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The first pterosaur from the Bauru Group: an azhdarchid from the Upper Cretaceous of Brazil

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Abstract: The vertebrate fossil record of the Bauru Group (Upper Cretaceous, southeastern Brazil) is remarkably rich, with a predominance of titanosaurs and crocodyliforms, alongside theropods, turtles, squamates, fishes and even small mammals. In contrast, pterosaur remains from the Bauru Group have remained elusive until now. Here, we describe a fragmentary jaw from the upper Maastrichtian Serra da Galga Formation, representing the first confirmed pterosaur discovery from the Bauru Group. The specimen was collected in the Serra da Galga Geosite and is interpreted as a rostrum (upper jaw tip), showing diagnostic features that support its identification as a new azhdarchid species: *Galgadraco zephyrius* gen. et sp. nov. This new taxon represents the first Brazilian azhdarchid and bears striking similarities to the coeval *Albadraco tharmisensis* from the Haţeg Basin, Romania. Phylogenetic analysis recovered *Galgadraco* as a sister taxon to *Albadraco*, both deeply nested within the clade Quetzalcoatlida. Additional indeterminate pterosaur fragments were also recovered from the same level of the fossil site and include another jaw fragment, a diminutive (? hatchling) lower jaw with azhdarchid affinities, a distal metacarpal IV, and ungual fragments. This highlights a previously unrecognized archosaurian diversity, with important implications for the palaeoecology of the Serra da Galga Formation.

Key words: Azhdarchoidea, systematics, Paraná Basin, Bauru Supersequence, Serra da Galga Formation, Maastrichtian.

UNEQUIVOCAL pterosaurs have been documented from as early as the Late Triassic (e.g. Dalla Vecchia 2003), when they were already relatively widespread and diverse (Martínez *et al.* 2022). Following the Turonian (Late Cretaceous), pterosaur phylogenetic diversity greatly declined (Butler *et al.* 2009; Pentland *et al.* 2019; Smith *et al.* 2023), even though species richness remained considerable (Longrich *et al.* 2018). During the Maastrichtian (the final age of the Mesozoic), although still widespread, pterosaurs were restricted mainly to three families: Pteranodontidae, Nyctosauridae and Azhdarchidae (Longrich *et al.* 2018).

Late Cretaceous pteranodontids are known from North America, Europe, North Africa, and East Asia (Kellner *et al.* 2016; Longrich *et al.* 2018; Averianov & Arkhangelsky 2021), while nyctosaurids occur in the Americas and North Africa (Price 1953; Longrich *et al.* 2018). In contrast, azhdarchids were distributed worldwide, having been found in Afroarabia, Europe, Central and East Asia, the Americas (e.g. Ibrahim *et al.* 2010; Averianov 2014; Rosenbach *et al.* 2024), and possibly Australia (Bennett & Long 1991). Azhdarchids are particularly abundant during the Turonian–Maastrichtian interval, and comprise at least 19 nominal species to date (Andres 2021; Ortiz-David *et al.* 2022; Thomas *et al.* 2024; Pêgas *et al.* 2025).

From South America, most of the pterosaur fossils come from the Lower Cretaceous (Aptian–Albian) Lagerstätte of the Araripe Basin (Northeastern Brazil), from which at least 25 species are generally regarded as valid (Pêgas *et al.* 2016; Cerqueira *et al.* 2021). Approximately coeval taxa are also present in Southern Brazil, including the tapejarids *Caiuajara dobruskii* and *Torukjara bandeirae* (Manzig *et al.* 2014; Pêgas 2024), and the azhdarchomorph *Keresdrakon vilsoni* (Kellner *et al.* 2019a), all recovered from the Cauiá Group.

Regarding the Upper Cretaceous of South America, only four nominal species are recognized so far. Of these, three species consist of Argentinian forms: the alanqid

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Argentinadraco barrealensis from the upper Turonian to lower Coniacian Portezuelo Formation (Kellner & Calvo 2017), and the azhdarchids *Thanatosdrakon amaru* from the upper Coniacian to lower Santonian Plottier Formation (Ortiz David *et al.* 2018), and *Aerotitan sudamericanus* from the middle Campanian to lower Maastrichtian Allen Formation (Novas *et al.* 2012; Pêgas *et al.* 2021). The fourth occurrence, based on a humerus from the uppermost Maastrichtian Gramame Formation, Northeast Brazil, is *Nyctosaurus lamegoi* (Price 1953), which probably represents a new genus related to the Moroccan *Barbaridactylus grandis* (Longrich *et al.* 2018) or *Simurghia robusta* (Pêgas 2024).

In this contribution we report on the first pterosaur remains from the Upper Cretaceous of the Bauru Group, Southeast Brazil. The specimens come from fluvial sediments of the late Maastrichtian Serra da Galga Formation at the Serra da Galga Geosite (Uberaba UNESCO Global Geopark). A well-preserved, three-dimensional rostrum fragment is identified as a new azhdarchid species, strikingly similar to the coeval European form *Albadraco tharmisensis* (Solomon *et al.* 2019). This new record enriches the diverse fossil assemblage of the Serra da Galga Formation and sheds light on the palaeoecology of this important unit of the Brazilian Upper Cretaceous and the azhdarchid diversity during the Maastrichtian.

GEOLOGICAL SETTING

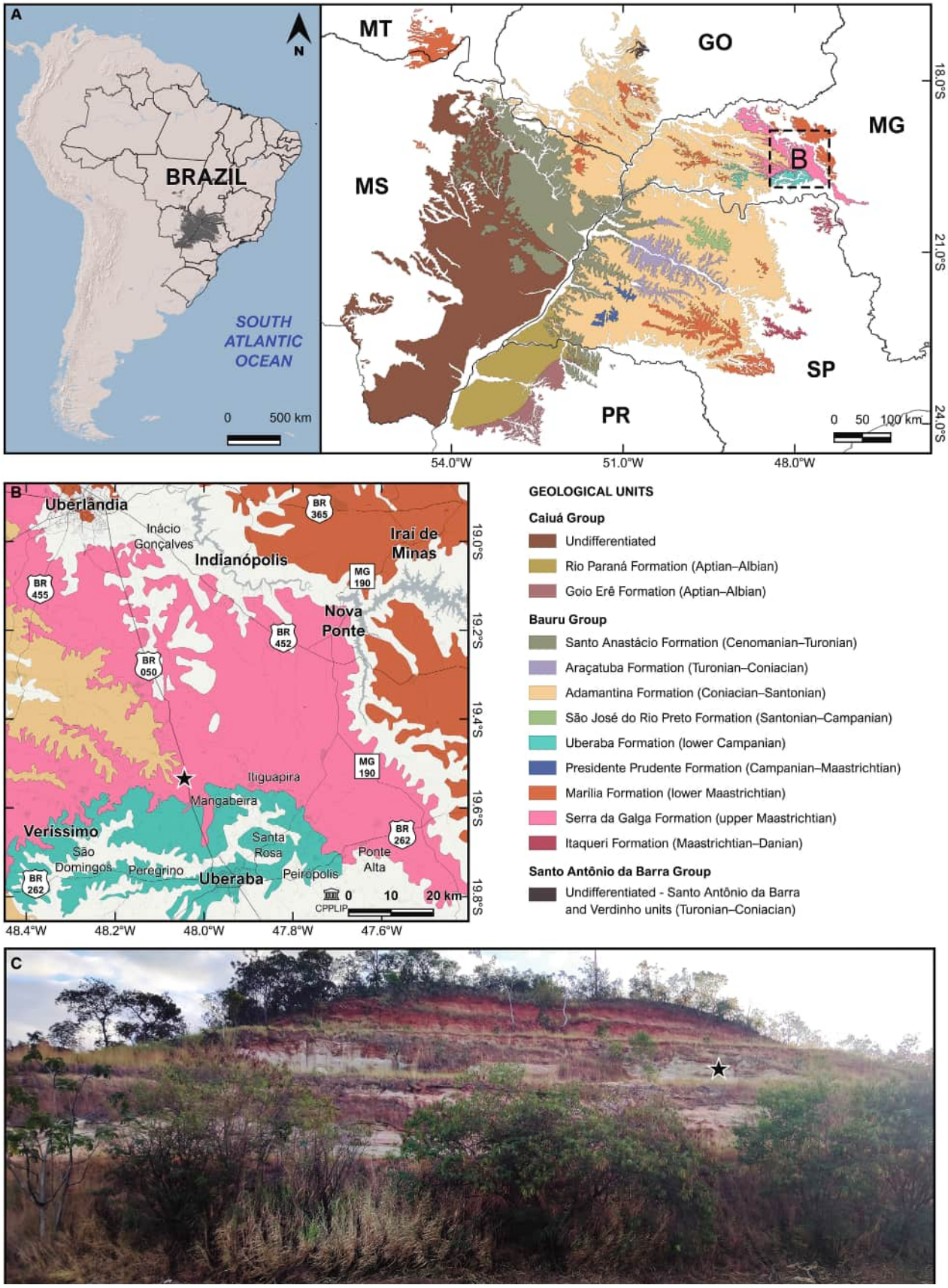
The Bauru Supersequence of the Paraná Basin (*sensu* Arai & Dias-Brito 2023; Fig. 1) comprises an extensive intracratonic siliciclastic deposit, covering *c.* 370 000 km^2 of south, southeastern and central Brazil, with a maximum thickness reaching up to 300 m. Based on biostratigraphic markers, such as ostracods and charophytes (e.g. Dias-Brito *et al.* 2001), as well as radiometric dating of igneous intrusions (e.g. Coutinho *et al.* 1982) and detrital zircons (Assis *et al.* 2021), it is inferred that the Bauru Supersequence developed from the Aptian to the Maastrichtian, potentially extending into the lower Paleocene (Menegazzo *et al.* 2016). During this interval, the region experienced a predominantly warm and arid climate, punctuated by brief humid phases (Dal'Bó *et al.* 2010).

The Bauru Supersequence is divided into two major lithostratigraphic units: the Caiuá and the Bauru groups (Soares *et al.* 1980). The Caiuá Group comprises the Rio Paraná and Goio Erê Formations, both predominantly composed of aeolian deposits, including extensive sand–sea systems and peripheral deposits of dunes and interdunes (Fernandes & Magalhães Ribeiro 2015). Conversely, the Bauru Group comprises the Santo Anastácio, Araçatuba, Adamantina, São José do Rio Preto, Uberaba, Presidente Prudente, Marília and Serra da Galga formations (Navarro *et al.* 2025, fig. S1), which were deposited in an endorheic context, characterized by lacustrine, fluvial and alluvial systems with intermittent aeolian influence.

The specimens described in this study came from the Serra da Galga Formation (SGF), recently erected from the former Serra da Galga and Ponte Alta Members of the Marília Formation (Soares *et al.* 2020a). The SGF consists predominantly of medium- to coarse-grained sandstones, pebbly sandstones, and conglomerates, with occasional fine sandstones, mudstones and calcrete beds. These lithologies reflect a distributive fluvial system with predominant NNW-directed palaeocurrents, characterized by interbedded channel fills, interchannels and palaeosol horizons (Soares *et al.* 2018). Eleven sedimentary facies and three pedotypes indicate dynamic deposition under a semiarid climate with episodic wetter intervals, evidenced by hyper-concentrated flow deposits, channel bar migration, and stable surface palaeosol development (Soares *et al.* 2020b).

Based on its fossil record, the SGF has been widely recognized as an upper Maastrichtian unit (Dias-Brito *et al.* 2001; Oliveira & Santucci 2020). The fossil assemblage of the SGF is remarkably diverse and provides a unique glimpse into South American continental ecosystems near the end of the Cretaceous, underscoring the palaeoecological importance of this formation. This biota includes charophytes, palynomorphs (gnetophytes, conifers and cycads), 'conchostracans' (clam shrimps), ostracodans, mollusks (gastropods and bivalves), several fishes (siluriforms, lepisosteiforms, amiids, characiforms, perciforms and dipnoans), anurans, podocnemidoid turtles, iguanian lizards, notosuchian crocodyliforms (peirosaurids, itasuchids and sphagesaurians), as well as sauropod (titanosaurian) and theropod (abelisaurid, unenlagiine

FIG. 1. Geographic and geological provenance of the new pterosaur material described here. A, location and range of the Bauru Supersequence in central Brazil (the dashed box shows the location of part B). B, detail of the Uberaba region, indicating the Serra da Galga Geosite (star) and the Centro de Pesquisas Paleontológicas 'Llewellyn Ivor Price' (CPPLIP). C, the Serra da Galga Geosite, with the source of the present specimens marked by a red star. Geological map follows 'Carta Geológica do Brasil ao milionésimo' (Schobbenhaus *et al.* 2004). Chronolithostratigraphic hierarchy follows Navarro *et al.* (2025). *Abbreviations*: GO, Goiás; MG, Minas Gerais; MS, Mato Grosso do Sul; MT, Mato Grosso; PR, Paraná; SP, São Paulo.



and ornithurine) dinosaurs (e.g. Candeiro 2007; Candeiro *et al.* 2008; Carbonaro *et al.* 2013; Martinelli & Teixeira 2015; Menegazzo *et al.* 2016; Brusatte *et al.* 2017; Delcourt *et al.* 2020; Brum *et al.* 2021; Giaretta *et al.* 2024, Muniz *et al.* 2025).

MATERIAL & METHOD

Material

The specimens described here came from the Serra da Galga Geosite (BR-050 km 153), located 25 km north of Uberaba County, at the Serra da Galga (Galga Hill; Figs 1, 2). This site corresponds to the type locality of the sauropod titanosaur *Uberabatitan ribeiroi*, and is also known as the BR-050 site (Salgado & Carvalho 2008). The herein described holotype (CPPLIP 1853) was discovered by the first author (AAG) as a rolled fragment and is thought to have originated nearby (0–3 m laterally, 1–2 m above), possibly excavated by himself before, and later exposed by rainfalls. Consistently, the specimen has the appearance of a freshly unearthed piece, showing no evidence of recent weathering. In support of this assumption, other pterosaur fragments were retrieved through dry sediment sieving from this rock layer.

Although the facies at the site are highly laterally heterogeneous, the sampled level (*c.* 1.5 m thick) could be correlated to the 37 m mark in the profile described by Salgado & Carvalho (2008) and the 22 m mark in Soares *et al.* (2020a). The sampling point consists of a friable coarse pebbly sandstone containing siliceous and

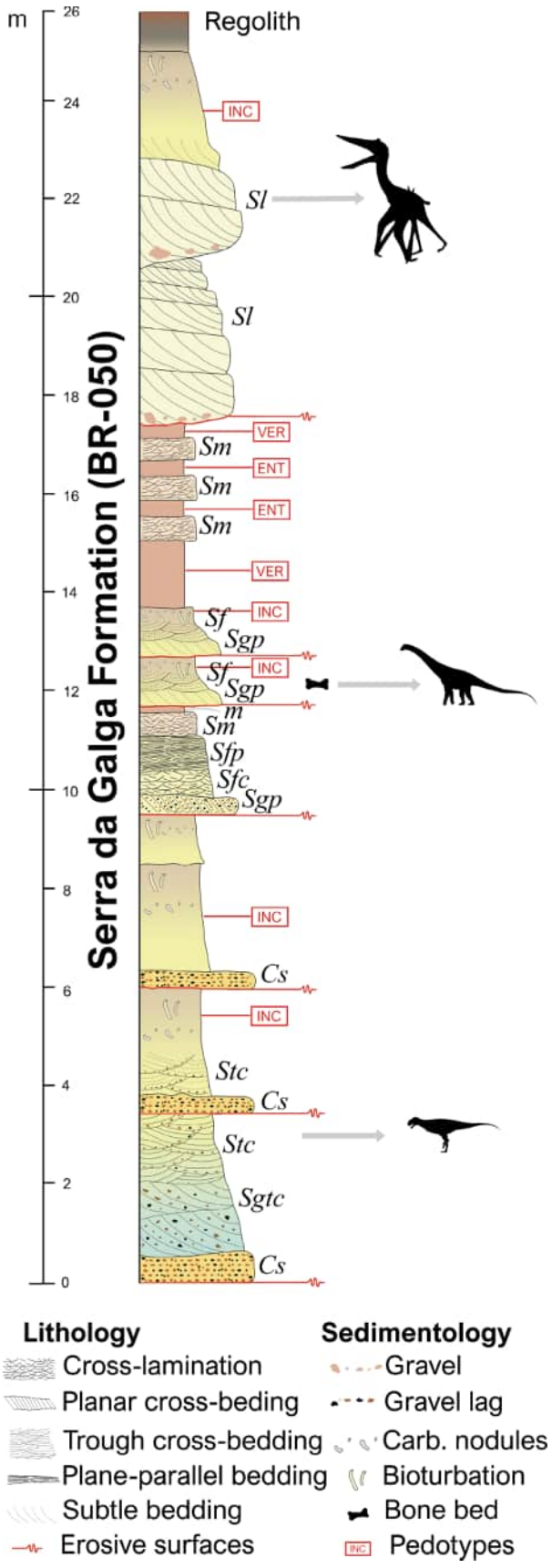


FIG. 2. Lithostratigraphic column of the Serra da Galga Geosite (BR-050 site), indicating the stratigraphic level of the remains of *Galgadraco zephyrius* gen. et sp. nov. (indicated by a pterosaur silhouette, near the 22 m mark), *Uberabatitan ribeiroi* (titanosaur silhouette, near the 12 m mark) and indeterminate abelisaurid remains (abelisaurid silhouette, between the 2 and 4 m marks). Modified from Soares *et al.* (2020b), reproduced with permission. *Galgadraco zephyrius* silhouette: courtesy of Matheus Gadelha. Titanosaur silhouette: artwork by Cy Marchant, from PhyloPic (https://www.phylopic.org/; CC BY 4.0). Abelisaurid silhouette: modified from artwork by Gabriel Martins, from WikiMedia Commons, (https://commons.wikimedia.org/wiki/File:Kurupi_itaata.jpg; CC BY-SA 4.0). Colour on the column roughly represents sediment colour. *Abbreviations*: Carb., carbonate; *Cs*, sandy conglomerate; ENT, entisol; INC, inceptisol; *m*, mudstone; *Sf*, fine sandstone; *Sfc*, cross-laminated fine-grained sandstone; *Sfp*, planar-laminated fine-grained sandstone; *Sgp*, planar cross-bedded conglomeratic sandstone; *Sgtc*, planar or trough cross-bedded pebbly sandstone; *Sl*, large-scale lenticular cross-bedded sandstone; *Sm*, muddy sandstone; *Stc*, trough cross-bedded sandstone; VER, vertisol.

mud clasts up to a few centimetres in size and rich in vertebrate microremains. The fossils described here were found in a channel fill, consistent with a fluvial channel, resembling an isolated crevasse channel as described by Burns *et al.* (2019). This suggests relatively close proximity to the parent feeder channel (Soares *et al.* 2020a). The fragile nature of the specimens (which, despite being fragmentary, show a low degree of abrasion) also suggests a transport distance not too far from their original location.

Excavation using hand tools and subsequent sieving of this level have yielded siluriform barb fragments (CPPLIP 1895 and CPPLIP 1896), scales of lepisosteiforms (CPPLIP 1897, CPPLIP 1898 and CPPLIP 1899), vertebrae and fused long bones of anurans (CPPLIP 1855, CPPLIP 1856, CPPLIP 1857 and CPPLIP 1858; Muniz *et al.* 2025), shell fragments of podocnemidoid turtles (CPPLIP 1900 and CPPLIP 1901), a notosuchian parietal (CPPLIP 1902), and several teeth of abelisaurid (CPPLIP 1903) and of titanosaurian dinosaurs (CPPLIP 1904 and CPPLIP 1905). All of these specimens, including those described here (CPPLIP 1853, CPPLIP 1854, CPPLIP 1906, CPPLIP 1907 and CPPLIP 1908), are housed at the Centro de Pesquisas Paleontológicas 'Llewellyn Ivor Price', Universidade Federal do Triângulo Mineiro, Uberaba, Brazil.

Photos of the specimen were taken with a Nikon D90 coupled to a micro 60 lens using built-in flash. Photos were edited in the software GIMP v2.10.34 to remove flash shadowing and to generate schematic drawings. Relevant anatomical details were emphasized by further delineating features over the scratches. The rostrum cross-section contour of the holotype was obtained by adjusting a thin (0.3 mm) flexible wire around the piece and taking photos of the resulting shape.

Institutional abbreviations. CPPLIP, Centro de Pesquisas Paleontológicas 'Llewellyn Ivor Price', Universidade Federal do Triângulo Mineiro, Uberaba, Brazil; LPB, Laboratory of Palaeontology of the Faculty of Geology and Geophysics, University of Bucharest, Romania; ME, Musée des Dinosaures, Espéraza, France; MN, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio da Janeiro, Brasil; MPC, Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MPM, Milwaukee Public Museum, Milwaukee, WI, USA; NJSM, New Jersey State Museum, Trenton, NJ, USA; PSMUBB, Palaeontology-Stratigraphy Museum, Babeş-Bolyai University, Cluj-Napoca, Romania; TMM, Texas Memorial Museum, Austin, TX, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; WAM, Western Australian Museum, Perth, WA, Australia.

Anatomical terminology. Standards for morphological description of pterosaur jaws mostly follow Pêgas *et al.* (2021) and Ortiz David *et al.* (2022). Noteworthy, 'tomial edges' refer to the elevated marginal edges of the beak, following analogous terms of the Nomina Anatomica Avium. Other orientational terminology follows 'Romerian' nomenclature (Wilson 2006). Lateral, dorsoventral and ventrolateral divergence angles were measured as in Martill *et al.* (2017, fig. 4). Furthermore, we introduce here the term 'foramination index', which represents the proportion of the axis length of a row (per side) that is occupied by the summed length of the slit-like foramina. Throughout this work, 'anterior foramination index' refers to the foramination index of the anterior region of the jaw.

Heuristic tree search

To assess the phylogenetic relationships of the new taxon, we coded the morphological data into the recently published dataset of Zhou *et al.* (2024; 533 characters, 204 terminals). Due to the preservation state of additional specimens and limitations in character sampling, only the holotype was scored for this analysis. Data matrix files (in Nexus and TNT formats) are available in Appendices S1 and S2. The matrix was analysed using equally weighted parsimony in TNT v1.5 (Goloboff *et al.* 2008). We conducted this analysis with new technology searches with the following major settings: *mxram* = 1024; *rseed* = 0; *hold* = 100 000; *collapse rule 1*; *outgroup* = 0; *xmult* = hits 100; *bbreak* = tbr. This approach combines the sectorial search, ratchet, drift, and tree fusing algorithms with traditional search methods, such as Wagner trees, tree branch reconnection, and subtree-pruning-regrafting algorithms, to identify the minimum length trees.

SYSTEMATIC PALAEONTOLOGY

PTEROSAURIA Owen 1842
PTERODACTYLOIDEA Plieninger 1901
AZHDARCHOIDEA Unwin 1995 (*sensu* Kellner 2003)
AZHDARCHIDAE Padian 1986 (*sensu* Pêgas *et al.* 2025)

Genus *Galgadraco* nov.

LSID. https://zoobank.org/NomenclaturalActs/130E9023-8D74-456E-928D-437F88DEA647

Derivation of name. From *Galga*, referring to the Serra da Galga Formation and the Galga Hill, and *draco*, Latin for 'dragon', a common suffix used to designate pterosaurs.

Type species. Galgadraco zephyrius sp. nov.

Diagnosis. As for the type and only known species, by monotypy.

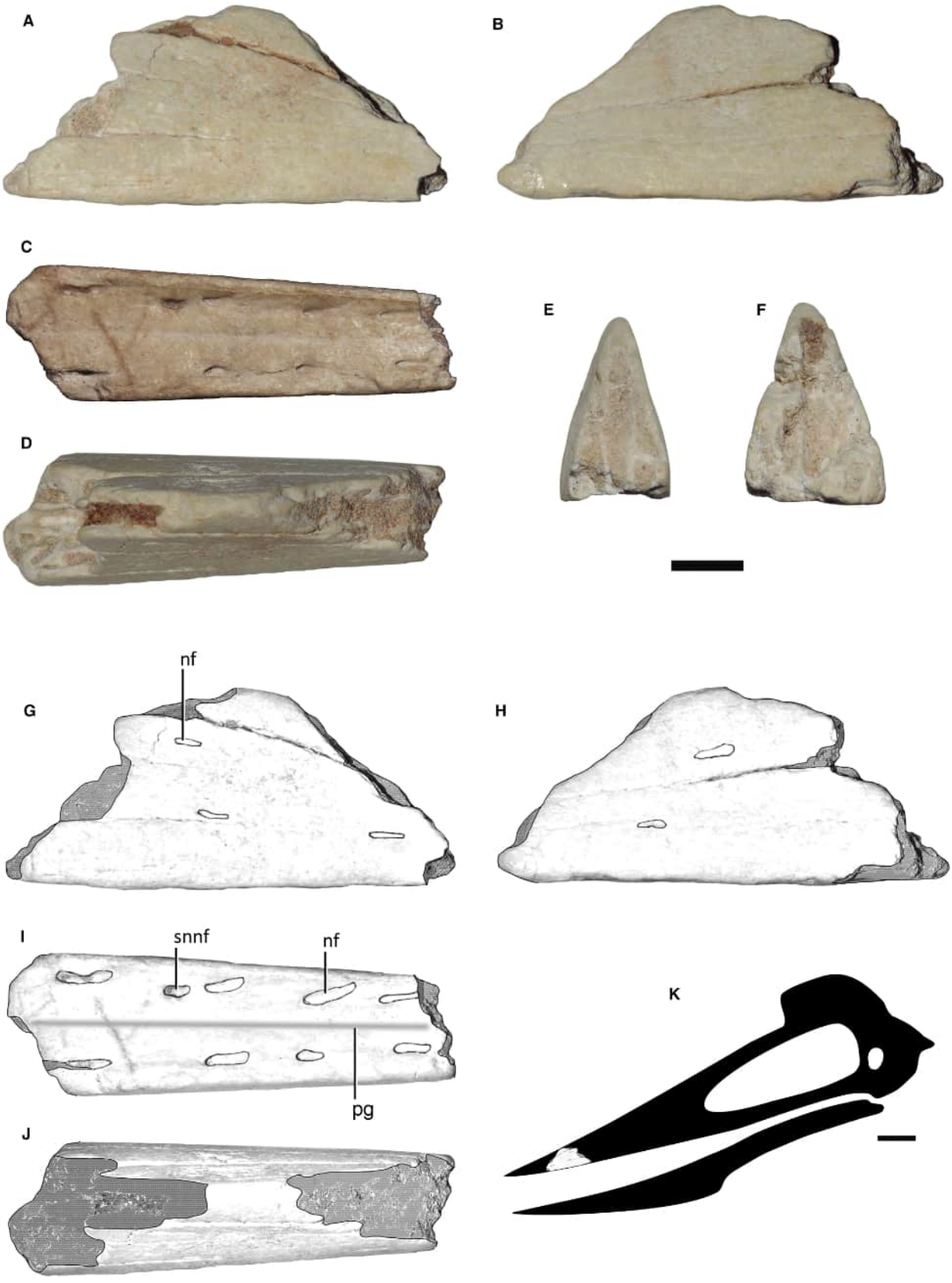


FIG. 3. Holotype of *Galgadraco zephyrius* gen. et sp. nov. (CPPLIP 1853). Rostrum fragment in: A, right lateral; B, left lateral; C, palatal; D, dorsal; E, anterior; F, posterior view. G–J, schematic drawings of A–D highlighting the slit-like foramina, the medial longitudinal groove, and broken parts (pattern). K, hypothetical reconstruction of a generalized *Hatzegopteryx*-like skull, showing the approximate anatomical position of the preserved fragment. *Abbreviations*: nf, neurovascular foramen; pg, palatal groove; snnf, supernumerary neurovascular foramen. Scale bar represents: 10 mm (A–J); 50 mm (K).

Galgadraco zephyrius sp. nov.
Figure 3

LSID. https://zoobank.org/NomenclaturalActs/0D77C4E2-FF7E-4C79-A3FF-B3B47C15DBC9

Derivation of name. From *Zéphuros* (Ζέφυρος), the personification of the west wind in Ancient Greek mythology.

Holotype. CPPLIP 1853, a tridimensional partial rostrum (upper jaw close to tip) fragment (Fig. 3).

Type locality. Serra da Galga Geosite, a roadcut located at kilometre 153 of the BR-050 highway, *c.* 25 km north of Uberaba city (19°35′32.8″S 48°01′42″W).

Horizon & age. Serra da Galga Formation, Bauru Group, late Maastrichtian.

Diagnosis. The new species can be diagnosed based on the following combination of features (autapomorphy marked with an asterisk): edentulous rostrum (upper jaw) tip with lateral divergence of *c.* 7°; dorsoventral divergence of *c.* 15°; ventrolateral divergence of *c.* 18°; roughly triangular cross-section; slit-like occlusal foramina larger than lateral foramina; occlusal foramina mostly organized in a symmetrical pair of rows; relatively dense occlusal foramina (jaw tip foramination index of *c.* 0.40); low and rounded tomial edges; and a shallow median palatal groove*.

Description & comparisons. The holotype (CPPLIP 1853) is an anterior (close to tip) edentulous upper jaw segment (Fig. 3), broken at its anterior and posterior ends. The maximum preserved anteroposterior length is 58.7 mm and the maximum height is 25.7 mm. The cortical bone is slender (*c.* 1 mm on the palatal surface; *c.* 2 mm on the lateral surface; and *c.* 3–4 mm at the dorsal edge), as are the trabeculae. An artefactual fracture runs longitudinally on the left lateral surface, and another one obliquely along the right surface.

The angles of divergence (*sensu* Martill *et al.* 2017) are: dorsoventral, *c.* 15°; lateral, *c.* 7°. Among azhdarchoids, a dorsoventral divergence of ≥15° is quite high, being found only in the upper jaws of some species (such as *Albadraco tharmisensis* and *Shenzhoupterus chaoyangensis*; Pêgas *et al.* 2021). This suggests that CPPLIP 1853 represents an upper jaw rather than a mandible (which typically have lower dorsoventral angles; Pêgas *et al.* 2021). In lateral view the preserved jaw margin is straight (no upward or downward inflection), and there is no indication of a crest.

TABLE 1. Foramination index (FI) of anterior jaw tips in azhdarchomorph taxa.

Taxon	Jaw	FI	References
Galgadraco zephyrius	Upper	0.43	This work
Albadraco tharmisensis	Upper	0.41	Solomon *et al.* (2019)
	Lower	0.44	
Leptostomia begaaensis	Upper	0.25	Smith *et al.* (2023)
	Lower	0.22	
Apatorhamphus gyrostega	Upper	0.25	McPhee *et al.* (2020)
	Lower	0.26	
Keresdrakon vilsoni	Upper	0.20	RVP pers. obs. 2025
	Lower	0.25	
Xericeps curvirostris	Lower	0.21	Martill *et al.* (2017)
Volgadraco bogolubovi	Lower	0.19	Averianov *et al.* (2008)
Aerotitan sudamericanus	Lower	0.14	Pêgas *et al.* (2021)
Mistralazhdarcho maggii	Lower	0.10	Vullo *et al.* (2018)

The palatal surface bears well-defined, deep, and paired neurovascular slit-like foramina organized mostly as symmetric pairs along two rows, as typical of azhdarchoids (Pêgas *et al.* 2016; Martill *et al.* 2017; Solomon *et al.* 2019; Smith *et al.* 2023). A supernumerary (unpaired) one is present on the right side. The slit-like foramina communicate with the medulla just posteriorly, tapering dorsoventrally towards the front. Four paired occlusal foramina are present along a 49 mm section, with a density of 0.82/cm and an anterior foramination index of 0.43 (i.e. the foramina occupy 43% of the anterior region of the foramen row). This is quite high among azhdarchoids (regarding jaw tips), comparable only to that of the azhdarchid *Albadraco tharmisensis* (Table 1).

The paired rows are aligned (symmetrical), similar to cf. *Hatzegopteryx thambema* (Vremir *et al.* 2018), *Albadraco tharmisensis* (Solomon *et al.* 2019), and the Laño azhdarchid (Buffetaut 1999); as well as the sinopterine tapejarid *Bakonydraco galaczi*, at least in the mid-symphysis (Ősi *et al.* 2005). This feature differs from most azhdarchids, in which the paired rows are offset, as in *Aerotitan sudamericanus*, *Mistralazhdarcho maggii*, and the isolated Bissekty Formation jaws (Averianov 2010), and the Bakony azhdarchid rostrum (Ősi *et al.* 2011). Occlusal foramina are also offset in alanqids, as seen in *Alanqa saharica*, *Xericeps curvirostris* and *Leptostomia begaaensis* (Smith *et al.* 2023); chaoyangopterids, as seen in *Apatorhamphus gyrostega* (McPhee *et al.* 2020); thalassodromids, as seen in *Tupuxuara* spp. (Kellner & Campos 1988, 1994); and caupedactylians, as seen in *Caupedactylus ybaka* (Kellner 2013) and *Aymberedactylus cearensis* (Pêgas *et al.* 2016). The new form also differs from tapejarids, in which the foramina may be organized in offset rows, as seen in the sinopterine *Afrotapejara zouhri* (Martill *et al.* 2020a); or in a dense cluster, as seen *Tapejara wellnhoferi*, *Caiuajara*

dobruskii and *Torukjara bandeirae* (Kellner 1989; Manzig *et al.* 2014; Pêgas 2024). Noteworthy, the new specimen also differs from *Quetzalcoatlus lawsoni*, in which the jaws are not foraminated (Andres & Langston 2021).

Still regarding the palatal surface, the bone texture is notably smooth, indicating osteological maturity (Bennett 1993). The palatal surface is transversely slightly concave, the tomial edges running along the length. There are no signs of palatal eminences or keels. Tomial edges are relatively low and rounded, being also mediolaterally thin in palatal view, and dorsoventrally low in cross-section. This is similar to the low tomial edges of *Albadraco tharmisensis* (Solomon *et al.* 2019) and *Quetzalcoatlus lawsoni* (Andres & Langston 2021), and different from the broad and tall tomial edges of *Aerotitan sudamericanus* (Novas *et al.* 2012; Pêgas *et al.* 2021) and *Mistralazhdarcho maggii* (Vullo *et al.* 2018). The tomial ridges are slightly higher on the left side (=collateral asymmetry), similar to the upper jaw of *Albadraco tharmisensis* (Solomon *et al.* 2019).

A shallow, slender median groove of uniform width runs along the preserved palatal surface. This feature is so far unreported for any other azhdarchoid with known jaws and represents an autapomorphy of *Galgadraco zephyrius*. This structure is not similar to the dentary groove of alanqids, which is restricted and produced by a pair of protruding marginal ridges (Kellner & Calvo 2017; Martill *et al.* 2017; Smith *et al.* 2023).

In cross-section the rostrum is V shaped, with a sharp dorsal apex. This is strikingly similar to *Albadraco tharmisensis*, and distinct from the D-shaped cross-sections (with a rounded dorsal apex) seen in the Argentinian azhdarchid *Aerotitan sudamericanus*, the chaoyangopterid *Apatorhamphus gyrostega* (McPhee *et al.* 2020), and in the alanqid *Xericeps curvirostris* (Smith *et al.* 2023).

The lateral surfaces have two and three unaligned slit-like foramina on the left and right sides, respectively. The lateral slit-like foramina are smaller and shallower than the occlusal ones and mostly parallel to the main axis.

cf. AZHDARCHIDAE Padian 1986 (*sensu* Pêgas *et al.* 2025)

Figures 4–6

Material. CPPLIP 1854 (upper jaw? fragment); CPPLIP 1906 (dentary symphysis); CPPLIP 1907 (distal end of metacarpal IV); CPPLIP 1908 (putative manual ungual).

CPPLIP 1854. A putative upper jaw fragment (Fig. 4) is herein attributed to Pterosauria based on the resemblance to the holotype (above) regarding bone thickness, trabeculae architecture, and its general shape. It comprises a segment originally recovered as four pieces, which could be combined (glued) into two pieces given outline complementarity. Possibly all four pieces were from the same specimen, given that they all seem to represent the dorsal surface of a rostrum (or the ventral surface of a symphysis). Given that the texture of the external surface is different to that of the holotype (CPPLIP 1853), they do not seem to be part of it.

The ventrolateral angle of divergence is *c.* 40°. This specimen has a thin cortical bone (1 mm) and even thinner (0.3 mm), regularly spaced trabeculae (*c.* 4 mm in length). The dorsal surface is transversely round or blunt, with no sign of a groove. The external bone surface is finely longitudinally striated (but smoother than the holotype). No slit-like foramina can be seen along these pieces.

CPPLIP 1906. This specimen consists of a fragment of a diminutive (12 mm) dentary symphysis (Fig. 5). Despite being fragmentary, it preserves the typical morphology of azhdarchoid jaws, with a V-shaped cross-section, well-defined tomial edges, and slit-like neurovascular foramen on the occlusal surface. It is regarded as a lower jaw due to the very low dorsoventral angle (*c.* 4°). The cross-section is approximately V shaped, with a sulcate occlusal surface bordered by dorsoventrally short tomial edges, and a sharp ventral apex. Its diminutive size and pitted lateral surface (one side) indicate a juvenile status (Bennett 1993). Even though this specimen is morphologically compatible with azhdarchids, it lacks any unambiguous features of the group. It is here cautiously regarded as possibly conspecific with the new species considering its compatible morphology, juvenile status and stratigraphic position (same level).

CPPLIP 1907. This specimen (Fig. 6A–C) comprises the distal end of a small left metacarpal IV. The element preserves the typical pulley-like articulation that characterizes the pterosaurian metacarpal IV, formed by two prominent ginglymoid condyles separated by a groove (e.g. Bennett 2001; Andres & Langston 2021). The condyles are positioned sub-horizontally, with their posterior edges slightly elevated dorsally. The dorsal condyle has a slightly quadrangular horizontal outline and is positioned more posteriorly. In contrast, the ventral condyle has a slightly circular outline and is offset more anteriorly, as in other

FIG. 4. A putative upper? jaw pterosaur fragment (CPPLIP 1854) from the Serra da Galga Geosite, collected approximately at the same level of the holotype. Scale bar represents 10 mm.

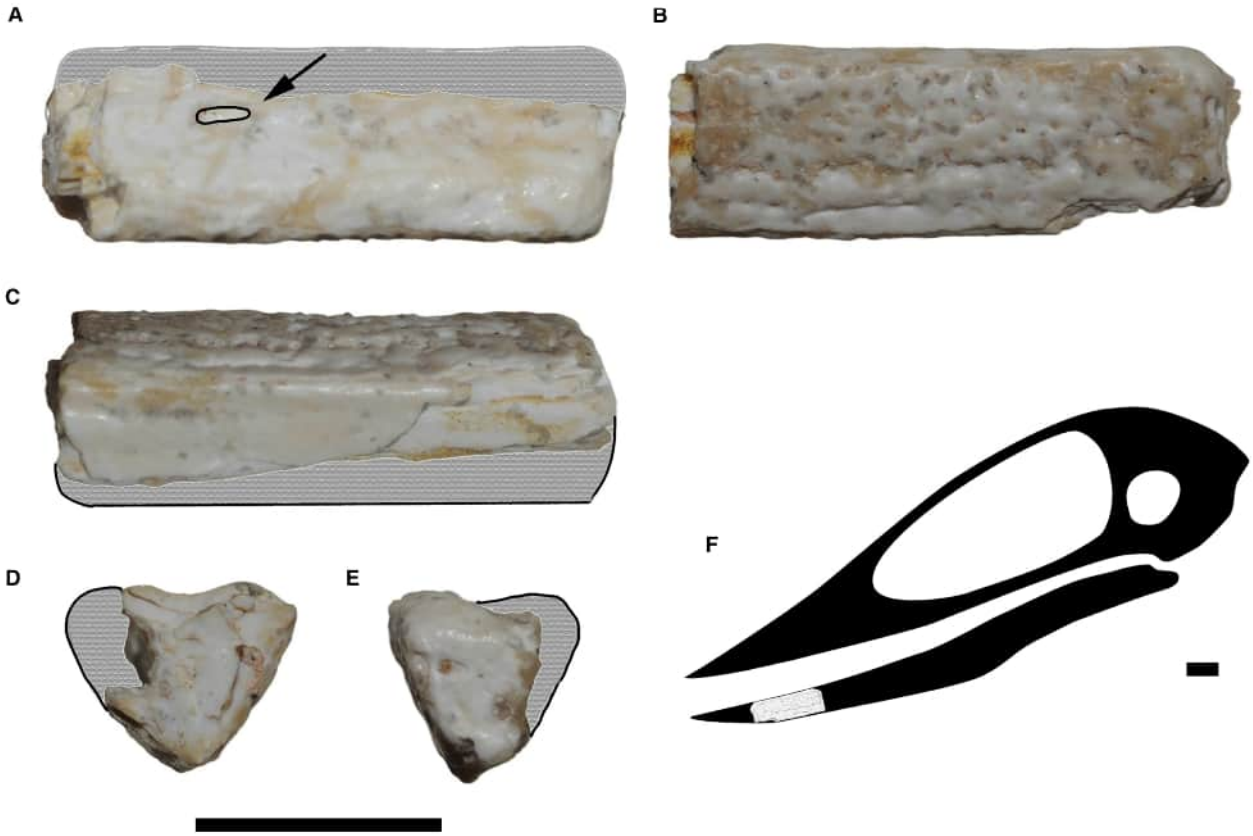


FIG. 5. A diminutive lower jaw fragment (CPPLIP 1906) from the Serra da Galga Geosite in: A, occlusal; B, right lateral; C, ventral; D, posterior; E, anterior view. Arrow (A) indicates a slit-like neurovascular foramen. F, hypothetical juvenile azhdarchid skull showing the approximate anatomical position of the fragment. Scale bars represent 10 mm.

pterosaurs (Bennett 2001; Cohen *et al.* 2018; Andres & Langston 2021). The dorsal condyle extends further distally than the ventral condyle and is oriented slightly distodorsally, giving the distal articulation an asymmetrical 'offset' appearance, as reported for the azhdarchiform *Montanazhdarcho minor* (McGowen *et al.* 2002) and the azhdarchid *Quetzalcoatlus lawsoni* (Andres & Langston 2021). This feature is suggestive of azhdarchoid affinities (Martill *et al.* 2013; Andres & Langston 2021). The small size of this element possibly indicates a juvenile status.

CPPLIP 1908. This specimen (Fig. 6D–G) represents a putative manual ungual. This ungual is laterally compressed and dorsoventrally shallow at the proximal region, as typical of manual pterosaur unguals (e.g. Andres & Langston 2021), and unlike theropod unguals, which are relatively more expanded proximally in both the manus (e.g. Novas *et al.* 2005) and pes (Delcourt & Grillo 2014). Unfortunately, the proximal region is broken, therefore we cannot ascertain whether it represents a right or a left element. The element has a strong degree of curvature (*c.* 100°), suggesting it is a manual rather than a pedal ungual (e.g. Wu *et al.* 2017). The degree of curvature is similar to the second manual ungual of *Quetzalcoatlus lawsoni* (95°; Andres & Langston 2021). Both sides bear a symmetric longitudinal groove, also similar to that of *Quetzalcoatlus lawsoni* (Andres & Langston 2021), and one neurovascular foramen symmetrically positioned on each side (Fig. 6D).

PHYLOGENETIC ANALYSIS

Our search produced 27 most parsimonious trees, with 2179 steps each. The strict consensus tree has an ensemble consistency index of 0.36 and an ensemble retention index of 0.80. *Galgadraco zephyrius* gen. et sp. nov. was recovered as the sister species of *Albadraco tharmisensis* in the strict consensus tree (Fig. 7), this relationship being supported by character 53(1), a dense (>0.40) anterior jaw tip foramination index. Furthermore, the inclusion of *Galgadraco zephyrius* in the *Hatzegopteryx–Albadraco* clade is supported by character 52(1), aligned (symmetrical) paired rows of occlusal foramina. Of further importance, character 37(1), reduced/rounded tomial edges, is recovered as a synapomorphy of Quetzalcoatlida, supporting the placement of the new species in this clade; and character 54(1), the presence of slit-like occlusal foramina, is recovered as a synapomorphy of Azhdarchoidea.

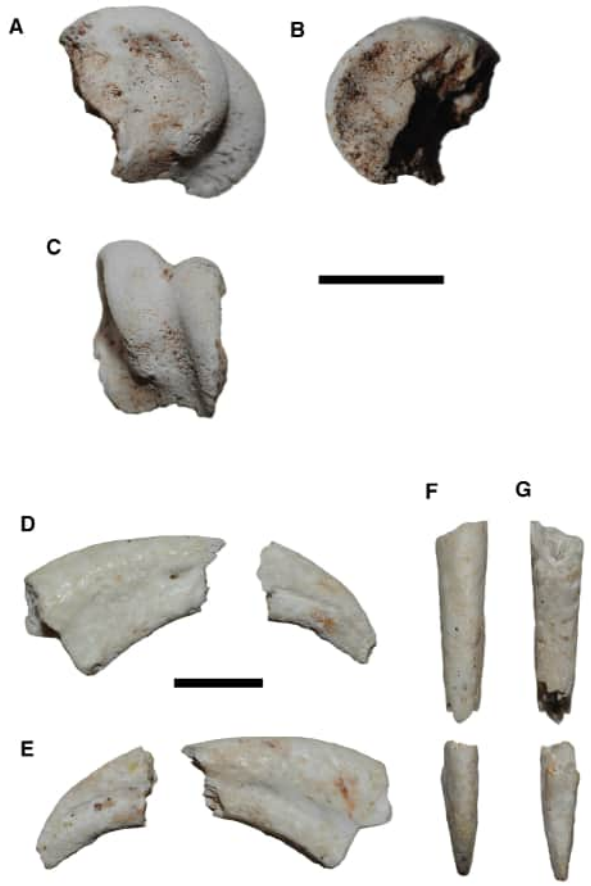


FIG. 6. Pterosaur (?azhdarchid) postcranial fragments from the Serra da Galga Geosite. A–C, CPPLIP 1907, a distal end of a left metacarpal IV in: A, mediolateral? view; B, opposite side of A; C, distal view. D–G, CPPLIP 1908, two portions of a fragmented ungual in: D–E, mediolateral; F, dorsal; G, ventral view. Scale bars represent 10 mm.

DISCUSSION

Phylogenetic affinities of Galgadraco zephyrius

The holotype specimen of *G. zephyrius* can be confidently identified as an azhdarchoid due to the presence of the typical slit-like occlusal neurovascular foramina (e.g. Pêgas *et al.* 2016; Martill *et al.* 2017; Smith *et al.* 2023). The rostrum of the new form bears a notable combination of features: a V-shaped cross-section with a sharp dorsal apex; anteriorly low/rounded tomial edges; mostly aligned (symmetrical) paired rows of occlusal foramina; and a high foramination index. Among azhdarchoids in general, a single taxon matches this combination of features: the Maastrichtian azhdarchid *Albadraco tharmisensis* from the Haţeg Basin (Solomon *et al.* 2019; further discussed below).

Individually, each of these features can be found elsewhere. V-shaped cross-sections can also be found in *Mistralazhdarcho maggii* (Vullo *et al.* 2018), *Alanqa saharica* (upper jaws; Smith *et al.* 2023) and *Keresdrakon vilsoni* (Kellner *et al.* 2019a); but these three forms differ from *Galgadraco zephyrius* in having sharp tomial edges and sparse offset occlusal foramina. A V-shaped cross-section is present in the jaws of cf. *Hatzegopteryx thambema* and *Albadraco tharmisensis* as well (Fig. 8).

Anteriorly low and rounded tomial edges can be found in some quetzalcoatlidans: cf. *Hatzegopteryx thambema*, *Quetzalcoatlus lawsoni* (Andres 2021; Andres & Langston 2021), and *Albadraco tharmisensis* (Solomon *et al.* 2019). Of note, some tapejarines bear laterally inflated, rounded tomial edges too (Kellner 1989; Pêgas 2024). In other azhdarchoids, tomial edges are generally sharp, as seen in the azhdarchids *Aerotitan sudamericanus* (Novas *et al.* 2012) and *Wellnhopterus brevirostris* (Andres & Langston 2021); alanqids (Smith *et al.* 2023); the chaoyangopterid *Apatorhamphus gyrostega* (McPhee *et al.* 2020); *Keresdrakon vilsoni* (Kellner *et al.* 2019a); thalassodromids (Pêgas *et al.* 2018; Smith *et al.* 2021); caupedactylians (Kellner 2013; Pêgas *et al.* 2016); and sinopterine tapejarids (Ősi *et al.* 2005; Martill *et al.* 2020a; Pêgas *et al.* 2023).

Symmetrical paired rows of occlusal neurovascular foramina, in turn, can be found in the azhdarchids cf. *Hatzegopteryx thambema*, the Laño azhdarchid, and *Albadraco tharmisensis* (Fig. 9); as well as in the tapejarid *Bakonydraco galaczi* (Ősi *et al.* 2005). Nonetheless, *Galgadraco zephyrius* differs from cf. *Hatzegopteryx thambema* and the Laño azhdarchid in having a higher foramination index; therefore, closely resembling *Albadraco tharmisensis*. The jaw tips of *Bakonydraco galaczi* differ from the upper jaw of *Galgadraco zephyrius* in having a D-shaped cross-section, sharper tomial edges, and a strongly concave occlusal margin in lateral view (Ősi *et al.* 2005).

Despite the striking similarity between *Albadraco tharmisensis* and *Galgadraco zephyrius*, the new species differs from the former in having a median palatal groove; regarded here as an autapomorphy of the new taxon. Notably, this slender median palatal groove may suggest the existence of a complementary median dentary ridge; such as the one found in cf. *Hatzegopteryx thambema* (Vremir *et al.* 2018).

In the present work we have recovered anteriorly low and rounded tomial edges as a synapomorphy of Quetzalcoatlida; and aligned (symmetrical) paired rows of occlusal foramina as a synapomorphy of a clade including *Hatzegopteryx thambema*, *Albadraco tharmisensis* and *Galgadraco zephyrius*. The high foramination index (>0.40) is recovered as a synapomorphy joining *Albadraco tharmisensis* and *Galgadraco zephyrius*. In this way, our phylogenetic analysis supports the referral of *Galgadraco zephyrius* to the Azhdarchidae, by virtue of the aforementioned character states shared with other group members.

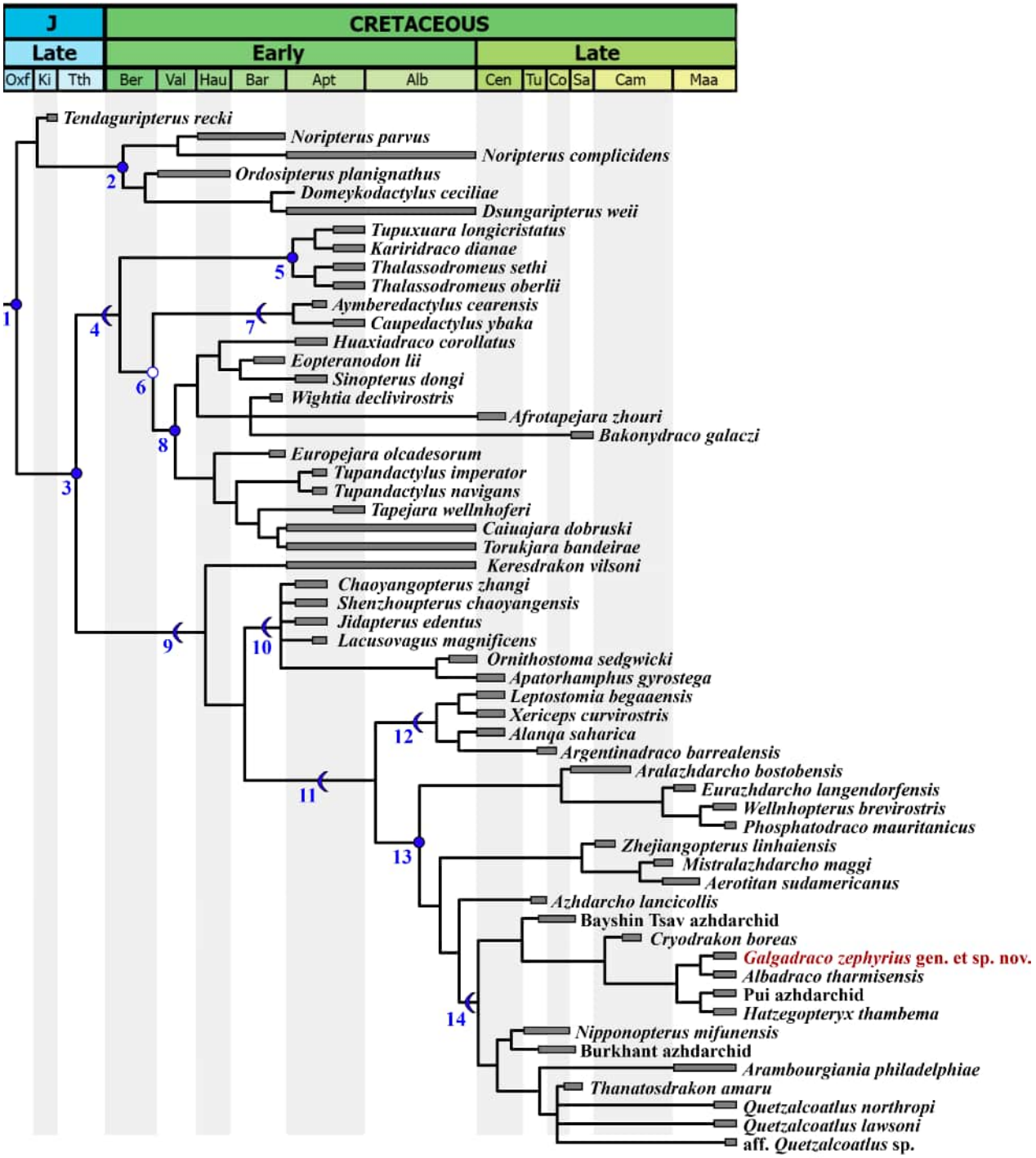


FIG. 7. Time-scaled strict consensus tree showing tapejaroid lower-level relationships. The remaining portion of the tree is identical to that of Pêgas (2024). Nodes: 1, Tapejaroidea; 2, Dsungaripteridae; 3, Azhdarchoidea; 4, Tapejaromorpha; 5, Thalassodromidae; 6, Tapejariformes; 7, Caupedactylia; 8, Tapejaridae; 9, Azhdarchomorpha; 10, Chaoyangopteridae; 11, Azhdarchiformes; 12, Alanqidae; 13, Azhdarchidae; 14, Quetzalcoatlida.

Wingspan estimates

The fragmentary nature of CPPLIP 1853 severely hampers a precise estimate of its wingspan in life. Still, cautious estimates can be made based on comparisons with more complete material from the literature. However, before useful comparisons can be made, its anatomical position needs to be further addressed.

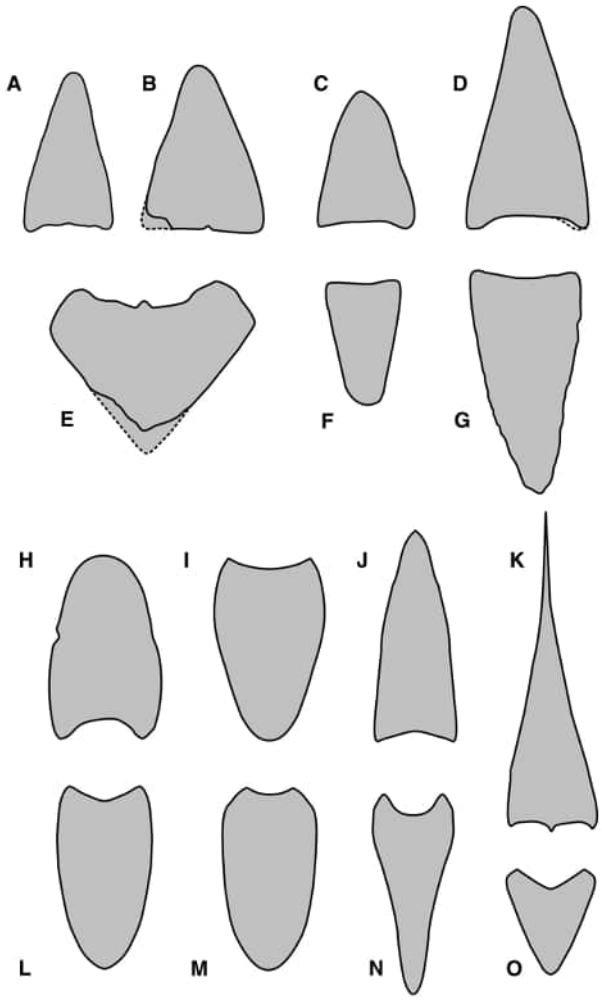


FIG. 8. Comparisons of jaw cross-sections of selected azhdarchoid pterosaurs. A–B, anterior and posterior views of CPPLIP 1853, the holotype of *Galgadraco zephyrius* gen. et sp. nov. C–D, upper jaw of *Albadraco tharmisensis* (based on Solomon *et al.* 2019, fig. 44). E, *Hatzegopteryx thambema* lower jaw (based on Vremir *et al.* 2018, fig. 3). F–G, lower jaw of *Albadraco tharmisensis* (based on Solomon *et al.* 2019, fig. 4). H, upper jaw of *Apatorhamphus gyrostega* (based on McPhee *et al.* 2020, fig. 14). I, lower jaw of *Volgadraco bogolubovi* (based on Averianov *et al.* 2008, fig. 1). J, upper jaw of *Wightia declivirostris* (based on Martill *et al.* 2020b, fig. 3). K, upper jaw of *Tupuxuara longicristatus* (based on Kellner & Campos 1994, fig. 4). L, lower jaw of *Apatorhamphus gyrostega* (based on Smith *et al.* 2021, fig. 14). M, lower jaw of *Aerotitan sudamericanus* (based on Novas *et al.* 2012, fig. 3). N, lower jaw of *Afrotapejara zouhri* (based on Smith *et al.* 2021, fig. 14). O, lower jaw of cf. *Tupuxuara* sp. (based on Smith *et al.* 2021, fig. 14). Drawings not to scale for comparative purposes.

Within azhdarchoids, divergence angles and height/width proportions vary anteroposteriorly along the jaws (e.g. Smith *et al.* 2023). Strikingly, the holotype rostrum tips of *Albadraco tharmisensis* (PSMUBB V651) and *Galgadraco zephyrius* gen. et sp. nov. have almost equal divergence angles and maximum height/width proportions (1.87 in PSMUBB V651, and 1.85 in CPPLIP 1853), indicating that these two fragmentary jaw tips are, most likely, roughly correspondent in anatomical position (assuming that the rostrum proportions are roughly similar). Noting that their absolute sizes (in maximum posterior width) are also almost equal (16.8 mm in CPPLIP 1853 and 16.3 mm in PSMUBB V651), this suggests that these two specimens represent individuals of roughly similar body sizes.

Still, the body size of the holotype of *Albadraco tharmisensis* also needs to be addressed. The fourth cervical PSMUBB V652, regarded as belonging to the same individual as the holotype of *Albadraco tharmisensis*, may provide a solid basis for estimating its wingspan. This vertebra is similar in width (*c.* 70 mm at the prezygapophyses, 35 mm minimum shaft width, and *c.* 40 mm at the condyle) to that of *Q. lawsoni* TMM 41544-8 (71.4 mm at the prezygapophyses, *c.* 33 mm minimum shaft width, and *c.* 39 mm at the condyle; Andres & Langston 2021), indicating that these two specimens are of roughly similar size (i.e. 4–5 m in wingspan; Andres & Langston 2021). Accordingly, we suggest that the holotype of *Albadraco tharmisensis* was *c.* 4–5 m in wingspan. Previous (larger) estimates based on comparisons between the jaws of *Albadraco tharmisensis* and those of *Bakonydraco galaczi* must be viewed with caution, especially considering that the latter has been reinterpreted as a tapejarid rather than an azhdarchid (Andres 2021; Pêgas 2024).

As discussed above, CPPLIP 1853 and PSMUBB V651 seem to represent rostrum fragments of similar anatomical position and are of similar preserved size, suggesting that these two specimens represent individuals of similar body size. This suggests that the wingspan of *Galgadraco zephyrius*, too, could be tentatively estimated at *c.* 4–5 m. Of course, many caveats confound body size estimates when it comes to fragmentary remains; our predictions rely on the premise that our anatomical interpretations of challenging fragments are accurate, and that body proportions are roughly equivalent between the compared taxa. It is reasonable that our tentative estimate comes with an unknown, considerable uncertainty. In any case, it seems safe to say that *Galgadraco zephyrius*, similar to its close relative *Albadraco tharmisensis*, apparently represents a medium-to-large pterosaur, not a small or a giant one.

Stratigraphic & palaeobiogeographic significance

The Azhdarchidae are the most diverse and widespread clade of pterosaurs during the Turonian–Maastrichtian

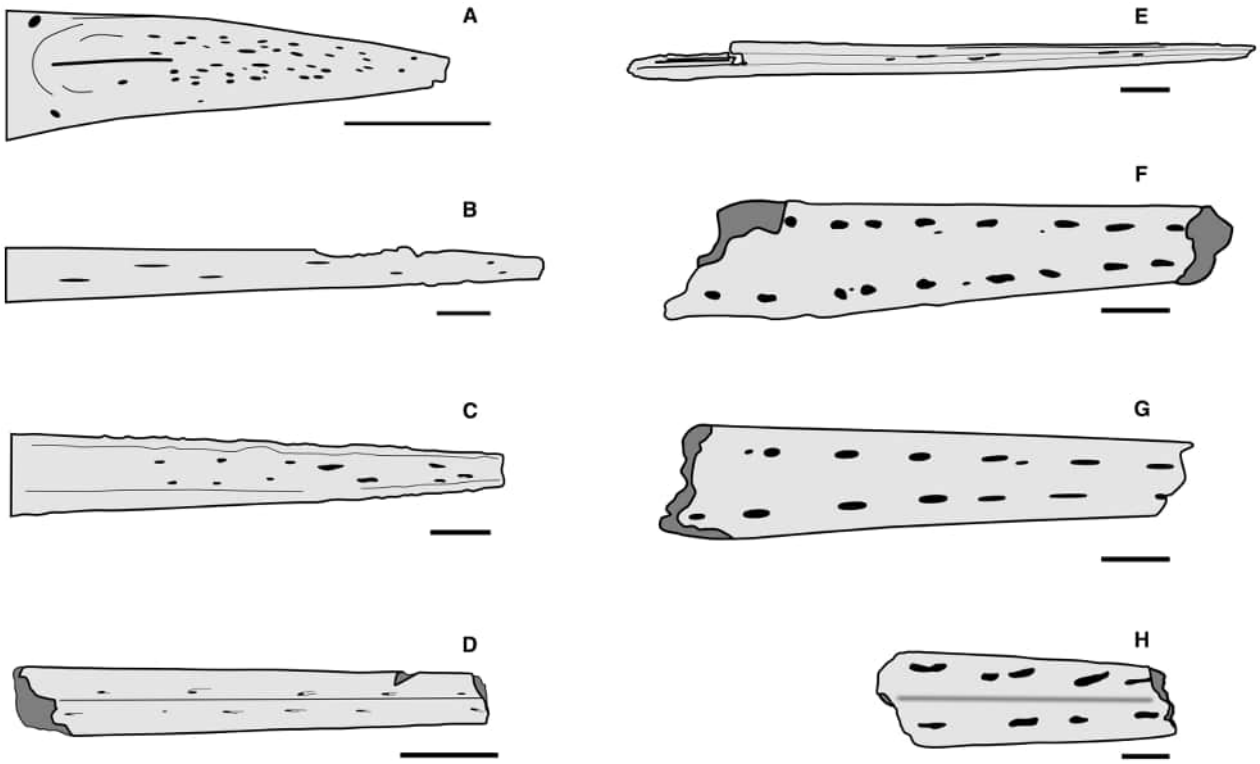


FIG. 9. Selected azhdarchoid jaw tips in occlusal view, showcasing their diversity in neurovascular foramination. A, upper jaw of the tapejarid *Torukjara bandeirae* (based on Pêgas 2024). B, lower jaw of the azhdarchomorph *Keresdrakon vilsoni* (based on Kellner *et al.* 2019a, fig. 4e). C, upper jaw of the alanqid *Leptostomia begaaensis* (based on Smith *et al.* 2023). D, upper jaw of the chaoyangopterid *Apatorhamphus gyrostega* (based on Smith *et al.* 2023). E, lower jaw of the azhdarchid *Aerotitan sudamericanus* (based on Pêgas *et al.* 2021); F, upper jaw of the azhdarchid *Albadraco tharmisensis* (based on Solomon *et al.* 2019). G, lower jaw of the azhdarchid *Albadraco tharmisensis* (based on Solomon *et al.* 2019). H, upper jaw of *Galgadraco zephyrius* gen. et sp. nov. All scale bars represent 10 mm.

interval, being an almost ubiquitous presence in pterosaur assemblages at that time (Longrich *et al.* 2018; Andres 2021) and particularly associated with inland environments (Witton & Naish 2008, 2013; Andres *et al.* 2014; Andres 2021). Considering this, the finding of an azhdarchid in the Bauru Group of Brazil (a fossil-rich Upper Cretaceous, inland deposit) should be expected. Before this work, the absence of pterosaur remains in the Bauru Group was notorious, especially considering the richness and diversity of its tetrapod fauna (Candeiro & Rich 2010; Menegazzo *et al.* 2016; Langer *et al.* 2022). Additionally, the discovery of *Galgadraco zephyrius* gen. et sp. nov. bridges a significant temporal gap in the regional record of pterosaurs, given that the most recent previous findings from the Bauru Supersequence date back to the Lower Cretaceous Caiuá Group.

Bauru Group vertebrates are mostly represented by fragmentary specimens (Brusatte *et al.* 2017; Bandeira *et al.* 2018, Muniz *et al.* 2025), with exceptions including some crocodyliforms (e.g. Carvalho *et al.* 2004, Martinelli *et al.* 2019). The degree of bone representativeness and preservation quality varies greatly across distinct vertebrate groups, suggesting that the Bauru fossil assemblage is greatly biased by taphonomic factors and does not reflect in-life diversity (Bandeira *et al.* 2018). Considering this scenario, it is conceivable that the Bauru Group pterosaur record is severely affected by taphonomic biases. Still, the scarcity of Bauru Group pterosaurs may be affected by collection biases as well; the findings herein reported came from microremains-bearing facies, which are rarely explored in the Bauru Group (Freitas *et al.* 2023). More fieldwork on similar facies may identify further remains of pterosaurs (and other vertebrates) in the future.

Apart from the new species herein reported, the South American azhdarchid record comprises Argentinian forms, including a partial mid-cervical vertebra from the Cenomanian Candeleros Formation (Agnolín *et al.* 2023), *Thanatosdrakon amaru* from the Coniacian–Santonian Plottier Formation, and *Aerotitan sudamericanus* from the Campanian–Maastrichtian Allen Formation (Novas *et al.* 2012; Pêgas *et al.* 2021). Nevertheless, within the limits of the available data, the form most closely related

FIG. 10. Maastrichtian world palaeomap showing pterosaur occurrences (map source: Scotese 2001). Sources: 1, Kellner *et al.* (2019b); 2, Bennett & Long (1991); 3, present study; 4, Fernandes *et al.* (2022); 5, Price (1953); 6, Rosenbach *et al.* (2024); 7, Pereda-Superbiola *et al.* (2003), Longrich *et al.* (2018); 8, Buffetaut (1999), Company *et al.* (1999); 9; Buffetaut (2008); 10, Buffetaut *et al.* (2003), Vremir *et al.* (2013, 2015, 2018), Solomon *et al.* (2019); 11, Tsuihiji *et al.* (2017); 12, Thomas *et al.* (2024); 13, Estes (1964); 14, Andres & Langston (2021); 15, Longrich *et al.* (2018); 16, Gallagher (1984). Pterosaur silhouettes were retrieved from PhyloPic or from Longrich *et al.* (2018). Pterodactyloidea: *Pterodactylus antiquus* by Gareth Monger, mirrored (CC BY 3.0). Pteranodontia: *Alcione elainus* by Dean Schnabel, CC0 1.0. Pteranodontidae: *Tethydraco regalis* by Dean Schnabel, CC0 1.0. Nyctosauridae: *Nyctosaurus gracilis* by Gareth Monger, mirrored (CC BY 3.0). Azhdarchoidea: *Inabtanin alarabia* by Cy Marchant (CC BY 4.0). Azhdarchidae (indeterminate), Azhdarchidae (robust, short-necked morph), and Azhdarchidae (slender, long-necked morph): *Phosphatodraco mauritanicus*, *Hatzegopteryx thambema*, and *Quetzalcoatlus northropi* from Longrich *et al.* (2018) (CC BY 4.0).

FIG. 11. Life reconstruction of a pair of *Galgadraco zephyrius* gen. et sp. nov. in a late Maastrichtian environment, showcasing the palaeobiota of the Serra da Galga Geosite. Artwork by Matheus Gadelha.

to the new species is the European taxon *Albadraco tharmisensis*, described from the Upper Cretaceous of Romania (Solomon *et al.* 2019), as discussed above. Interestingly, this relationship reflects the close affinities between two other azhdarchids: *Aerotitan sudamericanus* and the European *Mistralazhdarcho maggii* (Andres 2021; Pêgas *et al.* 2021). This pattern suggests recurrent pterosaur faunal interchanges between Europe and South America at the Campanian–Maastrichtian boundary.

Aside from the Campanian–Maastrichtian *Aerotitan sudamericanus*, other Maastrichtian pterosaurs from Gondwanaland have been reported in northeastern Brazil (Price 1953), Afroarabia (Longrich *et al.* 2018; Fernandes *et al.* 2022; Rosenbach *et al.* 2024), Antarctica (Kellner *et al.* 2019b) and Australia (Bennett & Long 1991). A Campanian–Maastrichtian record is also known from New Zealand (Molnar & Wiffen 1994). The finding of *Galgadraco zephyrius* extends the distribution of Maastrichtian pterosaurs into the continental palaeoenvironments of Brazil (Fig. 10).

Palaeoecological implications

The co-occurrence of adult and putative juvenile (CPPLIP 1906; possibly hatchling) pterosaur specimens in the Serra da Galga Geosite is noteworthy. Recent studies indicate that ontogenetic niche partitioning may have been common in pterosaurs (Bennet 2018; Bestwick *et al.* 2020; Naish *et al.* 2021). This is indicated by the relative abundance of immature versus mature specimens across several deposits (Bennett 2018), ontogenetic variation in diet (Bestwick *et al.* 2020), and ontogenetic variation in flight performance (Naish *et al.* 2021).

Taken together, these lines of evidence suggest that juveniles and adults did not live regularly in the same areas or ecosystems (Bennett 2018; Naish *et al.* 2021). Therefore, the presence of both hatchling and adult pterosaurs in the Serra da Galga Geosite depositional system could suggest that, prior to transport, these pterosaur specimens had originated from an area relatively close to nesting grounds.

However, at present it is not possible to ascertain that the juvenile specimen in question (CPPLIP 1906) is conspecific with *Galgadraco zephyrius*. While the reduced/rounded tomial edges do suggest affinities to Quetzalcoatlida, the single observed occlusal foramen is asymmetrical, suggesting that: (1) it may be distinct from *Galgadraco zephyrius*; (2) this feature is ontogenetically variable; or (3) it is a supernumerary one.

CONCLUSION

Specimen CPPLIP 1853 represents the long-expected first pterosaur specimen from the well-studied and diverse

Bauru Group (Upper Cretaceous of Brazil), from the uppermost Maastrichtian of the Serra da Galga Formation, Uberaba, State of Minas Gerais (Fig. 11). Despite being fragmentary, the specimen has a unique morphology (including an autapomorphic palatal groove) distinct from any other azhdarchoid, enabling its identification as a new taxon, *Galgadraco zephyrius*. It bears a particular suite of morphological characteristics that enable its identification as a close relative of the coeval European azhdarchid *Albadraco tharmisensis*, most particularly the V-shaped rostrum cross-section, low/rounded tomial edges, symmetrically paired rows of occlusal foramina, and a high foramination index. The sister-taxon relationship between the new form and *Albadraco tharmisensis* is supported by our phylogenetic analysis. Finally, the discovery of diminutive, potentially syntopic hatchling pterosaur specimens is of great significance due to the rarity of this association.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains have been registered in ZooBank: https://zoobank.org/References/177d903c-332b-4f0f-9ef7-8cc193f0f9d6

Editor. Felipe Pinheiro

SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1002/spp2.70039):

Appendix S1. Phylogenetic matrix in Nexus format.
Appendix S2. Phylogenetic matrix in TNT format.

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