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A new locality with ctenochasmatid pterosaurs (Pterosauria: Pterodactyloidea) in the Atacama Desert, Northern Chile

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ABSTRACT

We describe a new locality with ctenochasmatid pterosaurs found in a tidal estuarine paleoenvironment of the Quebrada Monardes Formation (Lower Cretaceous). The new locality, which is named "Cerro Tormento", is in Cerros Bravos in the northeast Atacama region, Northern Chile. Here, we describe four cervical vertebrae, one of them belonging to a small individual, the impression of a right scapulocoracoid, a left coracoid, an impression of a left humerus, an incomplete left humerus, a distal fragment of the right humerus, and impressions of a left femur and tibiotarsus. The presence of three humeri and a cervical vertebra belonging to a small pterosaur indicate that these materials represent more than one individual. The cervical vertebrae present diagnostic traits shared with ctenochasmatid pterosaurs, such as elongated vertebral centra, with integrated neural arch, low neural spines, and dorsally located neural canal. It is currently not possible to determine if there are one or more species represented. This finding is the second geographic occurrence of pterosaurs of the clade Ctenochasmatidae in the Atacama region, although it is currently uncertain if ctenochasmatids from both locations were contemporaneous. This suggests that the clade Ctenochasmatidae was widespread in what is now northern Chile. In addition, the presence of bones belonging to more than one individual preserved in Cerro Tormento suggest that pterosaur colonies were present at the southwestern margin of Gondwana during the Early Cretaceous.

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1. Introduction

The record of the Pterosauria in Chile is still scarce and most discoveries comprise fragmentary materials. Until now the most relevant fossil locality that yielded pterosaur remains in Chile is Cerro La Isla, discovered in 1988 by a team of geologists on the eastern side east of the Atacama Region (Bell and Suárez, 1989). In that locality previous authors reported a singular basin with an extensive layer mainly of sandstone and conglomerates that outcrops on the southern slope of Cerro La Isla, in which apparently hundreds of disarticulated bones are preserved (Bell and Padian, 1995). These deposits, assigned to Quebrada Monardes Formation, were interpreted as a result of a sudden flow of sediments (Bell and Padian, 1995). A rostrum, a possible dentary, and a proximal wing phalanx were described in 2006 by Martill and collaborators. These authors considered that they belonged to pterodactyloid

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pterosaurs of the clade Ctenochasmatidae, a group of pterosaurs characterized by having long necks and specialized dentition for filter feeding (Martill et al., 2006). Subsequent work has focused on the study of additional bones collected in that layer, which suggest that all these bones belong to pterosaurs of the clade Ctenochasmatidae (Alarcón-Muñoz et al., 2020).

In 2013, one of the authors (E.G.) and colleagues fortuitously discovered isolated bones and bone impressions in loose blocks of sedimentary rocks in Cerros Bravos, in the northeast Atacama Region. Subsequently, during field work carried out at the locality in December 2018, the layer in which the bones were preserved was identified (Alarcón-Muñoz et al., 2018). This locality, called here Cerro Tormento, in reference to the difficulty to access the site due to the slope and the high altitude (4200 m.a.s.l.), represents a new occurrence of pterosaurs from the Quebrada Monardes Formation, located approximately 65 km north from Cerro La Isla. The field work exposed several bones that were preserved disarticulated in a layer of sandstones and mud clast breccias, whose characteristics suggest that they were deposited in a tidal environment, unlike that interpreted in Cerro La Isla. Here, we describe pterosaur bones from Cerro Tormento. The remains correspond to well-preserved three-dimensional isolated bones, although mostly incomplete along with bone impressions. The fact that they are preserved three-dimensionally is particularly important, since most pterosaur bones are found crushed due to their great fragility (Unwin, 2006). Among the examples of Cretaceous pterosaurs three-dimensionally preserved are important finds made in Brazil, especially in Lower Cretaceous deposits of the Araripe Basin. Among these are pterosaurs such as *Tapejara wellnhoferi* Kellner, 1989, and *Caupedactylus ybaka* Kellner, 2013, among several other findings (e.g. Campos and Kellner, 1985; Kellner et al., 2013; Cerqueira et al., 2021). Additionally, in Upper Cretaceous rocks of the Goio-Erê Formation, Manzig et al. (2014) reported the discovery of a bonebed composed of hundreds of bones of pterosaurs three-dimensionally preserved, most belonging to the tapejarid *Caiuajara dobruskii* Manzig et al., 2014. A partial specimen preserved at this bonebed was identified as a different species, which was named *Keresdrakon vilsoni* by Kellner et al. (2019). The high bone accumulation led Kellner et al. (2019) to name this site as the "cemitério dos pterossauros".

The study of the pterosaur of Cerro Tormento can help answer more accurately questions related to the phylogenetic affinities of the pterosaurs of the Quebrada Monardes Formation to other pterosaur species from South America and the rest of the world.

1.1. Locality and geological setting

From the Late Jurassic to the Early Cretaceous, a dominant extensional regime in the southwestern margin of Gondwana, generated several retro-arc basins which were flooded by marine transgressions. These continental to shallow marine basins were connected to the proto-Pacific Ocean through narrow passages within the volcanic arc, characterizing a paleogeography similar to that currently present in the western Pacific (Chotin, 1981; Mpodozis and Allmendiger, 1993). Some of these marine basins were the Tarapacá, Chañarcillo and Aconcagua basins (Fig. 1A; Legarreta and Uliana, 1999, Aleman and Ramos, 2000; Ramos, 2009; Aguirre-Urreta et al., 2007; Ramos et al., 2019).

The Chañarcillo Basin was a NNE oriented retro-arc basin, with a linear and narrow configuration, generated at the east of the Lower Cretaceous volcanic arc (Punta del Cobre and Aeropuerto formations) and was filled with volcanic and sedimentary deposits of shallow marine, paralic and continental depositional environments of the Chañarcillo Group (Abundancia, Nantoco, Totoralillo and Pabellon formations) and Quebrada Monardes Formation (Fig. 1B; Mercado, 1982; Arévalo, 1995; Cornejo et al., 1998; Godoy and Lara, 1998; Lara and Godoy, 1998; Matthews et al., 2006; Mpodozis et al., 2012; Cornejo et al., 2013; Contreras et al., 2014; Mpodozis et al., 2018).

This stratigraphic record represents the last of the back-arc marine episodes in the north of Chile and gives evidence of the existence of corridors along which marine currents generated southward connections with the Aconcagua Basin and Neuquén Embayment during this period (Aguirre-Urreta, 2001; Mourgues 2004; Aguirre-Urreta et al., 2007; Fouquet, 2018).

The clastic deposits of the Quebrada Monardes Formation (300–~1000 m thick) have been interpreted as transitional to continental environments during Early Cretaceous times, located at the eastern edge of Chañarcillo Basin, and due to its wide geographical extension (26–29°S) different paleoenvironments have been described: lagoonal, estuarine, fluvial, alluvial and eolian systems (Muzzio, 1980; Mercado, 1982; Bell and Súarez, 1989; this paper). This formation conformably overlies shallow marine calcareous sandstones of the Pedernales and Lautaro formations of the Upper Jurassic–Lower Cretaceous (Muzzio, 1980; Mercado, 1982; Bell and Suarez, 1989; Cornejo et al., 1998; Mpodozis et al., 2018). The rocks of the Quebrada Monardes Formation extend for approximately 200 km in a north-south direction (26°–28°S and 69°–70° W; Bell and Suárez, 1989) and become thinner to the west where they probably interfinger with paralic and shallow marine deposits of the Pabellón, Nantoco and Bandurrias Formations, which comprise the Chañarcillo Group. Of these, the Bandurrias Formation represents the volcanic arc located to the west (Mercado, 1982; Arevalo, 1995).

The sparse fossils in the continental red beds of the Quebrada Monardes Formation, mainly pterosaur fossil bones and dinosaur footprints, have provided no specific ages. Marine fossils in underlying limestones of the Lautaro and Pedernales formations and Quebrada Vicuñita strata, indicate a Tithonian-Valanginian age for these successions (Arevalo, 1995; Mourgues et al., 2015; Mpodozis et al., 2018). However, recent questions have arisen concerning to the depositional age of this unit. A U-Pb detrital zircon analysis from a sandstone attributed to the Quebrada Monardes Formation, 105 Km south of Cerro Tormento gives a value *ca.* 94 Ma maximum depositional date, within the Cenomanian Stage (Mpodozis et al., 2018). Nevertheless, in the same work a conformable relationship of the Quebrada Monardes Formation with Lagunillas Formation is accepted, being the last unit assigned to the Upper Jurassic–lowermost Cretaceous. Therefore, the base of the Quebrada Monardes Formation would be, at least Early Cretaceous in age.

1.2. Stratigraphy

The new pterosaur-bearing horizon preserves several disarticulated bones. This layer corresponds to a 0.7–1.0 m thickness mud clast breccia and sandstone beds (Fig. 2) intercalated in the upper part of a 160 m thick succession of the Quebrada Monardes Formation exposed on the eastern flank of Cerro Tormento (4,200 m.a.s.l) in the Atacama Region, Northern Chile. It is located at 65 km north of the former pterosaur locality of Cerro La Isla, described by Bell and Súarez (1989), and Martill et al. (2006). This succession was measured at the eastern flank of Cerro Tormento (4200 m.a.s.l.) and consists of a set of red to brownish alternation of siliciclastic sandstones, siltstones and mudstones that reflect deposition in a tidal estuarine environment that overlies limestones from the Pedernales Formation. Principally based on Olariu et al. (2015) five sedimentary facies and two facies associations were determined.

1.2.1. Facies 1: Laminated mudstones and fine-grained sandstones

Facies 1(F1) represents a mixed sand and mud flat level that includes horizontal to sub horizontal mm-to cm thick dark purple to reddish mudstones and a minor proportion of fine-grained

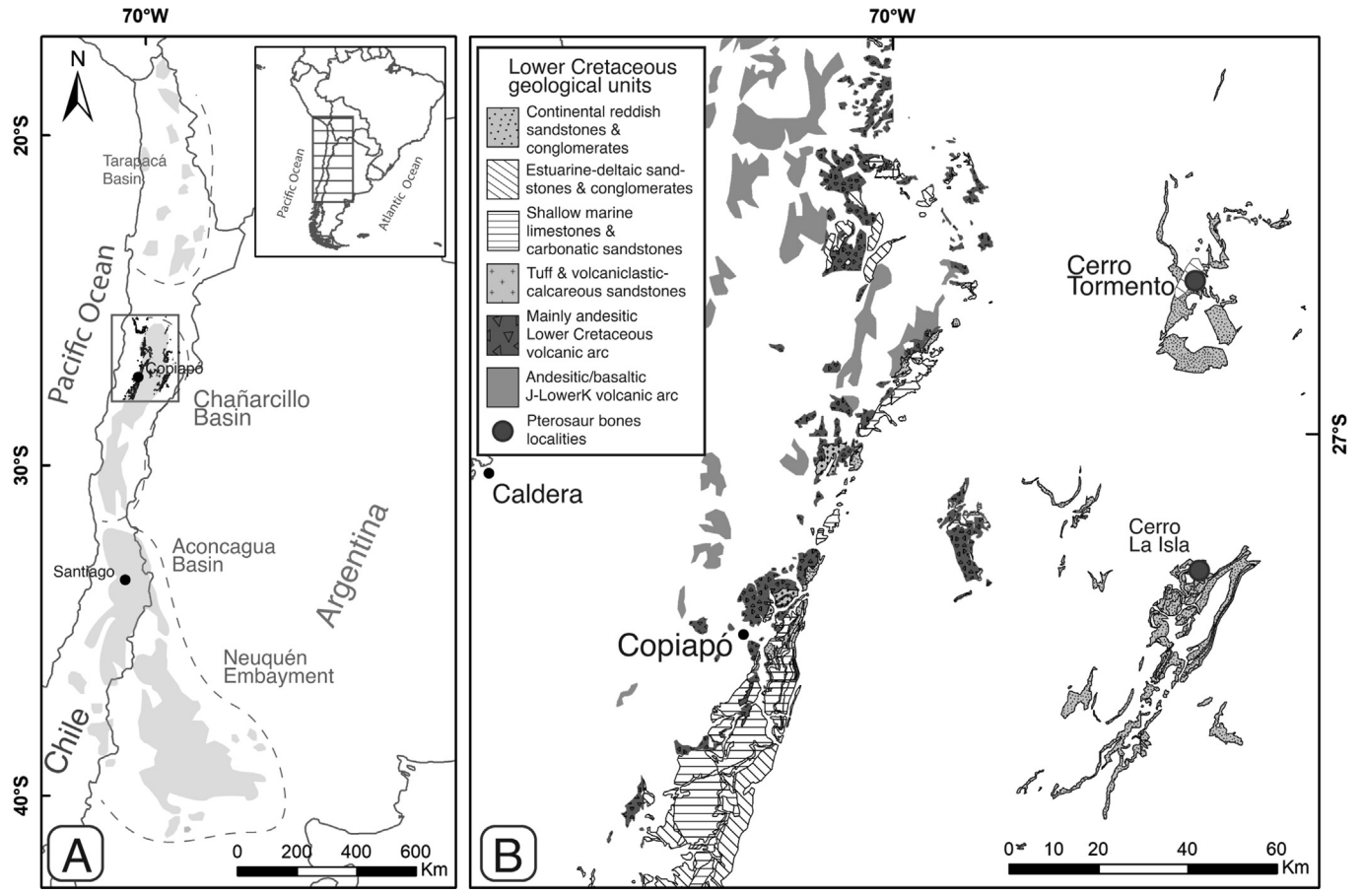


Fig. 1. A) The southwestern margin of Gondwana with the locations of Lower Cretaceous basins, modified from Aguirre-Urreta et al. (2007) B) Lower Cretaceous geological units of the Chañarcillo Basin and pterosaur bones localities: Cerro Tormento and Cerro La Isla. The geological units' polygons are based in (Arévalo, 1995; Cornejo et al., 1998; Godoy and Lara, 1998; Lara and Godoy, 1998; Matthews et al., 2006; Mpodozis et al., 2012; Cornejo et al., 2013; Contreras et al., 2014; Mpodozis et al., 2018).

sandstones (Fig. 3A) with gradual contacts to Facies 2 and frequent erosive surfaces at the top. Generally fining upward with rhythmic lamination (varve-type), desiccation and syneresis cracks, gypsum nodules, rain spots marks and locally horizontal bioturbations.

This facies, dominated by silt, represents a low-energy environment and a low sedimentary input, where rhythmic lamination was formed through cyclic deposition from suspension of slack water ponds and sandstones from low-density turbidity currents (Olariu et al., 2015; Tang et al., 2019). Rain spots, gypsum nodules, desiccation and syneresis cracks at top of mudstone levels indicate intermittent subaerial exposure (Tucker, 2003; Erin and Arnott, 2007; Boggs, 2009).

1.2.2. Facies 2: Rippled cross-laminated sandstone

Facies 2 (F2) is the dominant facies in Cerro Tormento, consists of unidirectional or less common bidirectional rippled cross-laminated fine to medium-grained sandstones. The grains are rounded and well-sorted with an important feldspar and lithic component; cement is siliceous to lightly calcareous. Rippled cross-laminated sets can be amalgamated, forming centimetric to decimetric thick beds with normal to reverse grading and occasionally separated by mm to cm thick mud layers (Fig. 3B). Other structures are flaser bedding, mud drapes, asymmetrical linguoid ripples and flute casts. F2 is variably bioturbated, ranging from no burrowing to intense bioturbation with *Planolites* isp. (Fig. 3C).

The rippled cross-lamination is interpreted as representing a subtidal or intertidal relatively low energy environment that can be widespread and unconfined as in an embayment or in the inner shelf, or confined within a channel (Olariu et al., 2015). The presence of oppositely directed ripples suggests reversing currents, and mud drapes on cross bed surfaces (foresets) and flaser bedding indicates periods of low flow velocity or of slack water in the trough of the dunes during tidal-current reversals (Fig. 2B; Reineck and Wunderli, 1968; Tucker, 2011; Olariu et al., 2012; Olariu et al., 2015). Local calcareous cement and variable rates of bioturbation indicate fluctuating salinity and sedimentation rates. In bioturbated levels (Fig. 3C), there was time for infauna to inhabit and churn Facies 2 (Pemberton et al., 1982; Tang et al., 2019).

1.2.3. Facies 3a: Planar stratified coarse pebbly sandstone

Facies 3a (F3a) consists in planar stratified coarse pebbly sandstone beds (Fig. 3D). It is present at the lower part of the section and is dominated by centimetric to decimetric alternations brownish of medium to very coarse-grained sandstones with fine to very fine feldspar and lithic pebbles and rounded quartz clasts in lag levels. The planar stratification is continuous and discontinuous in less cases. Beds range from 5 to 20 cm in thickness and may present normal grading. Flat and erosive top-base contacts and heterolithic intercalations are common. This facies rapidly upgrades to F4.

The relative bigger grain size and pebbly lag levels indicate high hydrodynamic conditions by strong subaqueous tractive current (Holz, 2003; Plint, 2010; Maahs et al., 2019), probably reflecting tractional transport during aggradation of longitudinal tidal bars (Miall, 1977, 1978).

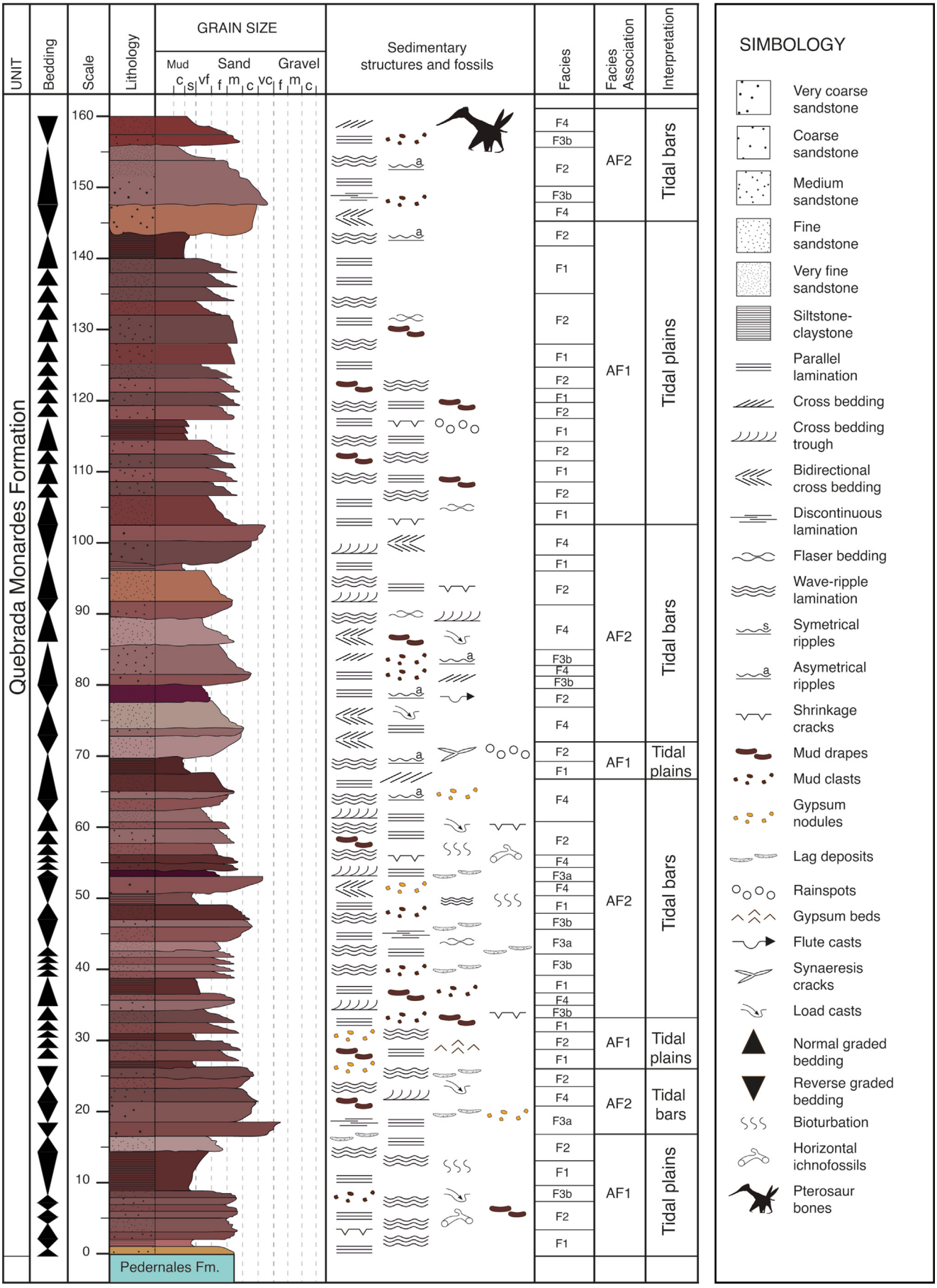


Fig. 2. Stratigraphic section of Quebrada Monardes Formation in Cerro Tormento locality.

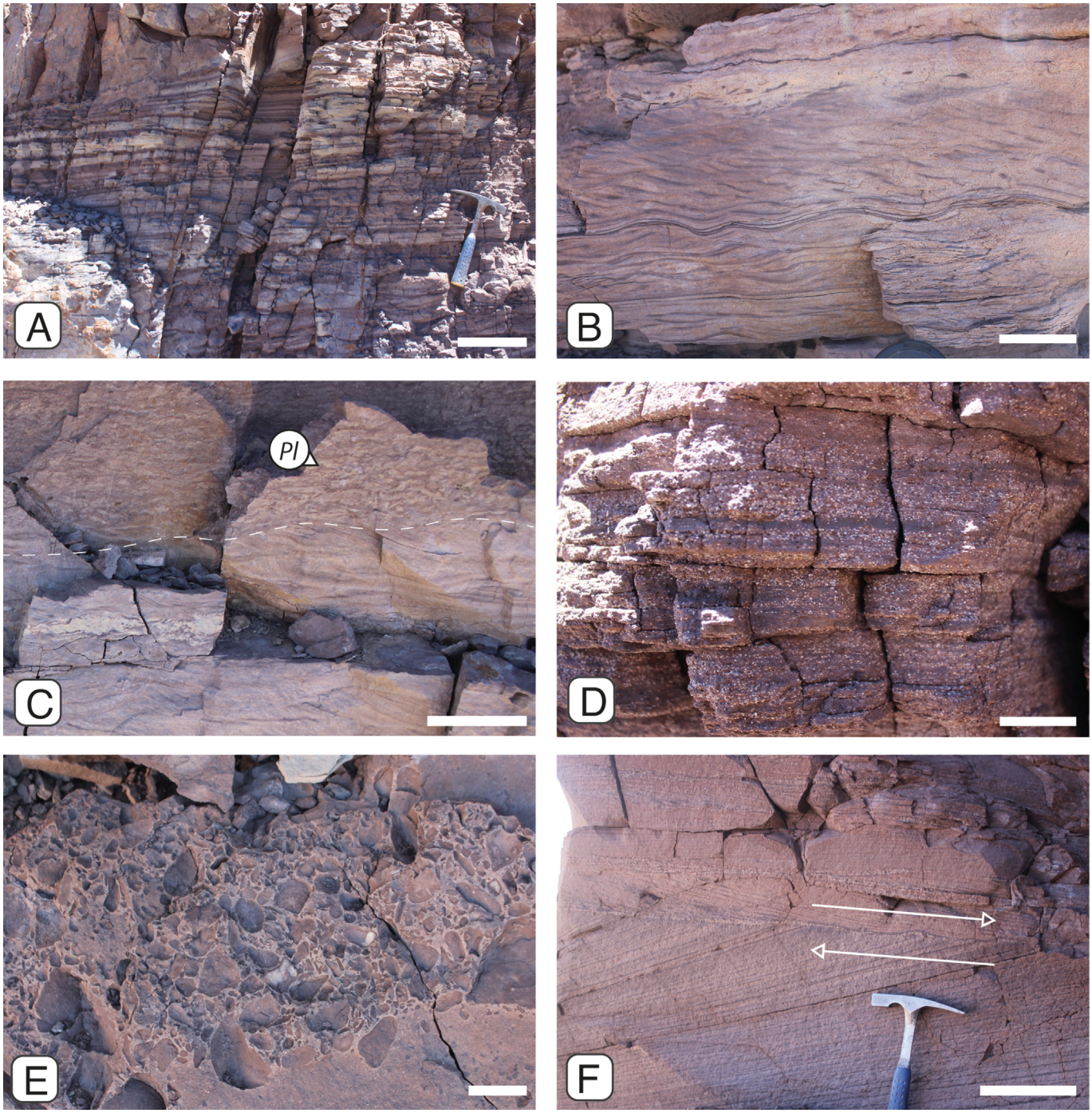


Fig. 3. Sedimentary facies in Cerro Tormento Section: (A) F1, laminated purple reddish mudstones and fine-grained sandstones; (B) Rippled cross lamination, flaser bedding and mud drapes in F2; (C) Rippled cross lamination and locally bioturbated sandstones in F2 *Pl*: *Planolites* isp.; (D) F3a, planar stratified coarse sandstone beds with rounded pebbles; (E) F3b mud clast breccia; and (F) Bi-directional crossbeds (herringbone cross stratification) in the lee-side area of a compound dune.

1.2.4. Facies 3b: Mud clast breccia

Facies 3b (F3b) is composed by reddish purple mud clast breccia beds that are 3–25 cm thick (Fig. 3E). This facies is matrix supported (60-55%), matrix is medium to fine gained sandstone, structureless to planar stratified. Clasts are planar "flakey" shape with very fine to coarse pebbles size (2–20 mm), slightly rounded to angular and locally imbricated. F3b generally is found an erosional based and is present at various stratigraphic positions, interbedded with gradual contact to F4. Disarticulated and apparently oriented pterosaur bones are found in F3b at the top of the section (Fig. 4A and B).

This facies is probably indicating reworking of previously deposited, thin, semi-lithified mud layers from intertidal or supratidal levels by flood tides when high energy currents agitate sandy sediments and mud clasts, forming high density and turbulent flows later deposited within tidal bars (Jablonski et al., 2016; Li et al., 2017). The high cohesiveness, "flakey" and angular shape of these clasts suggests minimal transport distances, due to short

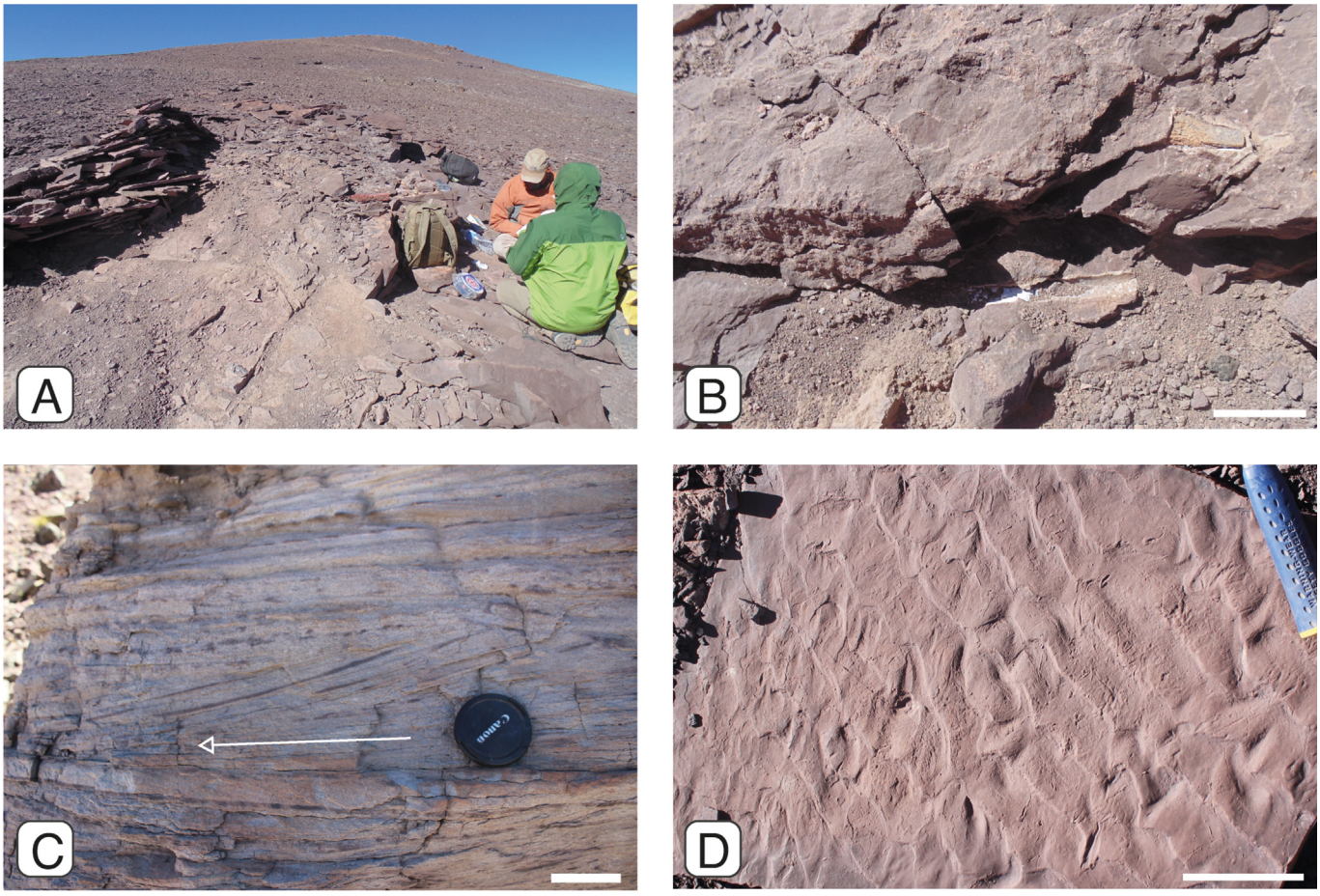


Fig. 4. (A) Site of pterosaur bones recollection; (B) Pterosaur bones at Facies 3b at the top of the section; (C) Inclined heterolithic lamination, note the thin mud drapes on the foresets and the ripples with mud drapes at the base of cross beds; (D) Asymetrical linguoid ripples in Facies 2 near the top of section.

periods (few hours) of each flood tide (Musial et al., 2012; Jablonski et al., 2016; Li et al., 2017). Pterosaur bones were probably transported by the same high density and turbulent flows, that are likely the result of upstream point bar erosion during fluvial or tidal flooding periods.

1.2.5. Facies 4: Cross-stratified sandstone

Facies 4 consists of series of upward coarsening units of cross-stratified unidirectional and bidirectional brownish medium to very coarse-grained sandstones (Fig. 3f) with occasional mud draped foresets (inclined heterolithic stratification) and thin mud layers (Fig. 4C). The cross strata are planar from low to high angle and set thickness range from 20 to 50 cm. It presents erosive and rarely channelized bases with load casts or gradual transitions from F3a and F3b. Calcareous cement and hummocky-like cross stratification in medium-grained sandstones were identified in few places.

Mud draped foresets, deposited during repeated slack water periods, and thick and orderly stacked sets of cross-stratified sandstones, with uni- and bidirectional paleocurrents, are believed to be consistent with tidal environments, indicating high energy tidal currents, probably confined by broad channels (Nio and Yang, 1991; Choi et al., 2004; Longhitano et al., 2012; Olariu et al., 2015; Tang et al., 2019). No indicators of subaerial exposures have been observed and most probably these dunes were formed in subtidal conditions. This facies association is interpreted as being a tidal bar deposit, and each up-coarsening unit is a single-stage tidal bar (Tang et al., 2019). The local hummocky-like cross-stratification are result of storm waves erosion (Tucker, 2011).

1.3. Facies association and paleoenvironment

With the conjunction and stacking of the previously described facies, two facies association were determined:

1.3.1. Facies Association 1: Muddy heterolithic inter-tidal deposits (tidal plains)

Facies Association 1 (FA1) is composed of intercalated F1 and F2 with wavy contacts and gradual transitions from F2 to F1. It has 5 to 40 m-thick silt deposits with fine to medium grained planar and rippled cross laminated sandstones. They are dominantly normal graded at the top of the section. The ripples are predominantly unidirectional but throughout the section they migrate in opposite directions. Sandstone beds are cm to dm thick and sometimes have lenticular like form. Locally presents 1–10 cm gypsum filled nodules.

FA1 is interpreted to be formed in an intertidal environment with weak bidirectional currents (Erin and Arnot, 2007). This environment evolves from aggradational to progradational at the top. Sand layers are laid down during high-energy ebb or flood tidal flow, while mud is deposited during low energy slack-water periods in between tidal flows (Chen et al., 2014). The systematic occurrence of mudstone drapes to mainly unidirectional ripples suggest a strong tidal influence and deposition in a fluvial channel

below the tidal limit (Tang et al., 2019). Filled gypsum cavities and mud cracks indicated dry and intense cyclic evaporation periods (Tucker, 2011) between tides, which allows FA1 to be interpreted as tidal plain deposits (Tucker, 2003; Erin and Arnott, 2007; Boggs, 2009).

1.3.2. Facies Association 2: Cross stratified tidal sandstone (tidal bars)

Facies Association 2 is mainly composed of F3a, F3b and F4 includes 8–30 m thick stacked bidirectional and unidirectional cross-stratified sandstones (individual beds 30–70 cm thick). The sandstone commonly presents mud drapes and thin mud layers. Local bioturbations occur in mudstones-wavy sandstone intercalations. The bases are principally sharp or erosional, usually presenting F3a or F3b. FA2 is dominantly normal graded at the top.

The deposits are interpreted as being tidal bar deposits, and each up-coarsening unit is a single-stage tidal bar (Tang et al., 2019) within an estuary mouth. The sharp and erosional bases of F3a, F3b that gradually pass to F4 suggest a broad channelized environment. Mud clasts breccias (F3b) indicates the erosion of a muddy sediment surface (tidal plains of FA1) by eddies in a passing turbulent current (Tucker, 2003) carrying them to the main tidal channel.

Observations of the stratigraphy suggest that the accumulation of pterosaur bones occurred in an estuarine environment, associated to tidal bar deposits, in which the tides would have had an important influence. It is probable that some specimens died in place or were carried short distances by the tidal flows, evidenced by the angular mud clasts (Li et al., 2017), previous to their deposition. Additionally, is possible that loose bones or specimens showing some degree of association were gradually buried by sediment that was washed away by the tides, or by river flooding.

2. Materials and methods

Most of the bones from Cerro Tormento are disarticulated and scattered throughout the stratum, which includes different parts of the axial and postcranial skeleton. The specimens are deposited in the Paleontology Area of the Museo Nacional de Historia Natural of Santiago de Chile (MNHN) under the code SGO.PV. The technical preparation of some of the fossils from this locality was carried out mechanically in the "Research Workstation" of the MNHN, and in the Laboratory of the Red Paleontológica U-Chile, in the Faculty of Sciences of the University of Chile.

3. Systematic paleontology

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Lophocratia Unwin, 2003
Archaeopterodactyloidea Kellner, 1996
Ctenochasmatidae Nopcsa, 1928

Ctenochasmatidae genus et sp. indet. (Figs. 5-6)

Material— four cervical vertebra of the middle series with the following numbers collection: SGO.PV.22800, SGO.PV.22801, SGO.PV.22804, SGO.PV.22815.

Cervical vertebrae. SGO.PV.22800 (Fig. 5) is an almost complete three dimensionally preserved middle cervical vertebra. It is procoelous, with a compressed neural arch, a little more integrated to the centrum than that observed in the ctenochasmatid vertebra from Cerro La Isla SGO.PV.350 (Alarcón-Muñoz et al., 2020). The transverse section of the middle zone of the vertebra is semicircular, with its dorsal surface flattened and its ventral surface convex. It can be appreciated in anterior view, that the cotyle is concave, its ventral margin is above the level of the ventral edge of the centrum. The preexapophyses correspond to rounded protrusions located under the base of the prezygapophyses; they are convex ventrally and concave dorsally. The anterior opening of the neural canal has an oval profile, with the horizontal axis greater than the vertical axis, and it is located dorsally with respect to the vertebral centrum. In the anterior section of the element, well conspicuous ventrolateral grooves arise almost from the base of both prezygapophyses, which continues posteriorly for approximately a quarter of the length of the element. The condyle is oval, well developed posteriorly, and is tilted laterally to the right. The ventral surface of the condyle is convex, while the dorsal surface is a little more flattened. The lateral surfaces of the condyle are approximately flattened and open slightly laterally. In ventral view, it is appreciated that the condyle arises from the vertebral centrum as ridges on both sides that separate like wings, diverging until reaching the postexapophysis. The postexapophyses are well preserved, especially the left, and they protrude from the condyle as small "rounded wings". Their articular surfaces are low and integrated with the condyle. In dorsal view, the neural spine was not preserved due to the erosion to which the vertebra was exposed. As a result, the filling of the neural canal is exposed, especially in the anterior half. The neural canal is approximately tubular.

The prezygapophyses and postzygapophyses of SGO.PV.22800 are well preserved and practically complete, except for the left prezygapophysis, which only retains its base. The right prezygapophysis is well developed, it exceeds anteriorly the level of the cotyle and is oriented laterally about 15° with respect to the main axis of the vertebra and rises slightly dorsally. The prezygapophyses show little lateral divergence and hardly rise dorsally, not exceeding the dorsal edge of the neural canal. The articular surface of the prezygapophysis is flattened and is directed dorsomedially. The postzygapophyses show great development, and do not exceed the posterior border of the condyle. The postzygapophyses are oriented dorsolaterally at an angle of about 30° with respect to the longitudinal axis of the vertebral centrum. The articular surfaces of the postzygapophyses are flat, oval in outline, and oriented ventromedially. In the ventral surface, the hypapophysis is observed, which is poorly preserved. The hypapophysis corresponds to a faint ridge that extends posteriorly from the cotyle to approximately one fifth of the element's extension. Due to deformation of the vertebra, the hypapophysis is displaced to the left. At this point, the hypapophysis is conspicuously protruding from the ventral edge of the vertebra. In its general dimensions, SGO.PV.22800 is less robust than the two vertebrae of ctenochasmatids from Cerro La Isla (Alarcón-Muñoz et al., 2020), being narrower in dorsal view and lower in lateral view.

Specimen SGO.PV.22801 (Fig. 6A-B) corresponds to a middle cervical vertebra preserved in two slabs. One of the slabs retains most of the element in dorsal view, while the other retains mostly its mold. SGO.PV.22801, like the other mid cervical vertebrae from Cerro Tormento, is elongated. It has a well-developed posterior condyle, which is quite expanded mediolaterally. The presence of postexapophyses integrated in the condyle is not clearly distinguished due to its poor state of preservation. The postzygapophyses are also not preserved. In dorsal and ventral view, the vertebral centrum has concave lateral surfaces, giving the vertebra an "hourglass" appearance. Because the vertebra lacks its midsection, the impression of the ventral surface is visible. A well-developed hypapophysis is observed, extending to at least the middle of the element. From posterior to anterior, the vertebra progressively expands mediolaterally, culminating in the prezygapophyses. Part of the left prezygapophysis is especially evident, which diverges slightly laterally, like SGO.PV.22800. In the impression of the dorsal surface of the vertebra, and in its anterior portion, it is possible to

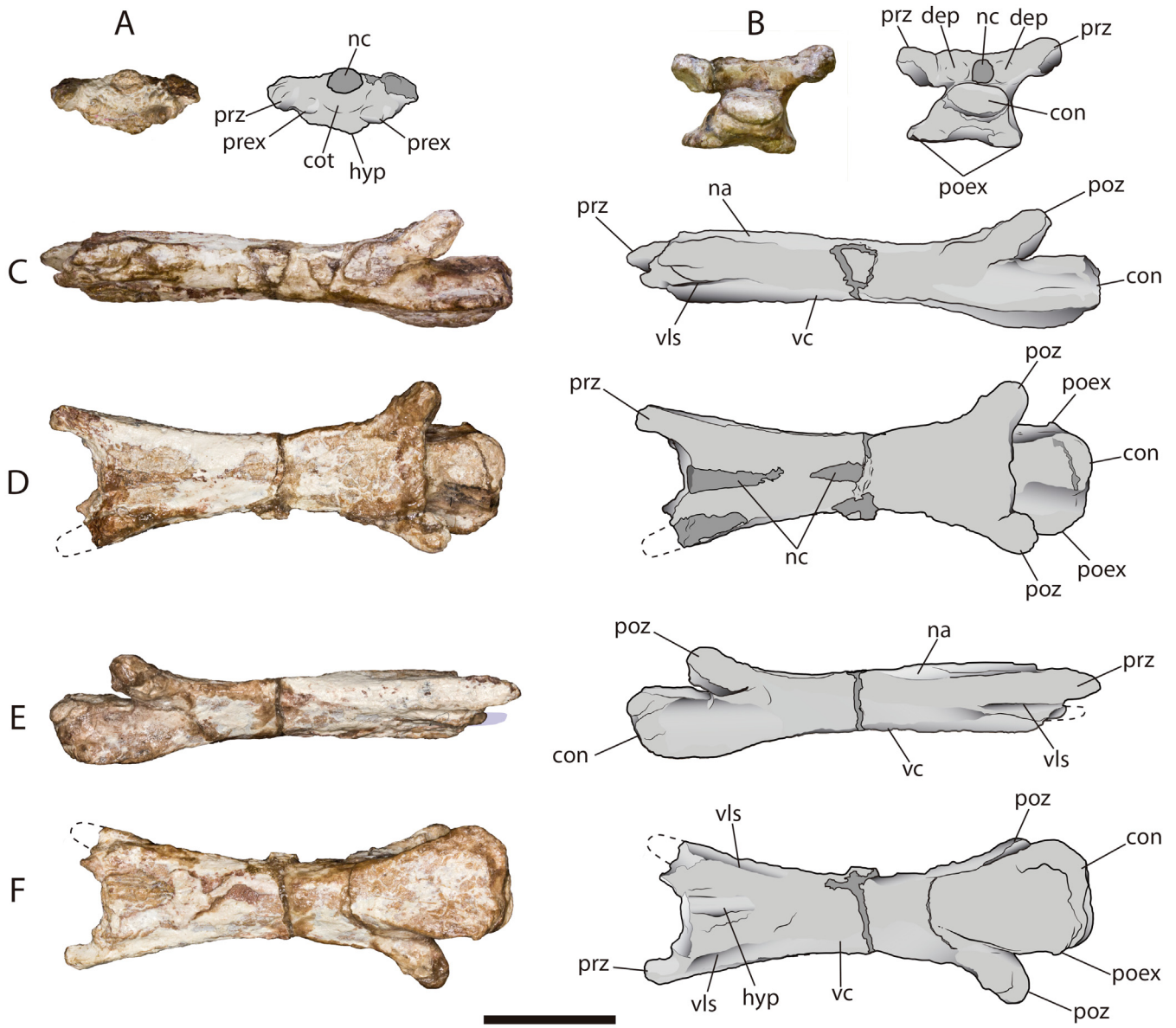


Fig. 5. Ctenochasmatidae indet., SGO.PV.22800, vertebra of the middle cervical series (left) and schematic representations (right), in anterior (A), posterior (B), left lateral (C), dorsal (D), right lateral (E) and ventral (F) views. Abbreviations: con: condyle; cot: cotyle; dep: depression; hyp: hypapophysis; na: neural arch; nc: neural canal; poex: postexapophysis; poz: postzygapophysis; prex: preexapophysis; prz: prezygapophysis; vc: vertebral centrum; vls: ventro-lateral sulcus. Scale bar: 20 mm.

observe the impression of the neural spine. This impression has a constant depth throughout the entire visible section (approximately 3 mm), which leads to the interpretation of a neural spine of relatively constant height, at least in that section.

Specimen SGO.PV.22804 (Fig. 6C) corresponds to a middle cervical vertebra represented only by the preserved posterior half in ventral view, while the rest of the element is preserved as the impression of its dorsolateral surface. The vertebra is elongated, its ends are expanded, and its lateral margins are concave, giving the vertebra an "hourglass" shape. The preserved portion of the vertebral centrum has an approximately tubular cross section, although its ventrolateral surfaces are almost flat. In the impression of the anterior portion, it is possible to see part of the neural spine, partially preserved as bone tissue embedded in the matrix and partially as an impression. It is difficult to elucidate its morphology, although it can be noted that the neural spine was long and low. Only the impression of the base of the right prezygapophysis is preserved, which is latero-anteriorly directed. The condyle is well developed, and its lateral margins were apparently straight, while its articular surface shows a closely convex profile. Judging from the preserved impressions, the postzygapophyses were elongated and projected posterolaterally. Unlike all the other vertebrae, this element is considerably small (see Table 1).

Specimen SGO.PV.22815 (Fig. 6D) corresponds to an incomplete middle cervical vertebra. Only the left prezygapophysis is preserved, which is robust and projected anteriorly, with a slight lateral displacement. Its lateral border is slightly convex while its medial border is concave and continues with the anterior border of the neural arch. The prezygapophysis has a medially oriented, rounded articular surface at its anterior end, with a slight dorsal orientation. The right lateral border of the neural arch is slightly concave and forms a lateral ridge that marks the boundary with the

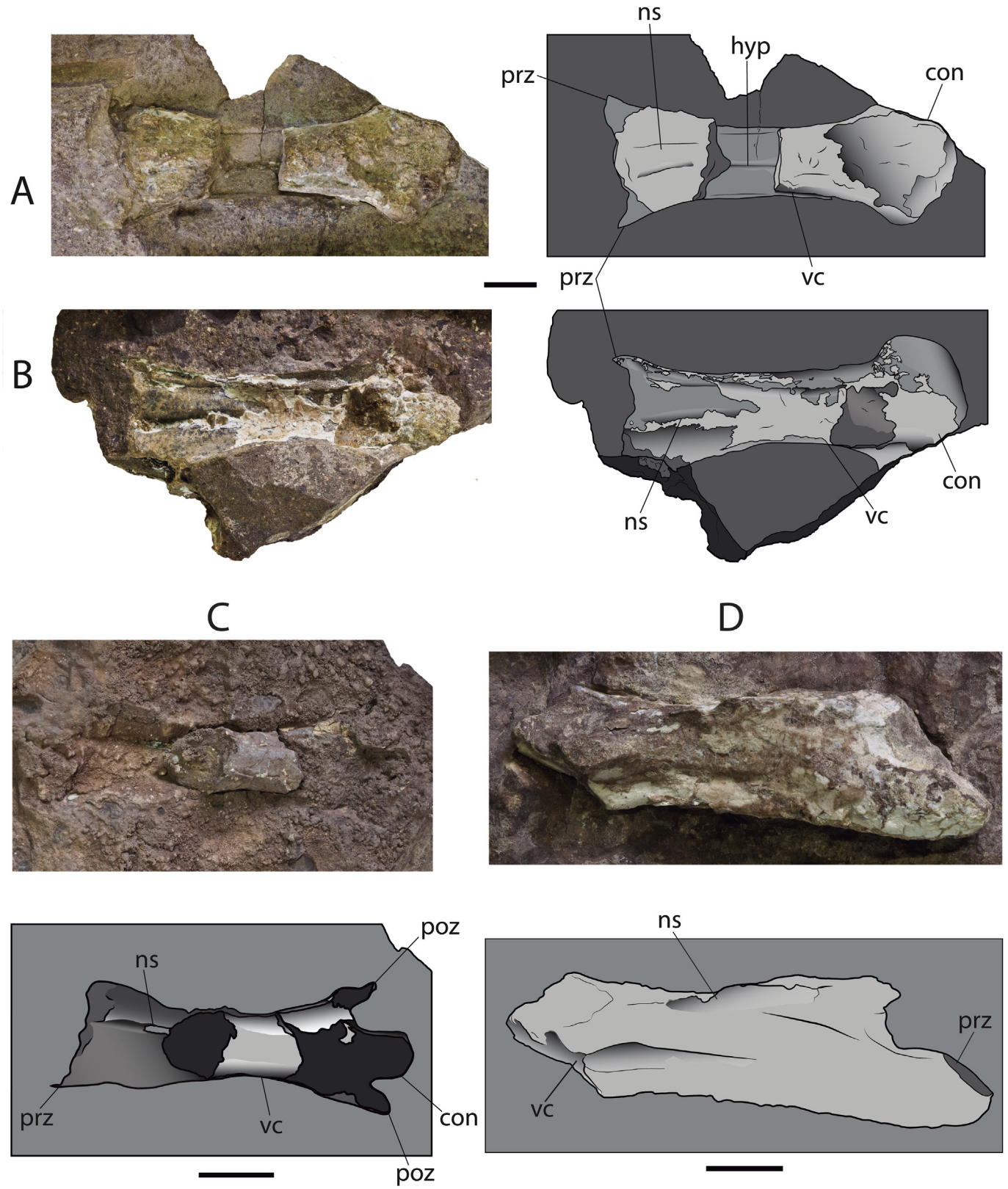


Fig. 6. Ctenochasmatidae indet., SGO.PV.22801, vertebra of the middle cervical series in dorsal view (A) and its cast (B) together with their respective diagrams. SGO.PV.22804, incomplete mid-series cervical vertebra in ventral view (C) and schematic interpretation. SGO.PV.22815, incomplete cervical vertebra of the middle series in dorsolateral view (D) and interpretive scheme. Abbreviations: con: condyle; hyp: hypapophysis; na: neural arch; nc: neural canal; ns: neural spine; poz: postzygapophysis; prz: prezygapophysis; vc: vertebral centrum; Scale bars: 10 mm.

Table 1
Measurements of cervical vertebrae in mm. The length of the centrum was taken from the ventral margin of the cotyle 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 the maximum preserved extent.

Specimen	Total length of centrum	Minimum width of the centrum	Minimum high of the centrum	Length of the hypapophysis	L/W Ratio
SGO.PV.22800	62.6	11.4	8.6	~10	5.5
SGO.PV.22801	~67.5	~16.1	–	–	~5.2
SGO.PV.22804	~46.4	7.7	–	–	~6
SGO.PV.22815	64.9[a]	~15	–	–	–

[a] Preserved.

vertebral centrum. The neural spine is partially preserved. This begins approximately 0.5 cm from the anterior border of the neural arch. The preserved section of the neural spine is low and maintains a relatively constant height.

Comparisons. Kellner (2003) proposed that elongated middle cervicals, but not to the same degree as in the Azhdarchidae, with low neural spines, are synapomorphies of the Archaeopterodactyloidea. This clade contains the Germanodactylidae and Euctenochasmatia, a group that in turn contains *Pterodactylus*, *Ardeadactylus* and Ctenochasmatoidea, which contains the Gallodactylidae and Ctenochasmatidae (Andres and Myers, 2013). A similar opinion is expressed by Unwin (2003), who mentioned that elongated cervical vertebrae with depressed neural arches and low, rectangular neural spines are diagnostic features of Euctenochasmatia.

Elongated vertebrae, with low, rectangular neural spines, and compressed neural arches are present especially in the clade Ctenochasmatidae. This group includes species such as *Gegepterus changae* Wang et al., 2007, *Elanodactylus prolatus* Andres and Ji, 2008, *Pterodaustro guinazui* Bonaparte, 1970, *Beipiaopterus chenianus* Lü, 2003, *Ctenochasma taqueti* Bennett, 2007, *Eosipterus yangi* Ji and Ji, 1997, and *Huanhepterus quingyangensis* Dong, 1982, which are characterized by having long compressed snouts, with fine, very closed spaced teeth.

A similar morphology to that described in vertebrae of the Ctenochasmatidae is observed in the Azhdarchidae, although in this group the neural arch is completely confluent with the vertebral centrum, forming a single tubular structure (Buffetaut et al., 1997; Martill et al., 1998; Unwin, 2003; Andres and Ji, 2008; Rodrigues et al., 2011; Buffetaut, 2012). As in the Ctenochasmatidae, the neural arch of the vertebrae of pterosaurs from Cerro Tormento, although depressed, remains distinguishable from the vertebral centrum (Unwin, 2003; Andres and Ji, 2008). Additionally, the elongation of the vertebrae from Cerro Tormento is not as marked as that described in the Azhdarchidae. In some azhdarchids such as *Quetzalcoatlus lawsoni* Andres and Langston, 2021, and *Arambourgiania philadelphiae* Arambourg, 1954, the cervical vertebrae are hyperelongated, with minimum centrum length/width ratios close to 12 in some species (Frey and Martill, 1996; Witton, 2007).

One feature observed in specimen SGO.PV.22800 that suggests that it belongs to a ctenochasmatid is the position of the neural canal. Martill et al. (2013) mentioned that in the Azhdarchidae the neural canal is centrally positioned, unlike the Ctenochasmatidae. In the specimen SGO.PV.22800, the neural canal is dorsally positioned, which contrasts with that described in the Azhdarchidae by Martill et al. (2013).

The cervical vertebrae of Cerro Tormento are procoelous, elongated, and with depressed neural arches. Some of them preserve evidence of a low and elongated neural spine. Its global morphology is like two middle cervical vertebrae attributed to the Ctenochasmatidae from Cerro La Isla (Alarcón-Muñoz et al., 2020). Like the middle cervical vertebrae of Cerro La Isla, the middle cervical vertebrae are elongated, and the neural arch is well integrated into the vertebral centrum. In addition, with the vertebrae of Cerro La Isla, in the SGO.PV specimen, it is appreciated that the neural arch is located dorsally, and not centralized, as in the Azhdarchidae. The fact that the cervical vertebrae of both localities coincide in morphology and in the geological unit of origin, suggests that the vertebrae of Cerro Tormento also belong to ctenochasmatids, and perhaps also the same species.

Archaeopterodactyloidea indet. (Figs. 7-10)

Materials—SGO.PV.22805, impression of a right scapulocoracoid associated with an incomplete tibiotarsus impression; SGO.PV.22810, left coracoid; SGO.PV.22806, impression of incomplete left humerus; SGO.PV.22807, distal portion of a left humerus

Table 2
Measurements in mm of the postcranial elements.

SGO.PV.22810	coracoid	total length 56.9	proximal width 16.7	middle width 7.2	distal width 19.3
SGO.PV.22805	scapulocoracoides	scapular length 25.5[a]	coracoidal length 38.9[a]	Anteroposterior length of the glenoid fossa 14.6	Dorsoventral height of the glenoid fossa 6.5
SGO.PV.22806	humerus	total length 100.6[a]	proximal width 21.6	middle width 9.6	width of the distal preserved end 16.8
SGO.PV.22807	humerus	total length 69.6[a]	width of the diaphysis 8.1	distal width 21.5	
SGO.PV.22808	humerus	total length 53.2[a]	width between ectepicondyle and entepicondyle 34.9	width of the diaphysis 16.1	
SGO.PV.22814	femur	total length 88.3[a]	dorsoventral height of the femoral head 13.8	length of the femoral neck 4.7	diaphysis width 8.1
SGO.PV.22805	tibiotarsus	total length 82.8[a]	width of the distal end 12.2		

[a] Preserved.

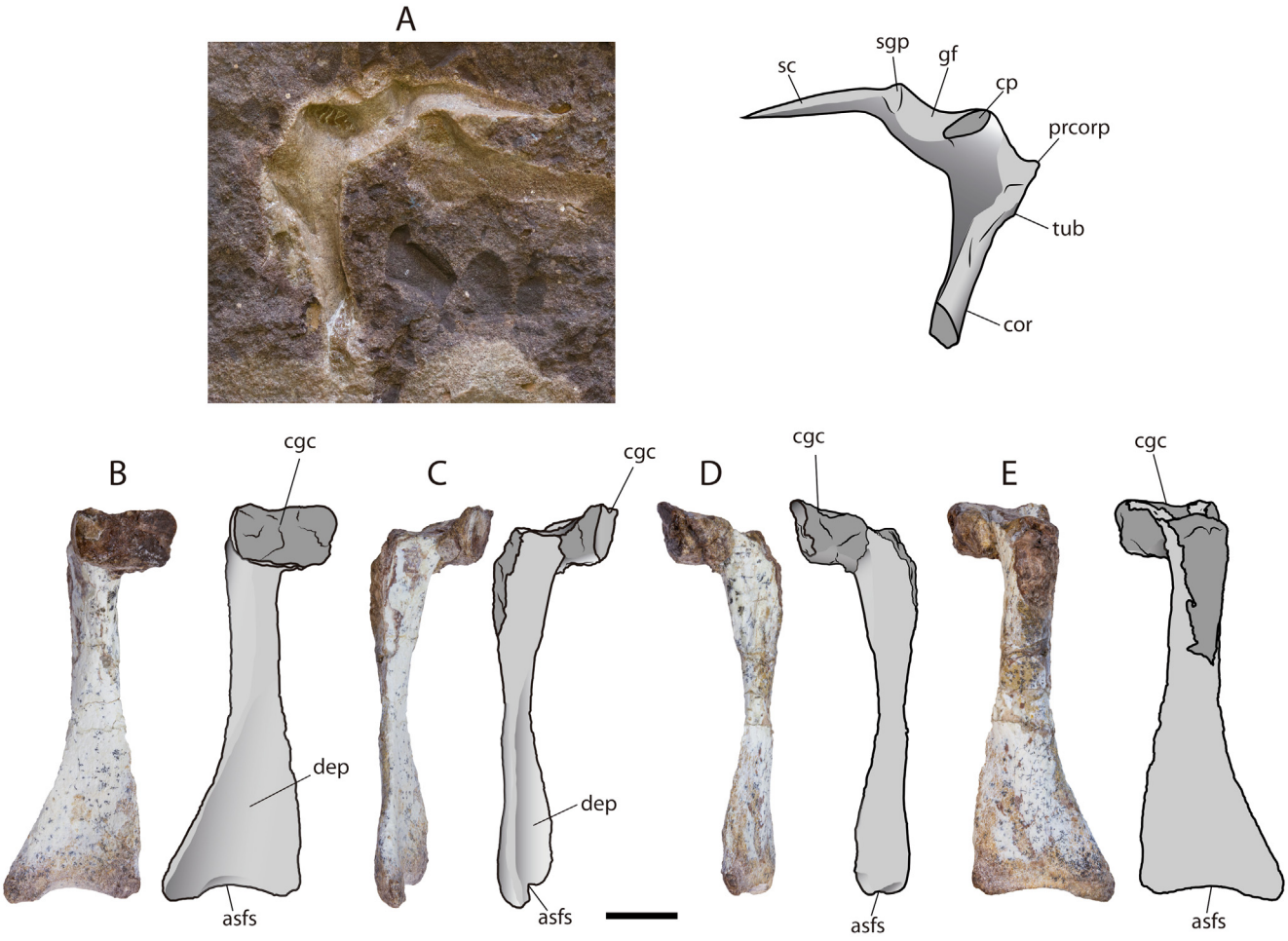


Fig. 7. Archaeopterodactyloidea indet., SGO.PV.22805, impression of a right scapulocoracoid (A) and schematic representation in lateral view from a silicone mold obtained from it. SGO.PV.22810, left coracoid in dorsal (B), posterior (C), anterior (D), and ventral (E) views and schematic interpretations. Abbreviations: asfs: articular surface for sternum; cgc: coracoidal glenoid cavity; cor: coracoid; cp: coracoid process; dep: depression; gf: glenoid fossa; prcorp: procoracoid process; sc: scapula; sgp: supraglenoid process; tub: tubercle. Scale bar: 10 mm.

preserved in a slab. SGO.PV.22808, distal section of right humerus; SGO.PV.22814, incomplete impression of the left femur.

Scapulocoracoid. Specimen SGO.PV.22805 (Fig. 7A) corresponds to a sandstone slab that preserves almost complete impression of a right scapulocoracoid in lateroventral view. A cast from the impression of the scapulocoracoid was made, which allowed a better description of this element (Fig. 7A). The scapula lacks the medial end. Its diaphysis is elongated and narrow, slightly curved and compressed dorsoventrally, with a thicker dorsolateral rim. The lateral end of the scapula is expanded, convex and it forms the posterior and dorsal part of the glenoid fossa, with a slightly subtriangular shape; this expansion is named here as a supraglenoid process. In *Pteranodon* this process is called supraglenoid buttress (Bennett, 2001). In addition, the lateral end of the coracoid is also expanded, robust, and forms the ventral region of the glenoid fossa. This thickening is named here the coracoid process.

Although the coracoid process is incomplete, its preserved portion suggests that it was more prominent than the supraglenoid process. The glenoid fossa remains almost complete, only lacking its most dorsal edge. The articular surface of the glenoid fossa is markedly concave, and it is saddle-shaped, a morphology that extends to its ventral edge, without the presence of any appreciable ridge. There is no evidence of a suture in the glenoid fossa separating the scapula from the coracoid. The coracoid lacks its medial end, the section that articulated with the sternum. The coracoid has a more robust constitution than the scapula. Its shaft is elongated, straight, and compressed anteroposteriorly, with a marked ventral ridge. The diaphysis expands anteriorly, separated some distance from the coracoid process, developing a marked procoracoid (Wellnhofer, 1991). Distally, from the procoracoid, there is a small tubercule.

Specimen SGO.PV.22810 corresponds to a left coracoid (Fig. 7B-E), is dorsoventrally compressed, and the preserved length is 56.9 mm (Table 2). The ventral surface (F) is almost flat, while the dorsal surface (C) is proximally flat and distally concave. The medial end of the coracoid that forms part of the glenoid fossa is robust, anteroposteriorly expanded, and concave in the center. The last feature is marked as coracoidal glenoid cavity in the specimen. The coracoidal tubercle is eroded. The shaft is anteroposteriorly narrow and slightly sigmoidal in its mid zone. The articular surface for the sternum (asfs) corresponds to the medial end; it is anteroposteriorlly wide with respect to the total length of the element, with a well-marked posterior expansion. This articular surface for the sternum is dorsoventrally narrow and proximally convex, with a concavity in the midpoint.

Comparisons. In adult pterosaurs, the scapula and coracoid fuse late in ontogeny and form a single bone, which can be V or U-shaped

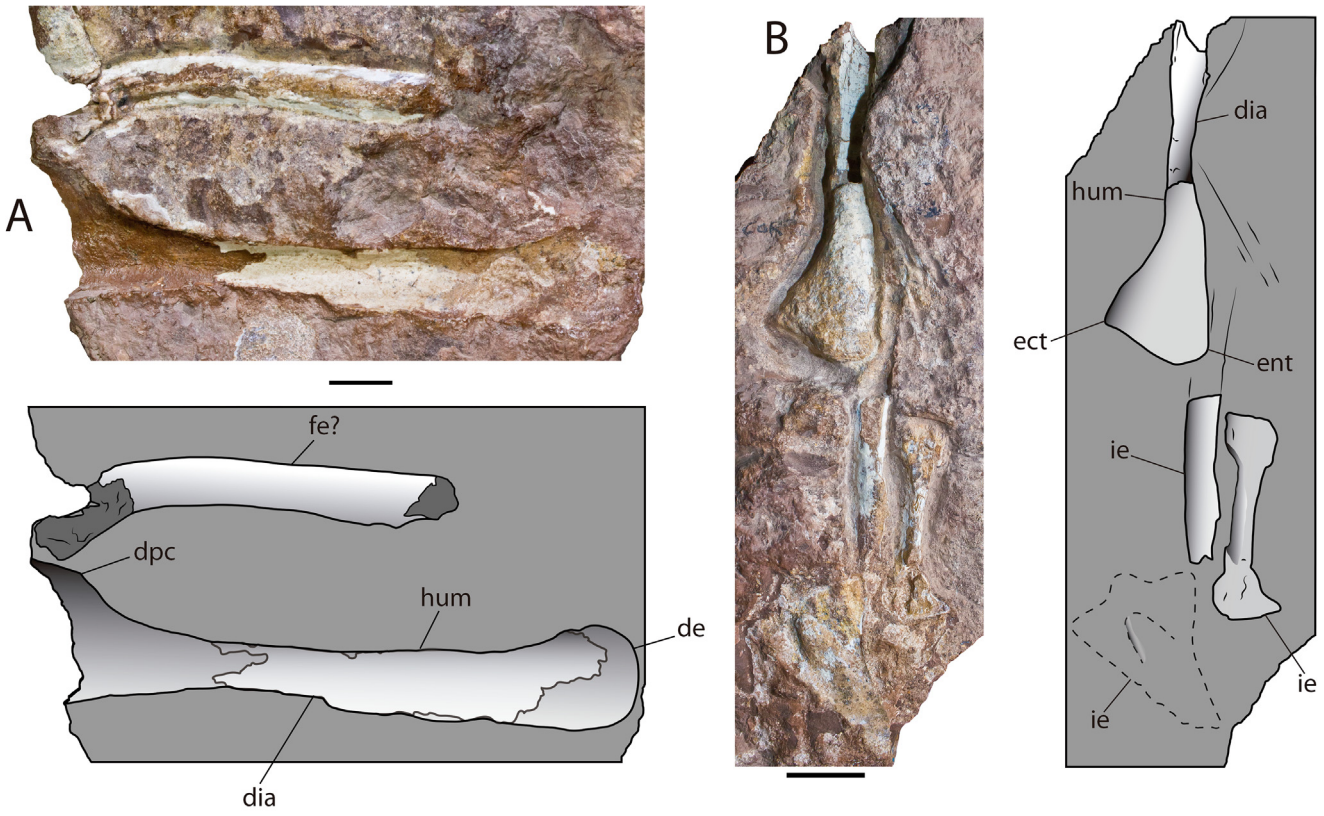


Fig. 8. Archaeopterodactyloidea indet., SGO.PV.22806, impression of the incomplete humerus and a fragment of an indeterminate appendicular element (A) and schematic interpretation. SGO.PV.22807, incomplete left humerus together with indeterminate elements, and schematic interpretation (B). Abbreviations: de: distal epiphysis; dpc: deltopectoral crest; dia: diaphysis; ect: ectepicondyle; ent: entepicondyle; fe?: femur?; hum: humerus; ie: indeterminate element. Scale bars: 10 mm.

(Wellnhofer, 1975; Bennett, 2001). Complete fusion of skeletal elements is one of the criteria proposed by Bennett (1993) to identify osteologically mature individuals. The absence of any suture signal between the scapula and the coracoid suggests that SGO.PV.22805 probably belonged to a mature individual, although this is difficult to ascertain from an impression. The glenoid fossa in SGO.PV.22805 is oriented anterolaterally, a feature that is proposed by Romer (1956) as a synapomorphy of the Pterosauria.

The morphological differences of the glenoid fossa of non-pterodactyloids and pterodactyloids appear to be related to the amplitude of movement of the humerus, which in turn is directly related to the morphology of the distal end of this element (Fujiwara and Hutchinson, 2012; Witton, 2015). In the Pterodactyloidea, the morphology of the glenoid fossa is described as "symmetric", since its dorsal and ventral articular surfaces are similar, and the latter does not present a ventral crest that limits the abduction of the humerus to a subvertical position, as in non-pterodactyloids (Witton, 2015). The morphology of the glenoid fossa provides clues about the posture of the forelimbs of a pterosaur when moving on land. This morphology allowed the pterodactyloids to acquire upright postures of the forelimbs when walking on land (Witton, 2015). The morphology of the glenoid fossa of SGO.PV.22805 is clearly symmetrical, without the presence of a prominent ridge on the ventral articular surface. Thus, this material is referred to the Pterodactyloidea based on its relatively large dimensions and in that the glenoid fossa is shared equally by the scapula and the coracoid. In contrast, in non-pterodactyloids the glenoid cavity is located mostly or completely on the scapula (Wellnhofer, 1975). Likewise, the scapulocoracoid SGO.PV.22805, is similar to the scapulocoracoid of *Pterodaustro* (L.C. *pers. obs*), as in that pterosaurs, apparently the two bones in SGO.PV.22805 are similar in length (subequal).

Humerus. Specimen SGO.PV.22806 (Fig. 8A) corresponds to the impression of an almost complete left humerus preserved next to the shaft of an indeterminate long bone (from the curvature it would seem an incomplete femur). A portion of the proximal end of the humerus is expanded with respect to the shaft, which corresponds to the impression of the deltopectoral crest. This structure curves anteroventrally, seems to be D-shaped and probably occupies approximately 30% of the length of the diaphysis. From the deltopectoral crest to the distal end, the element tapers very slightly, continuing in an approximately straight diaphysis, then gradually expanding again as it approaches the distal end. The distal end of the impression is markedly expanded with respect to the shaft, unfortunately no diagnostic morphological characters can be observed in this specimen, but they are preserved in other two fossils.

A distal portion of a left humerus (SGO.PV.22807, Fig. 8B) is exposed in posterodorsal view. The diaphysis is distorted, slightly sigmoidal and of approximately constant diameter in the preserved portion, culminating in a distal epiphysis that is especially expanded laterally.

Specimen SGO.PV.22808 (Fig. 9) corresponds to the distal end of a right humerus, very well preserved and almost tridimensional, with a sinuous distal edge. In anterior view, the distal epiphysis is greatly expanded with respect to the diameter of the diaphysis, an expansion that is given by the great development of the ectepicondyle and the entepicondyle. The ectepicondyle has a

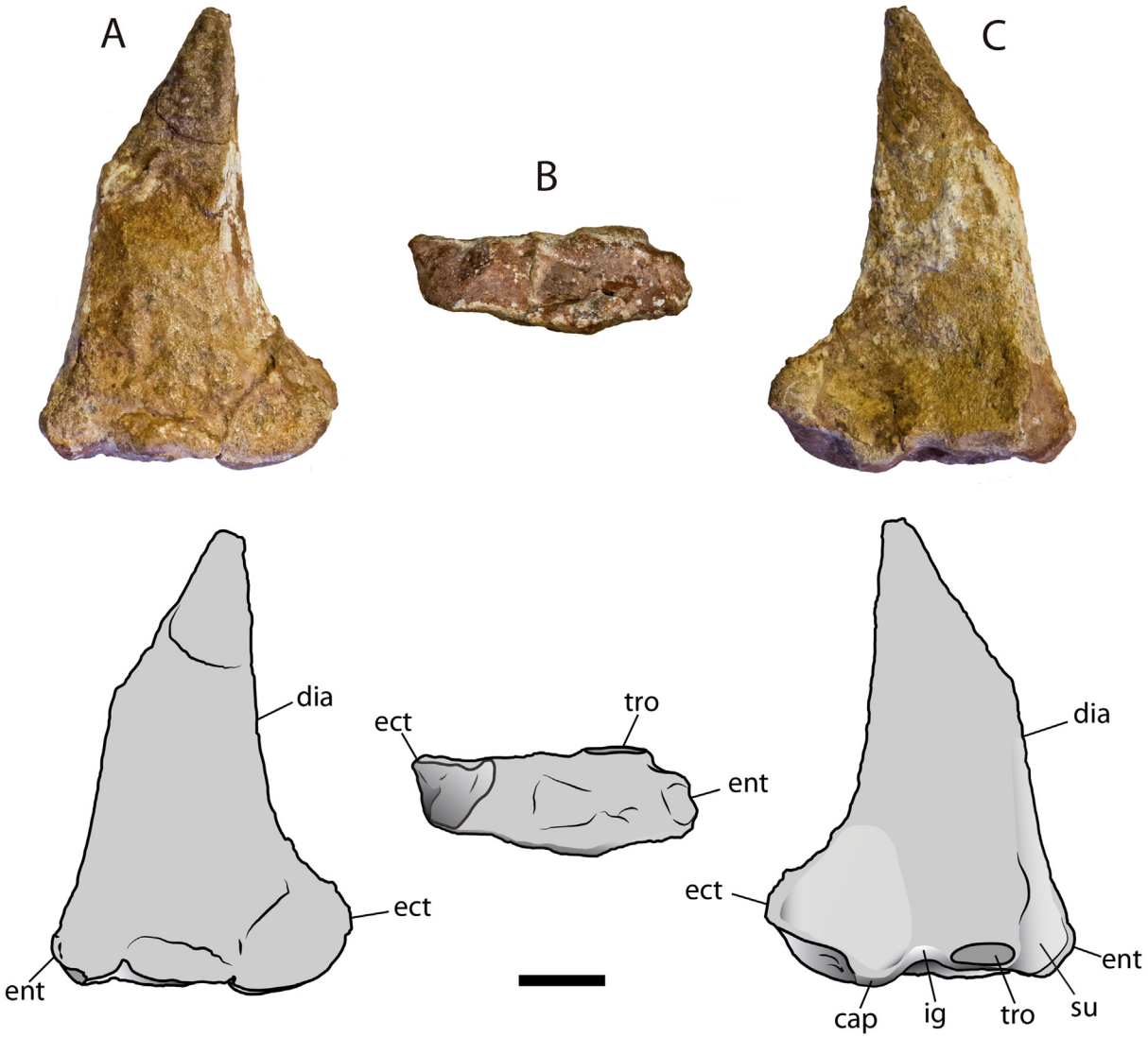


Fig. 9. Archaeopterodactyloidea indet., SGO.PV.22808, distal portion of the right humerus and their respective interpretative diagrams in posterior (A), distal (B) and anterior (C) views. Abbreviations: cap: capitulum; dia: diaphysis; ect: ectepicondyle; ent: entepicondyle; ig: intercondylar groove; su: sulcus; tro: trochlea. Scale bar: 10 mm.

subtriangular profile and is elevated relative to the level of the distal surface of the element, with its articular surface facing slightly anteriorly. The ectepicondyle limits a wide, but not very deep concavity restricted in the lateral half of the epiphysis, which extends to the edge of the distal end. The entepicondyle is less developed than the ectepicondyle. It has a rounded or elongated profile and is separated from the rest of the element by a groove that runs longitudinally along the proximo-distal axis of the bone, and it is deeper distally.

The trochlea (medial condyle) is partially eroded, and it is observed in anterior view, its profile is oval, with the lateral-medial axis longer than the proximal-distal one. The capitulum (lateral condyle) is oriented distally, it is oval shaped, with its most distal edge rounded. The capitulum and trochlea are separated by a well-marked intercondylar groove. In posterior view, expansion of the distal epiphysis is also evident; the entepicondyle shows the same rounded profile as in anterior view, and the ectepicondyle is conspicuously curved anteriorly. The dorsal edge of the bone is flattened along its entire length, while the ventral edge is concave. In distal view, SGO.PV.22808 has a subrectangular profile. Its posterior border is slightly convex, while the anterior border is slightly sinuous, although with a slight flattened elevation in its medial half, which is separated from the entepicondyle by the terminal of the sulcus that is described in anterior view. The entepicondyle sulcus is observed to be slightly displaced anteriorly. The subtriangular profile of the ectepicondyle is also observed, with its apex located well anteriorly and its lateral border obliquely in relation to the anteroposterior axis.

Comparisons. An expanded proximal humerus head (saddle-shaped) with a broad deltopectoral crest correspond to proposed synapomorphies for the Pterosauria (Romer, 1956; Wellnhofer, 1978). The deltopectoral crest has proven to be of systematic value in pterosaur phylogenies (Unwin, 2003). Unfortunately, in the only specimen that retains part of the deltopectoral crest (SGO.PV.22806), this structure is too incomplete for detailed comparisons. However, some conclusions can be drawn that would allow us to specify in a general way the systematic position of the pterosaur to which the humerus belonged. According to Kellner (1996), among pterodactyloids the deltopectoral crest has 3 types of basic morphology. The first type corresponds to deltopectoral crests that are located proximally and that are curved ventrally. This morphology is common in archeopterodactyloid and tapejaroid

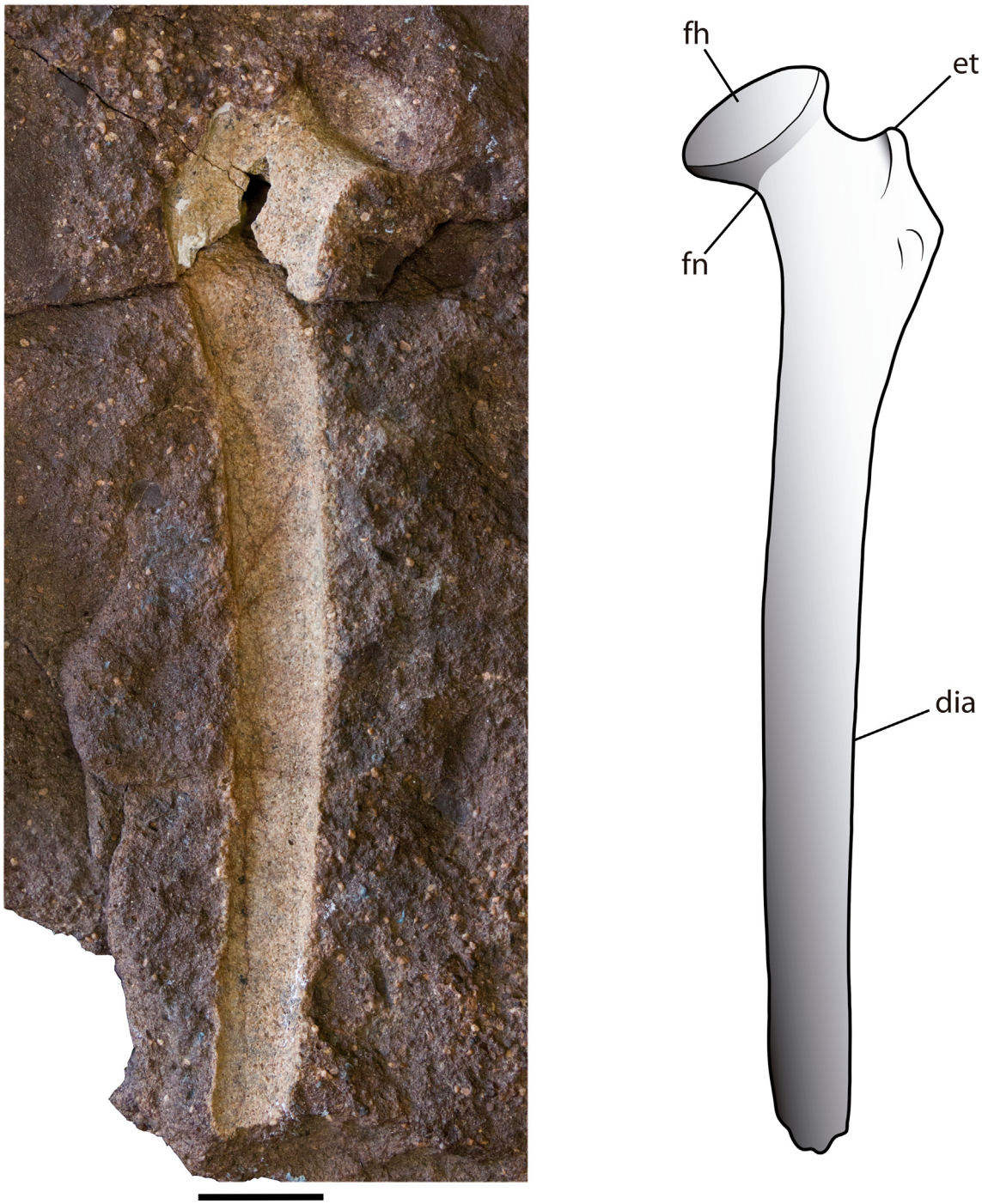


Fig. 10. Archaeopterodactyloidea indet., SGO.PV.22814. Impression of an incomplete left femur and schematic representation from a silicone counter mold. Abbreviations: dia: diaphysis; et: external trochanter; fh: femoral head; fn: femoral neck. Scale bar: 10 mm.

pterosaurs, which according to Kellner (1996), differs from that of all non-pterodactyloids. Examples of humeri with this deltopectoral crest morphology are observed in *Beipiaopterus chenianus* (Lü, 2003), *Gallodactylus suevicus, Pterodactylus kochi* (Wellnhofer, 1978) and *Pterodaustro guinazui* (Codorniú and Gasparini, 2007; fig. 1 in Codorniú et al., 2013). The second type is a distally displaced "hatchet-shaped" deltopectoral crests, a morphology that is characteristic of the Nyctosauridae (Kellner, 1991; 2003). This morphology of the deltopectoral crest is similar to that present in the Rhamphorhynchidae, but in them the deltopectoral crest is more proximally displaced (Kellner, 2003). The third type is the "warped" deltopectoral crests, typical of the clade Pteranodontoidea. A good example of this is the humerus of *Istiodactylus* (formerly *Ornithodesmus*) *latidens*, in which the deltopectoral crest practically rotates over the ventral surface of the bone (Hooley, 1913; Wellnhofer, 1978; Bennett, 1989). The deltopectoral crest of *Hatzegopteryx thambema* (Buffetaut et al., 2002) is much more developed; its upper and lower edges form a right

angle with respect to the longitudinal axis of the diaphysis. Judging by the visible portion in the Chilean specimen (SGO.PV.22806), the morphology of the deltopectoral crest does not agree with that observed in the Rhamphorhynchidae or Nyctosauridae (Wellnhofer, 1975, 1978; Kellner, 1991, 2003; Padian, 2008; Andres et al., 2010), and also differs from that present in the Azhdarchidae. The new specimens SGO.PV.22807 and SGO.PV.22808, show some features with informative value for the resolution of their systematic position. These fragments of the distal end of the humerus show an expanded distal epiphysis in relation to the diaphysis, due to the great development of the ectepicondyle and entepicondyle (principally the ectepicondyle), while their condyles (capitulum and trochlea) are proportionally reduced (SGO.PV. 22808). The great expansion of the distal portion of the humerus with respect to the diaphysis, due to the great development of the ectepicondyle and entepicondyle, and with underdeveloped condyles, constitutes a well-extended feature in the Pterodactyloidea (Fujiwara and Hutchinson, 2012; Witton, 2015). Fujiwara and Hutchinson (2012) describe a close relationship between the morphology of the distal humerus and the posture of the forelimbs in extant quadrupeds. These authors found a very close relationship between the degree of expansion of the distal end of the humerus, the degree of development of the condyles, and the posture they maintained when moving on land. It was found that expanded distal humerus ends with little development of the condyles seem to be related to upright postures of the forelimbs when walking on the ground, a feature that would characterize most pterodactyloids, while reduced distal humerus ends, with little development of the ectepicondyle and entepicondyle and great development of the condyles would be related to a more open posture of the forelimbs during their displacement on land, a trait that would characterize most non-pterodactyloids (Witton, 2015).

The morphology of SGO.PV.22808 agrees with what can be observed in members of the Pterodactyloidea, which also suggests that in life the extremities of this pterosaur would have remained upright during its movement on land. This type of morphology indicates a greater predominance of habits that imply movement on land, a characteristic that seems to have been well extended in the members of the clade Lophocratia, which includes pterosaurs for which a greater degree of activity in the terrestrial environment is inferred than those that integrate other more basal clades (Witton, 2013).

Bennett (2001) mentioned the shape of the distal epiphysis of the humerus as being of diagnostic value. Bennett (2001) and Kellner (2003) propose as a diagnostic feature of the clade Pteranodontoidea the subtriangular shape of the distal epiphysis of the humerus when observed in distal view. According to these authors, this morphology differs from the "D", oval or rectangular shape found in azhdarchoids. A similar proposal is made by Unwin (2003). He proposes that the triangular contour of the distal epiphysis in distal view is diagnostic for the clade Ornithocheiroidea, which is defined by this author as the most recent common ancestor of *Istiodactylus latidens* and *Pteranodon longiceps* plus all their descendants, and which includes a *Istiodactylus*, Ornithocheiridae, Pteranodontidae and *Nyctosaurus*. In contrast, Unwin (2003) mentions that in non-Ornithocheiroid pterosaurs the profile of the distal end is subrectangular or has a "D" shape. The distal view of SGO.PV.22808 clearly shows a subrectangular to D-shaped profile, which suggests ruling out the inclusion of the pterosaur to which this humerus belonged in the clade Pteranodontoidea proposed by Kellner (2003) and in the clade Ornithocheiroidea proposed by Unwin (2003).

The great expansion of the distal epiphysis and the very reduced condyles in relation to this expansion make it possible to assign SGO.PV.22808 to the Pterodactyloidea, while the non-triangular shape of this element in distal view makes it possible to rule out its inclusion in the Pteranodontoidea clade defined by Kellner (2003) and in the Ornithocheiroidea clade defined by Unwin (2003). This suggest the possibility open that SGO.PV.22808 belongs to a pterosaur of the clade Archaeopterodactyloidea.

Femur. Bone and impression of much of the anterior surface of a left femur is preserved in two blocks (SGO.PV.22814, Fig. 10). A cast from the impression of the femur was made, which allowed a better description of this bone. The specimen consists of the proximal end, almost complete shaft, and lacks the distal epiphysis. The total length preserved is 88.3 mm (Table 2). The shaft of the femur expands laterally from approximately one third of the length of the element in other pterosaurs (Young, 1964; Bonaparte, 1970; Kellner and Tomida, 2000). This lateral expansion is not evident in the preserved shaft of SGO.PV.22814. Based on this observation, the element lacks approximately one third of its total length, and the estimated total length is around 14 cm. The proximal end shows a well-developed femoral head, with a diameter greater than that of the diaphysis, with a rounded convex articular surface, with a dorsomedial orientation. The femoral neck is short and wide, and constricted in the middle. The approximate diameter in the narrowest area of the femoral neck is 70% of the diameter of the femoral head. The orientation of the femoral head with respect to the longitudinal axis of the shaft (specifically with respect to its medial surface) is approximately 130°. The diaphysis curves slightly medially and to a lesser extent anteriorly, and practically does not vary in diameter in the preserved section. The external trochanter, also called the great trochanter or greater trochanter (Bennett, 2001) is well developed, projects dorsomedially but does not exceed the median constriction of the femoral neck. Its shape is subrectangular, with its blunt proximal end. The external trochanter arises from the lateral surface, slightly below the level of the base of the femoral neck, continuing proximally obliquely with respect to the longitudinal axis of the diaphysis as a crest, which protrudes anteriorly. The external trochanter of SGO.PV.22814, as in most pterosaurs, gradually fuses distally into the diaphysis (Rauhut et al., 2017). It is not possible to observe the internal trochanter or the presence of any foramen on the intertrochanteric surface because there is a fracture in this zone.

Comparisons. In general, the femora of non-pterodactyloid pterosaurs are characterized by having straight shafts (Kellner, 1996). This can be seen in the femur of *Campylognathoides zitteli* (Plieninger, 1894; Wellnhofer, 1978), *Dorygnathus banthensis* (Theodori, 1852; Wellnhofer, 1978) and *Rhamphorhynchus muensteri* (Wellnhofer, 1975, 1978). In contrast, in the Pterodactyloidea the diaphysis is usually curved antero-medially, although the degree of curvature varies according to the species (Kellner, 1996). Examples of pterodactyloids with antero-medially curved shaft include *Pteranodon* (see Eaton, 1910; Wellnhofer, 1978; Bennett, 1991, 2001), *Nyctosaurus gracilis* (see Williston, 1903), *Dsungaripterus weii* Young, 1964, and *Herbstosaurus pigmaeus* Casamiquela, 1975. However, the pterodactyloid *Istiodactylus latidens* (previously *Ornithodesmus latidens*) has a femur whose diaphysis is quite straight, unlike the other pterodactyloids mentioned (Hooley, 1913; Wellnhofer, 1978). Relatively straight diaphyses are also observed in the femora of *Pterodactylus longicollum* (see Wellnhofer, 1970, 1978) and *Gallodactylus suevicus* (see Plieninger, 1907; Wellnhofer, 1978), although in the former the diaphysis presents a slight anteromedial curvature. The diaphysis of SGO.PV.22814 is slightly curved medially, and to a lesser degree anteriorly, in agreement with what is observed in most of the pterodactyloids. The shaft of the femur of *Anhanguera piscator* is slightly straighter than that of SGO.PV.22814 (Kellner and Tomida, 2000). On the other hand, the shaft of the femur of *Dsungaripterus weii* curves both anteriorly and medially more markedly than in SGO.PV.22814 (Young, 1964). In

the femur of *Pterodaustro guinazui* there is also a noticeable anterior curvature (Bonaparte, 1970; Codorniú et al., 2013). The marked curvature of the femur in two planes (both anteriorly and medially) has been cited as a diagnostic characteristic of the Dsungaripteridae (sensu Unwin, 2003), a proposal made mainly based on observations made in *Dsungaripterus weii* (Unwin, 2003; Fastnacht, 2005). However, this bidirectional curvature of the femur is also observed in other pterosaurs, such as *Dimorphodon* (see Padian, 1983), and in the pterodactyloid femurs mentioned above. This suggests that this trait is actually widespread among pterosaurs, especially among pterodactyloids (Unwin, 2006).

The shape of the femoral neck and head, together with their orientation with respect to the shaft, allow, to some extent, to discriminate between the different forms of known pterosaurs. Constrained necks that separate the femoral head from the rest of the element is a typical characteristic in pterosaurs, being proposed as a synapomorphy of the Pterosauria (Kellner, 1996; Kellner and Tomida, 2000). Among femora of non-pterodactyloids, SGO.PV.22814 differs from that of *Campylognathoides zitteli* in that in the latter the femoral head is oriented at a greater angle with respect to the diaphysis and there is practically no difference between the diameter of the head and of the femoral neck (Plieninger, 1894; Wellnhofer, 1978). SGO.PV.22814 differs from the femur of *Dorygnathus banthensis* in that the proximal portion of the element (from which the femoral head arises) is bulbous, and narrows distally, giving rise to a straight diaphysis (Theodori, 1852; Wellnhofer, 1978). In contrast, SGO.PV.22814 does not present this bulbous of the proximal portion, but rather continues distally in a slightly curved diaphysis with a relatively constant diameter. SGO.PV.22814 also differs from the femur of *Rhamphorhynchus muensteri* in that in this species there is little differentiation between the head and the femoral neck, not presenting a markedly constricted neck (Wellnhofer, 1975). Regarding pterodactyloids, SGO.PV.22814 differs from the femur of *Caiuajara dobruskii* (Azhdarchoidea, Tapejaridae) in that it has a proportionally longer, unconstrained, and more dorsally oriented femoral neck, and the external trochanter projects more dorsally, generating a more marked concavity between it and the dorsal surface of the femoral neck. These traits remain uniform throughout the ontogeny of this animal (Manzig et al., 2014). The femora of azhdarchids (Azhdarchoidea, Azhdarchidae) are poorly understood (Buffetaut et al., 2002), so making comparisons with members of this group is more complicated. For example, *Azhdarcho lancicollis* (see Nessov, 1984; Averianov, 2010) only conserves the proximal portion of the femur. This, unlike SGO.PV.22814 has a much narrower and elongated neck, with a constant thickness throughout its length, oriented at a much greater angle with respect to the diaphysis, as is characteristic of the clade Ornithocheiroidea (see discussion below) ending in a proportionally much smaller head, and also has a higher and sharper greater trochanter (see Averianov, 2010). On the other hand, the femur of *Zhejiangopterus linhaiensis* (M1323) is almost completely known, but few features are distinguishable in the femur illustrated in Cai and Wei (1994), although there are notable differences with SGO.PV.22814, mainly in its proximal portion. The femoral neck in *Zhejiangopterus linhaiensis* is proportionally shorter and is not constricted, but in anterior view its sides are approximately parallel, and also the angle between the femoral head and the diaphysis is greater, being markedly directed dorsally, as is common in the Ornithocheiroidea (Unwin, 2003). SGO.PV.22814 differs from the femur of *Anhanguera piscator* in that in this species there is less difference between the diameter of the femoral head and the femoral neck (Kellner and Tomida, 2000). A developed "mushroom-shaped" femoral head with a narrow neck has also been described in *Dsungaripterus weii*, a member of the Dsungaripteridae (Fastnach, 2005). However, in this species the femoral neck is proportionally longer than in SGO.PV.22814. In Chile, remains of a specimen belonging to the Dsungaripteridae have been recorded, which was given the name *Domeykodactylus ceciliae* by Martill et al. (2000). However, the femur of this species is unknown, and it is not possible to make comparisons. This morphology is also observed in the femur of the pterodactyloid *Herbstosaurus pigmaeus* (see Casamiquela, 1975), a pterosaur found in the Vaca Muerta Formation (Upper Jurassic, Tithonian), whose femoral neck appears to be shorter than in *Dsungaripterus weii*, keeping a greater similarity with SGO. PV.22814. The femur from Cerro Tormento bears a remarkable similarity with a femur not yet formally described referred to in cf. *Ardeadactylus* sp., figured in Rauhut et al. (2017), specifically in the morphology of the proximal epiphysis. As in SGO.PV.22814, this femur has a mushroom-shaped head separated from the diaphysis by a relatively short neck and constricted in its middle area. In addition, the femur of cf. *Ardeadactylus* sp. has a similar morphology and separation between the external trochanter and the lateral tuberosity. In the opinion of Rauhut et al. (2017), this femur probably belongs to the species *Ardeadactylus longicollum*, which is part of the clade Archaeopterodactyloidea (Bennett, 2012).

The angle between the femoral head and the diaphysis of SGO.PV.22814 (130°) is another useful feature to elucidate its relationship with other pterosaurs. In *Herbstosaurus pigmaeus* Casamiquela, 1975, and in the archaeopterodactyloid *Wenupterix uzi* Codorniú and Gasparini, 2013, from the Tithonian of Neuquén, the femoral neck and head are directed medially with an angle of approximately 100° with respect to the main axis of the diaphysis (Codorniú et al., 2006; Codorniú and Gasparini, 2013). This difference separates the femora of these pterodactyloids from the femora of the pterosaurs belonging to the clade Ornithocheiroidea sensu Unwin (2003), since an angle between the femoral neck and the diaphysis of the femur that exceeds 160° corresponds to a synapomorphy of this clade (Unwin, 2003). Derived non-pterodactyloids and non-ornitocheiroid pterodactyloids (the Ornithocheiroidea sensu Unwin, 2003) have a constricted femoral neck and a dorsomedially directed femoral head (caput) at an angle of approximately 135° with respect to the longitudinal axis of the diaphysis. This angle is interpreted as a plesiomorphic trait for pterodactyloids, while in ornithocheiroids (sensu Unwin, 2003) the femoral neck is relatively robust and markedly directed dorsally at an angle of about 160° with respect to the diaphysis. Examples of ornithocheiroids with separation angles between the femoral neck and the diaphysis of values greater than 160° are *Anhanguera piscator* (see Kellner and Tomida, 2000), *Pteranodon* (see Eaton, 1910; Wellnhofer, 1978; Bennett, 1991, 2001), *Nyctosaurus gracilis* (see Williston, 1903; Wellnhofer, 1978), *Istiodactylus latidens* (see Hooley, 1913; Wellnhofer, 1978), *Zhejiangopterus linhaiensis* (according to the illustration of the femur in Cai and Wei, 1994) and *Azhdarcho lancicollis* (see Nessov, 1984; Averianov, 2010).

SGO.PV.22814 is referred to the Archaeopterodactyloidea principally based on the angle between the femoral neck and the shaft less than 160°.

Pterodactyloidea indet. (Fig. 11)

Materials—SGO.PV.22805, partial impression of a left tibiotarsus associated with the impression of a scapulocoracoid.

Tibiotarsus. Specimen SGO.PV.22805 (Fig. 11) correspond to the impression of the distal end and part of the shaft of a left tibiotarsus in anterior view, associated with the impression of a scapulocoracoid. The shaft presents a slight curvature in the anteromedial direction. The distal epiphysis is expanded and appears to be slightly rotated laterally. In addition, the anterior surface of the lateral and medial condyle can be appreciated. The lateral condyle shows a

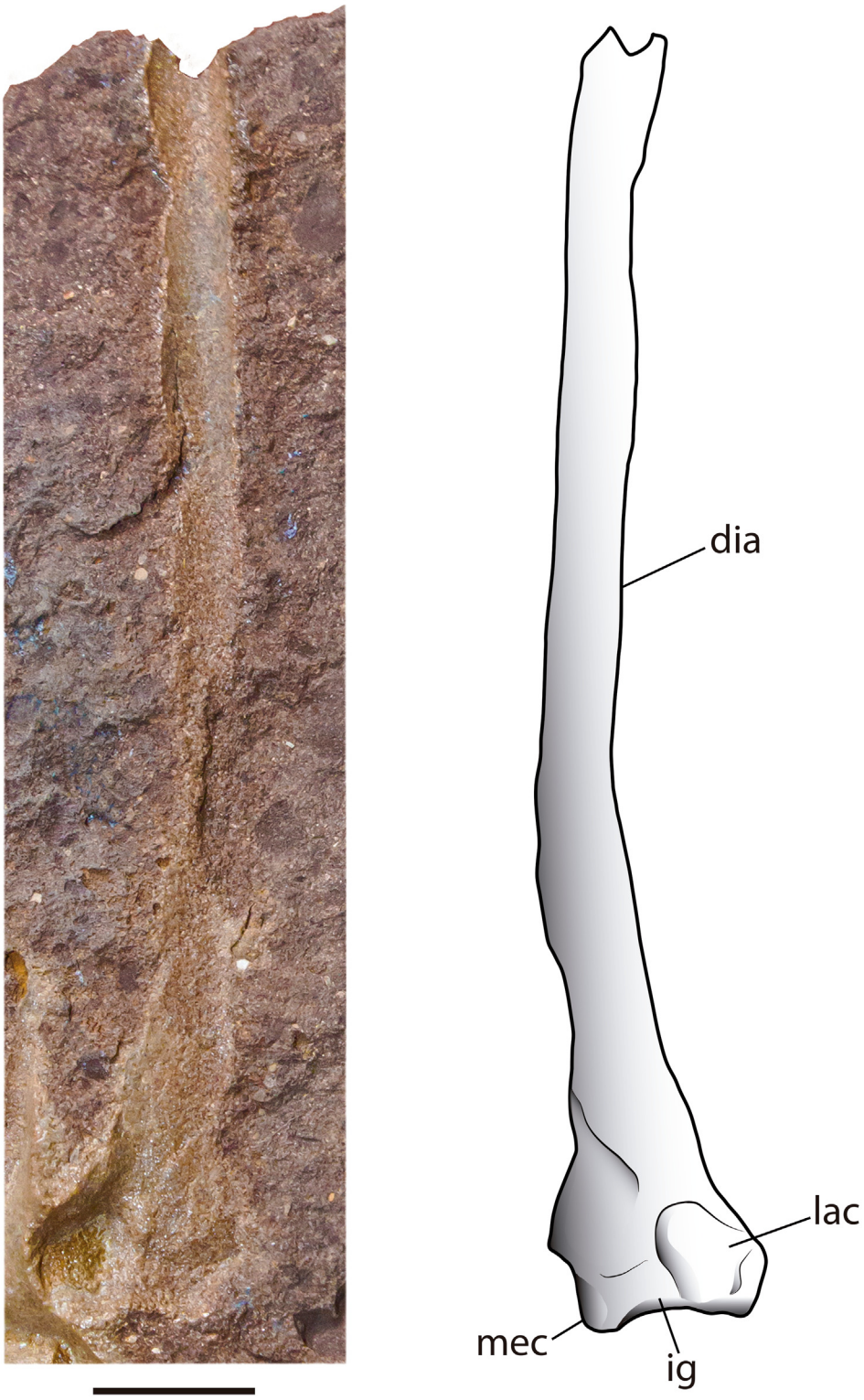


Fig. 11. Pterodactyloidea indet., SGO.PV.22805. Incomplete impression of the anterior surface of a left tibiotarsus and scheme made from a silicone mold obtained from the impression. Abbreviations: dia: diaphysis; ig: intercondylar groove; lac: lateral condyle; mec: medial condyle. Scale bar: 10 mm.

great development with respect to the diaphysis, with its proximal end rounded. The medial condyle, although incomplete, shows less development than the lateral condyle, forming a slightly concave rim medially. Between the medial and lateral condyles is a wide, shallow intercondylar groove.

Comparisons. The tibia in pterosaurs presents few informative features (Kellner, 2003; Unwin, 2003). In complete specimens, the most important features are related to the relative proportions with respect to the femur, although this only serves to position a taxon within the large groups of pterosaurs, but not among more

taxonomically specific groups (Kellner, 2003; Unwin, 2003). In the case of SGO.PV.22805, it is not possible to calculate proportions between the tibiotarsus and the femur, since, although both elements are available, they are incomplete and were not found in association. Morphological characters of taxonomic significance have only been described in some derived pterosaurs as *Anhanguera piscator* (see Kellner and Tomida, 2000) and *Pteranodon* (see Bennett, 2001). Also, some features were described in some archaeopterodactyloids, for example *Wenupteryx uzi* (MOZ 3625P, see Codorniú and Gasparini, 2013), in which the tibia has a straight shaft, wider proximally than distally. Its diameter becomes smaller for one-quarter of the length, and then is constant up to the distal end. In *Wenupteryx*, the proximal tarsals seem fused to the tibia, but this region cannot be seen clearly and distal tarsals are damaged (Codorniú et al., 2006).

In addition, the tibiotarsus was described in "*Puntanipterus globosus*" (PVL 3869, see Bonaparte and Sánchez, 1975), whose synonymy with *Pterodaustro guinazui* was confirmed in Codorniú and Gasparini (2007). Tibia-fibulae of *Pterodaustro guinazui* in specimens with less postmortem compression (MIC-V169, MIC-V90) were compared to that of "*Puntanipterus*". The presence of a wide globose articulation, formed by the proximal tarsal bones (astragalus and calcaneum) fused to the tibia, as well as the presence of spiny processes on the medial and lateral sides of the distal end of the tibia were the most significant diagnostic features for these specimens. However, the presence of a spiny process in the lateral condyle of the tibia of PVL 3869 has not been observed in any other specimen. This feature was reported not as diagnostic of *Pterodaustro* but probably as an ossified cartilage for the insertion of a tendon (lateral and medial ligamentous prominences described in Codorniú and Gasparini (2007). The great development of the wide globose articulation is also present in SGO.PV.22805, and it is similar to the tibiotarsus of *Pterodaustro* in that the lateral condyle extends proximomedially with a rounded proximal rim, while the medial condyle forms a rim with a medial concavity. The poor state of preservation of SGO.PV.22805 allows it to be referred to the Pterodactyloidea, probably an archaeopterodactyloid pterosaur.

4. Discussion

4.1. The pterosaurs of Cerro Tormento

Although some of the bones show some degree of association with each other, most are completely disjointed. In addition, the presence of three humeri and one cervical vertebra from a small individual suggests that the materials preserved at Cerro Tormento belong to more than one individual. One of the main limitations when trying to classify the bones is that it cannot be assumed *a priori* that the entire set of bones belongs to the same taxon. This scenario is faced with the problem that most of the diagnosis of pterosaurs that allow taxonomic assignments is based on cranial material and dental characteristics (Wellnhofer, 1978). To a lesser extent, the diagnosis is based on cervical elements (Howse, 1986), and to some extent based on the relative proportions of individual wing bones (Padian, 1991; Padian and Warheit, 1989; Padian and Wild, 1992).

The general morphology of the bones studied in this work suggests that they belonged to the clade Pterodactyloidea. Among these informative features are the large size of the bones, and the morphology of the glenoid of the scapulocoracoid, which is shared equally by both bones (Kellner, 2003; Unwin, 2003). Furthermore, the morphology of the glenoid and the distal epiphysis of the humerus suggests that these bones belonged to pterosaurs that moved efficiently on the ground with their forelimbs under the body, which is a more widespread body posture among pterodactyloid pterosaurs (Fujiwara and Hutchinson, 2012; Witton, 2015). Additionally, there are some anatomical similarities between the bones described here and those belonging to some members of the Archaeopterodactyloidea, such as *Pterodaustro* (see comparisons in this paper).

The cervical vertebrae are the most informative elements found so far at Cerro Tormento, and correspond to post-axial elements of the mid cervical series. These vertebrae are procoelous, elongated, with a depressed neural arch and low neural spine (when preserved), features that are shared by the Ctenochasmatidae and Azhdarchidae. In the cervical vertebrae of azhdarchids, the neural arch is usually completely confluent with the vertebral centrum; this causes that the vertebra acquire a tubular-like morphology (Martill et al., 1998; Unwin, 2003; Andres and Ji, 2008; Witton and Naish, 2008). In contrast to azhdarchids, in the cervical vertebrae of ctenochasmatids, the depressed neural arch remains distinct from the vertebral centrum (Howse, 1986; Unwin, 2003; Andres and Ji, 2008).

The cervical vertebrae from Cerro Tormento present a clear distinction between the neural arch and the vertebral centrum; the neural spine, when preserved, is low, rectangular, and anteroposteriorly elongated; so, these vertebrae are not tubular as in the Ctenochasmatidae. The presence of postexapophyses is a common feature in the Ornithocheiroidea (*sensu* Bennett, 1994; Kellner, 2003), and has been described in several azhdarchids (Andres and Ji, 2008; Andres et al., 2014; Lü et al., 2016). However, the postexapophyses are also present in some ctenochasmatids such as *Gegepterus changi* (Wang et al., 2007; Jiang and Wang, 2011) and *Elanodactylus prolatus* (Andres and Ji, 2008), although they seem to be absent in *Ctenochasma gracile* (Howse, 1986) and *Beipiaopterus chenianus* (Lü, 2003). In *Gegepterus changi*, the presence of cervical postexapophyses is one of the main features that suggest that this species is derived within the Archaeopterodactyloidea (Wang et al., 2007). Some authors have proposed that the independent acquisition of postexaphopyses in the 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 characteristic that suggests that the vertebrae from Cerro Tormento belong to the Ctenochasmatidae is the position of the neural canal. Martill et al. (2013) mentioned that in the Azhdarchidae the neural canal is centrally positioned with respect to the centrum, which according to these authors has not been reported so far in the Ctenochasmatidae. This feature seems to be more accentuated in anterior view, as can be observed in *Arambourgiania philadelphiae* (Martill et al., 1998) and *Azhdarcho lancicollis* (Nessov, 1984; Averianov, 2010). In the more complete mid cervical vertebra of Cerro Tormento, the neural canal in anterior view is very dorsally positioned as in the Ctenochasmatidae and contrary to that described in the Azhdarchidae by Martill et al. (2013). All these features mentioned are consistent with those described in the middle cervical vertebrae of pterosaurs of the Ctenochasmatidae (Kellner, 2003; Martill et al., 2013).

The evidence available so far suggests that the Cerro Tormento pterosaurs belong to the Archaeopterodactyloidea clade, and within this group, to the clade Ctenochasmatidae. These results confirm a second locality with ctenochasmatid pterosaurs in the Quebrada Monardes Formation. The middle cervical vertebrae found in Cerro Tormento are very similar in their morphology and size to that of two middle cervical vertebrae from Cerro La Isla, which were assigned to the Ctenochasmatidae by Alarcón-Muñoz et al. (2020). These findings demonstrate that this group of pterosaurs were widespread in northern Chile during the Early Cretaceous.

4.2. Paleoenvironment and paleobiology

Among the stratigraphic section at Cerro Tormento, we recognized the presence of diagnostic sedimentary structures such as heterolitic cross-stratification which support the existence of an estuarine environment influenced by tides. Upon this evidence we suggest that a possible scenario for the genesis of the pterosaur preservation may have been deposition of sediments as result of water flows produced by tides in the proximities of a tidal channel. In contrast with Cerro Tormento, the southernmost pterosaur basin located at Cerro La Isla, indicates that pterosaur bones were preserved in high-energy water flows and sediments produced in a mainly continental environment. Compared to the stratigraphy documented in the locality of Cerro La Isla (Bell and Suarez, 1993; Bell and Padian, 1995), we could lithologically correlate the Cerro Tormento Section with the 250–350 m part of the section of Bell and Padian (1995; Fig. 4), which also include fine-grained facies and a pterosaur horizon and were interpreted as alluvial flood plains with ephemeral streams. Despite the similarities, the fine-grained facies association of Cerro Tormento (FA1) where interpreted as tidal plains, mainly because are overlaid and underlaid by cross bedded sandstones with inclined heterolithic stratification with mud draped foresets that were interpreted as tidal bars, and indicates proximity to the coast (Nio and Yang, 1991; Choi et al., 2004; Longhitano et al., 2012; Olariu et al., 2015; Tang et al., 2019). In Cerro La Isla, the alluvial flood plain levels are intercalated between large scale cross bedded sandstones interpreted as aeolian dune fields and there is major presence of channel lags, conglomerates and larger clast size which indicates alluvial systems in a flat desert plain ten of kilometers inland from coast (Bell and Padian, 1995). Probably, the estuarine system of Cerro Tormento corresponds to river mouth and distal facies of the alluvial system of Cerro La Isla.

Preservation of pterosaur bones in marine or marine-influenced environments is relatively common. In fact, to date most of the currently known pterosaurs have been found in this type of environment (Butler et al., 2013; Upchurch et al., 2015). It is presumed this environment may have provided food to ctenochasmatid pterosaurs, probably consisting of crustaceans and other invertebrates (Qvarnström et al., 2019), as well as some small fishes.

Cerro Tormento would be one of the few cretaceous localities in the world in where several three-dimensional, well-preserved bones, belonging to more than one individual, have been preserved in the same constrained stratigraphic level. This new locality represents a valuable opportunity to carry out better and detailed stratigraphic studies comprising paleobiology and taphonomy of South American pterosaurs. Sequential stratigraphy studies in the Lower Cretaceous of Quebrada Monardes Formation will be certainly important in order to recognize correlations between the known layer with pterosaur from Cerro Tormento and the previously recorded Cerro La Isla locality. Bell and Padian (1995) postulated the existence of one or more colonies of pterosaurs that lasted for a long time to explain the accumulation of pterosaur bones in Cerro La Isla, an idea that they support based on the existence of bones of immature individuals. The existence of a possibly similar context in Cerro Tormento, suggests the presence of an additional colony of pterosaurs, although, for now, there is no evidence of immature individuals. Additional taphonomical and sedimentological data are required for testing this hypothesis.

Although in Cerro La Isla and Cerro Tormento at least some pterosaurs belong to the Ctenochasmatidae, at the moment it is uncertain whether these pterosaurs belong to the same species living along the extensive desert depression that existed in the area during the Early Cretaceous. It is also not known whether the pterosaurs from both locations were approximately contemporaneous or belonged to one or more populations. For now, the middle cervical vertebrae are the only comparable element between the two locations. The middle cervical vertebrae of Cerro La Isla and Cerro Tormento have a similar size, morphology and proportions. These similarities suggest that the ctenochamatids from both localities probably belong to the same taxon. However, more comparable elements are needed to better support this idea.

The current evidence suggests that big colonies of ctenochasmatids inhabited in an extensive desert area, and at least, of those from Cerro Tormento, inhabited a coastal area during the Early Cretaceous. Both localities suggest that these ctenochasmatids had a gregarious behavior, although there is no certainty that this behavior has been maintained permanently or only temporarily as in reproductive season.

Gregarious behavior has been suggested for a few species of pterosaurs, such as the ctenochasmatid *Pterodaustro guinazui*, whose remains come from lacustrine sediments from the “Loma del *Pterodaustro*”, Lagarcito Formation (Lower Cretaceous), Argentina (Chiappe et al., 1998). The same has also been suggested for the tapejarid *Caiuajara dobruskii*, found in lacustrine deposits of the Goio-Erê Formation (Upper Cretaceous), of the Caiuá Group, Brazil (Manzig et al., 2014). The latter bears a special resemblance to the pterosaurs of the Quebrada Monardes Formation, since these tapejarids also lived in colonies in a desert environment. This indicates that this type of habitat was occupied by more than one type of gregarious pterosaur at different times in the group's history. Another possible evidence of social behavior is restricted to the finding of some specimens of *Quetzalcoatlus* in close proximity (Kellner, 1994). Additional examples includes duplicate bones preserved in a concretion from the Romualdo Formation (Eck et al., 2011), two pterosaur specimens found in Kazakhstan (Costa et al., 2013), and an accumulation of eggs and bones from the pterosaur *Hamipterus tianshanensis* found in Lower Cretaceous rocks of China (Wang et al., 2017).

Considering the scarcity of sites in the world with accumulations of pterosaur bones, Cerro La Isla and Cerro Tormento have uncommon potential to provide evidence on social behavior in pterosaurs, which remains largely unknown in these animals.

5. Conclusions

A new locality with ctenochasmatid pterosaurs is described for the Lower Cretaceous in northern Chile. This deposit would have been formed in an estuarine environment, and bones would have been deposited under the influence of tides, and floods upon growth of river courses. Together with the “Cemitério dos pterossauros” in Brazil, the “Loma del *Pterodaustro*” in Argentina, the locality with *Hamipterus* in China, and Cerro La Isla in Chile, Cerros Bravos represents one of the few pterosaur localities in the world where associated remains belonging to several individuals have been found. The characteristics of this locality present an opportunity to carry out studies focused on aspects related to social behavior of these animals. On the other hand, the three-dimensional preservation of the bones allows the observation of characters that are not easily observed in other specimens, in which the bones are usually crushed, which often makes the analysis of osteological characters difficult.

The presence of the clade Ctenochasmatidae in Cerro Tormento and Cerro La Isla, separated from each other by more approximately 63 km, suggests that this clade, and potentially the same species, had an extensive distribution in what is now northern Chile, although for now it cannot be assured that the pterosaurs from both sites were contemporary.

Most of the appendicular elements (i.e., tibiotarsus, humerus, pectoral girdle) alone, do not provide enough information to refer to them at a generic or specific level, but they can be referred to Pterodactyloidea, many of them having a special affinity to the clade Archaeopterodactyloidea. The vertebral remains described in this work were the most informative elements to elucidate more specific relationships of the pterosaurs of the Quebrada Monardes Formation with other known pterosaurs. These elements are referred to the clade Ctenochasmatidae, constituting new records of this group of pterosaurs.

Future prospection for Cerro Tormento and also Cerro La Isla will possibly allow obtaining more eloquent materials that will help elucidate whether the same species of ctenochasmatid is found at both sites. In addition, new stratigraphic studies accompanied by dating will make it possible to determine if both sites are synchronous. Finally, the discovery of a new pterosaur site in the Quebrada Monardes Formation suggests that more intensive prospecting in outcrops of this formation will possibly allow the discovery of new pterosaur species for Gondwana.

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