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New ctenochasmatid pterosaur record for Gondwana: discovery in the Lower Cretaceous continental deposits of the Atacama Desert, northern Chile

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ABSTRACT

New pterosaur remains from Cerro La Isla, Quebrada Monardes Formation (Lower Cretaceous), Northern Chile, are described. The material comprises mandibular remains preserving dental bases and two vertebrae of the mid cervical series. The morphology and arrangement of the dental bases show a similar pattern to that observed in European and Chinese ctenochasmatids, but can be distinguished from those other South American ctenochasmatids reported from Argentina and Uruguay. The new vertebrae share certain characteristics with the mid cervical vertebrae of ctenochasmatids, such as very elongated centra with low neural arches, low and elongated neural spines, the presence of postexapophyses and a pair of oval pneumatic foramina on the lateral surfaces of the centra. Although most of these features are shared with the mid cervical vertebrae of azhdarchid pterosaurs, the lower integration of the neural arch, which does not acquire a tubular morphology in the mid-point of the vertebral centrum, together with the presence of oval pneumatic foramina, are characteristics that allow the referral of both vertebrae to the Ctenochasmatidae. The vertebral, mandibular and rostral remains from Cerro La Isla suggest the presence of a previously unknown ctenochasmatid pterosaur, distinct from *Pterodaustro*, the only other South American taxon.

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1. Introduction

Pterosauria is a clade of flying archosaurs, that appeared at the end of the Triassic and diversified during the Mesozoic, until its extinction alongside a wide range of other vertebrates and invertebrates at the end of the Cretaceous (Wellnhofer, 1991a; Unwin, 2006; Witton, 2013). The skeleton of these animals was highly pneumatic, with extremely thin bone walls (Unwin, 2003; Witton, 2013). Perhaps their most remarkable feature is a very complex wing membrane supported by the forelimb, more specifically by a hyper-elongate fourth wing finger (Wellnhofer, 1991a; Unwin, 2006; Elgin et al., 2011; Witton, 2013).

Records of pterosaurs in Chile are scarce and fragmentary. The first and so far only pterosaur species named in Chile is *Domeykodactylus ceciliae* (Martill et al., 2000), whose remains were previously referred to the ctenochasmatid *Pterodaustro guinazui* (Casamiquela and Chong, 1980). Most discoveries come from the regions of Antofagasta and Atacama (Soto-Acuña et al., 2015). Bell and Suárez (1989) and subsequently Bell and Padian (1995) reported an accumulation of disarticulated pterosaur bones in the Atacama Desert, northern Chile, preserved in a single sedimentary

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layer of the continental strata of the Quebrada Monardes Formation, in Cerro La Isla. This geological unit was originally assigned to the Upper Jurassic–Lower Cretaceous, and subsequently restricted to the Lower Cretaceous (Mercado, 1982; Martínez et al., 2015).

From among the pterosaur bones from Cerro La Isla, mandibular remains and a fragment of a first wing phalanx were described by Martill et al. (2006). These authors, based principally on the arrangement and morphology of the teeth, concluded that these specimens belong to the pterosaur family Ctenochasmatidae. Based on the apparent expansion of the anterior portion of two of the mandibular fragments, Martill et al. (2006) tentatively proposed their inclusion in the Gnathosaurinae. During the revision of the materials collected in 1988 and housed in the paleontological collection of the Natural History Museum of Santiago, new mandibular remains that had not previously been described were encountered. These bones have been identified as belonging pterosaurian and are presented here for the first time.

Rubilar et al. (2002) briefly described two cervical vertebrae found in Cerro La Isla, mentioning general aspects of their morphology and noting similarities shared by Archaeopterodactyloidea (a clade that includes the Ctenochasmatidae family) and Azhdarchidae, referring them to Pterodactyloidea without providing a more detailed identification. These remains were later reassigned to Ctenochasmatidae by Soto-Acuña et al. (2015), who also gave a general description of these vertebrae, with most of the traits mentioned also present in Archaeopterodactyloidea as well as in Azhdarchoidea, thus, the placement of these vertebrae in Ctenochamatidae was not well supported by these authors.

The fossil record of ctenochasmatid pterosaurs is distributed mainly in the Northern hemisphere, especially in China, where approximately ten genera have been described to date. In Europe, three genera have been identified (in the United Kingdom, France and Germany). In North America, only one species, *Kepodactylus insperatus* (Harris and Carpenter, 1996) is known, although its phylogenetic relationships are uncertain.

The record of ctenochasmatids in South America is represented by *Pterodautro guinazui* from Argentina (Bonaparte, 1970) and indetermined and very fragmentary specimens from Uruguay (Perea et al., 2018) and Chile (Martill et al., 2006). The only other record from Gondwana is from Tanzania, Africa, and consists of an isolated cervical vertebra, which is considered by some authors as belonging to a ctenochasmatid pterosaur, while other authors consider it belonging to an azdarchid (Sayão and Kellner, 2001; Andres and Ji, 2008; Costa et al., 2015). The aim of this work is to present, a detailed description of the vertebrae and mandibular remains from Chile. Additionally, we discuss the presence of ctenochasmatids in the Quebrada Monardes Formation and the global fossil record of the Ctenochasmatidae.

2. Locality and geological setting

The pterosaur remains studied in this work come from a single level in the Quebrada Monardes Formation (Mercado, 1982; Sepúlveda and Naranjo, 1982; Naranjo and Puig, 1984), exposed on the southwestern slopes of Cerro La Isla, approximately 80 km east of Copiapó in the Andes of the Atacama Region, Northern Chile (Fig. 1). The Quebrada Monardes Formation is a succession of continental redbeds (mainly sandstones) that conformably overlie the shallow Upper Jurassic limestones of the Lautaro Formation (Mercado, 1982). In places, evaporites occur at the contact between these two formations, reflecting a marine regression and sabkha conditions (Bell, 1991). In a different location, the same regressive succession comprises a 3 m-thick coral biostrome and oolitic grainstones (Bell and Suárez, 1985). Continental and marine coastal sabkhas in northern Chile can be traced back to the Late Triassic, implying warm and semi-arid to arid conditions in the region for more than 70–80 Ma.

The Quebrada Monardes Formation is essentially clastic, mainly derived from a calc-alkaline source during the Early Cretaceous and comprising approximately 90% sandstone and 10% pebbly sandstone, conglomerate and mudstone and very small proportions of non-marine evaporites and limestones (Bell, 1991; Bell and Suárez, 1993). The sandstones are well cemented and mainly consist of compositionally very immature lithic and feldspathic arenites, derived from volcanic rocks. The absence of sedimentary, plutonic or metamorphic clasts indicates that volcanic activity kept pace with erosion (Bell and Suárez, 1993).

The formation was deposited in warm, arid to semi-arid conditions, in an elongated N–S intra-arc basin on an active continental margin west of Gondwana during the early Cretaceous. Several depositional environments have been identified in these redbeds: aeolian dune fields, aeolian sand sheets and small dunes with vegetated paleosoils, braided streams on alluvial plains and alluvial fans, shallow braided alluvial channels and overbank flood plains, coastal and playa lake saline mud and sandflats, shallow, ephemeral evaporitic coastal plains, a regionally extensive and relatively deep perennial saline lake (Codocedo Limestone Member) and volcanic deposits. The regionally extensive saline lake, covering at least 1500 km^2, developed over alluvial plain and fan deposits and probably resulted from a catastrophic event such as the damming of the basin by a volcanic eruption or a landslide (Bell and Suárez, 1993). Some variations in the climate during deposition of the Quebrada Monardes Formation have been proposed by Bell and Suárez (1993), who suggest that the transition from aeolian to alluvial dominated sediments may indicate a temporal change to a more humid climate. The local occurrence of fossil trees in these fluvial deposits indicates transport from forested regions in the headwaters of the river system.

Stratigraphic logs recorded by Bell and Suárez (1985) at Cerro La Isla show that approximately the lower two-thirds of this red clastic sequence is composed of sandstones and siltstones with cross and horizontal lamination, while the upper third is formed by alternating sequences of conglomerates and sandstones with intercalation of evaporites of a thickness of two to three meters. The red sandstones were deposited in a system of braided rivers, while the conglomerates of the upper section represent deposits of alluvial fans and the evaporites are deposits of a “playa lake”, recording a dry climate during its deposition. The aeolian activity is evidenced by the presence of ventifacts between the clasts that are part of the conglomerates, together with possible “deflation lags” (Bell, 1991).

The Quebrada Monardes Formation has been assigned to the Lower Cretacous based on the inferred Kimmeridgian–Tithonian and Tithonian–Valangian ages of the underlying Lautaro and Pedernales formations respectively (Chong, 1976; Muzzio, 1980; Mercado, 1982; Reyes and Pérez, 1985; Cornejo et al., 1988), and the Maastrichtian–Danian age of the overlying Quebrada Seca Formation (Iriarte et al., 1999; Martínez et al., 2015). However, the latter does not provide a precise youngest age limit for the formation. Recently, a detrital zircon U–Pb age of 144, 8 ± 1, 8 Ma was obtained from rocks of the Quebrada Monardes Formation exposed in the Pulido River by Martínez et al. (2015), assigning a late Tithonian–early Berriasian age for the maximum deposition.

The pterosaur fossils were found together with crocodile remains in a 2-m-thick bed of matrix-supported conglomerate that was recognised for about 2 km along strike, without reaching its end, and always with abundant fragmentary fossil bones (Bell and Padian, 1995). This horizon is located in the upper section of the column, approximately 330 m from the base. The fossil-bearing

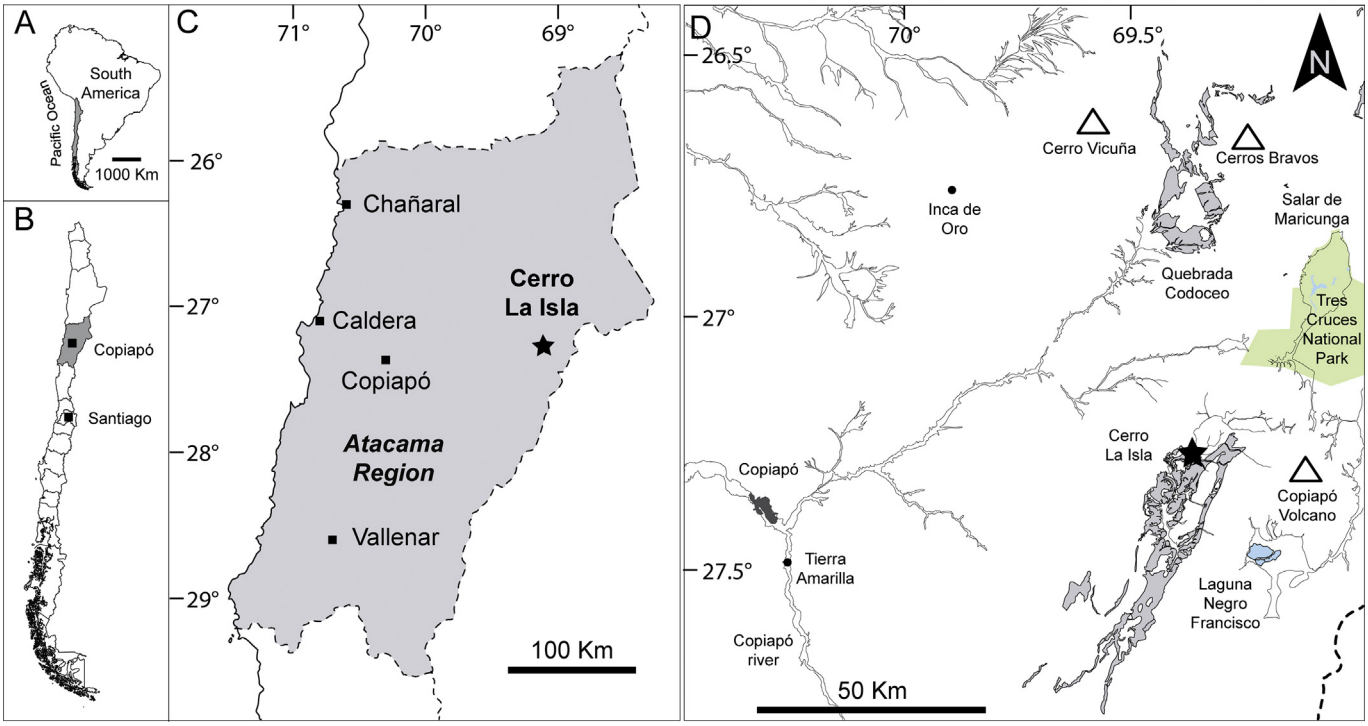


Fig. 1. A: Location of Chile in South America. B: Location of Atacama Region and Copiapó. C : Location of Cerro La Isla, 80 km east of Copiapó, Atacama Region, Northern Chile. D: Distribution of the outcrops of the Quebrada Monardes Formation and the location of Cerro La Isla.

conglomerate has been interpreted as a debris flow deposit resulting from a flash flood generated by heavy rains in far away mountains.

In addition to the pterosaurs, a diverse record of other fossil vertebrates has been found including dinosaur and fish bones, dinosaur footprints and other traces fossils. The documented remains come from several localities: Cerro La Isla, Quebrada El Patón, Quebrada Codocedo and Quebrada Tambería de los Pantanos (Bell and Suárez, 1989; Bell and Padian, 1995; Rubilar et al., 2002; Martill et al., 2006; Alarcón-Muñoz et al., 2016).

The pterosaurs lived in a warm and semi-arid climate, several tens of kilometers from an active volcanic chain. This volcanic chain, produced by the subduction of the oceanic plate beneath the continental margin of Gondwana, provided the source for almost all the clastic sediments (Bell, 1991).

3. Materials and methods

The pterosaur fossils from Cerro La Isla represent isolated and fragmentary remains from a single bed of sandstones and conglomerates and were collected by the researchers Larry Marshall, Michael Bell, Patricia Salinas and Manuel Suárez in 1988. It is uncertain whether the fragments belong to the same individual, due to the absence of information on the exact arrangement of the specimens (degree of articulation or connection) in the field. The fossils are deposited in the Department of Paleontology of the National Museum of Natural History in Santiago de Chile (MNHN). Some of the materials were prepared mechanically to remove part of the matrix covering the bone. The two cervical vertebrae described here were originally catalogued under the same number (SGO.PV. 350). However, it is unknown if the vertebrae were found in association. To facilitate the description, it was decided to maintain this number for only one of the fossils, while the others were assigned the new number SGO.PV. 351.

Institutional abbreviations—**SGO.PV.**, Vertebrate Collection of the Department of Paleontology of the National Museum of Natural History, Santiago, Chile. **UPMC,** Collection paleontológique de l' Université Paris 6, France. **SMNK-PAL**, Staatliches Museum für Naturkunde, Karlsruhe, Germany. **FC-DPV**, Vertebrate Fossil Collection, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

4. Systematic paleontology

Pterosauria Kaup, 1834.
Pterodactyloidea Plieninger, 1901.
Archaeopterodactyloidea Kellner, 1996.
Ctenochasmatidae Nopcsa, 1928.

Ctenochasmatidae gen. et. sp. indet.

Material: SGO.PV.364, a partial rostrum preserving palatal and rostral bones and dental crown bases; SGO.PV.362, SGO.PV.377 and SGO.PV.378, mandibular fragments with bases of dental crowns; SGO.PV.350 and SGO.PV.351, two midcervical vertebrae.
Locality and horizon: Cerro La Isla, 80 kms east of the city of Copiapó, Atacama Region, northern Chile. "Pterosaur horizon", approximately 330 m from the base of the Quebrada Monardes Formation, Lower Cretaceous.

4.1. Description of mandibular and rostral remains

Specimen SGO.PV.364 (Fig. 2) corresponds to a rostral fragment. In palatal view, several dental bases and alveoli without teeth are visible, aligned in a single row at the labial margins of the element. The orientation of the dental crown bases on the left side suggests that the fragment likely corresponds to the anterior portion of the rostrum, since the teeth in this region tend to be anteriorly

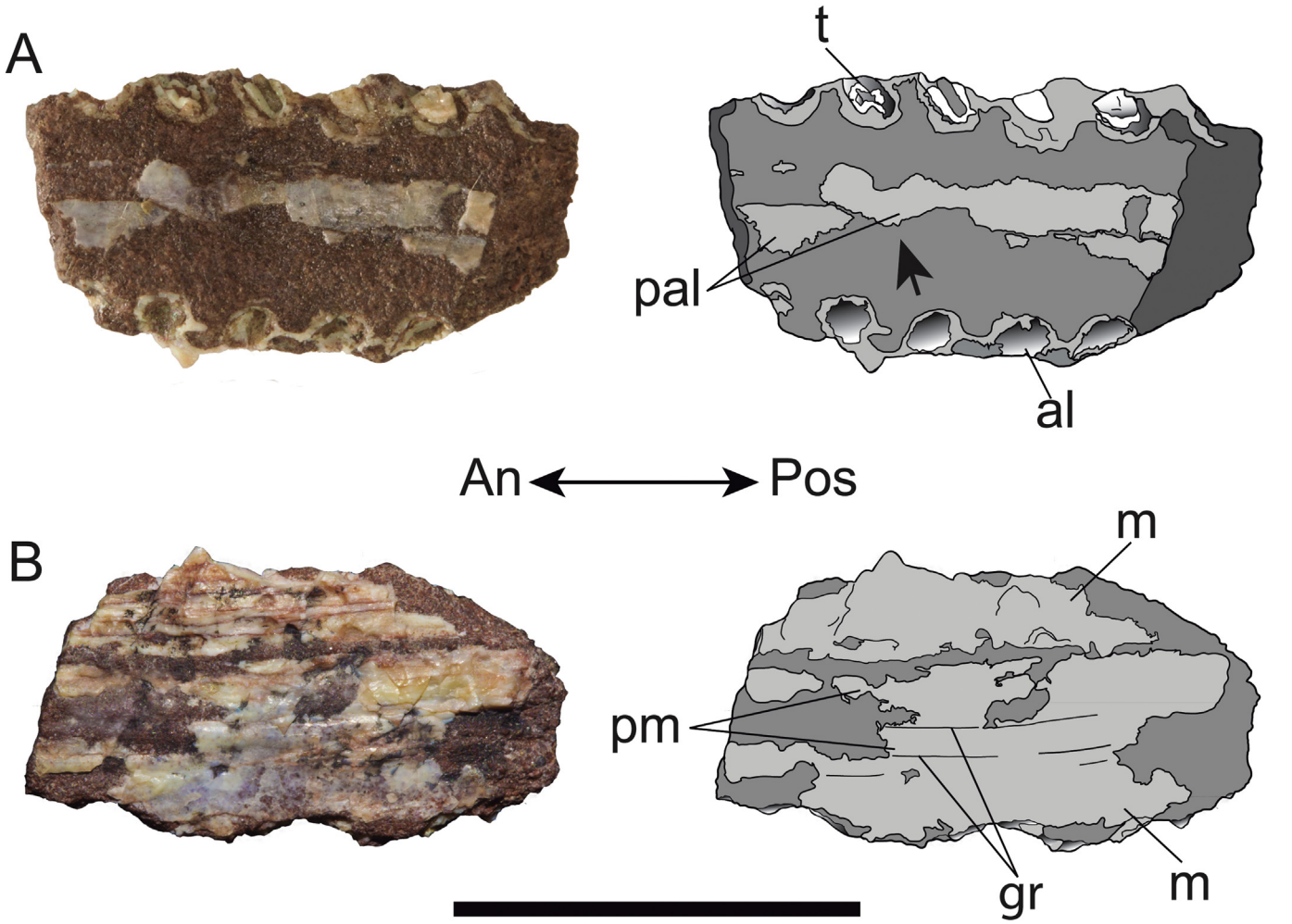


Fig. 2. SGO.PV. 364. Ctenochasmatidae indet. Rostral portion in palatal (A) and dorsal (B) view and its interpretative schemes. The arrow in the scheme of A indicates the site where deformation occurs. Abbreviations: al: alveolus; an: anterior; bb: bony bridge; gr: groove; mx: maxillary; pal: palatines; pmx: premaxillae; s: suture; t: teeth; pos: posterior. Scale bar: 10 mm.

orientated (He et al., 1983; Jouve, 2004; Lü and Ji, 2005; Wang et al., 2007; Jiang and Wang, 2011a, b). Five alveoli are present on the right border, which lack teeth. Their outline is oval, which is probably due to the fact that the sections are oblique, possibly related to the lateral orientation of the teeth, and the interalveolar spaces are subequal. Bony bridges separate the alveoli, which are especially evident between the third, fourth and fifth preserved tooth positions. On the left border, the well-preserved dental bases of four crowns are present, in addition to the poorly preserved anteriormost alveolus. This alveolus and the four dental bases are anterolaterally orientated and as on the right side, show a relatively constant interalveolar spacing. A pulp cavity is visible in the second and third tooth crowns on the left side, counting from the anterior end. They are very narrow and anterolaterally orientated. The estimated dental density of the preserved portion of the rostrum is 5 teeth/cm. Two elongated bones can be observed in the midline, aligned with the anteroposterior axis of the element. Both are incomplete and slightly deformed in the anterior half of the rostral fragment, due to a concavity on the palatal surface that was likely generated by crushing. These bones are identified as the palatines, based on interpretations of the palatal morphology of pterosaurs of several authors (Von Heune, 1914; Arthaber, 1919; Broili, 1919; Mayr, 1964; Wellnhofer, 1970, 1975, 1978, 1987, 1991a, b; Wellnhofer and Kellner, 1991; Gasparini et al., 2004; Bennett, 2007a, 2012). However, other authors suggest that the palatal bones usually identified as palatines correspond to extensive palatal plates of the maxilla (Ősi et al., 2010). In dorsal view, parts of the rostral bones are preserved. The fusion of these elements is quite advanced, but the sutures are still visible as faint longitudinally arranged grooves, making it possible to distinguish the maxillae from the premaxillae (which show no evidence of a premaxillary crest). According to some researchers, the complete fusion of the cranial elements occurs early in the ontogeny (Bennett, 1993). Considering the relatively low degree of maxillo-premaxillary fusion (given that the sutures are still visible) and the small size of the fossil, the specimen is interpreted as a juvenile or possibly a subadult.

Specimen SGO.PV.362 (Fig. 3A) is a fragment with six dental crown bases. The estimated dental density is 5.2 teeth/cm. A bony bar is preserved parallel to the fragment that holds the teeth. The oblique orientation of the dental crown bases indicates that the teeth projected anterolaterally, forming a row on the edge of the element. The outline of the pulp cavities is suboval, probably because the teeth are obliquely broken, which is highlighted by the lateral orientation of the teeth.

Specimen SGO.PV.377 (Fig. 3B) is a fragment that preserves six dental crown bases within their alveoli, some of them poorly preserved. The orientation of the crown bases is oblique with respect

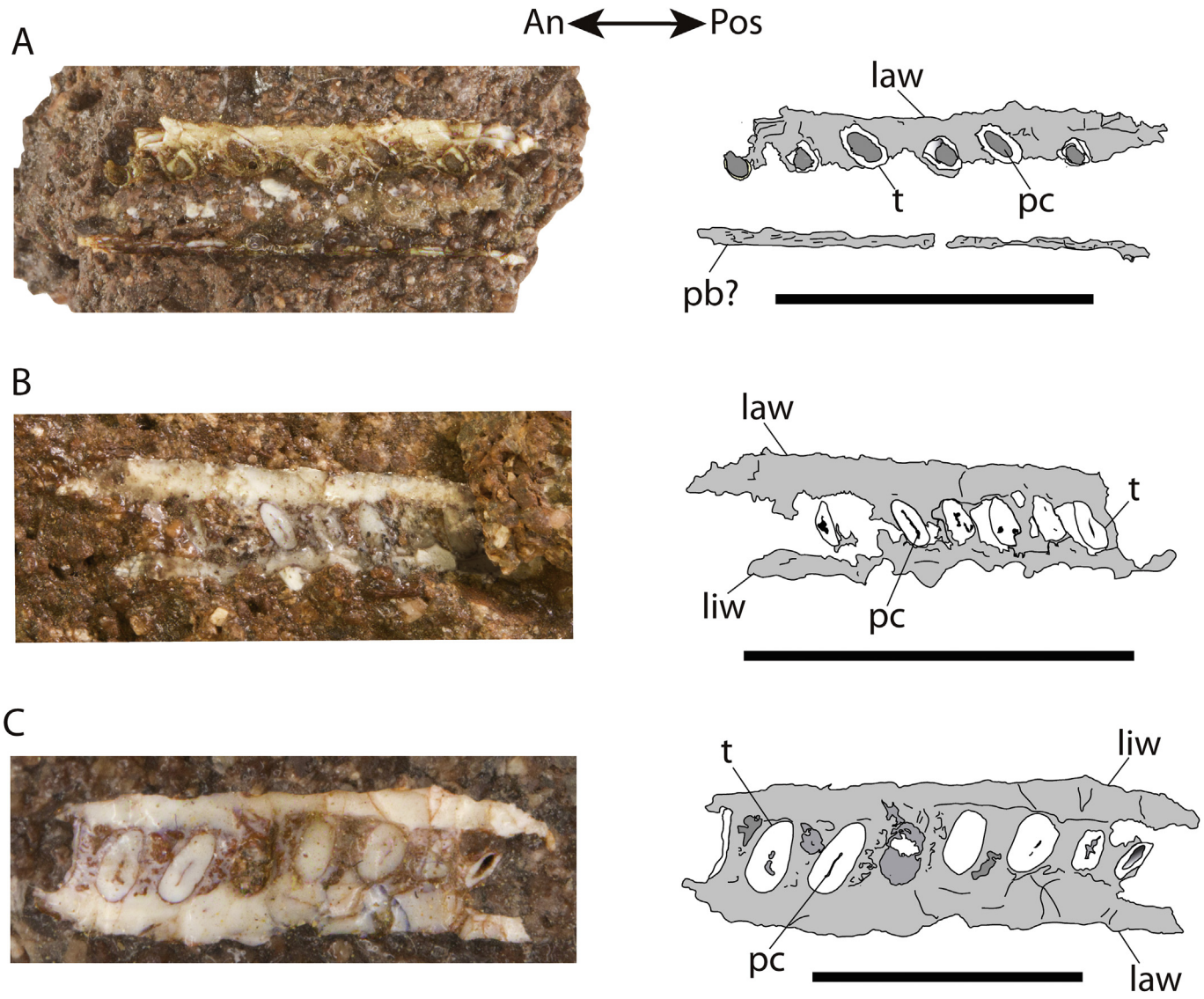


Fig. 3. Ctenochasmatidae indet. Mandibular remains (left) and interpretative schemes (right). A: SGO.PV. 362. Jaw fragment in occlusal view. B: SGO.PV. 377. Probable dentary fragment in occlusal view. C: SGO.PV. 378. Probable dentary fragment in occlusal view. The arrows indicate the antero-posterior orientation for all the materials. The orientation in B and C is tentative. Abbreviations: an: anterior; law: labial wall; liw: lingual wall; pc: pulp cavity; t: teeth; pos: posterior. Scale bar for A and B is 10 mm, while for C is 5 mm.

to the anteroposterior axis. The estimated dental density is 9.3 teeth/cm. The mediolateral thickness of the margins of the fragment shows a disparity on either side of the tooth row. The thicker margin is here interpreted as lateral and the thinner margin as medial.

Specimen SGO.PV.378 (Fig. 3C) is likely a mandibular fragment, exposed in occlusal view with the bases of six dental crowns and part of a seventh preserved in position. The estimated dental density is 8.5 teeth/cm. As in SGO.PV.377, one of the margins has a greater mediolateral thickness than the other. The presence of a single row of teeth suggests that the fossil represents a mandibular fragment posterior to the symphysis, however, the possibility that it corresponds to a maxillary fragment cannot be excluded. The bases of the dental crowns show a gradual change in diameter along the anteroposterior axis of the element, which may indicate their relative position in the tooth row. In *Gegepterus changi* for example, the alveoli decrease in diameter posteriorly (Wang et al., 2007; Jiang and Wang, 2011a). Counting from the proposed posterior end, the fifth alveolus does not preserve any trace of the crown, while the fourth dental base seems to correspond to a replacement tooth based on its lack of a pulp cavity. The margins of the fragment are subparallel and suggest that the intact element was elongate. The major axis of the dental crown bases is obliquely orientated with respect to the labio-lingual axis and the pulp cavities are very narrow. The oblique arrangement of the dental crown bases with respect to the anteroposterior axis of the element, together with the inclination of the pulp cavities suggest that the teeth were anterolaterally projected.

The specimens SGO.PV.362, SGO.PV.364 and SGO.PV. 378 differs from a probable dentary fragment (SMNK-PAL 4013) described by Martill et al. (2006) in which the outline of the teeth is morecircular, and the pulp cavities are comparatively larger and subcircular in cross-section. The differences in the shape of the cross-section of the teeth observed between the materials described by Martill et al. (2006) and the specimens described here probably relate to differences in the way these teeth broke. As noted above,

the oval cross-section of the teeth described in Chilean materials is probably due to the fact that they were broken obliquely, so that the oval profile is probably highlighted by the lateral orientation of the teeth, instead of representing differences in dental morphology with respect to the materials described by Martill et al. (2006).

Remarks: Cranial remains of pterosaurs are relatively rare and the reconstruction of their features, such as the palatal region, is difficult because much of the cranial material is exposed in lateral view, compressed or severely crushed due to the fragility of the bones (Wellnhofer, 1991a; Unwin, 2006; Ösi et al., 2010). Although the cranial remains described in this work are fragmentary, they provide new information regarding the morphology and disposition of the teeth, as well as the shape of the snout of these pterosaurs. In addition, specimen SGO.PV.364 makes it possible to observe palatal features for the first time. Our current knowledge of the cranial anatomy of ctenochasmatid pterosaurs is severely limited due to the lack of well-preserved specimens in the fossil record.

4.2. Description of mid cervical vertebrae

Specimen SGO.PV.350 (Fig. 4) is an elongated mid-cervical vertebra lacking part of its anterior portion. The cotyle is poorly preserved. Although the base of the left prezygapophysis is present, the right prezygapophysis is completely absent. In the posterior portion, only the bases of the postzygapophyses are preserved. The total length of the centrum is approximately 69.5 mm. This measurement was taken between the anterior ventral margin (following the line of the hypapophysis) and the distal tip of the condyle. The ratio between the centrum length to the minimum width of the element is 4.5 (see Table 1). It was not possible to measure the total length of the vertebra accurately (between the left prezygapophysis and the condyle) due to the partial preservation of the left prezygapophysis. However, the preserved length of 73.5 mm is probably very close to the original total length of the element. In lateral view, the vertebra shows dorsoventral constriction at its middle section, giving the vertebra an "hourglass" shape (Fig. 4A, B). The posterior half of the neural arch is

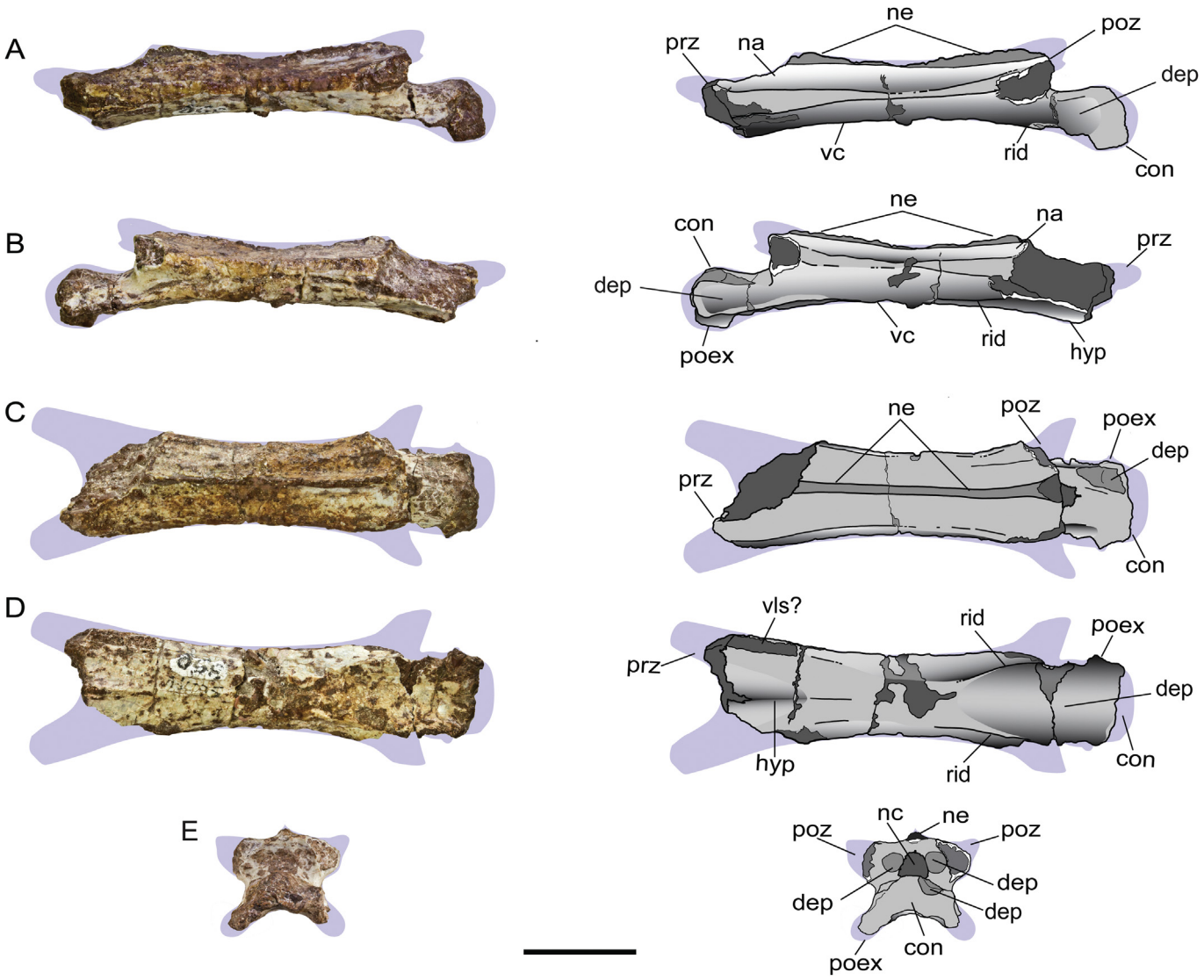


Fig. 4. Ctenochasmatidae indet. Photographs and interpretative schemes of mid cervical vertebra (SGO.PV. 350) in caudal (A) left lateral (B), dorsal (C), right lateral (D) and ventral (E) views. Abbreviations: con: condyle; dep: depression; hyp: hypapophysis; na: neural arch; nc: neural canal; ns: neural spine; pf: pneumatic foramen; poz: postzygapophysis; prz: prezygapophysis; poex: postexapophysis; rid: ridge; vc; vertebral centrum; vls?: ventrolateral sulcus? Scale bar: 20 mm.

Table 1
Measurements of SGO.PV.350 and SGO.PV.351 (in mm). The length of the centrum was taken from the ventral margin of the cotyla (poorly preserved in booth vertebrae) and the condyle. The minimum width was measured between the lateral margins of the vertebral centrum. The length of the neural spine and of the hypapophysis was taken considering its maximum preserved extent. Measurements such as the distance between zigapophyses (both from opposite sides and between pre and postzygapophyses of each side) were not possible to perform due to the lack of much of these structures.

	Total length of centrum	Minimum width of the centrum	Minimum high of the centrum	Preserved length of neural spine	Length of hypapophysis	L/W ratio
SGO.PV.350	69.5	15.3	10.7	42.4	13.3	4.5
SGO.PV.351	70.2	12.1	10.9	–	40.3	5.8

dorsoventrally lower and more concave when observed from the left side than it is when viewed from the right. This is due to a slight deformation, probably caused by compaction. The neural arch and the centrum are completely fused and lack any visible sutures between them, indicating an osteologically mature individual (Bennett, 1993). There are no pneumatic foramina on the lateral surface of the centrum, but their apparent absence may be the result of fractures hindering their identification. The neural spine is anteroposteriorly elongated and low, reduced to a long ridge with its middle zone partially eroded. It is slightly taller anteriorly and posteriorly, which is exaggerated by the erosion and deformation of its middle zone. This deformation causes the posterior half of the neural spine to appear taller in left lateral view than in right lateral view. In dorsal view, the vertebra shows concave lateral margins, with the minimum width approximately in the middle of the element, giving it an "hourglass" shape (Fig. 4C). In ventral view, the vertebra presents a posterior concavity, which begins posterior to the middle of the vertebra. It is weakly developed near the middle of the centrum and becomes more marked distally, between the postexapophyses (Fig. 4E). The lateral margins of this concavity form ridges proximally and distally they become separated from the centrum, forming two small flanges. In ventral view (Fig. 4D), a well-developed anteroventral hypapophysis can be observed in the midline of the vertebra. Its length is 13.3 mm (Table 1), extending from the anterior ventral edge to approximately a quarter of the total length of the vertebra posteriorly. Following Bennett (2001), this structure corresponds to the attachment site for the hipaxial muscles of the neck. There is no evidence of the preexapophyses due to the bad preservation of the anterior region. A sulcus is observed on the left ventrolateral edge of the element, but unfortunately, the state of preservation prevents a detailed description of this structure. The condyle is well-developed posteriorly. In posterior view, the dorsal surface of the condyle shows deformation and erosion that make its outline irregular (Fig. 4E). The ventral surface of the condyle is concave, which is exaggerated by the ventrolaterally projected postexapophyses. Only the base of the right postexapophysis is preserved, while the left one is almost complete. The left postexapophysis is small and rounded, with a dorsolaterally orientated articular surface. The elliptical neural canal is seen in posterior view, positioned above the level of the base of the postzygapophyses. It is dorsoventrally higher than wide and located dorsally to the condyle, extending slightly onto its dorsal surface. Two rounded depressions flank the neural canal, each approximately half the size (40%) of the neural canal.

The general morphology of SGO.PV.351 (Fig. 5) is very similar to that observed in SGO.PV.350, although this vertebra is more poorly preserved. It is elongated, with the centrum measuring approximately 70.2 mm in total length (see Table 1). The ratio between the centrum length to the minimum width (in dorsal view) of the element is 5.8. There are no obvious sutures between the vertebral centrum and the neural arch, suggesting that it belonged to an osteologically mature individual (Bennett, 1993). The body of the vertebra is approximately square in cross-section in anterior and posterior views, as in SGO.PV.350. This vertebra is procoelous and preserves much of the cotyle. The anterior region preserves no evidence of preexapophyses due to damage and the neural spine has been obliterated by erosion. In dorsal view (Fig. 5A), the anterior half of the element is slightly wider than the posterior and the lateral margins are concave. Its minimum width is in the posterior half of the vertebra. Only part of the right prezygapophysis is preserved, which is projected anterolaterally, while the postzygapophyses are completely absent. The condyle is also poorly preserved. It is well-developed, although less so than in SGO.PV.350, projecting posteriorly and showing a slightly concave ventral surface. Its dorsal surface is badly eroded, making observations about its outline impossible. The left postexapophysis is preserved, although very eroded. It is well integrated in the condyle and is ventrolaterally projected. In ventral view (Fig. 5B), the element shows a well-developed hypapophysis in its midline, which extends from the ventral edge of the cotyle and reaches slightly farther posteriorly than the mid-level of the element. The total length of the hypapophysis is 40.3 mm, making it much more extensive than in SGO.PV.350. A slightly marked sulcus is seen at the ventrolateral edge of the element. Unlike in SGO.PV.350, there is an oval pneumatic foramen on both lateral surfaces of the vertebral centrum (Fig. 5C-D). Each foramen is located approximately at the midpoint of the vertebra, just ventral to the neural arch-centrum contact.

Remarks: The mid cervical vertebrae of both ctenochasmatids and azhdarchids are usually anteroposteriorly elongated (Unwin, 2003; Andres and Ji, 2008, see Table 2), although extremely elongated mid-cervical vertebrae have been described in some azhdarchid genera such as *Quetzalcoatlus* (Lawson, 1975; Howse, 1986), *Phosphatodraco* (Pereda Suberbiola et al., 2010), and *Arambourgiania* (Frey and Martill, 1996; Martill et al., 1998) as well as in certain species of ctenochasmatid pterosaurs, such as *Huanhepterus quingyangensis* (Dong, 1982) and in *Moganopterus zhuiana* (Lü et al., 2012). In the case of *Phosphatodraco*, Pereda Suberbiola et al. (2010) describe a fifth cervical vertebra very elongated. However, Kellner (2010) points out that this supposed fifth vertebra is actually an element that is composed of the third and fourth cervical vertebra, which were mistakenly considered as a single vertebra due to their state of preservation. Conversely, some mid cervical vertebrae referred to Ctenochasmatidae and Azhdarchidae are considerably shorter (Table 2).

Considering Ctenochasmatidae, Chilean specimens SGO.PV.350 and SGO.PV.351 are proportionally shorter than the mid cervical vertebrae described in the genera *Moganopterus* and *Elanodactylus*. However, specimens SGO.PV.350 and SGO.PV.351 are longer than the same elements described for *Gegepterus* and *Beipiaopterus* (Table 2). These comparisons indicate that SGO.PV.350 and SGO.PV.351 belonged to a species that was larger than *Gegepterus* and *Beipiaopterus*, but smaller than *Elanodactylus* and *Moganopterus*.

It is important to mention that there is no standardized method for calculating the ratio between the length and width of mid cervical vertebrae, making results difficult to compare (for some values see Table 3). Some authors measure the maximum length of the element between the prezygapophyses and postexapophyses, while others consider it the distance between the prezygapophyses

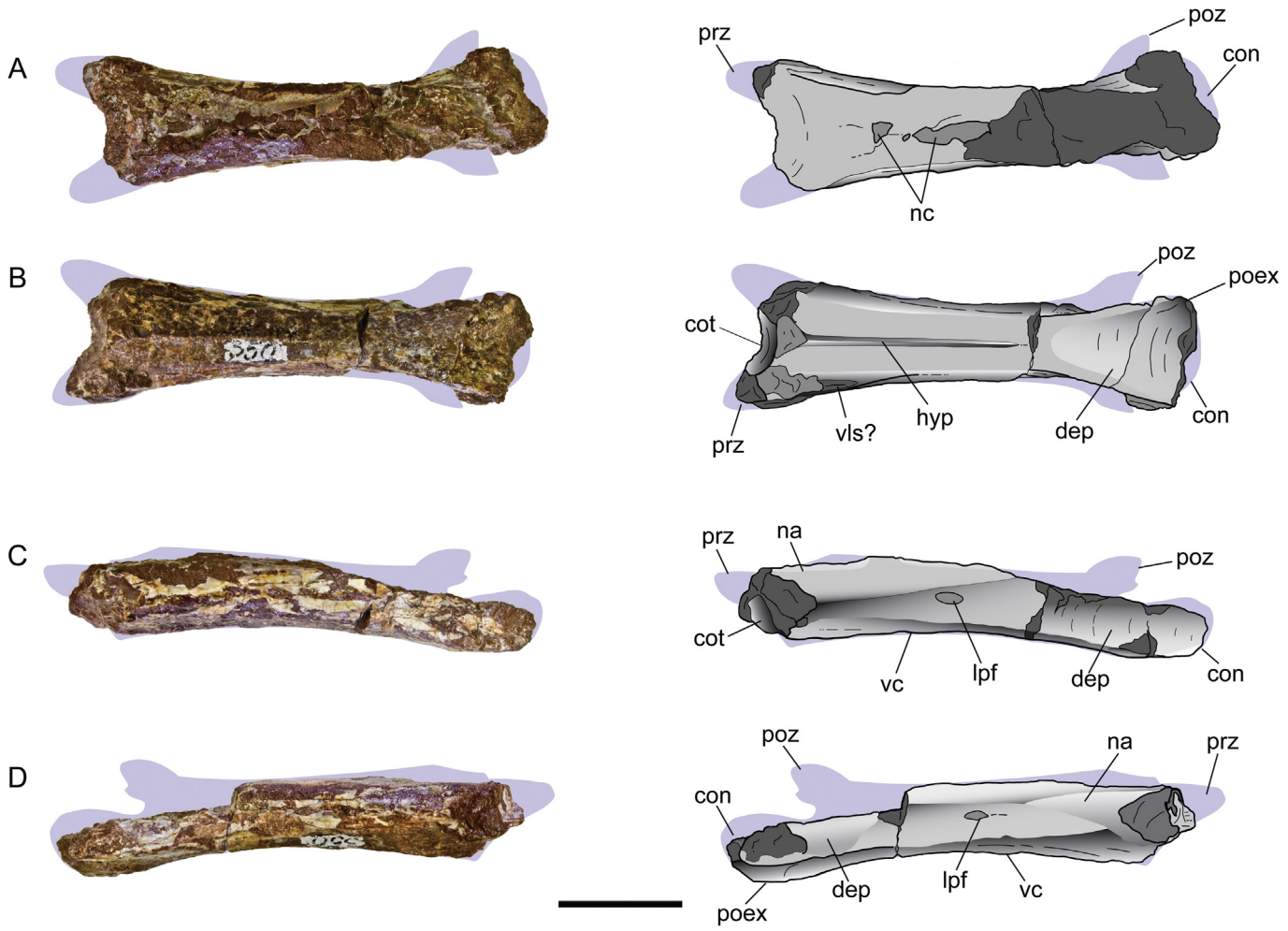


Fig. 5. Ctenochasmatidae indet. Photographs and interpretative schemes of mid cervical vertebra (SGO.PV. 351) in left lateral (A), dorsal (B), right lateral (C) and ventral (D) views. Abbreviations: con: condyle; hyp: hypapophysis; cot: cotyle; dep: depression; nc: neural canal; ns: neural spine; pf: pneumatic foramen; poz: postzygapophysis; prz: prezygapophysis; poex: postexapophysis; vc; vertebral centrum; vls?: ventrolateral sulcus? Scale bar: 20 mm.

and postzygapophyses. To complicate matters, in some calculations the width between prezygapophyses is used instead of the minimum width of the vertebra.

Although these differences in methodology make accurate comparisons difficult, the obtained values still provide an approximate idea of the general differences in vertebral proportions of different pterosaur species (Table 3).

In some azhdarchids, the ratio of the elongation of the centrum relative to centrum width is very high. For example, in *Quetzalcoatlus* it is approximately 11, while in *Arambourgiania* it is 12.6 (Frey and Martill, 1996). In other azhdarchids however, this ratio is lower than in *Quetzalcoatlus* and *Arambourgiania*. In *Phosphatodraco mauritanicus* the ratio between the maximum vertebral length and the anterior width between prezygapophyses is 4.1 for cervical V (Pereda Suberbiola et al., 2003), which was previously considered the sixth cervical vertebra (Costa et al., 2015). The cervical III of *Volgadraco bogolubovi* has a relatively short centrum, with the total length being 2.4 times the minimum width (Averianov et al., 2008). In two isolated mid cervical vertebrae referred to Azhdarchidae by Ősi et al. (2005), the lenght/width (l/w) ratio is 3.3. In a third vertebra from Mongolia (MPC-Nd 100/302) referred to Azhdarchidae by Watabe et al. (2009), the ratio of the length of the centrum to the minimum width of the element is approximately 4.4.

As in Azhdarchidae, the length/width ratio of the mid cervical vertebrae in Ctenochasmatidae is variable (Table 3). The ratio of the longest vertebra of *Gladocephaloideus jingangshanensis* is 4.14 (Lü et al., 2016) and in the longest cervical vertebrae of *Beipiaopterus chenianus* it is 3.4 (Lü, 2003). In *Elanodactylus prolatus*, the estimated length/width ratio of cervical VII is 4 (Andres and Ji, 2008). In *Moganopterus zhuiana*, the ratio between the total length and the minimum width is 5.5 for cervical III, while it is 7.5 for cervical IV (Lü et al., 2012).

The length-width ratios of cervical vertebrae do not provide diagnostic information when differentiating between azhdarchids and ctenochasmatids, due to their variation according to the position of the vertebra in the neck (Averianov, 2010; Costa et al., 2015). It is quite possible that the difference in the value of the ratios calculated for SGO.PV.350 and SGO.PV.351 (4.5 and 5.8 respectively) is due to their different positions in the cervical series.

5. Discussion

5.1. Taxonomical affinities

5.1.1. Mandibular remains

Specimens SGO.PV.362, SGO.PV.377 and SGO.PV.378 are incomplete mandibular remains. Their preservation makes their

Table 2
Lengths of cervical vertebrae of ctenochasmatids and azhdarchids obtained from the literature. The letter "a" indicates that the measurement corresponds to the length of the centrum, between the cotyle and condyle), "b" indicates that the measurement was taken between the prezygapophyses and postzygapophyses, while "c" indicates that the measurement corresponds to the length between the prezygapophyses and postexapophyses. For *Arambourguiania philadelphiae* the range of estimated measures of the reconstructed vertebra is provided. * Indicates that the position of the vertebra is tentative. **Estimated range. ***For Kellner (2010), this vertebra is not the fifth, but corresponds to the third and fourth vertebra preserved close together, so in his opinion each successive vertebra corresponds to a place ahead of what was identified by Pereda Suberbiola et al. (2003). Pres: preserved.

		1	2	3	4	5	6	7	8	9
Ctenochasmatidae	*Gegepterus changi* IVPP V 11981 (Wang et al., 2007) (a)	x	6.3	~17.5	21.3	21.3	20.5	16.4	x	x
	Gegepterus changi IVPP V 11981 (Wang et al., 2007) (b)	x	x	17.2	21.3	21	28	~20	x	x
	Elanodactylus prolatus NGMC 99-07-1 (Andres and Ji., 2008) (b)	x	x	x	x	x	x	>59,1	~77,5	45,4
	Beipiaopterus chenianus BPM 0002 (Lü, 2003) (c)	20	34	25	19	x	x	x	x	x
	Moganopterus zhuiana 41HIII0419 (Lü et al., 2012)(c)	x	25	110	145	x	x	x	x	x
	Gladocephaloideus jingangshanensis JPM-2014-004 (Lü et al., 2016) (c)	x	14	17.4	16.4	15.2	12.9	x	x	x
Azhdarchidae	*Quetzalcoatlus* sp. TMM 41544.15 (Howse, 1986) (a)	x	x	x	x	374	x	x	x	x
	Azdarchidae indet. CMN 50801 (Rodrigues et al., 2011) (a)	x	x	x	x	119*	x	x	x	x
	Azhdarchidae indet. LINHM 014 (Rodrigues et al., 2011) (a)	x	x	x	x	182*	x	x	x	x
	Azhdarchidae indet. UPMC-080 (Buffetaut, 2012) (a)	x	x	x	x	70 *	x	x	x	x
	Arambourgiania philadelphiae VF 1 (Arambourg, 1959) (c)	x	x	x	x	600-780**	x	x	x	x
	Zhejiangopterus linhaiensis M1323 (Cai and Wei, 1994) (c)	x	x	36	114	142	120	90	x	x
	Zhejiangopterus linhaiensis M1328 (Cai and Wei, 1994) (c)	x	x	57	92	98	81	56	x	x
	Zhejiangopterus linhaiensis M1330 (Cai and Wei, 1994) (c)	x	x	50	82	84	72	38	x	x
	Phosphatodraco mauritanicus OCP DEK/GE 111 (Pereda Suberbiola et al., 2003) (d)	x	x	x	x	~300***	~225	190 (pres)	150 (pres)	89 (pres)
	Azhdarchidae indet. MPC-Nd 100/302 (Watabe et al., 2009) (a)	x	x	90.6	x	x	x	x	x	x

accurate identification impossible; it is even uncertain whether they correspond to portions of maxilla or dentary. However, the dental density clearly varies between the specimens: in SGO.PV.364 (rostrum) and SGO.PV.362 the dental density is approximately 5 teeth/cm, while in SGO.PV.377 and SGO.PV.378 it is approximately 9 teeth/cm. This variation suggests that the fragments correspond to different parts of the snout (either dentary or maxilla), but the available information is insufficient to determine which fragments represent distal positions and which are more proximal.

All of the specimens share certain taxonomically informative characters: narrow, elongate and dorsoventrally compressed snout (interpretation based mainly on SGO.PV.364); anterolaterally projected teeth interpreted as likely elongated and gracile; oblique dental crowns with an oval cross-section (this oval shape is probably related to the oblique fracture of laterally oriented teeth); narrow pulpar cavities and similar dental density. Considering all of these features together allows us to regard them as the same taxon, which is assignable to the Ctenochasmatidae since the listed traits are diagnostic features of this group (Kellner, 2003; Unwin, 2003). Many of the features in the new mandibular and rostral material are similar to those previously described in mandibular remains (SMNK-PAL 4012, SMNK-PAL 4013 and SMNK-PAL 4014) from Cerro La Isla by Martill et al. (2006), also assigned to Ctenochasmatidae.

Due to the incomplete preservation of the teeth of the Chilean material, it cannot be asserted how long they were and if they had any degree of curvature, as it is reported in *Ctenochasma* and

Table 3
L/A ratio of some cervical vertebrae of ctenochasmatids and azhdarchids obtained from the literature. Letter "a" indicates that the ratio was calculated between the length of the vertebral centrum and the minimum width of the centrum, "b" indicates that the ratio was calculated from the length between prezygapophyses and postzygapophyses and the minimum width of the vertebral centrum, while "c" indicates that the ratio was calculated between the length of the element (without details about what structures the measurements were taken in) and its minimum width.

		1	2	3	4	5	6	7	8	9
Ctenochasmatidae	*Gegepterus changi* IVPP V 11981 (Wang et al., 2007) (a)	x	x	~4.5	4.4	3.7	3.4	~2.9	x	x
	Gegepterus changi IVPP V 11981 (Wang et al., 2007) (b)	x	x	4.4	4.4	3.6	3.5	~3.5	x	x
	Elanodactylus prolatus NGMC 99-07-1 (Andres and Ji., 2008) (b)	x	x	x	x	x	x	~4	~3.6	3.4
	Beipiaopterus chenianus BPM 0002 (Lü, 2003) (c)	~3.3	3.4	3.1	2	x	x	x	x	x
	Moganopterus zhuiana 41HIII0419 (Lü et al., 2012) (c)	x	x	5.5	7.25	x	x	x	x	x
	Gladocephaloideus jingangshanensis JPM-2014-004 (Lü et al., 2016) (c)	x	3.4	4.1	3.5	3.1	2.7	x	x	x
Azhdarchidae	Azdarchidae indet. CMN 50801 (Rodrigues et al., 2011) (a)	x	x	x	x	6.6	x	x	x	x
	Azhdarchidae indet. LINHM 014 (Rodrigues et al., 2011) (a)	x	x	x	x	5.7	x	x	x	x
	Arambourgiania philadelphiae (Arambourg, 1959) (c)	x	x	x	x	~6.9	x	x	x	x
	Volgadraco bogolubovi SGU n°47/104a (Averianov, 2010) (a)	x	x	2.4	x	x	x	x	x	x
	Azhdarchidae indet. MPC-Nd 100/302 (Watabe et al., 2009) (a)	x	x	4.4	x	x	x	x	x	x

Gnathosaurus (Wellnhofer, 1970). The teeth in the Chilean remains are set in alveoli as in *Ctenochasma*, without clear evidence of a longitudinal groove (Wellnhofer, 1970; Buisonjé, 1981). This is different from the condition in *Gegepterus changi* (Wang et al., 2007) where the premaxillary, maxillary and dentary teeth are held in deep alveoli arranged in a longitudinal groove flanked by bony walls, the thicker corresponding to the labial border and the thinner to the lingual.

Some examples of ctenochasmatids with this dental morphology are *Pterofiltrus qiui* (Jiang and Wang, 2011b); *Ctenochasma* sp. (Jouve, 2004), *Liaodactylus primus* (Zhou et al., 2017), *Gegepterus changi* (Wang et al., 2007; Jiang and Wang, 2011a), *Huanhepterus quingyangensis* (Dong, 1982), *Gladocephaloideus jingangshanensis* (Lü et al., 2012, 2016), *Cathayopterus grabaui* (Wang and Zhou, 2006a) and *Plataleorhynchus streptophorodon* (Howse and Milner, 1995). *Pterofiltrus qiui* from the Lower Cretaceous in China is characterized by having a multitude of long and slender teeth, whose orientation varies from lateral to ventrolateral. This morphology was considered a diagnostic trait when *Pterofiltrus qiui* was assigned to Ctenochasmatidae (Jiang and Wang, 2011a, b). *Ctenochasma*, a genus of the Ctenochasmatinae, has an elongated rostrum with anterolaterally oriented teeth that are long, thin and very closely spaced (Bennett, 2007b; Buisonjé, 1981; Wellnhofer, 1970). *Liaodactylus primus* from the Upper Jurassic of China is the oldest ctenochasmatid (Zhou et al., 2017). This pterosaur has an elongated rostrum with closely spaced slender teeth, interpreted as a filter-feeding specialization. The anterior teeth in both upper and lower jaws of this genus are long and needle-like, and projected anterolaterally to laterally, as inferred for the Chilean material.

The calculated dental density in SGO.PV.377 (9.3 teeth/cm) and SGO.PV.378 (8.5 teeth/cm) is similar to that observed in *Ctenochasma gracile* (10 teeth/cm) (Wang et al., 2007) and "*Ctenochasma*" *porocristata* (8–9 teeth/cm) (Buisonjé, 1981). This agrees with previous observations made in the Chilean material studied by Martill et al. (2006), who mentioned that the dental density is more similar to that observed in *Ctenochasma* than in *Gnathosaurus*. The similar dental density of SGO.PV.362 (5.2 teeth/cm) and SGO.PV.364 (5 teeth/cm) is close to the calculated value for the ctenochasmatinae *Gegepterus changi* (5.25 teeth/cm for the upper jaw and 5.8 teeth/cm for the dentary) (Wang et al., 2007). Additionaly, the dental density of *Huanhepterus quingyangensis* (1.6 teeth/cm) and *Pterofiltrus qiui* (2.5 teeth/cm) (Jiang and Wang, 2011b) is considerably lower than in the materials described here. However, it should be noted that the material described here is too fragmentary to obtain reliable averages and thus should be compared with those calculated for complete jaws with caution.

With respect to South American ctenochasmatids, the dental morphology of the Chilean material is also different from that of *Pterodaustro guinazui*, whose remains have been found in the Lagarcito Formation (Lower Cretaceous) of San Luis, Argentina (Bonaparte, 1970; Chiappe et al., 1998a, b; 2000, 2004; Codorniú and Chiappe, 2004; Codorniú, 2005; Codorniú and Paulina-Carabajal, 2013; Codorniú et al., 2013, 2015). The distal portion of the rostrum of *P. guinazui* curves upwards and the maxillaries hold hundreds of small teeth with narrow and conical bases. The teeth have wide and spatulate crowns that are not set in alveoli, but were possibly connected to the bone through soft tissue. Meanwhile, the lower jaw holds hundreds of much thinner, filament-like teeth, which are very closely spaced and arranged in a longitudinal groove, with only the anteriormost teeth thicker and held in individual alveoli (Chiappe et al., 2000; Codorniú et al., 2013). The teeth of the pterosaurs from Cerro La Isla described here are more robust and more widely separated from each other than those of *P. guinazui*. Another observed difference is that the teeth of the rostral fragment (SGO.PV.364) are set in alveoli at the edges of the maxillae, while *P. guinazui* lacks alveoli in these bones. These differences suggest that the mandibular and rostral remains do not belong to *P. guinazui*.

On the other hand, Perea et al. (2018) reported a rostral fragment (FC-DPV-2869) from the Upper Jurassic?-Lower Cretaceous of Uruguay that is very similar to specimen SGO.PV.364, both in the morphology and orientation of the teeth and in its width (~1.2 cm), although it lacks sutures on its dorsal surface. However, FC-DPV-2869 is different from SGO.PV.364 in that the former has deep interalveolar concavities, which are not observed in the Chilean material. These differences in the morphology of the interalveolar spaces suggest that the Chilean and Uruguayan material belong to different species.

The mandibular remains of the South American dsungaripterid *Domeykodactylus ceciliae* (Martill et al., 2000) are also different from the material described here. The dental morphology of this species is characterized by the presence of expanded tooth sockets that form protuberances, such as those observed in the genus *Dsungaripterus* (Young, 1964) and other members of the Dsungaripteridae family (Kellner, 2003; Unwin, 2003; Martill et al., 2006).

5.1.2. Cervical vertebrae

The cervical vertebrae from Cerro La Isla are procoelous and correspond to post-axial elements of the mid cervical series. These vertebrae are elongated, with a depressed neural arch and low neural spine (preserved in SGO.PV.350) and oval pneumatic foramina on the lateral surfaces of the vertebral centrum (preserved in SGO.PV.351).

Depressed neural arches and low neural spines are features present in both Ctenochasmatidae and Azhdarchidae, but they show certain differences. In Azhdarchidae, the neural arch is usually completely confluent with the vertebral centrum, that causes the vertebra to acquire a tubular-like morphology which is especially conspicuous in the middle of the element (Martill et al., 1998; Andres and Ji, 2008; Witton and Naish, 2008; Unwin, 2003). This morphology has been described in isolated vertebrae of the Azhdarchidae (Buffetaut et al., 1997; Martill et al., 1998; Unwin, 2003; Ösi et al., 2005; Andres and Ji, 2008; Rodrigues et al., 2011; Buffetaut, 2012) such as *Azhdarcho lancicollis* (Nessov, 1984; Unwin, 2003; Witton and Naish, 2008), *Phosphatodraco mauritanicus* (Pereda Suberbiola et al., 2003), *Eurazhdarcho langendorfensis* (Vremir et al., 2013) and *Arambourgiania philadelphiae* (Arambourg, 1959; Martill et al., 1998). In the cervical vertebrae of Ctenochasmatidae however, the depressed neural arch remains distinct from the vertebral centrum (Unwin, 2003; Andres and Ji, 2008), as described in *Elanodactylus prolatus* (Andres and Ji, 2008) and *Huanhepterus quingyangensis* (Dong, 1982). In SGO.PV.350 and SGO.PV.351, there is a clear distinction between the neural arch and the vertebral centrum, which is especially evident in SGO.PV.350. In addition, neither of the Chilean vertebrae are tubular. These features coincide with the midcervical vertebral morphology described in Ctenochasmatidae (Andres and Ji, 2008).

The morphology of the neural spine in Azhdarchidae is variable. This spine can be either low, absent (at least in the fifth cervical vertebra), or very tall in the first or last element of the mid cervical series (Howse, 1986; Kellner, 2003; Unwin, 2003), as described for *Phosphatodraco*, *Zhejiangopterus* and *Quetzalcoatlus* (Cai and Wei, 1994; Pereda Suberbiola et al., 2003; Andres and Ji, 2008). Moreover, in Azhdarchidae, Watabe et al. (2009) describe that, when present, the neural spine usually has a "double peak" morphology, characterized by being taller at both ends than in its middle region as in the case of *Azhdarcho* (Howse, 1986; Averianov, 2010) and *Quetzalcoatlus* (Howse, 1986). According to Watabe et al. (2009), this morphology is not observed in other pterosaurs, in which the height of the neural spine remains approximately constant in all its

extension. As for Ctenochasmatidae, the neural spine is low, rectangular, and anteroposteriorly elongated (Howse, 1986; Unwin, 2003; Andres and Ji, 2008), as in *Gegepterus changi* (Wang et al., 2007), *Elanodactylus prolatus* (Andres and Ji, 2008), *Gladocephaloideus jingangshanensis* (Lü et al., 2012) and *Huanhepterus quingyangensis* (Dong, 1982). In the case of SGO.PV.350, the neural spine is incomplete in the middle region, making it impossible to determine whether the vertebra showed the ctenochasmatid or azhdarchid morphology.

Both Cerro la Isla vertebrae preserve postexapophyses, a feature that is considered a synapomorphy of Dsungaripteroidea (*sensu* Kellner, 1996, 2003). In recent studies, Andres and Ji (2008) mentioned that the presence of postexapophyses is a common feature in a more inclusive clade. Most of these pterosaurs belong to Ornithocheiroidea (*sensu* Bennett, 1994; Kellner, 2003), a group that includes Azhdarchidae (Andres and Ji, 2008; Andres et al., 2014; Lü et al., 2016). In the case of the azhdarchid species *Azhdarcho* (Howse, 1986; Averianov, 2010), *Volgadraco* (Averianov et al., 2008), *Quetzalcoatlus* and *Arambourgiania* (Howse, 1986) the presence of postexapophyses has been described. These structures have also been reported in members of the Ctenochasmatidae such as *Gegepterus changi* (Wang et al., 2007; Jiang and Wang, 2011a), *Elanodactylus prolatus* (Andres and Ji, 2008), an isolated vertebra referred to Ctenochasmatidae (SMC J5340) (Howse and Milner, 1995; Andres and Ji, 2008), as well as the vertebrae described in this research. However, postexapophyses seem to be absent in the cervical vertebrae of *Ctenochasma gracile* (Howse, 1986) and *Beipiaopterus chenianus* (Lü, 2003), unlike most of the larger pterodactyloids. In *Gegepterus changi,* the presence of cervical postexapophyses is one of the main features that suggest that this species is derived within Archaeopterodactyloidea (Wang et al., 2007; Costa et al., 2015). Some authors have proposed that the independent acquisition of postexaphopyses in Ctenochasmatidae and Azhdarchidae is related to the strengthening and restriction of movement of the neck in large taxa, or those with a very long neck (Williston, 1897; Bennett, 2001; Andres and Ji, 2008).

Another feature that allows to differentiate between Ctenochasmatidae and Azhdarchidae is the presence or absence of pneumatic foramina on the lateral surface of the vertebral centrum (Andres and Ji, 2008). SGO.PV.351 has oval pneumatic foramina on both lateral surfaces of the cervical centum, whereas in SGO.PV.350 we cannot determine the presence of lateral pneumatic foramina due to the state of preservation. Lateral pneumatic foramina have been described in a cervical centrum of the ctenochasmatid *Gegepterus changi* (Wang et al., 2007), in a vertebra from the Upper Jurassic beds of Tendaguru [(Andres and Ji, 2008), though the latter has been questioned recently by Costa et al. (2015)] and in a vertebra from the Jurassic/Cretaceous boundary in the Purbeck Limestone of Southern England referred by Howse and Milner (1995) and Andres and Ji (2008) to Ctenochasmatidae. Wang et al. (2007) mention that the presence of lateral pneumatic foramina in the centrum of *Gegepterus changi* is a feature that is practically not observed in basal pterodactyloids. Thus, the presence of this structure as well as postexapophyses led these authors to propose that *G. changi* is a derived taxon within Archaeopterodactyloidea.

On the other hand, the azhdarchids seem to lack lateral pneumatic foramina, which may be the result of their having lost them secondarily, as proposed by Kellner (2003). For example, the lateral pneumatic foramina are absent in *Phosphatodraco mauritanicus* (Pereda Suberbiola et al., 2003), *Eurazhdarcho langendorfensis* (Vremir et al., 2013), *Azhdarcho lancicollis* (Nessov, 1984; Averianov, 2010), *Quetzalcoatlus* sp. (Howse, 1986), and in *Arambourgiania philadelphiae* (Arambourg, 1959; Martill et al., 1998). There are also several isolated mid cervical vertebrae that have been referred to Azhdarchidae based on the absence of pneumatic foramina on the lateral surfaces of the centrum (Buffetaut et al., 1997; Buffetaut, 2001, 2012; Ősi et al., 2005; Rodrigues et al., 2011; Costa et al., 2015). However, there is at least one record of an azhdarchid with a mid-series cervical centrum bearing lateral pneumatic foramina, which corresponds to *Volgadraco bogolubovi* from the Upper Cretaceous of Russia (Averianov et al., 2008). Cervical III of this pterosaur shows a series of small and irregular depressions on its lateral surfaces at the boundary between the neural arch and the centrum, some of which contain small pneumatic foramina. Thus, the shape of the lateral pneumatic foramina in this specimen differs from the oval foramina observed in the mid cervical vertebrae of ctenochasmatids (Howse, 1986; Wang et al., 2007). *Aralazhdarcho bostobensis* from the Upper Cretaceous of Kazakhstan, has pneumatic foramina on the lateral surfaces of its cervical vertebra, which corresponds to the atlas-axis complex (Averianov, 2007). Based on the exposed evidence, the presence of lateral oval pneumatic foramina allows us to assign the vertebra SGO.PV.351 to Ctenochasmatidae.

5.2. Fossil record of the clade ctenochasmatidae

Most currently known ctenochasmatid pterosaurs have been discovered in China (Fig. 6), being part of the Early Cretaceous Jehol Biota (Wang and Zhou, 2006b). Several species of ctenochasmatids are known from the Yixian Formation, including *Gegepterus changi* (Wang et al., 2007; Jiang and Wang, 2011a), *Eosipterus yangi* (Ji and Ji, 1997); *Pterofiltrus qiui* (Jiang and Wang, 2011b); *Elanodactylus prolatus* (Andres and Ji, 2008); *Beipiaopterus chenianus* (Lü, 2003); *Gladocephaloideus jingangshanensis* (Lü et al., 2012); *Cathayopterus grabaui* (Wang and Zhou, 2006a); *Feilongus youngi* (Wang et al., 2005) and *Moganopterus zhuiana* (Lü et al., 2012). *Feilongus youngi* was originally included in the clade Archaeopterodactyloidea, but not in a particular family, while *Moganopterus* was first considered a boreopterid pterosaur. In a subsequent analysis both species were recovered as ctenochasmatid pterosaurs (Andres et al., 2014). *Forfexopterus jeholensis* (Jiang et al., 2016) from the Jiufotang Formation (Lower Cretaceous), and *Huanhepterus quinyangensis* (Dong, 1982) from the Huachihuanhe Formation (Upper Jurassic) are other ctenochasmatids recorded from China. Zhou et al. (2017) described to *Liaodactylus primus*, based on a specimen found in the Tiaojishan Formation. The Oxfordian age assigned to the strata where it was discovered make this pterosaur the earliest known ctenochasmatid.

Remains of ctenochasmatids in Europe have been found in several localities, mainly in Germany, England and France. Most ctenochasmatid records in England come from the Purbeck Group, Jurassic/Cretaceous boundary, mostly Berriasian in age (Martill et al., 2013). Two ctenochasmatid species have been found in these outcrops; *Plataleorhynchus streptophorodon* (Howse and Milner, 1995) and *Gnathosaurus macrurus* (Seeley, 1869; *sensu*; Howse and Milner, 1995). A third discovery from the Purbeck Group corresponds to an isolated cervical vertebra found near Langton Matravers (SMC J5340). This vertebra was originally assigned to Azhdarchidae (Howse, 1986; Bennett, 1989, 1991, 1994), but was later reidentified as belonging to a ctenochasmatid (Howse and Milner, 1995; Andres and Ji, 2008). However, Martill et al. (2013), cast doubt on this last reassignment. Another find from England consists of an incomplete cervical vertebra (PV OR 48387) from Durlston Bay (Durlston Formation, Berriasian), which was assigned to Ctenochasmatidae by Howse and Milner (1995).

Ctenochasma is a genus well known in Europe. Remains of these pterosaurs have been found in the lower Tithonian Lithographic Limestone in Solnhofen, southern Germany (Bennett, 2007b). Among the *Ctenochasma* species are *Ctenochasma roemeri*, named by von Meyer (1851) and *Ctenochasma gracile* named by Oppel

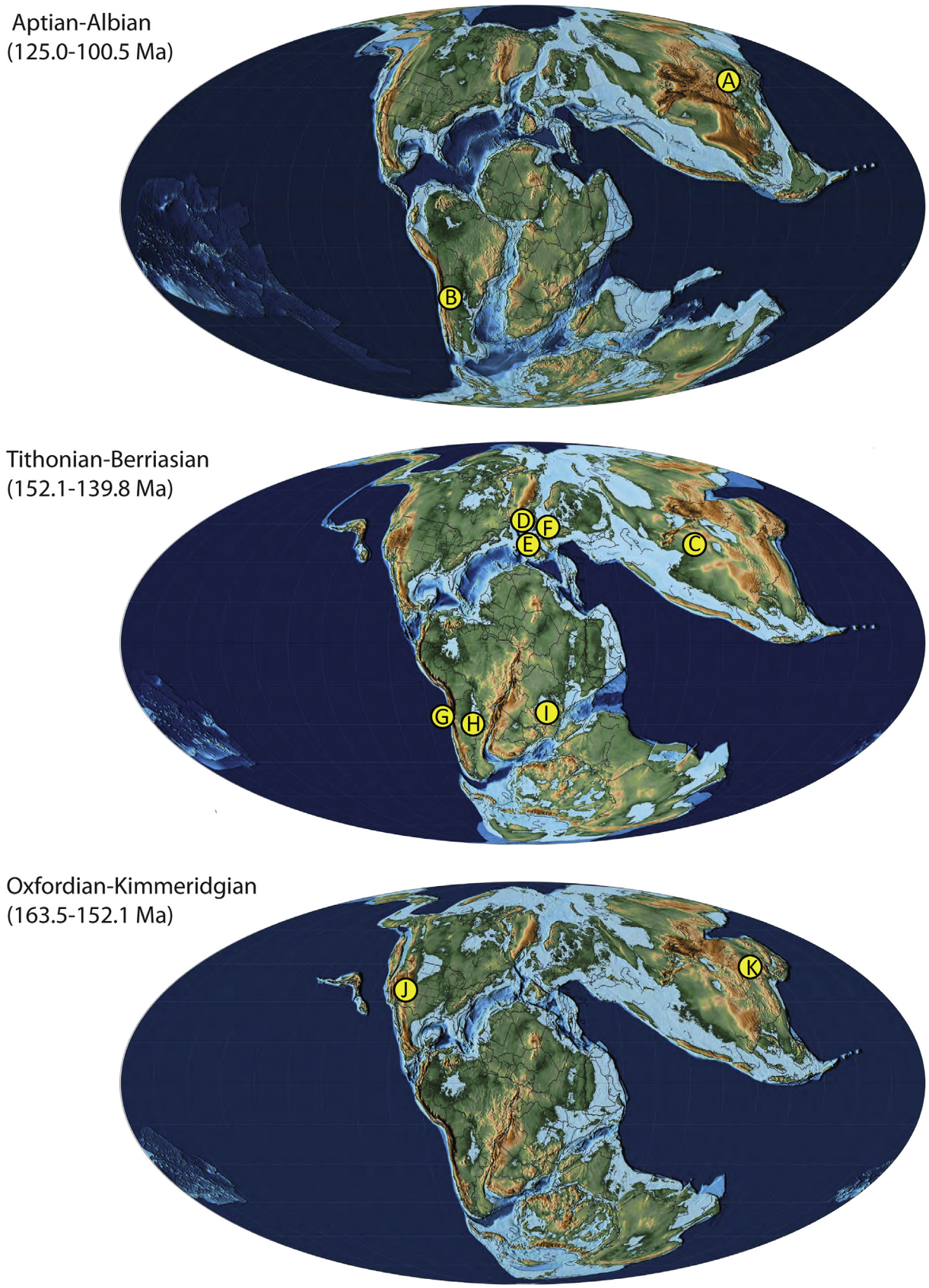


Fig. 6. Paleogeographic and temporal distribution of ctenochasmatid pterosaurs. A. *Gegepterus changi*, *Eosipterus yangi*, *Pterofiltrus qiui*, *Elanodactylus prolatus*, *Beipiaopterus chenianus*, *Gladocephaloideus jingangshanensis*, *Feilongus youngi*, *Cathayopterus grabaui* from Yixian Formation and *Forfexopterus jeholensis* from Jiufotang Formation, B. *Pterodaustro guinazui* from Lagarcito Formation, C. *Huanhepterus quinyangensis* from Huachihuanhe Formation, D. *Plataleorhynchus streptophorodon*, *Gnathosaurus macrurus*, SMC J5340 and PV OR 48387 from Purbeck Group, E. *Ctenochasma taqueti* from Calcaires tachetés, F. *Ctenochasma roemeri*, *Ctenochasma elegans*, *Gnathosaurus subulatus* and *Aurorazhdarcho micronyx*

(1862), the last species renamed by Bennett, 2007 as *Ctenochasma elegans*. *Ctenochasma porocristata* is another species from the Lithographic Limestones of Solnhofen (Buisonjé, 1981). However, the holotype of this species (an incomplete skull), was later reassigned to the species *Ctenochasma elegans* (Jouve, 2001, 2004). *Ctenochasma taqueti* was found in the lower Tithonian Calcaires tachetés of St. Diezer, France (Bennett, 2007b; Jouve, 2004; Taquet, 1972). *Gnathosaurus* is a second genus of ctenochasmatid pterosaur from the Lithographic Limestones of Solnhofen. A fragment of a lower jaw (Mayr, 1964) and a practically complete skull exposed in ventral view (Münster, 1832; Von Meyer, 1834) are assigned to *Gnathosaurus subulatus*. *Aurorazhdarcho micronyx* (Frey et al., 2011) was also discovered in the Lithographic Limestones of Solnhofen. This species was referred to its own family, Protazhdarchidae by Frey et al. (2011), but later Bennett (2012) referred this pterosaur to Ctenochasmatidae.

A possible ctenochasmatid from Africa is represented by an isolated cervical vertebra from the Upper Jurassic Tendaguru beds of East Africa. The vertebra was originally referred to Azhdarchidae by Sayão and Kellner (2001), but was later reassigned to Ctenochasmatidae by Andres and Ji (2008), mainly based on the presence of lateral foramina. However, Costa et al. (2015) questioned that assignment, since they found no signs of lateral foramina, so tentatively the vertebra was again referred to Azhdarchidae.

The records from North America are scarce, including only *Kepodactylus insperatus*, found in the Upper Jurassic Morrison Formation (Harris and Carpenter, 1996). Unwin (2003) considered this species a possible member of the Dsungaripteroidea. However, in a phylogenetic analysis carried out by Andres et al. (2014), *Kepodactylus insperatus* was recovered within Ctenochasmatidae.

The records in South America mostly belong to *Pterodautro guinazui*, a ctenochasmatid from the Lower Cretaceous Lagarcito Formation, San Luis Province, Argentina (Bonaparte, 1970). This pterosaur is represented by a large number of disarticulated specimens from several ontogenetic stages with differing degrees of completeness, even an embryo inside its egg (Bonaparte, 1970; Chiappe et al., 1998a, b, 2000, 2004; Codorniú and Chiappe, 2004; Codorniú, 2005; Codorniú et al., 2013, 2015). A fragment of rostrum and isolated teeth have been referred to Ctenochasmatidae from the Upper Jurassic? – Lower Cretaceous of Uruguay (Perea et al., 2018). Finally, the specimens from Cerro La Isla reported by Martill et al. (2006) and those described in this work are the only records of Ctenochasmatidae in Chile.

5.3. The pterosaur colony

Bell and Padian (1995) proposed the existence of at least one large pterosaur colony that could have persisted over a long period of time, as an explanation for the high accumulation of bones (some of them belonging to immature individuals) in Cerro La Isla. However, there is no definitive evidence supporting this proposal for the moment. Firstly, the origin of the fossil bone accumulation is unknown. Bell and Padian (1995) mention that the pterosaur bones do not form conforms a bonebed, but instead are dispersed in a single stratum. The sedimentary characteristics of this horizon, the preservation and the random distribution of the bones indicate that they were transported. Based on these observations, Bell and Padian (1995) propose the possibility that the pterosaur remains may have accumulated over a long period of time and were subsequently reworked. Bell and Padian (1995) also mention the existence of bone clusters within areas of approximately one square meter, but without any degree of articulation. This observation, together with the relatively good and tridimensional preservation of individual bones (however frequently wroken), led Bell and Padian (1995) to propose an alternative hypothesis; that the fossiliferous site may have originated from cadavers or parts of cadavers having been dragged and deposited by the flow of sediments before they completely decomposed.

Secondly, there is no certainty that the accumulation of pterosaur bones in Cerro La Isla represents a single species, since there are few remains that have been studied in detail (Martill et al., 2006; this study). Bell and Padian (1995) mention the difficulty of the taxonomic assignment of the pterosaur remains due to the fragmentary state of many of them and the high degree of disarticulation. There are few cases in the world of associated pterosaur bones that can be confidently referred to the same species. The ctenochasmatid *Pterodaustro guinazui*, from lacustrine sediments of the Lagarcito Formation (Lower Cretaceous), Argentina (Chiappe et al., 1998a, b), together with the tapejarid *Caiuajara dobruskii*, found in lacustrine deposits of the Goio-Erê Formation (Upper Cretaceous), of the Caiuá Group, Brazil (Manzig et al., 2014) and the accumulation of eggs and bones of the pterosaur *Hamipterus tianshanensis* in the Lower Cretaceous of China (Wang et al., 2017) represent good examples of pterosaur bone beds.

The present study provides new evidence that reinforces the presence of ctenochasmatid pterosaurs at Cerro La Isla, as proposed by Martill et al. (2006). However, it is not possible to demonstrate that the mandibular fragment materials described by Martill et al. (2006) and those described in this work belong to the same species due to its fragmentary state. It is also not possible to associate the mandibular remains and cervical vertebrae, since we do not have information about the disposition of these remains in the field. The systematic collection of sufficiently informative new material is required in the future to determine whether the accumulated bones represent a single species. At the same time, new stratigraphic, sedimentological and taphonomic studies are necessary to determine the origin of the site and to evaluate the degree and type of preservation of the remains. This set of information will make it possible to determine whether or not there had been a colony of pterosaurs in Cerro La Isla.

6. Conclusions

The features present in the mandibular remains (SGO.PV.362, SGO.PV.377 and SGO.PV.378) and in the rostral fragment (SGO.PV.364) allow us to refer the new material to Ctenochasmatidae. The new informative portions of the skull indicate a pterosaur with an elongated and narrow rostrum with the teeth positioned at its edges and, as can be inferred from the incomplete dental crowns, anterolaterally orientated, as observed in members of the family Ctenochasmatidae. Additionally, we identifiy the presence of a juvenile individual, represented by the fragment of a rostrum. This discovery is consistent with the observations made by Bell and Padian (1995), who suggested the presence of a possible breeding colony, although taphonomic studies are necessary to corroborate this hypothesis.

from Solnhofer Formation, G. Ctenochasmatidae indet. from Quebrada Monardes Formation, H. Gnathosaurinae indet. from Tacuarembó Formation, I. ?Ctenochasmatidae indet. from Tendaguru Formation, J. *Kepodactylus insperatus* from Morrison Formation, K. *Liaodactylus primus* from Tiaojishan Formation. The proposed age for Gnathosaurinae indet. from Tacuarembó Formation (h) is tentative, since the precise age of the outcrops in which it was found is unknown (see text for details). On the other hand, the proposed age for Ctenochasmatidae indet. from Quebrada Monardes Formation (g) is tentative, which is based on detrital zircon U–Pb age obtained by Martínez et al. (2015) in Pulido River. The paleomaps were modified from Scotese (2014a,b).

Considering the morphology of the cervical vertebrae, SGO.PV.350 can also be referred to the Ctenochasmatidae. Assignment is based on the following characters: general proportions; lack of a tubular shape, the neural arch and vertebral centrum are clearly distinguishable; and the neural spine is low. The specimen SGO.PV.351 also presents a pair of oval pneumatic foramina on the lateral surfaces of the centrum, a feature that reinforces its placement in Ctenochasmatidae. In conclusion, we consider that both vertebrae belong to the same species and that the few morphological differences they present are related to their differing positions in the cervical vertebral sequence.

Based on differences in dental and cervical morphology, we consider the taxon from Cerro La Isla to be different from the Argentinian *Pterodaustro guinazui* as well as from the ctenochasmatids discovered in Uruguay. In addition, the dimensions of these vertebrae suggest the existence of a medium-sized ctenochasmatid species for Chile. Although it is likely that the materials described here and those previously reported by Martill et al. (2006), belong to the same species, it is not possible to support this hypothesis since it is not possible to associate the remains, and the fragmentary state of the materials it does not allow adequate comparisons.

The Quebrada Monardes Formation has a great potential for paleontological research based on the relative richness of vertebrate fossils and other records (burrows, footprints) reported to date in several sites. Further systematic collection efforts and detailed taphonomic studies are needed to address the unresolved problems at the site in Cerro La Isla, such as the accurate identification of the new pterosaur species and the confirmation of the existence of a breeding colony.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2020.104378.