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 Argentine 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 Gondwana.

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

RESUMEN. 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, incluyendo 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 Antártida, 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 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 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) (Fig. 1). 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

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; Quinzio et al., 2000), including Isla Quiriquina, where the type-section of this unit was defined (Biró-Bagóczky, 1982; Frutos et al., 1982). 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 et al., 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).

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). 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., 2021; Davis et al., 2022; Alarcón-Muñoz et al., 2023), plants (Leppe et al., 2012; Trevisan et al., 2022), 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 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**, hemal 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 hemal 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).

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, 2020). 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, 2014, 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; O'Gorman et al., 2020). 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., 2014, 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 hemal 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 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 hemal 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 highly likely 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 hemal 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., 2014). 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.

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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.

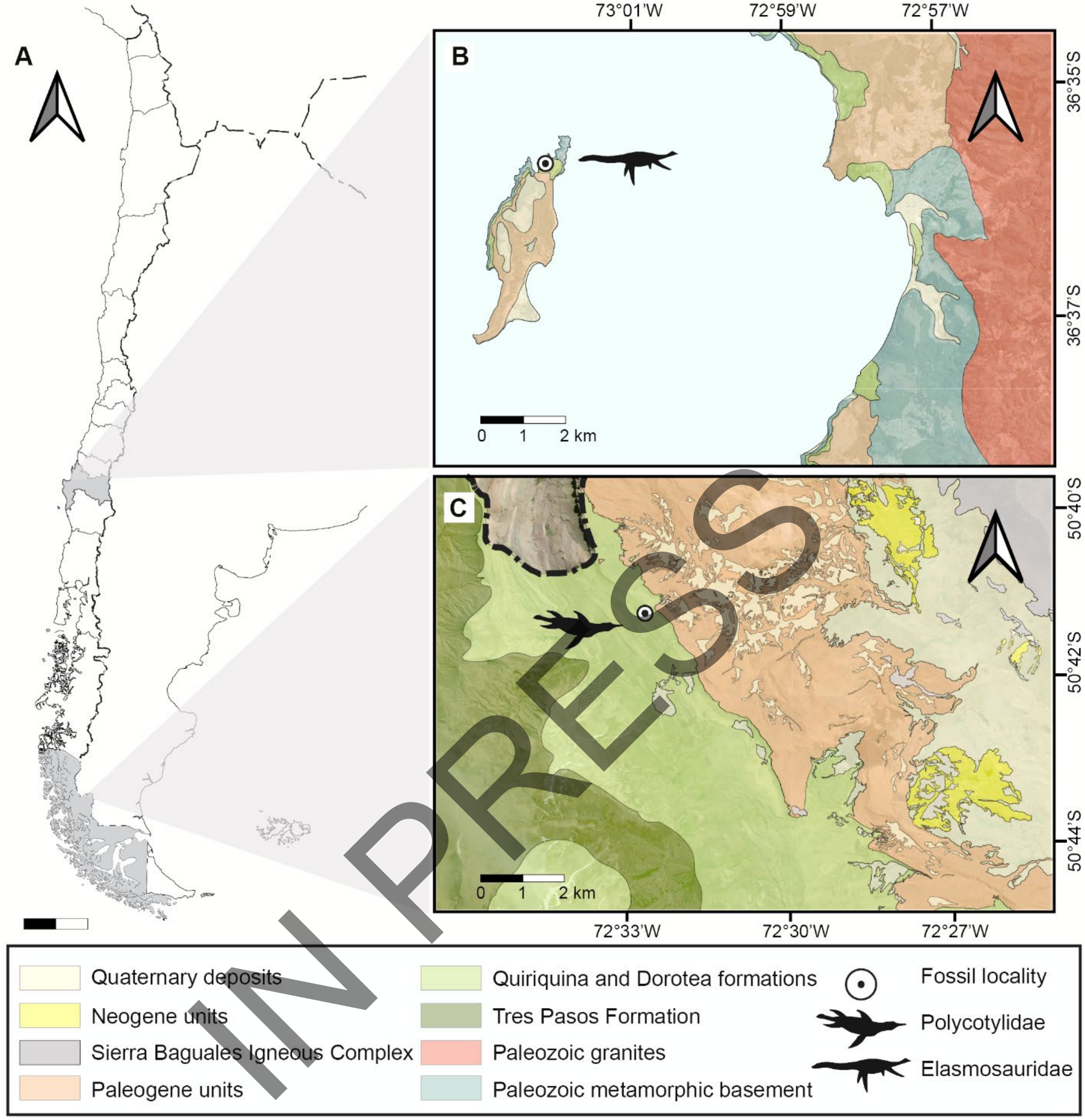

Fig. 1. Map of the provenance of the specimens studied in this work. **A.** Map of Chile indicating the two regions (in grey) where the material was collected. **B.** Geological map of the bay of Concepción, Biobío Region, showing the locality where Q/220-Q/227 were collected. **C.** Geological map of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

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.

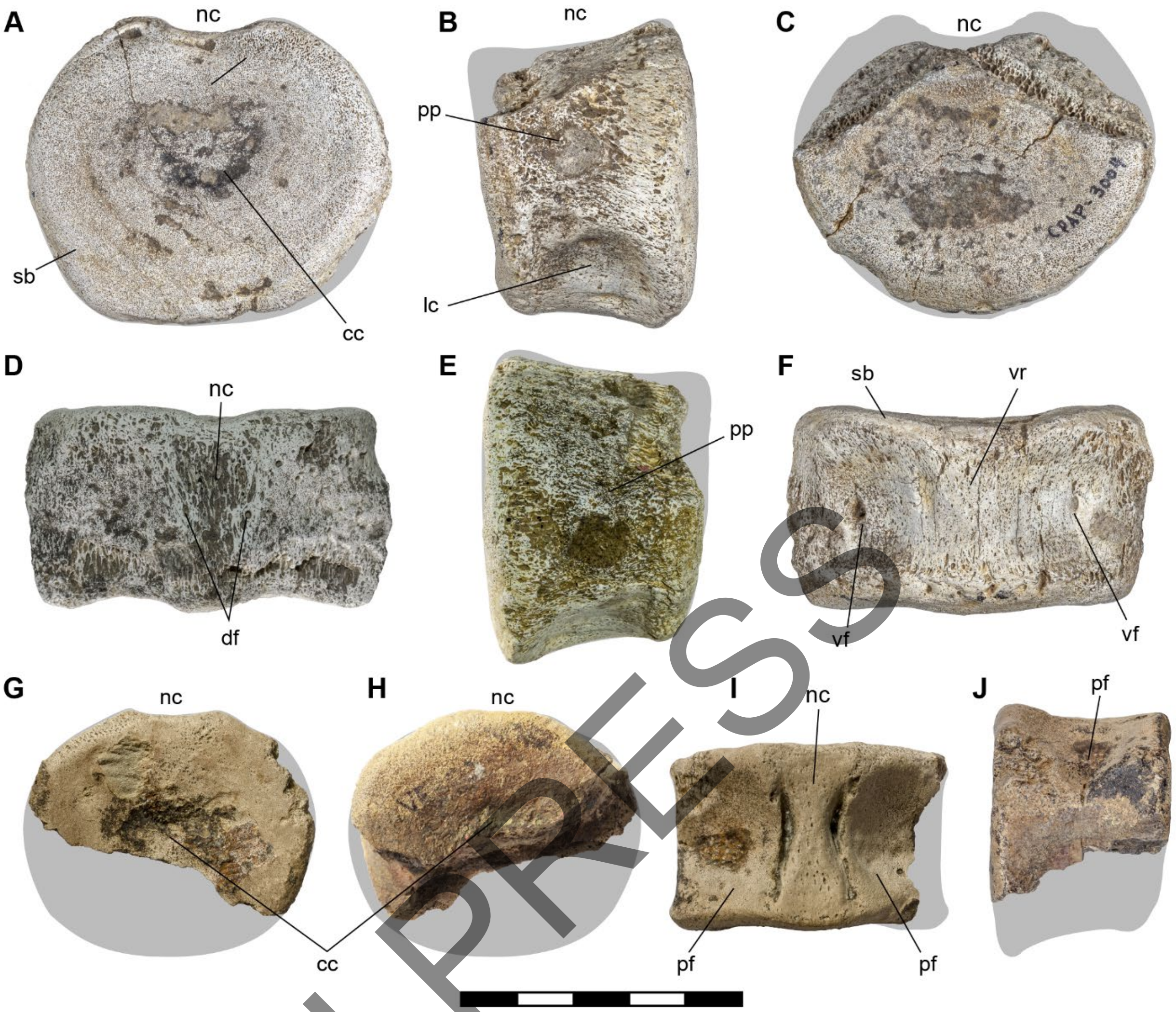

Fig. 3. Polycotylidae indet. from Río de las Chinas Valley, Magallanes Region. **A-F.** CPAP 3004, posterior cervical (or anterior pectoral) centrum; anterior view (A); right lateral view (B); posterior view (C); dorsal view (D); left lateral view (E); ventral view (F). **G-J.** CPAP 3014, anterior? 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.

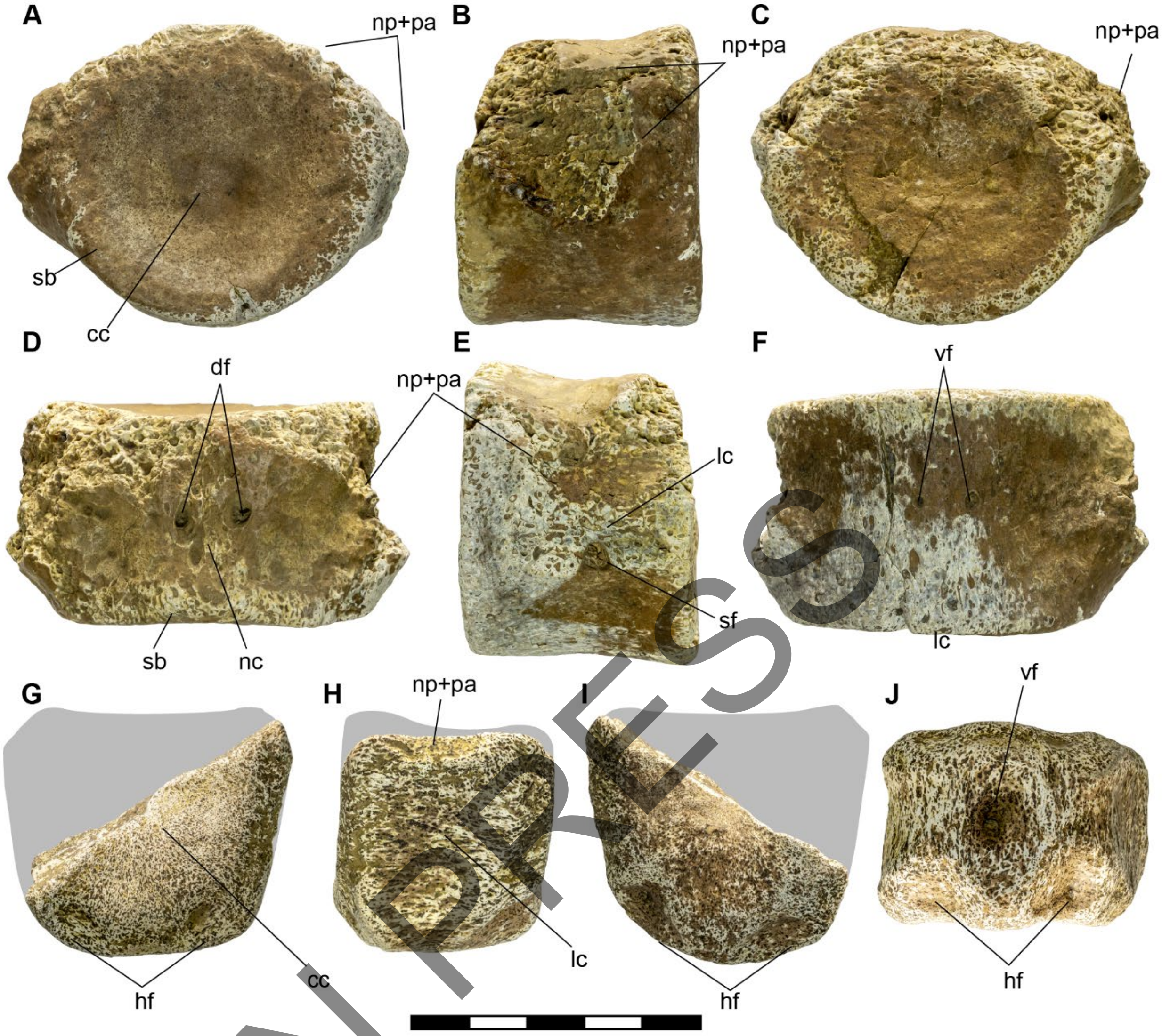

Fig. 4. Polycotylidae indet. from Río de las Chinas Valley, Magallanes Region. **A-F.** CPAP 3003, pectoral vertebra; anterior view (A); right lateral view (B); posterior view (C); dorsal view (D); left lateral view (E); ventral view (F). **G-J.** CPAP 3007, posterior caudal centrum; anterior view (G); 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.

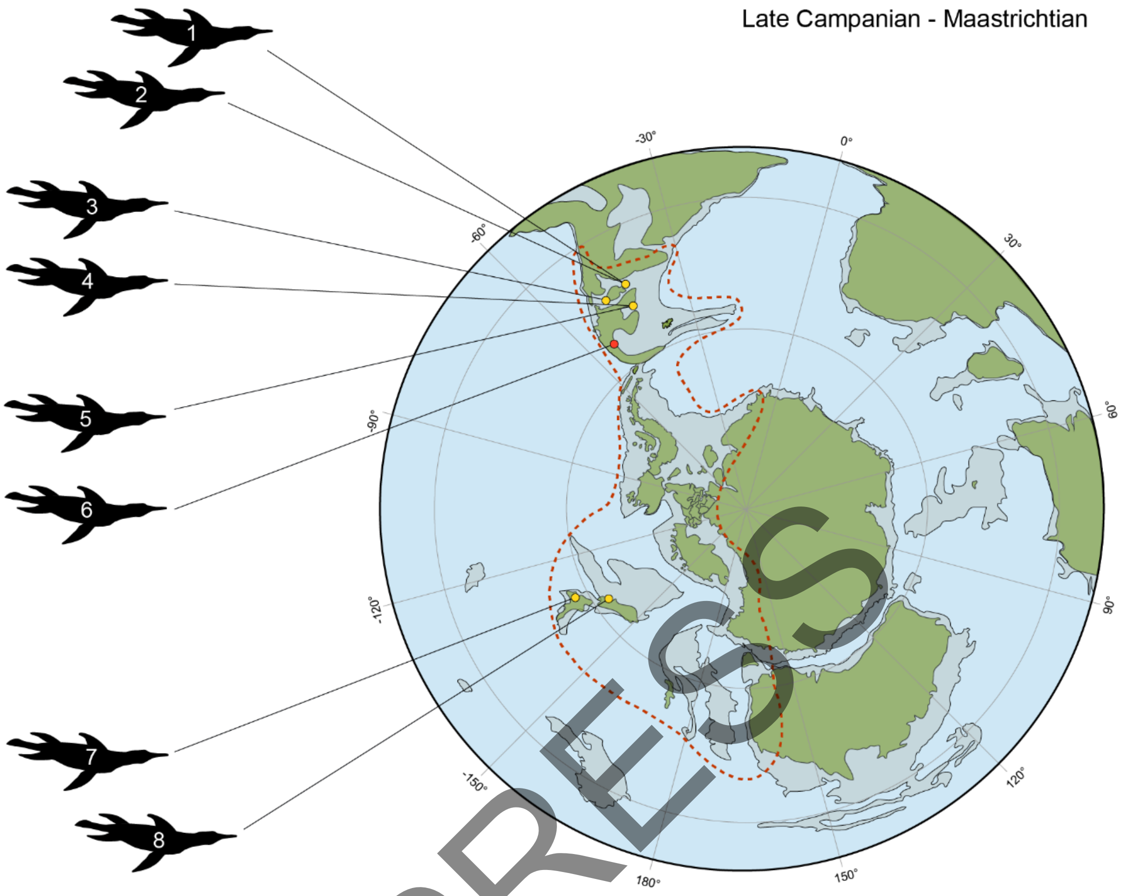

Fig. 5. Paleogeographical polar map of the latest Cretaceous with Weddellian polycotylids records. 1: MML-PV 43, Polycotylidae indet. from Loma Puntuda, Allen Formation (middle Campanian-lower Maastrichtian). 2: MACN-PV RN 1087c, Polycotylidae indet. from Salitral de Santa Rosa, Allen Formation (middle 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).