

Revision of the short-necked
Cretaceous plesiosaurians from New Zealand

José Patricio O'GORMAN & Rodrigo A. OTERO



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ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

Revision of the short-necked Cretaceous plesiosaurians from New Zealand

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Submitted on 31 July 2021 | Accepted on 18 November 2021 | Published on 14 March 2023

[urn:lsid:zoobank.org:pub:AB8DCA69-9BE5-44F1-877D-0E65F73B7186](https://zoobank.org/pub:AB8DCA69-9BE5-44F1-877D-0E65F73B7186)

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>

ABSTRACT

Polycotylidae Cope, 1869 is a clade of short-necked plesiosaurians that achieved a cosmopolitan distribution by the Late Cretaceous. Here, the material previously referred to Polycotylidae/Pliosauridae from the Upper Cretaceous of New Zealand is reviewed, concluding that only 2.4% and 7.7% respectively of the total plesiosaurians specimens recovered in these formations (late Campanian-early Maastrichtian Tahora Formation and Campanian-Maastrichtian Conway Formation) belong to Polycotylidae. This proportion is similar to that recorded in upper Campanian-Maastrichtian levels of the Allen, Los Alamitos and La Colonia formations, northern Patagonia (Argentina) and southernmost Chile, but contrasts with the coeval absence of polycotylids in Campanian-Santonian levels of Antarctica and central Chile. These new results improve our knowledge about the representation of Weddellian polycotylids and underline the relative scarcity of Campanian-Maastrichtian records in the Weddellia Province.

KEY WORDS
Polycotylidae,
Maastrichtian,
Campanian,
New Zealand.

RÉSUMÉ

Révision des plésiosaures du Crétacé à cou court de Nouvelle-Zélande.

Polycotylidae Cope, 1869 est un clade de plésiosaures à cou court qui a atteint une distribution cosmopolite à la fin du Crétacé. Ici, le matériel précédemment attribué aux Polycotylidae/Pliosauridae du Crétacé supérieur de la Nouvelle-Zélande est passé en revue, concluant que seuls 2,4 % et 7,7 % des spécimens de plésiosaures récupérés dans ces formations (Campanien supérieur-Maastrichtien inférieur, Formation Tahora et Campanien-Maastrichtien inférieur, Formation Conway) sont des poly-

MOTS CLÉS
 Polycotylidae,
 Maastrichtien,
 Campanien,
 Nouvelle-Zélande.

cotylidés. Cette proportion est similaire à celle enregistrée dans le niveaux Campanien-Maastrichtien supérieur des formations Allen, Los Alamitos et La Colonia, nord de la Patagonie (Argentine) et l’extrême sud du Chili, mais contraste avec l’absence de polycotylides contemporains en Antarctique et au centre du Chili. Ces nouveaux résultats améliorent nos connaissances sur la représentation des polycotylides weddelliens, prouvant la relative rareté des enregistrements Campanien-Maastrichtien dans la Province de Weddellia.

INTRODUCTION

Polycotylidae Cope, 1869 is a clade of short-necked plesiosaurs whose range extends from the Aptian to the K/Pg mass extinction (Kear 2003, 2005, 2006; Bardet *et al.* 2003; Sato 2005; Buchy *et al.* 2005; O’Gorman & Gasparini 2013; Fischer *et al.* 2018). Polycotylids show a peak of diversity during the Albian-Turonian, achieving a worldwide distribution, including Antarctica (Carpenter 1996; Sato & Storrs 2000; Bardet *et al.* 2003; Kear 2005; Buchy *et al.* 2005; Novas *et al.* 2015; Fischer *et al.* 2018). The Weddellian (i.e., New Zealand, Western Antarctica and southern South America) polycotylid record is markedly scarce. The historic studies regarding Late Cretaceous plesiosaurs from New Zealand starts with the first description by Owen (1861). Subsequent workers added specimens and a great number of species, most of them currently considered *nomina dubia* (Hector 1874; Lydekker 1889; see Welles & Gregg 1971 for a revision). More recent fieldwork on the South and North islands added a new collection of marine reptiles from New Zealand (Wiffen & Moislely 1986; Fig. 1). Among the specimens described by Welles & Gregg 1971 (41 specimens) and Wiffen & Moislely 1986 (39 specimens), about the 25% of the total have been referred historically to Polycotylidae or Pliosauridae (Welles & Gregg, 1971; Wiffen & Moislely, 1986), showing a marked differences with the scarce record of short-necked plesiosaur from the other coeval localities along the Weddellian Province and indicating an interesting anomaly that deserves a revision. Therefore, a reassessment of these short-necked plesiosaurians, their updated description, and a revision of their taxonomic affinities and the comparison with the records in other Weddellian localities are the main goals of this contribution.

MATERIAL AND METHODS

With the exception of five specimens housed in the United Kingdom, all the remaining material from New Zealand described in Welles & Gregg (1971) and Wiffen & Moislely (1986), were directly reviewed by the authors during March and April 2013. Together with these, other specimens not referred to Polycotylidae (mostly elasmosaurids) were also reviewed. For a descriptive purpose, the adimensional indices for the vertebral proportions coined by Welles (1952) were used. These indices capture vertebral centrum proportions, specifically height (H)/length (L) ratio (HI = 100*H/L) and breadth (B)/length (L) ratio (BI = 100*B / L).

ABBREVIATIONS

CM Canterbury Museum, Christchurch;
 DM Museum of New Zealand Te Papa Tongarewa, Wellington;
 NHMUK Natural History Museum, London;
 NPC CD National Paleontological Collection, GNS Science, Lower Hutt;
 SGO Museo Nacional de Historia Natural, Santiago.

SYSTEMATIC PALEONTOLOGY

Subclass SAUROPTERYGIA Owen, 1860
 Order PLESIOSAURIA de Blainville, 1835
 Superfamily PLESIOSAUROIDEA Welles, 1943
 Family POLYCOTYLIDAE Cope, 1869

Polycotylidae indet.
 (Fig. 2A-D)

Pliosauridae gen. et sp. indet. – Wiffen & Moislely 1986: 243.

MATERIAL. — NPC CD 459, anterior cervical vertebra.

LOCALITY AND HORIZON. — Mangahouanga Stream, a northern tributary of Te Hoe River, inland Hawke’s Bay, North Island, New Zealand. Maungataniwha Sandstone Member of the Tahora Formation, upper Campanian-lower Maastrichtian (Vajda & Raine 2010; Fig. 1).

REMARKS

NPC CD 459 possesses amphicelous articular facets, a large neural canal (near the half of the centrum breadth), high neural pedicels and pre- and postzygapophyses as broad as the centrum, which are traits commonly found among cervical vertebrae of polycotylids (Sato & Storrs 2000; Salgado *et al.* 2007; Sato *et al.* 2018).

NPC CD 459 was initially described by Wiffen & Moislely (1986), being then referred as an indeterminate pliosaurid. At that moment, polycotylids were considered as part of the clade Pliosauroida Welles 1943. This systematic placement of Polycotylidae was not questioned until O’Keefe (2001) recognized closer affinities to cryptoclidids and “cimoliasaurids” for this clade, based on large-scale phylogenetic analyses. A growing body of evidence currently recognizes the Polycotylidae as the sister taxon of Leptocleididae Benson & Druckenmiller, 2014 and part of the larger clade Leptocleidia. In addition, the Pliosauridae as currently understood were extinct by the Campanian-Maastrichtian (Druckenmiller & Russell 2008; Benson & Druckenmiller 2014).

Polycotyliidae indet.
(Fig. 2E-H)

Polycotylus tenuis – Hector 1874: 335, pl. 27. — Welles 1962: 73, *nomen dubium*.

Cimoliasaurus tenuis – Lydekker 1889: 188.

Polycotyliidae indet. – Welles & Gregg 1971: 44.

MATERIAL. — DM R1544, a cervical centrum.

LOCALITY AND HORIZON. — Haumuri Bluff, South Island, New Zealand. Conway Formation, Campanian (Wilson *et al.* 2005; Fig. 1).

REMARKS

Welles & Gregg (1971) provided the centrum indices (HI = 145 and BI = 168), pointing out the presence of deeply excavated articular facets and a subcircular articular outline. Such morphology differs from the typical cervical centra observed among Late Cretaceous elasmosaurids, characterized by platycelous articular facets and a bilobed articular contour (Gasparini *et al.* 2003). Otherwise, the elliptical and strongly concave articular facets indicate affinities with Polycotyliidae (Salgado *et al.* 2007). These are non-conclusive regarding a generic determination, as previously pointed out by Welles & Gregg (1971). DM R1544 is part of the hypodigm of '*Polycotylus tenuis*' Hector, 1874 (currently *nomen dubium*), and was designated as the paralectotype by Welles & Gregg (1971).

cf. Polycotyliidae
(Fig. 2I-L)

Polycotylus tenuis – Hector 1874: 335, pl. 27.

Polycotyliidae indet. Welles & Gregg 1971: 44.

MATERIAL. — DM R1548, a juvenile, indeterminate propodium.

LOCALITY AND HORIZON. — No information, but almost certainly from New Zealand (Welles & Gregg 1971; Fig. 1).

REMARKS

Based on its gracility, DM R1548 probably belongs to a polycotylid. It must be noted that the coeval plesiosaur record from New Zealand includes a very unusual, still indeterminate elasmosaurid (CMZfr 159) that possesses a distinctively elongate propodium (Hiller *et al.* 2014: fig. 7), although not so slender as the DM R1548. Similar unusually elongate propodia are known from the late Aptian of Australia, and have also been compared with polycotylids (see Kear 2005: fig. 3A, B). Based on these possibilities, we refer it, with doubts, to cf. Polycotyliidae.

cf. Polycotyliidae
(Fig. 2M)

Polycotylus tenuis – Hector 1874: 335, pl. 27.

Polycotyliidae indet. Welles & Gregg 1971: 47.

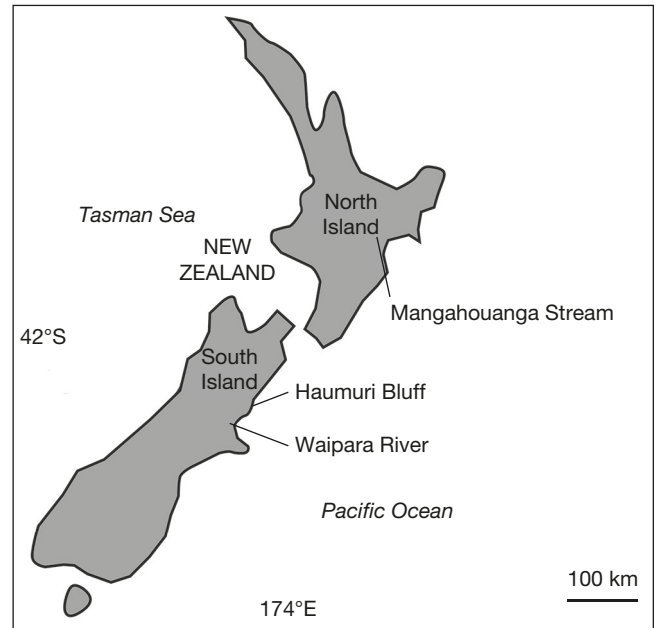


FIG. 1. — Map of New Zealand with the localities mentioned in the text (modified from Wilson *et al.* 2005).

MATERIAL. — NHMUK R838, an indeterminate propodium.

LOCALITY AND HORIZON. — Haumuri Bluff, South Island, New Zealand. Conway Formation, Campanian (Wilson *et al.* 2005; Fig. 1).

REMARKS

The general gracile outline (Fig. 2M) of this specimen is consistent with polycotylid propodia, but no clear diagnostic features are observed. The specimen was illustrated by Hector 1874: fig. XXVIIIB', but it was part of an exchange in 1880 (Lydekker 1889) and it is now in the Natural History Museum (London). The propodium is 22.8 cm in length (9 inches). It was designated by Welles & Gregg (1971) as the lectotype of '*Polycotylus tenuis*'. The latter authors referred the specimen to Polycotyliidae indet. Based on its gracility, it probably belongs to a polycotylid. Similar propodia were described from Australia and possible polycotyliidae affinities were commented (Kear 2005). However, as no clear diagnostic feature are observed, the specimen is referred as cf. Polycotyliidae.

Family ELASMOSAURIDAE Cope, 1869

Elasmosauridae indet.

Cimoliasaurus australis – Lydekker 1889: 221.

Polycotyliidae indet. Welles & Gregg 1971: 35.

MATERIAL. — NHMUK 36074, two posterior cervical centra (juvenile).

LOCALITY AND HORIZON. — NHMUK 36074 from Waipara River, South Island, New Zealand. Conway Formation, Maastrichtian (Wilson *et al.* 2005; Fig. 1).



FIG. 2. — Polycotyliidae indet.: **A-D**, NPC CD 459, cervical vertebra in: **A**, anterior; **B**, posterior; **C**, right; **D**, dorsal; **E-H**, DMR1544, cervical centrum in: **E**, posterior; **F**, left lateral; **G**, dorsal; **H**, ventral; **I-L**, DM 1548, left propodium in: **I**, dorsal; **J**, ventral; **K**, anterior; **L**, posterior; **M**, NHMUK R838, propodium in dorsal view. Scale bars: A-L, 20 mm; M, not in scale. Credits: M, taken from Hector 1874: fig. XXVIIIB’.



FIG. 3. — Elasmosauridae indet.: **A-D**, CM Zfr 99, proximal half of propodium in: **A**, dorsal; **B**, ventral; **C**, posterior; **D**, proximal views; **E, F**, CM Zfr 125, left promodium in: **E**, dorsal; **F**, ventral views; **G-J**, NPC CD 458; **G**, sacral vertebra in posterior view; **H-J**, femur in: **H**, dorsal; **I**, ventral; **J**, anterior views; **K**, NPC CD 458 and MLP 89- III-3-1 (aristonectine) digitally superposed showing similarities in their outlines. Scale bars: A-D, 50 mm; E-G, 20 mm; H-J, 100 mm.

REMARKS

NHMUK 36074 was not personally checked, but Lydekker (1889) stated the following: “These specimens cannot be distinguished from the cervicals of the type of *P. crassicostratus*, figured by Owen in the ‘Geol. Hag.’ dec. 1, vol. vii. pi. iii., and by Hector, op. cit. pi. xxviii” (Appendix 1). The latter specimen is clearly referable to a juvenile elasmosaurid (Welles & Gregg 1971: 36). Therefore, BM 36074 is here referred to *Elasmosauridae* indet.

Elasmosauridae indet.
(Fig. 3A-D)

Polycotyliidae indet. – Welles & Gregg 1971: 46.

MATERIAL. — CM Zfr 99, proximal part of a very large propodial.

LOCALITY AND HORIZON. — Waipara River, South Island, New Zealand. Conway Formation, Maastrichtian (Wilson *et al.* 2005; Fig. 1).

REMARKS

The presence of a distinctively prominent articular head and a dorsally elevated tuberosity is a feature commonly found in Weddellian elasmosaurids (Wiffen & Moisley 1986: figs 58, 59; O’Gorman *et al.* 2015, 2019; Otero *et al.* 2015). Furthermore, the presence of a tuberosity displaced with respect to the shaft axis of the femur is a feature observed in the femora of several very large Weddellian elasmosaurids such as DM R1529 (holotype of *Mauisaurus haasti* (Hector, 1874), currently considered *nomen dubium*, Hiller *et al.* 2017) from New Zealand, cf. *Aristonectes* Cabrera, 1941 (MLP-89-III-3-1) from Antarctica (O’Gorman *et al.* 2019), an isolated femur (SGO.PV.135) referred to *Aristonectes quiriquinensis* Otero, Soto-Acuña, O’Keefe, O’Gorman, Stinnesbeck, Suárez, Rubilar-Rogers, Salazar & Quinzio, 2014 from Chile (Otero *et al.* 2015: fig. 2) and in the holotype of *Kaiwheke katiki* Cruickshank & Fordyce, 2002 (Cruickshank & Fordyce 2002). The oval articular head/capitulum seen in CM Zfr 99 is probably consequence of taphonomic deformation. The tuberosity is partially eroded. As additional indirect evidence, the very large size of CM Zfr 99 is only comparable to the propodials of MLP-89-III-3-1, a giant elasmosaurid from the Maastrichtian of Antarctica, referred as cf. *Aristonectes* (O’Gorman *et al.* 2019). Thus, the presence of very large individuals such as CM Zfr 99 is so far documented among elasmosaurids of the Weddellian Province, but locally, CM Zfr 99 represents a novelty in terms of size among Late Cretaceous elasmosaurids from the Conway Formation.

Elasmosauridae indet.
(Fig. 3E, F)

Polycotyliidae indet. – Welles & Gregg 1971: 46.

MATERIAL. — CM Zfr 125, a juvenile propodial.

LOCALITY AND HORIZON. — No information, probably Waipara District (Fig. 1), according to Welles & Gregg (1971).

REMARKS

Based on propodial indices, Welles & Gregg (1971) identified this specimen as a juvenile “pliosaur” (*sensu lato*, following Welles 1943), noting a 90° angle between the capitulum and trochanter/tuberosity (as it is an indeterminate propodial). The presence of unexpanded distal end of the bone are features observed among juvenile. What is more these traits and the general proportions of CM Zfr 125 are remarkably similar to those described in the juvenile articulated postcranial skeleton SGO.PV.260 from the upper Maastrichtian of central Chile, referred to *Aristonectes quiriquinensis* (Otero *et al.* 2015: fig. 4A). While CM Zfr 125 could be narrowly comparable to the latter species, the lack of additional associated skeletal remains precludes its adscription to aristonectines. This is why it is kept as an indeterminate elasmosaurid.

Elasmosauridae indet.
(Fig. 3G-K)

Pliosauridae gen. et sp. indet. – Wiffen & Moisley 1986: 243.

MATERIAL. — NPC CD 458, a specimen comprising a left and right propodial, single sacral vertebra, and rib section (Fig. 3G-K).

LOCALITY AND HORIZON. — Mangahouanga Stream, a northern tributary of Te Hoe River, inland Hawke’s Bay, North Island, New Zealand. Maungataniwha Sandstone Member of the Tahora Formation. Upper Campanian-lower Maastrichtian (Vajda & Raine 2010; Fig. 1).

REMARKS

The NPC CD 458 propodial has features typically present among Weddellian elasmosaurids, with features slightly different from elasmosaurids elsewhere. These features are, particularly, the prominent, sub-hemispherical articular head/capitulum, stocky femoral shaft and high dorsal tuberosity of the propodial (Otero *et al.* 2015), while the sacral centrum has platyclous faces and a very narrow neural arch compared to the centrum breadth (Gasparini *et al.* 1984; Cruickshank & Fordyce 2002; Otero *et al.* 2015; O’Gorman *et al.* 2015, 2019). Therefore, it is reassessed as an indeterminate elasmosaurid. Moreover, the general outline is remarkably similar to that of MLP 89-III-3-1, a specimen from Antarctica referred to as an indeterminate aristonectine (O’Gorman *et al.* 2019).

Plesiosauria indet.

MATERIAL. — NHMUK 36075, part of a dorsal region comprising partial impressions of ribs and neural spines.

LOCALITY AND HORIZON. — Waipara River, South Island, New Zealand. Conway Formation, Maastrichtian (Wilson *et al.* 2005; Fig. 1)

REMARKS

NHMUK 36075 was referred by Welles & Gregg (1971) to *Polycotyliidae* based on their stout ribs, long transverse process, short centra and thick neural spines. None of these features are strictly diagnostic of *Polycotyliidae* since these could also be observed

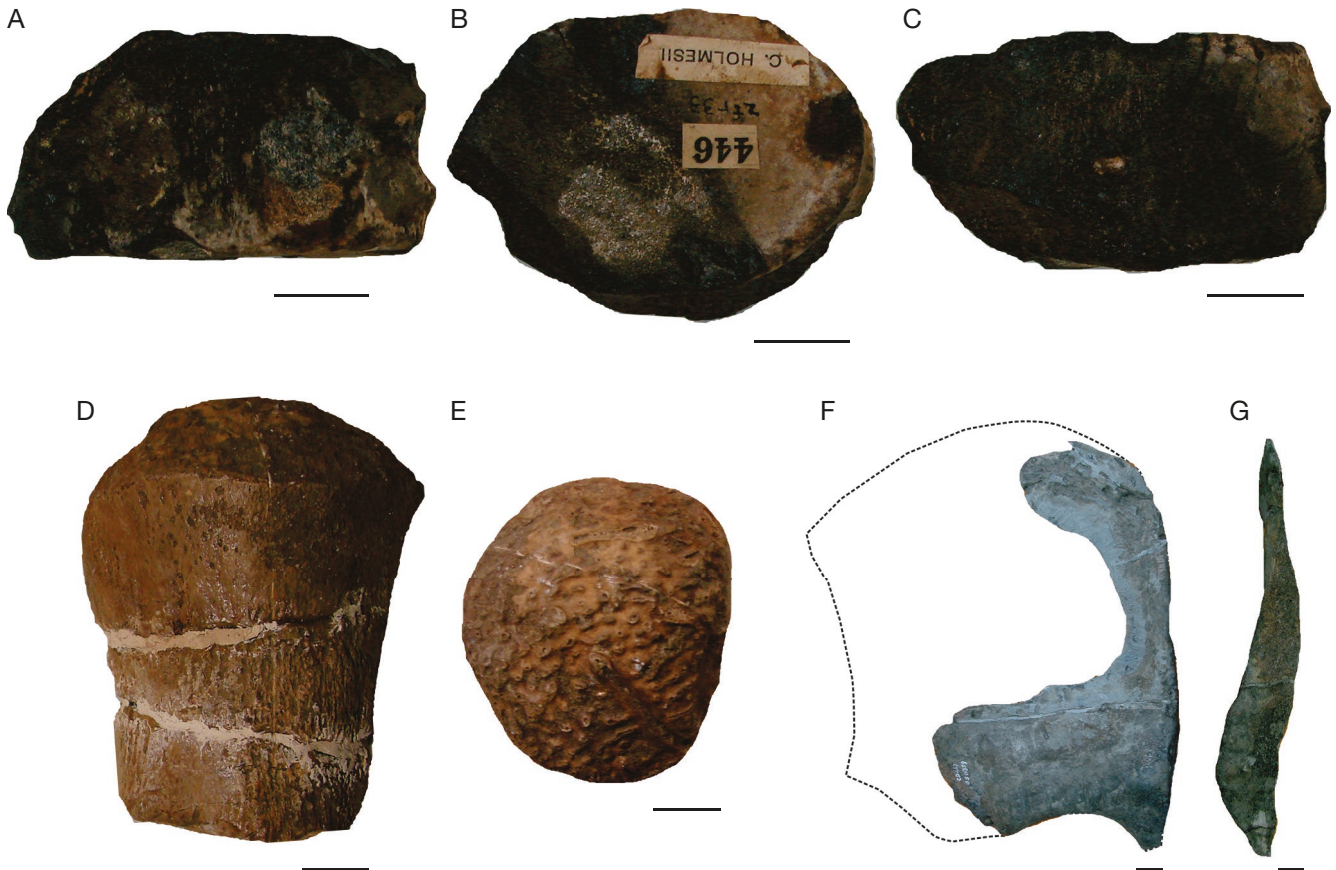


FIG. 4. — Plesiosauria indet.: A–C, CM Zfr 33, sacral centra: A, dorsal; B, anterior; C, ventral views; D, E, DM R 1547, proximal end of propodium in: D, ventral; E, proximal views; F, G, NPC CD 457, pubis in: F, dorsal; G, symphyseal views. Scale bars: 20 mm.

in juvenile elasmosaurids. Additionally, Lydekker (1889: 121) mentioned that NHMUK 36075 was probably part of the same individual as NHMUK 36073 (partial coracoid) and NHMUK 36073a (partial scapula); the latter specimens are currently referred as *Elasmosauridae* indet. However there are not direct evidence of the latter and therefore it is referred to *Plesiosauria* indet.

Plesiosauria indet.

MATERIAL. — NHMUK 37413, impression of six posterior cervical centra and four ribs.

LOCALITY AND HORIZON. — Probably Waipara river or Bobys Stream (Fig. 1).

REMARKS

Welles & Gregg (1971) mentioned that the matrix is similar to that observed in NHMUK 36073 and NHMUK 36075, also calculating the BI index of the last centra as 202. The vertebral measurements are remarkably similar (40 mm) in both specimens. Considering these indices and their associated collection, these likely belong to the same individual. The specimen is compatible with the morphology observed in *Elasmosauridae*; however, no clear synapomorphies of the later clade are observed and therefore, they are referred here to *Plesiosauria* indet.

Plesiosauria indet.

Plesiosaurus australis – Owen 1861: 122. — Lydekker 1889: 221.

Polycotylidae indet. Welles & Gregg 1971: 45.

MATERIAL. — NHMUK R831, a cervical centrum.

LOCALITY AND HORIZON. — Waipara River, South Island, New Zealand. Conway Formation, Maastrichtian (Wilson *et al.* 2005, Fig. 1).

REMARKS

Regarding this specimen, Lydekker (1889) described it as “the centrum of an early cervical vertebra of similar type”, in a direct comparison to the material previously described by Owen (1861), see Appendix 1. Following the comments of Lydekker (1889), they should be similar to those within the hypodigm of ‘*Plesiosaurus australis*’ (currently *nomen dubium*).

Plesiosauria indet.

(Fig. 4A, C)

Plesiosaurus holmesi – Hector 1874: 344.

Polycotylidae indet. Welles & Gregg 1971: 44.

MATERIAL. — CM Zfr 33, a sacral centrum.

LOCALITY AND HORIZON. — Waipara River, South Island, New Zealand. Conway Formation, Maastrichtian (Wilson *et al.* 2005; Fig. 1).

REMARKS

This specimen was regarded as a paralectotype of “*Plesiosaurus holmesi*” Hector, 1874 (*nomen dubium*), and considered as an indeterminate polycotyloid by Welles & Gregg (1971). The sacral features of the specimen preclude a referral to polycotyloids or elasmosaurids. Therefore, it is here considered as an indeterminate plesiosaurian.

Plesiosauria indet.

Plesiosaurus crassicostratus – Owen 1870: 49. — Hector 1874: 342.

Polycotyloidea indet. Welles & Gregg 1971: 43.

MATERIAL. — DM R1539, an isolated propodium.

LOCALITY AND HORIZON. — Haumuri Bluff, South Island, New Zealand. Conway Formation, Campanian (Wilson *et al.* 2005; Fig. 1).

REMARKS

This specimen is currently preserved as three fragments, clearly belonging to a propodium. No diagnostic features are observed on DM R1539 and therefore it is referred to Plesiosauria indet.

Plesiosauria indet.

(Fig. 4D-E)

Plesiosaurus crassicostratus – Owen 1870: 49. — Hector 1874: 43.

Polycotyloidea indet. Welles & Gregg 1971: 43.

MATERIAL. — DM R1547, proximal portion of propodium (Fig. 4D, E).

LOCALITY AND HORIZON. — Waipara River, South Island, New Zealand. Conway Formation, Maastrichtian (Wilson *et al.* 2005; Fig. 1).

REMARKS

The lack of distinctive features precludes us to refer it beyond Plesiosauria.

Plesiosauria indet.

(Fig. 4F-G)

Pliosauridae gen. et sp. indet. – Wiffen & Molesley 1986: 243.

MATERIAL. — NPC CD 457: an isolated, incomplete adult plesiosaurian pubis.

LOCALITY AND HORIZON. — Mangahouanga Stream, a northern tributary of Te Hoe River, inland Hawke’s Bay, North Island, New Zealand. Maungataniwha Sandstone Member of the Tahora Formation. Upper Campanian-lower Maastrichtian (Vajda & Raine 2010; Fig. 1).

REMARKS

This specimen was interpreted as a coracoid by Wiffen & Molesley 1986. These authors considered the symphysis as the posterior extension of a coracoid. Under that interpretation, the specimen indeed resembled a “pliosaurid or polycotyloid” coracoid. However,

the bone is much eroded. The side opposed to the symphysis (i.e., the external side) shows rough edges, indicating that the bone is broken. This is visible in the “two lateral prominences”, which are an artifact of the medial erosion of the tabular bone. In lateral view, the specimen lacks a transverse thickening typically present in plesiosaurian coracoids. The presence of a short medial anterior process in such a large (likely adult) specimen suggests the lack of a girdle bar (in this reinterpretation, a pelvic bar). In addition, typical features present in polycotyloid coracoids, such as the perforations on the symphyseal margin (Sato 2005; Albright *et al.* 2007; Schmeisser-McKean *et al.* 2012), although absent in *Plesiopleurodon wellesi* Carpenter, 1996 and *Mauriciosaurus fernandezii* Frey, Mulder, Stinnesbeck, Rivera-Sylva, Padilla-Gutiérrez & González-González, 2017 (Frey *et al.* 2017; Fischer *et al.* 2018), are not present. Therefore, the specimen CD 457 is considered a plesiosaur pubis. The large size and the lack of a pelvic bar suggest affinities to Elasmosauridae, but this cannot be assured. However, it is possible to discard CD 457 as the coracoid of a “pliosaur” *sensu lato*, or else, of a polycotyloid.

Plesiosauria indet.

(Fig. 5A, E)

Pliosauridae gen. et sp. indet. – Wiffen & Molesley 1986: 249.

MATERIAL. — NPC CD 460, three sacral and two caudal centra, disarticulated ribs, phalanges, and fragment of pubis? (Fig. 5A-E).

LOCALITY AND HORIZON. — Mangahouanga Stream, a northern tributary of Te Hoe River, inland Hawke’s Bay, North Island (Fig. 1), New Zealand. Maungataniwha Sandstone Member of the Tahora Formation. Upper Campanian-lower Maastrichtian (Vajda & Raine 2010).

REMARKS

The vertebrae were interpreted as cervicals by Wiffen & Molesley (1986). The pubis is severely damaged and it is not possible to assess its general outline. The phalanges are not diagnostic. Therefore, the vertebral series is the most diagnostic material of this specimen. The specimen is reinterpreted here as three sacral vertebrae and two caudal centra (Fig. 5A-G). This interpretation is consistent with the preserved ribs as the first and second are rod-shaped, as it is usual in elasmosaurids; while the third posterior rib is dorsoventrally compressed, being similar to the caudals. Thus, the referral to Polycotyloidea based on the typical short cervical centra is here discarded as they are considered sacral and caudal vertebrae.

Plesiosauria indet.

(Fig. 5F-H)

Pliosauridae gen. et sp. indet. – Wiffen & Molesley 1986: 249.

MATERIAL. — NPC CD 461, nine caudal articulated vertebrae, all damaged by erosion, three ribs and a pubis fragment.

LOCALITY AND HORIZON. — Mangahouanga Stream, a northern tributary of Te Hoe River, inland Hawke’s Bay, North Island (Fig. 1), New Zealand. Maungataniwha Sandstone Member of the Tahora Formation. Upper Campanian-lower Maastrichtian (Vajda & Raine 2010).



FIG. 5. — Plesiosauria indet.: **A-E**, NPC CD 460: **A**, **B**, sacral and caudal centra serie: **A**, left lateral; **B**, posterior view; **C-E**, caudal vertebrae: **C**, posterior; **D**, anterior; **E**, left lateral view; **F-H**, NPC CD 461: **F**, pubis, right lateral view; **G**, **H**, caudal serie: **G**, right lateral; **H**, posterior view; **I, J**, NPC CD 464, tooth in: **I**, lateral; **J**, anterior view; **K, L**, NPC CD 465: **K**, lateral; **L**, anterior view. Abbreviations: **cr**, caudal ribs; **lsa**, last sacral ventrum; **ca 1**, first caudal centrum; **pa**, parapophysis; **pf**, pedicellar facet. Scale bars: 20 mm.

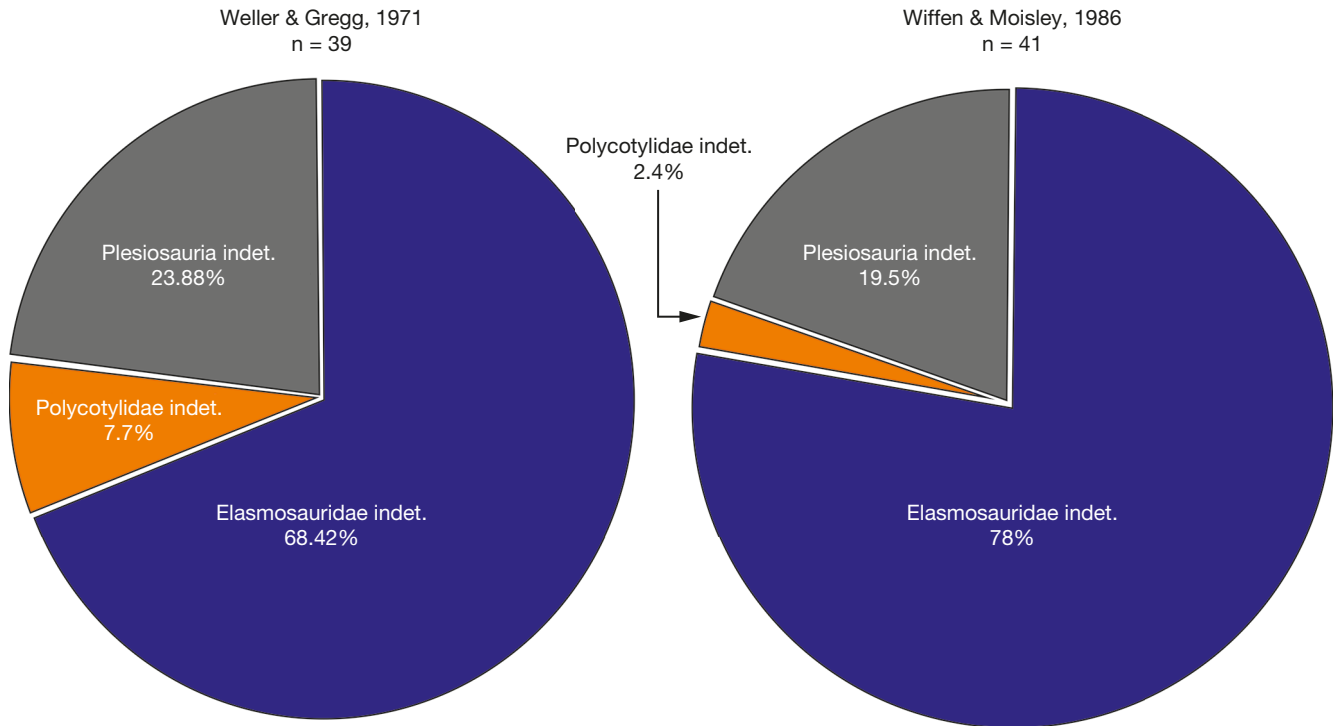


FIG. 6. — Plot showing the final results after revision of the material previously referred to Polycotylidae Cope, 1869: **A**, Welles & Gregg 1971 (mostly Conway Formation); **B**, Wiffen & Moisley 1986 (Tahora Formation).

REMARKS

These vertebrae were interpreted as a cervicals by Wiffen & Moisley (1986). This sequence is reinterpreted here as caudal vertebrae, as the associated ribs show typical elasmosaurid features (straight and dorsoventrally compressed). Therefore, pliosaurid affinities can be discarded. Wiffen & Moisley (1986) mentioned that both NZGS CD 460 and 461 could belong to the same specimen. The similar growth stage, similar size and the anatomically complementary remains of both specimens support that assumption. Additionally, both specimen preserved part of a pubis. If these are indeed a single specimen, these represent the sacral and anterior caudal part of a juvenile plesiosaur, probably belonging to an elasmosaurid.

Plesiosauria indet.
(Fig. 5I-L)

MATERIAL. — NPC CD 462, 463, 464, 465, four isolated teeth.

LOCALITY AND HORIZON. — Mangahouanga Stream, a northern tributary of Te Hoe River, inland Hawke’s Bay, North Island (Fig. 1), New Zealand. Maungataniwha Sandstone Member of the Tahora Formation. Upper Campanian-lower Maastrichtian (Vajda & Raine 2010).

REMARKS

These teeth have their enamel with few well-marked striations, and the crown comparatively shorter and blunter than those typically observed in elasmosaurids such as *Tuarangisaurus keyesi* Wiffen & Moisley, 1986 holotype (Wiffen & Moisley

1986: figs 1-3, 15, 16). The lack of distinctive dental traits the specimens are referred to Plesiosauria indet.

DISCUSSION

FAUNAL COMPOSITION OF THE PLESIOSAURIAN ASSEMBLAGE FROM THE LATE CRETACEOUS OF NEW ZEALAND
After this reassessment, we confirm/refer two specimens (NPC CD 459 and DM R1544) to Polycotylidae indet. Two specimens (DM R1548 and NHMUK R838) are doubtfully considered as possible polycotylids; six studied specimens (NHMUK 36074, CM Zfr 99, 125, NPC CD 458 and), formerly considered as polycotylids (Welles & Gregg 1971; Wiffen & Moisley 1986), are here referred to Elasmosauridae indet. Finally, eleven specimens (NHMUK 37413, NHMUK 36075, NHMUK R831, CM Zfr 33, DM R1539, DM R1547, NPC CD 457, NPC CD 460, NPC CD 461, NPC CD 462, NPC CD 463, NPC CD 464, NPC CD 465) are referred to Plesiosauria indet. due to the lack of diagnostic traits.

The material studied by Welles & Gregg (1971) included forty specimens. Several historical specimens, as indicated by these authors, were not found, so they are excluded from this account. From the reviewed material, Welles & Gregg (1971) referred twenty-two specimens to elasmosaurids, twelve to polycotylids, and five to indeterminate plesiosaurians. One specimen 64/6b of Hector (1874), later referred as the syn-type of ‘*Plesiosaurus mackayi*’ was regarded as not found by Welles & Gregg (1971). It was also excluded from this analysis. Our current review proposes the reassignment of NHMUK

36074, CM Zfr 99 and CM Zfr 125 to Elasmosauridae indet. and NHUMK 37413, BMNH 36075, BM R831, DM R1547, DM R1539 and CM Zfr 33 to Plesiosauria indet. With this, our proposed account of the specimens reviewed by Welles & Gregg (1971) includes twenty-five elasmosaurids, one confirmed polycotylid, two cf. polycotylidae (counted as Polycotylidae in Fig. 6), eleven indeterminate plesiosaurs, and one lost specimen.

Wiffen & Molesley (1986) studied a total of forty-two specimens, referring thirty-one of them to elasmosaurids, nine to indeterminate plesiosaurs and one specimen to an indeterminate plesiosaurian. After our review, we refer the former plesiosaurs to one polycotylid, one elasmosaurid, and seven indeterminate plesiosaurs. With this, our proposed account of the specimens reviewed by Wiffen & Molesley (1986) includes thirty-two elasmosaurids, one confirmed polycotylid, and eight indeterminate plesiosaurs.

The reviewed numbers of each taxon are summarized on the graphics of Fig. 6. Interestingly, the proportion of polycotylids in the material of Welles & Gregg (1971) and Wiffen & Molesley (1986) is 7.7 and 2.4 % respectively.

Among Weddellian records of polycotylids the Chilean records are restricted to isolated vertebral centra recovered from the marine Dorotea Formation, Magallanes Basin (Soto-Acuña *et al.* 2016). In the southwestern Pacific, particularly in central Chile, Late Cretaceous elasmosaurids are frequent and well-represented, but material unequivocally referable to polycotylids are not known to date (Otero *et al.* 2015). The record of polycotylids from Antarctica is restricted to two indeterminate records from lower levels of the marine Santa Marta Formation (Coniacian-Santonian), described by (Kellner *et al.* 2011; Novas *et al.* 2015). The overlying Campanian-Maastrichtian marine formations of Antarctic Peninsula (Snow Hill Island and López de Bertodano formations) of Antarctica has a rich and frequent record of elasmosaurids (Gasparini *et al.* 1984; O’Gorman 2012; Otero *et al.* 2014a; O’Gorman *et al.* 2018) even including endemic taxa (Chatterjee & Small 1989; O’Gorman *et al.* 2015; O’Keefe *et al.* 2017); however, despite thirty years of continuous field work by the Argentinean Antarctic Institute, post-Coniacian Antarctic polycotylids remain unknown to date.

At last, Argentinean Patagonic records of Atlantic Late Cretaceous polycotylids are restricted to one species, *Sulcusuchus erraini* Gasparini & Spalletti, 1990, and few postcranial remains (Gasparini & de La Fuente 2000; Salgado *et al.* 2007; O’Gorman *et al.* 2011) collected from marine marginal deposits of the upper Campanian-lower Maastrichtian Allen Formation and Maastrichtian levels of La Colonia Formation. However, no polycotylid specimens are recorded for the upper Maastrichtian levels of the marine Jagüel Formation, also from North Patagonia where elasmosaurids are frequently recorded (Gasparini *et al.* 2003). Therefore, the proportions of Polycotylid records observed in New Zealand is consistent with the general scarcity of Late Cretaceous polycotylids records in the Weddellian province, compared to coeval elasmosaurids (Welles & Gregg 1971; Wiffen & Molesley 1986; Cruickshank & Fordyce 2002; Hiller *et al.* 2005).

CONCLUSIONS

This revision concludes that among the plesiosaurian specimens from the Late Cretaceous of New Zealand, two specimens could be clearly referred to Polycotylidae and two other can be referred with doubts. The total number of specimens referred to polycotylids from the two main formations that have yielded plesiosaur material in New Zealand is 2.4 % (Tahora Formation) and 7.7 % (Conway Formation) respectively. This proportion is similar to the one observed in the plesiosaurian records from the Upper Campanian-Lower Maastrichtian, marine marginal Allen, Los Alamitos and La Colonia formations, and higher than the one observed in the same stages in the shallow-water, marine Quiriquina Formation of Chile, the coeval units with similar environment of the Austral (Magallanes) Basin, and the Campanian-Maastrichtian marine formations of the Antarctic Peninsula. The latter scarcity differs from the records of elasmosaurids that remain as the unique plesiosaurian clade recorded in several austral units (i.e., Jagüel, Quiriquina, Snow Hill Island, López de Bertodano formations).

Acknowledgements

This research was supported by grants PICT (proyecto de investigación en ciencia y técnica, Agencia de Promoción Científica y Tecnológica) PICT-2018-02443 and PICT 2017-0607. RAO was supported by Proyecto PIA-ANID-Chile, Anillo ACT-172099 (Registro Fósil y Evolución de Vertebrados). The author thanks the curators of the Canterbury Museum (R. P. Scofield), New Zealand Geology and Nuclear Sciences (M. Terezow) Museum of New Zealand Te Papa Tongarewa (A. J. D. Tennyson) who allowed the study of the material under their care, and the associated editor, Juliana Sterli, and the two reviewer, for their comments.

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Submitted on 31 July 2021;
accepted on 18 November 2021;
published on 14 March 2023.

APPENDICE

APPENDIX 1. — DMR 1527 type of *Plesiosaurus crassicostatus* Owen, 1870, figured by Owen 1870: pl. iii., and by Hector 1874: pi. xxviii”. Scale bars: 100 mm.

