



# First pliosaur remains (Sauropterygia, Pliosauridae) from the Oxfordian of the Atacama Desert

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## ABSTRACT

This research presents the first pliosaur remains from the Upper Jurassic of the Atacama Desert, in northern Chile. Two specimens recovered from Oxfordian levels, are represented by a fragmentary mandibular ramus and by an associated humerus and femur, respectively. Previous to this research, the Jurassic South American pliosaur records were restricted to Tithonian endemic taxa from the Neuquén Province, in Argentina. The studied material represents the first of Oxfordian age known in Gondwana, adding to the scarce pliosaur records of Oxfordian age known worldwide.

## RESUMEN

Esta investigación presenta los primeros restos de pliosaurio del Jurásico Superior del desierto de Atacama, en el norte de Chile. Dos especímenes recuperados de niveles de edad oxfordiana están representados por una rama mandibular fragmentaria y por un húmero y fémur asociados, respectivamente. Antes de esta investigación, los registros de pliosaurios jurásicos sudamericanos estaban restringidos a taxa endémicos de Titoniano de la provincia de Neuquén, en Argentina. El material estudiado representa el primero de edad oxfordiana conocido en Gondwana, y se suma a los escasos registros de pliosaurios oxfordianos conocido en todo el mundo.

## 1. Introduction

The Pliosauridae (Sauropterygia, Plesiosauria) was a group of marine diapsids that spanned from the Lower Jurassic until the mid Cretaceous. During the Jurassic, their occurrences are well-known in Europe (Lydekker, 1889; Andrews, 1913; Delair, 1959; Knutsen, 2012; Benson et al., 2013; Zverkov et al., 2018). The group seems to spread worldwide during the Upper Jurassic, but coupled to a reduction in its diversity

before the Jurassic-Cretaceous boundary (Benson and Druckenmiller, 2014). During the Lower Cretaceous until the mid-Cretaceous, pliosaurids have been recorded in United States (Williston, 1907; Albright et al., 2007), Mexico (Barrientos-Lara et al., 2015), Europe (Bardet et al., 2016; Buffetaut et al., 2005; Lukeneder and Zverkov, 2020), Russia (Zverkov, 2015), Colombia (Páramo-Fonseca et al., 2016, 2018) and Australia (Longman, 1924; Kear, 2006), indicating a widespread distribution along both hemispheres.

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Prior to the Cretaceous, records of Pliosauridae in the Southern Hemisphere are particularly scarce. The group is known by two species of *Pliosaurus* Owen, 1841 from the Tithonian of Argentinean Patagonia (Gasparini and O’Gorman, 2014; O’Gorman et al., 2018a, 2018b) and other still indeterminate pliosaurids (Fernández et al., 2020), while the oldest pliosaurid record from Gondwana is comprised by an isolated vertebra from the Callovian of the Argentinean Patagonia (Gasparini and Spalletti, 1993). The present contribution describes new specimens referable to Pliosauridae, recovered from lower Oxfordian strata of the Atacama Desert in northern Chile. These records represent the first South American records of this age, helping to fill the gap between the Callovian and Tithonian, proving a continuous presence of pliosaurids during the Middle and Upper Jurassic of Gondwana.

## 2. Locality and geological setting

The two specimens studied here were recovered from two different localities. Jurassic strata crop out in both sites, being exposed 20 km WSW Calama, northern Chile, in the central part of the Atacama Desert (Fig. 1A). The fossil-bearing levels were first described by Biese (1957, 1961), who indicated the presence of vertebrates in several strata of the section. The same outcrops were later re-studied by Lira (1989), who formalized them as the Cerritos Bayos Formation. Recently, this section was reassigned as the Cerro Campamento Formation by Duhart et al. (2018). The respective localities of the finds are described as following:

### 2.1. Loma Larga Sur

MUHNAL.20181 was recovered from this locality. The material was found in a fragment of a large concretion broken by effect of erosive processes. This has a matrix of dark-grey calcareous limestone. Following Biese (1961), the fossil-bearing level is part of the oolitic limestones with Spongiae. However, the material occurs in concretions and associated to *Subvinalesphinctes prophetae* Parent et al. (2006). Therefore, we assign the age of the material to the lower Oxfordian. The stratigraphic provenance of the material is correlated with the

‘*Perisphinctes*-Kalk’ of Biese (1961). Associated vertebrate remains comprise gill-rakers of large filter-feeding osteichthyans (Ossa-Fuentes et al., 2015). All these finds plus the ammonoid-bearing levels were integrated in a general stratigraphic section (Fig. 1B), with estimated thicknesses based in Biese (1961).

### 2.2. Biese 3

This is an informal field name, used here due to the lack of local formal toponymy. MUHNAL.20188 was found here, ca. 400 m south from El Loa River, in the northern part of Cerritos Bayos locality. The material was found scattered in fragments over the surface. It is associated to a larger concretion with *in situ* elements, awaiting extraction. Invertebrates associated in the concretion include abundant phragmocones of *S. prophetae* (=‘*Perisphinctes* limestone’, ‘Caliza de *Perisphinctes*’ in Biese, 1961). In addition, a phragmocone of the ammonoid genus *Reineckeia* was found in a level settled 5 m below the concretion horizon, indicating the presence of Callovian beds briefly below the hosting level of MUHNAL.20188, therefore, indicating a lower Oxfordian age for this specimen. Biese (1960) noted that the general section has 700–750 m covered by debris, obscuring the contact between the Callovian and the Oxfordian. The local presence of chronostratigraphically valuable ammonoids indicating both stages allows us to recognize the proximity of the Callovian-Oxfordian boundary, and even more, assigning a lower Oxfordian age for the studied material.

## 3. Material and methods

MUHNAL.20188 was found in October 2017 by two of the authors (ORM and JR). The specimen was scattered over the soil and fragmented into several pieces. A medial section of the femur diaphysis was naturally lost. Most of the fragments were partially covered by limestone and gypsum veins. Later, it was prepared with ME-9100 airscribe by one of the authors (RAO) during 2019. MUHNAL.20181 was found by one of the authors (SSA), being preserved as a natural slice section of a larger concretion. The rest of the mandible and/or skull was not found in the

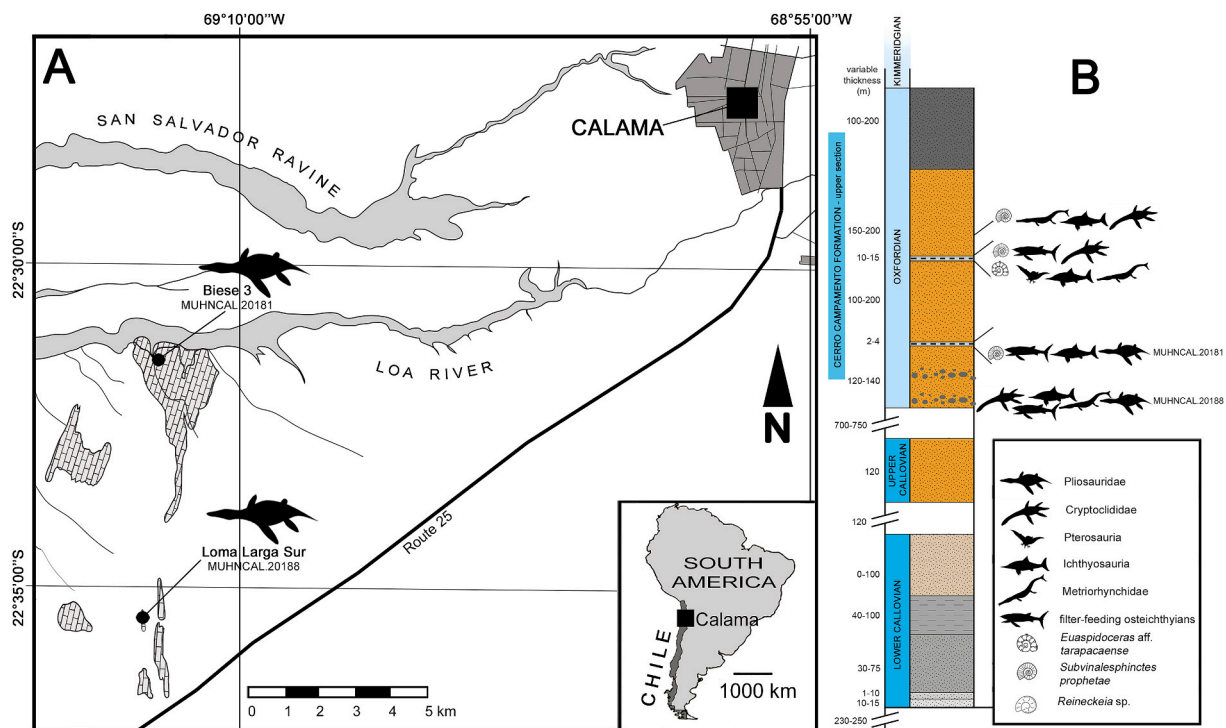
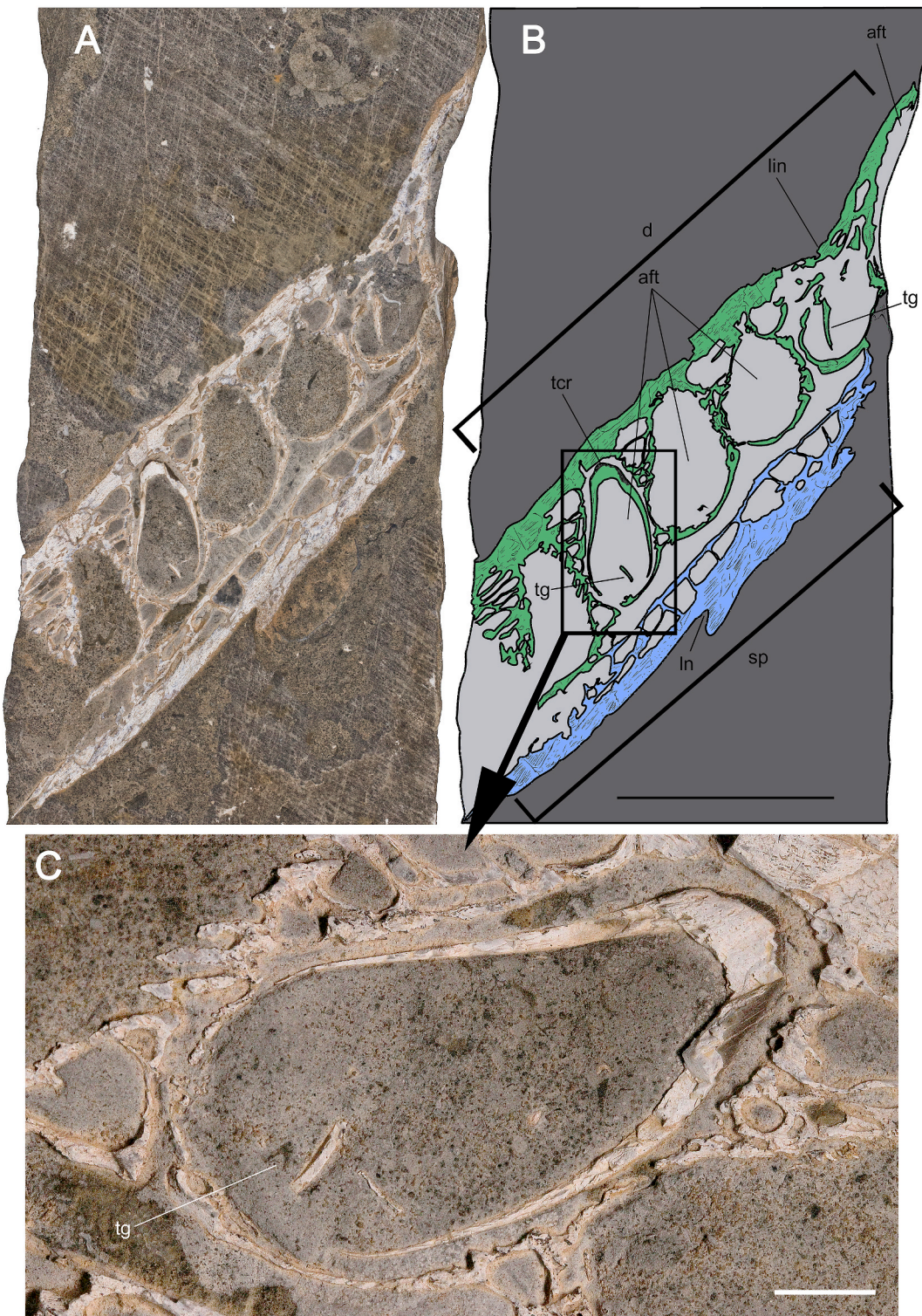


Fig. 1. A, map indicating the Oxfordian outcrops exposed in Cerritos Bayos east Calama, where the studied material was recovered. B, generalized stratigraphic section of the Cerro Campamento Formation. Based on Biese (1961) and Lira (1989).





**Fig. 2.** Pliosauridae indet.; MUHNCAL.20181. **A**, fragment of the left dentary naturally exposed in dorsolingual section. **B**, scheme of the same specimen. Scale bar = 10 cm. **C**, detail of the best preserved tooth, showing a fragment of the crown tip. Scale bar = 10 mm. Anatomical abbreviations. **aft**, alveoli of functional teeth; **d**, dentary (in green); **lin**, labial inflection; **ln**, lingual notch; **sp**, splenial (in light blue); **tcr**, tooth crown; **tg**, tooth germ. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



field. The natural exposure of the elements was used here for description, without further preparation.

3.1. Institutional abbreviations

MUHNAL, Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Chile; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; CAMSM, Sedgwick Museum, Cambridge, UK.

4. Systematic paleontology

- Diapsida Osborn, 1903.
- Sauropterygia Owen, 1860.
- Plesiosauria de Blainville (1835).
- Pliosauridae Seeley, 1874.
- Pliosauridae indet.
- Figs. 2–3

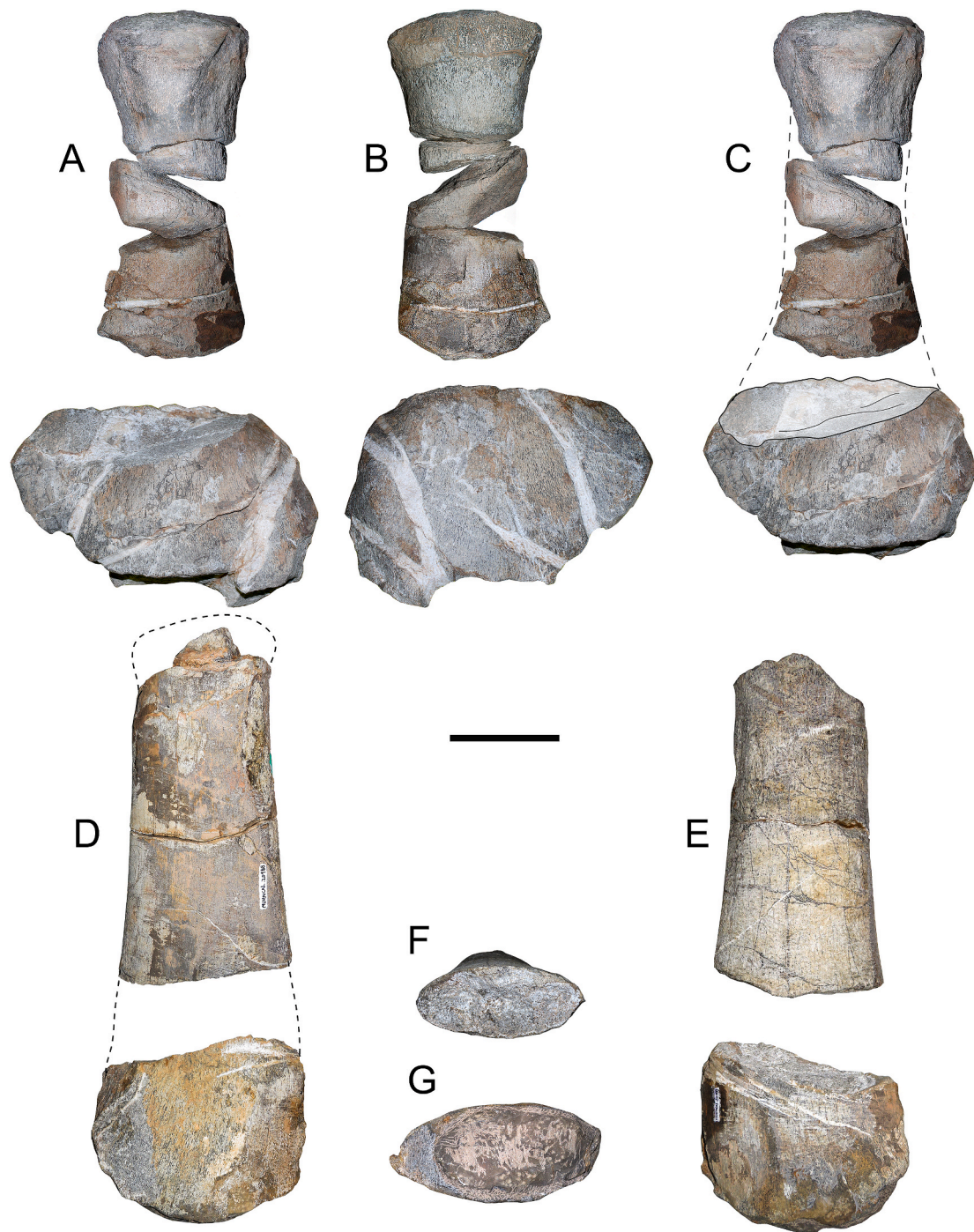


Fig. 3. Pliosauridae indet.; MUHNAL.20188, associated propodials. A, fragmented right humerus in dorsal view. B, same in ventral view. C, reconstruction of the humerus by digital relocation of the fragments separated by carbonate veins. D, right femur in dorsal view. E, same in ventral view. F, medial cross-section. G, distal view. Scale bar = 10 cm.



#### 4.1. Material

MUHNAL.20181. Incomplete left dentary; MUHNAL.20188. Incomplete femur and incomplete humerus, associated.

#### 4.2. Locality, horizon and age

MUHNAL.20181, Loma Larga Sur, 20 km WSW Calama, northern Chile. Cerro Campamento Formation, Zone of *Subvinialesphinctes prophetae*, middle Oxfordian; MUHNAL.20188, 'Biese 3' informal locality, 19 km WSW Calama, northern Chile. Levels with *Subvinialesphinctes prophetae*, briefly above *Reineckeia* zone, lower Oxfordian.

#### 4.3. Description

MUHNAL.20181. The material comprises a fragment of the left dentary (Fig. 2A and B). It is exposed in an oblique, dorsolingual view, which causes the view of the alveoli in oblique cross-section. Five alveoli are visible in dorsal view, with a sixth alveolus only visible in anterior view. One partial tooth is preserved, showing a small fragment of the lingual enamel with striations (Fig. 2C). The alveoli are surrounded by porous tissue which is interpreted as interdental and parodontal plates. The anterior part of the preserved portion has a marked rostral inflection over its labial surface. Over the exposed section, it can be noted a straight contact of two elements, one of them including the alveoli (i.e., the dentary) while the second element is placed ventrally with respect to the first. It is here identified as the splenial. Its lingual surface shows a notch, suggesting the articulation with a posterior element such as the coronoid or the angular.

MUHNAL.20188. The humerus (Fig. 3A and B) was found in four successive, associated fragments (Fig. 3A–C). Its distal part was probably fragmented during the burial, being filled by several carbonate veins. Its distal contour is preserved, but its continuity is interrupted by these veins. The medial part of the diaphysis is much eroded and cracked. The contact with the distal part was naturally lost due to the erosion. The proximal part preserves the articular head and the tuberosity. The articular head is slightly rounded, having a cross-section larger than that of the diaphysis. The tuberosity is centered over the shaft axis. A digital reconstruction of its distal fragment (Fig. 3C) shows articular faces without well-defined facets and a distal width expanded ca. twice of the articular width.

MUHNAL.20188 femur (Fig. 3D–G) lacks the contour of its articular head. It also lacks a fragment of the diaphysis section. The most proximal preserved part has a subcircular section, while its distal cross section is oval and dorsoventrally depressed. The femur is slender. Its distal width is ca. one third of its proximal width, without well-defined articular facets, preaxial nor postaxial expansions.

### 5. Discussion

#### 5.1. Comparison of MUHNAL.20181 with other pliosaurids

Despite its incomplete preservation, the fragmentary dentary MUHNAL.20181 preserves diagnostic aspects. The presence of a specialized tissue with interdental and parodontal plates, corresponds to a characteristic of Plesiosauria, and particularly, coincides with the topology of these structures described in Pliosauridae (Sassoon et al., 2015; Fig. 2). Although fragmentary, the best preserved tooth of MUHNAL.20181 has a crown tip with fine longitudinal striations in the lingual face. Other relevant dental features such as carinae, inserted ridges, ridglets and/or bands (see Zverkov et al., 2018) are not preserved. Considering the oblique cross-sections of the five preserved alveoli, the dental cross-section seems to be rounded, implying that the teeth are likely conical instead of trihedral (*sensu* Zverkov et al., 2018). The large pulp cavity seen in MUHNAL.20181 tooth is very similar to those of an indeterminate thalassophonean described by Zverkov (2018;

Fig. 5G). Also, the dentary/tooth proportion is typical of several genera within Pliosauridae (Knutsen, 2012; Fig. 4). Based on these features, we refer MUHNAL.20181 to Pliosauridae. In addition, the presence of a notch on the lingual surface of the splenial may reflect the contact with the angular or the coronoid. Based on its available fragment, MUHNAL.20181 can be morphologically separated from Lower Jurassic basal pliosaurids with elongated and constricted rostra (i.e., *Thalassiodracon*, *Attenborosaurus*, and *Hauffiosaurus*; see O'Keefe, 2001). The presence of a marked inflection over the labial surface at the level of the posterior end of the symphysis, associated to the presence of laterally expanded dentaries with larger alveoli, is only found among Middle-to-Upper Jurassic pliosaurids (Knutsen, 2012).

The relative size of MUHNAL.20181 teeth with respect to its dentary is considered a key feature for its classification. This proportion is similar to those present in few Kimmeridgian specimens from England, such as BRSMG Cc332 referred to the genus *Pliosaurus* (Knutsen, 2012), and CAMSM J.35991 referred to *Pliosaurus brachyspondylus* (Tarlo, 1959; Knutsen, 2012). The proportion between the dentary and the teeth is also similar to that of the Callovian genus *Simolestes* (Andrews, 1909, 1913). The only Oxfordian pliosaurid species known to date are *Gallardosaurus iturraldei* Gasparini (2009) from Cuba, known by a single partial skull, and *Anguanax zignoi* Cau and Fanti (2015), represented by a crushed skull and incomplete postcranium. Regrettably, *Gallardosaurus iturraldei* does not preserve the rostrum neither the symphyseal part of the mandibles, making impossible any comparison with MUHNAL.20181. On the other hand, *Anguanax zignoi* skull and dentary are laterally crushed, reason why their dental features cannot be assessed (Cau and Fanti, 2014).

#### 5.2. Comparison of MUHNAL.20188 with other pliosaurids

MUHNAL.20188 humerus shows a prominent articular head with a tuberosity centered in the shaft axis. Even fragmented, their distal contour can be assessed, showing a proximal width that represents ca. two thirds of its distal expansion. In addition, the slender femur shows a similar proportion between the proximal and distal width. These propodial features are similar to those observed in representatives of the genus *Pliosaurus*, particularly, in *Pliosaurus macromeris* (Tarlo, 1959). Within Pliosauridae, the occurrence of a femur shaft much larger than the humerus is absent in basal taxa such as *Thalassiodracon hawkinsi*, *Hauffiosaurus zannoni* and *Attenborosaurus conybeari* (O'Keefe, 2001), being instead more typical of taxa from the Middle Jurassic and onwards (Fig. 4). In addition, the presence of slender femora with a slightly expanded distal end in post-Middle Jurassic taxa (Fig. 4), is at least documented in the genera *Pliosaurus*, *Luskhan*, *Stenorhynchosaurus* and *Sachicasaurus* (Páramo-Fonseca et al., 2016: p. 95, Fig. 7; 2018: p. 233, Fig. 7). Both features are present in MUHNAL.20188. Even more, the general morphology of its propodials is similar to those of the species *Pliosaurus macromeris* (Tarlo, 1959: p. 48, Fig. 5 and Plate 9). By the moment, the lack of more significant features preserved in MUHNAL.20188 precludes a generic determination.

#### 5.3. Paleobiogeography of the Pliosauridae

The earliest known records of Pliosauridae are restricted to north Pangaea. During the Lower Jurassic, *Thalassiodracon hawkinsi* (Owen, 1838), *Attenborosaurus conybeari* (Sollas, 1881), *Cryonectes neustriacus* Vincent et al. (2013), *Hauffiosaurus* spp. (O'Keefe, 2001) and *Arminisaurus schuberti* Sachs and Kear (2018), represent an early pliosaurid diversity restricted to Europe. During the Middle Jurassic, a rich diversity is known in the Callovian of Europe, represented by the taxa *Liopleurodon ferox*, *Simolestes vorax* Andrews (1909), *Peloneustes philarchus* (Seeley, 1869), *Pachycostasaurus dawni* Cruickshank et al. (1996), and *Marmornectes candrewi* Ketchum and Benson (2011). The Oxfordian records of Pliosauridae includes large pliosaurid teeth from several units in England, spanning from the lower to upper Oxfordian

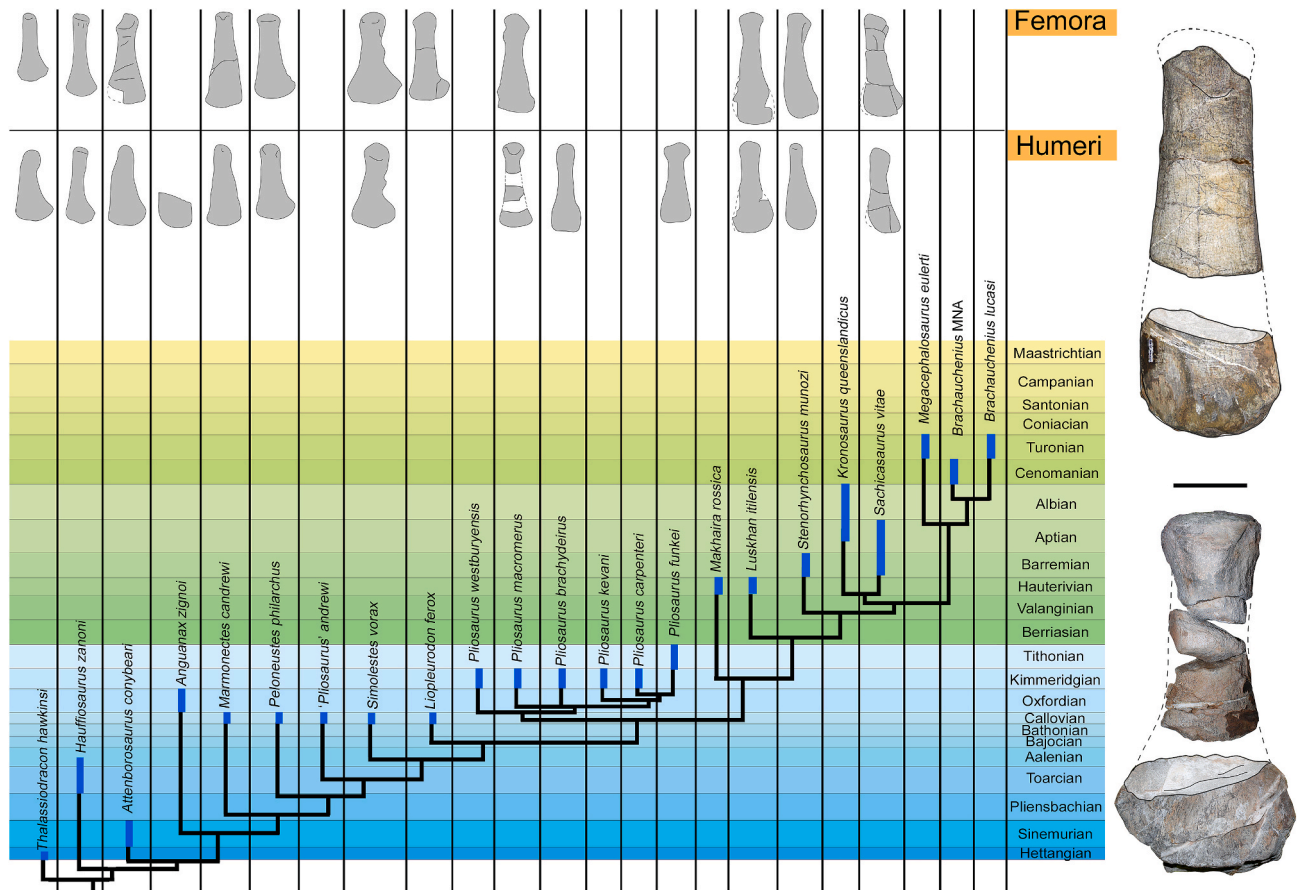


Fig. 4. Propodial comparison of MUHNAL.20188 with other pliosaurids. Cladogram was modified from Fischer et al. (2016). Outlines are based in O'Keefe (2001), Fanti and Cau (2015), Andrews (1911), Tarlo (1959), Knutsen et al. (2012b), Fischer et al. (2015), Fischer et al. (2017), and Páramo et al. (2016, 2018; 2019).

(Foffa et al., 2018). There are fragmentary records from the lower Oxfordian of Poland (Lomax, 2015). Callovian, Oxfordian and Tithonian pliosaurids have been reported from Russia (Zverkov, 2015). Skull material from the middle Oxfordian Rosso Ammonitico Veronese Formation of Italy was also referred to Pliosauridae (Cau and Fanti, 2014), being later identified as a new genus and species, *Anguanax zignoi*. Finally, *Megalneusaurus rex* from the Oxfordian of Wyoming and Alaska, has been described by few fragmentary specimens (Knight, 1895; Weems and Bloodgett, 1996; Wahl et al., 2007, 2010).

Outside Laurasia, the unique species so far identified during the Oxfordian is *Gallardosaurus iturraldei*, represented by an incomplete skull, atlas-axis and anterior cervical vertebrae, recovered from the middle-late Oxfordian Jagua Formation of Cuba. During the Tithonian, pliosaurids appeared in new localities including the Southern Hemisphere: Patagonian records in Argentina include two species, *Pliosaurus patagonicus* Gasparini and O'Gorman (2014), and *Pliosaurus almanzaensis* O'Gorman et al., 2018a, 2018b.

During the Upper Jurassic, the European records are mostly restricted to records of *Pliosaurus* spp. in the lower Kimmeridgian of England, and records of the same genus in the Tithonian of Russia and Norway (Knutsen et al., 2012b; O'Gorman et al., 2018a, 2018b and references therein). Outside Europe, postcranial elements of a giant pliosaurid were described from Kimmeridgian units of Mexico (Buchy et al., 2003). There is a record of a pliosaurid vertebral centrum from the Kimmeridgian-Tithonian Sabinal Formation, (Alvarado and Ortega, 2014), and a rostral fragment referred to *Liopleurodon* (Barrientos-Lara et al., 2015), both in Mexico. During the Lower Cretaceous and the lower part of the Upper Cretaceous, pliosaurids were only represented by the subfamily Brachaucheninae, which reached a wide geographical distribution. There are records in North America represented by the genus

*Brachauchenius* and *Megacephalosaurus* (Williston, 1907; Albright et al., 2007; Schumacher et al., 2013). Also, in Europe, represented by the genera, *Luskhan* (Fischer et al., 2017), *Makhaira* (Fischer et al., 2015), *Polyptychodon* (Bardet et al., 2016). Gondwanan records include Colombia, with the genera *Sachicasaurus*, *Stenorhynchosaurus* (Páramo-Fonseca et al., 2016, 2018) and *Acostasaurus* (Gómez-Pérez and Noè, 2018), and also Australia with the genus *Kronosaurus* (Longman, 1924; Kear, 2006; Kear et al., 2018).

Following Iturralde-Vinent (2005), the available stratigraphic information from sedimentary rocks from the Caribbean area allows demonstrating that the Caribbean Seaway (a marine corridor between the Tethys and Pacific) was completely functional at least since the Oxfordian. Even more, the beginning of the opening occurred even before the Oxfordian. The narrow phylogenetic relationships between the ammonoid assemblages from the Tethys and those from the Neuquén Basin during the Bajocian suggest the existence of this eventual connection ca. 7 Ma before the Oxfordian (Westermann and Riccardi, 1979). The presence of cryptoclidid and pliosaurid plesiosaurians now in southeastern Panthalassa (Gasparini and Spalletti, 1993; Otero et al., 2020; this study), reinforces the presence of a common marine diversity between northern Tethys, the Caribbean and South America during the Upper Jurassic, as previously pointed out by different authors (Gasparini, 1996; Iturralde-Vinent, 2005). The Oxfordian records from Wyoming (O'Keefe and Wahl, 2003; O'Keefe and Street, 2009; O'Keefe et al., 2011) could be the result of a marine corridor from the Caribbean Seaway into the north. The unusual diversity of long-necked cryptoclidids from the Tithonian of Norway (Knutsen et al., 2012a; b) includes the genera *Djupedalid* and *Spitasaurus*, which bear substantial anatomical differences compared to North American, Oxfordian forms with comparatively shorter necks, so far represented by the genera



*Pantosaurus* and *Tatenectes* (O'Keefe, 2001; O'Keefe and Street, 2009). Coeval records from Cuba includes a single genus and species, *Vinialesaurus caroli* (De La Torre and Rojas, 1949; emend. Gasparini et al., 2001).

On the other hand, pliosaurids are well-known in the Callovian, the Kimmeridgian and even in the Tithonian of England (Benson et al., 2013). Other Kimmeridgian specimens are known in Norway (Knutson et al., 2012b), however, there is scarce evidence on Oxfordian European pliosaurids, being restricted to indeterminate dental remains from lower Oxfordian of Poland (Lomax, 2015) and to the genus *Anguanax zignoi* Cau and Fanti (2015), from the middle Oxfordian of Italy.

Outside Europe, the unique Oxfordian pliosaurid records known to date are represented by *Gallardosaurus iturraldei* from Cuba, by *Megalneusaurus rex* (Knight, 1895) from USA, and by MUHNCAL.20181 here studied. Younger pliosaurid records are known in South America during the Tithonian (Gasparini and O'Gorman, 2014), the Berriasian (Fernández et al., 2020) and the Barremian-Aptian (Páramo-Fonseca et al., 2019). Despite being scarce, the presence of pliosaurids in the Oxfordian of Chile adds support for a full opening of the Caribbean Corridor fully during this lapse, as previously indicated by Iturralde-Vinent (2005).

On the other hand, the record of a Late Jurassic indeterminate plesiosaur from Antarctica (O'Gorman et al., 2018a, O'Gorman et al., 2018b) proved the coeval presence of the group in high austral latitudes. To this find are added the recent first unequivocal Late Jurassic ichthyosaur remains in Antarctica (Campos et al., 2019), referred to Ichthyosauria indet. and to Ophthalmosauridae indet.; this same clade is present during the Lower Cretaceous of southernmost Chile, current latitude 51°S (Stinnesbeck et al., 2014; Pardo-Pérez et al., 2015). In addition, there is a record of a late Kimmeridgian Pachycormiformes in Antarctica (Gouiric-Cavalli et al., 2019), a group also present in the Oxfordian of northern Chile (Arratia, 2015; Ossa-Fuentes et al., 2015).

Damborenea et al. (2012) extended this comparison to several Triassic-Jurassic bivalvian clades, finding similar distributional patterns. During the Middle Jurassic, similar evidences were noted on probably Bathonian-Callovian trigoniids from Caracoles, 65 km south Calama, considered as close relatives to South African taxa (Steinmann, 1881). Cecioni and Charrier (1974) discussed the common presence of Late Jurassic gryphaeids species between southern Chile and the Ethiopian-Indo-Malagasic Faunistic Paleoprovince, concluding that southern Chile was the transitional area of an interoceanic connection between the ancient Pacific and the Tethys, throughout the Mozambique Corridor (=Trans-Erythraean Seaway in Mutterlose, 1986). During the Late Jurassic and the Early Cretaceous, a similar distribution pattern was noted among Tithonian-Hauterivian trigoniids from South America, Magallanes (southernmost Chile) and South Africa (Fuenzalida (1964). An indopacific influence was also noted on Upper Jurassic-Lower Cretaceous ammonoids from central Chile (Salazar et al., 2020).

In this sense, the Middle and Upper Jurassic units of the Atacama Desert are strategical by providing geographic and chronostratigraphic intermediate localities between the Caribbean Seaway and the Mozambique Corridor. By the moment, the local vertebrate evidence is sparse, although in terms of their taxonomical composition it suggests a higher influence of the Caribbean Seaway (Arratia, 2015; Gasparini, 1996, 2009; Otero et al., 2020) at least during the Oxfordian.

#### 5.4. Comments on the putative previous record of pliosaurids from Chile

The presence of 'pliosaurids' (*sensu lato*) in Chile was historically restricted to a single Late Cretaceous species, '*Pliosaurus chilensis*' (Gay, 1847) (*nomen dubium*: Steinmann et al., 1895; Persson, 1963; Welles, 1962). Currently, all the material that conforms the hypodigm of '*Pliosaurus chilensis*' can be referred to different remains of elasmosaurid plesiosaurs (Otero et al., 2015); even more, the hypodigm includes an octagonal caudal centrum referable to the genus *Aristonectes* (Otero and O'Gorman, 2013). Considering this, the presence of pliosaurids in the

Late Cretaceous of Chile is totally discarded. Thus, the specimens studied here from lower Oxfordian levels of the Atacama Desert, represent the first materials from Chile confidently referable to pliosaurids.

## 6. Conclusions

The material studied here represents the first evidence of Oxfordian pliosaurids from South America. These new finds fill a chronostratigraphic gap in the South American pliosaurid record, previously represented by an isolated vertebra from the Callovian of Argentina, and by two endemic species from the Tithonian of Argentina. The studied specimens are fragmentary and cannot support a generic identification. However, these show partial affinities to Callovian-to-Kimmeridgian taxa from northern Tethys (e.g., *Pliosaurus*, *Simoolestes*). The Oxfordian pliosaurids from the Atacama Desert also complement the diversity of known marine vertebrates which are common between southeastern Panthalassa and the northern Tethys, reinforcing the hypothesis of a fully functional Caribbean Seaway during the Middle and Upper Jurassic.

### Credit authorship contribution statement

Rodrigo A. Otero: Conceptualization, Preparation of the material, Formal analysis, Investigation, Methodology, Writing - original draft. Sergio Soto-Acuña: Collection of one specimen, Conceptualization, Investigation, Writing - original draft. Jennyfer Rojas: Collection of one specimen, Specimen curation. Osvaldo Rojas: Collection of one specimen, Specimen curation.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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