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ARTICULO

AN ISOLATED MESOEUCROCODYLIAN TOOTH CROWN FROM THE LOWER CRETACEOUS CERRO LA ISLA PTEROSAUR SITE IN THE ATACAMA REGION, NORTHERN CHILE

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ABSTRACT

We describe the first crocodyliform tooth found in continental deposits from the Quebrada Monardes Formation (Lower Cretaceous) at Cerro La Isla, Atacama Region, northern Chile. Though the fossil (SGO.PV.1160) is poorly preserved, the enamel surfaces clearly bear tightly-packed apicobasal ridges. Comparisons of SGO.PV.1160 with the dental morphology of taxa that it may belong to suggest a hitherto unknown pholidosaurid or, more likely, notosuchian. Therefore, the tooth crown is here provisionally identified as belonging to an indeterminate mesoeucrocodylian, pending future discoveries of more complete material. This find increases our knowledge of the fauna in the Lower Cretaceous deposits of Cerro La Isla, as well as the importance of the fossil site, since pholidosaurids have not been reported from Chile, while if it proves to be notosuchian, it may represent one of the earliest known taxa of the group in South America, and the entire world.

Key words: Crocodyliformes, Quebrada Monardes Formation, Lower Cretaceous, Atacama Desert, Northern Chile

RESUMEN

Una corona dental Mesoucrocodiliana aislada del sitio de pterosaurios cerro La Isla del Cretácico inferior en la Región de Atacama, norte de Chile. Se describe el primer diente de un crocodiliforme descubierto en depósitos continentales de la Formación Quebrada Monardes (Cretácico Inferior) en Cerro La Isla, Región de Atacama, norte de Chile. Aunque el fósil (SGO.PV.1160) está pobremente preservado, sus superficies claramente poseen crestas apicobasales muy próximas entre sí. Las comparaciones de SGO.PV.1160 con la morfología dental de taxones a los cuales podría pertenecer sugieren un folidosáurido; o más probablemente, un notosuquio. Por lo tanto, la corona dental se identifica de manera provisional como perteneciente a un Mesoeucrocodylia indeterminado, hasta el descubrimiento de material más completo. El presente hallazgo aumenta tanto nuestros conocimientos sobre la fauna en los depósitos del Cretácico Inferior de Cerro La Isla, como la importancia del sitio fosilífero, dado que hasta el momento no se han reportado folidosáuridos en Chile, mientras que si resulta ser de notosuquio, podría representar uno de los taxones más tempranos de este grupo conocido de Sudamérica y del mundo entero.

Palabras clave: Crocodyliformes, Formación Quebrada Monardes, Cretácico Inferior, Desierto de Atacama, Norte de Chile

Institutional abbreviations – SGO.PV. Área de Paleontología, Museo Nacional de Historia Natural, Santiago, Chile.

INTRODUCTION

Cerro La Isla, in the Atacama Region, is one of the most interesting localities for the study of Lower Cretaceous continental vertebrates in Chile. Several pterosaur bones have been discovered at this locality, preserved in a single layer composed mainly of sandstone and conglomerates that would have originated in a high-energy event (Bell and Suárez 1989; Bell and Padian 1995). The fossil-bearing rocks are part of the Lower Cretaceous of the Quebrada Monardes Formation, deposited in a warm to arid paleoclimate with low and seasonal rainfall (Bell and Suárez 1993), and represent a continental braided alluvial and floodplain paleoenvironment (Bell and Suárez 1993; Bell and Padian 1995).

The overwhelming majority of the fossil remains at the site consists of disarticulated and partially preserved pterosaur bones, which have been identified as belonging to a hitherto unnamed member of the Ctenochasmatidae Nopcsa 1928 (Martill *et al.* 2006; Alarcón-Muñoz *et al.* 2020). In addition, the vertebrate material reported from the pterosaur horizon also includes extremely scarce, disarticulated and broken dinosaur (Bell and Suárez 1989, 1993; Bell and Padian 1995; Martill *et al.* 2006) and crocodyliform bones (Bell and Suárez 1989, 1993; Alarcón-Muñoz *et al.* 2020). However, the latter two taxa have so far only been mentioned in the scientific literature and, to date, no dinosaur or crocodilian fossils from Cerro La Isla have been described or figured.

In this study we describe a poorly preserved isolated tooth crown that differs markedly from the slender, needle-like pterosaur teeth that have been recovered from the site (Martill *et al.* 2006; Alarcón-Muñoz *et al.* 2020). Interestingly, the enamel surfaces bear apicobasal ridges. These structures are associated with feeding in an aquatic environment, typical in marine reptiles in general, spinosaurid theropods and some pterosaurs and crocodylomorphs (*e.g.*, Massare 1987; Brougham *et al.* 2017; McCurry *et al.* 2019). The aim of this contribution is to explore the taxonomic affinities of this isolated tooth crown and shed some light on the Lower Cretaceous vertebrate diversity of the Cerro La Isla locality.

LOCALITY AND GEOLOGICAL SETTING

Cerro La Isla is located approximately 95 km east of the city of Copiapó at 3,822 m.a.s.l., in the Atacama Region of northern Chile (Bell and Padian 1995; Figure 1). Several pterosaur bones are partially exposed in a single 0.6-4 m thick sedimentary horizon of braided alluvial and floodplain deposits on the southwestern slopes of the hill. The pterosaur horizon is part of the basal levels of the Quebrada Monardes Formation, representing a continental sequence of desert sediments (Bell and Padian 1995) that is considered early Cretaceous in age. This is based primarily on the age of the underlying Upper Jurassic-Lower Cretaceous sequences of the Pedernales and Lautaro formations (Chong 1976; Muzzio 1980; Mercado 1982; Reyes and Pérez 1985; Cornejo *et al.* 1998), and the overlying Quebrada Seca Formation, which is considered Maastrichtian-Danian in age (Iriarte *et al.* 1999; Martínez *et al.* 2015). Though this still leaves a degree of uncertainty about the precise age of the Quebrada Monardes Formation, Martínez *et al.* (2015) proposed a Tithonian-early Berriasian age for the maximum deposition based on detrital zircons obtained from outcrops exposed at Pulido river, which would support an early Cretaceous age.

The bones exposed in the pterosaur horizon are disarticulated, scattered and incomplete. The depositional event that created this horizon has been interpreted as a single high-energy flood, which swept across a north-south orientated inland desert basin enclosed by volcanic chains (Bell and Suárez 1993; Bell and Padian 1995). Though according to Bell and Padian (1995), such floods are usually caused by the alteration of barriers of bodies of water by lava flows and landslides, Alarcón-Muñoz *et al.* (2020) attributed the paleo-flood to heavy rains.

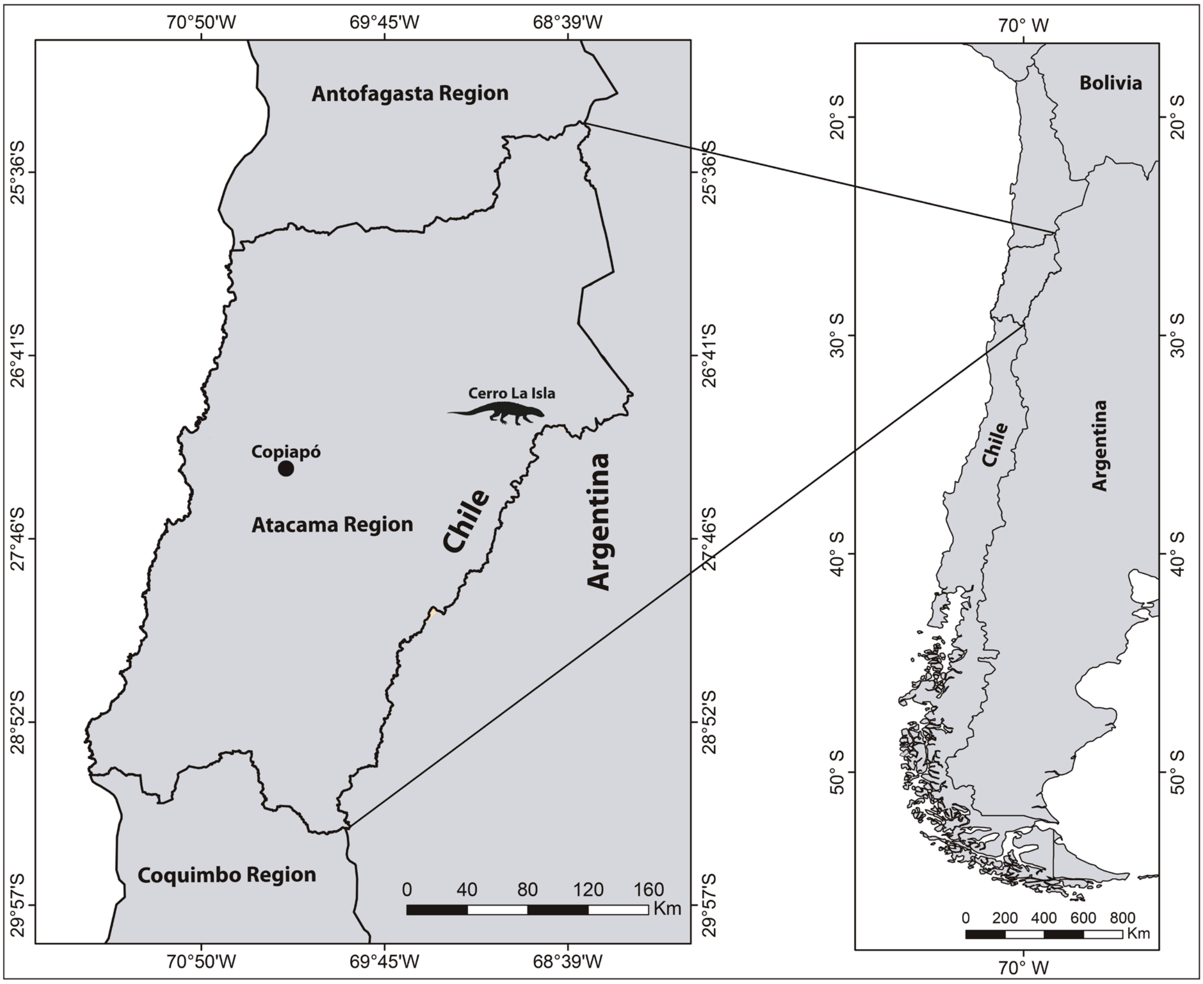

Figure 1. Map showing the locality where SGO.PV.1160 was found; Cerro La Isla, Atacama Region, northern Chile.

MATERIALS AND METHODS

SGO.PV.1160 is a poorly preserved isolated tooth missing its apex and most of the root and enamel surfaces (Figure 2). It was collected in the late 90's at the Cerro La Isla pterosaur site, and it is currently housed in the Paleontology Area of the Museo Nacional de Historia Natural (MNHN) in Santiago, Chile. For the description of the dental morphology, we broadly follow the terminology outlined by Hendrickx *et al.* (2015).

RESULTS

Systematic paleontology

Archosauria Cope 1869 (*sensu* Benton and Clark 1988)
Crocodylomorpha Hay 1930 (*sensu* Walker 1970)
Crocodyliformes Hay 1930 (*sensu* Benton and Clark 1988)
Mesoeucrocodylia Whetstone and Whybrow 1983
Mesoeucrocodylia indet.

Material – SGO.PV.1160; a poorly preserved isolated tooth missing its apex and most of the root and enamel surfaces (Figure 2).

DESCRIPTION

The specimen SGO.PV.1160 is a single-cusped caniniform tooth crown without cingula or accessory cusps. It is conical in shape, slender and elongated, tapering evenly towards the missing apex. It shows a gentle curvature that develops steadily along the entire crown height (Figure 2A), which is approximately 16 mm, as preserved. There is no constriction at the crown-root junction. However, the basal region is so poorly preserved that it is unclear where exactly this junction was located. The basal cross-section is elliptical (approximately 4.9 mm x 4.4 mm), and the gentle curvature of the crown is perpendicular to the plane of the longer basal diameter (Figure 2A; B). The crown lacks carinae.

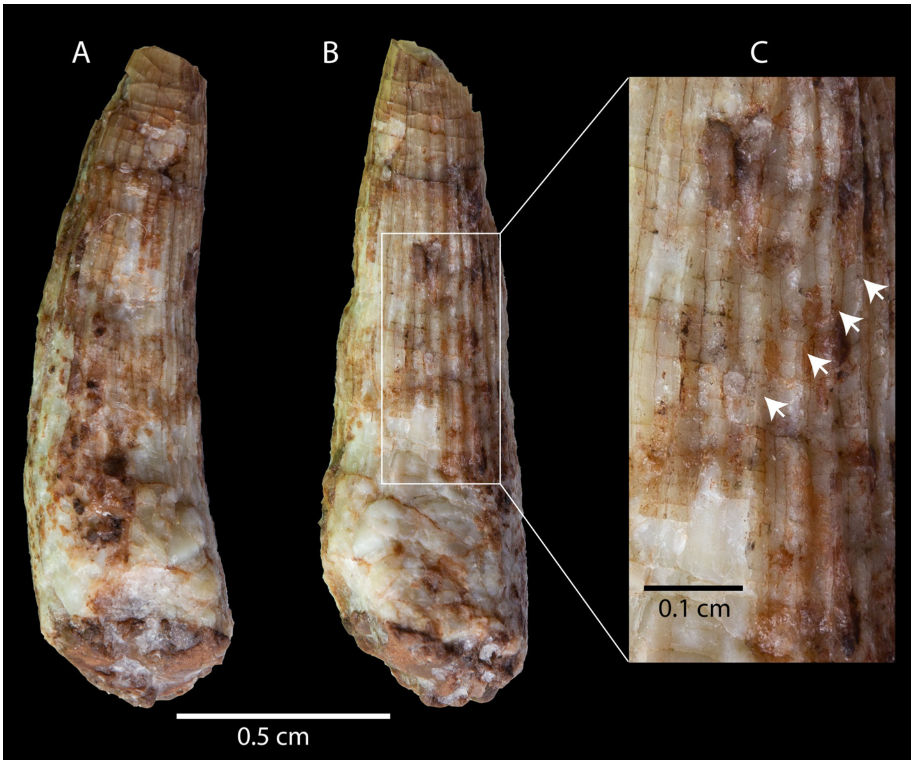

Figure 2. Mesoeucrocodylia indet. (SGO.PV.1160), in A) mesial/distal view, and B) labial/lingual view. C) shows the detail of the enamel ornamentation in a region of the crown where it is well-preserved. The white arrows point out apicobasal ridges that are present on the entire circumference of the crown.

The crown surfaces lack faceting but bear apicobasally orientated ridges that extend along the entire crown height (density in the best-preserved areas: approximately 3 ridges/mm; Figure 2C). The dentine participates in the formation of these ridges, as evidenced by some areas without enamel where these structures can still be distinguished. The preserved ridges are all equally developed, uniformly spaced and present on all crown surfaces. They become finer and show an anastomosed pattern in the apicalmost region. The ridges have been completely obliterated in some areas, exposing the smooth dentine. There are no distinguishable wear patterns.

DISCUSSION

To establish its taxonomic affinities, SGO.PV.1160 was compared with the dentition of all Lower Cretaceous South American taxa that may have occurred in a continental setting – as well as with that of other, less likely groups – whose representatives possess conical tooth crowns with apicobasal ridges.

Pterosauria Kaup 1834

The dentition of the Cerro La Isla ctenochasmatids consists of slender, needle-like teeth, which have been interpreted as a filter-feeding specialization (Alarcón-Muñoz *et al.* 2020). In the fragmentary tooth bearing elements described by Martill *et al.* (2006) and Alarcón-Muñoz *et al.* (2020), none of the teeth exceed 1 mm in basal diameter. The basal diameter of SGO.PV.1160 on the other hand is approximately 4.9 mm x 4.4 mm, making it considerably more robust than the teeth of the pterosaurs known from the site, as well as those of ctenochasmatids in general (Brougham *et al.* 2017).

Several pterosaur lineages became edentulous independently by the Cretaceous or disappeared during the Upper Jurassic (*e.g.*, Brougham *et al.* 2017; Bestwick *et al.* 2018), leaving few to which this Lower Cretaceous tooth crown may have belonged. Of these, apart from the Ctenochasmatidae, only the presence of Dsungaripteroidea Young 1964 and Ornithocheiroidea Seeley 1891 has been confirmed in the fossil record of South America (*e.g.*, Martill *et al.* 2000; Elias *et al.* 2007; Pinheiro and Rodrigues 2017; Bestwick *et al.* 2018). Among the representatives of these two clades, the ornithocheiroid Anhangueridae Campos and Kellner 1985 possess the most similar dentition to SGO.PV.1160; with slender, conical, slightly lingually curved tooth crowns with an elliptical basal cross-section, with or without carinae, and enamel surfaces ornamented with apicobasal striations (*e.g.*, Brougham *et al.* 2017; Pentland and Poropat 2019). However, rather than consisting of alternating ridges and grooves with a triangular cross-section, the enamel ornamentation of these pterosaurs typically consists of apicobasal grooves in otherwise smooth surfaces (Brougham *et al.* 2017) and where ridges are present, they are merely formed by the localized thickening of the enamel, without the participation of the underlying dentine (Pinheiro and Rodrigues 2017). We therefore consider that SGO.PV.1160 does not belong to a pterosaur.

Plesiosauroidea

The overall morphology and enamel ornamentation of SGO.PV.1160 is superficially similar to the dentition of some members of Plesiosauroidea Gray 1825 (Massare 1987), a group of predominantly marine aquatic reptiles that lived in the uppermost Triassic-uppermost Cretaceous interval (*e.g.*, Bardet *et al.* 1999; Benson *et al.* 2013). According to Bell and Suárez (1993) and Bell and Padian (1995), the Pacific coast was located 20 to 50 km to the west of the fossil site at the time of deposition, and no evidence of a marine influence has been uncovered at Cerro La Isla. However, Alarcón-Muñoz *et al.* (2022) interpreted the fossil locality Cerro Tormento, also in the Quebrada Monardes Formation but 65 km to the north from the site, as an estuarine paleoenvironment influenced by tides, indicating its proximity to the coast. The authors suggested that Cerro Tormento may correspond to the estuarine area of the same alluvial system that was present at Cerro La Isla, though it is currently unclear whether the two sites were coeval. Therefore, we examined Plesiosauroidea due to their sporadic occurrences reported from continental freshwater environments (*e.g.*, Vandermark *et al.* 2006; Benson *et al.* 2013; Gao *et al.* 2019; Campbell *et al.* 2021).

The apicobasal ridges in plesiosauroid tooth enamel are less uniformly and more widely spaced (*e.g.*, Benson *et al.* 2013; Gao *et al.* 2019), making them project from otherwise smooth crown surfaces, rather than forming alternating ridges and grooves (*i.e.*, forming fluted crown surfaces), as in SGO.PV.1160 and some spinosaurids and crocodyliforms (Benson *et al.* 2013). Additionally, the apicobasal ridges of sauropterygian teeth, as they are in pterosaurs, are formed only by the localized thickening of the enamel (*e.g.*, Massare 1987; McCurry *et al.* 2019), whereas in SGO.PV.1160 the underlying dentine also participates in these structures. Based on these morphological differences, we conclude that the tooth does not belong to a plesiosauroid.

Spinosauridae

In the Lower Cretaceous of South America, the unambiguous presence of Spinosauridae Stromer 1915 (*sensu* Sereno *et al.* 1998) has only been confirmed in Brazil so far (Martill *et al.* 1996; Sues *et al.* 2002; Sales *et al.* 2016). Compared to those of other theropod dinosaurs, spinosaurid tooth crowns show a reduction in labiolingual compression and distal curvature (*e.g.*, Charig and Milner 1997; Ruiz-Omeñaca *et al.* 1998), making them superficially similar to those of certain crocodyliforms (*e.g.*, Holtz 1998; Sereno *et al.* 1998; Rayfield *et al.* 2007; Amiot *et al.* 2010). Although the apicobasal ridges of some spinosaurid tooth crowns are quite similar to those of SGO.PV.1160, the teeth in this theropod group bear prominent mesial and distal carinae (*e.g.*, Fowler 2007; Buffetaut *et al.* 2008; Benson *et al.* 2013); structures that are absent in the tooth from Cerro La Isla.

Additionally, spinosaurid tooth crowns are either straight or distally recurved (*i.e.*, the plane of the crown curvature, when present, coincides with the plane of the greater basal diameter), whereas in SGO.PV.1160 the curvature appears to be lingual, which is typical in crocodyliform tooth crowns (*e.g.*, Fowler 2007; Sánchez-Hernández *et al.* 2007; Bertin 2010; Ősi *et al.* 2015).

Affinities within Crocodyliformes

Among the known Lower Cretaceous South American taxa that inhabited continental environments, the combination of the lack of carinae, the conical shape of the crown, the presence of apicobasal ridges on the crown surfaces and the orientation of the curvature with respect to the greater basal diameter (*i.e.*, the plane of the gentle curvature of the crown is perpendicular to the plane of the greater basal diameter) is only consistent with some crocodyliform teeth. In crocodyliform tooth crowns with a certain degree of labiolingual compression (*i.e.*, where the basal cross-section is at least sub-elliptical rather than circular), the greater basal diameter corresponds to the mesiodistal length of the crown, making the curvature of SGO.PV.1160 lingual (Ősi *et al.* 2015).

The taxon Crocodyliformes is a group that includes 'Protosuchia' Mook 1934, and Mesoeucrocodylia. The chronostratigraphic range of the group extends from the Upper Triassic to the present (*e.g.*, Pol and Gasparini 2007; Nesbitt 2011; Irmis *et al.* 2013).

‘Protosuchia’

‘Protosuchia’ Mook 1934 is a paraphyletic group formed by the most primitive crocodyliforms (Benton and Clark 1988). Following the Lower Jurassic, protosuchians have only been discovered in the Northern Hemisphere (*e.g.*, Fiorelli and Calvo 2007; Martínez *et al.* 2018; Dollman *et al.* 2021), with the only exception of *Neuquensuchus universitas* from the Santonian (Upper Cretaceous) of the Bajo de la Carpa Formation in Argentina (Fiorelli and Calvo 2007). The authors found the species to be a member of an Asian clade and proposed an early Cretaceous dispersal event from said continent to explain its presence in what is now South America. Aside from the apparent absence of ‘Protosuchia’ in the Middle Jurassic-Lower Cretaceous fossil record of Gondwana, none of the taxa in which the dentition is known possess teeth with apicobasal ridges (e.g., Pol *et al.* 2004; Clark 2011; Martínez *et al.* 2018). Therefore, SGO. PV.1160 is not a protosuchian tooth crown.

Mesoeucrocodylia

The group includes two major clades; the terrestrial Notosuchia Gasparini 1971 (*sensu* Sereno *et al.* 2001) and the semi-aquatic Neosuchia Benton and Clark 1988 (*sensu* Sereno *et al.* 2001) (*e.g.*, Leardi *et al.* 2015; Dal Sasso *et al.* 2017; Novas *et al.* 2021).

Notosuchia

Notosuchia is a terrestrial clade of mesoeucrocodylian crocodyliforms that showed a marked diversity in the Cretaceous of Gondwana, and particularly in South America (*e.g.*, Pol *et al.* 2014; Pol and Leardi 2015; Coria *et al.* 2019; Marinho *et al.* 2022). They are characterized by possessing heterodont dentition and a broad range of dental morphologies (*e.g.*, Pol *et al.* 2014; Martinelli *et al.* 2018; Melstrom and Irmis 2019; Figueiredo and Kellner 2021). Given their fully terrestrial ecology and the fact that several taxa, such as several members of the Peirosauridae Gasparini 1982 (*e.g.*, Larsson and Sues 2007; Campos *et al.* 2011) and the Sphagesauridae Kuhn 1968 (Pol *et al.* 2014), possess conical premaxillary and/or anterior dentary (incisiform or caniniform) teeth that bear apicobasal ridges, Notosuchia is the main group of interest for the present study.

The origin and early evolution of these crocodyliforms is not well understood. The fossil record suggests an initial radiation in the Aptian, giving rise to mainly African species (Pol *et al.* 2014; Pol and Leardi 2015). While their earliest known Lower Cretaceous occurrence is represented by *Amargasuchus minor* (Chiappe 1988), a peirosaurid known from the Barremian of the La Amarga Formation in Argentina, the three oldest notosuchian clades are the Uruguaysuchidae Gasparini 1971 (from the Aptian-Albian of South America and Africa), the Peirosauridae and closely related forms (from the Aptian-Cenomanian of Africa – without considering *Amargasuchus*) and the earliest members of Ziphosuchia Ortega *et al.* 2000 (from the Aptian-Albian of South America, Africa and China) (Pol *et al.* 2014; Pol and Leardi 2015). While according to Pol and Leardi (2015), the Aptian diversification implies the existence of at least early Lower Cretaceous ghost lineages, Dal Sasso *et al.* (2017) considered that as the sister taxon of Neosuchia, Notosuchia should have originated at the beginning of the Jurassic. The earliest and only known Jurassic notosuchian is the giant *Razanandrongobe sakalavae* (Maganuco *et al.* 2006) from the Bathonian of the Mahajanga Basin in northwestern Madagascar (Dal Sasso *et al.* 2017), whose discovery created a considerable gap in the fossil record of the group.

The only known likely notosuchian fossil from Chile to date was tentatively identified as Crocodyliformes indet. cf. Sebecosuchia and consists of a skull and associated postcranial material from the Albian-Cenomanian (mid-Cretaceous) of Los Estratos de Quebrada La Totora, Coquimbo Region, northern Chile (Chávez *et al.* 2016). Given that the specimen is still encased in the matrix, its dental morphology is currently unknown. Since SGO.PV.1160 was discovered in a horizon of the basal levels of the Lower Cretaceous of the Quebrada Monardes Formation (Bell and Padian 1995), whose deposition began in the late Tithonian-early Berriasian (Martínez *et al.* 2015), the fossil may prove to belong to one of the earliest Lower Cretaceous notosuchian crocodyliforms. Considering the above mentioned three early diverging Lower Cretaceous clades, the morphology of SGO.PV.1160 is not consistent with either Uruguaysuchidae (*e.g.*, Sereno and Larsson 2009; Figueiredo and Kellner 2021), or Ziphosuchia (*e.g.*, Ortega *et al.* 2000; Company *et al.* 2005; Sellés *et al.* 2020). Among the Peirosauridae however, species with tooth crowns bearing apicobasal ridges are quite common and most notably, some of the anteriormost teeth of *Hamadasuchus rebouli* from the Albian-Cenomanian of southeastern Morocco (Larsson and Sues 2007) and those of *Pepesuchus deiseae* from the Campanian-Maastrichtian of Brazil (Campos *et al.* 2011) are quite similar to SGO.PV.1160. Thus, it is possible that the tooth from Cerro La Isla belongs to an early peirosaurid – which would also be consistent with the presence of *Amargasuchus* in the Barremian of Argentina.

Neosuchia

Dyrosauridae di Stefano 1903

Most representatives of the group were large near-shore marine longirostrine forms, while some were recovered from freshwater environments (*e.g.*, Hastings *et al.* 2014; Sena *et al.* 2017; Scavezzoni and Fischer 2021). Though there are at least five South American species (two from Brazil and three from Colombia, Sena *et al.* 2017), the group originated in the Upper Cretaceous (*e.g.*, Hastings *et al.* 2014; Young *et al.* 2014; Sena *et al.* 2017) and according to Scavezzoni and Fischer (2021), as recently as the Campanian-Maastrichtian. Therefore, SGO.PV.1160 does not belong to a dyrosaurid.

Pholidosauridae Zittel and Eastman 1902

Pholidosaurids are a clade of semi-aquatic neosuchians, which lived in the Middle Jurassic-Upper Cretaceous interval (Hua *et al.* 2007; Fortier *et al.* 2011). The group is known from Europe, Africa, Asia and North- and South America (Fortier *et al.* 2011; Martin *et al.* 2013). Though most of them have been discovered in freshwater paleo-environments, some representatives were marine forms (Hua *et al.* 2007). Although their dentition is generally poorly preserved and described only superficially, the tooth crowns of some species are quite similar to SGO.PV.1160. Most notably, those of the Lower Cretaceous representatives of the genus *Pholidosaurus* von Meyer 1841, known from several European localities, have been described as slender, conical, slightly recurved, bearing enamel ornamentation formed by apicobasal ridges and either lacking carinae or possessing such weakly developed ones that they are difficult to differentiate from the rest of the ridges (Andrews 1913; Martin *et al.* 2016). *Oceanosuchus boecensis* (Hua *et al.* 2007) from the lower Cenomanian of western France and *Chalawan thailandicus* (Buffetaut and Ingavat 1980) from the Jurassic of northeastern Thailand are other pholidosaurids whose tooth crowns also bear apicobasal enamel ridges (Buffetaut and Ingavat 1980, 1984; Hua *et al.* 2007). Given the presence of these neosuchians in the Lower Cretaceous of South America – *Meridiosaurus vallisparadisi* from Uruguay (Fortier *et al.* 2011) and *Sarcosuchus hartti* from Brazil (Buffetaut and Taquet 1977; Souza *et al.* 2019) – and the similarities in dental morphology with some of their representatives, it is possible that SGO.PV.1160 belongs to a hitherto unknown freshwater pholidosaurid that inhabited northern Chile. Admittedly, this tooth is slenderer than pholidosaurid teeth in general, therefore its affinity with this group is tentative. However, it may be a replacement tooth or belong to a juvenile specimen.

Goniopholididae Cope 1875

Among crocodyliform groups, spinosaurid tooth crowns are most often considered similar to those of the Goniopholididae (Torcida *et al.* 1997; Fowler 2007; Canudo *et al.* 2008). Goniopholidid neosuchians originated in the Lower Jurassic and became extinct near the end of the Upper Cretaceous (Halliday *et al.* 2015; Ristevski *et al.* 2018). They were semiaquatic and inhabited continental freshwater and coastal environments (Buscalioni *et al.* 2013). Their dentition consists of conical tooth crowns with varying degrees of robustness and lingual curvature, and striated/fluted enamel surfaces. However, their teeth, as those of spinosaurids, are invariably bicarinate (Andrade *et al.* 2011; Puértolas-Pascual *et al.* 2015; Martin *et al.* 2016; Ristevski *et al.* 2018). Additionally, the distribution of these neosuchians was restricted to Laurasia (Allen 2012; Halliday *et al.* 2015; Puértolas-Pascual *et al.* 2015; Martin *et al.* 2016; Ristevski *et al.* 2018), therefore we consider it safe to conclude that SGO.PV.1160 does not belong to a goniopholidid either.

Atoposauridae Gervais 1871

Atoposaurids were small-bodied terrestrial to semi-aquatic neosuchians with heterodont dentition (Tennant *et al.* 2016; Young *et al.* 2016). Although some atoposaurids (*e.g.*, *Alligatorellus* Gervais 1871 and *Theriosuchus* Owen 1878) possess pseudo-caniniform teeth with apicobasal ridges in the anteriormost region of their jaws, their similarity with SGO.PV.1160 is only superficial (Tennant and Mannion 2014; Tennant *et al.* 2016). In addition, though Tennant *et al.* (2016) restricted the group to include only three genera, thereby reducing the biostratigraphic range of Atoposauridae to the Upper Jurassic of western Europe; even prior to this revision, the only tentative records from Gondwana were from Africa and Madagascar (Young *et al.* 2016) and no atoposaurid fossils have ever been discovered in South America. Therefore, SGO.PV.1160 belongs to a different crocodyliform taxon.

Thalattosuchia

Thalattosuchia Fraas 1901 (*sensu* Young and Andrade 2009) are marine crocodyliforms that lived during the Sinemurian (Lower Jurassic)-Barremian (Lower Cretaceous) interval (Gasparini *et al.* 2000; Jouve *et al.* 2016; Cortes *et al.* 2019). The phylogenetic affinities of the group are uncertain; though most recent analyses have recovered Thalattosuchia as non-eusuchian neosuchians (*e.g.*, Pol *et al.* 2014; Leardi *et al.* 2015; Dal Sasso *et al.* 2017; Ristevski *et al.* 2018; Arribas *et al.* 2019; Fernández Dumont *et al.* 2020; Novas *et al.* 2021). Thalattosuchia comprises two groups, the Teleosauroidea Geoffroy Saint-Hilaire 1831 (*sensu* Young and Andrade 2009) and the Metriorhynchoidea Fitzinger 1843 (*sensu* Young and Andrade 2009). Based on their similar morphology to extant crocodylians, teleosauroids are considered to have been relatively unspecialized to their marine ecology (e.g., Young *et al.* 2010; Wilberg 2015; Ősi *et al.* 2018). Though they predominantly inhabited coastal areas, lagoons and brackish estuarine waters, a few teleosauroids have been reported from Asian continental freshwater environments (*e.g.*, Young 1948; Martin *et al.* 2019). The presence of the group in South America has been recently confirmed by the discovery of the partial postcranial skeleton of a large indeterminate teleosauroid from the upper Barremian (Lower Cretaceous) of Colombia (Cortes *et al.* 2019). Regarding their dentition, possessing teeth with apicobasal ridges is a teleosauroid synapomorphy (Johnson *et al.* 2020). Johnson *et al.* (2020) separated Teleosauroidea into two families: Teleosauridae and Machimosauridae. Teleosauridae are characterized by their smaller body size and distribution restricted to Laurasia. Machimosauridae were considerably larger and more widely distributed, being present in what is now western Europe as well as northern and eastern Africa (Johnson *et al.* 2020). So far, only the genus *Machimosaurus* von Meyer 1837 is known to have survived into the Lower Cretaceous (Jouve *et al.* 2016), while all other taxa seem to have disappeared in the Kimmeridgian (Upper Jurassic) (Johnson *et al.* 2020). Due to its large size and Lower Cretaceous age, the teleosauroid specimen from Colombia is likely a representative of the tribe Machimosaurini (Jouve *et* *al.* 2016; Cortes *et al.* 2019). The comparatively wider distribution of Machimosauridae is also consistent with where it was discovered. Machimosaurins were large-bodied macro/durophagous teleosauroids, characterized by possessing blunt, bicarinate tooth crowns with serrated carinae (Jouve *et al.* 2016; Johnson *et al.* 2020). Based on our current knowledge of the teleosauroid fossil record, the tooth from Cerro La Isla could only belong to a machimosaurin. However, the dental morphology of this group differs so much from that of SGO.PV.1160 that we discard this possibility.

Regarding Metriorhynchoidea, at least four (Séon *et al.* 2020) and possibly six (Sachs *et al.* 2020) lineages survived into the Lower Cretaceous, the most recent currently known fossil being an isolated tooth crown from the lowermost Aptian of Sicily (Chiarenza *et al.* 2015). However, these lineages are all represented by derived forms (*i.e.*, metriorhynchids) with a battery of adaptations to their pelagic ecology (such as a hydrodynamic body plan, paddle-like limbs, a hypocercal tail fin and hypertrophied nasal exocrine salt glands; Young *et al.* 2010; Wilberg 2015; Ősi *et al.* 2018; Séon *et al.* 2020; Young *et al.* 2020), whose presence in a continental setting approximately 20-50 km inland is too unlikely to be considered. Therefore, SGO.PV.1160 is not a metriorhynchoid tooth crown.

Eusuchia Huxley 1875

The only known Lower Cretaceous South American non-crocodylian eusuchian is *Susisuchus anatoceps* from the Aptian of Brazil (Salisbury *et al.* 2003), whose dentition consists of needle-like teeth with smooth enamel surfaces (Leite and Fortier 2018). Regarding the extant Crocodylia Owen 1842, they originated in the Upper Cretaceous of the Northern Hemisphere, either in North America or Europe (*e.g.*, Salisbury *et al.* 2006; Mateus *et al.* 2018; de Celis *et al.* 2020). The only crocodylian eusuchian from the Mesozoic of South America is *Dolichochampsa minima* from the Maastrichtian to Danian of Argentina and Bolivia (Gasparini and Buffetaut 1980; Buffetaut 1987; Jouve *et al.* 2020). Therefore, based on our current knowledge, SGO.PV.1160 is excluded from Eusuchia.

CONCLUSIONS

Due to the fragmentary nature and poor preservation of the specimen, including this unusual tooth crown in any taxon more exclusive than Mesoeucrocodylia indet. would at present be imprudent. Still, the discovery of SGO.PV.1160 improves the resolution of our knowledge of the biodiversity at the Cerro La Isla pterosaur site and it represents the first evidence for the presence of crocodyliforms in the area to be described and figured.

Having examined several taxa with representatives that possess similar dentition to SGO.PV.1160, we have reached the conclusion that while this fossil tooth may belong to a freshwater pholidosaurid, its identification as an early notosuchian, possibly a peirosaurid, is more plausible. Though the depositional environment makes the presence of a pholidosaurid taxon possible, it is currently unknown how extensive and persistent the water courses and/or bodies were in the area, and thus whether they would have been sufficient to provide habitat for such a relatively large semi-aquatic predator. Notosuchians on the other hand are a group of fully terrestrial mesoeucrocodylians, whose presence in this warm to arid, desertic continental setting is quite plausible. Should SGO.PV.1160 prove to belong to a pholidosaurid once more complete material is recovered at Cerro La Isla, it will be the first of its kind in the Chilean fossil record. Alternatively, should it prove to belong to a notosuchian, it will help us start filling the considerable gap in the early fossil record of this highly successful and diverse clade.

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