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Reappraisal of the fossil record of Polycotylidae (Sauropterygia: Plesiosauria) from the Upper Cretaceous of Chile

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ABSTRACT. The polycotylids, mostly short-necked plesiosaurs, were a clade of marine reptiles with an almost cosmopolitan geographical distribution in the Cretaceous Period. In austral continents, like South America, Antarctica and Australia, the presence of this group has remained relatively poorly documented, where apart from some rare specimens, most records are limited to fragmentary material. Reports of this group from South America are infrequent, particularly from Chile. Therefore, a critical review of the fossil record of Upper Cretaceous polycotylids from Chile is presented here. Previous putative reports of the group from the Quiriquina Formation (upper Maastrichtian) of the Arauco Basin (central Chile) were exclusively supported by misidentified axial elements belonging to elasmosaurid plesiosaurs, and are thus dismissed here. On the contrary, the presence of Polycotylidae in upper Campanian-lower Maastrichtian levels of the Dorotea Formation, in the Magallanes Basin (southern Chile), is confirmed. The pattern of taxonomic diversity, including polycotylids together with abundant, mostly non-aristonectine elasmosaurs in uppermost Cretaceous rocks of the Magallanes Basin, is similar to that observed in coeval localities of Argentinean Patagonia and Antarctica, but different from that observed in the Quiriquina Formation and the upper levels of the Dorotea Formation, where aristonectine elasmosaurids dominate the plesiosaur fauna. Polycotylids of equivalent age have also been described in other regions of the Weddellian Province, such as New Zealand. Polycotylidae seem to disappear from the fossil record during the late Maastrichtian in high southern latitudes of former Gondwana territories.

Keywords: Polycotylidae, Quiriquina Formation, Dorotea Formation, Upper Cretaceous, Weddellian Province.

RESUMEN. Reevaluación del registro fósil de Polycotylidae (Sauropterygia: Plesiosauria) en el Cretácico Superior de Chile. Los policotílidos (plesiosaurios generalmente de cuello corto) fueron un clado de reptiles marinos con una distribución geográfica casi cosmopolita durante el periodo Cretácico. En continentes australes, como Sudamérica, la Antártida y Australia, la presencia de este grupo se ha mantenido relativamente poco documentada, y la mayoría de los registros, salvo algunos pocos especímenes, se limitan a material fragmentario. Los reportes de este grupo en Sudamérica son poco frecuentes, particularmente en Chile. Se presenta aquí, por lo tanto, una revisión crítica del registro fósil de policotílidos del Cretácico Superior en Chile. Reportes previos del grupo en la Formación Quiriquina (Maastrichtiano superior) de la Cuenca de Arauco (Chile central) se basaron exclusivamente en elementos axiales erróneamente identificados, pertenecientes a plesiosaurios elasmosáuridos, por lo que se descartan en esta contribución. Por el contrario, se confirma la presencia de Polycotylidae en los niveles campanianos y maastrichtianos de la Formación Dorotea, en la Cuenca de Magallanes (Chile austral). El patrón de diversidad taxonómica, que incluye policotílidos junto con la abundante presencia de elasmosaurios mayoritariamente no aristonectinos en el Campaniano superior-Maastrichtiano inferior de la Cuenca de Magallanes, es similar al observado en localidades coetáneas de la Patagonia argentina y la Antártica, pero diferente al observado en el Maastrichtiano superior de la Formación Quiriquina y en los niveles superiores de la Formación Dorotea, donde los elasmosáuridos aristonectinos dominan la fauna de plesiosaurios. También se han descrito policotílidos de edad equivalente en otras regiones de la Provincia Weddeliana, como Nueva Zelanda. Los policotílicos parecen desaparecer del registro fósil durante el Maastrichtiano tardío en las latitudes meridionales altas de territorios que fueron parte de Gondwana.

Palabras clave: Polycotylidae, Formación Quiriquina, Formación Dorotea, Cretácico Superior, Provincia Weddelliana.

1. Introduction

The Polycotylidae (Sauropterygia: Plesiosauria) were a distinctive clade of advanced plesiosauroids, with a fossil record spanning from Valanginian to Maastrichtian (Welles, 1943; O'Keefe, 2001; Druckenmiller and Russell, 2009; Fischer *et al.*, 2018). The phylogenetic divergence from other leptocleidians took place during the beginning of the Cretaceous or even earlier (Benson and Druckenmiller, 2014), suggesting that polycotylids could have a ghost lineage that might extend to the Berriasian (Fischer *et al.*, 2018) and that much of the early evolution of the group might be obscured by the lack of fossil records. Polycotylids are characterized by possessing elongated skulls with very long snouts (O'Keefe, 2001, 2004, 2008), hydrodynamic bodies, and relatively short necks compared to other plesiosauroids, although with some exceptions (Bardet *et al.*, 2003; Buchy *et al.*, 2005; Fischer *et al.*, 2018; Persons *et al.*, 2022). Their distribution was cosmopolitan; however, the fossil record obtained from the austral continents is significantly less complete than that from North Africa and other northern hemisphere continents (Williston, 1903; Carpenter, 1996; Buchy *et al.*, 2005; Fischer *et al.*, 2018). According to some recent phylogenetic analysis, within Polycotylidae, at least two main lineages are identified: Occultonectia and Polycotylinae (Fischer *et al.*, 2018). In South America, *Sulcusuchus erraini* Gasparini and Spalletti, 1990, known from a pair of partial skulls remains found in the La Colonia Formation (upper Campanian-Danian) and in lower levels of the Coli-Toro Formation (correlated with the upper Campanian-lower Maastrichtian Los Alamitos Formation), in Argentine Patagonia (Gasparini and Spalletti, 1990; Gasparini and de La Fuente, 2000; O'Gorman and Gasparini, 2013; O'Gorman *et al.*, 2025), is the only austral polycotylid identified at the species level (O'Gorman, 2022). Additionally, an almost complete, yet unnamed skeleton (Cruickshank *et al.*, 1999; Kear, 2003, 2005, 2006; Kear *et al.*, 2018), known as the 'Richmond plesiosaur', from the Allaru Mudstone (upper Albian-Cenomanian) in Queensland, Australia, may be phylogenetically related to *Sulcusuchus*. *Plesiopleurodon wellesi* Carpenter, 1996 (Fischer *et al.*, 2018), from the Cenomanian of the United States (Carpenter, 1996), may be another. Recent reviews suggest that the affinities of *Sulcusuchus* are far from being resolved (O'Gorman, 2022).

There are fragmentary specimens likely referable to polycotylids from localities in Australia, including the Aptian Bulldog Shale, the middle-late Albian Toolebuc Formation, the latest Albian-Cenomanian Mackunda Formation, and the late Cenomanian upper Gearle Siltstone (Kear, 2005, 2006, 2016; Kear *et al.*, 2018; Vakil *et al.*, 2021). In New Zealand, isolated material (primarily postcranial remains) assigned to the clade comes from the upper Campanian-lower Maastrichtian Tahora Formation and the Campanian Conway Formation (O'Gorman and Otero, 2023). In Western Antarctica, a partial postcranial skeleton was excavated from upper Coniacian levels of the Santa Marta Formation in James Ross Island, being referred to an indeterminate osteologically immature polycotylid (Novas *et al.*, 2015). Furthermore, from Santonian levels of the same unit, fragmentary postcranial remains were reported (Kellner *et al.*, 2011). First assigned to indeterminate plesiosaurians (Kellner *et al.*, 2011), they show polycotylid features (O'Gorman, 2012). In Argentine Patagonia, besides the cranial material of *Sulcusuchus*, fragmentary specimens have been recovered in Northern Patagonia from Loma Puntuda and Salitral Santa Rosa, from the Allen Formation (upper Campanian-lower Maastrichtian) (Salgado *et al.*, 2007; O'Gorman *et al.*, 2011), and from the La Colonia Formation at Cerro Bayo, Central Patagonia (O'Gorman, 2022).

In Chile, reports of polycotylids are scarce and primarily focused on the Quiriquina Formation (upper Maastrichtian, Arauco Basin) and the Dorotea Formation (upper Campanian-Danian, Magallanes Basin). Specifically, previous mentions of this group in the Arauco Basin are limited to vertebral elements

(Poblete-Huanca and Palma-Heldt, 2018; here reviewed) and an isolated coracoid (Otero *et al.*, 2010), both from Isla Quiriquina. However, in the last case, a subsequent revision reassigned the specimen to Elasmosauridae (Otero *et al.*, 2015a). In the Magallanes Basin, the only mention of polycotylids pertains to isolated axial material, described only preliminarily (Soto-Acuña *et al.*, 2016). In both basins, besides polycotylids, a taxonomical diversity of elasmosaurids has been documented in outcrops of the Quiriquina (Otero *et al.*, 2014a, b; Otero *et al.*, 2015a; Otero and Soto-Acuña, 2021), Dorotea (Otero *et al.*, 2009, 2010, 2015b; Soto-Acuña *et al.*, 2016) and Fuentes-Rocallosa (Ortiz *et al.*, 2013; Otero *et al.*, 2013) formations.

The present contribution provides a detailed review of the specimens found in Chilean Upper Cretaceous units that have been identified as polycotylids. As a result, it is proposed that the only indisputable presence of this clade occurs in the Magallanes Basin for the late Campanian to early Maastrichtian interval.

2. Geological setting

2.1. Quiriquina Formation

The Quiriquina Formation, formalized by Biró-Bagóczky (1982), constitutes a marine sedimentary unit with a few estuarine facies (Stinnesbeck, 1986; Salazar *et al.*, 2010). Intermittent outcrops are exposed between the Maule and Biobío regions (Cecioni, 1983; Stinnesbeck, 1986; Collao *et al.*, 2000[1]), including Isla Quiriquina, where the type-section of this unit was defined (Biró-Bagóczky, 1982; Frutos *et al.*, 1982) (Fig. 1). This formation overlies Paleozoic metamorphic basement in angular and erosive discordance and similarly underlies the Paleogene sediments of the Lebu Group (Gajardo, 1981; Le Roux and Elgueta, 1997). It comprises glauconitic sandstones, conglomerates and siltstones with calcareous concretions with abundant marine invertebrates (Thiele and Tavera, 1967; Förster and Stinnesbeck, 1987; Bandel and Stinnesbeck, 2000; Salazar *et al.*, 2010), vertebrates (Lambrecht, 1929; Fuenzalida, 1956; Gasparini, 1979; Gasparini and Biro-Bagoczky, 1986; Suárez *et al.*, 2003; Jiménez-Huidobro *et al.*, 2015; Otero *et al.*, 2015a), palynomorphs and xylopals (Doubinger, 1972; Torres and Biró-Bagóczky, 1986; Nishida and Nishida, 1987). Specifically, in Las Tablas, Isla Quiriquina, where the specimens studied here were probably collected, coquinaceous levels dominate with abundant *Cardium* (*Bucardium*) *acuticostatum* d'Orbigny, 1842, and *Pacitrigonia hanetiana* (d'Orbigny, 1842) (Salazar *et al.*, 2010). Once regarded as Campanian to Maastrichtian in age (Biró-Bagóczky, 1982), it was then considered Maastrichtian by Stinnesbeck (1986) and ulteriorly as late Maastrichtian, based mostly on ammonoid biostratigraphy (Stinnesbeck, 1996; Salazar *et al.*, 2010).

2.2. Dorotea Formation

The Dorotea Formation, formalized by Katz (1963), is a marine to transitional sedimentary sequence which crops out in the eastern flank of the Última Esperanza Province, Magallanes Region (Hoffstetter *et al.*, 1957; Katz, 1963; Rivera *et al.*, 2020). It overlies the Tres Pasos Formation (Campanian) and underlies the Man Aike/Río Turbio Formation (middle to late Eocene) in erosive unconformity: it has a variable thickness, reaching more than 1 km in the Río de las Chinas valley sector (Fosdick *et al.*, 2011; George *et al.*, 2020) (Fig. 1). The formation is composed of siltstones, mudstones, sandstones, conglomerates, and intercalations of clay and calcareous levels with sandy concretions (Manríquez *et al.*, 2019). This unit preserves abundant fossils of invertebrates (Katz, 1963; Pérez and Reyes, 1978), continental and marine vertebrates (Cecioni, 1955; Otero *et al.*, 2009; Goin *et al.*, 2020; Martinelli *et al.*, 2021; Soto-Acuña *et al.*, 2015; Soto-Acuña *et al.*,2021; Davis *et al.*, 2022; Alarcón-Muñoz *et al.*, 2023), plants (Leppe *et al.*, 2012; Trevisan *et al.*, 2020), and microfossils (Martínez-Pardo, 1965).

The fossiliferous section that includes the polycotylid-bearing level in the Río de las Chinas Valley includes sandstones and conglomerates with abundant remains of indeterminate plesiosaurs, sharks, mollusks and crustaceans (Soto-Acuña *et al.*, 2016; Manríquez *et al.*, 2021). This horizon is stratigraphically below the hadrosaur bonebed of *Gonkoken nanoi* Alarcón-Muñoz *et al.*, 2023 (Manríquez *et al.*, 2019, 2021). The locality is on a deflation plain, on a slope; therefore, vertebrate fossils from different levels were dragged by gravity to the same point. Recent field data allowed reinterpretation of the local stratigraphic context, revealing at least two different horizons with *in situ* plesiosaur bones (Manríquez *et al.*, 2021). Remains referable to polycotylids are older than the uppermost levels where elasmosaurids and particularly aristonectines have previously been documented (Otero *et al.*, 2015b; Soto-Acuña *et al.*, 2016). The depositional environment of this unit

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[1] Collao, S.; Alfaro, G.; Cecioni, A.; González, A.; Quinzio, A. 2000. Evaluación de los Recursos Metálicos de la Región del Bio Bío. Proyecto FNDR. BIP 20107632. Informe inédito, Depto. Ciencias de la Tierra, Universidad de Concepción. 2 Vols. p. 207.

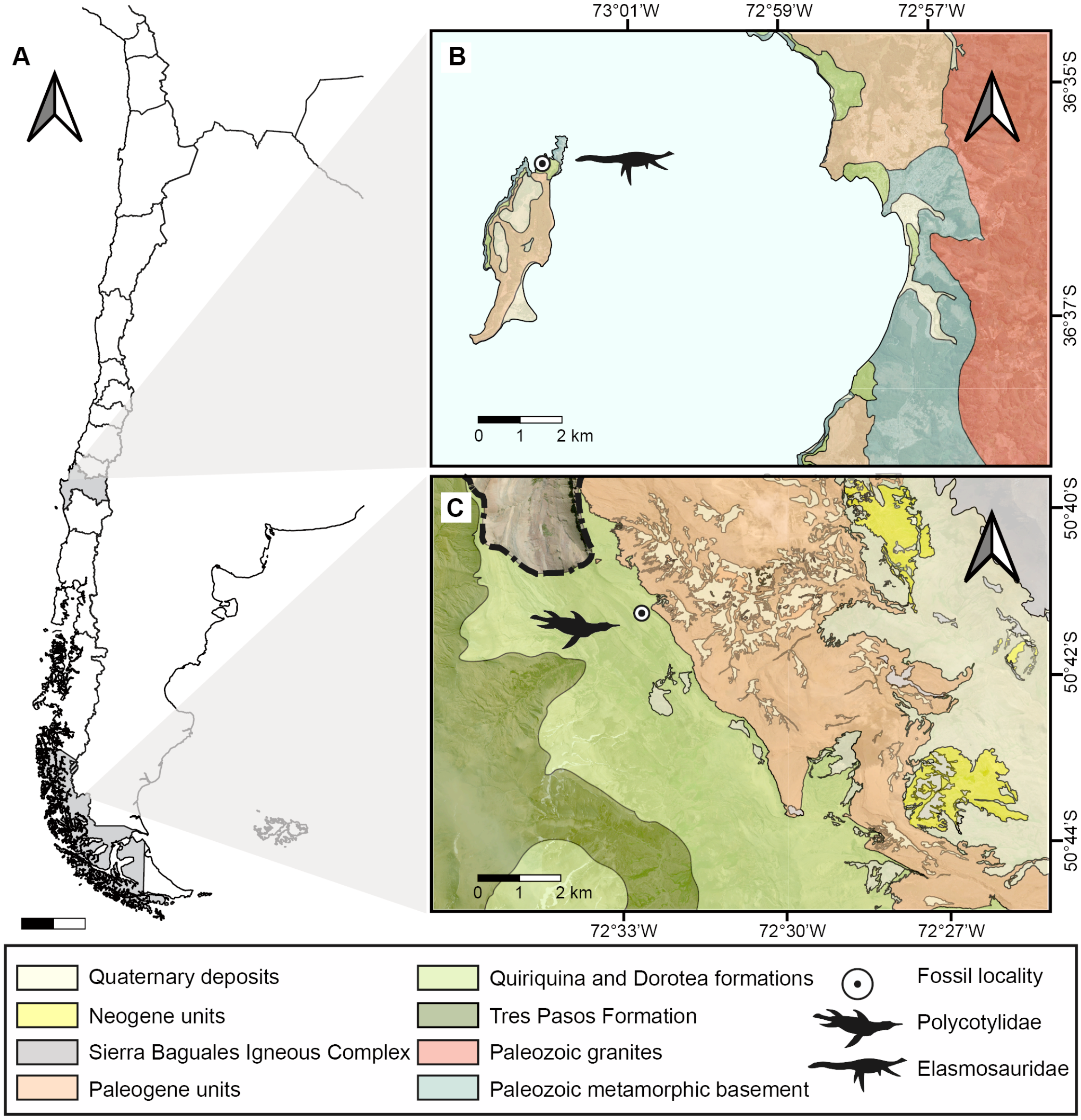

FIG. 1. Map of the provenance of the specimens studied in this work. **A.** Map of Chile indicating the two regions (in grey) where the material was collected. **B.** Geological map of the bay of Concepción, Biobío Region, showing the locality where Q/220-Q/227 were collected. **C.** Geological map of Río de las Chinas Valley, Magallanes Region, where CPAP specimens were collected.

has been interpreted as channels and tidal bars in a highstand system (Manríquez *et al.*, 2021). U-Pb dating on detrital zircon in the fossiliferous horizon indicates an age of 72±1 Ma (Gutiérrez *et al.*, 2017) and 69±2 Ma (Schwartz *et al.*, 2016), which would date the top of the section as upper Campanian-lower Maastrichtian.

3. Material and methods

Institutional abbreviations: CPAP, Colección de Paleontología de Antártica y Patagonia, Instituto Antártico Chileno, Punta Arenas, Chile; **DM**, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; **MACN-PV**, Colección Paleontología de

Vertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciudad Autónoma de Buenos Aires, Argentina; **MLP-PV**, División Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina; **MML-PV**, Museo Municipal de Lamarque, Lamarque, Argentina; **MPEF-PV**, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **NPC CD**, National Paleontological Collection, GNS Science, Lower Hutt, New Zealand; **Q**, Museo Geológico Profesor Lajós Biró, Universidad de Concepción, Concepción, Chile; **QM**, Queensland Museum, Brisbane, Australia; **SGO.PV,** Área de Paleontología, Museo Nacional de Historia Natural, Santiago, Chile.

Anatomical abbreviations: br, broken sacral rib; **cc**, central concavity on anterior face; **cm**, central mammilla; **df**, dorsal foramina; **hf**, haemal facet; **lc**, ventrolateral concavity; **na**, neural arch; **nc**, neural canal; **np**, neural pedicle; **np+pa**, neural pedicle + parapophysis; **pa**, parapophysis; **pf**, pedicle facet; **po**; postzygapophysis; **pp**, parapophysis; **pr**, prezygapophysis; **sb**, swollen border; **sf**, subcentral foramina; **vf**, ventral foramen; **vr**, ventral ridge.

Material: The studied specimens are hosted in the Museo Geológico Profesor Lajós Biró under acronym Q, and in the Instituto Antártico Chileno (INACH), under the code CPAP. The material housed in the INACH was collected by the lead author of this contribution (SSA) in the Río de las Chinas Valley. No mechanical preparation was needed, and only consolidants were applied to the specimens. The specimens from Museo Geológico Profesor Lajós Biró were probably collected during field campaigns of the geology career of the University of Concepción in Isla Quiriquina.

4. Results

Systematic paleontology

Superorder Sauropterygia Owen, 1860
Order Plesiosauria de Blainville, 1835
Clade Xenopsaria Benson and Druckenmiller, 2014
Family Elasmosauridae Cope, 1869
Elasmosauridae indet.
(Fig. 2)

Material: Q/220-Q/221, Q/222-Q/223, and Q/224, Q/225, Q/226, Q/227. Articulated sacral and anterior caudal vertebrae, possibly belonging to the same individual.

Locality and horizon: Probably from Las Tablas, Isla Quiriquina, Biobío Region. Quiriquina Formation.

Description: Q/224-Q/227 consists of a block with four vertebrae articulated, with large centra in comparison to the neural arches, oval in articular view, and wider than high and short (Fig. 2A, D). The series is rotated to the right side at the posterior end (Fig. 2D). The prezygapophyses, well preserved in the third vertebra, are oval and elongated (Fig. 2F). The anterior articular face is slightly concave; however, the border is sharp and not swollen (Fig. 2A). In the second vertebra, a broken rib of subtrapezoidal contour in cross-section is preserved in articulation to an expanded parapophysis in the left side. This rib moves away from the centrum and curve, heading lateroventrally. The following two posterior vertebrae have comparatively smaller and ovoidal parapophyses restricted to the centrum (Fig. 2F).

Q/222-Q/223 comprises two articulated vertebrae of coincident characteristics of the posterior vertebra of the previous block, although slightly shorter (Fig. 2E, G). The articular faces are oval, and the neural canal is relatively small relative to the centrum, this last slightly excavated at the high of the neural canal floor in articular view, as in the posterior vertebrae of Q/224-Q/227 and Q/221 (Fig. 2C). The lateral parapophyses are articulated with robust ribs of subcircular cross-section in the proximal end but oval immediately distal to the articulation (Fig. 2G). Both centra are wider than they are high and proportionally short.

Q/220-Q/221 consists of two caudal vertebrae, likely anterior, that are semi-articulated (Fig. 2B, C). The vertebral centra are broader than they are high and long. The articular surfaces exhibit a subcircular outline and are either platycoelous or slightly amphicoelous, but they lack a prominent articular rim (Fig. 2B, C). At the center of both articular surfaces, a subtle bulge or central mammilla (*sensu* Storrs, 1999) is noticeable (Fig. 2B). The articular facets for the ribs are proportionally large relative to the centrum, reaching at least two-thirds of its height. These facets are projected laterally from the center (Fig. 2B, C). The neural arches are incomplete, but it is evident that the pedicles are completely fused to each vertebral centrum, with no visible suture. The neural canal is proportionally small compared to the vertebral centrum (Fig. 2B, C). Finally, while in Q/224-Q/227 and Q/222-Q/223 there is no trace of haemal facets, in Q/220-Q/221 it is not possible to confirm its presence due to poor preservation of the ventral surface.

Remarks: These specimens were regarded as cervical vertebrae referred to Polycotylidae? by Poblete-Huanca (2018) and to Polycotylidae by Poblete-Huanca and Palma-Heldt (2018). They were described assuming a posterior position within the cervical series; however, an alternative location in the axis was not considered. The assignation to Polycotylidae was based on the alleged presence of amphicoelous articular faces on the putative cervical centra, along with the presence of a "ring" surrounding the articular surface (thickened articular margin) adding to the proportions of the centra, which are taller than they are long (Poblete-Huanca and Palma-Heldt, 2018).

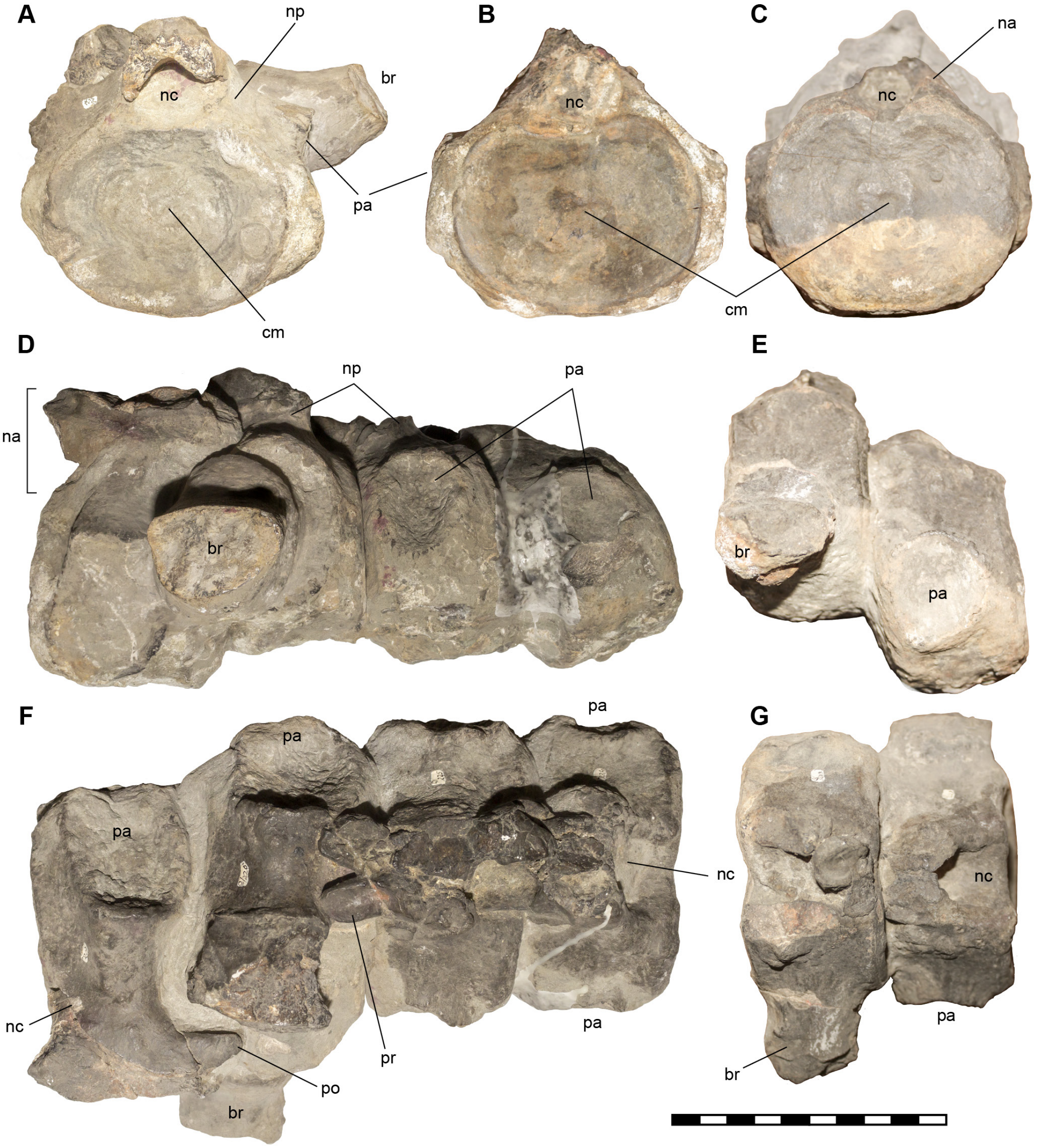

FIG. 2. Elasmosauridae indet. from Isla Quiriquina, Biobío Region. **A, D, F.** Q/224-Q/227, sacral and proximal caudal vertebrae; articulated portion, anterior view (A); left lateral view (D); dorsal view (F). **B, C.** Q/220-Q/221, proximal caudal vertebrae: anterior view (B); posterior view (C). **E, G.** Q/222-Q/223, anterior caudal vertebrae; left lateral view (E); dorsal view (G). Scale bar=10 cm.

The Q/224-Q/227 series preserves one vertebra with its respective neural arch, together conforming a combined rib facet ("transverse process", *sensu* Welles, 1962) with continuous double contribution (Fig. 2D). The preserved prezygapophyses of the third vertebra of this series allows assessing its cranio-caudal orientation, showing that the combined rib facet is in an anterior position with respect to the rest of the vertebrae and, therefore, confirming its anatomical identity as a sacral vertebra instead of a posterior cervical or pectoral element (Fig. 2F). Thus, the following two elements of the series are the first and second caudal vertebrae. Q/224-Q/227 has neural pedicles anteriorly shifted, with prezygapophyses overlapping the immediately anterior centrum. The same features are present in Q/220-Q/221 and Q/222-Q/223, which are also dorsoventrally depressed (*i.e.*, not a taphonomic deformation) and coincident in size with Q/224-Q/227 (Fig. 2B, C, E, G). In addition, the relative size of all the centra and their respective neural arches are successively coincident. Also, between the first and second caudal of Q/224-Q/227, and in the remaining two blocks as well, there is a vertical offset between the articular surfaces (Fig. 2E, F). These facts (plus the successive numeration) strongly suggest that all the vertebrae belong to an articulated axial portion of a single individual. Regrettably, the lack of field information prevents confirmation. Even if this is not the case, at least all represent the same morphotype.

The assignment to Polycotylidae can be dismissed based on the following anatomical observations: 1) the presence of a neural arch and, most important, a neural canal that is considerably smaller in comparison to the diameter of the vertebral centrum; 2) robust lateral parapophyses and ribs; 3) the presence of slightly amphicoelous articular faces bordered by a thin margin; 4) the presence of a small notochordal bulk or central mammilla; and 5) the absence of a prominent ventral longitudinal keel. Furthermore, the presence of thickened ribs directed ventrolaterally, without a lateral crest, and the absence of bilobed centra with a ventral notch, allow discarding the assignment to the cervical vertebrae of other Late Cretaceous plesiosaurs like Elasmosauridae (Welles, 1952; Gasparini *et al.*, 2003; O'Gorman, 2019). The assignment to dorsal centra (as initially proposed by Poblete-Huanca and Palma-Heldt, 2018) is also dismissed due to the presence of parapophyses on the centrum rather than on the neural arch (diapophysis). Moreover, polycotylids usually show the dorsal vertebrae with subrounded centra which are strongly amphicoelous and possess large, rectangular pedicle facets (O'Gorman, 2022; Zverkov *et al.*, 2024, 2026). On the other hand, it is possible to rule out the described specimens belonging to the caudal portion of a polycotylid based on the following: 1) the articular contour of the vertebrae is circular to ovoid, different from the polygonal contour present in caudals of Polycotylidae; 2) there are no chevrons protruding laterally; and 3) the parapophyses in the caudals are present in the centrum, while in polycotylids these are found shared between the neural arch and the vertebral centrum, even in the vertebrae of the middle portion of the tail (Williston, 1903; Sato, 2005; Schmeisser McKean, 2012; Schumacher and Martin, 2016; O'Gorman, 2022; Zverkov *et al.*, 2024, 2026).

With respect to the caudal vertebrae, the absence of a distinctive octagonal contour allows for the exclusion of the genus *Aristonectes* (Otero *et al.*, 2012, 2014a, 2018) or indeterminate aristonectines (Otero *et al.*, 2015a). Additionally, caudal morphology differs from some Weddellian elasmosaurids, where the contour of the centra in this region is roughly polygonal, such as *Chubutinectes* (O'Gorman *et al.*, 2023) and *Marambionectes* (O'Gorman *et al.*, 2024), or smaller in adult size, with long laterally projected parapophyses as seen in *Kawanectes* (O'Gorman, 2016). On the other hand, similar characteristics can be observed in *Vegasaurus* (O'Gorman *et al.*, 2015) and other indeterminate weddellonectian elasmosaurs like MLP-PV 14-I-20-16 (O'Gorman *et al.*, 2018). Furthermore, all the sacro-caudal anatomical features present in Q/220-Q/227 have been previously described in SGO.PV.6506, a specimen recovered from levels of the Quiriquina Formation exposed at Pelluhue (95 km north from Isla Quiriquina). While this specimen is not resolved to genus level, it aids understanding of the '*Cimoliasaurus*' *andium* Deecke (in Steinmann *et al.*, 1895) morphotype, especially improving knowledge of the caudal portion, which is indeed compatible with the anatomy of Q/220-Q/227 (Otero *et al.*, 2014b, figs. 5 and 6). While the generic assignment of Q/220-Q/227 cannot be resolved now, the available information allows its reassessment as an indeterminate Elasmosauridae, referable to the same general morphotype of '*Cimoliasaurus*' *andium*.

Family Polycotylidae Cope, 1887

Polycotylidae indet.
(Figs. 3 and 4)

Material: CPAP 3003, pectoral vertebra; CPAP 3004, posterior cervical or anterior pectoral vertebra; CPAP 3007, posterior caudal vertebra; CPAP 3014, anterior? cervical vertebra.

Locality and horizon: Río de las Chinas Valley, Estancia Cerro Guido, Magallanes Region. Middle to upper section of the Dorotea Formation.

Description: CPAP 3004 consists of a posterior cervical or anterior pectoral centrum, lacking the articular facets for neural pedicles (Fig. 3A-F). The centrum is wider than it is high and anteroposteriorly short (see Table 1 for measurements). The anterior articular face is concave and bordered by a swollen edge, which forms a well-developed ventral lip (Fig. 3A, B). In the middle part of the centrum there is a marked concavity. Below the neural canal, the border projects ventrally, forming a heart-shaped concavity in the articular face. The posterior articular face is platycoelous, lacking the anterior thickened edge (Fig. 3C). The cervical rib facets are subcircular and are located slightly over half the high of the centrum (Fig. 3B, E). Two small dorsal foramina are visible on each side of the neural canal in dorsal view (Fig. 3D). A marked lateral concavity is developed in the lateroventral zone, which ventrally meets in a rounded longitudinal ridge. Two large nutritive subcentral foramina are located on each side of the longitudinal ridge, in the center of the ventrolateral concavities (Fig. 3F).

CPAP 3014 consists of a fragmentary centrum, preserving the dorsal half and part of the left side (Fig. 3G-J). As CPAP 3004, the anterior articular face is slightly amphicoelous, with a conspicuous swollen border, however it is approximately 20% smaller than CPAP 3004 (Fig. 3G; Table 1). In dorsal view, two longitudinal excavations bordering the neural canal are visible, the latter being hourglass-shaped (Fig. 3I). Lateral to this, conspicuous dorsolaterally oriented concavities are observed, corresponding to the facets for the neural arch pedicles (Fig. 3I, J). No signs of erosion or fractures are observed, indicating that there was no neurocentral fusion.

CPAP 3003 is a pectoral vertebra, preserving the parapophyses. The centrum is wider than it is high and anteroposteriorly short (see Table 1 for measurements), subcircular in articular contour. The anterior face is concave, with a thickened border, similar to CPAP 3004, but without conforming a heart-shaped contour or a ventral lip (Fig. 4A). The pedicle facets are continuous with the parapophyses, combined in a single facet located in the upper third of the centrum (Fig. 4B, E). The posterior articular face is slightly concave, but flatter than the anterior one (Fig. 4C). There are two conspicuous dorsal foramina in the neural canal (Fig. 4D) and two smaller subcentral foramina are present on the ventral side (Fig. 4F). There is no sign of ventral ridge and ventrolateral concavities.

CPAP 3007 is a fragment of caudal centrum, probably from the posterior half of the tail. The centrum is longer than wide (Table 1) and has a polygonal shape, with the ventral side narrower than the upper half (Fig. 4J). Both articular faces are markedly amphicoelous and a dorsal articulation is preserved in the left side of the centrum, corresponding to the combined parapophysis and the neural pedicle. Four concave facets for haemal arches are preserved in the ventrolateral edges, those of the posterior half being deeper (Fig. 4G, I, J). A single, comparatively large ventral foramen is located in the ventral surface (Fig. 4J).

Remarks: CPAP 3004 was preliminary described as part of an assemblage of marine reptiles (Soto-Acuña *et al.*, 2016); nevertheless, new field data has indicated that there are at least two marine reptile assemblages in different horizons, separated by continental levels bearing hadrosaurs (Alarcón-Muñoz *et al.*, 2023; see geological setting above). The levels above the dinosaurs preserve abundant remains of chondrichthyans, aristonectine and non-aristonectine elasmosaurs, and few mosasaurs (Otero *et al.*, 2015b; Soto-Acuña *et al.*, 2016), while the oldest levels preserve the polycotylid remains. Two caudal vertebrae (CPAP 3005 and CPAP 3006), previously collected from the same site, but coming from higher levels (Manríquez *et al.*, 2021), were also referred to Polycotylidae (Soto-Acuña *et al.*, 2016), but a close inspection of the material allows any plesiosaur affinities to be discarded. In fact, portions without periosteum in both vertebrae allow visualization of the internal tissue, which is not osteoporotic but rather fibrolamellar, highly vascularized, with a dense trabecular architecture. The articular contour is hexagonal, and the heart-shaped surface of the articular face is produced by

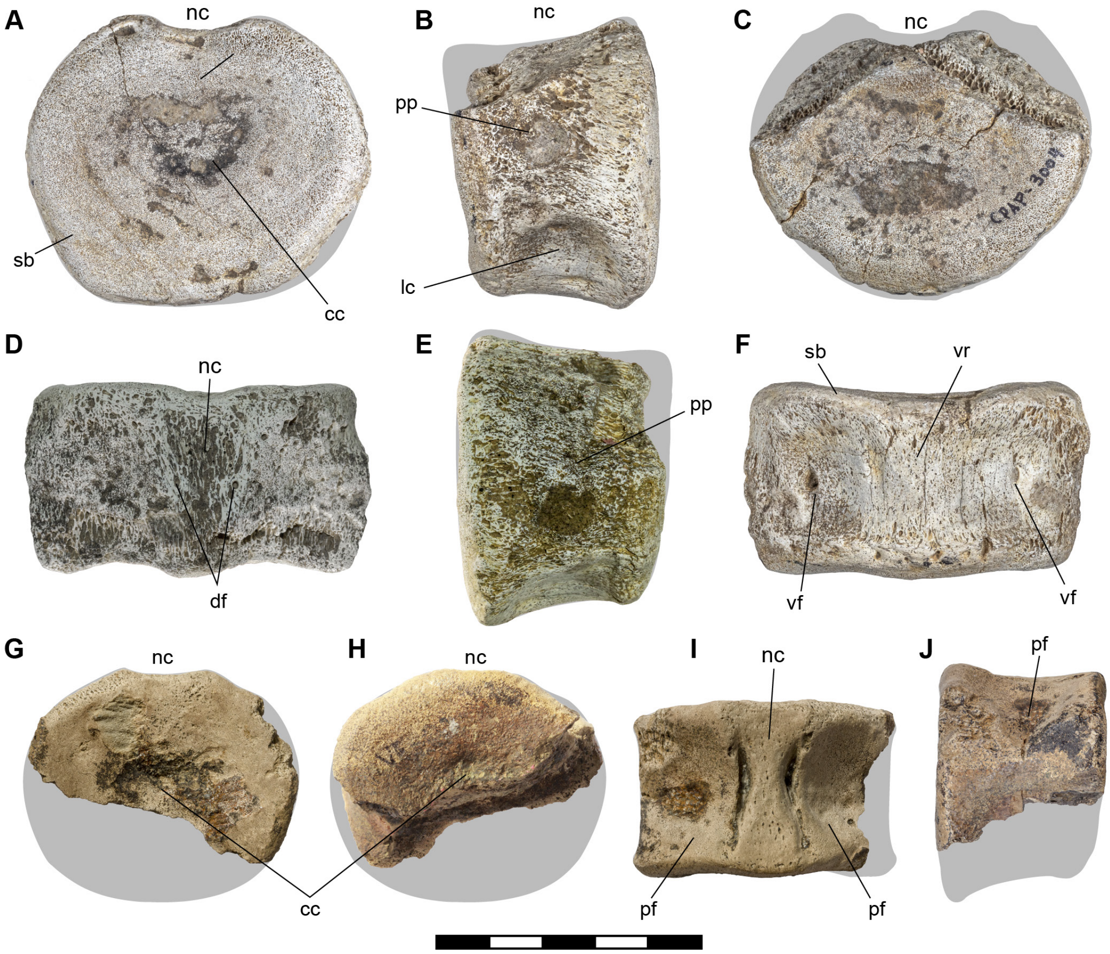

FIG. 3. Polycotylidae indet. from Río de las Chinas Valley, Magallanes Region. **A-F.** CPAP 3004, posterior cervical (or anterior pectoral) centrum; anterior view (A); right lateral view (B); posterior view (C); dorsal view (D); left lateral view (E); ventral view (F). **G-J.** CPAP 3014, anterior? cervical centrum; anterior view (G); posterior view (H); dorsal view (I); left lateral view (J). The grey silhouettes in the background are the inferred contour of the vertebra. Scale bar=5 cm.

TABLE 1. MEASUREMENT OF VERTEBRAE OF POLYCOTYLIDAE INDET. FROM THE RÍO DE LAS CHINAS VALLEY.

Collection number of specimen	Position within the axial skeleton	Length (mm)	Height (mm)	Breath (mm)
CPAP 3014	Cervical vertebra	33.0	-	45.0
CPAP 3004	Posterior cervical vertebra or anterior pectoral vertebra	33.5	49.0	58.0
CPAP 3003	Pectoral vertebra	38.0	48.0	55.0
CPAP 3007	Posterior caudal vertebra	32.0	-	50.0*

*approximate measurement due to poor preservation.

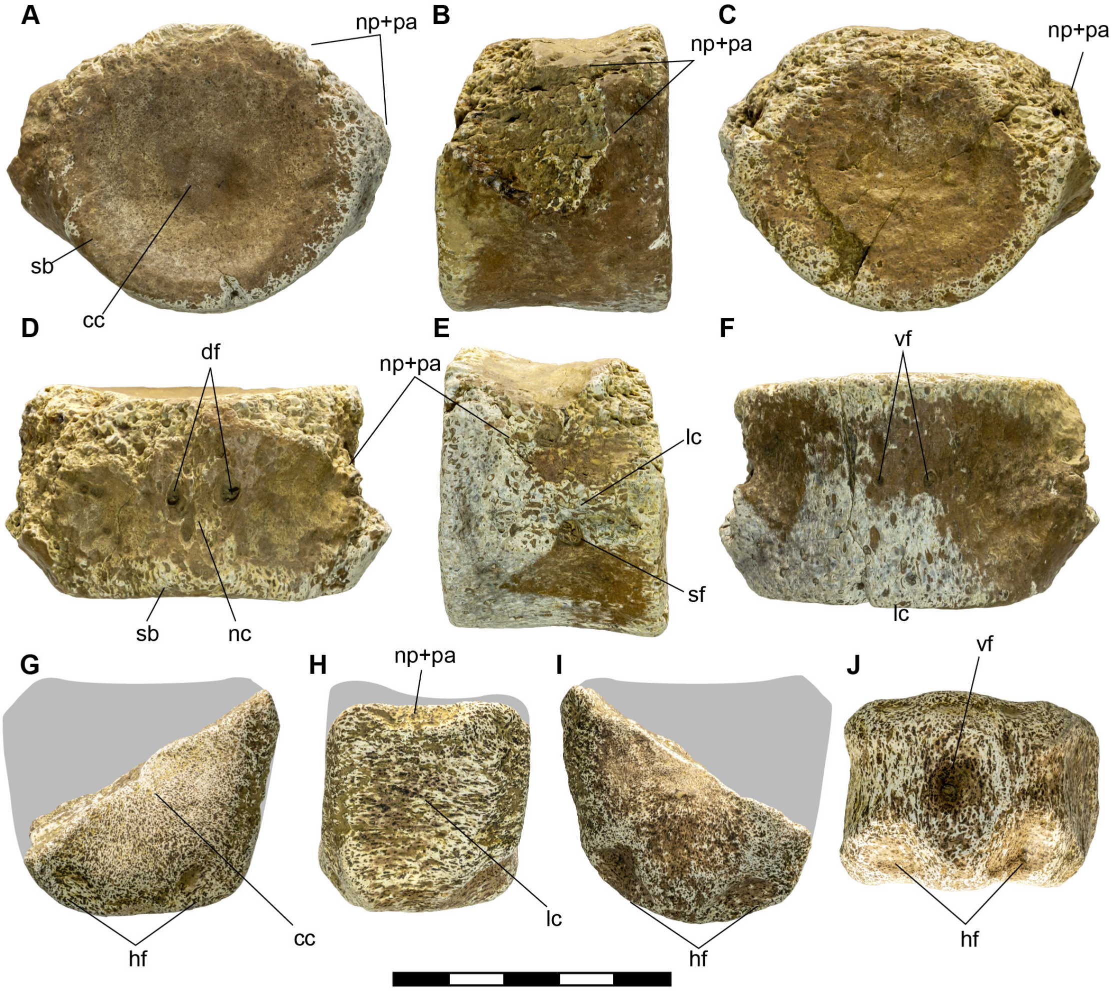

FIG. 4.Polycotylidae indet. from Río de las Chinas Valley, Magallanes Region. **A-F.** CPAP 3003, pectoral vertebra; anterior view (A); right lateral view (B); posterior view (C); dorsal view (D); left lateral view (E); ventral view (F). **G-J.** CPAP 3007, posterior caudal centrum; anterior view (G); left lateral view (H); posterior view (I); ventral view (J). The grey silhouettes in the background are the inferred contour of the vertebra. Scale bar=5 cm.

the excavation of the neural canal in the centrum rather than by the swollen border itself. While continuity between the pedicles of the neural arch and parapophyses is common in polycotylid caudal vertebrae (Sato, 2005; Novas *et al.*, 2015), this is not exclusive to this group. Also, there are no marked and concave facets for the articulation of haemal arches. Finally, the neural canal is reduced compared to the centrum, and while ventral foramina are present, they are not arranged in an aligned pattern and are asymmetrical in distribution. Collectively, these features are typical of hadrosauroid caudal vertebrae. Given the stratigraphic proximity to the horizon of the hadrosauroid *Gonkoken*, it is much probable that the caudal vertebrae CPAP 3005 and CPAP 3006 previously described by Soto-Acuña *et al.* (2016) correspond to this taxon; however, well-preserved proximal caudal vertebrae are not yet known in this species (Alarcón-Muñoz *et al.*, 2023). Nonetheless, direct comparison with proximal caudal vertebrae of the saurolophine hadrosauroid *Huallasaurus australis* (Bonaparte *et al.*, 1984), in particular with MACN-PV RN 02, reveals a strong resemblance between those specimens.

In polycotylids, the cervical centra are typically characterized by the possession of a distinctive swollen edge on the articular faces, combined with a marked concavity in anterior articular faces and cervical neural arches slightly narrower than the centrum breadth (Salgado *et al.*, 2007). Also, there is a well-developed and thick ventral longitudinal ridge, usually with two large nutritious foramina on each side (Fischer *et al.*, 2018), as observed in CPAP 3004 and partially in CPAP 3014. CPAP 3004 and CPAP 3014 differ in their proportions, with CPAP 3014 being relatively longer than CPAP 3004. Although these differences could be attributed to taxonomic distinctions or even to pathologies, different anatomical positions along the neck are more likely; in fact, in well-preserved axial series of polycotylids, the anterior cervical vertebrae are longer while the posterior ones are considerably shorter (Schmeisser McKean, 2012). In addition, there is a noticeable difference in size between the two specimens, with CPAP 3004 being larger than CPAP 3014. In the latter specimen, clear pedicle facets are visible, indicating an immature condition for this specimen. While it is not possible to establish the presence of neurocentral fusion in CPAP 3004 due to poor preservation, both specimens may represent different ontogenetic stages. On the other hand, both CPAP 3003 and CPAP 3004 are of roughly similar size and proportions, so there is no solid evidence to suggest the presence of polycotylids of different sizes.

Despite slightly different proportions of the centra, they are comparatively shorter than those observed in the cervical vertebrae of the indeterminate Patagonian polycotylids MML-PV 43 and MACN-PV RN 1087c from the Allen Formation (Salgado *et al.*, 2007; O'Gorman *et al.*, 2011), as well as the indeterminate polycotylid MPEF-PV 11546 from the La Colonia Formation (O'Gorman, 2022). New Zealand polycotylids NPC CD 459 and DM R1544, from the Tahora and Conway formations, respectively (O'Gorman and Otero, 2023), have proportionally elongated cervical centra. In contrast, comparatively very short centra relative to width and height have been described in the cervical vertebrae of *Dolichorhynchops osborni* Williston, 1903, *Dolichorhynchops herschelensis* Sato, 2005, *Dolichorhynchops tropicensis* Schmeisser McKean, 2012, *Trinacromerum bentonianum* Cragin, 1888, *Eopolycotylus rankini* Albright *et al.*, 2007, *Mauriciosaurus fernandezi* Frey *et al.*, 2017, *Polycotylus sopozkoi* Efimov *et al.*, 2016, and *Unktaheela specta* Clark *et al.*, 2024 (Williston, 1903; Sato, 2005; Schumacher and Everhart, 2005; Albright *et al.*, 2007; Schmeisser McKean, 2012; Clark *et al.*, 2024; Zverkov *et al.*, 2024, 2026).

CPAP 3003, identified here as a pectoral vertebra, has a similar morphology and proportions of the equivalent element described in the polycotylid MPEF-PV 11546 (O'Gorman, 2022). Furthermore, pectoral vertebrae described in *Polycotylus sopozkoi* Efimov *et al.*, 2016, also have the same traits (Zverkov *et al.*, 2024, 2026), although in that case there is a raised central mammilla. On the other hand, the caudal centrum CPAP 3007 has a distinctive combination of traits present in polycotylids, such as a polygonal contour, amphicoelous articular faces, marked haemal facets and a single, large ventral foramen (Williston, 1906; Novas *et al.*, 2015; Schumacher and Martin, 2016; O'Gorman, 2022; Zverkov *et al.*, 2024).

5. Discussion

5.1 Remarks on taxonomy

The presence of Polycotylidae during the uppermost Late Cretaceous of South America, Western Antarctica and New Zealand has been alleged, except for *Sulcusuchus erraini* Gasparini and Spalletti, 1990, and the upper Coniacian polycotylid from Santa Marta Formation (Novas *et al.*, 2015), on scattered remains, some of which were based on non-diagnostic material. In New Zealand, several Campanian to Maastrichtian records initially assigned to this clade (Welles and Gregg, 1971; Wiffen and Moisley, 1986) have been recently reassigned to Plesiosauria indet. or Elasmosauridae (O'Gorman and Otero, 2023). Only two cervical vertebrae, from the upper Campanian-lower Maastrichtian Tahora Formation (NPC CD 459) and from the Campanian Conway Formation (DM R1544), are unambiguously referable to Polycotylidae (O'Gorman and Otero, 2023). The traits that support NPC CD 459 are: concave articular facets, neural canals large in comparison with the centrum, high neural pedicles, and zygapophyses as broad as the centrum (Sato and Storrs, 2000; Salgado *et al.*, 2007; Sato *et al.*, 2018; O'Gorman and Otero, 2023), some of which are also present in the cervical centra from the Río de las Chinas Valley.

On the other hand, previous mentions of the presence of Polycotylidae during the Maastrichtian of the Arauco Basin are here dismissed on the base of anatomical features. Particularly, the material previously regarded as articulated cervicals of polycotylids from the Quiriquina Formation, are here reassigned to a sacral-anterior caudal sequence of an elasmosaurid; same geological unit from which similar vertebral morphology has been ascribed to non-Aristonectinae elasmosaurids (Otero *et al.*, 2014b). Therefore, at present, there is no undoubtable evidence of Polycotylidae in the Maastrichtian of the Arauco Basin.

The former mention of caudal vertebrae referred to Polycotylidae in the Dorotea Formation was also reviewed, finding that these have a greater affinity with caudal vertebrae of hadrosaurs. Thus, the material referable to Polycotylidae from the Río de las Chinas Valley is restricted to two cervical vertebrae which preserve unambiguous diagnostic traits of the clade. Additionally, two specimens found in association with the cervicals are also recognizable as polycotylids, including a pectoral and a true caudal vertebra. These specimens come from conglomerates immediately below the horizon which contains the *Gonkoken* hadrosauroid.

Minor differences in the proportions of the cervical centra among the specimens studied here suggest that the polycotylids from the Magallanes Basin may belong to a distinct taxon compared to those found in northern and central Patagonian basins. Further and more comprehensive material is needed to facilitate proper comparisons among South American polycotylids and evaluate their potential taxonomical diversity.

5.2 Biogeographical comments

According to the known fossil record, polycotylids were a clade of plesiosaurs that reached their peak diversity during the Turonian, which subsequently declined drastically towards the end of the Cretaceous, with at least three named species remaining during the Maastrichtian (Fischer *et al.*, 2018), one of which is the Argentine taxon *Sulcusuchus erraini* Gasparini and Spalletti, 1990 (O'Gorman, 2022; O'Gorman *et al.*, 2025). A fourth record comes from the late Maastrichtian in Harrana, Jordan, Asia, where a fragmentary rostrum represents the taxon *Rarosaurus singularis* Kaddumi, 2009. Although doubts have been raised regarding its classification, due to the potential presence of crocodylomorph characteristics (Alhalabi *et al.*, 2024), this requires confirmation through direct analysis of the specimen. Therefore, to date, the few polycotylid records from the latest Cretaceous are confined to the so-called Weddellian Province (Zinsmeister, 1979, 1982; Gasparini *et al.*, 2003) (Fig. 5). The absence of polycotylids in upper Maastrichtian rocks (see O'Gorman and Otero, 2023) has led to the suggestion of possible extinction of the group (Otero *et al.*, 2015b), an observation that is consistent with the reviewed record of this clade in the Arauco and Magallanes basins. In contrast, large-sized weddellonectians and particularly aristonectines are well documented in upper Maastrichtian rocks from the Weddellian Province, which suggests a faunal turnover (Otero *et al.*, 2015b). Thus, each new record of this clade in the southern regions of Gondwana is significant for understanding the evolution and biogeography of the group at the end of the Mesozoic, a period during which they appear to be in ecological decline.

6. Conclusions

A critical review of the specimens attributed to the family Polycotylidae discovered in Chile was conducted. The presence of polycotylids in the Arauco Basin during the late Maastrichtian is here dismissed on the grounds of improved anatomical identification and taxonomical adscription of the former material. In contrast, their presence in the Magallanes Basin during the late Campanian to early Maastrichtian interval is verified, although some specimens previously identified as polycotylids are here reassigned to Hadrosauroidea.

The specimens from the Dorotea Formation in the Magallanes Basin may represent a different form than those found in central and northern Patagonia, although better evidence is needed to assess taxonomic diversity and to assure a more precise stratigraphic provenance. Furthermore, the scarcity of records for this group in Maastrichtian rocks in Chile is consistent with the global pattern observed for the family, contrasting with that of contemporaneous plesiosaurs such as Weddellonectia in general and Aristonectinae in particular, which appear to reach greater diversity shortly before the K-Pg event.

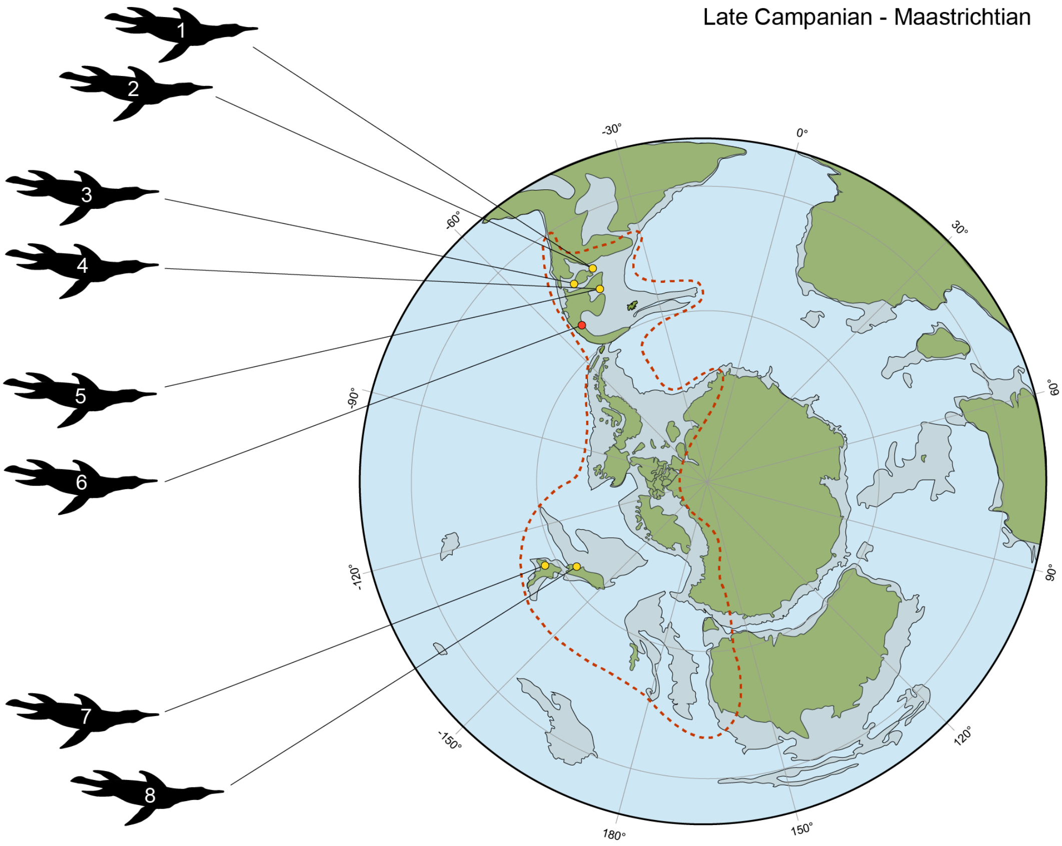

FIG. 5. Paleogeographical polar map of the latest Cretaceous with Weddellian polycotylids records. **1:** MML-PV 43, Polycotylidae indet. from Loma Puntuda, Allen Formation (middle Campanian-lower Maastrichtian). **2:** MACN-PV RN 1087c, Polycotylidae indet. from Salitral de Santa Rosa, Allen Formation (middle Campanian-lower Maastrichtian). **3:** MLP 88-IV-10-1, Sulcusuchus erraini (holotype), from Laguna Cari-Laufquén Grande, Los Alamitos Formation (upper Campanian-lower Maastrichtian). **4:** MPEF 650, Sulcusuchus erraini from Cerro Bosta, La Colonia Formation (Maastrichtian). **5:** MPEF-PV 11546, Polycotylidae indet. from Cerro Bayo, La Colonia Formation (Maastrichtian). **6:** CPAP 3003, CPAP 3004, CPAP 3007, and CPAP 3014, Polycotylidae indet. (this work), from Río de las Chinas Valley, Dorotea Formation (upper Campanian-lower Maastrichtian). **7:** NPC CD 459, Polycotylidae indet. from Mangahouanga Stream, Tahora Formation (upper Campanian-lower Maastrichtian). **8:** DM R1544 Polycotylidae indet. from Haumuri Bluff, Conway Formation (Campanian). The yellow circles are previous findings, while the red circles are the records described in this work. The dotted red line corresponds to the approximate outline of the Weddellian Province (*sensu* Zinsmeister, 1979). The paleogeographic reconstruction was based on Casamiquela (1978), Urien *et al*. (1995), Quattrocchio (2009), and Scotese (2014).

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References

Alarcón-Muñoz, J.; Vargas, A.O.; Püschel, H.; Soto-Acuña, S.; Manríquez, L.; Leppe, M.; Kaluza, J.; Milla, V.; Simon-Gutstein, C.; Palma-Liberona, J.; Stinnesbeck, W.; Frey, E.; Pino, J.P.; Bajor, D.; Núñez, E.; Ortiz, H.; Mansilla, H.; Rubilar-Rogers, D.; Cruzado-Caballero, P. 2023. Relict duck-billed dinosaurs survived into the last age of the dinosaurs in subantarctic Chile. Science Advances 9 (24): eadg2456.

Albright, L.B.; Gillette, D.D.; Titus, A.L. 2007. Plesiosaurs from the Upper Cretaceous (CenomanianeTuronian) Tropic shale of southern Utah, part 2: polycotylidae. Journal of Vertebrate Paleontology 27: 41-58. https://doi.org/10.1671/0272-4634(2007)27[41:PFTUCC]2.0.CO;2

Alhalabi, W.A.; Bardet N.; Sachs S.; Kear B.P.; Joude I.B.; Yazbek, M.K.; Godoy P.L.; Langer, M.C. 2024. Recovering lost time in Syria: New Late Cretaceous (Coniacian-Santonian) elasmosaurid remains from the Palmyrides mountain chain. Cretaceous Research 159: 105871.

Bandel, K.; Stinnesbeck W. 2000. Gastropods of the Quiriquina Formation (Maastrichtian) in Central Chile: Paleobiogeographic relationships and the description of a few new taxa. Zentralblatt für Geologie und Paläontologie (7-8): 757-788.

Bardet, N.; Pereda Suberbiola, X.; Jalil, N.-E. 2003. A new polycotylid plesiosaur from the Late Cretaceous (Turonian) of Morocco. Comptes Rendus Palevol 2 (5): 307-315. https://doi.org/10.1016/S1631-0683(03)00063-0

Benson, R.B.; Druckenmiller, P.S. 2014. Faunal turnover of marine tetrapods during the Jurassic-Cretaceous transition. Biological Reviews 89 (1): 1-23. https://doi.org/10.1111/brv.12038

Biró-Bagóczky, L. 1982. Revisión y redefinición de los 'Estratos de Quiriquina', Campaniano-Maastrichtiano, en su localidad tipo, Isla Quiriquina, Chile, con un perfil complementario en Cocholgüe. *In* Congreso Geológico Chileno No. 3, Actas 1: A29-A64. Concepción.

Bonaparte, J.F.; Franchi, M.R.; Powell, J.E.; Sepúlveda, E.G. 1984. La Formación Los Alamitos (Campaniano-Maastrichtiano) del sudeste de Río Negro, con descripción de *Kritosaurus australis* n. sp. (Hadrosauridae). Revista de la Asociación Geológica Argentina 39 (3-4): 284-299.

Buchy, M.-C.; Metayer, F.; Frey, E. 2005. Osteology of *Manemergus anguirostris* n. gen. et sp., a new plesiosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Morocco. Palaeontographica Abteilung A 272 (5-6): 97-120. https://doi.org/10.1127/pala/272/2005/97

Carpenter, K. 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 201: 259-287.

Casamiquela, R. 1978. La zona litoral do la transgresión Maastrichtense en el norte de Patagonia. Aspectos ecológicos. Ameghinina 15: 137-148.

Cecioni, G. 1955. Distribuzione verticale di alcune Kossmaticeratidae della Patagonia cilena. Bollettino della Società Geologica Italiana 74: 141-148.

Cecioni, G. 1983. Chanco Formation, a potential Cretaceous reservoir, Central Chile. Journal of Petroleum Geology 6 (1): 89-93.

Clark, R.O.; O'Keefe, F.R.; Slack, S.E. 2024. A new genus of small polycotylid plesiosaur from the Upper Cretaceous of the Western Interior Seaway and a clarification of the genus *Dolichorhynchops*. Cretaceous Research 157: 105812. https://doi.org/10.1016/j.cretres.2023.105812

Callao, S.; Alfara, G.; Cecioni, A.; González, A.; Quinzio, A. 2000. Evaluación de los Recursos Metálicos de la Región del Bio Bío. Proyecto FNDR. BIP 20107632. Informe inédito, Depto. Ciencias de la Tierra, Universidad de Concepción. 2 Vols. p. 207.

Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Transactions of the American Philosophical Society (new series) 14: 1-252. https://doi.org/10.5962/bhl.title.60499

Cope, E.D. 1887. The sea-saurians of the Fox Hills Cretaceous. The American Naturalist 21: 563-566.

Cragin, F. 1888. Preliminary description of a new or little-known saurian from the Benton of Kansas. American Geologist 2: 404-407.

Cruickshank, A.R.I.; Fordyce, R.E.; Long, J.A. 1999. Recent developments in Australasian sauropterygian palaeontology (Reptilia: Sauropterygia). Records of the Western Australian Museum (Supplement) 57: 201-205.

Davis, S.N.; Soto-Acuña, S.; Fernández, R.A.; Amudeo-Plaza, J.; Leppe, M.A.; Rubilar-Rogers, D.; Vargas, A.O.; Clarke, J.A. 2022. New records of Theropoda from a Late Cretaceous (Campanian-Maastrichtian) locality in the Magallanes-Austral Basin, Patagonia, and insights into end-Cretaceous theropod diversity. Journal of South American Earth Sciences 122: 104163. https://doi.org/10.1016/j.jsames.2022.104163

de Blainville, H.D. 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. Nouvelles Annales du Muséum d'Histoire Naturelle, Paris (série 3) 4: 233-296.

d'Orbigny, A.D. 1831-1847. Voyage dans l'Amérique Méridionale. Vol. 5, part 3, Mollusques. P. Bertrand, Paris: 758 p. + Atlas 85 pls.

Doubinger, J. 1972. Évolution de la flore (pollen et spores) au Chili Central (Arauco) du Crétacé supérieur au Miocène. Société de Biogéographie 49: 17-25.

Druckenmiller, P.S.; Russell, A.P. 2009. Earliest North American occurrence of polycotylidae (Sauropterygia: Plesiosauria) from the Lower Cretaceous (Albian) Clearwater Formation, Alberta, Canada. Jorunal of Paleontology 83: 981-989.

Efimov, V.M.; Meleshin, I.A.; Nikiforov, A.V. 2016. A new species of the plesiosaur genus Polycotylus from the Upper Cretaceous of the Southern Urals. Paleontological Journal 50 (5): 494e503. https://doi.org/10.1134/S0031030116050051

Fischer, V.; Benson, R.B.; Druckenmiller, P.S.; Ketchum, H.F.; Bardet, N. 2018. The evolutionary history of polycotylid plesiosaurians. Royal Society Open Science 5 (3): 172-177. https://doi.org/10.1098/rsos.172177

Förster, R.; Stinnesbeck, W. 1987. Zwei neue Krebse, *Callianassa saetosa* n. sp. und *Homolopsis chilensis* n. sp. (Crustacea: Decapoda) aus der Oberkreide Zentral-Chiles. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 27: 51-65.

Fosdick, J.C.; Romans, B.W.; Fildani, A.; Bernhardt, A.; Calderón, M.; Graham, S.A. 2011. Kinematic evolution of the Patagonian retroarc fold-and-thrust belt and Magallanes foreland basin, Chile and Argentina (51°30'S). Geological Society of America Bulletin 123: 1679-1698.

Frey, E.; Mulder, E.W.; Stinnesbeck, W.; Rivera-Sylva, H.E.; Padilla-Gutiérrez, J.M.; González-González, A.H. 2017. A new polycotylid plesiosaur with extensive soft-tissue preservation from the early Late Cretaceous of northeast Mexico. Boletín de la Sociedad Geológica Mexicana 69 (1): 87-134. https://doi.org/10.18268/BSGM2017v69n1a5

Frutos, J.; Mencarini, P.; Pincheira, M.; Bourret, Y.; Alfaro, G. 1982. Geología de la Isla Quiriquina. Congreso Geológico Chileno No. 3. Actas: 307-338. Concepción.

Fuenzalida, V.H. 1956. Los saurios de la Isla Quiriquina. Noticiario Mensual, Museo Nacional de Historia Natural (Santiago) 5: 2.

Gajardo, A.C. 1981. Hoja Concepción-Chillán, escala 1:250 000. Instituto de Investigaciones Geológicas: 36 p. Santiago.

Gasparini, Z.; Biro-Bagóczky, L. 1986. *Osteopygis* sp. (Reptilia: Testudines: Toxochelyidae) de la Formación Quiriquina, Cretácico Superior de Chile. Revista Geológica de Chile 27: 85-90.

Gasparini, Z.; Spalletti, L.A. 1990. Un nuevo cocodrilo en los depósitos mareales maastrichtianos de la Patagonia noroccidental. Ameghiniana 27: 141-150.

Gasparini, Z.; de la Fuente, M.S. 2000. Tortugas y plesiosaurios de la Formación La Colonia (Cretácico Superior) de Patagonia. Revista Española de Paleontología 15 (1): 23-35.

Gasparini, Z.; Bardet, N.; Martin, J.E.; Fernández, M. 2003. The elasmosaurid plesiosaur *Aristonectes* Cabrera from the latest Cretaceous of South America and Antarctica. Journal of Vertebrate Paleontology 23: 104-115.

George, S.W.; Davis, S.N.; Fernández, R.A.; Manríquez, L.M.; Leppe, M.A.; Horton, B.K.; Clarke, J.A. 2020. Chronology of deposition and unconformity development across the Cretaceous-Paleogene boundary, Magallanes-Austral Basin, Patagonian Andes. Journal of South American Earth Sciences 97. https://doi.org/10.1016/j.jsames.2019.102237

Goin, F.; Martinelli, A.; Soto-Acuña, S.; Vieytes, E.; Manríquez, L.; Fernández, R.; Pino, J.P.; Trevisan, C.; Kaluza, J.; Reguero, M.; Leppe, M.; Ortiz H.; Rubilar-Rogers, D.; Vargas, A. 2020. First Mesozoic mammal from Chile: the southernmost record of Late Cretaceous gondwanatherian. Boletín del Museo de Historia Natural, Chile 69: 5-31.

Gutiérrez, N.M.; Le Roux, J.P.; Vásquez, A.; Carreño, C.; Pedroza, V.; Araos, J.; Oyarzún, J.L.; Pino, J.P.; Rivera, H.A.; Hinojosa, L.F. 2017. Tectonic events reflected by palaeocurrents, zircon geochronology and palaeobotany in the Sierra Baguales of Chilean Patagonia. Tectonophysics 695: 76-99.

Hoffstetter, R.; Fuenzalida, H.; Cecioni, C. 1957. Lexique Stratigraphique International, Amérique Latine, Chili. Centre National de la Recherche Scientifique: 444 p.

Jiménez-Huidobro, P.; Otero, R.A.; Soto-Acuña, S.; Suárez, M. 2015. Mosasaurios (Squamata: Mosasauroidea) del Cretácico Superior de Chile. *In* Vertebrados fósiles de Chile (Rubilar-Rogers, D.; Otero, R.; Vargas A.O.; Sallaberry, M.; editors). Publicación Ocasional del Museo Nacional de Historia Natural, Chile 63: 99-111.

Kaddumi, H.F. 2009. On the remains of the first plesiosaur (Reptilia: Sauropterygia) from Harrana with a description of a new genus and species of Polycotylidae. Fossils of the Harrana Fauna and the Adjacent Areas, Eternal River Museum of Natural History: 158-162.

Katz, H. 1963. Revision of Cretaceous stratigraphy in the Patagonian Cordillera of Última Esperanza, Magallanes

Province, Chile. Bulletin of the American Association of Petroleum Geologist 47 (3): 506-524.

Kear, B.P. 2003. Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. Cretaceous Research 24 (3): 277-303. https://doi.org/10.1016/S0195-6671(03)00046-6

Kear, B.P. 2005. Marine reptiles from the Lower Cretaceous (Aptian) deposits of White Cliffs, southeastern Australia: implications of a high-latitude cold-water assemblage. Cretaceous Research 26 (5): 769-782. https://doi.org/10.1016/j.cretres.2005.04.006

Kear, B.P. 2006. Marine reptiles from the Lower Cretaceous of South Australia: elements of a high-latitude cold-water assemblage. Palaeontology 49 (4): 837-856. https://doi.org/10.1111/j.1475-4983.2006.00569.x

Kear, B.P. 2016. Cretaceous marine amniotes of Australia: perspectives on a decade of new research. Memoirs of Museum Victoria 74: 17-28.

Kear, B.P.; Schroeder, N.I.; Lee, M.S.Y. 2006. An archaic crested plesiosaur in opal from the Lower Cretaceous high-latitude deposits of Australia. Biology Letters 2: 615-619. https://doi.org/10.1098/rsbl.2006.0504

Kear, P.; Fordyce, E.; Hiller, N.; Siversson, M. 2018. A palaeobiogeographical synthesis of Australasian Mesozoic marine tetrapods. Alcheringa 42 (4): 461-486. https://doi.org/10.1080/03115518.2017.1397428

Kellner, A.W.A.; Rodrigues Simões, T.; Riff, D.; Grillo, O.; Romano, P.; de Paula, H.; Ramos, R.; Carvalho, M.; Sayão, J.; Oliveira, G.; Rodrigues, T. 2011. The oldest plesiosaur (Reptilia: Sauropterygia) from Antarctica. Polar Research 30: 7265. https://doi.org/10.3402/polar.v30i0.7265

Lambrecht, K. 1929. *Neogeornis wetzeli* n. gen. n. sp., der erste Kreidevogel der südlichen Hemisphäre. Paläontologische Zeitschrift 11: 121-129.

Leppe, M.; Mihoc, M.; Varela, N.; Stinnesbeck, W.; Mansilla, H.; Bierma, H.; Cisterna, K.; Frey, E.; Jujihara, T. 2012. Evolution of the Austral-Antarctic flora during the Cretaceous: new insights from a paleobiogeographic perspective. Revista Chilena de Historia Natural 85: 369-392. http://dx.doi.org/10.4067/S0716-078X2012000400002

Le Roux, J.P.; Elgueta, S. 1997. Paralic parasequences associated with Eocene sea-level oscillations in an active-margin setting: Trihueco Formation of the Arauco Basin, Chile. Sedimentary Geology 110: 257-276. https://doi.org/10.1016/S0037-0738(96)00086-3

Manríquez, L.M.E.; Lavina, E.L.; Fernández, R.A.; Trevisan, C.; Leppe, M.A. 2019. Campanian-Maastrichtian and Eocene stratigraphic architecture, facies analysis and paleoenvironmental evolution of the northern Magallanes Basin (Chilean Patagonia). Journal of South American Earth Sciences 93: 102-118.

Manríquez, L.M.; Lavina, E.L.; Netto, R.G.; Horodyski, R.S.; Leppe, M. 2021. Evolution of a high-latitude high-energy beach system (Maastrichtian-Eocene, Magallanes/Austral Basin, Chilean Patagonia). Sedimentary Geology 426: 106026. https://doi.org/10.1016/j.sedgeo.2021.106026

Martinelli, A.G.; Soto-Acuña, S.; Goin, F.J.; Kaluza, J.; Bostelmann, J.E.; Fonseca, P.H.M.; Reguero, M.A.; Leppe, M.; Vargas, A.O. 2021. New cladotherian mammal from southern Chile and the evolution of mesungulatid meridiolestidans at the dusk of the Mesozoic era. Scientific Reports 11: 7594. https://doi.org/10.1038/s41598-021-87245-4

Martínez-Pardo, R. 1965. The presence of *Bolivinoides draco dorreeni* Finlay in the Magellan Basin, Chile. Micropaleontology 11 (3): 360-364.

Nishida, M.; Nishida, H. 1987. Petrified woods from the Upper Cretaceous of Quiriquina Island, Chile. *In* Contributions to the Botany in the Andes II (Nishida, M.; editor). Academia Scientific Book: 5-11. Tokyo.

Novas, F.E.; D'Angelo, J.S.; O'Gorman, J.P.; Agnolín, F.L.; Lirio, J.M.; Isasi, M.P. 2015. First record of Polycotylidae (Sauropterygia: Plesiosauria) from the Upper Cretaceous of Antarctica. Cretaceous Research 56: 563-568. https://doi.org/10.1016/j.cretres.2015.06.015

O'Gorman, J.P. 2012. The oldest elasmosaurs (Sauropterygia: Plesiosauria) from Antarctica, Santa Marta Formation (upper Coniacian?-upper Campanian) and Snow Hill Island Formation (upper Campanian-lower Maastrichtian), James Ross Island. Polar Research 31: 1-10. https://doi.org/10.3402/polar.v31i0.11090

O'Gorman, J.P. 2016. A small-bodied non-aristonectine elasmosaurid (Sauropterygia: Plesiosauria) from the Late Cretaceous of Patagonia, with comments on Patagonian and Antarctic elasmosaurid relationships. Ameghiniana 53: 245-268. https://doi.org/10.5710/AMGH.29.11.2015.2928

O'Gorman, J.P. 2019. Elasmosaurid phylogeny and paleobiogeography, with a reappraisal of Aphrosaurus furlongi from the Maastrichtian of the Moreno Formation. Journal of Vertebrate Paleontology 39 (5): e1692025. https://doi.org/ 10.1080/02724634.2019.1692025

O'Gorman, J.P. 2020. First record of Kawanectes lafquenianum (Plesiosauria, Elasmosauridae) from the La Colonia Formation of Argentina, with comments on the mandibular morphology of elasmosaurids. Alcheringa: An Australasian Journal of Palaeontology

44: 176-193. https://doi.org/10.1080/03115518.2019.1687754

O'Gorman, J.P. 2022. Polycotylidae (Sauropterygia, Plesiosauria) from the La Colonia Formation, Patagonia, Argentina: Phylogenetic affinities of sulcusuchus erraini and the late Cretaceous circum-Pacific polycotylid diversity. Cretaceous Research 14: 105339. https://doi.org/10. 1016/j.cretres.2022.105339

O'Gorman, J.P.; Gasparini, Z. 2013. Revision of *Sulcusuchus erraini* (Sauropterygia: Polycotylidae) from the Upper Cretaceous of Patagonia, Argentina. Alcheringa 37 (2): 163-176. https://doi.org/10.1080/03115518.2013.736788

O'Gorman, J.P.; Otero, R.A. 2023. Revision of the short-necked Cretaceous plesiosaurians from New Zealand. Comptes Rendus Palevol 22 (6): 77-90. https://doi.org/10.5852/cr-palevol2023v22a6

O'Gorman, J.P.; Salgado, L.; Gasparini, Z. 2011. Plesiosaurios de la Formación Allen (Campaniano-Maastrichtiano) en el área del Salitral de Santa Rosa (Provincia de Río Negro, Argentina). Ameghiniana 48 (1): 129-135. https://doi.org/10.5710/AMGH.v48i1(308)

O'Gorman, J.P.; Salgado, L.; Olivero, E.B.; Marenssi, S.A. 2015. *Vegasaurus molyi* gen. et sp. nov. (Plesiosauria: Elasmosauridae) from the Cape Lamb Member (Lower Maastrichtian) of the Snow Hill Island Formation, Vega Island, Antarctica, and remarks on Weddellian Elasmosauridae. Journal of Vertebrate Paleontology 35 (3): e931285. https://doi.org/10.1080/02724634.2014.931285

O'Gorman, J.P.; Panzeri, K.M.; Fernández, M.S.; Santillana, S.; Moly, J.J.; Reguero, M. 2018. A new elasmosaurid from the Upper Maastrichtian of the López de Bertodano Formation: new evidence on the Weddellonectia diversity. Alcheringa 42 (4): 575-586. https://doi.org/10.1080/03115518.2017.1339233

O'Gorman, J.P.; Carignano, A.P.; Calvo-Marcilese, L.; Pérez-Panera, J.P. 2023. A new elasmosaurid (Sauropterygia: Plesiosauria) from the upper levels of the La Colonia Formation (Upper Maastrichtian), Chubut Province, Argentina. Cretaceous Research 152: 105674. https://doi.org/10.1016/j.cretres.2023.105674

O'Gorman, J.P.; Canale, J.I.; Bona, P.; Tineo, D.E.; Reguero, M.; Cárdenas, M. 2024. A new elasmosaurid (Plesiosauria: Sauropterygia) from the López de Bertodano Formation: new data on the evolution of the aristonectine morphology. Journal of Systematic Palaeontology 22 (1): 2312302. https://doi.org/10.1080/14772019.2024.2312302

O'Gorman, J.P.; Aspromonte, F.R.; Matelo Mirco, G. 2025. First record of lithophagy in *Sulcusuchus erraini* (Plesiosauria; Polycotylidae) with comments on the taphonomic and collect bias in gastroliths. Historical Biology. https://doi.org/10.1080/08912963.2025.2548329

O'Keefe, F.R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). Acta Zoologica Fennica 213: 1-63.

O'Keefe, F.R. 2004. On the cranial anatomy of the polycotylid plesiosaurs, including new material of *Polycotylus latipinnis* from Alabama. Journal of Vertebrate Paleontology 24 (2): 326-340. https://doi.org/10.1671/1944

O'Keefe, F.R. 2008. Cranial anatomy and taxonomy of *Dolichorhynchops bonneri* (Sauropterygia: Polycotylidae) from the Pierre Shale of Wyoming and South Dakota. Journal of Vertebrate Paleontology 28 (10): 664-676. https://doi.org/10.1671/0272-4634(2008)28[664:CAATOD]2.0.CO;2

Ortiz, H.; Mansilla, H.; Manríquez, L.; Leppe, M. 2013. Registro de los plesiosaurios más australes de América. Sistemática, paleoambiente y estratigrafía. *In* Congreso Latinoamericano de Ciencia Antártica, No. 7, Libro de resúmenes: 183-186. La Serena.

Otero, R.; Soto-Acuña, S. 2021. *Wunyelfia maulensis* gen. et sp. nov., a new basal aristonectine (Plesiosauria: Elasmosauridae) from the Upper Cretaceous of central Chile. Cretaceous Research 118: 104651. https://doi.org/10.1016/j.cretres.2020.104651

Otero, R.A.; Suárez, M.E.; Le Roux, J.P. 2009. First record of elasmosaurid plesiosaurs (Sauropterygia: Plesiosauria) in upper levels of the Dorotea Formation (Late Cretaceous, Maastrichtian), Puerto Natales, Chilean Patagonia. Andean Geology 36 (2): 342-350. https://doi.org/10.5027/andgeoV36n2-a08

Otero, R.A.; Soto-Acuña, S.; Rubilar-Rogers, D. 2010. La discutida presencia de pliosauroideos en Chile (Sauropterygia: Pliosauroidea): evidencias del clado en el Cretácico Superior de la Región del Biobío. *In* Simposio Paleontología en Chile, No. 2, Libro de resúmenes: p. 57. Concepción. Concepción.

Otero, R.A.; Soto-Acuña, S.; Rubilar-Rogers, D. 2012. A postcranial skeleton of an elasmosaurid plesiosaur from the Maastrichtian of central Chile, with comments on the affinities of Late Cretaceous plesiosauroids from the Weddellian Biogeographic Province. Cretaceous Research 37: 88-99. https://doi.org/10.1016/j.cretres.2012.03.010

Otero, R.A.; Soto-Acuña, S.; Yury-Yáñez, R.; Rubilar-Rogers, D. 2013. Southernmost occurrence of an elasmosaurid plesiosaur in the Late Cretaceous of South America (Magallanes Basin). *In* Geosur 2013, Bollettino di Geofisica teorica ed applicata (Supplement B) 54: 334-336.

Otero, R.A.; Soto-Acuña, S.; O'Keefe, F.R.; O'Gorman, J.P.; Stinnesbeck, W.; Suárez, M.E.; Rubilar-Rogers, D.; Salazar, C.; Quinzio, L.A. 2014a. *Aristonectes quiriquinensis* sp. nov., a highly derived elasmosaurid from the Upper Maastrichtian of central Chile. Journal of Vertebrate Paleontology 34: 100-125. https://doi.org/10.1080/02724634.2013.780953

Otero, R.A.; Soto-Acuña, S.; Vargas, A.O.; Rubilar-Rogers, D. 2014b. A new postcranial skeleton of an elasmosaurid plesiosaur from the Upper Cretaceous of central Chile and a reassessment of the historic species *Cimoliasaurus andium*. Cretaceous Research 50: 318-331. https://doi.org/10.1016/j.cretres.2014.05.008

Otero, A.O.; Soto-Acuña, S.; Rubilar-Rogers, D. 2015a. El registro fósil de plesiosaurios (Sauropterygia) en Chile. *In* Vertebrados fósiles de Chile (Rubilar-Rogers, D.; Otero, R.; Vargas A.O.; Sallaberry M.; editors). Publicación Ocasional del Museo Nacional de Historia Natural, Chile 63: 151-188.

Otero, R.A.; Soto-Acuña, S.; Salazar, C.S.; Yury-Yáñez, R.; Oyarzún, J.L. 2015b. New elasmosaurids (Plesiosauria: Sauropterygia) from the Upper Cretaceous of the Magallanes Basin, Chilean Patagonia: evidence of a faunal turnover during the Maastrichtian along the Weddellian Biogeographic Province. Andean Geology 42 (2): 237-267.

Otero, R.A.; Soto-Acuña, S.; O'Keefe, F.R. 2018. Osteology of *Aristonectes quiriquinensis* (Elasmosauridae: Aristonectinae) from the Upper Maastrichtian of central Chile. Journal of Vertebrate Paleontology 38 (1): e1408638. https://doi.org/10.1080/02724634.2017.1408638

Owen, R. 1860. On the orders of fossil and recent Reptilia, and their distribution in time. Reports of the British Association for the Advancement of Science 29: 153-166.

Pérez, E.; Reyes, R. 1978. Las trigonias del Cretácico Superior de Chile y su valor cronoestratigráfico. Instituto de Investigaciones Geológicas (Chile), Boletín 34: 71 p. Santiago.

Persons, W.S.; Street, H.P.; Kelley, A. 2022. A long-snouted and long-necked polycotylid plesiosaur from the Late Cretaceous of North America 25 (10). https://doi.org/10.1016/j.isci.2022.105033

Poblete-Huanca, A.V. 2018. Identificación del registro de Plesiosaurios depositados en el Museo Geológico Lajos Biró-Bagóczky. Undergraduate tesis, University of Concepción: p.111

Poblete-Huanca, A.V.; Palma-Heldt, S. 2018. Identification of plesiosaurs of the collection of the Geological Museum Lajos Biró-Bagóczky. *In* Congreso Chileno de Paleontología, No. 1, Resúmenes: 385-389. Punta Arenas.

Quattrocchio, M.E. 2009. Paleogene dinoflagellate cysts from Punta Prat, southern Chile. Palynology 33: 141-156.

Rivera, H.A.; Le Roux, J.P.; Farías, M.; Gutiérrez, N.; Sánchez, A.; Palma-Heldt, S. 2020. Tectonic controls on the Maastrichtian-Danian transgression in the Magallanes-Austral foreland basin (Chile): Implications for the growth of the Southern Patagonian Andes. Sedimentary Geology 403. https://doi.org/10.1016/j.sedgeo.2020.105645

Salazar, C.; Stinnesbeck, W.; Quinzio, L.A. 2010. Ammonites from the Maastrichtian (Upper Cretaceous) Quiriquina Formation in central Chile. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 257 (2): 181-236. https://doi.org/10.1127/0077-7749/2010/0072

Salgado, L.; Parras, A.; Gasparini, Z. 2007. Un plesiosaurio de cuello corto (Plesiosauroidea, Polycotylidae) del Cretácico Superior del norte de Patagonia. Ameghiniana 44 (2): 349-358.

Sato, T. 2005. A new polycotylid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous Bearpaw Formation in Saskatchewan, Canada. Journal of Paleontology 79 (5): 969-980. https://doi.org/10.1666/0022-3360(2005)079[0969:ANPPRS]2.0.CO;2

Sato, T.; Storrs, G.W. 2000. An early polycotylid plesiosaur (Reptilia: Sauropterygia) from the Cretaceous of Hokkaido, Japan. Journal of Paleontology 74 (5): 907-914. https://doi.org/10.1017/S0022336000033096

Sato, T.; Hanai, T.; Hayashi, S.; Nishimura, T. 2018. A Turonian polycotylid plesiosaur (Reptilia: Sauropterygia) from Obira town, Hokkaido, and its biostratigraphic and paleoecological significance. Paleontological Research 22 (3): 265-278. https://doi.org/10.2517/2017PR024

Schmeisser McKean, R.S. 2012. A new species of polycotylid plesiosaur (Reptilia: Sauropterygia) from the Lower Turonian of Utah: extending the stratigraphic range of *Dolichorhynchops*. Cretaceous Research 34: 184-199. https://doi.org/10.1016/j.cretres.2011.10.017

Schumacher, B.A.; Everhart, M.J. 2005. A stratigraphic and taxonomic review of plesiosaurs from the old "Fort Benton Group" of central Kansas: a new assessment of old records. Paludicola 5 (2): 33-54.

Schumacher, B.A.; Martin, J.E. 2016. *Polycotylus latipinnis* Cope (Plesiosauria, Polycotylidae), a nearly complete skeleton from the Niobrara Formation (Early Campanian) of southwestern South Dakota. Journal of Vertebrate Paleontology 36 (1). https://doi.org/10.1080/02724634.2015.1031341

Schwartz, T.M.; Fosdick, J.C.; Graham, S.A. 2016. Using detrital zircon U-Pb ages to calculate Late Cretaceous sedimentation rates in the Magallanes-Austral basin, Patagonia. Basin Research 29 (6): 725-746.

Scotese, C.R. 2014. Atlas of Late Cretaceous Maps, PALEOMAP Atlas for ArcGIS, volume 2, The Cretaceous, Maps 16-22, Mollweide Projection, PALEOMAP Project, Evanston, IL.

Soto-Acuña, S.; Otero, R.; Rubilar-Rogers, D. 2015. First record of mosasaurs (Lepidosauria: Mosasauridae) from the late Cretaceous (Maastrichtian) of the Magallanes Basin. Boletín del Museo Nacional de Historia Natural, Chile 64: 69-79.

Soto-Acuña, J.; Alarcón, J.P.; Guevara, R.; Fernández, M.; González, E.; Leppe, M.; Vargas, A.O. 2016. Nuevos hallazgos de reptiles marinos en la Formación Dorotea (Maastrichtiano) en la Región de Magallanes, extremo austral de Chile. Ameghiniana 53 (Supplement 6): 76R.

Soto-Acuña, S.; Vargas, A.O.; Kaluza, J.; Leppe, M.A.; Botelho, J.F.; Palma-Liberona, J.; Simon-Gutstein, C.; Fernández, R.A.; Ortiz, H.; Milla, V.; Aravena, B.; Manríquez, L.M.; Alarcón-Muñoz, J.; Pino, J.P.; Trevisan, C.; Mansilla, H.; Hinojosa, L.F.; Muñoz-Walther, V.; Rubilar-Rogers, D. 2021. Bizarre tail weaponry in a transitional ankylosaur from subantarctic Chile. Nature 600: 259-263. https://doi.org/10.1038/s41586-021-04147-1

Steinmann, G.; Deecke, W.; Möricke, W. 1895. Das Alter und die Fauna der Quiriquina-Schichten in Chile. Neues Jahrbuch für Mineralogie Geologie und Paleontologie 14: 1-118.

Stinnesbeck, W. 1986. Zu den Faunistischen und Palökologischen Verhältissen in der Quiriquina Formation (Maastrichtium) Zentral-Chiles. Palaeontographica (A) 194: 99-237.

Stinnesbeck, W. 1996. Ammonite extinctions and environmental changes across the Cretaceous-Tertiary boundary in central Chile. *In* The Cretaceous-Tertiary Boundary Mass Extinction (Macleod, N.; Keller, G.; editors). Biotic and Environmental Events: 289-302. New York.

Storrs, G.W. 1999. An examination of Plesiosauria (Diapsida: Sauropterygia) from the Niobrara Chalk (Upper Cretaceous) of central North America 11: 1-15. The University of Kansas Paleontological Contributions: 1e13. https://doi.org/10.17161/PCNS.1808.3766

Suárez, M.E.; Quinzio, L.A.; Fritis, O.; Bonilla, R. 2003. Aportes al conocimiento de los vertebrados marinos de la Formación Quiriquina. *In* Congreso Geológico Chileno, No. 10, Actas: 1-7. Concepción.

Thiele, R.; Tavera, J. 1967. Estudio sobre muestreos paleontológicos practicados en el sector de costa comprendido entre Constitución y Pelluhue (latitudes 35°21' a 35°47') con una información adicional sobre existencia de Terciario carbonífero en Cobquecura. Informe inédito, Departamento de Geología, Universidad de Chile: 38 p.

Torres, T.; Biró, L. 1986. Xilotomía de coníferas fósiles de la Isla Quiriquina, Chile. Comunicaciones 37: 65-80.

Trevisan, C.; Dutra, T.; Wilberger, T.; Leppe, M.; Manríquez, L. 2020. An austral fern assemblage from the Upper Cretaceous (Campanian) beds of Cerro Guido Magallanes Basin, Chilean Patagonia. Cretaceous Research 106. https://doi.org/10.1016/j.cretres.2019.104215

Urien, C.M.; Zambrano, J.J; Yrigoyen, M.R. 1995. Petroleum basins of southern South America: an overview. *In* (Tankard, A.J.; Suárez, S.R.; Welsink, H.J.; editors). Petroleum basins of South America, vol 62. American Association of Petroleum Geologists Memorial: 63-77.

Vakil, V.; Webb, G.; Cook, A. 2021. Taxonomic utility of Early Cretaceous Australian plesiosaurian vertebrae. Palaeontologia Electronica 24 (3): a30. https://doi.org/10.26879/1095

Welles, S.P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs of the University of California 13: 125-254.

Welles, S.P. 1952. A review of the North American Cretaceous elasmosaurs. University of California Publications in Geological Sciences 29 (3): 47-144.

Welles, S.P. 1962. A new species of Elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. University of California, Publications in Geological Sciences 44: 1-96.

Welles, S.P.; Gregg, D.R. 1971. Late Cretaceous marine reptiles of New Zealand. Records of the Canterbury Museum 9: 1-111.

Wiffen, J.; Moisley, W.L. 1986. Late Cretaceous reptiles (Families Elasmosauridae and Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. New Zealand Journal of Geology and Geophysics 29 (2): 205-252. https://doi.org/10.1080/00288306.1986.10427535

Williston, S.W. 1903. North American plesiosaurs, Part I. Field Columbian Museum Geological Series 2: 1-77.

Williston, S.W. 1906. North American plesiosaurs: *Elasmosaurus*, *Cimoliasaurus* and *Polycotylus*. American Journal of Science 21: 221-236.

Williston, S.W. 1908. North American plesiosaurs: *Trinacromerum*. Journal of Geology 16: 715-736.

Zinsmeister, W.J. 1979. Biogeographic significance of the Upper Mesozoic and Early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final break-up of Gondwanaland. *In* Historical Biogeography, Plate Tectonics and the Changing Environment (Gray, J.; Boucot, A.J.; editors). Oregon State University Press: 349-355. Corvallis.

Zinsmeister, W.J. 1982. Late Cretaceous-Early Tertiary molluscan biogeography of the southern Circum-Pacific. Journal of Paleontology 56: 84-102.

Zverkov, N.G.; Grigoriev, D.V.; Meleshin, I.A.; Nikiforov, A.V. 2024. Revision of the plesiosaur *Polycotylus sopozkoi* from the Southern Urals (Russia) confirms the wide distribution of *Polycotylus* in the Late Cretaceous of the Northern Hemisphere. Cretaceous Research 160: 105879. https://doi.org/10.1016/j.cretres.2024.105879

Zverkov, N.G.; Grigoriev, D.V.; Nikiforov, A.V. 2026. New polycotylid plesiosaur skeletons from the Upper Cretaceous of the Southern Urals provide additional diagnostic features of *Polycotylus sopozkoi* and demonstrate its variation. Historical Biology 38 (1): 54-87. https://doi.org/10.1080/08912963.2025.2472161

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