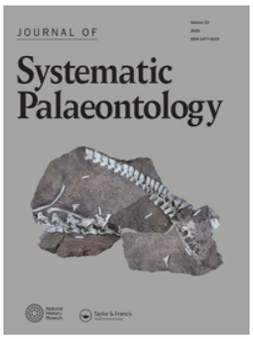

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Enter the dragons: the phylogeny of Azhdarchoidea (Pterosauria: Pterodactyloidea) and the evolution of giant size in pterosaurs

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Azhdarchidae is a clade of pterosaurs which includes the largest-ever flying animals. The evolutionary history of this clade and its closest relatives remains incompletely understood and highly debated. To investigate this, we combined multiple preexisting datasets with 29 new operational taxonomic units and 57 new characters, resulting in the most comprehensive phylogenetic analysis of pterosaurs published to date, with a focus on Azhdarchomorpha. Higher level phylogenetic taxonomy of Azhdarchomorpha is revised based on the results of this analysis, and three new clade names are established: Shenzhoupterinae (cl. nov.) for the subgroup of Chaoyangopteridae containing *Shenzhoupterus* that is sister to the existing Chaoyangopterinae; Concilazhia (cl. nov.) for the clade uniting Chaoyangopteridae and Azhdarchiformes; and Serpennata (cl. nov.) for the clade with highly elongated cervical series that includes the giant (~10 m wingspan) *Quetzalcoatlus* and *Arambougiania*. The iconic genus *Quetzalcoatlus* is recovered as polyphyletic, with its giant and moderately large species belonging to separate clades within Serpennata. Gigantism evolved convergently at least four times in quetzalcoatline azhdarchids: in *Cryodrakon*, once in a clade containing *Hatzegopteryx* and its closest relatives, and twice independently in different lineages of Serpennata.

Keywords: Pterosauria; phylogeny; Pterodactyloidea, Azhdarchoidea; gigantism

Introduction

Pterosaurs (e.g. Jagielska & Brusatte, 2021; Wellnhofer, 1978; Witton, 2013) are a clade of Mesozoic archosaurian reptiles (Ezcurra et al., 2020) known for being the first vertebrate group to achieve powered flight. Particular research interest has been focused on the Late Cretaceous Azhdarchidae (Fig. 1), characterized by extreme elongation of the cervical vertebrae, relatively large and toothless skulls, elongate limbs, and proportionally short wing fingers (Thomas et al., 2025; Witton, 2013; Witton & Naish, 2008). The earliest Azhdarchidae are known from the Cenomanian (Agnolín et al., 2023; Andres, 2021; Zhou et al., 2024), and the clade persisted until the end of the Maastrichtian, making them one of the last pterosaur lineages to exist (Lehman, 2021; Longrich et al., 2018).

Azhdarchids are culturally and scientifically notable for including the largest ever flying animals (e.g. Andres & Myers, 2013), with *Arambourgiania philadelphiae*, *Hatzegopteryx thambema* and *Quetzalcoatlus northropi* having estimated wingspans possibly in excess of 10 metres, comparable to the wingspans of general aviation aircraft (e.g. Cessna Aircraft Co., 1956), and masses up to *c*. 260 kg (Witton, 2008b; Witton & Habib, 2010). It has been proposed that giant size in azhdarchids either evolved once, in a giant clade (Andres, 2021; Longrich et al., 2018), or that large size evolved separately in different lineages of azhdarchids (Naish & Witton, 2017; Witton, 2013). Not all azhdarchids reached this large size however, with many having wingspans between 3 and 5 m, while a possible azhdarchid from Campanian British Columbia has an estimated wingspan of 1.5 m (Martin-Silverstone, Witton, et al., 2016). Azhdarchid ecology has historically been disputed, with hypotheses including obligate scavenging, aerial predation, piscivory and durophagy (e.g. Bestwick et al., 2018; Nesov, 1991), but they are now largely considered to be generalist carnivores that forage terrestrially (Naish & Witton, 2017; Witton & Naish, 2008, 2015).

Azhdarchids have been included in phylogenetic analyses for as long as modern phylogenetic methods have been applied to pterosaurs (Kellner, 2003; Unwin, 2003). Since then, there has been considerable disagreement about the interrelationships of pterosaur clades (e.g. Vidovic, 2016). The interrelationships of Azhdarchidae are one example of this (compare Andres, 2021; Longrich et al., 2018; Pêgas, 2024; Pêgas et al., 2022; Thomas, 2021; Vidovic & Martill, 2018; Zhou et al., 2024), which has been complicated by the quality of the azhdarchid

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Figure 1. Reconstructions of giant azhdarchid pterosaurs. From left to right: *Cryodrakon boreas*, *Hatzegopteryx thambema*, *Arambourgiania philadelphiae* and *Quetzalcoatlus northropi*. Original artwork by Kyra Zhuravel.

fossil record: many taxa are known solely from isolated skeletal elements (e.g. Thomas et al., 2025; Zhou et al., 2024), and more complete specimens are often disarticulated (e.g. Andres & Langston, 2021) or not preserved three-dimensionally (e.g. Unwin & Lü, 1997). This follows the general patterns of the pterosaur fossil record (Dean et al., 2016). However, a wealth of new data and analyses from the past two decades (e.g. Andres & Langston, 2021; Averianov, 2010; Hone et al., 2019; Longrich et al., 2018; Manzig et al., 2014; Ortiz David et al., 2022; Pêgas, 2024; Pêgas et al., 2025; Thomas et al., 2025; Zhou et al., 2024) enables the more detailed interpretation and resolution of previously unanswered questions regarding pterosaur phylogeny. Here, we present the most comprehensive phylogenetic analysis of pterosaurs to date, with a focus on Azhdarchomorpha. We also reconstruct the evolution of size within pterosaurs to track the appearance of the largest flying organisms in Earth's history.

Methods

Phylogenetic analysis

The phylogenetic analysis in this study is derived from that presented in Pêgas (2024), which was previously the most comprehensive phylogenetic analysis of pterosaurs published to date. Independent forks of this dataset were reported by Hone et al. (2024), Thomas et al. (2025), and Zhou et al. (2024), which are hereby consolidated into a single dataset. Codings for *Allkaruen koi* (Codorniú et al., 2016), *Darwinopterus linglongtaensis* (Wang et al., 2010), *Darwinopterus robustodens* (Lü et al., 2011), *Douzhanopterus zhengi* (Wang et al., 2017), *Petrodactyle wellnhoferi* (Hone et al., 2023), *Skiphosoura bavarica* (Hone et al., 2024), 'Rhamphodactylus' (Rauhut, 2012), and IVPP V 23674 (Cheng et al., 2017) were imported from Hone et al. (2024). Codings for *Apatorhamphus gyrostega* (McPhee et al., 2020), '*Gnathosaurus*' *macrurus* (Seeley, 1869), *Gobiazhdarcho tsogtbaatari* (Pêgas et al., 2025; Watabe et al., 2009), *Nipponopterus mifunensis* (Zhou et al., 2024), *Ornithostoma sedgwicki* (Seeley, 1891), *Postosuchus kirkpatricki* (Chatterjee, 1985), *Tsogtopteryx mongoliensis* (Pêgas et al., 2025; Watabe et al., 2009), and LPB R.2395 (Vremir et al., 2015) were imported from Zhou et al. (2024). Codings for *Infernodrakon hastacollis* (Thomas et al., 2025), *Montanazhdarcho minor* (Padian et al., 1995), MPPM 2000.23.1 (Harrell et al., 2016), and UCMP 114286 (Estes, 1964) were imported from Thomas et al. (2025). Codings for *Thanatosdrakon amaru* (Ortiz David et al., 2022) were combined from the datasets of Thomas et al. (2025) and Zhou et al. (2024).

In total, 23 new ingroup operational taxonomic units (OTUs) have been added to the dataset: *Bennettazhia oregonensis* (Gilmore, 1928; Nesov, 1991), *Eoazhdarcho liaoxiensis* (Lü et al., 2006), *Inabtanin alarabia* (Rosenbach et al., 2024), *Lonchognathosaurus acutirostris* (Maisch et al., 2004), *Meilifeilong sanyainus* (Ji et al., 2023), *Meilifeilong youhao* (Wang et al., 2023), *Microtuban altivolans* (Elgin & Frey, 2011), *Radiodactylus langstoni* (Andres & Myers, 2013), *Vectidraco daisymorrisae* (Naish et al., 2013), *Volgadraco bogolubovi* (Averianov et al., 2008), '*Palaeornis*' *cliftii* (Mantell, 1844), the 'Tous pterosaur' (Company et al., 1999), CAMSM J5340 (Howse, 1986), LPB R.2347

(Vremir et al., 2018), MB. R. 2832 (Costa et al., 2015), MC SF69 (Buffetaut, 2001), ME1 04 (Buffetaut et al., 1997), MN 6588-V (Sayão & Kellner, 2007), MPCA PV 2003 (Agnolín et al., 2023), MTCO 21.269 (Dyke et al., 2011), RGM.631745 (de Buisonjé, 1980), UFC 721 (Leal et al., 2018), and ctenochasmatid material from the Quebrada Monardes Formation ('Quebrada Monardes pterosaur'; Alarcón-Muñoz et al., 2020, 2022; Martill et al., 2006). Additionally, *Lagosuchus talampayensis* (Agnolin & Ezcurra, 2019; Romer, 1971, 1972; Sereno & Arucci, 1994), *Coelophysis bauri* (Bugos & McDavid, 2024; Colbert, 1989; Cope, 1887, 1889), *Dromomeron romeri* (Irmis et al., 2007; Nesbitt et al., 2009), *Ixalerpeton polesinensis* (Cabreira et al., 2016), *Venetoraptor gassenae* (Müller et al., 2023), and *Scleromochlus taylori* (Foffa et al., 2024; Woodward, 1907) were added to the dataset to improve outgroup sampling.

Bogolubovia orientalis (Bogolubow, 1914; Nesov & Yarkov, 1989), *Navajodactylus boerei* (Sullivan & Fowler, 2011), *Palaeocursornis corneti* (Kessler & Jurcsák, 1984), *Samrukia nessovi* (Averianov et al., 2015; Buffetaut, 2011; Naish et al., 2011), '*Ornithocheirus*' *buenzeli* (Buffetaut et al., 2011; Seeley, 1881), the 'Sidi Chennane azhdarchid' (FSAC-OB 203; Longrich et al., 2018), RBCM.EH.2009.019.0001 (Martin-Silverstone, Witton, et al., 2016), and the large-bodied azhdarchid from the Nemegt Formation (Tsuihiji et al., 2017) were excluded from the analysis due to a lack of phylogenetically informative characters present in the preserved material. The azhdarchid cervical vertebra from Late Cretaceous Senegal (Monteillet et al., 1982) was excluded as the current location of this specimen is unknown (Averianov, 2014; Pentland & Poropat, 2023). The 'Wessex humerus' (Witton et al., 2009) was excluded as the original specimen is held in a private collection, although casts are available in public institutions. The chaoyangopterid specimens LPM-L112113 and LPM-N081607 (Wu et al., 2017) were excluded as these specimens lack proper descriptions. The azhdarchid material from the Laño site in Spanish Basque Country (Astibia et al., 1990; Buffetaut, 1999) was excluded as this material has yet to be fully described (Pereda-Suberbiola et al., 2015). The pterosaur taxon from the Merchantville Formation (Baird & Galton, 1981), which has sometimes been considered an azhdarchid (e.g. Averianov, 2014) was excluded as it is currently under study (Thomas & McDavid, 2025a). The putative azhdarchid cervical vertebra YPM VPPU 23497 from the Navesink Formation (Gallagher, 1984; Schwimmer et al., 1985) tentatively assigned to aff. *Arambourgiania* sp. by Thomas et al. (2025) is actually a badly damaged ulna (Thomas & McDavid, 2025a) and not phylogenetically informative; therefore, was excluded. This specimen will be described in further detail elsewhere.

Data for *Bakonydraco galaczi* were modified following interpretation of this taxon as an azhdarchid instead of a tapejarid (see Discussion). In light of evidence for multiple anatomically similar yet size-separated species in the *Bakonydraco* hypodigm (Prondvai et al., 2014), the OTU was renamed to simply *Bakonydraco*. Data for *Pteranodon longiceps* and *Pteranodon sternbergi* were modified based on our observations of material in the YPM and USNM. Data for '*Quetzalcoatlus*' *lawsoni* were modified based on the description provided in Andres and Langston (2021). The *Hatzegopteryx thambema* OTU was divided such that the cervical vertebra EME 315 has been split into a separate OTU. EME 315 ('Râpa Roşie azhdarchid') has been referred to *Hatzegopteryx* sp. (Naish & Witton, 2017; Vremir, 2010), but this specimen does not overlap with the *H. thambema* type material. Furthermore, *H. thambema* is known from the Early Maastrichtian Vălioara locality of the Densuş-Ciula Formation (Albert et al., 2025; Buffetaut et al., 2002), whereas EME 315 is known from the Late Maastrichtian Râpa Roşie locality of the overlying Sebeş Formation (Albert et al., 2025; Naish & Witton, 2017), making a referral to *H. thambema* provisional at best. The original composite *Hatzegopteryx* OTU is retained in the dataset for posterity with the name '*Hatzegopteryx* composite', but was deactivated for analysis. Additional data modifications are described in the Supplemental File 1.

Characters added to the dataset in Hone et al. (2024), Thomas et al. (2025) and Zhou et al. (2024) were added to our dataset and were scored for taxa not present in other forks of the dataset. We ordered or reordered states for 48 characters, so the states form a progressive sequence, and added new states to six characters. We also added one character modified from Andres (2021), three from Garcia and Müller (2025) and 53 novel characters to the dataset. All character modifications are described in the Supplemental File 1. The final dataset contains 241 active OTUs and 615 characters. The dataset was constructed using Mesquite 3.81 (Maddison & Maddison, 2023).

The *Kryptodrakon progenitor* OTU was deactivated because this taxon is very poorly known and should be considered a *nomen dubium* (Hone et al., 2024). The *Pteranodon maiseyi* (= *Geosternbergia maiseyi* Kellner, 2010) OTU was deactivated as it only differs from the revised *P. longiceps* codings in one character (20, 'nasoantorbital fenestra, dorsal and ventral margins, orientation') which is only based on the posterior-most part of the nasoantorbital fenestra in *P. maiseyi* (Kellner, 2010). In some more complete *Pteranodon* specimens

(e.g. *P. sternbergi* UALVP 24238, Martin-Silverstone, Glasier, et al., 2016; *P. longiceps* AMNH FARB 7515, S. McDavid, pers. obs.), the dorsal and ventral margins of the nasoantorbital fenestra are subparallel only in the posterior-most portion of the fenestra, and otherwise forming an acute angle, so the differing coding for this character probably does not represent an actual morphological difference between *P. maiseyi* and other *Pteranodon* species. The holotype of *P. maiseyi* (KUVP 27821) has been assigned to both *P. longiceps* (Bennett, 1994) and *P. sternbergi* (Brandão, 2018) in different studies; consequently, we regard *P. maiseyi* as a *species inquirenda* and assign KUVP 27821 to *Pteranodon* sp. pending further study. Characters 236, 414 and 433 were deactivated *a priori* as these characters are pseudoreplicates, but are retained in the dataset for continuity, following Hone et al. (2024). These taxa and characters are deactivated by default with the commands `taxcode` and `ccode`.

Parsimony-based phylogenetic analysis was performed in TNT v.1.6 (Goloboff et al., 2008; Goloboff & Morales, 2023). *Euparkeria capensis* was used as the outgroup taxon following Pêgas (2024). In total, 98 characters were treated as additive (ordered), as they have three or more states that form a progressive sequence: 1–5, 14–16, 22, 25, 26, 32, 34, 46, 50, 63, 66, 67, 70, 76, 78, 105, 106, 121, 123, 125, 130, 133, 135, 140–142, 164, 165, 180, 187–189, 191, 215, 221, 234, 241–246, 248, 253, 254, 268, 270, 286, 295, 298, 302, 320, 322, 345, 346, 354, 358, 371, 372, 409, 413, 417, 418, 430, 440, 450, 451, 459, 470, 479, 483, 485, 489, 491, 501, 503, 504, 507, 509, 511, 517, 518, 520, 522, 532, 534, 562, 571, 574, 581, and 589. 1000 replicates, each saving 100 trees each, of a TBR analysis using TNT's 'Traditional search' function were performed. Analyses were performed using both equal weights and implied weights with concavity constant values (k) between 14 and 26, following the recommendation of Ezcurra (2024). Information on the implied weights analyses and clade support metrics can be found in the Supplemental File 2. Tree diagrams were produced using TreeGraph (Stöver & Müller, 2010) and Inkscape.

Phylogenetic taxonomy

Phylogenetic nomenclature has been applied to pterosaurs since the origins of pterosaur phylogeny (Kellner, 2003; Unwin, 2003), but phylogenetic taxonomy of pterosaurs is a historically contentious subject. Many pterosaur clades have multiple definitions that have been used in recent literature (see Pêgas, 2025, and Pêgas et al., 2023 for discussion). Notably, there exist two competing frameworks for the usage of Tapejaridae, Tapejarinae and Thalassodrominae (Pêgas et al., 2023). In the taxonomic framework of Kellner (2003) and Kellner and Campos (2007), Tapejaridae is a broadly inclusive clade that includes *Tapejara wellnhoferi* and *Thalassodromeus sethi* as internal specifiers, and Tapejarinae and Thalassodrominae are defined as branch-based clades to form a node-stem triplet with Tapejaridae. Conversely, in the taxonomic framework of Andres (2021) and Andres et al. (2014), Tapejaridae is a narrower clade with *Tapejara wellnhoferi* and *Sinopterus dongi* as internal specifiers, forming a node-stem triplet with Sinopterinae and Tapejarinae. Thalassodrominae is defined as a narrower clade pertaining to *Thalassodromeus sethi* and its closest relatives, with *Tupuxuara longicristatus* listed as an external specifier, and the clade Thalassodromidae encompasses them both. We adopt the latter taxonomic framework here, following Pêgas et al. (2023). Furthermore, competing minimum- and maximum-clade definitions exist for Azhdarchidae (Pêgas et al., 2022; Vidovic & Martill, 2018), Azhdarchinae (Andres, 2021; Vidovic & Martill, 2018), and Chaoyangopteridae (Andres et al., 2014; Lü et al., 2008). Chaoyangopterinae has been defined with either *Jidapterus edentus* (Andres, 2021) or *Shenzhoupterus chaoyangensis* (Andres et al., 2014) as an internal specifier, and Azhdarchidae *sensu* Kellner (2003, p. 125) listed "any other pterosaur [than *Quetzalcoatlus*]" as an external specifier, which would enforce perpetual monotypy. A review of previous phylogenetic definitions for azhdarchoid clades is provided in the Supplemental File 1. Phylogenetic definitions used in this study are presented in Table 1. A system of phylogenetic taxonomy for Azhdarchomorpha is provided in the Systematic Palaeontology section. Phylogenetic taxonomy for Tapejaromorpha follows Pêgas (2024).

Phylogenetic nomenclature follows the *PhyloCode* (Cantino & De Queiroz, 2020), following Pêgas et al. (2022; 2023), Pêgas (2024), and several recent reviews of fossil diapsid systematics (e.g. Fonseca et al., 2024; Madzia et al., 2021; M. T. Young et al., 2024). New clades and clade definitions are registered in PhyloRegNum, following the best practices of Cantino et al. (2022).

Wingspan estimation

Wingspan was chosen as a proxy for body size because wingspan estimates can be calculated more reliably for fragmentary pterosaur specimens than body mass. Although mass and wingspan are closely associated in pterosaurs (Venditti et al., 2020; Witton, 2008b) and mass can be estimated from wingspan (see Witton, 2008b for equations and Hone & McDavid, 2025 for an

Table 1. Phylogenetic definitions of clades used in this study. Abbreviation style for phylogenetic definitions follows Cantino and de Queiroz (2020). 'Preexisting name' designates clades that were given phylogenetic definitions prior to the *PhyloCode* entering into force.

Clade name	Original authorship	Definition	Reference for definition	Applicable codes	Comments
Archosauriformes	Gauthier, 1994	min ∇ (*Gallus gallus* & *Alligator mississippiensis* & *Proterosuchus fergusi*)	Gauthier, 2020	PhyloCode	
Pseudosuchia	Zittel, 1890	max ∇ (*Crocodylus niloticus* ~ *Passer domesticus*)	Nesbitt, 2011	PhyloCode	Preexisting name
Pan-Aves	Gauthier & de Queiroz, 2001	max ∇ (*Vultur gryphus* ~ *Alligator mississippiensis*)	Ezcurra et al., 2020	PhyloCode	Preexisting name
Dinosauromorpha	Benton, 1985	max ∇ (*Passer domesticus* ~ *Pterodactylus antiquus* ∨ *Ornithosuchus longidens* ∨ *Crocodylus niloticus*)	Nesbitt, 2011	PhyloCode	
Pterosauromorpha	Kuhn-Schnyder & Rieber, 1986	max ∇ (*Pterodactylus antiquus* ~ *Alligator mississippiensis* & *Compsognathus longipes*)	Andres & Padian, 2020a	PhyloCode	
Lagerpetidae	Arcucci, 1986	max ∇ (*Lagerpeton chanarensis* ~ *Eudimorphodon ranzii* ∨ *Silesaurus opolensis* ∨ *Vultur gryphus*)	Ezcurra et al., 2020	ICZN, PhyloCode	Preexisting name
Pterosauria	Owen, 1842	apo ∇ fourth manual digit hypertrophied to support wing membrane [*Pterodactylus antiquus*]	Andres & Padian, 2020b	PhyloCode	
Preondactylia	Andres et al., 2014	min ∇ (*Prenodactylus buffarinii* & *Austriadactylus cristatus*)	Andres et al., 2014	PhyloCode	Preexisting name
Eudimorphodontoidea	Andres et al., 2014	min ∇ (*Eudimorphodon ranzii* & *Raeticodactylus filisurensis*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Eudimorphodontidae	Wellnhofer, 1978	max ∇ (*Eudimorphodon ranzii* ~ *Raeticodactylus filisurensis*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Raeticodactylidae	Andres et al., 2014	max ∇ (*Raeticodactylus filisurensis* ~ *Eudimorphodon ranzii*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Novialoidea	Kellner, 2003	min ∇ (*Campyloganthoides zittelli* & *Quetzalcoatlus northropi*)	Kellner, 2003	PhyloCode	Preexisting name
Breviquartossa	Unwin, 2003	min ∇ (*Rhamphorhynchus muensteri* & *Quetzalcoatlus northopi*)	Unwin, 2003	PhyloCode	Preexisting name
Rhamphorhynchinae	Nopcsa, 1928	max ∇ (*Rhamphorhynchus muensteri* ~ *Scaphognathus crassirostris*)	Andres, 2021	ICZN, PhyloCode	
Rhamphorhynchae	Seeley, 1870	min ∇ (*Rhamphorhynchus muensteri* & *Angustinaripterus longicephalus*)	Andres, 2021	PhyloCode	
Rhamphorhynchini	Andres et al., 2014	max ∇ (*Rhamphorhynchus muensteri* ~ *Angustinaripterus longicephalus*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Angustinaripterini	Andres et al., 2014	max ∇ (*Angustinaripterus longicephalus* ~ *Rhamphorhynchus muensteri*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Scaphognathinae	Hooley, 1913	min ∇ (*Scaphognathus crassirostris* & *Sordes pilosus*)	Unwin, 2003	ICZN, PhyloCode	Preexisting name

(*Continued*)

Table 1. (*Continued*).

Clade name	Original authorship	Definition	Reference for definition	Applicable codes	Comments
Anurognathidae	Kuhn, 1937	apo ∇ skull wider than long [*Anurognathus ammoni*]	Andres, 2021	ICZN, PhyloCode	
Anurognathinae	Nopcsa, 1928	max ∇ (*Anurognathus ammoni* ∼ *Batrachognathus volans*)	Wei et al., 2021	ICZN, PhyloCode	
Batrachognathinae	Kellner et al., 2009	max ∇ (*Batrachognathus volans* ∼ *Anurognathus ammoni*)	Kellner et al., 2009	ICZN, PhyloCode	Preexisting name
Pterodactylomorpha	Andres et al., 2014	max ∇ (*Pterodactylus antiquus* ∼ *Rhamphorhynchus muensteri*)	Andres et al., 2014	PhyloCode	Preexisting name
Caelidracones	Unwin, 2003	min ∇ (*Anurognathus ammoni* & *Quetzalcoatlus northopi*)	Unwin, 2003	PhyloCode	Preexisting name
Monofenestrata	Lü et al., 2010	apo ∇ confluent naris and antorbital fenestra [*Pterodactylus antiquus*]	Andres et al., 2014	PhyloCode	Preexisting name
Darwinoptera	Andres et al., 2014	min ∇ (*Darwinopterus modularis* & *Pterorhynchus wellnhoferi*)	Andres et al., 2014	PhyloCode	Preexisting name
Wukongopteridae	Wang et al., 2009	min ∇ (*Wukongopterus lii* & *Kungpengoperus sinensis*)	Wang et al., 2010	ICZN, PhyloCode	Preexisting name
Pterodactyliformes	Andres et al., 2014	max ∇ (*Pterodactylus antiquus* ∼ *Darwinopterus modularis*)	Andres et al., 2014	PhyloCode	Preexisting name
Pterodactyloidea	Plieninger, 1901	apo ∇ fourth metacarpal at least 80% as long as humerus [*Pterodactylus antiquus*]	Andres & Padian, 2020c	PhyloCode	
Archaeopterodactyloidea	Kellner, 2003	min ∇ (*Pterodactylus antiquus* & *Ctenochasma elegans* & *Germanodactylus cristatus*)	Kellner, 2003	PhyloCode	Preexisting name
Ctenochasmatoidea	Unwin, 1995	min ∇ (*Cycnorhamphus suevicus* & *Pterodaustro guinazui*)	Unwin, 2002	ICZN, PhyloCode	This definition violates the PhyloCode as it does not include *Ctenochasma* as an internal specifier but a redefinition of this clade is beyond the scope of the present study.
Aurorazhdarchia	Vidovic & Martill, 2018	min ∇ (*Aurorazhdarcho micronyx* & *Aerodactylus scolopaciceps*)	Vidovic & Martill, 2018	PhyloCode	
Moganopterinae	Lü et al., 2012	min ∇ (*Moganopterus zhuianus* & *Feilongus youngi*)	Lü et al., 2012	ICZN, PhyloCode	
Ctenochasmatidae	Kuhn, 1967	min ∇ (*Ctenochasma elegans* & *Gnathosaurus subulatus*)	Andres, 2021	ICZN, PhyloCode	
Ctenochasmatinae	Nopcsa, 1928	max ∇ (*Ctenochasma elegans* ∼ *Gnathosaurus subulatus*)	Andres et al., 2014	ICZN, PhyloCode	
Ornithocheiroidea	Seeley, 1891	min ∇ (*Ornithocheirus simus* & *Anhanguera blittersdorffi* & *Pteranodon longiceps* & *Dsungaripterus weii* & *Quetzalcoatlus northopi*)	This study	PhyloCode	Unrestricted emendation; see Systematic Paleontology

(*Continued*)

Table 1. (*Continued*).

Clade name	Original authorship	Definition	Reference for definition	Applicable codes	Comments
Pteranodontoidea	Kellner, 2003	min ∇ (*Anhanguera blittersdorfii* & *Pteranodon longiceps*)	Kellner, 2003	ICZN, PhyloCode	Preexisting name
Boreopteridae	Lü et al., 2006	min ∇ (*Boreopterus cuiae* & *Zhenyuanopterus longirostris*)	Jiang et al., 2014	ICZN, PhyloCode	Preexisting name
Pteranodontia	Marsh, 1876	min ∇ (*Pteranodon longiceps* & *Nyctosaurus gracilis*)	Unwin, 2003	PhyloCode	
Nyctosauromorpha	Andres, 2021	max ∇ (*Nyctosaurus gracilis* ∼ *Pteranodon longiceps*)	Andres, 2021	PhyloCode	
Nyctosauridae	Marsh, 1876	min ∇ (*Nyctosaurus gracilis* & *Muzquizopteryx coahuilensis*)	Andres et al., 2014	ICZN, PhyloCode	
Lanceodontia	Andres et al., 2014	min ∇ (*Anhanguera blittersdorffi* & *Istiodactylus latidens*)	Andres et al., 2014	PhyloCode	
Istiodactyliformes	Kellner, Caldwell, et al., 2019	max ∇ (*Istiodactylus latidens* ∼ *Anhanguera blittersdorffi*)	Kellner, Caldwell, et al., 2019	PhyloCode	Preexisting name
Mimodactylidae	Kellner, Caldwell, et al., 2019	max ∇ (*Mimodactylus libanensis* ∼ *Istiodactylus latidens*, *Ikrandraco avatar*, *Anhanguera blittersdorffi*)	Kellner, Caldwell, et al., 2019	ICZN, PhyloCode	
Istiodactylidae	Howse et al., 2001	min ∇ (*Istiodactylus latidens* & *Nurhachius ignaciobritoi*)	Andres et al., 2014	ICZN, PhyloCode	
Istiodactylinae	Andres et al., 2014	max ∇ (*Istiodactylus latidens* ∼ *Nurhachius ignaciobritoi*)	Andres et al., 2014	ICZN, PhyloCode	
Ornithocheiridae	Seeley, 1870	max ∇ (*Ornithocheirus simus* ∼ *Anhanguera blittersdorffi*)	Andres & Myers, 2013	ICZN, PhyloCode	Preexisting name
Targaryendraconia	Pêgas et al., 2019	max ∇ (*Targaryendraco wiedenrothi* ∼ *Anhanguera blittersdoeffi*)	Pêgas et al., 2019	PhyloCode	Preexisting name
Targaryendraconidae	Pêgas et al., 2019	max ∇ (*Targaryendraco wiedenrothi* ∼ *Cimoliopterus cuvieri*)	Pêgas et al., 2019	ICZN, PhyloCode	
Cimoliopteridae	Pêgas et al., 2019	max ∇ (*Cimoliopterus cuvieri* ∼ *Targaryendraco wiedenrothi*)	Pêgas et al., 2019	ICZN, PhyloCode	
Anhangueria	Rodrigues & Kellner, 2013	max ∇ (*Anhanguera blittersdorffi* ∼ *Istiodactylus latidens* & *Cimoliopterus cuvieri)*	Rodrigues & Kellner, 2013	PhyloCode	Preexisting name
Hamipteridae	Holgado et al., 2019	max ∇ (*Hamipterus tianshanensis* ∼ *Ludodactylus sibbicki* & *Coloborhynchus clavirostris* & *Anhanguera blittersdorffi*)	Holgado et al., 2019	ICZN, PhyloCode	Preexisting name
Anhangueridae	Campos & Kellner, 1985	min ∇ (*Anhanguera blittersdorffi* & *Coloborhynchus clavirostris* & *Tropeognathus mesembrinus*)	Holgado et al., 2019	ICZN, PhyloCode	
Anhanguerinae	Holgado et al., 2019	max ∇ (*Anhanguera blittersdorffi* ∼ *Coloborhynchus clavirostris*)	Holgado et al., 2019	ICZN, PhyloCode	
Tropeognathinae	Holgado and Pêgas, 2020	max ∇ (*Tropeognathus mesembrinus* ∼ *Coloborhynchus clavirostris* ∨ *Anhanguera blittersdorffi*)	Holgado and Pêgas, 2020	ICZN, PhyloCode	Preexisting name

(*Continued*)

Table 1. (*Continued*).

Clade name	Original authorship	Definition	Reference for definition	Applicable codes	Comments
Mythungini	Richards et al., 2024	max ∇ (*Mythunga camara* ∼ *Tropeognathus mesembrinus*, *Amblydectes crassidens*, *Siroccopteryx moroccensis*)	Richards et al., 2024	ICZN, PhyloCode	
Coloborhynchinae	Holgado et al., 2019	max ∇ (*Coloborhynchus clavirostris* ∼ *Anhanguera blittersdorffi*)	Holgado et al., 2019	ICZN, PhyloCode	Preexisting name
Tapejaroidea	Kellner, 1989	min ∇ (*Dsungaripterus weii* & *Tapejara wellnhoferi* & *Quetzalcoatlus northopi*)	Kellner, 2003	ICZN, PhyloCode	Preexisting name
Dsungaripteromorpha	Andres et al., 2014	max ∇ (*Dsungaripterus weii* ∼ *Quetzalcoatlus northopi*)	Andres et al., 2014	PhyloCode	Preexisting name
Dsungaripteridae	C. C. Young, 1964	min ∇ (*Dsungaripterus weii* & *Noripterus complicidens*)	Unwin, 2003	ICZN, PhyloCode	Preexisting name
Dsungaripterinae	Andres et al., 2014	max ∇ (*Dsungaripterus weii* ∼ *Noripterus complicidents*)	Andres et al., 2014	ICZN, PhyloCode	
Azhdarchoidea	Unwin, 1995	min ∇ (*Azhdarcho lancicollis* & *Tapejara wellnhoferi*)	this study	ICZN, PhyloCode	Unrestricted emendation; see Systematic Paleontology
Neoazhdarchia	Unwin, 2003	min ∇ (*Tupuxuara longicristatus* & *Quetzalcoatlus northropi*)	Unwin, 2003	PhyloCode	This definition violates the PhyloCode as it does not include *Azhdarcho* as an internal specifier. Since this clade is equivalent to Azhdarchoidea in our topology, we consider a redefinition unnecessary in this work
Tapejaromorpha	Andres et al., 2014	max ∇ (*Tapejara wellnhoferi* ∼ *Azhdarcho lancicollis*)	Andres et al., 2014	ICZN, PhyloCode	
Thalassodromidae	Witton, 2008b	min ∇ (*Thalassodromeus sethi* & *Tupuxuara longicristatus*)	Andres, 2021	ICZN, PhyloCode	
Thalassodrominae	Kellner & Campos, 2007	max ∇ (*Thalassodromeus sethi* ∼ *Tupuxuara longicristatus*)	Andres, 2021	ICZN, PhyloCode	
Tapejariformes	Pêgas, 2024	apo ∇ downturned rostrum [*Tapejara wellnhoferi*]	Pêgas, 2024	PhyloCode	
Caupedactylia	Pêgas et al., 2023	max ∇ (*Caupedactylus ybaka* ∼ *Tapejara wellnhoferi*)	Pêgas *et al.* 2023	PhyloCode	
Eutapejaria	Pêgas et al., 2023	max ∇ (*Tapejara wellnhoferi* ∼ *Caupedactylus ybaka*)	Pêgas et al., 2023	PhyloCode	
Tapejaridae	Kellner, 1989	min ∇ (*Tapejara wellnhoferi* & *Sinopterus dongi*)	Lü et al., 2006	ICZN, PhyloCode	Preexisting name
Sinopterinae	Lü et al., 2016	max ∇ (*Sinopterus dongi* ∼ *Tapejara wellnhoferi*)	Andres, 2021	ICZN, PhyloCode	
Tapejarinae	Kellner, 1989	max ∇ (*Tapejara wellnhoferi* ∼ *Sinopterus dongi*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name

(*Continued*)

Table 1. (*Continued*).

Clade name	Original authorship	Definition	Reference for definition	Applicable codes	Comments
Tapejarini	Kellner, 1989	min ∇ (*Tapejara wellnhoferi* & *Tupandactylus imperator*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Caiuajarina	Pêgas, 2024	max ∇ (*Caiuajara dobruskii* ∼ *Tapejara wellnhoferi*)	Pêgas, 2024	ICZN, PhyloCode	
Azhdarchomorpha	Pêgas et al., 2022	max ∇ (*Azhdarcho lancicollis* ∼ *Tapejara wellnhoferi*)	Pêgas et al., 2022	PhyloCode	
'Neopterodactyloidea'	Andres et al., 2014	min ∇ (*Quetzalcoatlus northropi* & *Chaoyangopterus zhangi*)	Andres et al., 2014	PhyloCode	This definition violates the PhyloCode as it does not include *Pterodactylus* as an internal specifier, and a redefinition that includes *Pterodactylus* would be equivalent to Lophocratia
Concilazhia	Thomas & McDavid, new clade	min ∇ (*Azhdarcho lancicollis* & *Chaoyangopterus zhangi* & *Alanqa saharica*)	This study	PhyloCode	New clade name, new definition
Chaoyangopteridae	Lü et al., 2008	max ∇ (*Chaoyangopterus zhangi* ∼ *Quetzalcoatlus northropi*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Chaoyangopterinae	Pinheiro et al., 2011	max ∇ (*Chaoyangopterus zhangi* & *Jidapterus edentus)*	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Shenzhoupterinae	Thomas & McDavid, new clade	max ∇ (*Shenzhoupterus chaoyangensis* ∼ *Chaoyangopterus zhangi*)	This study	ICZN, PhyloCode	New clade name, new definition
Azhdarchiformes	Andres, 2021	max ∇ (*Azhdarcho lancicollis* ∼ *Chaoyangopterus zhangi*)	This study	PhyloCode	Unrestricted emendation; see Systematic Paleontology
Alanqidae	Pêgas et al., 2022	max ∇ (*Alanqa saharica* ∼ *Azhdarcho lancicollis* ∨ *Chaoyangopterus zhangi*)	Pêgas et al., 2022	ICZN, PhyloCode	
Azhdarchidae	Padian, 1986	min ∇ (*Azhdarcho lancicollis* & *Quetzalcoatlus northopi* & *Phosphatodraco mauritanicus*)	Pêgas et al., 2022	ICZN, PhyloCode	
Azhdarchinae	Nesov, 1984	max ∇ (*Azhdarcho lancicollis* ∼ *Quetzalcoatlus northopi*)	Andres, 2021	ICZN, PhyloCode	
Quetzalcoatlinae	Andres et al., 2014	max ∇ (*Quetzalcoatlus northopi* ∼ *Azhdarcho lancicollis*)	Andres et al., 2014	ICZN, PhyloCode	Preexisting name
Serpennata	Thomas & McDavid, new clade	min ∇ (*Quetzalcoatlus northopi* & *Arambourgiania philadelphiae*)	This study	PhyloCode	New clade name, new definition

Table 2. Summary of skeletal elements used for new wingspan estimates.

Element	# of taxa
Complete wing skeletons	66
Skull (complete)	8
Skull (estimated complete)	4
Rostrum (tip of premaxilla to anterior border of naris/nasoantorbital fenestra)	1
Mandible	12
Cervical vertebrae	18
Humerus	40
Ulna	18
Metacarpal IV	2
Wing phalanx I	17
Wing phalanx II	15
Wing phalanx IV	1
Previous estimates (regression)	4
Previous estimates (isometric scaling)	4
Previous estimates (unspecified)	8

example), estimates of body mass based on wingspan would require a further transformation of the data, possibly contributing to a loss of accuracy. Although other definitions of wingspan do exist (e.g. Kellner et al., 2013; Witton, 2008b), the most commonly used definition of wingspan in pterosaur research is the two times the sum of the lengths of the humerus, ulna or radius, fourth metacarpal, and all four wing phalanges (Andres & Langston, 2021; Bennett, 2001; Benson et al., 2014; Hone & McDavid, 2025; Jagielska et al., 2022). This is the definition we adopt here.

Our dataset of pterosaur wingspans was based on the dataset provided in Benson et al. (2014), augmented with additional complete pterosaur specimens. Using the proportions of these complete specimens, linear regression equations were calculated relating various individual elements in the pterosaur skeleton to the total wingspan. These equations were used to calculate wingspans for incompletely known pterosaurs. The humerus, ulna, wing phalanx I, and wing phalanx II all predict wingspan with $r^2 > 0.95$, so wingspan estimates of each OTU were calculated using the total length of each of these elements if preserved. If more than one of these elements were preserved in an OTU, a mean of all calculated estimates was adopted for analysis. If none of these elements were preserved, linear regression using the length of the mandible was adopted if applicable for members of Pteranodontoidea ($r^2 = 0.956$) and Azhdarchoidea ($r^2 = 0.931$). It should be noted that, since our wing element dataset includes many non-azhdarchoids, regression estimates for azhdarchoids based on wing elements may be slightly overestimated, as azhdarchoids have a proportionally shorter wing phalanx IV relative to other pterosaurs (Andres & Langston, 2021).

Wingspan estimations for ctenochasmatoid pterosaurs that lack complete appendicular elements were calculated from the length of the skull, using the regression equation presented in Gao et al. (2022). Published estimates of total skull length were adopted for the incompletely known *Lusognathus almadrava* (Fernandes et al., 2023), *Plataleorhynchus streptophorodon* (Howse & Milner, 1995), and *Tacuadactylus luciae* (Soto et al., 2021), while the skull length for '*Gnathosaurus*' *macrurus* (Howse & Milner, 1995) was calculated from the mandible length based on the proportions of *Gnathosaurus subulatus*. Wingspan estimations for azhdarchiform pterosaurs known only from cervical vertebrae were made using the methodology presented in Thomas et al. (2025). Total neck length was first estimated using linear regression from an individual cervical vertebra, and from this neck length the proportions of either '*Quetzalcoatlus*' *lawsoni* (for members of Serpennata) or *Zhejiangopterus linhaiensis* (for others) were isometrically scaled to match the estimated neck length. The variation in proportional length of the cervical series within Azhdarchidae serves as a caveat; we caution that wingspan may be underestimated for taxa with proportionally shorter cervical series. Wingspan for *Hatzegopteryx thambema* was calculated by isometrically scaling humeral proportions of *Quetzalcoatlus northropi* to the shaft width of the holotype humerus (90 mm; Buffetaut et al., 2002) and using the resulting length (544 mm) for linear regression. However, given the unique robusticity of *Hatzegopteryx* (Naish & Witton, 2017), isometric scaling based on shaft width may result in an overestimated wingspan.

Due to a lack of preservation of elements that can be reliably used in regression analyses, isometric scaling of the proportions of closely related taxa was used

to estimate the wingspans of *Angustinaripterus longicephalus*, *Caeletiventus hanseni*, *Cuspicephalus scarfi*, '*Dimorphodon*' *weintraubi*, *Hongshanopterus lacustris*, *Klobiodon rochei*, *Lacusovagus magnificens*, *Maaradactylus kellneri*, the 'Quebrada Monardes pterosaur', MB.R 2832, and UFC 721. The results of the regression analyses performed in Jagielska et al. (2022) were adopted for *Dearc sgiathanach*. Due to the quality of preservation, wingspans for *Hamipterus tianshanensis*, *Iberodactylus andreui*, *Istiodactylus latidens*, *Jianchangnathus robustus*, *Thapunngaka shawi*, *Torukjara bandeirae*, *Tropeognathus mesembrinus* and *Vectidraco daisymorrisae* were sourced from previous estimates in the literature. Although smaller complete specimens are included in our dataset, published wingspan estimates of the largest known individuals were adopted for *Nurhachius ignaciobritoi* (Wang et al., 2005), *Pteranodon longiceps* (Bennett, 2001), and *Rhamphorhynchus muensteri* (Hone & McDavid, 2025).

A pruned consensus tree derived from the strict consensus of the equal weights analysis, with OTUs without reliable wingspan estimates and non-pterosaurian outgroups removed, was used for reconstruction. *Arcticodactylus cromptonellus*, *Bellubrunnus rothgaengeri*, *Jidapterus edentus*, *Luopterus mutoudengensis*, *Propterodactylus frankerlae* and *Qinglongopterus guoi* were also removed *a priori* since these taxa are only known from early juvenile individuals (ontogenetic stage 2 of Kellner, 2015). Ancestral state reconstruction was performed in R (R Core Team, 2024) using the package phytools (Revell, 2024). Maximum likelihood estimates of wingspan for each node on the tree was calculated using the function fastAnc. Figures were produced using the packages svglite (Wickham et al., 2023) and viridis (Garnier et al., 2023).

For the purposes of this study, we adopt the definition of gigantism in pterosaurs proposed by Kellner et al. (2013) of 7.4 m. This is greater than the largest specimen of *Pteranodon longiceps* (FMNH PR 468, estimated at 7.25 m by Bennett, 2001), historically considered the largest pterosaur prior to the discovery of azhdarchids (Witton, 2010), as well as the largest bird (*Pelagornis sandersi*, estimated at 6.06–7.38 m by Ksepka, 2014). The only non-azhdarchid pterosaur that possibly meets this definition of gigantism is a specimen of *Tropeognathus* cf. *mesembrinus* (MN 6594-V) estimated at 8.2 m (using our definition of wingspan and individual bone length estimates of Kellner et al., 2013, scaled based on AMNH FARB 22552). We consider pterosaurs with a wingspan up to 2 m to be small (following Martin-Silverstone, Witton, et al., 2016), 2–5 m to be medium, and 5–7.4 m to be large.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; **BSPG,** Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CAMSM,** Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, UK; **CMN,** Canadian Museum of Nature, Ottawa, Ontario, Canada; **EME,** Transylvanian Museum Society, Cluj-Napoca, Romania; **FMNH,** Field Museum of Natural History, Chicago, IL, USA; **FSAC,** Faculté des Sciences Aïn Chock, Université Hassan II de Casablanca, Casablanca, Morocco; **KUVP,** Vertebrate Paleontology, University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, KS, USA; **LF,** Lauer Foundation for Paleontology, Science, and Education, Wheaton, IL, USA; **LPB,** (FGGUB) Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; **LPM,** Liaoning Paleontological Museum, Chaoyang National Geopark, Chaoyang, China; **MANCH,** Manchester Museum, University of Manchester, Manchester, UK; **MB,** Museum für Naturkunde, Berlin, Germany; **MC,** Musée de Cruzy, Cruzy, France; **MCSNB,** Museo Civico di Scienze Naturali E. Caffi, Bergamo, Italy; **MCT,** Museu de Ciências da Terra, Rio de Janeiro, Brazil; **ME,** Musée des Dinosaures, Espéraza, France; **MN,** Museu Nacional, Rio de Janeiro, Brazil; **MPC,** Mongolian Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **MPCA,** Carlos Ameghino Provincial Museum, Cipolletti, Argentina; **MPPM,** Memphis Museum of Science and History, Memphis, TN, USA; **MTCO,** Marinescu Collection, Țării Crișurilor Museum, Oradea, Romania; **MTM,** Hungarian Natural History Museum, Budapest, Hungary; **NHMUK,** (ex BMNH) The Natural History Museum, London, UK; **NJSM,** New Jersey State Museum, Trenton, NJ, USA; **RBCM,** Royal British Columbia Museum, Victoria, British Columbia, Canada; **RGM,** Geological Collection, Naturalis Biodiversity Center, Leiden, Netherlands (includes specimens formerly held at UvA; de Clercq, 2004); **SMNK,** Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; **TMM,** Texas Vertebrate Paleontology Collections, Austin, TX, USA; **TMP,** Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP,** University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; **UCMP,** University of California Museum of Paleontology, Berkeley, CA, USA; **UFC,** Federal University of Ceará, Fortaleza, Brazil; **UNCUYO-LD,** Laboratorio y Museo de Dinosaurios, Universidad Nacional de Cuyo, Mendoza, Argentina; **UPMC,** Collection paléontologique de l'Université Paris 6, Paris, France; **USNM,** National Museum of Natural History, Washington, DC, USA; **UvA,** University of Amsterdam, Amsterdam, Netherlands (collections now at other Dutch institutions; de Clercq, 2004); **YPM,** Yale Peabody Museum, New Haven, CT, USA (VPPU designates

specimens formerly held at Princeton University, now held at YPM; Gallagher et al., 1986); **ZIN,** Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Systematic palaeontology

Pterosauromorpha Kuhn-Schnyder & Rieber, 1986 *sensu* Andres & Padian, 2020a
Pterosauria Owen, 1842 *sensu* Andres & Padian, 2020b

1834 Pterosaurii Kaup: 311

Remarks. Pterosauria is often incorrectly attributed to Kaup, 1834. The correct authorship is Owen, 1842, p. 156; see Andres and Myers (2013) and Andres and Padian (2020b) for discussion.

Pterodactyloidea Plieninger, 1901 *sensu* Andres & Padian, 2020c
Ornithocheiroidea Seeley, 1878, converted clade name

RegNum registration number. 1180.

Definition. The least inclusive clade containing *Ornithocheirus simus* (Owen, 1861), *Anhanguera blittersdorffi* Campos & Kellner, 1985, *Pteranodon longiceps* Marsh, 1876, *Dsungaripterus weii* C. C. Young, 1964, and *Quetzalcoatlus northopi* Lawson, 1975b.

Reference phylogeny. This study (Figs 2, 3).

Included taxa. Pteranodontoidea, Dsungaripteromorpha, Azhdarchoidea.

Remarks. Kellner (2003) defined Ornithocheiroidea as a minimum clade without *Ornithocheirus* as an internal specifier. This violates the *PhyloCode* (Art. 11.9), as the namesake taxon of the Ornithocheiroidea is not an internal specifier. We revise the definition to add *Ornithocheirus simus* as an internal specifier. This does not alter the clade content as *Ornithocheirus*, although poorly known, is universally recovered within the Tapejaroidea + Pteranodontoidea clade (e.g. Andres, 2021; Pêgas, 2024, 2025; this study). Additionally, the name Ornithocheiroidea is often attributed to Seeley, 1891; the name was first used in Seeley (1878) and is attributed to Seeley (1878) in Seeley (1891). Despite the -oidea suffix (cf. ICZN Art. 29.2) this is not a superfamily name. It was established as a suborder by Seeley (1878, 1891) and is treated as an unranked clade herein.

Azhdarchoidea Unwin, 1995, converted clade name

RegNum registration number. 1181.

Definition. The least inclusive clade containing *Azhdarcho lancicollis* Nesov, 1984 and *Tapejara wellnhoferi* Kellner, 1989.

Reference phylogeny. This study (Fig. 3).

Included taxa. Azhdarchomorpha, Tapejaromorpha, *Keresdrakon vilsoni*, MN 6588-V

Remarks. Unwin (2003) defined Azhdarchoidea as a minimum clade using *Quetzalcoatlus northopi* as an internal specifier. This violates the *PhyloCode* (Art. 11.9), as the namesake taxon *Azhdarcho lancicollis* is not included as an internal specifier. We revise the definition to include *Azhdarcho lancicollis* as the internal specifier instead of *Quetzalcoatlus northropi*. Under the phylogenetic hypothesis in this study, Neoazhdarchia *sensu* Unwin, 2003 (which, not including *Azhdarcho lancicollis* as an internal specifier, also violates Article 11.9 of the *PhyloCode*) is a synonym of Azhdarchoidea. As Nesov (1984) established the subfamily name Azhdarchinae, the Principle of Coordination (ICZN, 1999, Art. 36) specifies that Nesov, 1984 is the author of the superfamily name Azhdarchoidea. The *PhyloCode* has no such principle, so the author of the clade Azhdarchoidea (as opposed to the superfamily Azhdarchoidea) is the first to use the spelling Azhdarchoidea (see *PhyloCode* note 9.15A.3). The first author to use the spelling Azhdarchoidea is Unwin, 1995. We treat Azhdarchoidea as a clade under the *PhyloCode*, so the authorship is Unwin, 1995.

Azhdarchomorpha Pêgas, Holgado, Ortiz David, Baiano & Costa, 2022

Definition. The most inclusive clade containing *Azhdarcho lancicollis* Nesov, 1984, but not *Thalassodromeus sethi* Kellner & Campos, 2002 or *Tapejara wellnhoferi* Kellner, 1989 (Pêgas et al., 2022).

Included taxa. Concilazhia, *Inabtanin alarabia*, *Microtuban altivolans*, RGM.631745

Concilazhia Thomas & McDavid, new clade name

RegNum registration number. 1177.

Definition. We propose this clade as the least inclusive clade containing *Azhdarcho lancicollis* Nesov, 1984, *Chaoyangopterus zhangi* Wang & Zhou, 2003, and *Alanqa saharica* Ibrahim, Unwin, Martill, Baidder, & Zouhri, 2010.

Reference phylogeny. This study (Fig. 4).

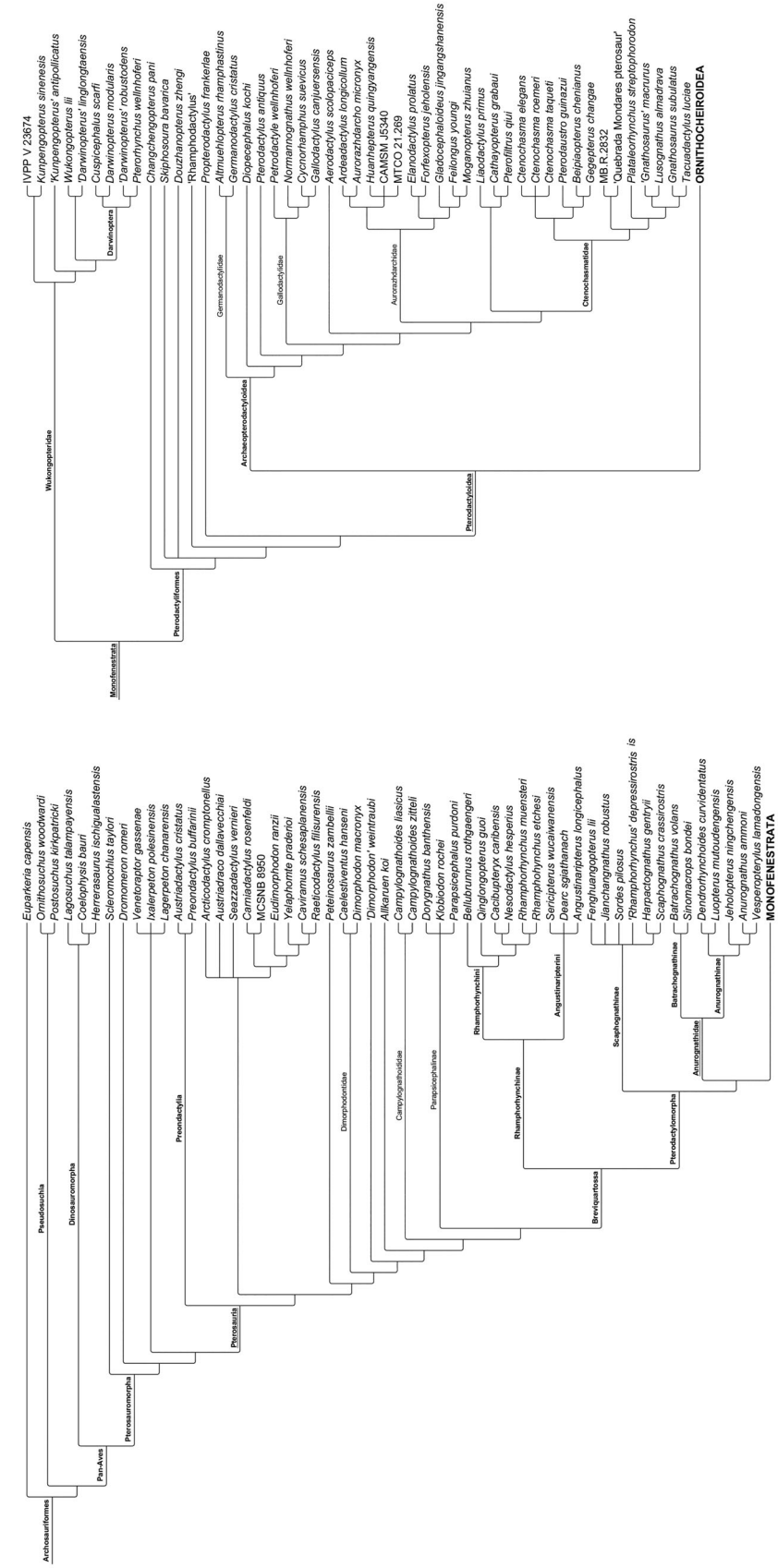

Figure 2. Strict consensus phylogeny of non-pterodactyloid pterosaurs based on the phylogenetic analysis of this study. Branches labelled with bold text are phylogenetically defined clades; branches labelled with underlined bold text are phylogenetically defined clades with apomorphy-based definitions.

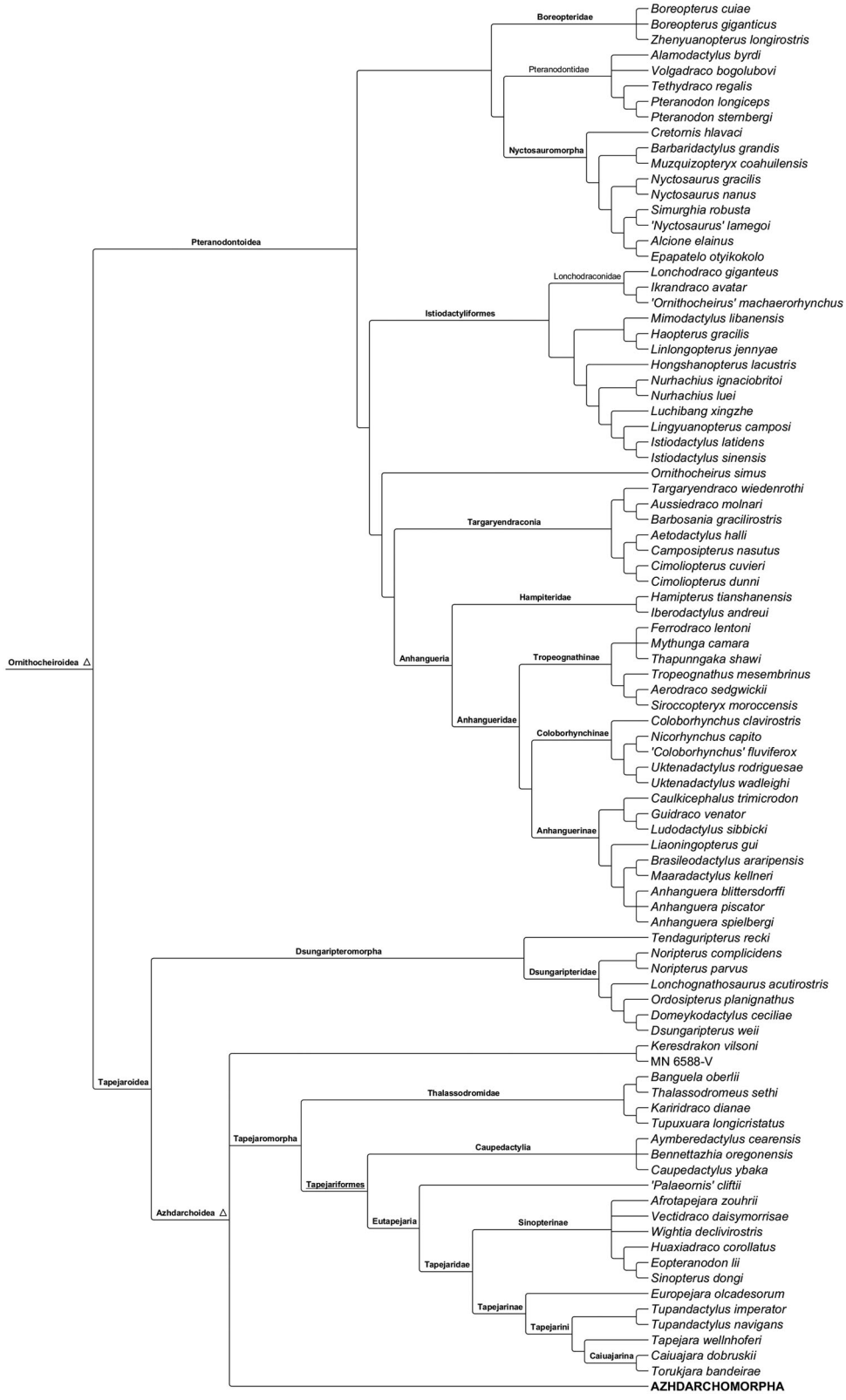

Figure 3. Strict consensus phylogeny of Pterodactyloidea based on the phylogenetic analysis of this study. Branches labelled with bold text are phylogenetically defined clades; branches labelled with underlined bold text are phylogenetically defined clades with apomorphy-based definitions. White triangles next to clade names indicate new definitions.

Derivation of name. 'Concil' from Latin *concilium* meaning 'council' or 'assembly' (Gaffiot, 1934); '-azhia' from Avestan *azhi* meaning 'snake', a word which would be incorporated into the names of many draconic and serpentine mythical beings, and from which the name *Azhdarcho* ultimately derives (Shakiba, 2018). The name therefore loosely translates to 'council of dragons'.

Included taxa. Azhdarchiformes, Chaoyangopteridae.

Remarks. 'Neopterodactyloidea' was defined by Andres et al. (2014) as "the least inclusive clade containing *Quetzalcoatlus northopi* Lawson [1975b] and *Chaoyangopterus zhangi* Wang and Zhou [2003]". This violates *PhyloCode* Art. 11.9 as the clade name is derived from *Pterodactylus*, which is not part of this clade under the topology of Andres et al. (2014), and was universally recovered as a much more early-diverging member of Pterodactyloidea in then-preexisting analyses (e.g. Andres, 2010; Andres & Ji, 2008; Lü & Ji, 2006; Lü et al., 2010) and subsequent analyses (e.g. Andres, 2021; Hone et al., 2024; Longrich et al., 2018; Lü et al., 2016; Pêgas, 2024; Pêgas et al., 2022; Vidovic & Martill, 2014, 2018). 'Neopterodactyloidea' is not an acceptable name for this clade under the *PhyloCode*. We establish Concilazhia as a new clade that serves a similar purpose and has a similar definition to 'Neopterodactyloidea' of Andres et al. (2014), though we use *Azhdarcho* as an internal specifier rather than *Quetzalcoatlus* in order to be consistent with the definitions of Azhdarchoidea, Azhdarchomorpha, Azhdarchiformes, and Azhdarchidae. *Alanqa saharica* is listed as an internal specifier to account for topologies where Alanqidae nests outside the (Azhdarchidae + Chaoyangopteridae) clade (e.g. Pêgas et al., 2022).

Chaoyangopteridae Lü, Unwin, Xu, & Zhang, 2008 *sensu* Andres, Clark, & Xu, 2014

Definition. The most inclusive clade containing *Chaoyangopterus zhangi* Wang & Zhou, 2003 but not *Quetzalcoatlus northropi* Lawson, 1975b (Andres et al., 2014).

Included taxa. Chaoyangopterinae, Shenzhoupterinae.

Chaoyangopterinae Pinheiro, Fortier, Schultz, de Andrade, & Bantim, 2011 *sensu* Andres, 2021

Definition. The least inclusive clade containing *Chaoyangopterus zhangi* Wang & Zhou, 2003 and *Jidapterus edentus* Dong, Sun, & Wu, 2003.

Included taxa. *Chaoyangopterus zhangi*, *Jidapterus edentus*, *Lacusovagus magnificens*, UFC 721.

Remarks. This clade was defined in Andres et al. (2014) using *Shenzhoupterus chaoyangensis* as an internal specifier instead of *Jidapterus edentus*. Under the phylogenetic hypotheses in Andres (2021), Pêgas (2024), Pêgas et al. (2022), and this paper, Chaoyangopterinae *sensu* Andres (2021) is equivalent to Chaoyangopteridae. As Lü et al. (2008) established the family name Chaoyangopteridae, the Principle of Coordination (ICZN, 1999, Art. 36) specifies that Lü et al., 2008 are the authors of the subfamily name Chaoyangopterinae. The *PhyloCode* has no such principle, so the authors of the clade Chaoyangopterinae (as opposed to the subfamily Chaoyangopterinae) are the first to use the spelling Chaoyangopterinae (see *PhyloCode* note 9.15A.3). The first authors to use the spelling Chaoyangopterinae were Pinheiro et al. (2011). We treat Chaoyangopterinae as a clade under the *PhyloCode*, so the authorship is Pinheiro et al., 2011.

Shenzhoupterinae Thomas & McDavid, new clade name

RegNum registration number. 1178.

Definition. We propose this clade as the most inclusive clade containing *Shenzhoupterus chaoyangensis* Lü, Unwin, Xu, & Zhang, 2008, but not *Chaoyangopterus zhangi* Wang & Zhou, 2003.

Reference phylogeny. This study (Fig. 4).

Derivation of name. From the internal specifier *Shenzhoupterus chaoyangensis*.

Included taxa. *Eoazhdarcho liaoxiensis*, *Meilifeilong youhao*, *Melifeilong sanyanius*, *Shenzhoupterus chaoyangensis.*

Remarks. *Meilifeilong* and *Shenzhoupterus* display relatively deep skulls with large nasoantorbital fenestrae, a convex dorsal margin of the skull roof, and short sagittal crests.

Azhdarchiformes Andres, 2021

RegNum registration number. 1182.

Definition. The most inclusive clade containing *Azhdarcho lancicollis* Nesov, 1984 but not *Chaoyangopterus zhangi* Wang & Zhou, 2003.

Reference phylogeny. This study (Fig. 4).

Included taxa. Alanqidae, Azhdarchidae, *Montanazhdarcho minor*, *Radiodactylus langstoni*

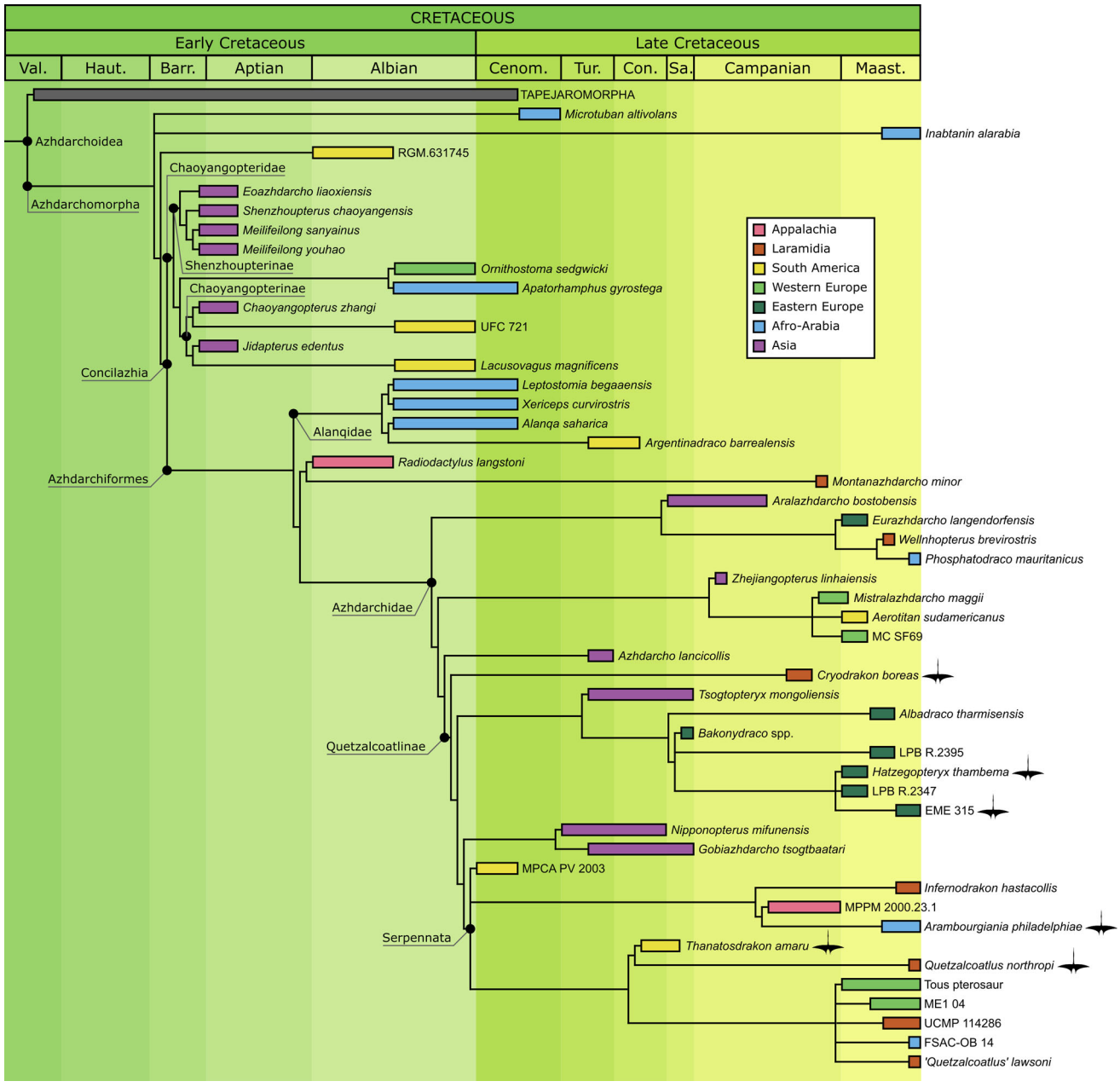

Figure 4. Strict consensus time-calibrated phylogeny of Azhdarchomorpha based on the equal weights phylogenetic analysis of this study. Clade labels at the base of a node indicate minimum clades; clade labels on a branch indicate maximum clades.

Remarks. This clade was originally defined in Andres (2021) using *Quetzalcoatlus northropi* as an internal specifier. This violates the *PhyloCode*, as the namesake taxon *Azhdarcho lancicollis* is not included as an internal specifier (*PhyloCode* Art 11.9). We revise the definition to include *Azhdarcho lancicollis* as the internal specifier instead of *Quetzalcoatlus northropi*. This does not alter clade content.

Alanqidae Pêgas, Holgado, Ortiz David, Baiano, & Costa, 2022

Definition. The most inclusive clade containing *Alanqa saharica* Ibrahim, Unwin, Martill, Baidder, & Zouhri, 2010 but not *Azhdarcho lancicollis* Nesov, 1984, or

Chaoyangopterus zhangi Wang & Zhou, 2003 (Pêgas et al., 2022).

Included taxa. *Alanqa saharica*, *Argentinadraco barrealensis*, *Leptostomia begaaensis*, *Xericeps curvirostris.*

Azhdarchidae Padian, 1986 *sensu* Pêgas, Zhou, & Kobayashi, 2025

1984 Titanopterygiidae Padian: 522 (unavailable because *Titanopteryx* was preoccupied; see Padian, 1986)
1984 Titanopterygidae Gallagher: 23 (unavailable, *lapsus calami*)

Definition. The least inclusive clade containing *Azhdarcho lancicollis* Nesov, 1984, *Quetzalcoatlus northropi* Lawson, 1975b, *Zhejiangopterus linhaiensis* Cai & Wei, 1994, and *Phosphatodraco mauritanicus* Pereda-Suberbiola, Bardet, Jouve, Iarochène, Boya, & Amaghzaz, 2003 (Pêgas et al., 2025).

Included taxa. Quetzalcoatlinae, *Aerotitan sudamericanus*, *Aralazhdarcho bostobensis*, *Azhdarcho lancicollis*, *Eurazhdarcho langendorfensis*, *Mistralazhdarcho maggii*, *Phosphatodraco mauritanicus*, *Wellnhopterus brevirostris*, *Zhejiangopterus linhaiensis*, MC SF69.

Remarks. Azhdarchidae was initially defined in Unwin (2003) with *Azhdarcho lancicollis* and *Quetzalcoatlus northropi* as internal specifiers. Pêgas et al. (2022) provided an unrestricted emendation, adding *Phosphatodraco mauritanicus* as an internal specifier. An alternate definition for Azhdarchidae was provided in Vidovic and Martill (2018): the most inclusive clade containing *Azhdarcho* but not *Tapejara* or *Tupuxuara*; this definition is equivalent to Azhdarchomorpha *sensu* Pêgas et al. (2022). As Nesov (1984) established the subfamily name Azhdarchinae, the Principle of Coordination (ICZN, 1999, Art. 36) specifies that Nesov, 1984 is the author of the family name Azhdarchidae. The *PhyloCode* has no such principle, so the author of the clade Azhdarchidae (as opposed to the family Azhdarchidae) is the first to use the spelling Azhdarchidae (see *PhyloCode* note 9.15A.3). The first author to use the spelling Azhdarchidae is Padian (1986). We treat Azhdarchidae as a clade under the *PhyloCode*, so the authorship is Padian, 1986.

Quetzalcoatlinae Andres, Clark, & Xu, 2014

Definition. The most inclusive clade containing *Quetzalcoatlus northropi* Lawson, 1975b but not *Azhdarcho lancicollis* Nesov, 1984 (Andres et al., 2014).

Included taxa. Serpennata, *Albadraco*, *Bakonydraco*, *Cryodrakon*, *Gobiazhdarcho*, *Hatzegopteryx*, *Nipponopterus*, *Tsogtopteryx*, LPB R.2395.

Serpennata Thomas & McDavid, new clade name

1985 '*Titanopteryx-Quetzalcoatlus* group' Baird in Schwimmer et al.:674
2025 '*Quetzalcoatlus-Arambourgiania* clade' Thomas, Hone, Gomes, & Peterson: 3

RegNum registration number. 1179.

Definition. We propose this clade as the least inclusive clade containing *Quetzalcoatlus northropi* Lawson, 1975b and *Arambourgiania philadelphiae* (Arambourg, 1959).

Reference phylogeny. This study (Fig. 4).

Derivation of name. Portmanteau of the Latin *serpens* meaning 'snake' and 'pennata' (fem.) meaning 'feathered' (Gaffiot, 1934). 'Feathered serpents', in allusion to the extremely long cervical series of azhdarchids in this clade, and to the internal specifier *Quetzalcoatlus*, named for the Aztec deity Quetzalcoatl, depicted as a flying feathered serpent.

Included taxa. *Arambourgiania philadelphiae*, *Infernodrakon hastacollis*, '*Quetzalcoatlus*' *lawsoni*, *Quetzalcoatlus northropi*, *Thanatosdrakon amaru*, 'Tous pterosaur', FSAC-OB 14, ME1 04, MPCA-PV 2003, MPPM 2000.23.1, UCMP 114286.

Remarks. This clade includes the azhdarchids with the most gracile and elongate cervical vertebrae, with elongation ratios of cervical V exceeding 8 (Pêgas et al., 2022; Thomas et al., 2025). These are among the most gracile vertebrae of any tetrapod (Thomas et al., 2025). A clade containing *Arambourgiania* and *Quetzalcoatlus* to the exclusion of *Azhdarcho*, *Hatzegopteryx*, and *Phosphatodraco* has previously been recovered in Andres (2021), Pêgas (2024), Pêgas et al. (2022, 2023), Thomas et al. (2025), and Zhou et al. (2024).

Results

The equal weights analysis returned 48 most parsimonious trees (length = 2835; CI = 0.301; RI = 0.784), and the implied weights analysis (with $k = 14$) returned nine (fit = 101.05915; CI = 0.300; RI = 0.784). The broader scale topologies of each analysis are largely in agreement,

although there are minor differences in the arrangement of a handful of nodes on the tree. The following description of results, as well as further analyses, follows the equal weights analysis; the full topology of the implied weights analyses can be found in the Supplemental File 2.

Pterosaur macroevolution

The status of Lagerpetidae as either the sister group to Pterosauria (Ezcurra et al., 2020) or a grade paraphyletic with respect to Pterosauria (Garcia & Müller, 2025) is an area of active research. We recover a Lagerpetidae containing *Ixalerpeton*, *Lagerpeton* and *Venetoraptor*, but *Dromomeron* and *Scleromochlus* are recovered as earlier-diverging pterosauromorphs. This being said, our dataset lacks the characters to accurately resolve this portion of the tree and the inclusion of these non-pterosaurian pterosauromorphs serves to optimize character states for the ingroup (e.g. Baron, 2020), so these results should not be taken as support for either hypothesis.

The topology of non-azhdarchoid Pterosauria is overall similar to that presented in Pêgas (2024). We recovered a monophyletic Rhamphorhynchinae, equivalent to Rhamphorhynchae *sensu* Andres, 2021, uniting the Angustinaripterini (*Angustinaripterus*, *Sericipterus* and *Dearc*; Jagielska et al., 2022) as the sister taxon to Rhamphorhynchini. The two named pterosaur species from Cuba, *Cacibupteryx caribensis* (Gasparini et al., 2004) and *Nesodactylus hesperius* (Colbert, 1969), are sister taxa, supported by a synapomorphic helical quadrate-mandible articulation (character 139). Scaphognathinae encompasses *Scaphognathus*, *Harpactognathus*, *Sordes*, *Jianchangnathus*, *Fenghuangopterus*, and '*Rhamphorhynchus*' *depressirostris*. *Parapsicephalus* and *Klobiodon* clade with *Dorygnathus* rather than as Rhamphorhynchines or Scaphognathines as previously suggested (O'Sullivan & Martill, 2017, 2018) with this group forming the earliest-diverging 'Rhamphorhynchid' lineage. Parapsicephalinae Kuhn, 1967 is available as a family-group name for this clade, although we choose not to convert it to a phylogenetically defined clade name in this study, as non-pterodactyloid taxonomy is outside the scope of this paper. 'Rhamphorhynchidae' as traditionally understood (i.e. uniting Rhamphorynchinae with Scaphognathinae to the exclusion of pterodactyloids) is paraphyletic, with Parapsicephalinae, Rhamphorhynchinae and Scaphognathinae representing successive branches on the lineage leading to the Monofenestrata + Anurognathidae clade (i.e. Caelidracones *sensu* Unwin, 2003, though note that the content of this named clade is highly variable given the unstable position of Anurognathidae within Pterosauria).

We recovered Anurognathidae as the sister taxon to Monofenestrata within Pterodactylomorpha. The position of Anurognathidae within Pterosauria is highly unstable with different analyses recovering vastly different results (see Dalla Vecchia, 2022; Wei et al., 2021). Anurognathidae are highly morphologically divergent from other pterosaurs, presumably due to their unique niche as aerial insectivores, making their relationships to other pterosaurs difficult to accurately resolve (Clark & Hone, 2022; Dalla Vecchia, 2022; Hone, 2020). Within Anurognathidae, we recover a Batrachognathinae encompassing *Batrachognathus* and *Sinomacrops*, with the remaining anurognathids forming Anurognathinae, as in Pêgas (2024) and Wei et al. (2021).

We recovered a monophyletic Wukongopteridae, which contains Darwinoptera *sensu* Andres et al., 2014. This is in contrast to the results recently obtained by Hone et al. (2024) in which 'Wukongopteridae' is a grade on the lineage leading to Pterodactyloidea, and Darwinoptera includes Pterodactyloidea. The internal relationships of Wukongopteridae are poorly resolved, but they seem to represent a radiation independent of pterodactyloids and 'rhamphorhynchoids' (*sensu* e.g. Wellnhofer, 1975) rather than a grade. The intriguing taxon *Changchengopterus pani*, originally assigned to Rhamphorhynchidae (Lü, 2009) and subsequently assigned to Wukongopteridae (Cheng et al., 2017; Martin-Silverstone et al., 2023; Wang et al., 2010), is here recovered as the earliest-diverging member of Pterodactyliformes, as in several recent phylogenetic analyses (e.g. Andres, 2021; Hone et al., 2024; Pêgas, 2024). It is equally parsimonious for *Skiphosoura* and *Douzhanopterus* to be sister taxa as it is for *Douzhanopterus* to be one step closer to Pterodactyloidea (i.e. as in Hone et al., 2024). The informally named 'Rhamphodactylus' and *Propterodactylus* then represent successive branches from the lineage leading to Pterodactyloidea. This topology is similar, but not identical, to that recovered by Hone et al. (2024).

We also recovered a topology similar but not identical to that of Hone et al. (2024) for Archaeopterodactyloidea. Notably, we recovered a monophyletic *Ctenochasma* sister to a monophyletic Pterodaustrini encompassing *Pterodaustro*, *Beipiaopterus* and *Gegepterus*. CAMSM J5340 and MTCO 21.269 are two cervical vertebrae from Berriasian Europe, the former from the Purbeck Group of England (Howse, 1986; Howse & Milner, 1995) and the latter from the bauxite mines of Cornet, Romania (Dyke et al., 2011). Each has been suggested to represent an azhdarchid pterosaur, on account of their extreme elongation and dorsoventral compression of the centrum (Dyke et al., 2011; Howse, 1986). Here they are both recovered deeply nested within Ctenochasmatoidea in a polytomy with

Huanhepterus quingyangensis, which similarly displays extremely elongated cervical vertebrae convergent with azhdarchids (Andres & Ji, 2008). Ctenochasmatoids are well documented in the Purbeck Group (Howse & Milner, 1995) and had been previously reported from Cornet (Jurcsák & Kessler, 1985, 1991), though Dyke et al. (2011) rejected this identification. MB. R. 2832, a cervical vertebra from the Tendaguru Formation which has been suggested to represent a Late Jurassic azhdarchid (Costa et al., 2015), is recovered within Ctenochasmatidae as the sister taxon to the 'Quebrada Monardes pterosaur' (Alarcón-Muñoz et al., 2020, 2022; Martill et al., 2006). '*Gnathosaurus*' *macrurus*, limited to the lectotype rostrum (Howse & Milner, 1995), is recovered as the sister taxon to *Lusognathus almadrava*, as in Zhou et al. (2024).

The topology of Pteranodontoidea is nearly identical to that presented in Pêgas (2024). *Volgadraco bogolubovi*, originally described as an azhdarchid (Averianov et al., 2008), is recovered as an early-diverging pteranodontid, in a polytomy with *Alamodactylus byrdi* and a *Pteranodon*+*Tethydraco* clade. Within Istiodactyliformes, *Lonchodraco* and '*Ornithocheirus*' *machaerorhynchus* form a clade (i.e. Lonchodraconidae) with *Ikrandraco avatar*. '*O*'. *machaerorhynchus* is recovered as the sister taxon to *Ikrandraco avatar*, as suggested in Averianov (2020). This contrasts with the results of Pêgas (2024), in which *Lonchodraco giganteus* and '*Ornithocheirus*' *machaerorhynchus* form a clade that is sister to *Mimodactylus*.

Tapejaroidea *sensu* Kellner (2003) is recovered as monophyletic, containing Dsungaripteromorpha and Azhdarchoidea. The topology of Dsungaripteromorpha closely agrees with that of Pêgas (2024). *Tendaguripterus recki* is recovered as the sister taxon to Dsungaripteridae, which consists of *Noripterus* and Dsungaripterinae. *Lonchognathosaurus acutirostris* (Maisch et al., 2004) is recovered as the earliest-diverging member of Dsungaripterinae, outside a clade containing *Domeykodactylus*, *Dsungaripterus* and *Ordosipterus*. This position supports the recognition of *Lonchognathosaurus acutirostris* as a valid dsungaripterid taxon (Augustin et al., 2021), contrary to previous suggestions that it may be a junior synonym of *Dsungaripterus weii* (Andres et al., 2010) or *Noripterus complicidens* (Hone et al., 2018).

Azhdarchoidea

As with most recent phylogenetic analyses (e.g. Hone et al., 2024; Ortiz David et al., 2022; Pêgas, 2024; Pêgas et al., 2022; Thomas, 2021; Zhou et al., 2024), Azhdarchoidea contains two major clades: one containing Tapejaridae and Thalassodromidae, and one containing Chaoyangopteridae and Azhdarchidae. Neoazhdarchia, defined by Unwin (2003) as a minimum clade containing azhdarchids and thalassodromids, is a junior synonym of Azhdarchoidea under this topology.

Keresdrakon vilsoni has been variously recovered as the earliest-diverging tapejaromorph (Kellner, Weinschütz, et al., 2019; Thomas, 2021), the earliest-diverging azhdarchomorph (Pêgas, 2024), an alanqid (Pêgas et al., 2022), or a tapejarid (Andres, 2021). This taxon shows a mixture of azhdarchoid plesiomorphies and derived characters not evident in other azhdarchoids, making it difficult to place phylogenetically. We recover it as an unresolved early-diverging azhdarchoid, in a polytomy with Azhdarchomorpha and Tapejaromorpha. None of the synapomorphies of each clade are present in *Keresdrakon*. The azhdarchoid specimen MN 6588-V (Sayão & Kellner, 2006), a partial skeleton lacking the head and limbs previously referred to the genus *Tupandactylus* (Beccari et al., 2021), is recovered as the sister taxon to *Keresdrakon vilsoni*; this is supported by similarities in the cervical vertebrae and sternum (characters 310, 365).

The topology we recovered for Tapejaromorpha is generally similar to that obtained by Pêgas (2024). '*Palaeornis*' *cliftii*, a pterosaur humerus referred to Lonchodectidae in Witton et al. (2009), is recovered as the sister taxon to Tapejaridae; it shares with this clade an expanded lateral condyle (character 396) and a proximally oriented deltopectoral crest of the humerus (character 588). *Bakonydraco* is recovered as an azhdarchid closely related to *Hatzegopteryx* rather than a tapejaromorph, following our modification of character coding for this taxon (see Discussion). Among newly added OTUs, *Vectidraco daisymorrisae* (Naish et al., 2013) is recovered as a member of Sinopterinae, in a polytomy with *Afrotapejara*, *Wightia*, and a clade containing *Eopteranodon*, *Sinopterus* and *Huaxiadraco*. If *Vectidraco* is removed *a posteriori*, *Afrotapejara* and *Wightia* form a clade. *Bennettazhia oregonensis*, originally assigned to *Pteranodon* (Gilmore, 1928) and assigned to its own genus by Nesov (1991) is based only on a humerus and two free dorsal vertebrae. It has at times been considered dubious (Bennett, 2018) and while a full reassessment of *Bennettazhia* is beyond the scope of this work, our examination of the holotype (USNM V 11925) suggests it is a unique humeral morphotype and, therefore, potentially valid. We recover it within the clade Caupedactylia in a polytomy with *Caupedactylus* and *Aymberedactylus*, supported by a flattened anterior surface of the distal humerus (character 591, ambiguous in *Aymberedactylus*). The dsungaripteromorph material assigned to *Bennettazhia* by Retallack et al. (2023) does not overlap with the holotype specimen and was seemingly assigned to *Bennettazhia* only based on its stratigraphical and geographical origin. This material includes teeth and undoubtedly represents a

different taxon; the *Bennettazhia* hypodigm is here restricted to only include the holotype.

Azhdarchomorpha

Inabtanin alarabia is a recently described azhdarchoid from the Maastrichtian of Jordan (Rosenbach et al., 2024). It was assigned to Azhdarchoidea without a phylogenetic analysis based on its "long, edentulous beak" and "humerus with a deltopectoral crest that originates from a distally placed position on the shaft and is rectangular, flat, and elongate in shape" (p. 2). Our analysis confirms this. Specifically, we recover it as an early-diverging member of Azhdarchomorpha in a polytomy with *Microtuban altivolans* and a clade containing all other azhdarchomorphs. Azhdarchomorpha is supported by the development of the ventral coracoid into an enlarged flange (character 353) and a round distal articulation of the wing metacarpal (character 438). *Inabtanin* and *Microtuban* are excluded from Concilazhia by the plesiomorphic morphology of the cervical vertebrae: they are short (elongation ratio <3; character 322) and have tall neural spines (characters 301, 302), distinct neural arches (character 538), well-developed transverse processes (character 581) and lateral pneumatic foramina (character 313). The presence of an early-diverging azhdarchomorph in the Maastrichtian is surprising, suggesting a ghost lineage extending to at least the Cenomanian but possibly the Aptian. *Microtuban altivolans*, from the Cenomanian of Lebanon, was described as potentially being either a chaoyangopterid or thalassodromine (Elgin & Frey, 2011). It is also recovered as an early-diverging azhdarchomorph due to the aforementioned characters of the cervical vertebra. *Inabtanin* and *Microtuban* show that early-diverging azhdarchomorphs survived into the Late Cretaceous in West Asia and imply the existence of at least one but possibly two ghost lineages of early-diverging azhdarchomorphs from the Aptian to Cenomanian.

RGM.631745 is the paratype of *Santanadactylus brasilensis* de Buisonjé, 1980. The specimen was originally catalogued at the Geological Institute of the University of Amsterdam, with the catalogue number UvA M 4895 (de Buisonjé, 1980). The geological collections of UvA have since been divested to other Dutch institutions (de Clercq, 2004); this specimen is currently stored at the Naturalis Biodiversity Center (Naturalis Biodiversity Center, 2017). RGM.631745 was not found associated with the holotype of *S. brasilensis*, which appears to be an anhanguerid (Kellner & Tomida, 2000), and there is no reason to refer it to *Santandactylus* (Bennett, 1989; Kellner, 1995, 2004; Leal et al., 2018). Here, RGM.631745 is recovered as the sister taxon to Concilazhia. The morphology of the vertebra is very similar to that of chaoyangopterids (e.g. UFC 721: Leal et al., 2018) and contrasts with the shorter cervical vertebrae of tapejaromorphs, *Keresdrakon*, *Inabtanin* and *Microtuban*. Namely, the vertebra is moderately elongate (character 322), the neural spine is reduced and rectangular (character 302), and the transverse processes are reduced (character 580). RGM.631745 is excluded from Concilazhia due to the presence of pneumatic foramina on the lateral centrum surface (character 313) and absence of well-excavated sulci ventral to the prezygapophyses (character 578). RGM.631745 was also recovered in this position in the analysis of Pêgas et al. (2022).

Chaoyangopteridae is resolved as a clade of early-diverging azhdarchomorphs. The previously defined Chaoyangopterinae (Andres et al., 2014) is resolved as monophyletic, and is the sister taxon to Shenzhoupterinae, cl. nov. Shenzhoupterinae contains *Eoazhdarcho liaoxiensis*, *Shenzhoupterus chaoyangensis* and *Meilifeilong* spp. *Eoazhdarcho* has been variously considered an azhdarchid (Lü & Ji, 2005), chaoyangopterid (Andres, 2021; Andres et al., 2014; Lü & Ji, 2006; Lü et al., 2008), basal azhdarchoid (Vidovic & Martill, 2018), and basal azhdarchiform (Longrich et al., 2018). It is recovered as the earliest-diverging member of Shenzhoupterinae, although this is supported by a single synapomorphy, an elongate deltopectoral crest of the humerus (character 384). '*Shenzhoupterus*' *sanyainus* is recovered as the sister taxon to *Meilifeilong youhao* by seven synapomorphies, supporting the referral of the former species to the genus *Meilifeilong* by Wang et al. (2023). *Apatorhamphus gyrostega* and *Ornithostoma sedgwicki* are recovered as sister taxa, as in Zhou et al. (2024). UFC 721, an articulated series of cervical vertebrae IV–VII recovered from the Crato Formation (Leal et al., 2018), is recovered as the sister taxon to *Chaoyangopterus zhangi*. *Lacusovagus magnificens*, which has been variously considered a chaoyangopterid (Pêgas, 2024; Witton, 2008a), a thalassodromine (Wu et al., 2017), or a tapejarid (Andres, 2021), is recovered here as the sister taxon to *Jidapterus edentus* within Chaoyangopterinae. *Lacusovagus magnificens* and UFC 721 are both known from the Crato Formation, and as the material is non-overlapping it is not impossible that they represent the same taxon (Leal et al., 2018). When a constraint is applied to force the two OTUs to form a monophyletic clade (effectively forming a composite taxon), they form a polytomy with *Chaoyangopterus zhangi* and *Jidapterus edentus*.

Alanqidae is a recently defined (Pêgas et al., 2022) clade of azhdarchomorphs known primarily from the Kem Kem Group in Morocco (Ibrahim et al., 2010; Martill et al., 2018; Smith et al., 2020) but also from

the Portezuelo Formation in Argentina (Kellner & Calvo, 2017). The topology of Alanqidae is identical to that recovered in Pêgas (2024), containing *Alanqa saharica*, *Argentinadraco barrealensis*, *Leptostomia begaaensis* and *Xericeps curvirostris*. These taxa all bear distinctive modifications to the jaws inferred to reflect molluscivory (Kellner & Calvo, 2017; Martill & Ibrahim, 2015) or probe-feeding (Smith et al., 2020), and may represent a Gondwanan radiation of coastal and riparian azhdarchoids, with the Kem Kem taxa filling different niches in the same ecosystem (Smith et al., 2023).

Montanazhdarcho minor is recovered as one step closer to Azhdarchidae, as in Andres (2021) and Thomas et al. (2025). This contrasts with the analysis of Carroll (2015), which recovered *Montanazhdarcho* as a tapejaromorph, and of Pêgas et al. (2023), which recovered it as an alanqid. *Radiodactylus langstoni*, previously recovered as a non-azhdarchid azhdarchomorph (Andres, 2021; Andres & Myers, 2013; Pêgas et al., 2022) is here recovered as the sister taxon to *Montanazhdarcho minor*. This clade is supported by four character states of the humerus: pneumatic foramen between distal condyles present (character 398); pneumatic foramen on distal surface present (character 400); short projection on radial surface of humerus near base of deltopectoral crest present (character 588); transverse groove on distal humerus present (character 592).

Azhdarchidae

The topology of Azhdarchidae is broadly similar to that of Zhou et al. (2024). The first branch in Azhdarchidae contains *Aralazhdarcho bostobensis*, *Eurazhdarcho langendorfensis*, *Phosphatodraco mauritanicus* and *Wellnhopterus brevirostris*. This grouping has previously been recovered in Pêgas (2024), Pêgas et al. (2022, 2023), and Zhou et al. (2024), and was defined as Phosphatodraconia in Pêgas et al. (2025). The next branch is a clade encompassing *Zhejiangopterus linhaiensis*, MC SF69, *Aerotitan sudamericanus*, and *Mistralazhdarcho magii*, which we informally term the '*Zhejiangopterus* clade'. *Aerotitan* and *Mistralazhdarcho* are united by several derived features of the lower jaw (characters 57, 187, 206), which were first identified in Pêgas et al. (2022). MC SF69 is recovered in a polytomy with *Aerotitan* and *Mistralazhdarcho*, supported by the presence of a ventrally expanded hypapophysis (character 552, unknown in *Aerotitan*). Both *Mistralazhdarcho maggii* and MC SF69 are known from late Campanian-early Maastrichtian sediments of France (Buffetaut, 2001; Vullo et al., 2018), and may represent closely related taxa.

The '*Zhejiangopterus* clade' is the sister taxon to the clade encompassing *Azhdarcho* and Quetzalcoatlinae. The known members of Phosphatodraconia and the '*Zhejiangopterus* clade' are all Santonian to Maastrichtian in age (Andres & Langston, 2021; Averianov, 2007; Buffetaut, 2001; Novas et al., 2012; Pereda-Suberbiola et al., 2003; Unwin & Lü, 1997; Vremir et al., 2013; Vullo et al., 2018), though the presence of members of Serpennatain the early Cenomanian (the 'Candeleros azhdarchid'; Agnolín et al., 2023) implies that these clades diverged from the *Azhdarcho*-Quetzalcoatlinae lineage in the earliest Cenomanian at the latest. Phosphatodraconia and the '*Zhejiangopterus clade*' both include mid-sized azhdarchids.

After Phosphatodraconia, the '*Zhejiangopterus* clade', *Azhdarcho*, and *Cryodrakon* represent successive branches on a lineage. Azhdarchinae (*sensu* Andres, 2021) is monotypic, containing only *Azhdarcho lancicollis*, which is the sister taxon to Quetzalcoatlinae. All the giant species are included within Quetzalcoatlinae, though importantly not all quetzalcoatlines are giant. *Cryodrakon* is the earliest diverging quetzalcoatline, the sister taxon to a clade containing all other quetzalcoatlines. After *Cryodrakon*, there is a divergence between two major lineages. The first clade contains *Albadraco*, *Bakonydraco*, *Hatzegopteryx* and *Tsogtopteryx*, defined as Hatzegopterygia in Pêgas et al. (2025), and the second clade, defined as Quetzalcoatlini in Pêgas et al. (2025), consists of *Gobiazhdarcho*, *Nipponopterus*, and the newly defined clade Serpennata.

A clade containing *Hatzegopteryx* and other robust eastern European quetzalcoatlines, which we informally term the '*Hatzegopteryx* clade', has been previously recovered by Thomas (2021) and Zhou et al. (2024), and a clade uniting *Hatzegopteryx* with *Albadraco* has been recovered in several previous analyses (Hone et al., 2024; Pêgas, 2024; Pêgas et al., 2022; Thomas, 2021; Zhou et al., 2024). This clade is supported by four synapomorphies of the mid-cervical vertebrae: centrum length shorter than 7 times mid-width (character 322), prezygapophyses laterally extend beyond level of postzygapophyses (character 310), hypapophysis anterior margin forms a smooth intumescence (character 315), and ventrolateral sulci extend onto bases of the prezygapophyseal pedicles (character 579). All members of the clade are known from Eastern Europe: *Albadraco tharmisensis* (Solomon et al., 2020), EME 315 (Naish & Witton, 2017; Vremir, 2010), LPB R.2395 (Vremir et al., 2015), LPB R.2347 (Vremir et al., 2018), and *Hatzegopteryx thambema* (Buffetaut et al., 2002) are all known from the Haţeg and Transylvanian basins of Romania, whereas *Bakonydraco* (Ősi et al., 2005; Prondvai et al., 2014) is known from the Csehbanya

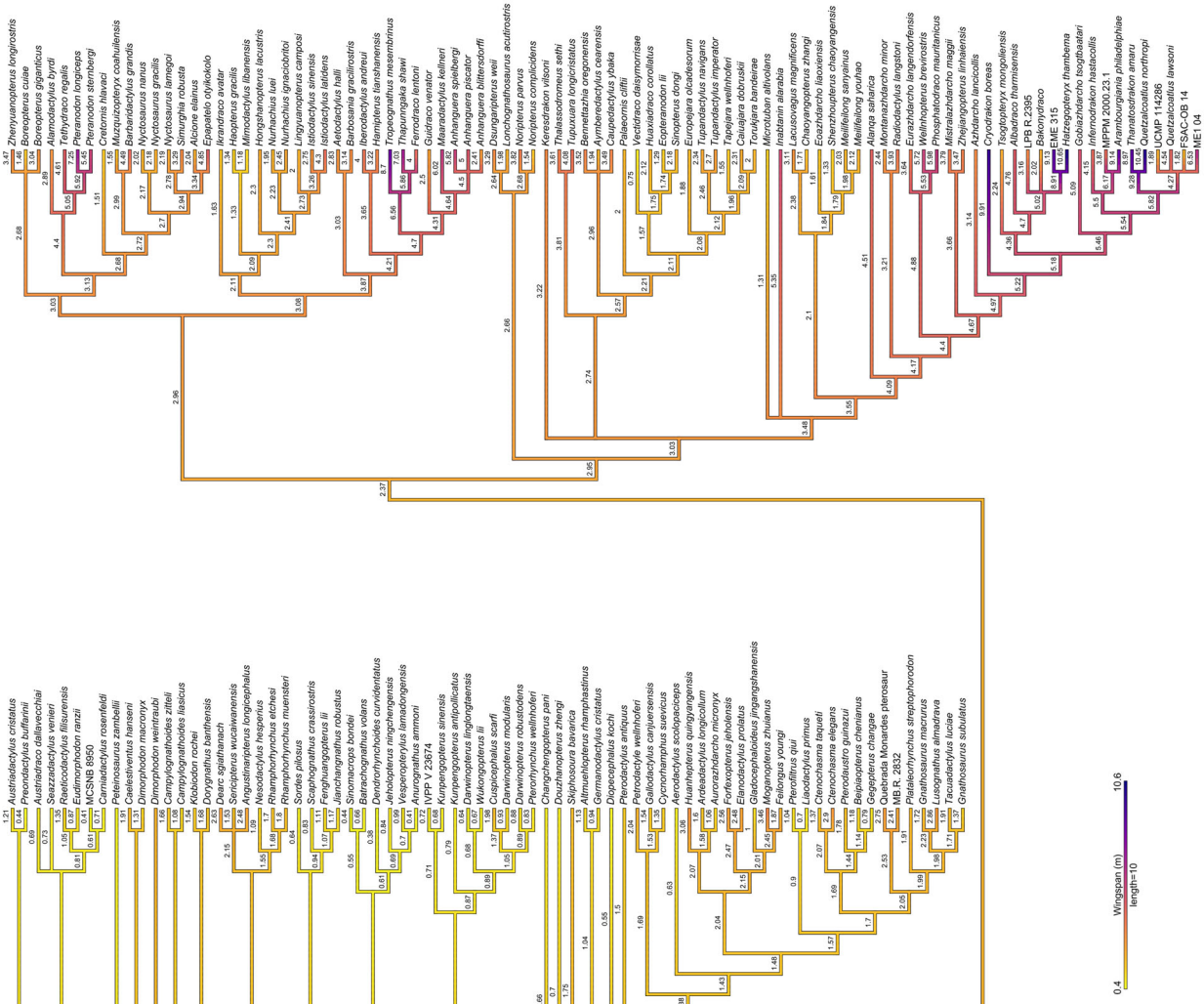

Figure 5. Pruned consensus tree with reconstruction of wingspan. Numbers positioned above the branches of terminal taxa are known or estimated values as reported in Supplemental File 4. Numbers positioned above deeper branches are reconstructed values.

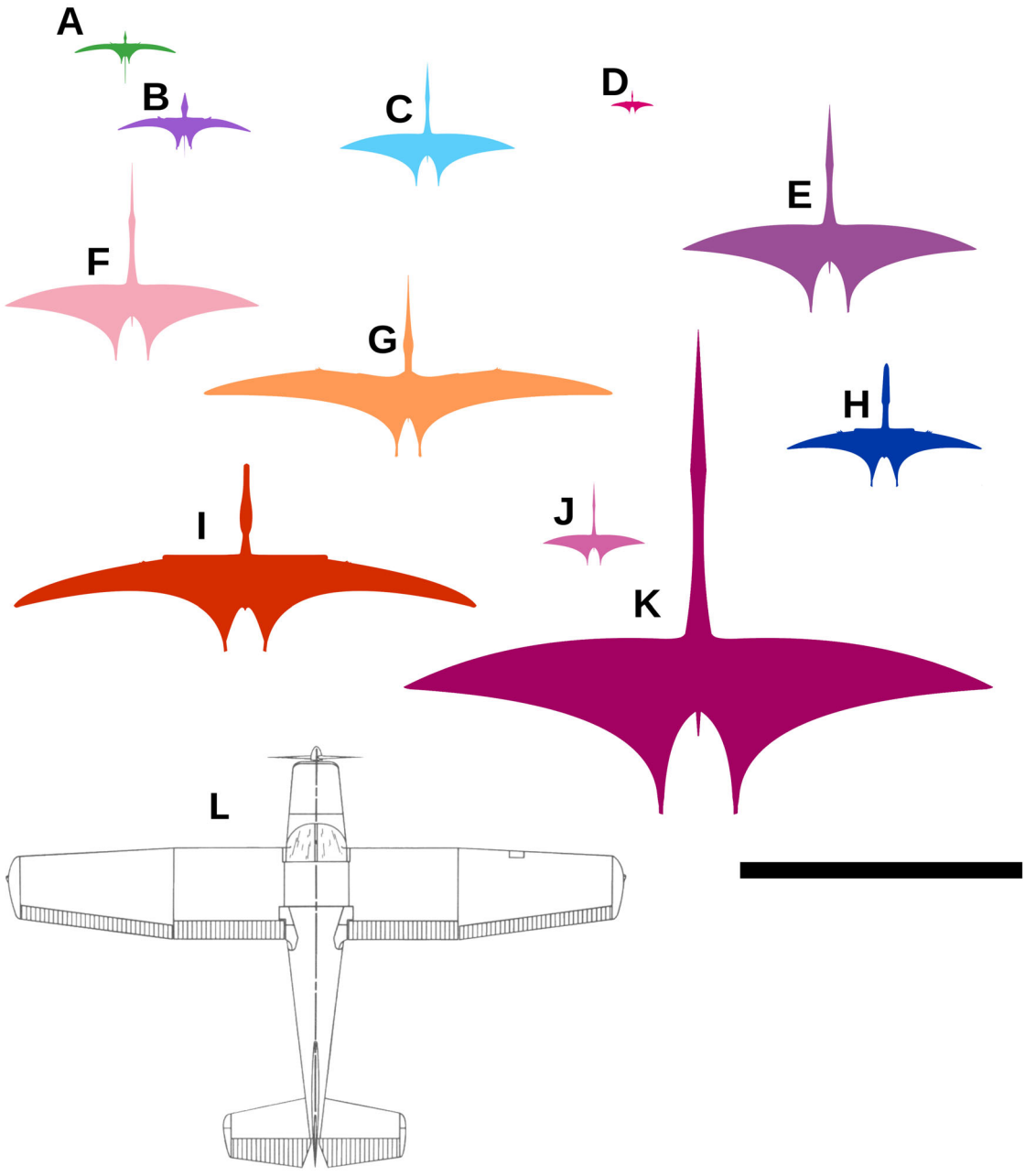

Figure 6. Size comparison of various pterosaurs and a general aviation aircraft: **A**, *Rhamphorhynnchus muensteri* (a typical large non-pterodactyloid); **B**, *Dearc sgiathanach* (the largest well-preserved non-pterodactyloid); **C**, *Lacusovagus magnificens* (the largest chaoyangopterid); **D**, *Vectidraco daisymorrisae* (the smallest azhdarchoid); **E**, *Inabtanin alarabia* (the largest non-azhdarchid azhdarchoid); **F**, *Alanqa saharica* (the largest alanqid); **G**, *Pteranodon longiceps* (the largest Late Cretaceous non-azhdarchid); **H**, *Moganopterus zhuianus* (the largest archaeopterodactyloid); **I**, *Tropeognathus mesembrinus* (the largest non-azhdarchid); **J**, FSAC-OB 14 (the smallest azhdarchid); **K**, *Quetzalcoatlus northopi* (the largest azhdarchid and the largest pterosaur for which size can be reliably estimated); **L**, Cessna 172 general aviation aircraft. Silhouette A reproduced from Hone and McDavid (2025, fig. 7); B and H based on skeletal diagrams by S. McDavid in Hone et al. (2024, fig. 3); D and I based on Chatterjee and Templin (2004, figs. 2, 3); G based on Dempsey (2025); L reproduced from Cessna Aircraft Co. (1956, p. ii); all others modified from Witton and Habib (2010, fig. 7). Scale bar = 5 m.

Formation of Hungary. *Bakonydraco* was originally described as an azhdarchid (Ősi et al., 2005) but subsequently treated as a tapejaromorph (e.g. Andres, 2021; Andres et al., 2014; Pêgas, 2024). We once again recover it as an azhdarchid. Large- and giant-sized azhdarchid material from Maastrichtian Romania, including the *Hatzegopteryx thambema* type material, form a polytomy. Although there is no overlap between the material, this clade is supported by the presence of thickened cortical bone walls (>4 mm; character 611) and a distinctly spongiose internal bone texture, a combination unique to giant Romanian azhdarchid material (Naish & Witton, 2017; Vremir et al., 2018). This result supports tentative referral of other giant Romanian specimens to the genus *Hatzegopteryx*, though not necessarily to *H. thambema* (Naish & Witton, 2017).

Nipponopterus (Zhou et al., 2024) is a recently described quetzalcoatline azhdarchid from the Mifune group of Kyushu, Japan. In their analysis, Zhou et al. (2024) recovered it as the sister taxon to the 'Burkhant azhdarchid' (MPC-Nd 100/302: Watabe et al., 2009), later named as *Gobiazhdarcho tsogtbaatari* (Pêgas et al., 2025), from the Eastern Gobi, Mongolia, with the clade formed by these two OTUs being the sister group to Serpennata (unlabelled clade containing *Arambourgiania* and *Quetzalcoatlus* of Zhou et al., 2024). We recover the same result here. The 'upper formation' of the Mifune group which yielded *Nipponopterus* is dated from the Turonian to possibly earliest Coniacian stages (Tsutsumi et al., 2018), and while the age of the Burkhant locality is less precisely constrained, it has been assigned to the Bayn Shire Formation (Watabe et al., 2009) which is dated to the Cenomanian to Coniacian stages (Kurumada et al., 2020). Zhou et al. (2024) noted that the phylogenetic placement of the *Gobiazhdarcho-Nipponopterus* clade was 'quite consistent with' their geological ages. However, we note that MPCA PV 2003 from the Candeleros Formation of Argentina is early Cenomanian (Agnolín et al., 2023), and therefore unambiguously older than *Nipponopterus* and probably older than *Gobiazhdarcho*. MPCA PV 2003 is recovered within Serpennata, diverging later than the *Gobiazhdarcho-Nipponopterus* clade, implying a divergence of the two lineages in or before the earliest Cenomanian.

Serpennata

Serpennata is a newly defined clade within the Quetzalcoatlinae, defined as the least inclusive clade containing *Arambourigiania philadelphiae* (Arambourg, 1959; Nesov in Nesov & Yarkov, 1989) and *Quetzalcoatlus northropi* (Lawson, 1975b). This clade is supported by two character states of the mid-cervical vertebra: deep ventral fossa present between postexapophyses (character 319), and maximum vertebral length more than ten times width (character 321). An additional ambiguous synapomorphy may support the clade: humerus with proximally tapered shaft (character 399, unknown in *Gobiazhdarcho* and *Nipponopterus*). Though it is newly defined, a clade containing *Arambourgiania* and *Quetzalcoatlus* but not *Azhdarcho*, *Hatzegopteryx* or *Phosphatodraco* has been recovered in several previous studies (Andres, 2021; Pêgas, 2024; Pêgas et al., 2022; 2023; 2025; Thomas, 2021; Thomas et al., 2025). Similarly, a clade uniting *Arambourgiania* and *Quetzalcoatlus* to the exclusion of *Azhdarcho* and *Zhejiangoperus* was recovered by several earlier analyses (Andres, 2010; Andres & Myers, 2013; Andres et al., 2014; Longrich et al., 2018). Within Serpennata, we recover a polytomy between the 'Candeleros Azhdarchid' MPCA PV 2003 (Agnolín et al., 2023), and two clades: the '*Arambourgiania* clade' includes *Arambourgiania philadelphiae sensu stricto*, the referred cervical vertebra of *Arambourgiania* sp. from Tennessee MPPM 2000.23.1 (Harrell et al., 2016; Thomas et al., 2025), and *Infernodrakon hastacollis*, while the '*Quetzalcoatlus* clade' contains *Quetzalcoatlus northopi*, *Thanatosdrakon amaru*, '*Quetzalcoatlus*' *lawsoni*, the referred cervical vertebra of aff. *Quetzalcoatlus* FSAC-OB 14 (Longrich et al., 2018), ME1 04 (Buffetaut et al., 1997), the 'Tous pterosaur' (Company et al., 1999), and UCMP 114286 (Estes, 1964). The genus *Quetzalcoatlus* as described by Andres and Langston (2021) is polyphyletic: the type species *Quetzalcoatlus northropi* is the sister taxon to *Thanatosdrakon amaru*, united by the entepicondyle of the humerus being larger than the ectepicondyle (character 401), a triangular and proximodorsally oriented proximal radius (character 593), presence of an intercondylar ridge on the proximal ulna (character 548), and sub-triangular cross-section of wing phalanx I (character 610). '*Quetzalcoatlus*' *lawsoni* forms a clade with FSAC-OB 14, ME1 04, the 'Tous pterosaur', and UCMP 114286, united by cervical vertebrae with an accentuated constriction of the posterior-most centrum just anterior to the postzygapophyses (character 316), absent in *Q. northropi* (TMM 42889-1: Andres & Langston, 2021). As *Thanatosdrakon* is Coniacian-Santonian in age (Ortiz David et al., 2022), the split between the *Q. northropi* and '*Q*'. *lawsoni* lineages is at least that old. Given this time depth and the morphological differences between the two species, the longstanding placement of '*Q*'. *lawsoni* within the genus *Quetzalcoatlus* is called into question (see Discussion).

Wingspan evolution

Pterosauria is reconstructed as having an ancestral wingspan of 1.25 m, and wingspan is reconstructed as gradually but consistently increasing leading to the base of Pterodactyloidea, which has an estimated ancestral wingspan of 1.57 m. This trend of increasing size continues separately within Pteranodontia, Lanceodontia

and Azhdarchoidea, terminating with the large- or giant-sized *Pteranodon longiceps* (7.25 m), *Tropeognathus mesembrinus* (8.2 m), and Azhdarchidae (largest taxa ~10 m).

All non-pterodactyloid pterosaurs have relatively small wingspans; the majority are <2 m, with larger size evolving in Angustinaripterini and '*Dimorphodon*' *weintraubi*, although the fragmentary nature of the latter taxon makes its size estimation tenuous. Wingspans below 1 m are present in Triassic pterosaurs, Scaphognathinae, Anurognathinae, and Wukongopteridae. Archaeopterodactyloidea contains taxa with wingspans ranging between 55 cm (*Diopecephalus kochi*) and 3.46 m (*Moganopterus zhuianus*), with no clearly visible trends observed in size evolution.

The majority of Pteranodontoidea have wingspans between 2 and 5 m, although smaller size is present in *Cretornis hlavaci*, *Muzquizopterx coahuilensis*, and the subadult holotype of *Boreopterus cuiae*. The genus *Pteranodon* attains large size (wingspan >5.45 m). The majority of Lanceodontia have wingspans between 2 and 5 m. Large size (>5 m) appears several times within Anhangueridae, being present in *Anhanguera piscator*, *A. spielbergi*, *Maaradactylus kellneri*, *Tropeognathus mesembrinus* and *Thapunngaka shawi*. Similarly large size has also been inferred for additional anhanguerid taxa (e.g. *Nicorhynchus capito*: Martill & Unwin, 2011) that were excluded from this analysis due to their fragmentary nature precluding reliable wingspan estimates. *Tropeognathus mesembrinus* is the only member of Lanceodontia to qualify as 'giant' by our definition, with a wingspan exceeding 8 m (Kellner et al., 2013). Dsungaripteridae ranges between 1.53 and 3.82 m in wingspan; ironically, *Noripterus parvus* is the largest dsungaripterid in our analysis.

Azhdarchoidea is reconstructed as having an ancestral wingspan of 3.03 m. A general trend of increasing wingspan leading up to Serpennata is reconstructed. Small size (<2 m wingspan) is independently attained in Tapejaridae, Chaoyangopteridae and *Microtuban*, with the smallest azhdarchoid being the sinopterine *Vectidraco* (~0.75 m; Naish et al., 2013). The only non-azhdarchid azhdarchoid that exceeds 5 m wingspan is *Inabtanin*, which we estimate as having a 5.35 m wingspan. Azhdarchidae is estimated to have had an ancestral wingspan of 4.4 m, and the majority of azhdarchids have wingspans between 3 and 6 m. We reconstruct four separate instances of gigantism evolving in azhdarchids: *Cryodrakon boreas*, *Hatzegopteryx* spp. (i.e. *H. thambema* and EME 315), *Arambourgiania philadelphiae*, and the *Quetzalcoatlus northropi-Thantosdrakon amaru* clade. A decrease in size (wingspan <2.5 m) is reconstructed for *Tsogtopteryx mongoliensis*, *Bakonydraco*, FSAC-OB 14 and UCMP 114286. The pterosaur with the largest wingspan that can reliably be estimated from a complete appendicular element is *Quetzalcoatlus northopi*, estimated at 10.5 m. *Hatzegopteryx thambema*, estimated at 10.6 m wingspan, may be slightly larger, though this estimate may be less reliable as it is based on an incomplete humerus and the proportions of this species remain unknown. Regardless, the size difference is well within the expected range of expected individual variation among skeletally mature individuals, as at least some pterosaurs show significant size variation among skeletally mature individuals (Hone & McDavid, 2025). Therefore, it is best to consider the largest (>9 m) azhdarchids as part of a maximum pterosaur size class; to declare a particular taxon the largest based on present knowledge would be premature (Witton & Habib, 2010).

Discussion

The earliest azhdarchids

There have been many previous reports of azhdarchids being present in the Early Cretaceous or even the Late Jurassic. Nearly all of these records have been refuted; these are summarized by Andres (2021). These include the putative Solnhofen 'protazhdarchid' *Aurorazhdarcho primordius* (a junior synonym of *Pterodactylus micronyx*, recombined as *Aurorazhdarcho micronyx*; Bennett, 2013), isolated tapejaroid humeri from the Doushan Formation (Zhou, 2010) and Elrhaz Formation (Blackburn, 2002; Sereno et al., 1998), and the postcranial specimens MN 4729-V, SMNK PAL 2342, 3843, and 3830 (Averianov, 2014; Frey et al., 2003; Martill & Frey, 1998), all from the Crato Formation. The putative Early Cretaceous azhdarchids *Bennettazhia oregonensis* (Bennett, 1989; Gilmore, 1928; Murry et al., 1991), *Eoazhdarcho liaoxiensis* (Lü & Ji, 2005) and *Radiodactylus langstoni* (Andres & Myers, 2013; Murry et al., 1991) are all phylogenetically tested here and found to be non-azhdarchid azhdarchoids.

Elongate cervical vertebrae from the Kimmeridgian and Berriasian have occasionally been referred to Azhdarchidae. These include CAMSM J5340 from the Purbeck Group (Howse, 1986; Martill et al., 2013), MB. R. 2832 from the Tendaguru Formation (Costa et al., 2015; Kellner et al., 2007), and MTCO 21.269 from Cornet (Dyke et al., 2011). CAMSM J5340 has been referred to '*Gnathosaurus*' *macrurus* (Andres, 2021; Averianov, 2014), but as this specimen was not associated with the lectotype CAMSM J5339 and multiple ctenochasmatoid species are known from the Purbeck Group (Howse & Milner, 1995), it cannot be referred to that taxon with confidence. MB. R. 2832 is the more complete of two putative azhdarchid cervical vertebrae from the Tendaguru Formation, which are

morphologically consistent with each other and probably pertain to the same taxon (Costa et al., 2015). A non-azhdarchid nature for CAMSM J5340 and MB. R. 2832 has been previously argued due to the presence of a lateral pneumatic foramen on the centrum, which is absent in azhdarchids but typical in ctenochasmatoids (Andres, 2021; Andres & Ji, 2008). MTCO 21.269 was referred more broadly to Azhdarchoidea without comment in Averianov (2014). Notably, this specimen lacks an anterior accessory pneumatic foramen on the centrum, the vertebra has a pentagonal cross-section, and the neural arch and centrum are distinct, all plesiomorphic character states for Pterodactyloidea absent in azhdarchids. The affinities of these three specimens are phylogenetically tested here and all are recovered within Ctenochasmatoidea. CAMSM J5340 and MTCO 21.269 are recovered as closely related to *Huanhepterus*, while MB. R. 2832 is recovered as a ctenochasmatid. The similarities that these specimens have to azhdarchid cervical vertebrae are the result of convergently evolved elongation of the cervical series in Ctenochasmatoidea and Azhdarchidae (Andres & Ji, 2008).

Martill et al. (2013) described a pterosaur metacarpal IV from the Durlston Formation, Purbeck Group, and considered it a possible azhdarchid. This apparently unnumbered specimen is held at the fossil display in the Square and Compass pub in Worth Matravers, England, but casts are available at the NHMUK, SMNK and University of Portsmouth. The affinities of this specimen were narrowed down to Dsungaripteridae and Azhdarchidae on the basis of its length, a constricted shaft just proximal to the distal condyles, and the dorsal condyle being offset from the long axis of the metacarpal shaft. Martill et al. (2013) argued that a dsungaripterid identity was unlikely due to a lack of thickened cortical bone characteristic of the clade and tentatively referred the specimen to Azhdarchidae based on comparison with *Azhdarcho lancicollis*. However, dsungaripterid long bones do not universally bear thickened bone walls (Jiang et al., 2023), so a dsungaripterid identity cannot be eliminated. The specimen also shares the aforementioned characters with the metacarpal IV of the thalassodromid *Tupuxuara* sp. (Wellnhofer, 1991, p. 130) and the gallodactylids *Cycnorhamphus suevicus* (GPIT 80, H. Thomas, pers. obs.), *Gallodactylus canjuerensis* (Wellnhofer, 1978), *Petrodactyle wellnhoferi* (Hone et al., 2023; LF 2809, S. McDavid, pers. obs.), and LF 1414 (S. McDavid, pers. obs.; McDavid et al., in prep.). We therefore consider the Square and Compass specimen an indeterminate pterodactyloid and based on stratigraphy a probable gallodactylid.

Palaeocursornis corneti (not to be confused with *Eurolimnornis corneti*; see Bock & Bühler, 1996 for nomenclature) is a distal fragment of a putatively pterosaurian humerus from Cornet (Agnolin & Varricchio, 2012). Although interpreted as an avian femur by Dyke et al. (2011), it has since been reinterpreted as the distal humerus of a pterosaur, with possible affinities to Azhdarchidae (Agnolin & Varricchio, 2012). This specimen is very poorly preserved and does not display many phylogenetically informative characters. Of the characters noted to be shared with *Azhdarcho* by Agnolin and Varricchio (2012), one of them, a 'D'-shaped distal humerus, is a synapomorphy of Tapejaroidea. The other two, a deep fovea supratrochlearis ventralis and deep trochlear groove, can only be determined in three-dimensionally preserved humeri and cannot yet be said to be unique to azhdarchids. We consider *Palaeocursornis corneti* a nomen dubium and an indeterminate tapejaroid pterosaur.

The earliest unambiguous azhdarchid material dates from the Cenomanian. The 'Candeleros azhdarchid' MPCA PV 2003 is the oldest azhdarchid for which a precise date is known, being from the early Cenomanian (Agnolín et al., 2023). The ages of *Gobiazhdarcho tsogtbaatari* and *Tsogtopteryx mongoliensis* are less precisely constrained but are no older than the Cenomanian (Kurumada et al., 2020; Pêgas et al., 2025; Watabe et al., 2009). Additional azhdarchids are known from the Turonian, including *Azhdarcho lancicollis* (Averianov, 2010), *Nipponopterus mifunensis* (Zhou et al., 2024), and indeterminate specimens from Armenia and Kazakhstan (Averianov, 2007). *Gobiazhdarcho*, *Tsogtopteryx*, and the 'Candeleros azhdarchid' are Cenomanian-Turonian in age but occupy rather late-diverging positions in the Azhdarchomorph tree. This implies a divergence time of early Cenomanian at the latest for Serpennata and the *Gobiazhdarcho-Nipponopterus* clade, and an earlier, probably earliest Cenomanian or perhaps latest Albian divergence for the Phosphatodraconia, the '*Zhejiangopterus* clade', Hatzegopterygia, *Azhdarcho* and *Cryodrakon*. This indicates that the early Cenomanian was a time of significant diversification for azhdarchids.

This rapid diversification of azhdarchids shortly precedes the Cenomanian-Turonian extinction event, which saw the demise of 'mid'-Cretaceous faunas. The Cenomanian-Turonian extinction, typically attributed to ocean anoxia (Harries & Little, 1999; Jenkyns, 1980; Schlanger et al., 1987), is well-documented for its impact on marine biota (e.g. Elder, 1989; Harries & Little, 1999; Monnet, 2009; Tur, 1997; Wan et al., 2003). Its impact on terrestrial fauna is less well documented (Eaton et al., 1997; Galasso et al., 2023; Heimhofer et al., 2018; Kirkland, 1987), though there does appear to be a turnover among terrestrial dinosaurs (Candeiro et al., 2018; Coria & Salgado, 2005; Meso et al., 2021). Toothed pterosaurs, mostly notably anhanguerians, disappear from the fossil record in this interval (Averianov,

2014). As many anhanguerians likely fed on marine prey (Bestwick et al., 2018), the disruption of marine ecosystems during this event may have contributed to their extinction (Frey et al., 2020; Pentland et al., 2019). In contrast, azhdarchid pterosaurs diversified during the Cenomanian-Turonian. Groups that thrive and diversify during biotic crises have been termed 'disaster taxa' (e.g. Rodland & Bottjer, 2001), though this term implies only a brief period of abundance that dissipates in later phases of ecosystem recovery (Modesto, 2020). This definition cannot be applied to azhdarchids, which survived with high diversity until the end-Maastrichtian (e.g. Lehman, 2021; Longrich et al., 2018). Rather, azhdarchids can be described as 'bloom taxa' (Hansen, 1988) which diversify during biotic crises then maintain their diversity afterwards.

At least eight lineages of azhdarchomorphs survived the Cenomanian-Turonian event. *Inabtanin*, despite belonging to one of the earliest-diverging lineages within Azhdarchomorpha, is known from the Maastrichtian (Rosenbach et al., 2024); the alanqid *Argentinadraco* is late Turonian-early Coniacian in age (Kellner & Calvo, 2017); and the non-azhdarchid azhdarchiform *Montanazhdarcho* is known from the Campanian (McGowen et al., 2002). Within Azhdarchidae, *Cryodrakon* (Eberth et al., 2023; Hone et al., 2019) is known from the Late Campanian, while members of Phosphatodraconia (e.g. *Phosphatodraco*, Pereda-Suberbiola et al., 2003; *Eurazhdarcho*, Vremir et al., 2013; *Wellnhopterus*, Lehman, 2021), the '*Zhejiangopterus* clade' (e.g. *Aerotitan*, Novas et al., 2012), the '*Hatzegopteryx* clade' (e.g. *Hatzegopteryx*, Buffetaut et al., 2002; *Albadraco*, Solomon et al., 2020), and Serpennata (e.g. *Arambourgiania*, Frey & Martill, 1996; *Quetzalcoatlus,* Lehman, 2021; *Infernodrakon*, Thomas et al., 2025) persisted to the Maastrichtian. In contrast, tapejaromorphs and chaoyangopterids seemingly went extinct during or soon after the Cenomanian-Turonian turnover. The youngest examples of each, *Afrotapejara zouhri* and *Apatorhamphus gyrostega*, are both known from the Kem Kem Group, which is poorly constrained but early Cenomanian at the youngest (Martill, Smith, et al., 2020; McPhee et al., 2020; Smith et al., 2023).

Azhdarchoid and putative lonchodectid postcrania from Cretaceous Europe

'*Palaeornis*' *cliftii* (Mantell, 1844) was named based on a humerus from the Valangianian Hastings Beds Group of West Sussex, England. The genus name is preoccupied by the extant red-breasted parakeet *Palaeornis alexandri* Vigors, 1825, an objective synonym of *Psittacula* (Mathews, 1917, p. 169). Witton et al. (2009) summarized the taxonomic and nomenclatural history of this specimen and discussed its affinities. While pointing out many traits shared with non-azhdarchid azhdarchoids, they assigned it to Lonchodectidae based on a proximally placed deltopectoral crest and a swollen lateral condyle. These traits are shared with CAMSM B54.081, an isolated humerus from the Cambridge Greensand, previously referred to *Lonchodectes* without justification by Unwin (2001, 2003). The lonchodectid identification of these two humeri was rejected by Averianov (2012, 2020), who referred CAMSM B54.081 first to the putative azhdarchoid *Ornithostoma sedgwicki* (Averianov, 2012), then as simply a 'basal azhdarchoid' (Averianov, 2020). *Ornithostoma sedgwicki* was restricted to edentulous jaw material by Smith et al. (2021) and based on this material we recover it as a chaoyangopterid. No comment on the affinities of the postcranial specimens was provided.

The lectotype of *Lonchodectes compressirostris* is a fragmentary and nondiagnostic mandibular symphysis (Rodrigues & Kellner, 2013); its affinities within Lanceodontia are obscure, making *Lonchodectes*-based family-group or clade names (i.e. Lonchodectidae) untenable, and no postcranial material can be referred to the genus with certainty. Other nominal species referred to *Lonchodectes* in Unwin (2001) have been moved to the genera *Lonchodraco* (Rodrigues & Kellner, 2013), *Serradraco* (Rigal et al., 2018), *Ikrandraco* (Averianov, 2020), and *Draigwenia* (Holgado, 2021). Although most of these are also only known from craniomandibular material, the lonchodraconid *Ikrandraco avatar* (Wang et al., 2020) preserves a humerus, which is clearly different from '*Palaeornis*' *cliftii*, having a diaphysis of approximately the same width as its distal end and a distally angled deltopectoral crest (Wang et al., 2014). As noted by Averianov (2012) and Witton et al. (2009), '*Palaeornis*' *cliftii* closely resembles azhdarchoid humeri. The sole feature cited to support a position within 'Lonchodectidae' instead of Azhdarchoidea, a proximal margin of the deltopectoral crest confluent with the ulnar crest (Witton et al., 2009), is not evident in the photographs and illustrations of NHMUK 2353. We recovered '*P*'. *cliftii* as a tapejaromorph within the clade Eutapejaria. Though not included in our phylogenetic analysis, CAMSM B54.081 is indeed very similar to '*Palaeornis*' *cliftii* and bears an enlarged lateral condyle, a synapomorphy of Eutapejaria in our analysis and therefore, most likely also belongs to this clade.

Two elongated pterosaur vertebra (CAMSM B54.394 and B54.493) from the Cambridge Greensand have also been referred to both Lonchodectidae (Unwin, 2001) and *Ornithostoma* (Averianov, 2012). These vertebrae were initially reported as caudal vertebrae (Owen, 1859; Seeley, 1870), before being reidentified as cervical

vertebrae (Hooley, 1914; Seeley, 1875). The elongation of these vertebrae has prompted comparisons with azhdarchids (Howse, 1986; Padian, 1986). As with the humeri, this material was referred to Lonchodectidae without comment by Unwin (2001), subsequently reassigned to *Ornithostoma* by Averianov (2012) and then removed from *Ornithostoma* by Smith et al. (2021). The moderate elongation of these vertebrae (length:mid-width ratio < 3; Owen, 1859, pl. 10, fig. 37), distinct neural arch, unreduced neural spine, and possible lateral pneumatic foramina (Averianov, 2012) do not suggest particularly close affinities to Azhdarchidae and support a position outside Concilazhia. The general shape of these vertebrae enlarged neural canal openings, and oval-shaped anterior cotyle are strikingly similar to the cervical vertebrae of *Tapejara wellnhoferi* (Eck et al., 2011) and *Tupandactylus navigans* (Beccari et al., 2021). We consequently refer these two specimens to Tapejaridae indet.

Azhdarchoid material was reported from the Albian Gault Formation of England by Smith and Martill (2022). These included a cervical vertebra, MANCH LL 14954a, and a fragmentary humerus, NHMUK PV R 8715. The humerus closely resembles that of '*Palaeornis*' *cliftii*, including in the angle of the humeral head relative to the shaft and the expansion of the distal half of the shaft; it may represent an additional European tapejariform. The cervical vertebra is slightly elongated, with a preserved length:mid-width ratio of 3.6 (measurements from Smith & Martill, 2022) and preserves the base of a low neural spine. A lateral pneumatic foramen is absent on the centrum, and the transverse processes are reduced, indicating a position within Concilazhia. The elongation ratio of the vertebra and low but not vestigial neural spine are most consistent with the mid-cervical vertebrae of Chaoyangopteridae. If MANCH LL 14954a is a chaoyangopterid cervical vertebra, it is one of the few three-dimensionally preserved examples. Notably, an accessory pneumatic foramen is present dorsal to the anterior neural canal opening, and adjacent pneumatic foramina are absent lateral to the posterior neural canal opening (Smith & Martill, 2022), a configuration unique among azhdarchomorphs. The Gault specimens add further support for the presence of tapejariform and chaoyangopterid pterosaurs in mid-Cretaceous (Aptian-Cenomanian) Europe.

An azhdarchoid cervical vertebra, UPMC-080, was reported from the lower Albian 'Sables verts' (=Greensand, unnamed unit: Magniez-Jannin & Demonfaucon, 1980) of Grandpré in north-eastern France (Buffetaut, 2012). This specimen was originally referred to Azhdarchidae, but Averianov (2014) considered it an indeterminate azhdarchoid on the basis of an unreduced neural spine. This vertebra has a length:mid-width ratio of approximately 5, and strongly developed transverse processes and lateral pneumatic foramina are absent. The anterior and posterior faces of the vertebra are damaged and largely uninformative, and much of the neural spine is absent. The elongation ratio is consistent with a position in Azhdarchiformes, but the development of the neural spine indicates a position outside of Azhdarchidae. UPMC-080 bears a particular resemblance to azhdarchoid cervical vertebrae from the Kem Kem Beds, such as CMN 50801 (Rodrigues et al., 2011) and FSAC-KK 5215 (Smith et al., 2023), some of which probably represent the cervical vertebrae of alanqids. We consider this specimen an indeterminate non-azhdarchid azhdarchiform, possibly an alanqid.

Azhdarchoids from Late Cretaceous eastern Europe

Four named azhdarchoid taxa are known from the Late Cretaceous of eastern Europe: *Albadraco tharmisensis*, *Bakonydraco galaczi*, *Eurazhdarcho langendorfensis*, and *Hatzegopteryx thambema*. Additional Romanian specimens, including EME 315 ('Râpa Roşie azhdarchid': Naish & Witton, 2017; Vremir, 2010), LPB R.2395 ('Pui azhdarchid'; Vremir et al., 2015), the 'PT specimen' of Vremir (2010), an unpublished short-necked azhdarchid from the lower Sebeş Formation (Vremir et al., 2014), and unpublished giant material nicknamed 'Dracula' in press releases (e.g. Saplakoglu, 2018), may represent further diversity in the region. Of these, *Albadraco*, *Eurazhdarcho* and *Hatzegopteryx* have been universally considered azhdarchids. Longrich et al. (2018) recovered *Eurazhdarcho* as an early-diverging member of Quetzalcoatlinae and *Hatzegopteryx* in a trichotomy with *Arambourgiania* and *Quetzalcoatlus*. Andres (2021) recovered *Albadraco* within Azhdarchinae and *Eurazhdarcho* and *Hatzegopteryx* within Quetzalcoatlinae, with *Hatzegopteryx* being the sister taxon to an *Arambourgiania-Quetzalcoatlus* clade (=Serpennata). The phylogenetic analyses of Hone et al. (2024), Pêgas (2024), Pêgas et al. (2022, 2023, 2025), and Thomas et al. (2025) recovered a clade containing *Albadraco* and *Hatzegopteryx*, excluding all non-European azhdarchids, with *Eurazhdarcho* recovered as a close relative of *Phosphatodraco* and *Wellnhopterus*.

The affinities of *Bakonydraco galaczi* are less clear. Although previously considered an azhdarchid (Averianov, 2010; 2014; Martill, Smith, et al., 2020; Ősi et al., 2005), the majority of recent phylogenetic studies (e.g. Andres, 2021; Andres & Myers, 2013; Andres et al., 2014; Longrich et al., 2018; Pêgas, 2024; Pêgas et al., 2022, 2023; Wu et al., 2017) have recovered *Bakonydraco galaczi* as a tapejarid, supported by characters shared between

the mandibles of these taxa. However, this is a consequence of artefactual coding and inconsistent application of character states to *Bakonydraco galaczi* compared to other azhdarchoids. Notably, the mandibular symphyses of *Bakonydraco galaczi* and *Albadraco tharmisensis* are consistently coded differently (e.g. Andres, 2021; Pêgas, 2024) despite the remarkable morphological similarity between the anterior mandibles of these taxa (Solomon et al., 2020). Here we provide justification for our reinterpretation of *Bakonydraco galaczi*. It must be noted that histological sampling of *Bakonydraco* mandibular symphyses supports the presence of two separate taxa, one of which having a much smaller adult body size than the other (Prondvai et al., 2014). However, the symphyses of these two taxa are morphologically identical, and considering the coexistence of closely related azhdarchoids in the same geological formations (e.g. Lehman, 2021; Pêgas, 2024; Pêgas et al., 2023), it is probable that the two Iharkút pterosaurs also represent sister taxa: *Bakonydraco galaczi* and *Bakonydraco* sp. For the purposes of this analysis, all this material will be treated under the OTU *Bakonydraco*.

Bakonydraco galaczi is coded as having a lateral expansion of the jaws level with the anterior margin of the nasoantorbital fenestra (character 38), which is a synapomorphy of Tapejariformes (Pêgas, 2024). This cannot be reliably coded in *Bakonydraco* as the position of the lateral expansion relative to the nasoantorbital fenestra is unknown due to lack of associated cranial material. The lateral expansion also differs from the condition in tapejarids in that the lateral margins of the dentary are distinctly concave anterior the 'expanded' point and straight posterior to it, with a well-defined junction between them. In tapejariforms, the entire lateral margin of the anterior mandible is smoothly convex in this region, as in *Caupedactylus ybaka* (Kellner, 2013), *Caiuajara dobruskii* (Manzig et al., 2014), and *Tupandactylus navigans* (Beccari et al., 2021). The straight sides of the posterior half of the dentary symphysis compare well with LPB R.2347, a fragmentary mandibular symphysis of a giant azhdarchid from the Densuș-Ciula Formation which may represent *Hatzegopteryx* (Vremir et al., 2018). The distinctly angled lateral margins of the jawline in *Bakonydraco* also resemble the 'flaring' lateral margins of the jawline in the chaoyangopterids *Chaoyangopterus zhangi* (Zhou, 2010) and *Lacusovagus magnificens* (Witton, 2008a), where the left and right margins of the jawline are alternatingly tapered and subparallel. *Bakonydraco* is therefore recoded to lack a lateral expansion of the jaws.

Bakonydraco galaczi is coded as having well-defined tomial margins of the anterior jaw (characters 40, 41), but the dentary of *Bakonydraco* has a nearly flat anterior occlusal surface (Prondvai et al., 2014) and MTM V 2010.80.1, a referred rostrum figured in Ősi et al. (2011), does not have prominent tomial margins either. Indeed, the tomial margins of *Albadraco tharmisensis*, which are coded as being 'reduced', are comparably sharply defined as those of *Bakonydraco. Bakonydraco* is recoded to have 'reduced' tomial edges to match. The rostrum of *Bakonydraco* (MTM V 2010.80.1; Ősi et al., 2011) is coded as being downturned (character 58), but this rostrum is visibly distorted in dorsoventral view and a break is present posteriorly where the apparent curvature is. This opens the possibility that this downturn may be exaggerated by taphonomic distortion, and we opt to code this character as unknown in *Bakonydraco*. The surface of anterior palatal tip is coded as being concave in *Bakonydraco*, but the condition does not appear to differ from *Albadraco tharmisensis* (Solomon et al., 2020) and is recoded 'straight' to match.

Bakonydraco is coded as 'unknown' for the presence of neurovascular foramina on the palate, despite the fact that these foramina are visibly present on MTM V 2010.80.1 (Ősi et al., 2011) and *Bakonydraco* is coded for characters 153 and 154, pertaining to the morphology of these foramina. *Bakonydraco* is coded as having 'pit-like' foramina (character 154), in contrast to the 'slit-like' foramina of most other azhdarchoids. The palatal foramina are visibly elongated on the anterior rostrum of MTM V 2010.80.1 (Ősi et al., 2011). The mandibular foramina in the holotype MTM 2007.110.1 (Ősi et al., 2005) show a pattern of decreasing length posteriorly; the anterior-most foramina are more elongate than those in the rostrum and mandible of *Albadraco* (Solomon et al., 2020), which is coded as 'slit-like'. This character is recoded to 'slit-like', as in most other azhdarchoids. This was a putative synapomorphy with *Afrotapejara zouhrii*, which does indeed have sub-circular foramina on its palate. The foramina of *Afrotapejara zouhrii* are coded as being organized in rows, which appears to be the case on the holotype, but is less evident in the referred specimens (Martill, Smith, et al., 2020). These instead more closely resemble the 'cluttered' state of *Wightia declivirostris*, which also has sub-circular neurovascular foramina (Martill, Green, et al., 2020). *Afrotapejara zouhrii* and *Wightia declivirostris* are recoded as both having cluttered, 'pit-like' neurovascular foramina.

Bakonydraco galaczi is coded as having a secondary row of slit-like foramina on the lateral surface of the mandibular symphysis, parallel with the ventral margin of the symphysis. This character is also coded as being present in *Afrotapejara zouhrii*, but only two foramina are clearly preserved on the referred mandibular symphysis BSPG 1997 I 67 (Wellnhofer & Buffetaut, 1999), so this arrangement cannot be determined with

certainty and is recoded as unknown in that taxon. However, a descending row of foramina is visible on the mandibular symphysis of *Albadraco tharmisensis* (Solomon et al., 2020). The main axis of the mandible is coded as being downturned in *Bakonydraco galaczi*, as in tapejarids, but this downturn is not as strongly evident in *Bakonydraco* as in tapejarids. The degree of decurvature, which is limited to the dorsal dentary margin at the anterior half of the mandibular symphysis, more closely resembles the conditions in *Aerotitan sudamericanus* (Novas et al., 2012; Pêgas et al., 2022) and *Mistralazhdarcho maggii* (Vullo et al., 2018). *Bakonydraco* is therefore recoded to match this state.

The holotype of *Bakonydraco galaczi* displays a transverse ridge on the occlusal surface of the mandibular symphysis (character 212). A similar horizontal ridge is present in the holotype of *Huaxiapterus benxiensis* (=*Huaxiadraco corollatus*; Pêgas et al., 2023), and this is coded as a shared feature in the dataset of Pêgas (2024). However, some specimens of *Bakonydraco* do not display this ridge (Prondvai et al., 2014; Smith et al., 2021); consequently, this feature has been recoded as being ambiguous in *Bakonydraco*. The anterior occlusal surface is coded as having a fossa (character 206), but the holotype and referred material of *B. galaczi* do not bear the deeply excavated anterior fossa of tapejarids (e.g. Manzig et al., 2014), and differs little from the slightly concave surface of *Albadraco tharmisensis* (Solomon et al., 2020) and *Azhdarcho lancicollis* (Averianov, 2010), and is recoded to match.

Bakonydraco galaczi has also frequently been coded as bearing a crest on the ventral surface of the dentary (character 222). This would be a shared feature with tapejarids, but not with azhdarchids, which have a deep, broader keel to the mandibular symphysis. Although *Bakonydraco* certainly has a crest-like structure, a closer examination demonstrates that this structure is not closely comparable to the crests of tapejarids. The dentary crests of tapejariforms are mediolaterally narrow, giving the dentary concave lateral sides in cross-sectional view, as is present in *Aymberedactylus cearaensis* (Pêgas et al., 2016), *Afrotapejara zouhrii* (Martill, Smith, et al., 2020), *Caiuajara dobruskii* (Manzig et al., 2014), *Tapejara wellnhoferi* (Eck et al., 2011), and *Tupandactylus navigans* (Beccari et al., 2021); this is also the case for the dentary crest of *Argentinadraco barrealensis* (Kellner & Calvo, 2017). The dentary of *Bakonydraco* is ventrally broadened with convex lateral margins in cross-section, with no offset between the 'crest' and the rest of the dentary externally or internally (Prondvai et al., 2014). Morphologically, it more closely resembles a ventrally expanded dentary symphysis, rather than a narrow crest. It particularly resembles the state in *Albadraco tharmisensis* (Solomon et al., 2020), which is coded as having a 'smooth' ventral margin of the dentary, although it is unclear how this differs from the keeled state present in other azhdarchids. It is also reminiscent of the inferred morphology of LPB R.2347, which likely bore a wide ventral keel on the dentary (Vremir et al., 2018). Accordingly, *Bakonydraco* and *Albadraco* are both recoded as having keeled dentaries. Characters 223 to 226, describing the morphology of the dentary crest, are recoded as inapplicable in *Bakonydraco.*

Additionally, a large amount of azhdarchoid postcranial material has been recovered from the Iharkút locality of the Csehbánya Formation (Ősi et al., 2005, 2011). This material includes distinctively elongated cervical vertebrae that clearly belonged to an azhdarchid (Ősi et al., 2005), and other postcranial material is consistent with an azhdarchid identity (Ősi et al., 2011). None of this material is indicative of tapejarids being present in the sample, although a pterosaur metacarpal IV is consistent with a possible pteranodontoid identity (Ősi et al., 2011). Although not impossible, it is highly unlikely that all known azhdarchoid craniomandibular material from Iharkút (all referred to *Bakonydraco*; Csiki-Sava et al., 2015) pertains to a different taxon from all of the azhdarchoid postcranial material. It is likely that at least some of this postcranial material pertains to *Bakonydraco* (Csiki-Sava et al., 2015; Ősi et al., 2012), and indeed the Iharkút cervical vertebrae were implicitly referred to *B. galaczi* in Averianov (2010, 2014), Hone et al. (2019), and Solomon et al. (2020). It is perhaps noteworthy that the cervical vertebra MTM Gyn/451 (Ősi et al., 2005, fig. 5B) displays some shared characters with *Albadraco tharmisensis* and LPB R.2395, including a dorsoventrally compressed centrum, laterally broadened prezygapophyses, and an expanded anterior neural spine. Although some of this postcranial material probably belongs to *Bakonydraco*, we conservatively do not include it in the OTU.

With these characters recoded, *Bakonydraco* is recovered within a clade of eastern European azhdarchids (the '*Hatzegopteryx* clade'), which also contains *Albadraco tharmisensis*, *Hatzegopteryx thambema*, LPB R.2347 and LPB R.2395. This clade is sister to *Tsogtopteryx mongoliensis* (Pêgas et al., 2025; Watabe et al., 2009). The '*Hatzegopteryx* clade' displays an unusual set of morphologies for azhdarchids, including robust skulls, relatively short and broad cervical vertebrae, and thickened postcranial cortical bone (>3 mm) in large taxa. This morphology has been suggested to relate to macropredatory behaviour hypothesized in *Hatzegopteryx* (Naish & Witton, 2017). It is possible that these eastern European azhdarchids were more

macropredatory due to the absence of medium-to-large theropods from the ecosystem and the abundance of medium-sized herbivorous dinosaurs. The largest terrestrial predator currently known in Maastrichtian Romania is *Allodaposuchus precedens* (Delfino et al., 2008), and the largest possibly carnivorous theropod dinosaur is *Balaur bondoc* (Csiki et al., 2010). Dinosaurs in eastern Europe are smaller-bodied than related taxa due to insular dwarfism, with none exceeding 1000 kg in body mass (Benton et al., 2010; Nopcsa, 1923). Azhdarchids, being able to travel between islands aerially (Witton & Habib, 2010), may have been able to overcome the limited resources of these insular environments (Naish & Witton, 2017), permitting the larger body size present in *Albadraco* and *Hatzegopteryx*.

In contrast, *Eurazhdarcho* probably represents a more typical azhdarchid ecotype in the Hateg ecosystem. It is significantly smaller than *Albadraco* and *Hatzegopteryx*, and is nested within Phosphatodraconia. While the '*Hatzegopteryx* clade' represents a local radiation of azhdarchids to fill a niche elsewhere filled by medium to large theropod dinosaurs, members of this clade may have filled a generalist mesopredator niche in various ecosystems, coexisting with other, often larger azhdarchids (Andres & Langston, 2021; Lehman, 2021; Longrich et al., 2018; Vremir et al., 2013). The pterosaur fauna of eastern Europe also contrasts with the pterosaur fauna of Campanian-Maastrichtian western Europe, which consists of Serpennata ('Tous pterosaur', ME1 04) and the '*Zhejiangopterus* clade' (*Mistralazhdarcho maggii*, MC SF69). An additional fragmentary specimen (ME FO1-20) of pterosaur longbone from the Maastrichtian of Aude, France was noted as having 'azhdarchid affinities' based on comparisons to *Quetzalcoatlus* and *Montanazhdarcho* (Buffetaut et al., 1996). Although it does not preserve sufficient characters to inform a more specific phylogenetic placement, it can be excluded from the '*Hatzegopteryx* clade' based on its plesiomorphically thin (1 to 2 mm thick; Buffetaut et al., 1996, p. 754) cortical bone.

Systematics of *Quetzalcoatlus*

Remains of azhdarchids from Texas were first reported by Lawson (1975a) then further described and named *Quetzalcoatlus northopi* in a subsequent publication (Andres et al., 2017; ICZN, 2019; Lawson, 1975b). Lawson (1975a, 1975b) noted the presence of a giant morph and a moderately large morph found approximately 40 km apart but treated all the material as conspecific due to 'the similarity of their humeri, proximal carpals, and second [wing] phalanges'. Kellner and Langston (1996) proposed that the referred specimens of the moderately large morph represented a species within the genus *Quetzalcoatlus* distinct from the giant type species *Q. northopi*. This moderately large species remained unnamed for 25 years until the publication of a volume dedicated to *Quetzalcoatlus* (Brown & Padian, 2021), including a detailed osteological description in which the moderately large species was named *Quetzalcoatlus lawsoni* (Andres & Langston, 2021). Kellner and Langston (1996) were correct to separate the moderately large and giant species, though subsequent finds of other azhdarchids provide further context in which to analyse the characters uniting and separating the two species. Material from the Dinosaur Park Formation of Alberta (Currie & Russell, 1982) and Hell Creek Formation of Montana (Henderson & Peterson, 2006) was also assigned to the genus *Quetzalcoatlus*, but reanalysis of those remains has established them as representing distinct genera and species: *Cryodrakon boreas* from Alberta (Hone et al., 2019) and *Infernodrakon hastacollis* from Montana (Thomas et al., 2025). Additionally, two isolated cervicals of moderately large azhdarchids, UCMP 114286 from the Lance Formation of Wyoming (Estes, 1964; Thomas et al., 2025) and FSAC-OB 14 from the Maastrichtian 'Couche III' of Morocco (Longrich et al., 2018) have been referred to cf. *Quetzalcoatlus* sp. more recently.

Although previous analyses (Andres, 2021; Thomas et al., 2025) have recovered a sister-group relationship between *Q. northopi* and *lawsoni*, this relationship is not recovered here. The sister taxon of *Quetzalcoatlus northopi* is *Thanatosdrakon amaru*, united by the entepicondyle of the humerus being larger than the ectepicondyle and the presence of an intercondylar ridge on the proximal ulna. The sister to the *Quetzalcoatlus northopi–Thanatosdrakon* clade is a clade containing *Quetzalcoatlus lawsoni*, FSAC-OB 14, UCMP 114286, ME1 04, and the 'Tous pterosaur' (hereafter the '*lawsoni* group'). The taxa in the '*lawsoni* group' all display cervical vertebrae with an accentuated constriction of the posterior-most centrum just anterior to the postzygapophyses, which is absent in *Q. northropi* (TMM 42889-1: Andres & Langston, 2021). The separation of these two clades is not an artefact of which material is known, as both *Q. northopi* and '*Q*'. *lawsoni* are known from both forelimb and cervical material (Andres & Langston, 2021). This is also not an artefact of size, as the characters that unite *Q. northropi* and *T. amaru* are not directly size-related and are not present in other giant azhdarchids (e.g. *Cryodrakon boreas* Hone et al., 2019; 'Sidi Chennane azhdarchid' FSAC-OB 203, Longrich et al., 2018). Although each of these clades only has limited character support, our results challenge the longstanding referral of the two species to

a single genus. Further characters should be sought to improve resolution of this area of the azhdarchoid tree.

Placement of '*Q*'. *lawsoni* within the genus *Quetzalcoatlus* would render the genus polyphyletic or require that the genus be expanded to include *Thanatosdrakon* and several additional unnamed morphotypes that may represent distinct species, ranging from the late Coniacian to Maastrichtian. Additionally, both *Thanatosdrakon* and *Quetzalcoatlus northropi* are giants (9–10 m wingspan) while all the members of the '*lawsoni* group' range between 2 and 6 m wingspans. The continued placement of '*Q*'. *lawsoni* within the genus *Quetzalcoatlus* is therefore problematic: a new genus is most likely needed to accommodate '*Q*'. *lawsoni* and potentially also its closest relatives (e.g. UCMP 114286 and FSAC-OB 14). A rediagnosis of *Quetzalcoatlus* in light of the probable polyphyly of the genus as historically understood is required, though this is beyond the scope of the present study.

The femur TMM 41047-1, referred to *Q. northopi* (Andres & Langston, 2021), is of interest due to its exceptional robusticity in comparison to '*Q*'. *lawsoni*. The femur of '*Q*'. *lawsoni* (TMM 41544-2 and other TMM specimens: see Andres & Langston, 2021) is broadly similar to most azhdarchid femora. It exhibits a constriction at the proximal end of its diaphysis which expands distally, which is typical of azhdarchid femora (e.g. *Azhdarcho lancicollis* ZIN PH 16/44, Averianov, 2010; *Zhejiangopterus linhaiensis*, Cai & Wei, 1994; *Cryodrakon boreas* TMP 1988.36.92, Godfrey & Currie, 2005, Hone et al., 2019; *Hatzegopteryx thambemba* LPB R.1625, Buffetaut et al., 2003; Azhdarchidae indet. NJSM GP 18772, Parris et al., 2004; pers. obs.). In contrast, the *Q. northropi* referred femur lacks this constriction, having "a relatively constant diameter over [the] length" of the shaft (Andres & Langston, 2021, p. 84), which Andres and Langston compared to *Dsungaripterus*. However, in stark contrast to the 'slender' (C. C. Young, 1964) femur of *Dsungaripterus*, TMM 41047-1 is 'the most robust' of any pterosaur (Andres & Langston, 2021). This extreme robusticity is most likely an adaptation to support the increased weight of the giant pterosaur during terrestrial location. Notably, the femur of *Thanatosdrakon amaru* (UNCUYO-LD 307-24) shows an intermediate condition between that of typical azhdarchids including '*Q*'. *lawsoni* and that of *Q. northopi*, lacking a strong constriction of the diaphysis but not displaying the extreme robusticity of TMM 41047-1. The increasing femoral robusticity in the *northopi*-*Thantosdrakon* clade is likely associated with the evolution of gigantism in the *Quetzalcoatlus northopi* lineage.

Pterosaur size evolution

Large size (>5 m wingspan) in pterosaurs is only present within Ornithocheiroidea. *Moganopterus zhuianus* (originally spelled *zhuiana* by Lü et al., 2012; here emended to *zhuianus* under ICZN Art. 34.2, as *zhuiana* is an adjective and therefore must agree in gender with masculine -pterus) was initially estimated as having a wingspan of 7 m (Lü et al., 2012), but this has been reduced to 3.5 m (Gao et al., 2022), a number we accept for our analysis. Within ornithocheiroids, large size emerges in *Pteranodon* and Anhangueridae, with the only giant-sized taxon being *Tropeognathus mesembrinus*. The largest wingspans known in both extinct birds (*Pelagornis sandersi*, wingspan 6.06–7.38 m) and extant birds (*Diomedea exulans*, wingspan 3.5 m) are present in oceangoing piscivores (Kspeka, 2014) with similar foraging strategies to what has been inferred for pteranodontids and anhanguerids (Bestwick et al., 2018; Witton, 2013). Selection for soaring efficiency was a likely driver for large size in albatrosses and *Pelagornis* (Ksepka, 2014), and the wing anatomy of pteranodontids and anhanguerids is consistent with similar marine soaring flight styles (Witton, 2013; Witton & Habib, 2010). It is therefore plausible that selection for soaring efficiency contributed to the appearance of large size in anhanguerids and pteranodontids.

Giant size (>7.4 m wingspan) is very rare in pterosaurs. Wingspans of >7.4 m have been estimated for indeterminate pterodactyloid specimens from the Romualdo Formation (Dalla Vecchia & Ligabue, 1993) and the Vectis Formation (Martill et al., 1996), but the extremely fragmentary nature of these specimens and variability in pterosaur wing proportions mean that these estimates should not be considered greatly reliable (Buffetaut, 2004; Kellner et al., 2013). More recently, a specimen of *Tropeognathus* cf. *mesembrinus* (MN 6594-V) has been estimated to have a 'maximized wingspan' of 8.7 m based on comparison with *Anhanguera piscator* and AMNH FARB 22552; an even larger size of 9 m was estimated for the indeterminate anhanguerid specimen MCT 1838-R (Kellner et al., 2013). Our recalculation based on our differing definition of wingspan (see Methods and compare to Kellner et al., 2013) reduces this number to 8.2 m for MN 6594-V, but these specimens nevertheless represent an instance of giant size evolving outside of Azhdarchidae.

Azhdarchids, on the other hand, evolved large or giant sizes frequently. Giant azhdarchid specimens insufficiently diagnostic to include in the phylogenetic analysis include FSAC-OB 203 ('Sidi Chennane azhdarchid'), an ulna from the Ouled Abdoun Basin with an estimated wingspan of *c*. 9 m (Longrich et al., 2018); a large-bodied taxon from the Nemegt Formation,

known only from posterior cervical vertebrae (Tsuihiji et al., 2017); and azhdarchid trackways from the Uhangri Formation referred to the ichnotaxon *Haenamichnus uhangriensis* (Hwang et al., 2002), the largest of which indicate trackmakers with wingspans in excess of 8 m (Kubo, 2011; Witton & Naish, 2008). The repeated evolution of gigantism may partially be due to Cope's rule (Benson et al., 2014), but furthermore, the azhdarchid bauplan is one well-suited for gigantism, facilitating effective terrestrial and aerial locomotion even at large size (Witton & Habib, 2010; Witton & Naish, 2008). Among the proposed benefits of evolving a larger size are defence against predation, more effective predation, and the ability to hunt larger prey (e.g. Hone & Benton, 2005; Stanley, 1973). Such factors are certainly plausible drivers for the evolution of gigantism in terrestrially stalking predators capable of flight (Witton & Naish, 2008), and azhdarchids may have been more susceptible to these factors than other clades given their ecology and bauplan. Additionally, the fragile membranous wings of pterosaurs made them somewhat vulnerable (Frey & Tischlinger, 2012), so the intimidation ability of a larger animal may have also provided a fitness advantage.

It has been hypothesized that the large size and soaring flight style of giant azhdarchids could have allowed them to travel on the wing over 16,000 km at a time, allowing them to cross oceans and potentially have ranges encompassing multiple continents (Habib, 2010). However, it is uncertain how frequently this capacity for cross-continental distribution was exploited in life. Azhdarchids likely had a flight style best suited for soaring over terrestrial environments (Witton & Habib, 2010); such a flight style would be relatively ill-equipped for crossing large oceanic boundaries (Witton & Naish, 2008). There is currently no direct evidence for multicontinental distribution in giant azhdarchids. Indeed, the presence of three independent, geographically separated lineages of giant azhdarchids (*Arambourgiania*, *Hatzegopteryx* and *Quetzalcoatlus*) in the Maastrichtian opens the possibility that these pterosaurs may not have attained global distributions. As discussed above, the unusual morphology and inferred ecology of *Hatzegopteryx* was likely a result of a lack of competing predatory dinosaurs in its environment, making it unlikely that this taxon's range extended far beyond the unique island environments of eastern Europe. However, there are several cases of giant azhdarchids whose closest relatives are found on other continents: *Arambourgiania* is known from Afro-Arabia, but its closest relatives MPPM 2000.23.1 and *Infernodrakon* are found in Appalachia and Laramidia respectively; *Quetzalcoatlus northopi* and *Thanatosdrakon* are sister taxa but are found in Laramidia and South America respectively. Similar patterns are also present among smaller azhdarchids, with members of Phosphatodraconia, the '*Zhejiangopterus* clade', and the '*lawsoni* group' being present on both sides of the Atlantic Ocean. This suggests that while transoceanic ranges for individual species were not the norm, transoceanic dispersal may have been frequent within azhdarchids.

Conclusions

This study presents the most comprehensive phylogenetic analysis of pterosaurs to date, with implications for their phylogenetic systematics, especially in the Azhdarchomorpha. Despite its Maastrichtian age, the recently described *Inabtanin alarabia* is one of the earliest-diverging azhdarchomorphs. Chaoyangopterids can be divided into two clades, the Chaoyangopterinae and Shenzhoupterinae (cl. nov.). The earliest azhdarchids are from the Early Cenomanian, and putative older records of azhdarchids either represent non-azhdarchid azhdarchoids or belong to distantly related pterosaur clades whose similarities to azhdarchids are convergent. Azhdarchids significantly diversified around the Cenomanian and Turonian, perhaps representing a 'bloom taxon' that diversified during a faunal turnover and remained diverse afterwards. *Bakonydraco* is not a tapejaromorph but an azhdarchid; some of the azhdarchid postcranial material from Iharkút probably pertains to it. *Bakonydraco*, *Albadraco* and *Hatzegopteryx* belong to a clade of robust, possibly macropredatory azhdarchids seemingly endemic to Eastern Europe. Serpennata (cl. nov.) is a clade that includes the giant quetzalcoatline azhdarchids *Quetzalcoatlus* and *Arambourgiania*, along with several other relatives of various sizes, notable for having extremely elongated cervical vertebrae. The iconic genus *Quetzalcoatlus* as understood for nearly three decades is polyphyletic: the type species *Q. northopi* is most closely related to *Thanatosdrakon amaru*, while '*Q*'. *lawsoni* belongs to a clade that also includes several unnamed morphotypes of non-giant azhdarchids. Gigantism in azhdarchids is limited to Quetzalcoatlinae but independently evolved at least four times: in the lineage of *Cryodrakon*, in the '*Hatzegopteryx* clade', in the clade including *Quetzalcoatlus northopi* and *Thanatosdrakon amaru*, and in the lineage of *Arambourgiania philadelphiae.* This repeated evolution of gigantism may have been facilitated by the unique bauplan and ecology of azhdarchids.

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Author contributions

Study conception and design: HNT and SNM; Data collection: HNT and SNM; Analysis: HNT and SNM; Manuscript writing: SNM and HNT; Figures: SNM and HNT.

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Data availability statement

The data that support the findings of this study are openly available from MorphoBank at https://doi.org/10.7934/P6060 (Thomas and McDavid, 2025b).

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