a poor sample in and of itself will not bias a scientific analysis; it just means a less robust framework to test hypotheses (Kearney, 2002; Kearney and Clark, 2003; Wiens, 2003; Wilkinson, 2003). Also, such assumptions feed into the bias that the pterosaurs have a poor fossil record.

There is another possibility, however, in which this stratigraphic incongruence can be reconciled with a robust fossil record and a precise phylogeny. All of the putative azhdarchid specimens older than the Late Cretaceous (Turonian Age) were referred to the Azhdarchidae without the use of phylogenetic analysis. The phylogenetic relationships could be correct and the fossil record adequately sampled, but the hypothesized referrals for these specimens could be incorrect. This has been tested before. In the description of *Elanodactylus prolatus* Andres and Ji, 2008, the authors noted similarity between the cervical vertebrae of this Early Cretaceous species and the azhdarchid species. When they subjected both to a phylogenetic analysis of the Pterodactyloidea, they recovered *E. prolatus* as a ctenochasmatid pterosaur instead and determined that the vertebral similarities were due to convergence. Andres and Ji (2008) noted that the oldest of the putative azhdarchid specimens, from the Tendaguru Beds (Kimmeridgian–Tithonian) (Sayão and Kellner, 2001; Kellner et al., 2007) and Purbeck Group (Tithonian–Berriasian, but now identified as the Berriasian Durlston Formation) (Howse and Milner, 1995), were identical in codings to some of the ctenochasmatid vertebrae, and when analyzed phylogenetically they were recovered in the Ctenochasmatidae as well. These codings include the presence of postexapophyses, now known to occur in non-ornithocheiroid pterosaurs (Andres and Ji, 2008; Andres et al., 2010). Andres and Ji (2008) referred these specimens to the contemporaneous Ctenochasmatidae, instead of regarding them as inordinately early azhdarchids, and suggested that the known Azhdarchidae remained exclusively from the Late Cretaceous. Since then, however, the Tendaguru specimens have been again regarded as azhdarchids (Costa et al., 2013, 2015), a Solnhofen species has been placed in the 'Protazhdarchidae' (Frey et al., 2011), and a number of new species have been referred to the Azhdarchidae (Averianov, 2007; Averianov et al., 2008; Ibrahim et al., 2010; Buffetaut et al., 2011; Sullivan and Fowler, 2011; Agnolin and Varricchio, 2012; Novas et al., 2012; Vremir et al., 2013, 2015; Averianov and Ekrt, 2015; Kellner and Calvo, 2017; Vullo et al., 2018; Hone et al., 2019; Solomon et al., 2020), all without explicit phylogenetic analysis. A phylogenetic analysis of the species referred to the Azhdarchidae and the relationships of the Pterosauria is presented here to delineate the evolutionary origin and history of the azhdarchid pterosaurs in order to resolve these issues.

Although the origin of the azhdarchids is in dispute, their prevalence in the Late Cretaceous is not. Until recently, they were the only reported lineage to survive to the latest Cretaceous (Maastrichtian Age), with the possible exception of *Nyctosaurus lamegoi* Price, 1953, although the resolution of the dating of this species has been called into question (Longrich et al., 2018). Whereas the Azhdarchidae are a rather speciose pterosaur group (roughly 10% of valid pterosaur species sensu lato) and the Maastrichtian has the largest number of pterosaur species since the Early Cretaceous, it is difficult to describe pterosaurs as diverse at the end of the Cretaceous Period if there is just one surviving lineage. This has led some authors to suggest that pterosaurs were going extinct before the K-Pg boundary, or at least declining in diversity, and that this could be the result of competition with birds and/or due to the large size of the azhdarchids (Unwin, 1987, 1988, 2006; Slack et al., 2006; McGowan and Dyke, 2007; Butler et al., 2009, 2012, 2013; Benson et al., 2014; Chan, 2017). There has also been a tendency to refer Late Cretaceous pterosaurs to the Azhdarchidae uncritically, and so this epoch may appear to be less taxonomically diverse than it actually was. When considering taxic diversity (species number), there is actually an increase in species in the latest Cretaceous (Longrich et al., 2018). When considering phylogenetic diversity (species plus ghost lineage number), there is a decrease in lineages from an explosive radiation in the Early Cretaceous (Longrich et al., 2018). However, it should be noted that this Early Cretaceous radiation would be more accurately described as a spike in diversity because Late Cretaceous pterosaur diversity was rather constant and comparable to that of the Late Jurassic (Longrich et al., 2018). Conversely, if the referral of the early specimens to the Azhdarchidae is valid, then that explosive radiation would be pushed into the Late Jurassic and the pterosaurs had been declining ever since. If those referrals are not valid, such a hypothesized Late Jurassic radiation is due to the mistaken placement of young taxa in basal positions extending the lineages of less basal lineages back into a short time span, as has been documented in some reconstructions of the early history of the Pterosauria (Andres, 2012). Therefore, the phylogenetic relationships of the Azhdarchidae can determine whether pterosaurs were decreasing in diversity and possibly going extinct before the end of the Cretaceous. To test this hypothesis, numerous Late Cretaceous pterosaur species were included in the phylogenetic analysis of *Quetzalcoatlus* and the relationships of the Pterosauria. This analysis mirrors the work of Longrich et al. (2018), which reported an assemblage of marine pterosaurs in the Maastrichtian Age and addressed terminal pterosaur diversity.

Institutional Abbreviations—**BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; **CAMSM**, Sedgwick Museum, Cambridge, U.K.; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **FSAC**, Faculté des Sciences Aïn Chock, Casablanca, Morocco; **LINHM**, Long Island Natural History Museum, New York; **MB.R.**, Museum für Naturkunde, Leibniz, Institut für Evolutions und Biodiversitätsforschung, Berlin, Germany; **MN**, Museu Nacional Universidade Federal do Rio de Janeiro, Brasil; **NHMUK**, Natural History Museum, London, U.K.; **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; **SMU**, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas; **TMM**, Texas Vertebrate Paleontology Collections, The University of Texas at Austin, Austin, Texas.

MATERIALS AND METHODS

The phylogenetic analysis of *Quetzalcoatlus northropi*, *Q. lawsoni*, *Wellnhopterus brevirostris*, and the relationships of the Pterosauria follows the data and protocols put forward in the supplement of Andres et al. (2014). This has been updated by Wu et al. (2017) and Longrich et al. (2018), as well as the addition of new species and characters unique to this analysis to produce a phylogenetic matrix of 177 taxa by 275 characters. This incorporates the phylogenetically informative characters and the majority of valid species from previous systematic studies of pterosaurs, comprising 70 studies from over 150 years of literature. The input data file for executing the phylogenetic analysis including all taxa, codings, character descriptions, and analysis settings is provided online as SupplementalData1.tnt and curated on MorphoBank as Project 2774 (http://morphobank.org/permalink/?P2774).

Included in the phylogenetic analysis are the azhdarchids from previous analyses: *Arambourgiania philadelphiae* (Arambourg, 1959), *Azhdarcho lancicollis* Nesov, 1984, *Zhejiangopterus linhaiensis* Cai and Wei, 1994, *Hatzegopteryx thambema* Buffetaut et al., 2002, *Phosphatodraco mauritanicus* Pereda-Suberbiola

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et al., 2003, *Aralazhdarcho bostobensis* Averianov, 2007, and *Eurazhdarcho langendorfensis* Vremir et al., 2013; as well as all putative azhdarchid species: '*Pterodactylus macrurus*' (= *Gnathosaurus macrurus*) Seeley, 1869, *Cretornis hlavaci* Frič, 1881, *Montanazhdarcho minor* Padian et al., 1995, *Eoazhdarcho liaoxiensis* Lü and Ji, 2005a, *Bakonydraco galaczi* Ősi et al., 2005, *Volgadraco bogolubovi* Averianov et al., 2008, *Alanqa saharica* Ibrahim et al., 2010, *Aerotitan sudamericanus* Novas et al., 2012, *Radiodactylus langstoni* Andres and Myers, 2013, *Mistralazhdarcho maggii* Vullo et al., 2018, *Cryodrakon boreas* Hone et al., 2019, and *Albadraco tharmisensis* Solomon et al. 2020; and putative azhdarchoids that may have a close relationship to the Azhdarchidae: *Ornithostoma sedgwicki* Seeley, 1891b, *Lacusovagus magnificens* Witton, 2008, *Microtuban altivolans* Elgin and Frey, 2011, and *Aurorazhdarcho primordius* Frey et al., 2011. It should be noted that Bennett (2013a) synonymized '*Pterodactylus*' *micronyx* Meyer, 1856, and *Aurorazhdarcho primordius* into *Aurorazhdarcho micronyx* and referred it to the Ctenochasmatidae. They are kept separate for the purposes of this analysis, but this is not intended as a taxonomic act. The fragmentary possible azhdarchids '*Ornithocheirus*' *buenzeli* Bunzel, 1871, *Ornithostoma orientalis* (= *Bogolubovia orientalis*) Bogolubov, 1914, *Navajodactylus boerei* Sullivan and Fowler, 2011, and *Limnornis corneti* (= *Palaeocursornis corneti*) Kessler and Jurcsák, 1984, are taxonomic equivalents (Wilkinson and Benton, 1995) with other more complete species and were therefore excluded from the analysis; their validity will not be addressed here.

The alpha taxonomy of the species in the phylogenetic analysis follows the literature with the following specifications. The taxonomy of the Solnhofen Limestone Formation pterosaur species follows Jouve (2004) and Bennett (2006, 2007, 2013a, 2013b); Niobrara and Pierre Shale formation taxonomy follows Bennett (1991, 1994, 2001) and Martin-Silverstone et al. (2017); Cambridge Greensand Formation taxonomy follows Rodrigues and Kellner (2013) except that '*Pterodactylus*' *compressirostris* (= *Lonchodectes compressirostris*) Owen, 1851, is considered valid; Araripe Basin taxonomy follows Kellner and Tomida (2000) as updated by Pinheiro and Rodrigues (2017); *Thalassodromeus sethi* Kellner and Campos, 2002, taxonomy follows Pêgas et al. (2018); *B. galaczi* taxonomy follows Ősi et al. (2005, 2011); *Nurhachius ignaciobritoi* Wang et al., 2005, taxonomy follows Lü et al. (2008a); and *Feilongus youngi* Wang et al., 2005, taxonomy follows Wang et al. (2014). *Arambourgiania philadelphiae* and *H. thambema* were coded with all specimens referred to them in the literature. *Ornithostoma sedgwicki*, *Peteinosaurus zambellii* Wild, 1978, *Sinopterus dongi* Wang and Zhou, 2003a, and *Zhenyuanopterus longirostris* Lü, 2010, are restricted to their holotypes. The previously coded *Eosipterus yangi* Ji and Ji, 1997, *Sinopterus gui* Li et al., 2003, and *Nemicolopterus crypticus* Wang et al., 2008, are excluded from the analysis because they are likely juvenile specimens of other known species. The specimens identified as *A. saharica* or cf. *A. saharica* by Ibrahim et al. (2010) and Martill and Ibrahim (2015) were coded for *A. saharica* (except for BSPG 1993 IX 338 that has since been referred to *Apatorhamphus gyrostega* McPhee et al., 2020), but with the rostrum and mandible identifications switched (Longrich et al., 2018; Ibrahim et al., 2020). Similarly, the rostrum and mandible identifications for *M. maggii* are switched and the holotype of *A. sudamericanus* is maintained as a rostrum fragment based on the preponderance of anatomical evidence. Individual specimens were directly coded instead of coding supraspecific taxa or exemplars.

The format for writing character descriptions was taken from Sereno's (2007) review of character argumentation. Both continuous and discrete character partitions were used, with continuous characters automatically rescaled to unity using the 'nstates stand' command (Goloboff and Catalano, 2016). Rescaling to unity results in the maximum change along a branch for a continuous character being equivalent to the maximum change along a branch for a binary character (i.e., 1 step) and is the only accurate method to prevent continuous characters from swamping or being swamped by discrete characters (Thiele, 1993; Wiens, 2001). The continuous characters were coded to four significant figures, and characters greater than the maximum value of 65 were divided by a hundred or a thousand to fit in this range. Meristic, continuous, and any characters that have intermediate states in their transformational series were coded as ordered. Characters were typically given a 0 for their most plesiomorphic state or the end of their transformation series closest to the most plesiomorphic state. All characters were equally weighted. Inapplicable features were reductively coded (Strong and Lipscomb, 1999), that is, neomorphic characters were kept separate from transformational characters. Inapplicable codings were denoted with a hyphen (-) to distinguish them from true missing data, except in the continuous character partition that cannot handle hyphens and so question marks (?) were used instead. Polymorphic coding was used to denote either variation within species or instances where preservation could exclude all but a couple of the possible states.

The analysis was executed using the phylogenetic software TNT (Tree analysis using New Technology) 1.5 (Goloboff et al., 2008). Ambiguous branch support was not used ('rule 1'), that is, branches are collapsed if at least one optimization lacks support (default setting of TNT, Nona, and Pee-Wee), which is compatible with reductive coding of inapplicable states (Strong and Lipscomb, 1999). These zero-length branches were automatically collapsed, and the resultant trees were filtered for best score. Four outgroups were used: *Euparkeria capensis* Broom, 1913, *Ornithosuchus longidens* Huxley, 1877, *Herrerasaurus ischigualastensis* Reig, 1963, and *Scleromochlus taylori* Woodward, 1907. *Euparkeria capensis* was used as the primary outgroup and is therefore listed first in the matrix. Basic tree searches of 2,000 random addition sequence replicates were conducted followed by branch swapping phases using tree bisection reconnection (TBR) and subtree pruning and regrafting (SPR) heuristic searches with trees kept from all replications. The ratchet was also implemented, but it was found to make no difference in the results. Ensemble consistency and retention indices were calculated using the Stats.run script available at the PhyloWiki Web site (http://phylo.wdfiles.com/local--files/tntwiki/Stats.run). It should be noted that TNT starts numbering taxa and characters from 0 instead of 1. Therefore, taxa and characters are listed in SupplementalData1.tnt starting at 0; their true number in succession would be incremented by 1. This has led to some confusion in the literature before (Maisch and Matzke, 2017; Maisch et al., 2017).

RESULTS

The phylogenetic analysis of *Quetzalcoatlus*, *Wellnhopterus*, and the relationships of the Pterosauria resulted in a single most parsimonious tree with a tree length of 1364.991 steps (consistency index [CI] = 0.289, retention index [RI] = 0.788). Support indices are provided in Table S1 in Supplemental Data 2. *Quetzalcoatlus northropi* and *Q. lawsoni* are recovered as sister taxa in a monophyletic *Quetzalcoatlus*, with *Arambourgiania philadelphiae*, *Hatzegopteryx thambema*, a trichotomy with *Cryodrakon boreas* and *Wellnhopterus brevirostris*, *Zhejiangopterus linhaiensis*, *Eurazhdarcho langendorfensis*, a *Phosphatodraco mauritanicus* + *Aralazhdarcho bostobensis* clade, as well as a *Mistralazhdarcho maggii* + *Albadraco tharmisensis* + *Azhdarcho lancicollis* clade as successive outgroups to *Quetzalcoatlus* in the Azhdarchidae. The topology for these relationships is depicted in Figure 1, and the phylogenetic taxonomy based on these relationships is listed in Table 1.

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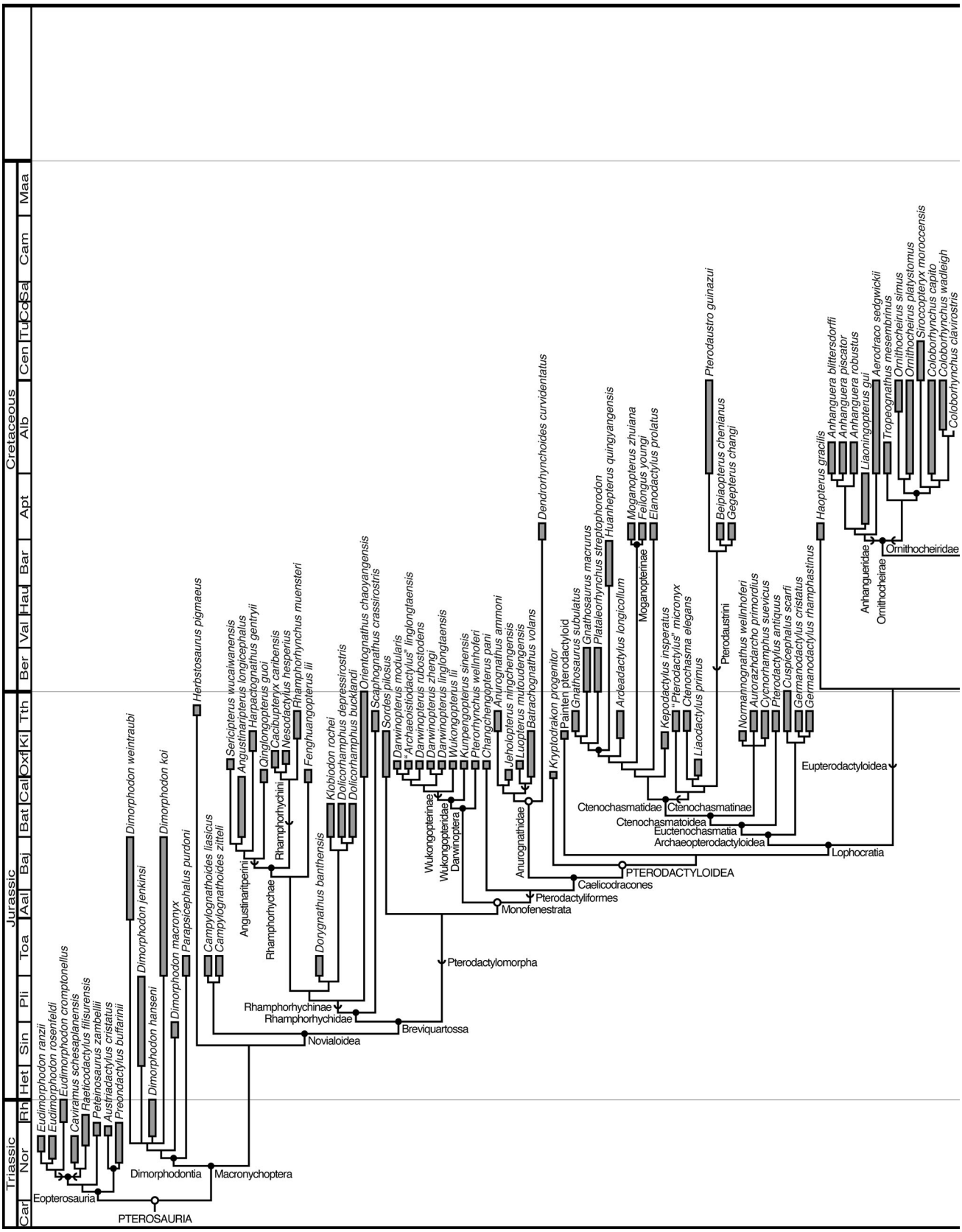


FIGURE 1. Phylogenetic range diagram of pterosaur species in the single most parsimonious tree resulting from the phylogenetic analysis of *Quetzalcoatlus* and the relationships of the Pterosauria. Ranges represent the maximum stratigraphic resolution of species occurrences. Outgroup relationships are not depicted. Clade names with phylogenetic definitions in Table 1 are labeled with a closed circle (●) for node-based definitions, an open circle (○) for apomorphy-based definitions, and a half circle (◡) for branch-based definitions. Not all defined clade names are depicted because of space limitations. Highly uncertain dates for species ranges are omitted, and branch lengths are drawn for visibility. **Mesozoic age name abbreviations: Aal**, Aalenian; **Alb**, Albian; **Apt**, Aptian; **Baj**, Bajocian; **Bar**, Barremian; **Bat**, Bathonian; **Ber**, Berriasian; **Cal**, Callovian; **Cam**, Campanian; **Car**, Carnian; **Cen**, Cenomanian; **Co**, Coniacian; **Hau**, Hauterivian; **Het**, Hettangian; **Ki**, Kimmeridgian; **Maa**, Maastrichtian; **Nor**, Norian; **Oxf**, Oxfordian; **Pli**, Pliensbachian; **Rh**, Rhaetian; **Sa**, Santonian; **Sin**, Sinemurian; **Toa**, Toarcian; **Tth**, Tithonian; **Tu**, Turonian; and **Val**, Valanginian ages.

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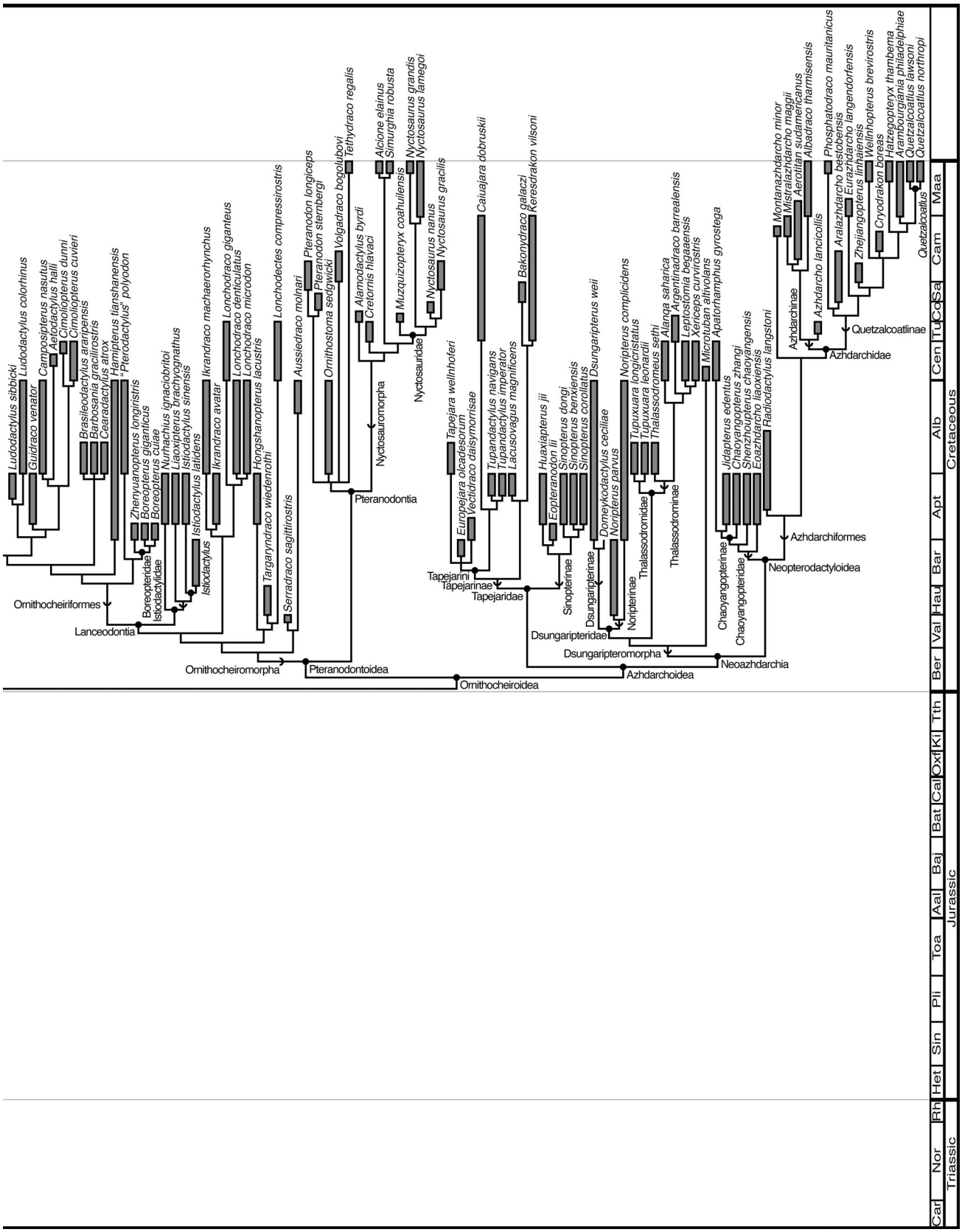


FIGURE 1. (Continued).

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TABLE 1. Phylogenetic nomenclature derived from the analysis of *Quetzalcoatlus* and the relationships of the Pterosauria.

Taxon	Authorship and conversion	Phylogenetic definition
Pterosauria	Owen (1842), sensu Andres and Padian (2020a)	Most inclusive clade exhibiting fourth metacarpal and digit hypertrophied to support wing membrane synapomorphic with that in *Pterodactylus antiquus* (Sömmerring, 1812).
Eopterosauria	Andres et al. (2014)	Least inclusive clade containing *Preondactylus buffarinii* Wild, 1984, and *Eudimorphodon ranzii* Zambelli, 1973.
Preondactylia	Andres et al. (2014)	Least inclusive clade containing *Preondactylus buffarinii* Wild, 1984, and *Austriadactylus cristatus* Dalla Vecchia et al., 2002.
Eudimorphodontoidea	Andres et al. (2014)	Least inclusive clade containing *Eudimorphodon ranzii* Zambelli, 1973, and *Raeticodactylus filisurensis* Stecher, 2008.
Eudimorphodontidae	Wellnhofer (1978), sensu Andres et al. (2014)	Most inclusive clade containing *Eudimorphodon ranzii* Zambelli, 1973, but not *Raeticodactylus filisurensis* Stecher, 2008.
Raeticodactylidae	Andres et al. (2014)	Most inclusive clade containing *Raeticodactylus filisurensis* Stecher, 2008, but not *Eudimorphodon ranzii* Zambelli, 1973.
Macronychoptera	Unwin (2003)	Least inclusive clade containing *Dimorphodon macronyx* (Buckland, 1829) and *Quetzalcoatlus northropi* Lawson, 1975.
Dimorphodontia	Andres et al. (2014)	Least inclusive clade containing *Dimorphodon macronyx* (Buckland, 1829) and *Parapsicephalus purdoni* (Newton, 1888).
Novialoidea	Kellner (2003)	Least inclusive clade containing *Campylognathoides zitteli* (Plieninger, 1894) and *Quetzalcoatlus northropi* Lawson, 1975.
Breviquartossa	Unwin (2003)	Least inclusive clade containing *Rhamphorhynchus muensteri* (Goldfuß, 1831) and *Quetzalcoatlus northropi* Lawson, 1975.
Rhamphorhynchidae	Hoernes (1884), sensu Unwin (2003)	Least inclusive clade containing *Rhamphorhynchus muensteri* (Goldfuß, 1831) and *Scaphognathus crassirostris* (Goldfuß, 1831).
Rhamphorhynchinae	Nopcsa (1928), converted clade name	Most inclusive clade containing *Rhamphorhynchus muensteri* (Goldfuß, 1831) but not *Scaphognathus crassirostris* (Goldfuß, 1831).
Rhamphorhynchae	Seeley (1870), converted clade name	Least inclusive clade containing *Rhamphorhynchus muensteri* (Goldfuß, 1831) and *Angustinaripterus longicephalus* He et al., 1983.
Rhamphorhynchini	Andres et al. (2014)	Most inclusive clade containing *Rhamphorhynchus muensteri* (Goldfuß, 1831) but not *Angustinaripterus longicephalus* He et al., 1983.
Angustinaripterini	Andres et al. (2014)	Most inclusive clade containing *Angustinaripterus longicephalus* He et al., 1983, but not *Rhamphorhynchus muensteri* (Goldfuß, 1831).
Pterodactylomorpha	Andres et al. (2014)	Most inclusive clade containing *Pterodactylus antiquus* (Sömmerring, 1812) but not *Rhamphorhynchus muensteri* (Goldfuß, 1831).
Monofenestrata	Lü et al. (2010), sensu Andres et al. (2014)	Most inclusive clade exhibiting confluent external naris and antorbital fenestra (nasoantorbital fenestra) synapomorphic with that in *Pterodactylus antiquus* (Sömmerring, 1812).
Darwinoptera	Andres et al. (2014)	Least inclusive group containing *Darwinopterus modularis* Lü et al., 2010, and *Pterorhynchus wellnhoferi* Czerkas and Ji, 2002.
Wukongopteridae	Wang et al. (2009)	Least inclusive clade containing *Wukongopterus lii* Wang et al., 2009, and *Kunpengopterus sinensis* Wang et al., 2010.
Wukongopterinae	Zhou et al. (2021)	Most inclusive clade containing *Wukongopterus lii* Wang et al., 2009, but not *Kunpengopterus sinensis* Wang et al., 2010.
Pterodactyliformes	Andres et al. (2014)	Most inclusive clade containing *Pterodactylus antiquus* (Sömmerring, 1812) but not *Darwinopterus modularis* Lü et al., 2010.
Caelicodracones	Unwin (2003)	Least inclusive clade containing *Anurognathus ammoni* Döderlein, 1923, and *Quetzalcoatlus northropi* Lawson, 1975.
Anurognathidae	Kuhn (1937), converted clade name	Most inclusive clade exhibiting a skull wider than long synapomorphic with that in *Anurognathus ammoni* Döderlein, 1923.
Batrachognathinae	Kellner et al. (2010)	Most inclusive clade containing *Batrachognathus volans* Rjabinin, 1948, but not *Anurognathus ammoni* Döderlein, 1923.
Pterodactyloidea	Plieninger (1901), sensu Andres and Padian (2020b)	Most inclusive clade exhibiting metacarpus at least 80% as long as humerus synapomorphic with that in *Pterodactylus antiquus* (Sömmerring, 1812).
Lophocratia	Unwin (2003)	Least inclusive clade containing *Pterodaustro guinazui* Bonaparte, 1970, and *Quetzalcoatlus northropi* Lawson, 1975.
Archaeopterodactyloidea	Kellner (2003), converted clade name	Least inclusive clade containing *Pterodactylus antiquus* (Sömmerring, 1812), *Ctenochasma elegans* (Wagner, 1861), and *Germanodactylus cristatus* (Wiman, 1925).
Euctenochasmatia	Unwin (2003)	Least inclusive clade containing *Pterodactylus antiquus* (Sömmerring, 1812) and *Pterodaustro guinazui* Bonaparte, 1970.
Ctenochasmatoidea	Unwin (1995), sensu Unwin (2003)	Least inclusive clade containing *Cycnorhamphus suevicus* (Quenstedt, 1855) and *Pterodaustro guinazui* Bonaparte, 1970.
Ctenochasmatidae	Kuhn (1967), converted clade name	Least inclusive clade containing *Ctenochasma elegans* (Wagner, 1861) and *Gnathosaurus subulatus* Meyer, 1834.
Ctenochasmatinae	Nopcsa (1928), sensu Andres et al. (2014)	Most inclusive clade containing *Ctenochasma elegans* (Wagner, 1861) but not *Gnathosaurus subulatus* Meyer, 1834.
Pterodaustrini	Andres et al. (2014)	Most inclusive clade containing *Pterodaustro guinazui* Bonaparte, 1970, but not *Ctenochasma elegans* (Wagner, 1861).
Moganopterinae	Lü et al. (2012), sensu Andres et al. (2014)	Least inclusive clade containing *Moganopterus zhuiana* Lü et al., 2012, and *Feilongus youngi* Wang et al., 2005.
Gnathosaurinae	Unwin et al. (2000), sensu Unwin (2002)	Least inclusive clade containing *Gnathosaurus subulatus* Meyer, 1834, and *Huanhepterus quingyangensis* Dong, 1982.
Eupterodactyloidea	Bennett (1994), sensu Andres et al. (2014)	Least inclusive clade containing *Pteranodon longiceps* Marsh, 1876, but not *Pterodactylus antiquus* (Sömmerring, 1812).

(*Continued*)

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TABLE 1. Continued.

Taxon	Authorship and conversion	Phylogenetic definition
Ornithocheiroidea	Seeley (1891a), sensu Kellner (2003)	Least inclusive clade containing *Anhanguera blittersdorffi* Campos and Kellner, 1985, *Pteranodon longiceps* Marsh, 1876, *Dsungaripterus weii* Young, 1964, and *Quetzalcoatlus northropi* Lawson, 1975.
Pteranodontoidea	Kellner (2003)	Least inclusive clade containing *Anhanguera blittersdorffi* Campos and Kellner, 1985, and *Pteranodon longiceps* Marsh, 1876.
Pteranodontia	Marsh (1876), sensu Unwin (2003)	Least inclusive clade containing *Pteranodon longiceps* Marsh, 1876, and *Nyctosaurus gracilis* (Marsh, 1876).
Nyctosauromorpha	New clade name	Most inclusive clade containing *Nyctosaurus gracilis* (Marsh, 1876) but not *Pteranodon longiceps* Marsh, 1876.
Nyctosauridae	Hay (1902), sensu Andres et al. (2014)	Least inclusive clade containing *Nyctosaurus gracilis* (Marsh, 1876) and *Muzquizopteryx cohuilensis* Frey et al., 2006.
Ornithocheiromorpha	Andres et al. (2014)	Most inclusive clade containing *Ornithocheirus simus* (Owen, 1861) but not *Pteranodon longiceps* Marsh, 1876.
Boreopteridae	Lü et al. (2006a), sensu Jiang et al. 2014	Least inclusive clade containing *Boreopterus cuiae* Lü and Ji, 2005a, and *Zhenyuanopterus longirostris* Lü, 2010.
Lanceodontia	Andres et al. (2014)	Least inclusive clade containing *Anhanguera blittersdorffi* Campos and Kellner, 1985, and *Istiodactylus latidens* (Seeley, 1901).
Istiodactylidae	Howse et al. (2001), sensu Andres et al. (2014)	Least inclusive clade containing *Istiodactylus latidens* (Seeley, 1901) and *Nurhachius ignaciobritoi* Wang et al., 2005.
Istiodactylinae	Andres et al. (2014)	Least inclusive clade containing *Istiodactylus latidens* (Seeley, 1901) but not *Nurhachius ignaciobritoi* Wang et al., 2005.
Istiodactylus	Howse et al. (2001), sensu Andres et al. (2014)	Least inclusive clade containing *Istiodactylus latidens* (Seeley, 1901) and *Istiodactylus sinensis* Andres and Ji, 2006.
Ornithocheiriformes	New clade name	Most inclusive clade containing *Ornithocheirus simus* (Owen, 1861) but not *Istiodactylus latidens* (Seeley, 1901).
Ornithocheirae	Seeley (1870), sensu Andres and Myers (2013)	Least inclusive clade containing *Ornithocheirus simus* (Owen, 1861) and *Anhanguera blittersdorffi* Campos and Kellner, 1985.
Ornithocheiridae	Zittel (1890), sensu Andres and Myers (2013)	Most inclusive clade containing *Ornithocheirus simus* (Owen, 1861) but not *Anhanguera blittersdorffi* Campos and Kellner, 1985.
Ornithocheirinae	Fürbringer (1900), sensu Andres et al. (2014)	Least inclusive clade containing *Ornithocheirus simus* (Owen, 1861) and *Coloborhynchus clavirostris* Owen, 1874.
Anhangueridae	Campos and Kellner (1985), sensu Andres and Myers (2013)	Most inclusive clade containing *Anhanguera blittersdorffi* Campos and Kellner, 1985, but not *Ornithocheirus simus* (Owen, 1861).
Azhdarchoidea	Unwin (1995), sensu Kellner (2003) and Unwin (2003)	Least inclusive clade containing *Tapejara wellnhoferi* Kellner, 1989, and *Quetzalcoatlus northropi* Lawson, 1975.
Tapejaridae	Kellner (1989), sensu Lü et al. (2006b)	Least inclusive clade containing *Tapejara wellnhoferi* Kellner, 1989, and *Sinopterus dongi* Wang and Zhou, 2003a.
Tapejarinae	Kellner and Campos (2007), sensu Andres et al. (2014)	Most inclusive clade containing *Tapejara wellnhoferi* Kellner, 1989, but not *Sinopterus dongi* Wang and Zhou, 2003a.
Tapejarini	Andres et al. (2014)	Least inclusive clade containing *Tapejara wellnhoferi* Kellner, 1989, and *Tupandactylus imperator* (Campos and Kellner, 1997).
Sinopterinae	Lü et al. (2016), converted clade name	Most inclusive clade containing *Sinopterus dongi* Wang and Zhou, 2003a, but not *Tapejara wellnhoferi* Kellner, 1989.
Neoazhdarchia	Unwin (2003)	Least inclusive clade containing *Tupuxuara longicristatus* Kellner and Campos, 1988, and *Quetzalcoatlus northropi* Lawson, 1975.
Dsungaripteromorpha	Andres et al. (2014)	Most inclusive clade containing *Dsungaripterus weii* Young, 1964, but not *Quetzalcoatlus northropi* Lawson, 1975.
Thalassodromidae	Witton (2008), converted clade name	Least inclusive clade containing *Thalassodromeus sethi* Kellner and Campos, 2002, and *Tupuxuara longicristatus* Kellner and Campos, 1988.
Thalassodrominae	Kellner and Campos (2007), converted clade name	Most inclusive clade containing *Thalassodromeus sethi* Kellner and Campos, 2002, but not *Tupuxuara longicristatus* Kellner and Campos, 1988.
Dsungaripteridae	Young (1964), sensu Unwin (2003)	Least inclusive clade containing *Dsungaripterus weii* Young, 1964, and *Noripterus complicidens* Young, 1973.
Noripterinae	Andres et al. (2014)	Most inclusive clade containing *Noripterus complicidens* Young, 1973, but not *Dsungaripterus weii* Young, 1964.
Dsungaripterinae	Andres et al. (2014)	Most inclusive clade containing *Dsungaripterus weii* Young, 1964, but not *Noripterus complicidens* Young, 1973.
Neopterodactyloidea	Andres et al. (2014)	Least inclusive clade containing *Chaoyangopterus zhangi* Wang and Zhou, 2003b, and *Quetzalcoatlus northropi* Lawson, 1975.
Chaoyangopteridae	Lü et al. (2008b), sensu Andres et al. (2014)	Most inclusive clade containing *Chaoyangopterus zhangi* Wang and Zhou, 2003b, but not *Quetzalcoatlus northropi* Lawson, 1975.
Chaoyangopterinae	Andres et al. (2014), converted clade name	Least inclusive clade containing *Chaoyangopterus zhangi* Wang and Zhou, 2003b, and *Jidapterus edentus* Dong et al., 2003.
Azhdarchiformes	New clade name	Most inclusive clade containing *Quetzalcoatlus northropi* Lawson, 1975, but not *Chaoyangopterus zhangi* Wang and Zhou, 2003b.
Azhdarchidae	Padian (1986), sensu Unwin (2003)	Least inclusive clade containing *Azhdarcho lancicollis* Nesov, 1984, and *Quetzalcoatlus northropi* Lawson, 1975.
Azhdarchinae	Nesov (1984), converted clade name	Most inclusive clade containing *Azhdarcho lancicollis* Nesov, 1984, but not *Quetzalcoatlus northropi* Lawson, 1975.
Quetzalcoatlinae	Andres et al. (2014)	Most inclusive clade containing *Quetzalcoatlus northropi* Lawson, 1975, but not *Azhdarcho lancicollis* Nesov, 1984.
Quetzalcoatlus	Lawson (1975), converted clade name	Least inclusive clade containing *Quetzalcoatlus northropi* Lawson, 1975, and *Quetzalcoatlus lawsoni* Andres and Langston, 2021.

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Systematics of *Quetzalcoatlus*

With the exception of referring *Quetzalcoatlus* to the Pterodactyloidea (Wellnhofer, 1978; Langston, 1981) and the suggestion by Langston (1978, 1981) that it may be a junior synonym of *Titanopteryx* (= *Arambourgiania*), the evolutionary relationships of *Quetzalcoatlus* were not discussed until almost a decade after its discovery. Langston's (1978, 1981) initial concerns turned out to be unwarranted: *Titanopteryx* was a junior homonym of a black fly previously named by Enderlein (1934), the pterosaur was renamed *Arambourgiania* (Nesov et al., 1987) after *Quetzalcoatlus* had been named, and *Quetzalcoatlus* has since been considered distinct from *Arambourgiania* (Martill et al., 1998).

After a decade's lack of systematic interest, two papers published in the same year classified *Quetzalcoatlus*. In the first of these, Nesov (1984) erected the Azhdarchinae within the Pteranodontidae and placed within it three genera: his new *Azhdarcho*, *Quetzalcoatlus*, and *Titanopteryx* (= *Arambourgiania*). This group was named unbeknownst to Padian (1984), who diagnosed the Pteranodontidae and erected the Titanopterygiidae later in the same year for the reception of *Titanopteryx* (= *Arambourgiania*) and *Quetzalcoatlus*. Later, Padian (1986) addressed this taxonomic issue. He believed that the diagnoses of the cervical vertebrae were identical and so awarded priority to the name Azhdarchinae, but removed it from the Pteranodontidae and elevated it to the family rank, creating the name Azhdarchidae in the process. Padian's (1984) Titanopterygiidae (= *Arambourgiania* + *Quetzalcoatlus*) has a significantly smaller circumscription than Nesov's (1984) Azhdarchinae (= *Azhdarcho* + *Quetzalcoatlus* + *Arambourgiania*) and could theoretically be considered a subset of the latter. To have a clade with a family name suffix inside a clade with a subfamily name suffix would cause consternation to followers of ranked taxonomy; also, the nominotypical genus of the Titanopterygiidae has been changed to *Arambourgiania*. We honor historical usage in referring *Quetzalcoatlus* to the Azhdarchidae. Following Recommendation 9.8A of the PhyloCode, authorship and date of Azhdarchidae is Padian (1986), referring to the original publication of that name spelled the same way as when it was converted into a phylogenetic name and regardless of the rank and composition originally associated with the name (Cantino and de Queiroz, 2010).

The year 1986 also marked the first phylogenetic analysis of *Quetzalcoatlus* and pterosaurs in general. Howse (1986) conducted a phylogenetic analysis of the cervical vertebrae of the pterodactyloids that included casts of *Quetzalcoatlus* cervicals (TMM 41544-8, 41544-15, and 41544-16) reposited in the NHMUK (NHMUK R 9323, 9325, and 9326, respectively). He recovered *Quetzalcoatlus* in a polytomy with *Doratorhynchus* (= *Gnathosaurus macrurus*), Cambridge Greensand Formation long cervical vertebrae, *Azhdarcho*, and *Titanopteryx* (= *Arambourgiania*) within a group he called 'Long-necked Pterodactyloids' or 'advanced pterodactyloids'. He mirrored Padian (1986) in independently linking *Doratorhynchus* (= *G. macrurus*), *Azhdarcho*, *Titanopteryx* (= *Arambourgiania*), and *Quetzalcoatlus* in the single taxonomic group Azhdarchidae. However, Howse (1986) did not publish a matrix or any analytical procedures to replicate these results. Andres and Ji (2008) later tested these conclusions with a larger analysis of pterodactyloids with characters from the entire skeleton. They recovered *G. macrurus* as a ctenochasmatid pterodactyloid and noted the convergence in cervical vertebrae between the Azhdarchidae and Ctenochasmatidae, pointing out that the earliest reported occurrences of azhdarchids are more likely contemporary occurrences of ctenochasmatids.

Quetzalcoatlus, to the extent that it was accurately known, was present in the first phylogenetic analysis and almost all analyses of pterodactyloids since, but with much the same results—recovery in an unresolved Azhdarchidae. Bennett (1991, 1994) put forward that *Quetzalcoatlus* and *Azhdarcho* were more closely related to each other than *Doratorhynchus* (= *G. macrurus*) or *Arambourgiania*, based on edentulous jaws (Bennett, 1991, 1994) and the inverted 'T-shaped' cross-section of the second and third wing phalanges (Bennett, 1994). However, the former condition is unknown in *Arambourgiania* and the latter condition is unknown in both, and so this group could not have been fully resolved. Also, Figure 8 of Bennett (1994) depicts *Quetzalcoatlus* and *Arambourgiania* as more closely related to each other than to *Azhdarcho* and *Doratorhynchus* (= *G. macrurus*), and so there seems to be some confusion.

This lack of resolution presented a problem for defining the Azhdarchidae in the first phylogenetic taxonomies of Kellner (2003) and Unwin (2003). These first large-scale pterosaur phylogenies and taxonomies were published back to back in the same publication. Fortunately, the new names erected by Kellner (2003) and Unwin (2003) used different specifiers for the most part, and when their data were combined (e.g., Andres and Ji, 2008; Andres et al., 2010; Andres and Myers, 2013; Andres et al., 2014; Wu et al., 2017; Longrich et al., 2018), they resulted in different names for different clades. Unfortunately, different specifiers were also used for previous clade names that both publications converted into phylogenetic nomenclature, such as the Azhdarchidae. Kellner (2003:125) defined the Azhdarchidae as "All pterosaurs closer related to *Quetzalcoatlus* than to any other pterosaur". This definition is problematic. A strict reading would suggest that the Azhdarchidae would only include *Quetzalcoatlus*. Even if the definition referred to the sister group of *Quetzalcoatlus* and another pterosaur, the clade to which the name would refer would change with whatever the closest taxon happens to be in analysis. Unwin (2003:181) defined the Azhdarchidae as "*Azhdarcho lancicollis, Quetzalcoatlus northropi*, their most recent common ancestor, and all its descendants". The specifiers date back to two of Nesov's (1984) original three taxa, and subsequent analyses have recovered nearly all of the traditional azhdarchids in this group (e.g., Andres and Myers, 2013; Longrich et al., 2018). Therefore the phylogenetic definition of Unwin (2003) is the one used here for this group: Azhdarchidae Padian, 1986, sensu Unwin (2003). Numerous specimens have been referred to the Azhdarchidae over the years (see Averianov, 2014, for a review), and not all these specimens fall within this definition.

Since the inclusion of *Quetzalcoatlus* and other azhdarchids in the first phylogenetic analysis and over 30 years of pterosaur phylogenetic analyses, only four publications have resolved their relationships: Andres and Myers (2013), Andres et al. (2014), Wu et al. (2017), and Longrich et al. (2018) recovered *A. philadelphiae* Arambourg, 1959, *Z. linhaiensis* Cai and Wei, 1994, and *A. lancicollis* Nesov, 1984 as successive sister groups to *Quetzalcoatlus* in the Azhdarchidae. Andres and Myers (2013) went further to analyze the Texas pterosaur specimens SMU 72547 and TMM 42489 (= *W. brevirostris*) in relation to the azhdarchids. SMU 72547 is a left humerus originally described and referred to the Azhdarchidae by Murry et al (1991), but the authors noted that some of the characters used to do so might be plesiomorphic for the clade. It is not surprising that this specimen was recovered as the sister group to the Azhdarchidae, especially considering that it is significantly older than that clade. Andres and Myers (2013) diagnosed and named this specimen *Radiodactylus langstoni* Andres and Myers, 2013, after the Comanche Peak Nuclear Power Plant where this specimen was discovered during the construction of an emergency spillway, and in honor of Wann Langston, Jr.

Evolutionary History of the Pterosauria

The resultant phylogeny is the largest analysis of the pterosaurs to date, with 48,675 separate codings. Despite its size, it remains highly congruent with stratigraphy, surpassed only by the perfect congruence of Maisch et al.'s (2004) seven-taxon ingroup (Andres, 2010). This stratigraphic congruence means

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that there are not extensive ghost lineages obscuring the history of the pterosaurs; therefore, various evolutionary patterns can be recognized: the initial adaptive radiation of the pterosaurs consisted only of Triassic species followed by a phylogenetic bottleneck at the end of the Triassic; the Early Jurassic is dominated by dimorphodontians possibly representing a disaster taxon surviving the end Triassic extinction; rhamphorhynchids, darwinopterans, anurognathids, and pterodactyloids radiated in the Middle Jurassic followed by the end-Jurassic extinctions; the explosive radiation of the pterodactyloids in the Early Cretaceous is succeeded by steady diversity afterward; and the origin of the Azhdarchidae occurs in the Late Cretaceous with a spike in diversity before the end-Cretaceous extinctions. This last evolutionary pattern is discussed in detail.

Origins of the Azhdarchidae—A multitude of specimens has been referred to the Azhdarchidae. Pterosaurs from essentially every major pterosaur-bearing formation since the Late Jurassic and from every major group of the Pterodactyloidea have been referred to this group. Such a specimen-level review of hundreds of individuals is beyond the scope of an analysis of *Quetzalcoatlus* and the species of the Azhdarchidae. Therefore, this discussion will delineate the relationships of the species and the early specimens referred to the Azhdarchidae. No specimen or species was found to extend the range of the Azhdarchidae before the Turonian, the age of *Azhdarcho lancicollis*.

The oldest putative azhdarchids are two mid-cervical vertebrae housed in the MB.R. and are from the Upper Jurassic (Kimmeridgian–Tithonian) Tendaguru Beds of Tanzania (Sayão and Kellner, 2001; Kellner et al., 2007; Costa et al., 2013, 2015). A nearly complete mid-cervical vertebrae (MB.R. 2832) was identified as an azhdarchid by Sayão and Kellner (2001) based on its dimensions and termed Azhdarchidae indet. by Kellner et al. (2007), to which Costa et al. (2013, 2015) later added the posterior end of a mid-cervical vertebrae (MB.R. 2823). Before the discovery of *Kryptodrakon progenitor* Andres et al., 2014, the oldest pterodactyloids were Kimmeridgian in age, making the highly derived azhdarchids possibly the oldest known pterodactyloids at the time. This referral has been questioned by Andres and Ji (2008) and Averianov (2014), and the contemporaneous Ctenochasmatidae was put forward as a more defensible identification instead. Costa et al. (2015) stated that the argument presented by Andres and Ji (2008) was based on similarity to *Elanodactylus prolatus*; this is incorrect. Placement in the Ctenochasmatidae by Andres and Ji (2008) was the result of phylogenetic analysis. The codings of MB.R. 2832 were identical to the Durlston Formation cervicals, and when analyzed separately they were recovered in a monophyletic Ctenochasmatidae. Costa et al. (2015) were correct that the absence of pneumatic foramina on the lateral surface of the mid-cervical centrum would result in MB.R. 2832 being recovered as an azhdarchid. However, MB.R. 2832 does have pneumatic foramina on the lateral surfaces of the centrum. The observations of this material in Costa et al. (2015) appear to have been made on casts and photographs of admittedly imperfectly preserved material, and the area that preserves the pneumatic foramina in MB.R. 2832 in their figure 2 is in shadow. Even without this observation, Costa et al. (2015) do not identify pneumatic foramina lateral to the neural canal in the neural arch of these cervicals. Subsequent phylogenetic analyses have included this character and shown these neural foramina to be present in the Azhdarchidae and absent in the Ctenochasmatidae. In addition, Andres and Ji (2008) recovered the postexapophyses present in MB.R. 2832 to be convergently present in ctenochasmatid and ornithocheiroid (including the azhdarchids) pterosaurs. An elongate wing metacarpal from the Tendaguru Beds was identified as that of a possible azhdarchid by Sayão and Kellner (2001) and Kellner et al. (2007), but Costa et al. (2015) allocated it to just within the 'Tapejaroidea' (= Azhdarchoidea). There are no known azhdarchids in the Kimmeridgian Age.

One pterosaur taxon from the Solnhofen Limestone was listed as ?Azhdarchidae by Barrett et al. (2008). This early Tithonian specimen was later named *Aurorazhdarcho primordius* by Frey et al. (2011) and placed by itself in the new family 'Protazhdarchidae'. The rationale for this was the referral of the specimen to the Azhdarchoidea and the listing of the azhdarchid features that it lacked. Frey et al. (2011) eschewed a phylogenetic analysis in favor of a functional argument, but from their discussion it appears that they consider *A. primordius* to be either a basal azhdarchoid or sister group to the Azhdarchoidea. It is correct that *A. primordius* has some features found in azhdarchoid pterosaurs. However, those features are also found in *Cycnorhamphus suevicus* (Quenstedt, 1855), which the authors stated was complete enough to compare but did not do so in the text. When subjected to phylogenetic analysis, *A. primordius* is recovered in a trichotomy with *C. suevicus* and *Normannognathus wellnhoferi* Buffetaut et al., 1998, in the Ctenochasmatoidea instead of the Azhdarchoidea. Bennett (2013a) considered *A. primordius* a junior synonym of '*Pterodactylus*' *micronyx* but still distinct from *Pterodactylus*, and so he subsumed it into the new combination *Aurorazhdarcho micronyx*. He referred this taxon to the Ctenochasmatidae. These species were not combined in this phylogenetic analysis to assess the taxonomy of Frey et al. (2011), with *A. primordius* recovered as a non-ctenochasmatid ctenochasmatoid and *'Pterodactylus' micronyx* recovered as a ctenochasmatine ctenochasmatid. There are no known azhdarchids in the Solnhofen Limestone.

The only other possible Jurassic azhdarchid was an elongate mid-cervical, CAMSM J5340, and associated mandible, CAMSM J5339, from the Purbeck Group, which is dated to the Tithonian–Berriasian (Howse, 1986; Howse and Milner, 1995), although the pterosaur-bearing Durlston Formation of this group has been more specifically dated to the Berriasian Age of the Cretaceous (Allen and Wimbledon, 1991; Barrett et al., 2008). These were originally named '*Pterodactylus*' *macrurus* Seeley, 1869, but Seeley (1875) referred this material to '*Pterodactylus validus*' Owen, 1870 (an isolated wing phalanx), and erected the genus name '*Doratorhynchus*' for the latter species. One or both of these elements, listed as '*Doratorhynchus validus*', were recovered in the Azhdarchidae by the phylogenetic analyses of Howse (1986) and Bennett (1989, 1991, 1994). '*Doratorhynchus validus*' ironically turned out to be not valid and was restricted to its holotype wing phalanx by Howse and Milner (1995), who made the cervical a lectotype of the '*P.*' *macrurus* species and referred it to *Gnathosaurus*. The cervical and mandible were presumed to belong to the same individual (Seeley, 1869) and in association (Seeley, 1875), and so Howse and Milner (1995) may have been overly cautious in their taxonomy. Either way, Howse and Milner (1995) referred both CAMSM J5339 and CAMSM J5340, as well as the posterior end of a mid-cervical, NHMUK 48387, to the Ctenochasmatidae. Andres and Ji (2008) phylogenetically analyzed CAMSM J5339 and CAMSM J5340 together and apart, and both times recovered these specimens as ctenochasmatids. Subsequent analyses, including this one, have kept both specimens in *Gnathosaurus macrurus*. Martill et al. (2013) also referred to an incomplete wing metacarpal from the same locality as ?Azhdarchidae, gen. et sp. indet., but Averianov (2014) stated that there are no reasons to attribute this specimen to the Azhdarchidae and it can be referred to *G. macrurus* instead. There are no azhdarchids in the Jurassic Period.

Some Early Cretaceous specimens previously referred to the Azhdarchidae have since been reassigned to other groups. The anterior end of a cervical vertebra from the Berriasian Age Cornet Bauxite Mine of Romania was tentatively referred to the Azhdarchidae by Dyke et al. (2011) but later identified as just Azhdarchoidea by Averianov (2014). *Eoazhdarcho liaoxiensis* from the Aptian Age Jiufotang Formation of China

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was originally referred to the Azhdarchidae by Lü and Ji (2005b), but it was referred to the Chaoyangopteridae when it was erected by Lü et al. (2008b), which was confirmed by the present analysis as well as by Andres and Ji (2008), Andres et al. (2014), Wu et al. (2017), and Zhou et al. (2017), although Andres and Myers (2013) recovered it as a branch azhdarchid (i.e., on the branch subtending the Azhdarchidae). Sereno et al. (1998) reported an azhdarchid from the Aptian Elrhaz Formation of Niger, but Blackburn (2002) later identified this as a tapejaroid (= azhdarchoid) humerus. A partial humerus from the Aptian Doushan Formation of China identified by Zhou (2010) as Azhdarchidae indet. has since been referred to the Dsungaripteridae (Averianov, 2014). SMNK PAL 2342 and 3830 from the Aptian Crato Formation were identified as azhdarchids because the cross-section of the wing phalanges was said to be 'T'-shaped (Martill and Frey, 1998, 1999; Frey et al., 2003), but this shape results here from the crushing of a triangular cross-section and is missing in SMNK PAL 3830, and these specimens have since been reidentified as tapejarids (Unwin, 2002; Frey et al., 2003; Kellner, 2004; Sayão and Kellner, 2006; Unwin and Martill, 2007; Elgin and Campos, 2011; Vila Nova and Sayão, 2012). Conversely, two tapejarids from the Crato Formation (MN 4729-V and SMNK PAL 3843) were referred to the Azhdarchidae by Averianov (2014), based on a similar 'T'-shaped cross-section that has not been confirmed and a coracoid crest that is also found in tapejarids, respectively. An isolated humerus, SMU 72547, from the Upper Aptian–Lower Albian Glen Rose Formation of Texas, was originally identified as an azhdarchid pterosaur by Murry et al. (1991), but it was later named *Radiodactylus langstoni* and phylogenetically recovered as the sister group to the Azhdarchidae by Andres and Myers (2013); it is recovered as the second sister group to the Azhdarchidae basal to *M. minor* in the current analysis. A pterosaur vertebra from the Sables Vert de l'Albien (Albian Greensand) Formation of France was referred to the Azhdarchidae but later identified as an indeterminate azhdarchoid by Averianov (2014). *Bennettazhia oregonensis* (Gilmore, 1928) from the Albian Hudspeth Formation of Oregon was first suggested to be an azhdarchid by Bennett (1989) and later given the name *Bennettazhia* and placed in the Azhdarchidae by Nesov (1991). Andres and Myers (2013), Andres et al. (2014), Wu et al. (2017), Zhou et al. (2017) and Longrich et al. (2018) recovered *B. oregonensis* as the sister group to the Tapejaridae. Bennett (2018) has since considered it a nomen dubium, and so it is excluded from this analysis. There are no known azhdarchids in the Early Cretaceous.

The basal-most azhdarchid is *Azhdarcho lancicollis* from the middle–late Turonian of Uzbekistan (Averianov, 2010), but a few slightly older specimens in the Late Cretaceous have also been referred to the Azhdarchidae. *Alanqa saharica* from the Cenomanian Kem Kem Beds of Morocco (Ibrahim et al., 2010) is one of these. Averianov (2014) referred all pterosaur specimens from the Kem Kem Beds to *A. saharica*. This phylogenetic analysis coded only the specimens described in Ibrahim et al. (2010) and Martill and Ibrahim (2015) with the exception of BSPG 1993 IX 338, the most defensible action, but much of the material is similar and likely formed a clade if not a species. *Alanqa saharica* was recovered as a thalassodromine in a clade with *Xericeps curvirostris* Martill et al., 2018, *Argentinadraco barrealensis* Kellner and Calvo, 2017, and *Leptostomia begaaensis* Smith et al., 2020. Slightly elongate cervical vertebrae from the Kem Kem Beds (CMN 50801, FSAC-KK 5077, and LINHM 014) were referred to the Azhdarchidae by Rodrigues et al. (2011) and Williams et al. (2021), but they have unreduced blade-like neural spines indicating that they do not belong to azhdarchids and may represent non-azhdarchid azhdarchiforms instead. Averianov (2014) also lists some fragments from the Cenomanian Khodzhakul Formation of Uzbekistan as Azhdarchidae indet., but this material is so incomplete that it is not possible to determine whether it belongs in or outside the Azhdarchidae. No azhdarchids can be confirmed before the Turonian Age.

Relationships of the Azhdarchidae—In addition to the azhdarchid specifiers *Azhdarcho lancicollis* and *Quetzalcoatlus northropi*, only the species *Quetzalcoatlus lawsoni*, *Wellnhopterus brevirostris*, *Phosphatodraco mauritanicus*, *Aralazhdarcho bostobensis*, *Eurazhdarcho langendorfensis*, *Zhejiangopterus linhaiensis*, *Hatzegopteryx thambema, Aerotitan sudamericanus, Mistralazhdarcho maggii, Cryodrakon boreas, Albadraco tharmisensis*, and *Arambourgiania philadelphiae* are recovered in the Azhdarchidae by the present phylogenetic analysis. The topology of the Azhdarchidae is predominantly pectinate (comb-like). Successive outgroups to *Quetzalcoatlus* are *A. philadelphiae*, *H. thambema*, a trichotomy with *C. boreas* and *W. brevirostris*, *Z. linhaiensis*, *E. langendorfensis*, the sister group of *P. mauritanicus* + *A. bostobensis*, a clade of *M. maggii* + *A. sudamericanus* + *A. tharmisensis* + *A. lancicollis*. Of note is that the co-occurring *E. langendorfensis*, *A. tharmisensis*, and *H. thambema* are not recovered as sister groups or even as particularly closely related within the Azhdarchidae, suggesting that they are not conspecifics.

The topology of the Azhdarchidae is largely resolved here by the characters of the cervical vertebrae. For example, the *P. mauritanicus* + *A. bostobensis* sister group is supported by the reduction of pneumatic foramina lateral to the neural canal. This reliance on cervical vertebrae is due to a number of factors. They are rather robust elements that are often preserved in the fossil record and are the most common elements in the Big Bend National Park pterosaur material; *Arambourgiania philadelphiae* and *P. mauritanicus* are known almost entirely from cervical material. The first phylogenetic analysis of pterosaurs (Howse, 1986) was conducted only on cervical vertebrae, and these characters have been well represented in phylogenetic analyses ever since. Also, a large number of morphological features in pterosaurs cervical vertebrae can be described and coded.

One of the most surprising results of the phylogenetic analysis is that the giant pterosaurs form a monophyletic clade to the exclusion of all other pterosaur species. Although still one of the largest pterosaurs, *Q. lawsoni* is in this group but about half the estimated sizes of *Q. northropi*, *A. philadelphiae*, and *H. thambema*. The rationale for erecting *Q. lawsoni* as a distinct species from *Q. northropi* is based on diagnostic apomorphies and depositional environment. Such a large reversal in size is unexpected and is about the only observation not supporting the distinctness of these species, but size is highly variable in pterosaurs.

Late Cretaceous Pterosaurs—Although there has been a tendency to refer Late Cretaceous pterosaurs to the Azhdarchidae, the phylogenetic analysis recovered up to 19 pterosaur lineages extending into this epoch: *Siroccopteryx moroccensis* Mader and Kellner, 1999; *Aetodactylus halli* Myers, 2010; *Cimoliopterus cuvieri* (Bowerbank, 1851); *Cimoliopterus dunni* Myers, 2015; *Lonchodraco giganteus* (Bowerbank, 1846); *Lonchodectes compressirostris* (Owen, 1851); *Pteranodon* with possibly *Volgadraco bogolubovi* Averianov et al., 2008, and *Tethydraco regalis* Longrich et al., 2018; the Nyctosauromorpha; *Caiuajara dobruskii* Manzig et al. 2014; a *B. galaczi* + *Keresdrakon vilsoni* Kellner et al., 2019, clade; *X. curvirostris*; *A. saharica*; *A. barrealensis*; *L. begaaensis*; *Microtuban altivolans* Elgin and Frey, 2011; *A. gyrostega* and the Azhdarchiformes.

In addition, not all Late Cretaceous pterosaur species that have been referred to the Azhdarchidae belong to that group: The Turonian *Cretornis hlavaci* from the Jizera Formation of Czech Republic was suggested to be an azhdarchid by Averianov (2010) but later identified as a non-azhdarchid azhdarchoid by Averianov and Ekrt (2015); the phylogenetic analysis recovers *C. hlavaci* as a nyctosauromorph. Similarly, *Volgadraco bogolubovi* from the Campanian Rybushka

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Formation of Russia was originally referred to the Azhdarchidae by Averianov et al. (2008) but is recovered here in the Pteranodontidae. *Bakonydraco galaczi* from the Santonian Csehbánya Formation of Hungary was originally referred to the Azhdarchidae, recovered as the sister group to the Azhdarchidae by Andres and Ji (2008) and Averianov and Ekrt (2015) in part, in a trichotomy with the Azhdarchidae by Averianov (2010) in part, and as sister group to the Neopterodactyloidea by Averianov and Ekrt (2015) in part. Andres and Myers (2013), Andres et al. (2014), Wu et al. (2017), and Zhou et al. (2017), and the current analysis recover *B. galaczi* as a late surviving tapejarid. *Argentinadraco barrealensis* from the upper Turonian–early Coniacian Portezuelo Formation of Argentina, as well as *A. saharica* and *Xericeps curvirostris* from the Cenomanian Kem Kem Beds, were originally regarded as at least possible azhdarchids but are recovered as thalassodromines by this analysis. Finally, the Campanian *Montanazhdarcho minor* from Montana was originally referred to the Azhdarchidae by Padian et al. (1995) and is recovered here as the sister group to the Azhdarchidae.

Up to 19 pterosaur lineages enter the first age of the Late Cretaceous (Cenomanian) and 13 or 14 species are present in the last stage of the Late Cretaceous (Maastrichtian Age), 12 of which are dated to the very end of the Mesozoic Era. In between, pterosaur phylogenetic diversity was more or less the same for the last 34 million years of the Mesozoic (Longrich et al., 2018). When considering taxic diversity (species number) instead, there is a spike in species number at the end of the Cretaceous that surpasses the species number of any other time in the Late Cretaceous (Longrich et al., 2018). The Maastrichtian is still dominated by azhdarchids, but there is evidence that nyctosaurids and pteranodontids (Longrich et al., 2018) also survived into this age. Much discussion has been put forward about whether pterosaur diversity was declining in the Late Cretaceous and the possible causes thereof (Unwin, 1987, 1988; Slack et al., 2006; Unwin, 2006; McGowan and Dyke, 2007; Butler et al., 2009, 2012, 2013; Benson et al., 2014; Chan, 2017). This phylogenetic analysis of *Quetzalcoatlus* and the relationships of the Pterosauria does not support a terminal decline in pterosaur diversity and indicates that pterosaurs were a successful group of flying vertebrates up until the Cretaceous–Paleogene extinction event**.**

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