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First temnodontosaurid (Ichthyosauria, Parvipelvia) from the Lower Jurassic of the Atacama Desert, northern Chile

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ABSTRACT

We describe fragmentary ichthyosaur skull remains of a single individual recovered from Lower Jurassic marine strata in northern Chile. The preserved teeth display distinctive features such as a very long, robust and coarsely infolded roots; as well as low, labio-lingually compressed, large triangular crowns with carinae. Dental features are consistent with those of the genus *Temnodontosaurus*, previously known in the Lower Jurassic of Europe. This find represent the first record of a temnodontosaurid ichthyosaur in the southern hemisphere, reinforcing a pattern of faunal interchange between the northern Tethys and southern Panthalassa, prior to the separation of Laurasia and Gondwana, and before the full establishment of the Caribbean Seway.

RESUMEN

Describimos restos craneales fragmentarios de ictiosaurio pertenecientes a un único individuo, recuperado desde estratos marinos del Jurásico Inferior del norte de Chile. Los dientes preservados muestran características distintivas, como una raíz muy larga, robusta y con gruesos pliegues, así como también coronas bajas, triangulares, masivas, labio-lingualmente comprimidas y con carenas. Las características dentales son consistentes con las del género *Temnodontosaurus*, anteriormente conocido en el Jurásico Inferior de Europa. Este descubrimiento representa el primer registro de un ictiosaurio temnodontosáurido en el hemisferio sur, reforzando un patrón de intercambio faunístico entre el Tetis norte y Panthalassa sur, antes de la separación de Laurasia y Gondwana, y antes del establecimiento completo de la vía marítima del Caribe.

1. Introduction

Ichthyosaur records from northern Chile are abundant (Pardo-Pérez et al., 2015) but mostly comprised by fragmentary remains of indeterminate taxa. The oldest local record is represented by indeterminate ichthyosaur remains from Triassic beds of Quebrada Doña Inés Chica, Región de Atacama (Suárez and Bell, 1992). Lower Jurassic records include ichthyosaur vertebrae from Sinemurian levels of Quebrada Punta del Viento, Región de Antofagasta (Casamiquela, 1970). Also, Chong and Gasparini (1972) mentioned ichthyosaur vertebrae from Sinemurian beds of the Profeta Formation in Alto de Varas, Región de Antofagasta. Chong and Gasparini (1976) also reported ichthyosaur remains near Quebrada Incahuasi, in strata of middle Toarcian age. Later, Suárez and Otero (2010) described 10 vertebrae of a single and large individual, from Hettangian beds in Pan de Azúcar, Región de Atacama. These authors also described an incomplete juvenile specimen from Quebrada Tres Cruces, Región de Coquimbo, recovered from Lower Jurassic strata. Importantly, none of the specimens mentioned above had enough diagnostic features for a determination beyond ordinal level.

This research describes the first Lower Jurassic ichthyosaur remains from northern Chile, which can be referred to Temnodontosauridae, a monogeneric group that only includes the genus *Temnodontosaurus*. The studied specimen is the first temnodontosaurid found in the southern hemisphere. Paleogeographic implications are discussed.

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2. Material and methods

The material (SGO.PV.324) was collected during 1988 by geologists Patricio Sepúlveda and Nelson Muñoz (ENAP, Empresa Nacional del Petróleo, Chile). The remains were collected as fragments found over the soil, scattered due to the erosion. Once collected, it was housed in the Museo Nacional de Historia Natural (Santiago, Chile), being rediscovered during 2016 by S. Soto-Acuña (U. de Chile) during the review of old collections. Most of the teeth are preserved as moulds in the matrix, while few rostral bones are only visible in cross-section. The fragments were prepared by one of the authors (RAO) during 2017 with Dremel Engraver Tool and hand tools, allowing the visualization of several complete teeth. Most of the fragments cannot be attached to successive portions because the broken sections are much eroded. However, they can be ordered based in a straight margin present in most fragments. One large block shows in cross-section the articulated dentary and rostrum, verifying that the straight margin seen in other fragments corresponds to the occlusion between the skull and the mandible. Anatomical comparisons follows Maisch and Matzke (2000).

2.1. Institutional Abbreviations

SGO.PV, Paleontología de Vertebrados, Área Paleontología, Museo Nacional de Historia Natural, Santiago, Chile; LEICT, Leicester Arts and Museums Service (New Walk Museum and Art Gallery), Leicester, England.

3. Locality and geologic setting

SGO.PV.324 was naturally transported from its stratigraphic occurrence, being found over the soil in a ravine ca. 7 km south from Mantos Blancos Mine, Antofagasta Region, northern Chile (Fig. 1). The lithology of the ichthyosaur-bearing level comprised calcareous sandstones with medium grain, and grey to yellowish colour. Available geologic studies have recognized two Mesozoic or older sedimentary units cropping out in the studied area. A geologic map procured by Sernageomin (2003; 1:1,000,000 scale map) of the area where the specimen was found, indicates the presence of volcanic and volcaosedimentary beds of La Negra Formation (García, 1967). The basal half of this unit comprises a section of ca. 450 m mostly conformed by lithic riodacytic tuffs, with intercalations of andesitic lavas, reddish quartz-rich sandstones, and calcareous sandstones with ammonoids of the taxa *Arnioceras* sp. and *Paracoroniceras*(?) sp. indicating a Sinemurian age (Pérez and Reyes, 1998).

In addition, the Estratos de Rencoret unit (Tobar, 1966) underlies La Negra Formation through an angular discordance. According to Cortés (2000), the Estratos de Rencoret is a ca. 400 thick section of sandstones and calcareous, marine, fossiliferous shales, characterized by a very fine stratification and by a grey to yellowish colour. The mid-section of shales includes the trigoniid *Myophorigonia* cf. *pascoensis*, and the brachiopods *Terebratula* and *Spiriferina* (Pérez and Reyes, 1998), while the upper 200 m of massive, yellow calcareous limestones include ammonoids (*Caloceras* sp.), bivalvians (*Astarte* sp.) and echinoderms (*Pentacrinites* sp.), indicating an Hettangian age. In addition, Muñoz (1989) reported the presence of the ammonoids *Arietites* sp. and *Arnioceras* sp. in the same unit, assigning it a Sinemurian age. The lithology of the sediment attached to the studied material is consistent with the upper section of the Estratos de Rencoret. Thus, a Hettangian-Sinemurian age can be assigned to the specimen.

4. Systematic paleontology

Ichthyosauria de Blainville (1835).
Parvipelvia Motani, 1999.
Neoichthyosauria Sander, 2000.
Temnodontosauridae McGowan, 1974.

Genus *Temnodontosaurus* Lydekker, 1889.

4.1. Type species

Temnodontosaurus platyodon (Conybeare, 1822), Lower Jurassic (Upper Hettangian-Lower Sinemurian), Lyme Regis, Dorset, England.

***Temnodontosaurus* sp.**

Figs. 2-4

4.2. Referred specimen

SGO.PV.324. Fragmentary dentary and rostrum including at least 11 teeth, few of them preserved as a cast.

4.3. Locality, Horizon and age

South Mantos Blancos Mine, Antofagasta Region, northern Chile. Estratos de Rencoret Unit, Hettangian-Sinemurian.

4.4. Description

SGO.PV.324 includes eleven main blocks and several small fragments. These represents part of de dentary and likely, the premaxilla (Fig. 2). Both remained in occlusion during the burial. Only few blocks can be re-joined, being most of them eroded. This makes difficult an accurate interpretation of the dentary, however, in most blocks the occlusal margin is preserved and filled with sandstone, which helps as a guide for the orientation of each block. No sutures were visible. A large block preserves the dentary labial wall as well as a tooth in anatomical position (Fig. 3). In the latter, it is possible to identify the ventral part of the dentary and assess its cross-section, which is almost three times dorsoventrally higher than labiolingually broad. SGO.PV.324 also preserves several dissarticulated, bivalve shells consistently oriented, suggesting it was deposited with the skull lying over its side.

The teeth of SGO.PV.324 originated within a dental groove and without a proper socket. This aulacodont condition (sensu Motani, 1997) is typical of post-Triassic ichthyosaurs. All SGO.PV.324 teeth are robust, with roots at least twice as high as its respective crown and coarsely infolded. The measurements of the best preserved teeth are provided on Table 1. Crowns are triangular, low and robust, labio-lingually compressed, with longitudinal striations over its crown, and having a distal and a mesial carinae without serrations (Fig. 4). In one tooth cast (Fig. 4A and B) we observed that the teeth have a compressed oval cross-section.

5. Discussion

5.1. Remarks

Temnodontosauridae (as originally proposed by McGowan, 1974) includes, among other features, an adult jaw between 60 cm and 100 cm of length. McGowan (1974) also indicates that the clade was restricted to the lower division of the Liassic. Even in its fragmentary condition, the preserved mandibular fragments of SGO.PV.324 exceed 60 cm in length and 22 cm high, although, its total size cannot be assessed.

Triassic ichthyosaurs having teeth with carinae include the genera *Himalayasaurus* Dong, 1972, and *Thalattoarchon* Fröbisch et al., 2013. Teeth of *Himalayasaurus* possess a crown that looks like a thick dagger blade, being labiolingually compressed, with well-developed cutting edges and coarse, deep longitudinal striations over the crown. The best available tooth of *Himalayasaurus tibetensis* holotype shows a crown that represents the half of the whole tooth length (Motani, 1999). Teeth of *Thalattoarchon* are also bicarinate and laterally compressed, with

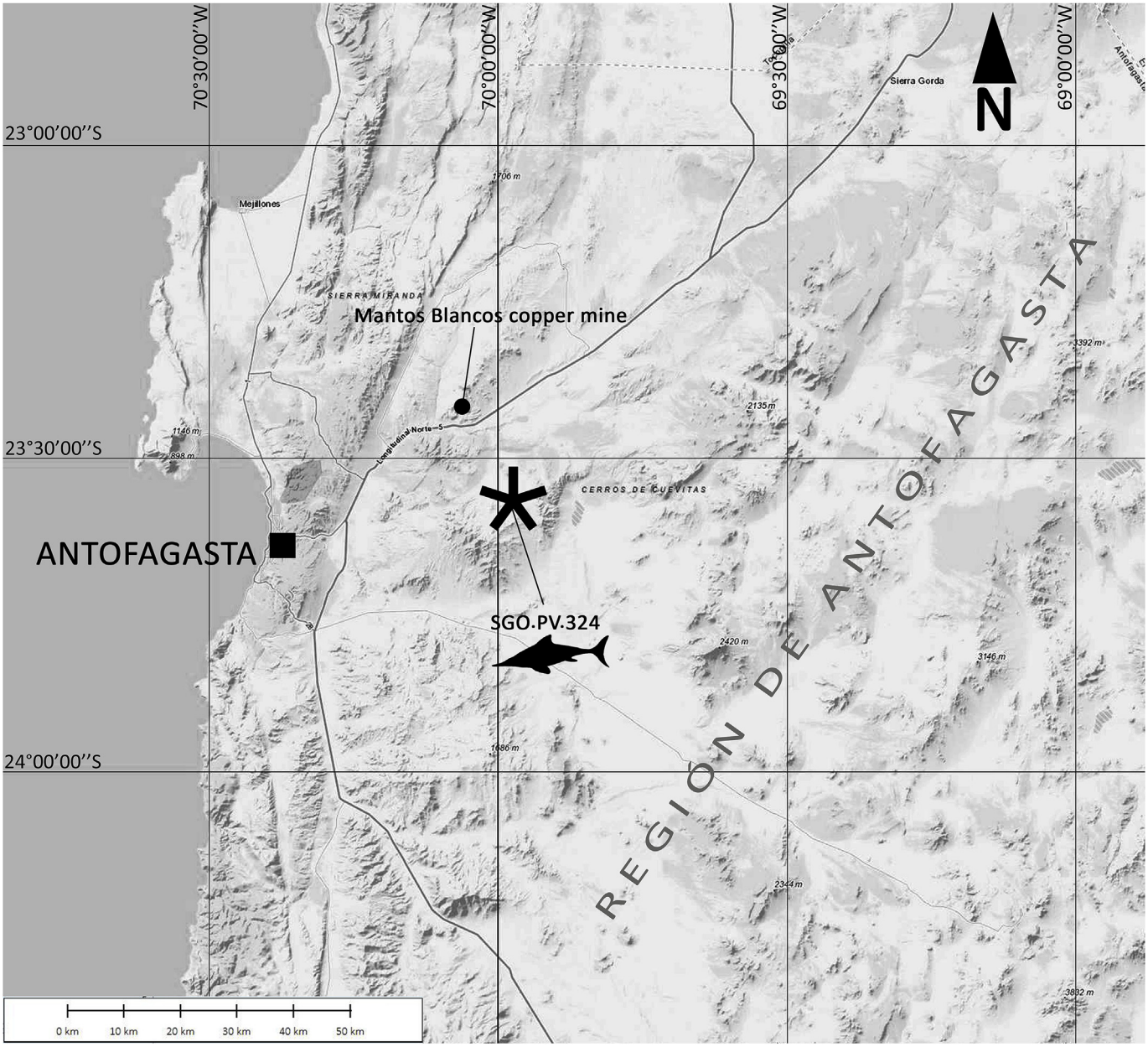

Fig. 1. Map indicating the area where SGO.PV.324 was discovered in 1988, south from Mantos Blancos mine, Región de Antofagasta, northern Chile (map from World Topomap, online source 2018).

crowns larger than 5 cm (Fröbisch et al., 2013).

Hettangian–Sinemurian taxa include the genera *Leptonectes*, *Protoichthyosaurus*, *Ichthyosaurus*, *Wahlisaurus* and *Excalibosaurus*. *Leptonectes* teeth are characterized by slender crowns larger than its respective root (Maisch and Matzke, 2000: Fig. 17). *Protoichthyosaurus* teeth possess triangular crowns higher than broad, with strong striations (or folds in both the enamel and dentine), and these have a crown similarly high as the root (Lomax and Massare, 2018: Fig. 4). In addition, the teeth of *Ichthyosaurus* possess striated crowns with a root more massive and thicker than the crown, and a root as high as the crown (Maisch and Matzke, 2000: Fig. 17). The teeth of *Wahlisaurus* show very slender crowns higher than the root, with soft striations and finely pointed apices, with roots thicker than their respective crowns (Lomax, 2016). Finally, the teeth of *Excalibosaurus* have very slender, needle-like crowns (McGowan, 1989: Fig. 3C).

The clade Temnodontosauridae is documented during the Hettangian–Toarcian. Temnodontosauridae includes only one genus, *Temnodontosaurus* Lydekker, 1889. Maisch and Matzke (2000) listed five species for the genus, being these *Temnodontosaurus platyodon*, *T. trigonodon*, *T. acutirostris* (removed from the genus by Maisch, 2010), *T. nuertingensis*, *T. eurycephalus*. Later, Martin et al. (2012) added another species, *T. azerguensis*. Maisch and Matzke (2000) indicated for the diagnosis of *T. platyodon*, the presence of teeth with mesial and distal carinae in adults; for *T. trigonodon*, teeth with two to four carinae; in *T. nuertingensis*, teeth without carinae; for *T. eurycephalus,* jaws with few but very large teeth. Adding to this record, Lomax and Gibson (2015) referred to *Temnodontosaurus* sp. a specimen from the Hettangian of Nothinghamshire, UK, indicating robust teeth with roots coarsely infolded, and with crowns subtly striated.

SGO.PV.324 can be distinguished from Triassic ichthyosaurs with carinated teeth (i.e., *Himalayasaurus* and *Thalattoarchon*). The material from northern Chile differs from *Himalayasaurus* in the lack of deep longitudinal striations in the crown, and by a having roots at least twice larger than its respective crown. Regarding *Thalattoarchon*, their crowns

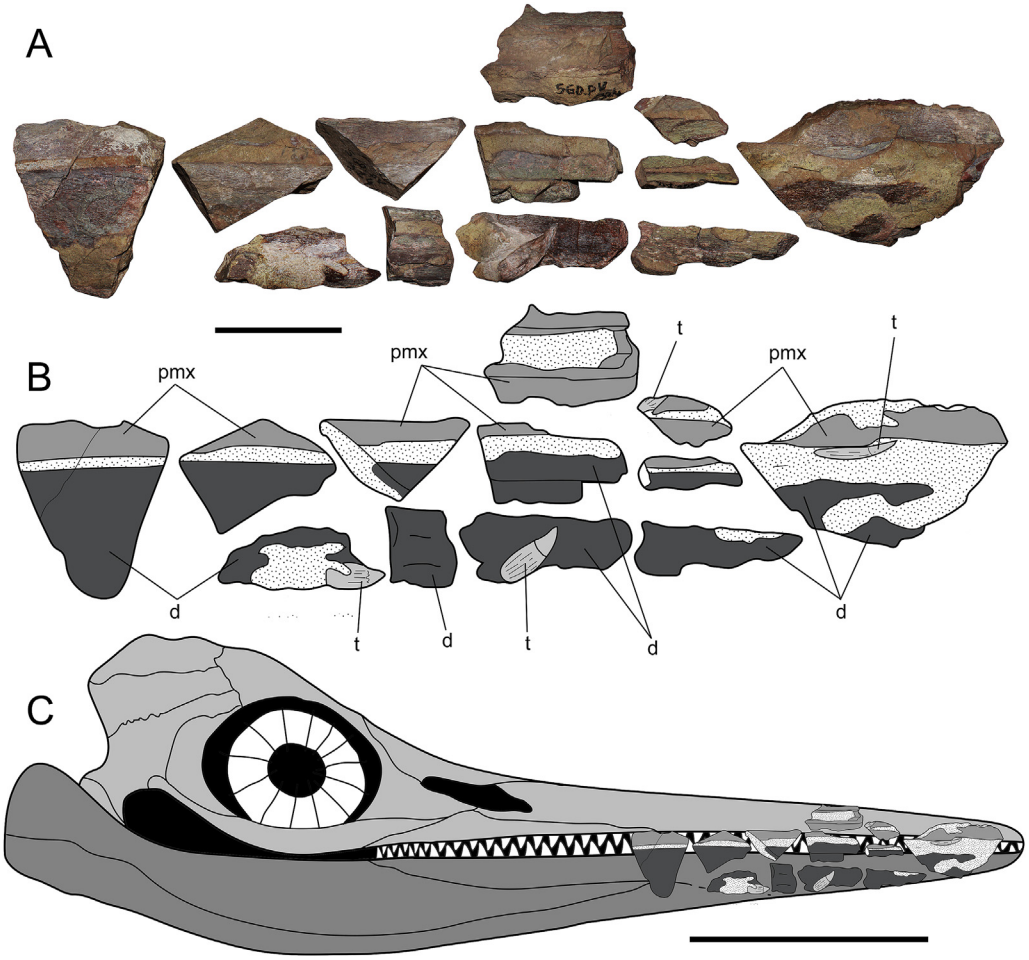

Fig. 2. SGO.PV.324, *Temnodontosaurus* sp.; A) fragmentary rostrum and dentary in occlusion, lateral view. B) Scheme of the material. C) Estimated anatomical position of the preserved fragments. Skull outline modified from Maisch and Matzke (2000). **Anatomical abbreviations: d,** dentary; **pmx,** premaxilla; **t,** teeth. Scale bar equals 10 cm in A, and 50 cm in C.

(Fröbisch et al., 2013: Fig. 1E–I) are comparatively more slender than those of SGO.PV.324. Also, the size of *Thalattoarchon* teeth is clearly larger than those of SGO.PV.324.

In addition, SGO.PV.324 dentition can be distinguished from those of the Hettangian–Sinemurian genera *Leptonectes*, *Protoichthyosaurus*, *Wahlisaurus* and *Excalibosaurus*. All these taxa have high and slender (even needle-like) crowns, contrary to the thick triangular and robust crowns present in SGO.PV.324. The studied specimen also differs from *Ichthyosaurus* in having crowns comparatively shorter, and roots as thick as the crown.

The presence of robust teeth with roots coarsely infolded and crowns subtly striated, are features shared by SGO.PV.324 and the specimen referred by Lomax and Gibson (2015) to *Temnodontosaurus* sp. (LEICT: G463.1972). Also, its large size and its Hettangian-Sinemurian age are ecologically and chronostratigraphically consistent with the size and known bichron of *Temnodontosaurus*. Based on these observations, SGO.PV.324 is here referred to *Temnodontosaurus*. All the available teeth of SGO.PV.324 exclusively show crowns with mesial and distal carinae, as those of *T. platyodon*. However, the fragmentary condition of the specimen precludes a specific determination.

5.2. Paleobiogeography

Early Jurassic ichthyosaurs are best known from Europe, with well-documented material from the UK, Germany, France, Belgium, Luxembourg, Switzerland, Spain and Portugal (Maisch and Matzke, 2000; Maisch, 2010). In addition, there are known records in the Hettangian-Sinemurian of western North America, referred to the genus *Ichthyosaurus* (Dennison et al., 1990). In Chile, Lower Jurassic ichthyosaur records are documented at least in 6 localities (including this study), geographically located between latitudes 23°10′S and 30°16′S, with three occurrences restricted to the Hettangian–Sinemurian (Casamiquela, 1970; Chong and Gasparini, 1972, 1976; Suárez and Otero, 2010; Pardo-Pérez et al., 2015). All of these records occurred in southeastern Panthalassian basins, considering that the break-up of Gondwana was not established yet (Cecca, 2002; Benedetto, 2010).

Riccardi (1991) analyzed the paleobiogeography of ammonoids, finding a Hettangian–Pliensbachian pattern of distribution through the Australian margin of Gondwana, with sporadic openings of the Caribbean Seaway from the Pliensbachian onwards. The (still scarce) marine vertebrate fossil record from northern Chile is not opposed to this proposal. Arratia (2015) pointed out the bi-hemispheric presence of leptolepid fishes, with occurrences in Europe and also in the lower Sinemurian of northern Chile, being the oldest leptolepids from the southern hemisphere. Also, Sinemurian indeterminate marine thalattosuchians are known in northern Chile (Chong and Gasparini, 1972), while the group is also represented in Europe during the Lower Jurassic (Young et al., 2013). Finally, the presence of indeterminate plesiosaurs in the Sinemurian of northern Chile (Chong and Gasparini, 1976) shows the early presence of this group of marine reptiles in southeastern Panthalassa, while in Europe, these are also well-represented (Benson et al., 2012).

The Pliensbachian-Toarcian, marine invertebrate and vertebrate assemblages from northeastern Panthalassa (e.g., Alberta, Canada)

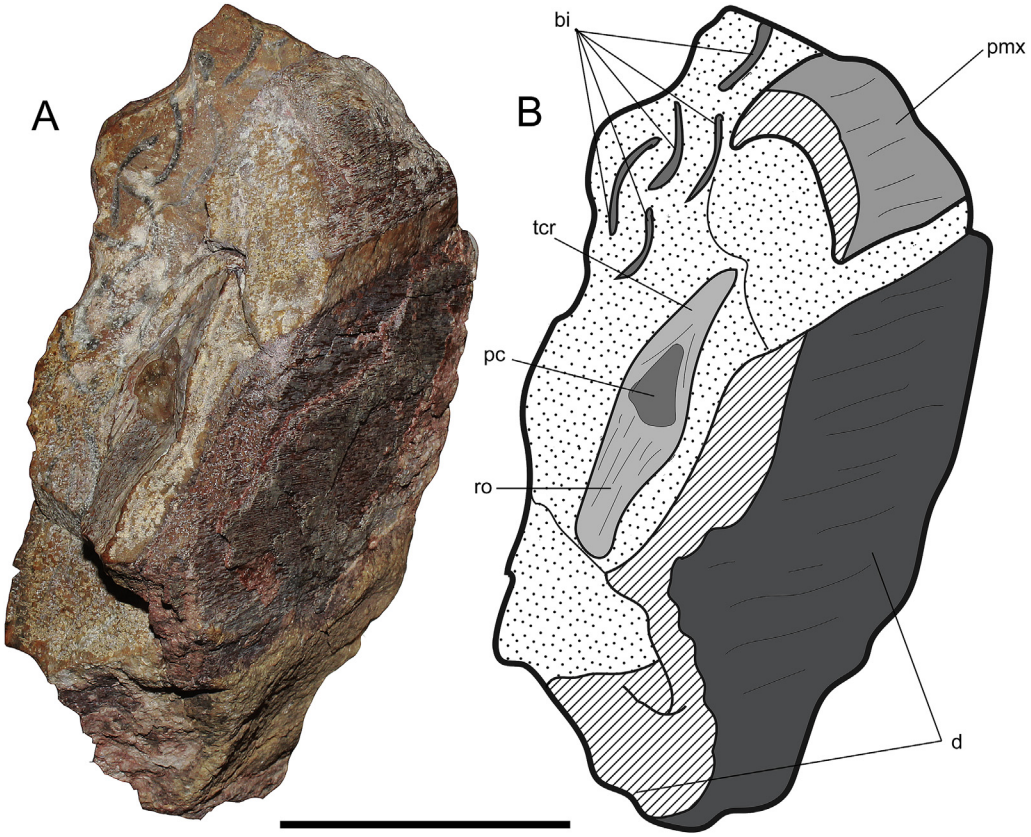

Fig. 3. SGO.PV.324, *Temnodontosaurus* sp.; detail of a rostrum and dentary section in occlusion. **Anatomical abbreviations: bi,** bivalves; **d,** dentary; **pc,** pulp cavity; **pmx,** premaxilla; **tcr,** tooth crown. Scale bar equals 10 cm.

were similar to coeval assemblages from Europe. Common vertebrates include icthyosaurs, leptolepiform fishes and saurichthyform fishes (Martindale et al., 2017; Maxwell and Martindale, 2017). This evidence partially supports an interchange through the Boreal corridor during the early Lower Jurassic.

Considering all these records, the emerging pattern suggests a Tethyan-Panthalassan marine faunal interchange during the early Lower Jurassic. By the moment, the evidence from the southern hemisphere is still sparse for a clear picture regarding the path(s) and direction(s) of the faunal interchange. The bi-hemispheric distribution of Lower Jurassic marine vertebrate fauna could occur through the boreal corridor, the Austral corridor and/or through the Mozambique seaway (Benedetto, 2010), but more robust evidence is needed for a better understanding of this matter.

6. Conclusions

The dental features and large size of SGO.PV.324's rostrum and dentary from Lower Jurassic strata of northern Chile described herein, are coincident with features present in the genus *Temnodontosaurus*. In addition, its Hettangian-Sinemurian age is also consistent with the known biochron of the latter genus. Based on these observations, the studied specimen is referred to *Temnodontosaurus* sp. precluding a species determination due to its fragmentary preservation. SGO.PV.324 represents the first occurrence of the genus in the southern hemisphere. The presence of *Temnodontosaurus* adds to a growing body of evidence regarding an interoceanic and bi-hemispheric interchange of marine fauna during the Lower Jurassic, prior to the full establishment of the Caribbean Seaway. To date, Lower Jurassic European basins as well as southeastern Panthalassian basins from Chile, share the presence of the typical groups of marine reptiles (i.e., Ichthyosauria, Plesiosauria, Thalattosuchia) and also leptolepid fishes, giving partial support to this hypothesis; however, by the moment, more evidence is needed for revealing clear marine routes and the direction of the migration of the different groups.

CRediT authorship contribution statement

Rodrigo A. Otero: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - original draft. **Patricio Sepúlveda:** Data curation, Investigation, Methodology, Writing - original draft.

Table 1
Measurements of the most relevant teeth preserved in SGO.PV.324. Incomplete elements are indicated with (*).

	Crown height	Crown width at the base	Root height	Maximum root width	Figure
large tooth	26*	22	31*	23	4 A, B
best preserved tooth	20	18	40	19	4C, E
replacement tooth	21	11	41	12	4D
replacement tooth	26	16	27*	16	4 F, G
functional tooth	14*	17	38	18	4H

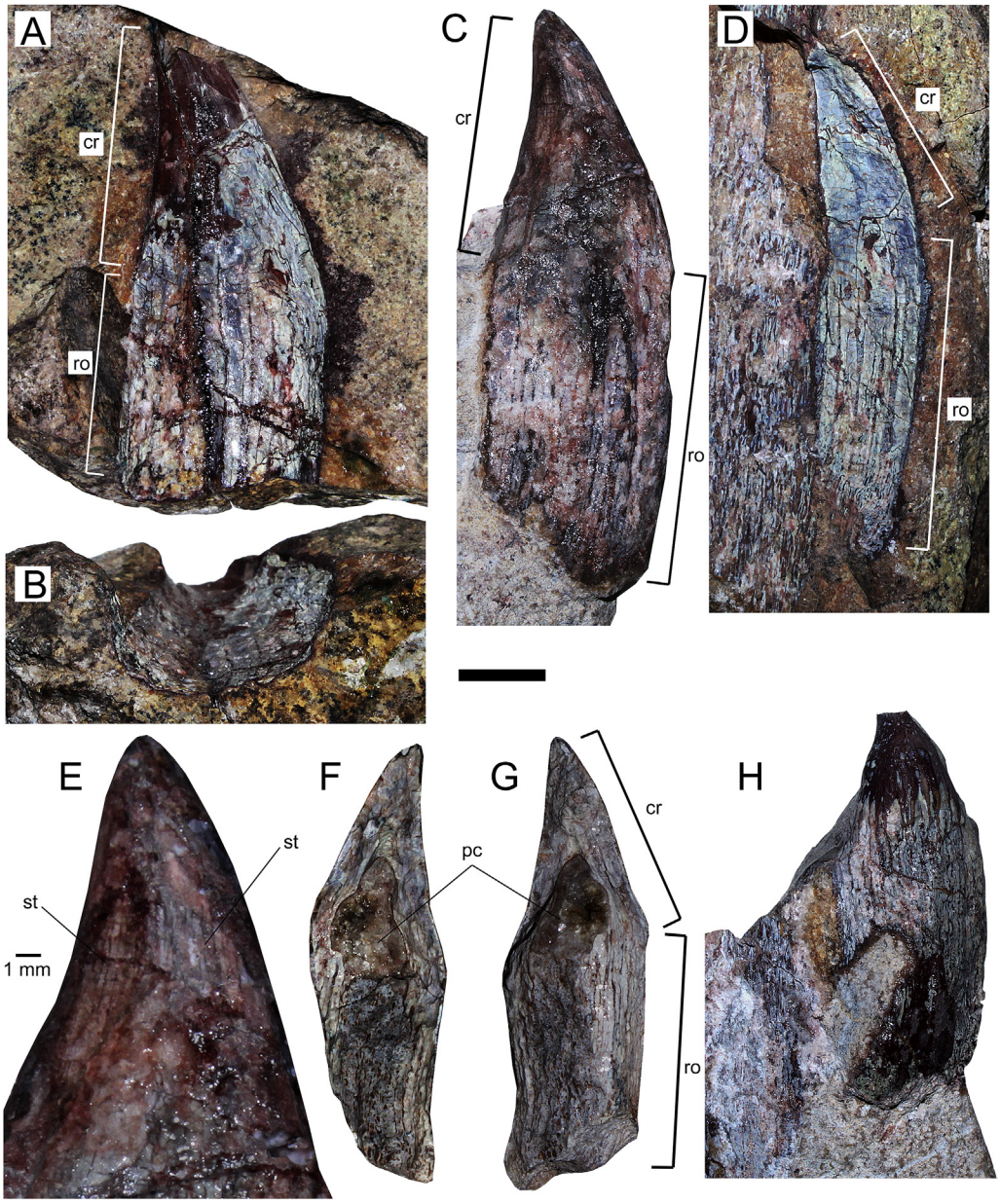

Fig. 4. SGO.PV.324, *Temnodontosaurus* sp.; A) Tooth cast showing the low, triangular crown and the coarsely infolded root. B) basal view of the previous block, showing the oval cross-section of the tooth. C) complete and well-preserved tooth, showing the same morphological features. D) Replacement tooth embedded in the matrix behind the dentary. The low triangular crown and the coarsely infolded roots are present even in early stages of the tooth growth. E) Detail of the fine striations over the crown of the best preserved tooth (same in C). F) Young functional dentary tooth with the same morphology. G) Counterpart of the previous. H) Functional tooth with the resorption pit in its root. **Anatomical abbreviations: cr,** crown; **pc,** pulp cavity; **ro,** root; **st,** striations. Scale bar equals 10 mm.

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