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Fernando E. Novas, Martin Kundrat, Federico L. Agnolín, Martín D. Ezcurra, Per Erik Ahlberg, Marcelo P. Isasi, Alberto Arriagada, and Pablo Chafrat

A NEW LARGE PTEROSAUR FROM THE LATE CRETACEOUS OF PATAGONIA

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South America has yielded abundant and diverse Early Cretaceous pterosaur remains, mainly from the highly productive Santana Group (Aptian–Albian) in the Araripe Basin, northeastern Brazil (Kellner, 2001; Unwin and Martill, 2007). Several pterosaur taxa have been reported from these beds, including *Tapejara*, *Tupuxuara*, and *Anhangüera* as the most outstanding examples (Kellner, 2001). Another highly productive Lower Cretaceous South American pterosaur-bearing unit is the Lagarcito Formation (Albian) of central Argentina that has yielded a monospecific assemblage of the pterodactyloid *Pterodaustro guinazui* (Bonaparte, 1970; Chiappe et al., 1998; Codorniú and Gasparini, 2007). The La Amarga Formation (Barremian–early Aptian) in northwestern Patagonia has provided an isolated pterosaur femur (Montanelli, 1987) and the Río Belgrano Formation (Barremian) in southern Patagonia has yielded an ulna and a probable partial wing metacarpal of a probable anhangüerid pteranodontoid (Kellner et al., 2003). In the Lower Cretaceous of Chile, a partial jaw with teeth and a proximal wing phalanx were assigned to an indeterminate ctenochasmatid (Martill et al., 2006). In addition, some fragmentary pterosaur remains have been reported from the Lower Cretaceous of Venezuela and Peru (Codorniú and Gasparini, 2007; Barrett et al., 2008). By contrast, the Late Cretaceous pterosaur bone record of South America is still scarce and restricted to a handful of fragmentary specimens, including remains referred to the nyctosaurid *Nyctosaurus lamegoi* from the Maastrichtian of Brazil (Price, 1953; Lima and Koutsooukos, 2006) and azhdarchoid long bones, probably from a taxon closely related to or a member of Azhdarchidae, from the Turonian–Coniacian Portezuelo Formation (Calvo and Lockley, 2001; Kellner et al., 2004, 2006; Apesteguía et al., 2007; Codorniú and Gasparini, 2007).

Here, we expand the meager record of Late Cretaceous South American pterosaurs with the description of a partial rostrum belonging to a large azhdarchid pterodactyloid. The specimen was collected close to the Bajo de Arriagada locality, corresponding to the uppermost Cretaceous Allen Formation of Argentina, around 80 km northwest of the well-sampled Bajo de Santa Rosa locality (Martinelli and Foriasepi, 2004) (Fig. 1). The Azhdarchidae were the most abundant pterosaurs during latest Cretaceous times (Company et al., 1999; Butler et al., 2009). This clade comprises several species of long-necked pterosaurs ranging from 2.5 to 10 m in wing span, thus including the largest known flying vertebrates, such as the gigantic *Quetzalcoatlus* and *Hatzegopteryx* (Kellner and Langston, 1996; Buffetaut et al., 2002; Witton and Naish, 2008; Witton and Habib, 2010). Azhdarchid remains have been documented from almost all continental landmasses, includ-

ing Europe, North America, Africa, Asia, and probably Oceania (Bennett and Long, 1991; Company et al., 1999; Averianov et al., 2005; Barrett et al., 2008; Kear et al., 2010; Ósi et al., 2011). In South America, probable azhdarchid remains consist of a fragmentary postcranial skeleton from the Aptian of Brazil (Martill and Frey, 1998, 1999) and partial long bones from the Turonian–Coniacian of Argentina (Kellner et al., 2006; Codorniú and Gasparini, 2007). However, recent reassessments of this material suggested that the Brazilian specimen is more closely related to tapejarids than to azhdarchids and that the Argentinean records are dubious (Kellner, 2004; Kellner et al., 2006; Unwin and Martill, 2007). As a result, the specimen reported here represents the first unambiguous evidence of an azhdarchid pterosaur from South America. This specimen represents a new genus and species, *Aerotitan sudamericanus*, which is diagnosed based on a unique combination of characters, including one autapomorphy, and represents one of the largest known South American pterosaurs. The fossil here described resulted from a joint Argentine–Swedish paleontological expedition to Patagonia.

Institutional Abbreviations—BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; MPCN-PV, Vertebrate paleontology Collection, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina.

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

AZHDARCHOIDEA Nessov, 1984, sensu Unwin, 1992

AZHDARCHIDAE Nessov, 1984

AEROTITAN SUDAMERICANUS, gen. et sp. nov.

(Figs. 2–3A, B, and F)

Holotype—MPCN-PV 0054, partial rostrum.

Etymology—The generic name is a combination of ‘aeros,’ meaning air in Greek, and ‘titan,’ after the giants of the Greek mythology, because the new genus was a large flying reptile. The specific epithet is for the South American continent.

Diagnosis—*Aerotitan sudamericanus* is a large pterosaur that differs from other azhdarchoids in the presence of the following combination of characters (autapomorphy indicated with an asterisk): rostrum elongated and transversely compressed (dorsoventrally deeper in *Alanqa* and transversely wider in both *Alanqa* and *Bakonydraco*) with several (i.e., at least six), large slit-like lateral neurovascular foramina aligned parallel to the alveolar margin* (the foramina are aligned parallel to the ventral margin of the rostrum in *Alanqa* and fewer foramina are present in *Bakonydraco*), and each pair of palatal foramina not aligned to

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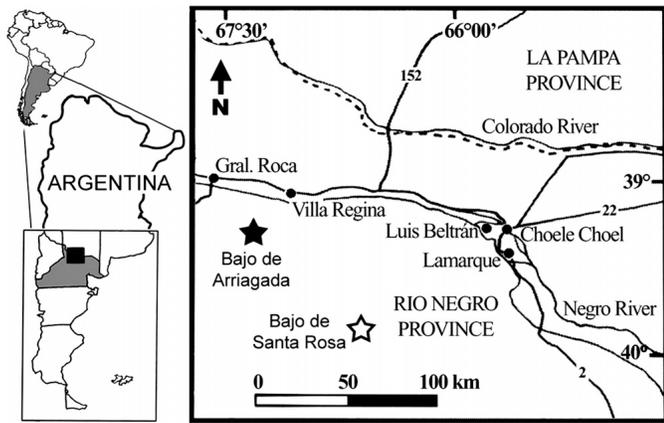


FIGURE 1. Map of north-central Río Negro Province showing the Bajo de Santa Rosa (white star) and the Bajo de Arriagada localities (black star), the latter being the type locality of *Aerotitan sudamericanus*, gen. et sp. nov. Modified from Martinelli and Foriasepi (2004).

each other (the palatal foramina of at least one pair are perfectly aligned to each other in *Bakonydraco*).

Type Locality and Horizon—Allen Formation (Campanian–Maastrichtian) (Martinelli and Foriasepi, 2004), Cerro de Guerra (39°27'80"S, 67°19'61"W), close to the Bajo de Arriagada fossil site (Salgado et al., 2007), around 90 km southeast of General Roca and 80 km northwest of the well-sampled Bajo de Santa Rosa locality, Río Negro Province, Argentina (Fig. 1). Other fossils collected from the same horizon and locality include indeterminate fishes (isolated vertebrae and scales), fragmentary chelid turtle shells, and elasmosaurid plesiosaur remains (isolated vertebrae and the articular portion of a lower jaw), indicating a near-shore marine depositional environment.

Description—The holotype of *Aerotitan sudamericanus* consists of a partial snout with a maximum preserved length of 264 mm (Fig. 2). The specimen probably represents a rostrum, rather than a dentary symphysis, for the following reasons: it is dorsoventrally deeper than the strongly compressed dentaries of *Alanqa saharica* (BSPG 1996 I 36) and *Quetzalcoatlus* sp. (Kellner and Langston, 1996); the palatal margin is convex, resembling the condition of the rostra of *Azhdarcho* (Averianov, 2010) and *Alanqa* (BSPG 1993 IX 338) (Fig. 3A, C), but contrasting with the mostly concave or straight alveolar margin of the dentary symphyses of the those taxa (Averianov, 2010; BSPG 1996 I 36); the palatal surface is concave along all of its preserved length, as occurs in the rostra of *Alanqa saharica* (BSPG 1993 IX 338) (Fig. 3F, G) and *Bakonydraco* (Ósi et al., 2011), but contrasting with azhdarchid dentary symphyses that possess a planar or slightly convex palatal surface anteriorly (e.g., *Alanqa saharica*, BSPG 1996 I 36; *Quetzalcoatlus* sp., Kellner and Langston, 1996; *Azhdarcho*, Averianov, 2010); and finally *Aerotitan* possesses a 'D'-shaped cross-section, as in the rostrum of *Alanqa saharica* (BSPG 1993 IX 338) (Fig. 3F, G), rather than the typical 'Y'-shaped cross-section of the posterior region of azhdarchid dentaries (BSPG 1996 I 36; Ibrahim et al., 2010). However, the identification of MPCN-PV 0054 as a partial rostrum should be considered with caution, as is the case for other isolated remains of azhdarchid snouts, until new discoveries and detailed descriptions of more complete and articulated azhdarchid skulls become available.

The rostrum of *Aerotitan* is completely edentulous and its external surface is longitudinally striated and highly vascularized by numerous small pits (Fig. 2A, E). The internal microstructure is composed of cancellous bone, as typically occurs in pterosaurs.

As in most pterosaurs, the cortical bone is very thin, being approximately 1.0 mm in thickness. The rostrum of *Aerotitan* is strongly elongated with a length–height ratio >7.7 (Fig. 2A, B, E, F). This value approaches that of long-beaked azhdarchids, such as *Alanqa* (Fig. 3C), *Bakonydraco*, and *Quetzalcoatlus* sp. (Fig. 3E) (Kellner and Langston, 1996; Ibrahim et al., 2010; Ósi et al., 2011). In lateral view, both dorsal and ventral margins converge anteriorly at a very low angle (approximately 10°), a condition that resembles that of several azhdarchids (e.g., *Alanqa*, BSPG 1993 IX 338; *Quetzalcoatlus* sp., Kellner and Langston, 1996; *Bakonydraco*, Ósi et al., 2011). The palatal margin of the rostrum of *Aerotitan* is concave and the dorsal one is almost straight in lateral view as far as is preserved. The lateral surface possesses a single row of at least six large slit-like neurovascular foramina that are aligned approximately parallel to the alveolar margin and situated slightly below the midheight of the bone (Fig. 2B, F).

In palatal view, the rostrum of *Aerotitan* is extremely narrow and its lateral margins converge anteriorly at a very low angle. The strong transverse compression of the rostrum of *Aerotitan* does not seem to be a taphonomic artifact because of the absence of longitudinal breakages along the ventral surface of the rostrum. The palatal surface is deeply concave and surrounded by thick dental margins formed by elevated crests (Figs. 2D, H, 3F), resembling the condition of *Alanqa* (Fig. 3D, G) (BSPG 1993 IX 338). The palatal surface possesses a low and well-defined median longitudinal eminence (Fig. 2H). At least three pairs of slit-like foramina are present within the palatal surface of *Aerotitan* (Fig. 2D, H), a condition described as diagnostic for Azhdarchidae (Ibrahim et al., 2010). The foramina in each pair are not aligned to each other, but are set obliquely, a condition that also occurs in *Alanqa* (Fig. 3D) (BSPG 1993 IX 338). The slit-like lateral and palatal foramina, as well as the numerous small pits on the external surface of the bone, were likely related to the blood vessels and nerves that supplied the rhamphothecae covering the jaws (Frey et al., 2003). In cross-section, the mandibular symphysis of *Aerotitan* has a transversely compressed 'V'- to 'D'-shaped profile, resembling the condition of other azhdarchid rostra (Ibrahim et al., 2010).

DISCUSSION

The most salient feature of the rostrum of *Aerotitan sudamericanus* is the complete absence of dental alveoli, a condition that allows the new genus to be distinguished from most pterosaur taxa with the exception of *Pteranodon*, nyctosaurids, the basal dsungaripteroid *Nemicolopterus*, and *Azhdarchoidea* (Andres and Ji, 2008; Wang et al., 2008; Ibrahim et al., 2010). *Aerotitan* differs from *Pteranodon* in lacking a strongly dorsally curved snout (Bennett, 1993) and from nyctosaurids in the presence of a proportionally deeper rostrum (Bennett, 2003). The small-sized *Nemicolopterus* can be distinguished from *Aerotitan* due to the presence of a longitudinal lateral ridge close to the dorsal margin of the rostrum (Wang et al., 2008). Among azhdarchoids, the partial rostrum of *Aerotitan* exhibits a morphology almost identical to that observed in some azhdarchids (e.g., *Alanqa*, BSPG 1993 IX 338; *Bakonydraco*, Ósi et al., 2011) (Fig. 3) and possesses a feature considered diagnostic for the clade: the presence of prominent paired foramina on the palatal surface of the rostrum (Ibrahim et al., 2010). The rostral and dentary symphyses have proved to be some of the most diagnostic elements of the azhdarchid skeleton, allowing previous authors to refer isolated partial snouts to this clade (e.g., Averianov et al., 2008; Averianov 2010; Ibrahim et al., 2010). As a result, we assign *Aerotitan sudamericanus* to Azhdarchidae.

The overall morphology of azhdarchid rostra exhibits limited interspecific variation within the group. However, *Aerotitan*

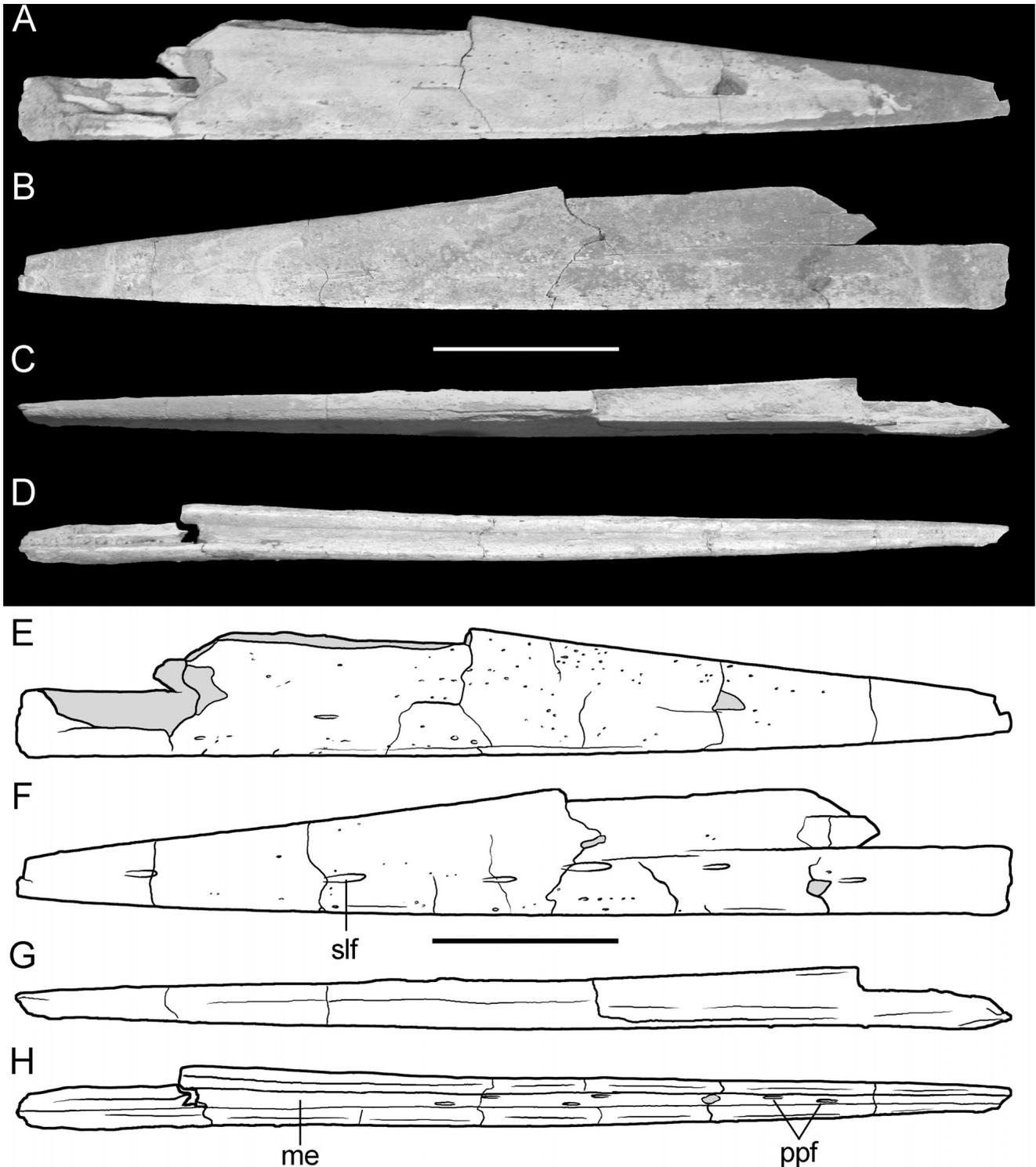


FIGURE 2. Partial rostrum of the holotype of *Aerotitan sudamericanus*, gen. et sp. nov., in right lateral (A, E), left lateral (B, F), ventral (C, G), and palatal (D, H) views. **Abbreviations:** me, median eminence; ppf, paired palatal foramina; slf, slit-like lateral foramen. Scale bar equals 5 cm.

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215 differs from *Azhdarcho* in the presence of a straight dorsal margin and a more transversely compressed rostrum, contrasting with the concave dorsal margin and wider snout of the Asian genus (Averianov, 2010). *Zhejiangopterus* differs from *Aerotitan* in the presence of a proportionally shorter rostrum (Cai and Wei, 1994),

and *Aerotitan* differs from *Quetzalcoatlus* in possessing slit-like lateral foramina on the rostrum (Kellner and Langston, 1996). *Bakonydraco* can be differentiated from *Aerotitan* based on the presence of at least some palatal foramina aligned to each other in the anterior end of the rostrum, a lower number of slit-like

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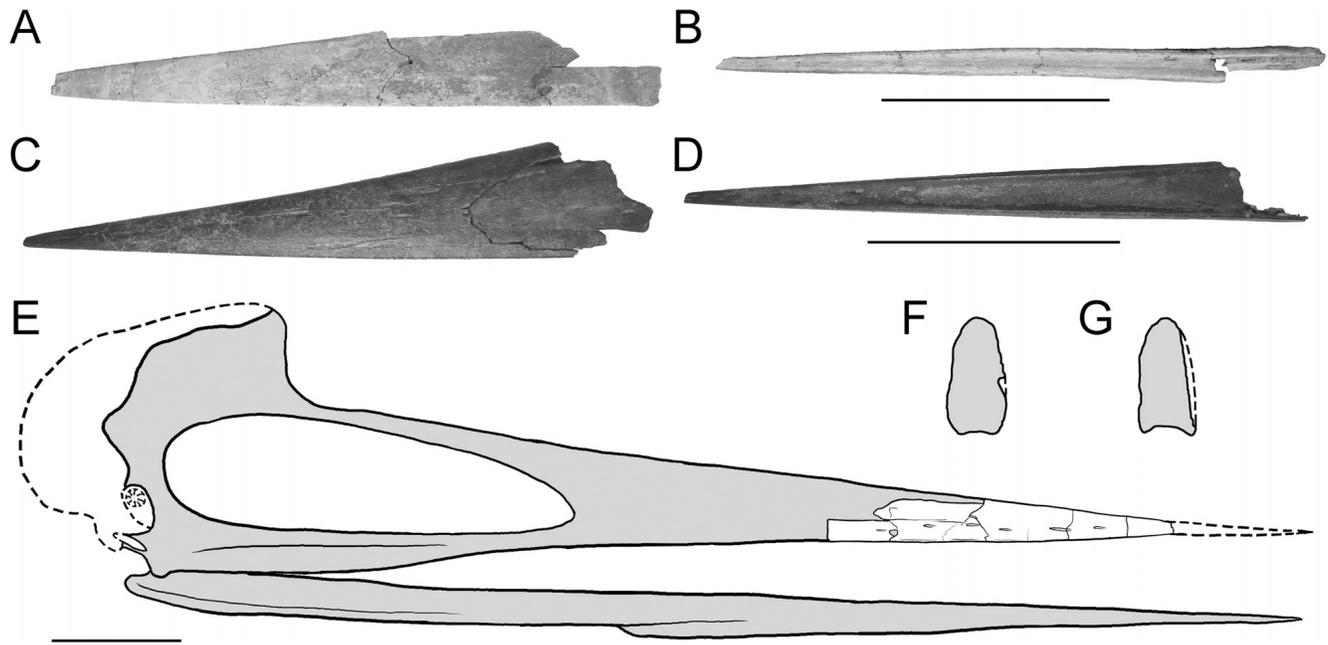


FIGURE 3. Comparisons of the partial rostra of the azhdarchid pterosaurs *Aerotitan sudamericanus* (A, B, F) and *Alanqa saharica* (C, D, G), and the overall size of the skull of *Quetzalcoatlus* sp. and *Aerotitan sudamericanus* (E). In E, the gray silhouette depicts the skull of *Quetzalcoatlus* sp. and the white filled drawing depicts the partial rostrum of *Aerotitan sudamericanus* to the same scale. E redrawn from Kellner and Langston (1996). Scale bars equal 10 cm and F and G not to scale.

lateral foramina, and a transversely wider snout (Ósi et al., 2011). In particular, *Aerotitan* closely resembles the rostra of *Alanqa* (BSP 1993 IX 338) and *Volgadraco*. The latter was previously identified as a dentary symphysis (Averianov et al., 2008), but appears to represent a partial rostrum based on the same characters listed in support of the anatomical identification of the holotype of *Aerotitan*. The features shared among these taxa are a gently convex palatal margin in lateral view, each pair of palatal foramina not aligned to each other, and a deeply concave palatal surface with thick lateral edges (BSP 1993 IX 338; Averianov et al., 2008) (Fig. 3A–G). However, the rostrum of *Aerotitan* clearly differs from the snout of *Volgadraco*, because the former is considerably more elongated and possesses a larger number of slit-like lateral foramina aligned parallel to the palatal margin, whereas the latter has only a few foramina disposed in a random pattern (Averianov et al., 2008). Although the rostrum of *Alanqa* appears to be most similar to that of *Aerotitan*, the rostrum of the former increases more rapidly in depth posteriorly, is transversely wider, and the row of lateral foramina is more dorsally positioned and aligned more parallel to the dorsal margin than in *Aerotitan* (Fig. 3A–G) (BSPG 1993 IX 338). Accordingly, *Aerotitan sudamericanus* can be differentiated from all other known azhdarchids with preserved rostra and, as a result, is identified here as a new genus and species.

It is worth noting that giant azhdarchids are represented by the latest Cretaceous species *Quetzalcoatlus northropi*, *Hatzegopteryx liaoxiensis*, and *Arambourgia philadelphiae*, with a wing span ranging from 8 to 10 m (Averianov et al., 2005; Witton and Naish, 2008; Witton and Habib, 2010). The preserved rostrum of *Aerotitan* corresponds to an animal that approached or exceeded the size of *Quetzalcoatlus* sp. (Fig. 3E), which had a wing span of around 5 m (Kellner and Langston, 1996), suggesting that the new Patagonian genus represents the first large pterosaur from the Upper Cretaceous of South America. In addition, *Aerotitan* is the second named pterosaur from the Upper

Cretaceous of South America. The other named Late Cretaceous South American pterosaur is the Maastrichtian *Nyctosaurus lamegoi*, which is represented by an incomplete humerus assigned to *Nyctosaurus* due to the presence of a hatchet-shaped deltopectoral crest (Price, 1953; Wellnhofer, 1991; Bennett, 2003). Previous reports of South American azhdarchids consist of a late Early Cretaceous Brazilian specimen (Martill and Frey, 1998, 1999), which was subsequently identified as non-azhdarchid by Kellner (2004), and a partial forelimb bone from the early Late Cretaceous of South America (Codorniu and Gasparini, 2007). Kellner et al. (2006) provided a description of the latter specimen and the detailed comparisons provided by these authors suggested that it should be considered an indeterminate azhdarchoid. Codorniu and Gasparini (2007) did not provide evidence for the suggested azhdarchid affinities of this specimen and as a result we follow the taxonomic assignment proposed by Kellner et al. (2006). Accordingly, *Aerotitan* represents the first unambiguous record of Azhdarchidae in South America. The record of an azhdarchid in South America is not unexpected because Azhdarchidae was a geographically widespread clade during the Late Cretaceous (Averianov et al., 2005; Barrett et al., 2008). Nevertheless, the Patagonian *Aerotitan* also constitutes the southernmost record of an unambiguous azhdarchid to date, given that the referral of a proximal ulna from Australia to this group is considered tentative (Bennett and Long, 1991; Kear et al., 2010). Thus, *Aerotitan* indicates that large pterosaurs also inhabited southern South America during the latest Cretaceous and that azhdarchids were distributed from northern to southern high paleolatitudes before the Cretaceous-Tertiary mass extinction that resulted in the complete extinction of the group 65 million years ago.

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