A new postcranial skeleton of an elasmosaurid plesiosaur from the Upper Cretaceous of central Chile and reassessment of *Cimoliasaurus andium* Deecke

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ABSTRACT

We describe a new specimen of an elasmosaurid plesiosaur from the upper Maastrichtian of central Chile. The specimen includes a relatively complete dorso-caudal series, a few cervical vertebrae, and a fragmentary pelvic girdle. The specimen is identified as a sub-adult non-artistonectine elasmosaurid (Sauropterygia, Plesiosauria) based on graphic bivariate analysis of the cervical vertebral proportions. The caudal vertebrae have distinctive features such as neural arches that are recurved cranially, with pedicels overlapping the dorso-posterior surface of the immediately anterior centrum, and terminal centra with two pairs of deep dorsal articulations for the neural arches. These unusual features are present in several late Maastrichtian adult specimens from the Quiriquina Formation of central Chile, and have been included within the hypodigm of the historic taxon *Cimoliasaurus andium* Deecke (nomen dubium). The specimen studied here likely represents the same taxon or a closely related form, showing slight differences in both size and ontogenetic stage. The preserved elements of this new skeleton afford comparison with several other late Maastrichtian specimens from Chile that were previously, albeit tentatively, referred to "*C. andium*". The similarity of these specimens suggests that the late Maastrichtian elasmosaurid diversity of central Chile (excluding aristonectines) may be represented by taxa with low morphological disparity, or by a single taxon.

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1. Introduction

During the early 1990s, marine reptile remains were discovered in the town of Pelluhue, central Chile (Fig. 1). The first fossils were described by Castillo et al. (1992), who identified them as Plesiosauria indet. and assigned a Late Cretaceous age without additional chronostratigraphic resolution. The figured material includes 6 most anterior cervical vertebrae (including the atlas-axis), a mid posterior cervical vertebra, one tooth, and one ilium (misidentified as a fragment of humerus). Among non-figured elements are twenty-nine vertebrae, 25 fragments of neural spines (regarded as 'spinal apophyses'), 25 rib fragments, eight fragmentary teeth (comprising plesiosaur and sclerorhynchid teeth), one phalanx, two additional ilia (making three total for this specimen association), and ten indeterminate bone fragments. These authors recovered additional remains in the following years, including elements that

were found by locals. These new elements comprised a second skeleton (reported here), and were found a few centimetres below the first. The neck was oriented to the north while the trunk region was twisted and crushed, leaving the caudal elements oriented to the west. Later, both specimens were combined into a display that, together, included the parts of a near complete postcranial skeleton. This display was kept on exhibit in a private Museum on the city of Santiago until 2010. When the skeletons were returned to the Museo Nacional de Historia Natural (National Museum of Natural History, Santiago, Chile), a preliminary inspection revealed the parts of at least two individuals. Unfortunately, much of the relevant information about the original discovery was lost. Therefore, the specimens had to be separated using criteria that included preservation, morphology, relative size, and vertebral measurements (including graphic bivariate analysis of cervical proportions). One of the two specimens (SGO.PV.6507) is preliminary identified as an indeterminate aristonectine (subfamily Aristonectinae O'Keefe and Street, 2009, sensu Otero et al., 2012). This skeleton includes the atlas-axis and anterior cervicals firstly described by

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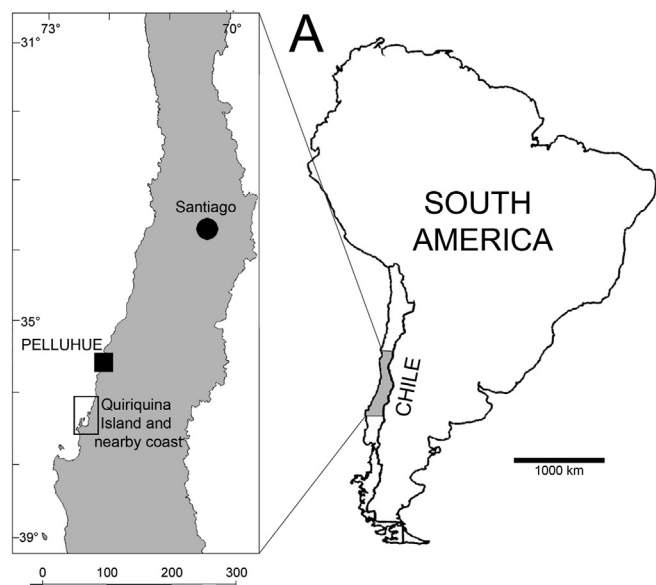
Fig. 1. Map indicating the locality of Pelluhue in central Chile (35°48′2″S, 72°34′5″W) and its relative distance to the main outcrops of the Quiriquina Formation in the area of the homonymous island.

Castillo et al. (1992). The second postcranial specimen studied here (SGO.PV.6506) preserves a good part of its axial skeleton and fragments of the pelvic girdle, which show that it is not an aristonectine, but rather closely related to the long-necked plesiosaurs more common to the Cretaceous of the Northern Hemisphere.

The remains of the SGO.PV.6506 include a nearly complete caudal series with interesting features. The neural arches bear distinctive morphologies such as an anterior displacement of the neural pedicels, causing the posterior vertebrae to have an overlap of the neural arch into the immediately anterior centrum. The extreme representation of this condition is observed in the caudal-most centra where an additional pair of facets appears on the dorsal surface of these centra. Displaced neural arches overlapping their anterior centra have been observed among other Late Cretaceous fossils from Chile, particularly, in the specimens regarded as cervical vertebrae of the taxon *Cimoliasaurus andium* Deecke (in Steinmann et al., 1895) (nomen dubium) from upper Maastrichtian beds of Quiriquina Island, central Chile. The cervical vertebrae of "*C. andium*" are actually caudal vertebrae with neural arches similar to those present in the specimen SGO.PV.6506. In addition, the combination of characters form the caudals, cervical vertebrae, and pelvic girdle of SGO.PV.6506 were compared with other Late Cretaceous specimens from the Weddellian Biogeographic Province (Zinsmeister, 1979, WBP hereafter) where similar anatomical elements are preserved and/or described. Based on these comparisons, we group these Chilean specimens within a single morphotype, which appears to be different from other non-aristonectine elasmosaurids from the WBP (at least based on the distinctive ilium and the caudal features). However, because of the lack of the skull material and the incompleteness of each specimen, we conservatively refrain any attempt of generic or specific determination.

2. Locality and geologic setting

Pelluhue (35°48′2″S, 72°34′5″W) is in central Chile, about 320 km southwest of Santiago (Fig. 1). The southern part of the town, Mariscadero, has basement rocks conformed by massive sandstones with intercalated levels of concretionary nodules and cross-bedding, including a rich fossil diversity of both invertebrates and vertebrates. Thiele and Tavera (1967) analyzed fossil vertebrates and invertebrates collected from Loanco (25 km N from the studied locality), assigning for first time a Senonian age to the fossil-bearing levels. Later, Biró-Bagóczky (1982) formalized the name of Quiriquina Formation for those Upper Cretaceous beds exposed 100 km southwest from the locality studied here, constraining the age of the formation to the Campanian–Maastrichtian based on biostratigraphic correlations. In addition, offshore wells studied by Mordojovich (1976) and taken 100 km in front of Faro Carranza (35 km north from Pelluhue) showed 1000 m of Upper Cretaceous marine sediments, a basin large enough to include the deposits from type locality of the Quiriquina Formation and those from Pelluhue, located 100 km N from the first. Cecioni (1983) attempted to formalize the status of the sandstones of Faro Carranza-Pelluhue, by erecting the Chanco Formation. Cecioni (1983) indicated that the Chanco Formation was correlated to the base of the Quiriquina Formation, and assigned it a late Campanian age based on fossil invertebrates. Mordojovich (1976) and Cecioni (1980, 1983) recognized the existence of Eocene beds in the area, based on drillings performed offshore. These studies indicate that the Quiriquina Formation and the sandstones of Faro Carranza-Pelluhue belong to the same basin that existed at least since the Upper Cretaceous, and was deposited until the Eocene. Stinnesbeck (1986) considered the beds of the 'Chanco Formation' as equivalent to the Quiriquina Formation based on the fossil invertebrates, refining its age to the Maastrichtian. Later, Tavera (1988) correlated the levels of Pelluhue with the lower levels of the Quiriquina Formation.

Based on field data collected during this current research, the section exposed at Pelluhue (Fig. 2) comprises a basal conglomeratic, yellowish, sandstone with fine conglomerate lenses including variable clasts under 10 cm. The base of this level is not visible and the exposed thickness is estimated close to 2 m. Conglomerate sandstones are overlaid by near 1 m of very bioturbated sandstones with abundant traces of *Thalassinoides* isp. The bioturbated layer is conformably overlain by approximately 2 m of massive medium grain, yellow to grey, sandstones. The plesiosaur specimens SGO.PV.6507 and 6506 were found in this sandstone layer. SGO.PV.6507, tentatively identified as aristonectine elasmosaurid, was found a few centimetres above SGO.PV.6506. Fossiliferous concretions are present near the roof of the bioturbated sandstone and include remains of vertebrates represented by *Ischyrhiza chilensis* (Rajiformes, Sclerorhynchidae), *Carcharias* sp. (Lamniformes, Odontaspididae), and indeterminate osteichthyan vertebrae. Invertebrates are represented by the bivalves *Cardium* (*Bucardium*) *acuticostatum* (D'Orbigny), *Cymbophora araucana* (D'Orbigny), as well as indeterminate gastropods. Above the concretions there are few lenses comprised by fine and well-sorted conglomerates, with clasts smaller than 5 mm, that are partially fossiliferous. Reworked shark teeth of indeterminate odontaspidids have been found in this level. The top of the sandstones is eroded.

The section exposed on Pelluhue correlates with the lower levels of the section exposed in Las Tablas Bay and Cocholgüe (Stinnesbeck, 1986: fig. 3), the type and paratype locality of the Quiriquina Formation, respectively. This is concordant with the previous observation of Tavera (1988), and indicates that the fossil-bearing level that includes the studied specimen is early late Maastrichtian in age.

3. Materials and methods

The observed size difference of vertebrae from the same anatomic position was the first criterion used to separate elements
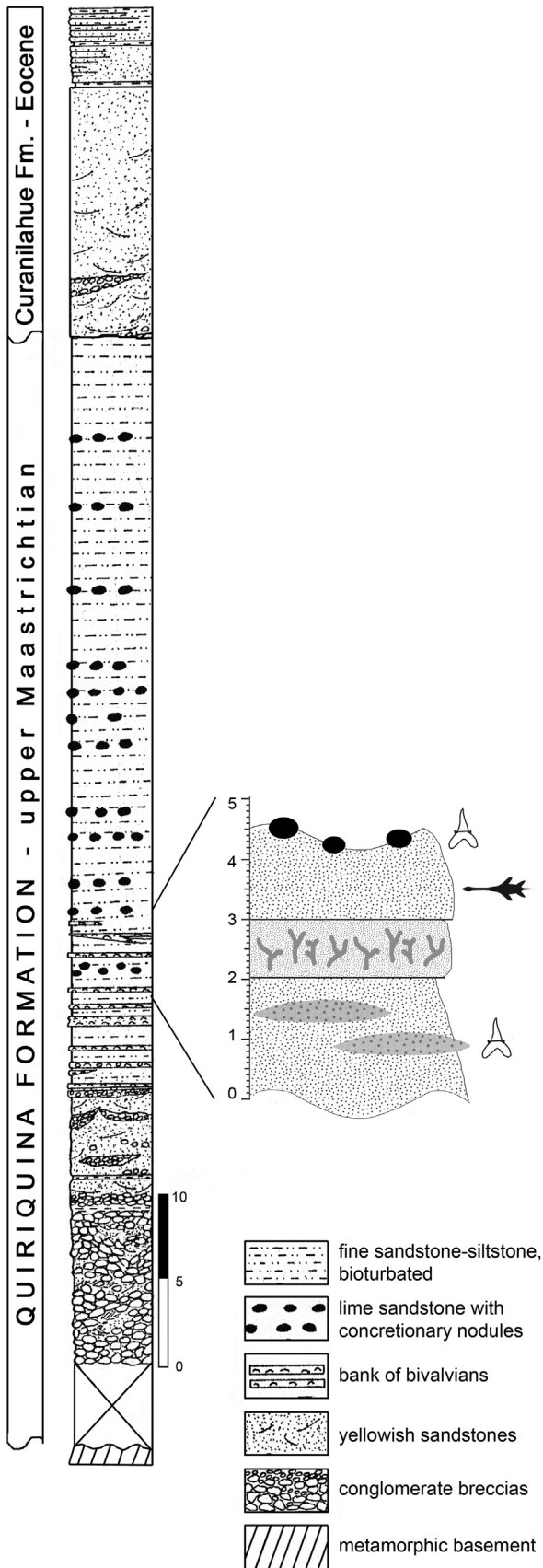
Fig. 2. General stratigraphic column of the Quiriquina Formation in its type locality of Las Tablas, Quiriquina Island, indicating the relative position of the small section exposed at Pelluhue, where the studied specimen was recovered. Modified from Stinnesbeck (1986).

of each skeleton included in the composite mounting. In addition, the following criteria were used:

3.1. Deformation by stress

Several posterior cervicals and anterior caudal vertebrae can be distinguished by being deformed, with a lateral shear that caused the posterior articular facets to be displaced left with respect to the axis, in addition to showing vertical compression. This is exclusively observed in the larger centra, while the set of smaller vertebrae is not deformed.

3.2. Mineralization of the bones

Each specimen shows different mineralization. SGO.PV.6506 is the larger (based on vertebrae size) and has dorsal elements that are dorso-ventrally crushed. The thinner elements are very brittle and can be easily broken. In contrast, SGO.PV.6507 shows centra and thin portions of the neural spines that are harder and less fragile. Even though they were found close together, the different mineral replacement is different reveals the stratigraphic provenance for each specimen. The same criterion was useful to associate the girdle elements. After segregation of the vertebral elements belonging to each specimen, they were re-ordered based on their relative anatomic position, comparative size, and best match of the articular facets. As a result, we can assign 50 vertebrae belonging to a long-necked elasmosaurid specimen (SGO.PV.6506), and 35 (including the atlas-axis) belonging to a second different specimen of an indeterminate aristonectine (SGO.PV.6507).

3.3. Graphic bivariate analysis

O'Keefe and Hiller (2006) recognized a broad trend towards elongation of the cervical centra in the mid-section of the column and especially in extremely long-necked specimens. Regretfully, the SGO.PV.6506 only preserves 12 cervicals, six of them dorso-ventrally crushed and laterally deformed, making it difficult to interpret the relative position of each vertebra along the neck or get accurate cervical measurements.

The cervical proportions of the SGO.PV.6506 were evaluated using a bivariate graphic analysis following O'Gorman et al. (2013). The indices here considered follow those defined by Welles (1952), particularly the height/length ratio (HI = $100^*H/L$), the breadth/length ratio (BI = $100^*B/L$), as well as the rate of vertebral elongation (VLI = $100^*L/(0.5^*(H + B))$). SGO.PV.6506 represents a near adult individual; because of this, comparisons were included adult representatives from the Upper Cretaceous of North America, particularly *Hydrotherosaurus alexandrae*, *Elasmosaurus platyurus*, as well as *Callawayasaurus colombiensis*, from the Upper Cretaceous of Colombia (measurements of these specimens were taken from Welles 1943, 1952, 1962). Data regarding adult elasmosaurids from the WBP were included, particularly the indices of the holotype of *Tuarangisaurus keyesi* from the Maastrichtian of New Zealand, as well as those of SGO.PV.957, an adult specimen referred to *Aristonectes* sp. by Suárez and Fritis (2002) and later referred to a new species, *A. quiriquinensis* by Otero et al. (2014). No phylogenetic analysis was attempted since SGO.PV.6506 is fragmentary, making it scoreable for few characters.

Institutional abbreviations—DM, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; MUCPv, Museo de Geología y Paleontología de la Universidad del Comahue, Colección de Paleontología de Vertebrados, Neuquén, Argentina; MLP, Museo de La Plata, Argentina; MML-PV, Museo Municipal de Lamarque, Río Negro, Argentina; CM, Canterbury Museum, New Zealand., NZGS CD, New Zealand Geologic Survey; SGO.PV., Paleontología de

Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; OU, Otago University, Department of Geology, Dunedin, New Zealand; ZPAL, ZPAL R., Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Institutional abbreviations—**SGO.PV.**, Museo Nacional de Historia Natural, Santiago, Chile.

Anatomical abbreviations—**af**, acetabulum facet; **ak**, anterior keel; **bcr**, broken cervical rib; **bm**, bite mark; **c**, concavity; **c19**, ninetenth last caudal centrum; **car**, caudal rib; **cc**, caudal centra; **cm**, caudal mass; **cr**, cervical rib; **de**, dorsal end; **dg**, dorsal groove; **ff**, femoral facet; **fha**, facets for the haemal arches; **fna**, facets for the neural arches; **fp**, fused pedicel; **if**, ischium facet; **lc**, last caudal element; **lcr**, last caudal rib; **lns**, last neural spine; **lrf**, last rib facet; **na**, neural arch; **nc**, neural canal; **np**, notochordal pit; **ns**, neural spine; **pd**, pedicel; **pk**, posterior keel; **pna**, pedicels of neural spines; **poz**, postzygapophyses; **prz**, prezygapophyses; **rf**, rib facet; **vf**, ventral foramina; **vk**, ventral keel; **vn**, ventral notch.

4. Systematic paleontology

Sauropterygia Owen, 1860
Plesiosauria de Blainville, 1835
Family Elasmosauridae Cope, 1869 (sensu Ketchum and Benson 2010)

Elasmosauridae indet.
(Fig. 3)

Material—SGO.PV.6506. Postcranial skeleton preserving 12 posterior cervical vertebrae, 10 dorsals, and 28 caudals (with two probably missing centra), and a fragmentary pelvic girdle including part of one pubis and two ilia.

Locality, Horizon and Age—Mariscadero, south of Pelluhue, central Chile. Lower levels of the Quiriquina Formation, lower upper Maastrichtian.

Remarks—Relevant morphologic characters include nine posterior-most caudal vertebrae with dorsal surface having two pairs of deep, subtriangular articular facets, two in the antero-dorsal half of each centrum for its respective neural arch, and two over the postero-dorsal half for the neural arch of the successive vertebra. The ilia show a unique morphology, a slender and recurved shape with a laterally expanded ventral portion. The ischium facet is almost twice the length of the acetabular facet, and an internal (dorsal) groove along the shaft extends from between the ischial and acetabular facets into the mid of the shaft. The caudal-most vertebrae have neural spines that are angled anteriorly with neural arches that overlap the immediately anterior centrum. The last 19 caudal vertebrae have facets for haemal arches. There are three additional successive caudals, giving a total of at least 22 caudal vertebrae with facets for haemal arches. There are well-fused neural arches until the last nine caudal centra, and reappearing fused in final three centra. Caudal ribs are present until the final eight centra. Haemal arches are present until the final two

centra, being all of them settled under the articular surfaces of each pair of successive centra. The anterior caudal centra have an oval articular outline that is broader than high. The caudal-most centra are reduced in size and have hexagonal articular outlines. Two parallel ventral keels between each facet for haemal arches are present between the seventh and fourteenth (last) caudal centra. There is a gradual reduction in length, breadth and height of the caudal-most centra. The last caudal centra have neural arches that are anteriorly displaced and probably conforming a pygostyle in the adult.

5. Description

Anatomical position of each vertebra—Cervical vertebrae were recognized by having a typical bilobed shape in articular view (Gasparini et al., 2003b) and by the presence of low facets for the cervical ribs in lateral view. Dorsal centra were identified by the presence of two dorsal facets for the neural pedicels and by having nearly circular articular outlines. Anterior caudal vertebrae were identified by the presence of dorso-ventrally compressed centra with marked lateral facets for the ribs as well as neural facets.

Posterior cervical vertebrae—These are preserved in three non-successive series. The anterior group has five, probably successive and well-preserved centra. A sixth cervical is isolated and much deformed, while the 6 posterior-most cervicals are the best preserved. Cervical centra (Fig. 4) are broader than high and as high as long. In articular view, they have a bilobed outline with a well-marked ventral notch, and bear platycoelous facets. In lateral view, they have profuse striations near the articular margins, and lack lateral keels. The ventral surface also bears similar striations near the articular facets, having reduced foramina with a laterally compressed oval contour, and separated by a conspicuous bridge that turns into a sharp keel in the more anterior centra. Cervical ribs are broken, but had oval to blade-like proximal cross-section depending on the break point. The ribs are slightly displaced into the posterior half of the centra. Neural arches are very incomplete, but a few of them show that the neural canal is reduced in diameter. The last cervical centra are very deformed and slightly crushed. No pectoral vertebrae are recognized.

Dorsal vertebrae—Ten dorsal centra are preserved, most of them crushed. In ventral view they bear a medial constriction, while in dorsal view the facets for the neural arches occupy almost all the length of each centrum. Neural pedicels are broken, thereby indicating that these were fused to each centrum. The strong deformation suffered in the anterior dorsals makes it difficult to establish accurate measurements for each vertebra.

Anterior caudal vertebrae—Seven centra are identified as caudals based on the migration of the rib facets into the centrum and by the absence of facets for the haemal arches. Evidence of distinctive lateral facets for the ilium attachment is not observed in any centrum, indicating that no sacral centra are present. This section comprises two probably successive but poorly preserved centra with fused neural arches, as well as a second group of five, likely

Fig. 3. Elasmosauridae gen. et sp. indet. SGO.PV.6506. Partial postcranial skeleton including the complete caudal-most portion. Pelluhue, central Chile. Lower levels of the Quiriquina Formation, lower upper Maastrichtian. Scale bar equals 500 mm.
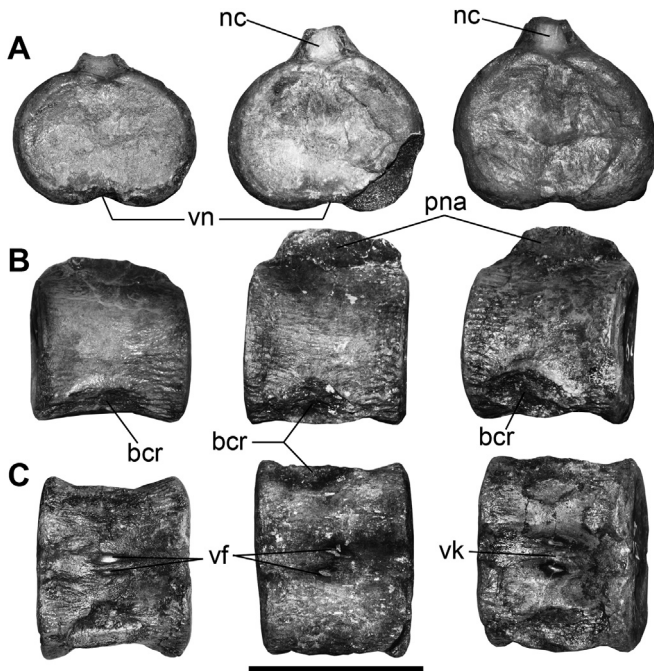
Fig. 4. Elasmosauridae gen. et sp. indet. SGO.PV.6506. Detail of cervical vertebrae. A, anterior view; B, right lateral view; C, ventral view. Scale bar equals 100 mm.

successive vertebrae (based on their matching articular faces and relative size). Anterior caudal centra have a more marked dorsoventral compression compared with dorsal elements, although, the anterior-most caudals are strongly crushed. The anterior caudal centra are broader than high and higher than long, with an oval articular outline. The latero-dorsal surface between the pedicels of the neural arch and the rib facet is slightly concave, becoming flat in the posterior centra. Several caudal vertebrae have concave rib facets, indicating that the ribs were not fused to the centrum. Interestingly, a few centra preserve part of their respective ribs still attached, showing a deep suture line (Fig. 5A—C). Each centrum has rib facets that occupy almost the entire length of the vertebral body. The posterior elements progressively acquire a postero-ventral sinusoidal edge of the articular facets that merge with the facets for the haemal arches from the successive caudals.

Posterior caudal vertebrae—Nineteen successive caudal vertebrae (Fig. 5D—F) are determined to belong to the posterior-most axial elements. All of them have two pairs of ventral facets (two anterior and two posterior) for articulation of haemal arches. In the anterior centra these ventral facets are shallow, becoming even more excavated to the posterior end, then, acquiring a larger and more rounded contour in the successive posterior centra. The largest haemal facets can be observed between twelfth and ninth to last caudals. Each posterior caudal has anterior articular facets larger than the respective posterior facet, giving them a trapezoidal outline in dorsal view (Fig. 6A). The anterior caudal centra have oval articular outlines, being broader than high and as high as long. The rib facets have oval contours, and are dorso-ventrally compressed in the anterior caudals and become more rounded between the thirteenth and ninth last centrum. All of these facets are slightly excavated and located over the lateral midline of the centra. They have oval articular facets, while the preserved ribs are flattened. The rib facets fade in posterior elements, having a last, incipient facet in the last eight centra.

The surfaces of the articular facets of the anterior caudals are shallowly amphycoelous, becoming strongly amphycoelous starting at the tenth centrum. The last centra (especially the last four)

show a deep notochordal pit in both articular faces. Their respective neural arches are poorly preserved, but several pedicels fused to the centrum are still attached. These show that the neural arches were anteriorly displaced with respect to the middle half of the centrum. The tenth to last centrum preserves a broken pedicel that occupies most of the dorsal length of the vertebral body, while a small pair of facets appears on the dorso-posterior articular margin, leaving a small gap without neurocentral contact over the dorsal surface of these vertebrae. These two pairs of complementary facets appear in each successive centrum starting from the ninth to tenth pair of centra, and articulate with a single neural arch that is anteriorly displaced and overlap into the immediately anterior centrum. Most of the overlapped arches are not fused, based on the excavated facets observed since the ninth last centrum (Fig. 7A). The exceptions to this are the fused pedicel preserved in the posterior half of the sixth to last caudal, as well as the fused pedicel in the anterior half of the third to last caudal. The last nine terminal caudal vertebrae are laterally compressed with respect to the rest of the caudals. These last caudal vertebrae acquire a slightly hexagonal articular face, which becomes variable in the smaller last centrum (Fig. 6B—E).

Dorsal and anterior caudal neural spines—Two types of neural arches can be distinguished. One type is smaller with thickened dorsal ends. These neural arches are referred to the specimen SGO.PV.6507 (indeterminate aristonectine). The larger neural spines matches with the length of dorsal centra of the specimen SGO.PV.6506, and are subsequently considered as part of that specimen. These dorsal neural spines (Fig. 7A, B) are blade-like, laterally compressed, and lack dorsal thickening. Other much similar spines (but smaller in size) match the length of posterior caudal centra as well as their respective neural pedicels. These spines are also blade-like but bear a distinctive anterior and posterior keel. The prezygapophyses are poorly preserved being difficult to evaluate their shape, although, postzygapophyses are short and they do not extend posteriorly to the blade of the spine. The neural pedicels of these spines are reduced and match with the respective scars near the fourteenth posterior caudal (Fig. 7C—E).

Pelvic girdle—The right ilium is almost complete, being slender, with the medial part of the shaft recurved and its ventral portion expanded, keeping an oval cross-section dorso-ventrally that is higher than laterally broad. The ventral end is noticeably broader than the rest of the shaft (Fig. 8A—D) and has a ventral (internal) groove that extends from between both ischial and acetabular faces into the shaft. The internal surface of the dorsal end bears a rugosity that indicates the sacral attachment of the ilium to the axial skeleton. The left ilium (Fig. 8E, F) only preserves its ventral portion, which is ventrally eroded and bears a single triangular bite mark over its lateroventral surface. The right pubis preserves just the acetabular portion (Fig. 8G, H), which shows an asymmetric length of the articular facets. The smaller articular facet is interpreted as the facet for the ischium whereas the larger one is for the femur. Most of the outline of the pubis is lost.

Tooth—A single tooth was recovered (Fig. 8I). This tooth bears soft ridges over the labial enamel and has an oval cross-section. The root is massive and slightly shorter than the crown. Since the other specimen from the same site (SGO.PV.6507) is an indeterminate aristonectine, we compared the tooth with representatives of that clade. The teeth of *Morturneria seymourensis* Chatterjee and Small, 1989 from the upper Maastrichtian of Antarctica differ by being very slender with marked labial ridges. These teeth are similar to *Aristonectes quiriquinensis* Otero et al. (2014: fig. 7B—D). Finally, the holotype of *Kaiwhekea katiki* Cruickshank and Fordyce (2002) from the lower Maastrichtian of New Zealand has slender teeth but these cannot be directly compared since none of them have enough
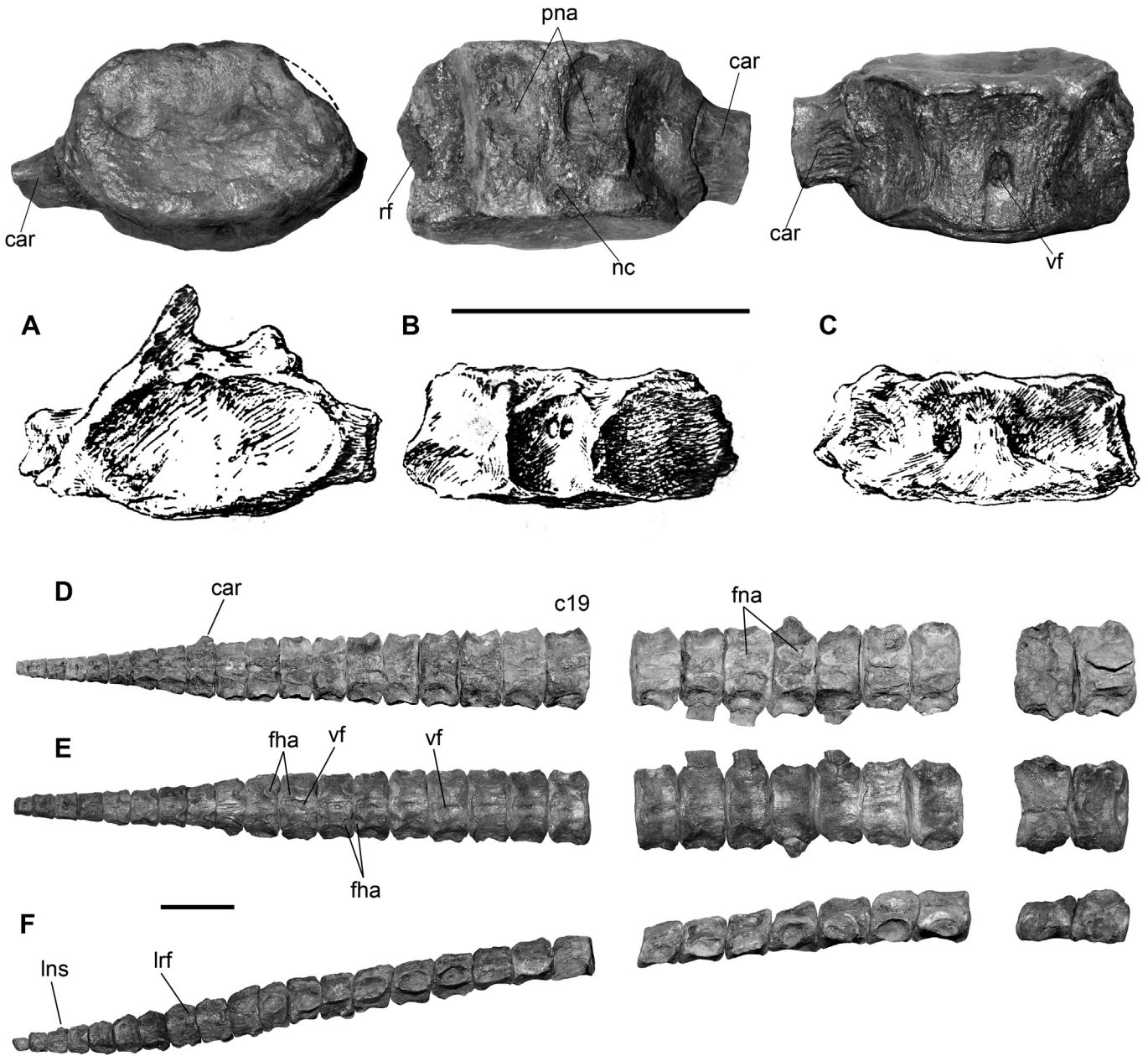
Fig. 5. Elasmosauridae gen. et sp. indet. Comparison of the anterior caudal vertebra (c22) of the SGO.PV.6506 (above) and the caudal vertebra (originally regarded as cervical) described by Broili (1930) and referred to 'Cimoliasaurus' andium Deecke. A, anterior articular view; B, dorsal view; C, ventral view. Elasmosauridae gen. et sp. indet. SGO.PV.6506. D, dorsal view of the caudal portion. E, ventral view of the same. F, right lateral view. All scale bars equals 100 mm.

preservation of the enamel. These observations suggest that the teeth of aristonectines can be distinguised by their crowns, which are comparatively higher and thinner than those of other elasmosaurids. Aristonectine teeth also lack prominent ridges in the labial and lingual enamel. These characters are observed among cryptoclidids such *Cryptoclidus* (Brown, 1981: fig.5), *Muraenosaurus* (Brown, 1981: fig. 19) and *Tricleidus seeleyi* (Brown, 1981: Fig. 24), although, in the two first the labial face lack striations, while the crown of *T. seeleyi* is comparatively broader than that of *M. seymourensis* and *A. quiriquinensis*. Because of this, we do not refer the tooth to the indeterminate aristonectine SGO.PV.6507, and instead associate it with SGO.PV.6506.

Phalanges—Five isolated phalanges were recovered. All of them are small, short, and dorso-ventrally flattened, with dorso-ventrally compressed articular facets, expanded only in axial direction, and having oval articular outline (Fig. 8K–O). Few of them bear scavenging marks, probably made by odontaspidid sharks. Based on the well-known phalanges of the genus *Aristonectes*, which are elongated, without dorsoventral compression, and spool-shaped with expanded polygonal articular facets (Gasparini et al., 2003b), we include the recovered phalanges among the remains of the SGO.PV.6506. Interestingly, these phalanges match with those of the forelimb described by Broili (1930: fig. 1) that he referred to "*C.*" *andium* with doubts about the generic identification.

6. Ontogenetic observations of SGO.PV.6506

The specimen has cervical and dorsal vertebrae with neural spines strongly fused to the centra. In contrast, caudal vertebrae have a low degree of neurocentral fusion and also lack fusion
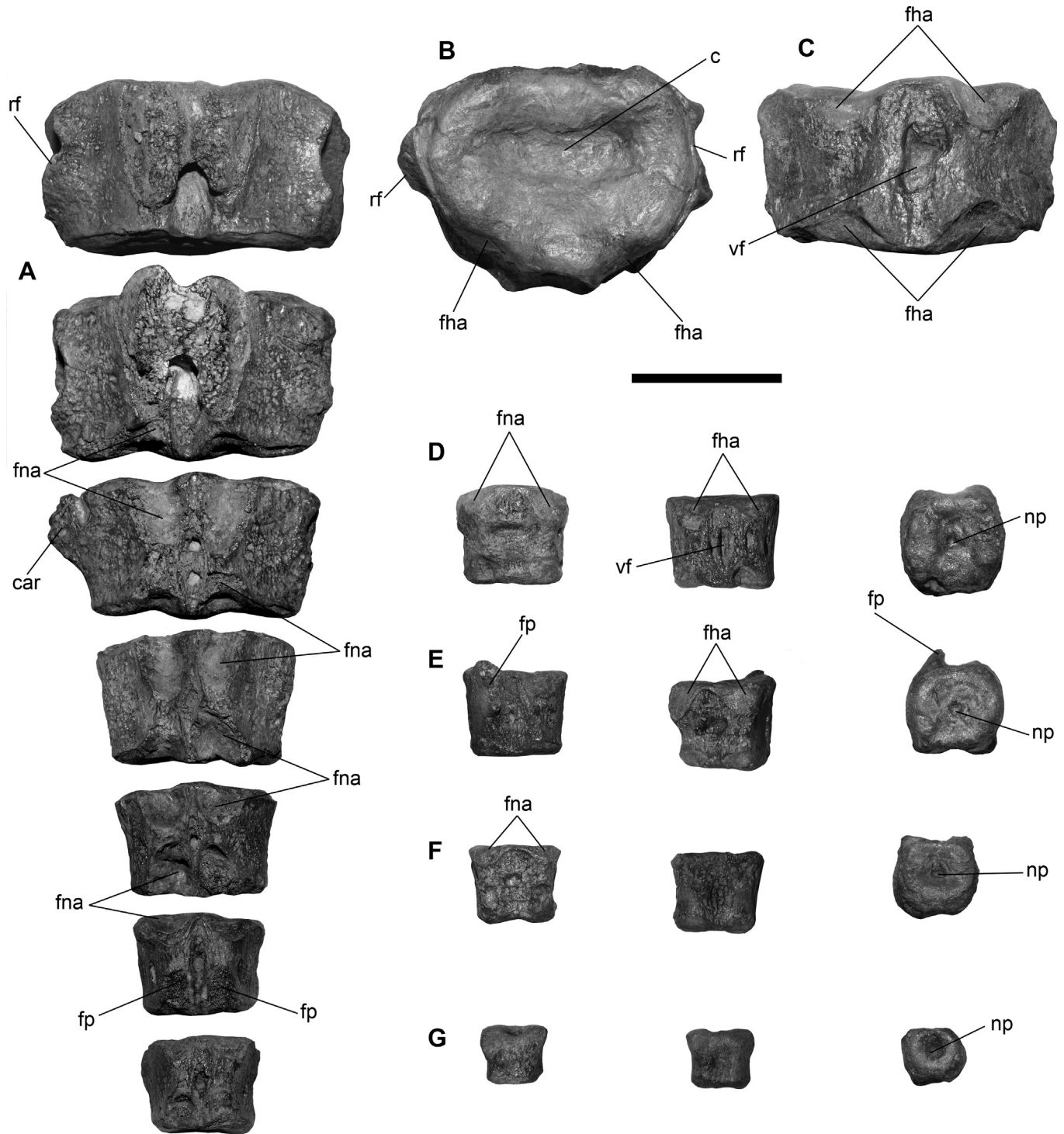
Fig. 6. Elasmosauridae gen. et sp. indet. SGO.PV.6506. Caudal-most centra. A, c11 to c5 in dorsal view. Last four caudal centra in ventral, anterior, and dorsal views, respectively. B, c4; C, c3; D, c2; E, last caudal centrum (c1). Scale bar equals 100 mm.

between the caudal ribs and the centra. Anterior caudal vertebrae have neural arches fused to the centrum, whereas in posterior caudals the neural arches are fused from the tenth to the last centrum, non-fused from the ninth to fourth to last, and fused again in the final three caudals. Also, cervical ribs are partially fused in anterior caudals, but at least one centrum has a partially fused rib with the opposite rib facet visible, indicating that fusion could occur in an asymmetrical way in few centra. Despite the fact that

dorsal vertebrae support an adult stage based on the criteria of Brown (1981), the non-fused caudal elements suggest a near adult stage. This specimen verifies a pattern of fusion from the anterior to posterior end as in ichthyosaurs (Kear and Zammit, 2014), and in different from the fusion pattern seen in some other reptiles, such as crocodiles (Brochu, 1996).

The caudal-most elements of the SGO.PV.6506 (last nine vertebrae) have two pairs of deep facets for the neural arches,
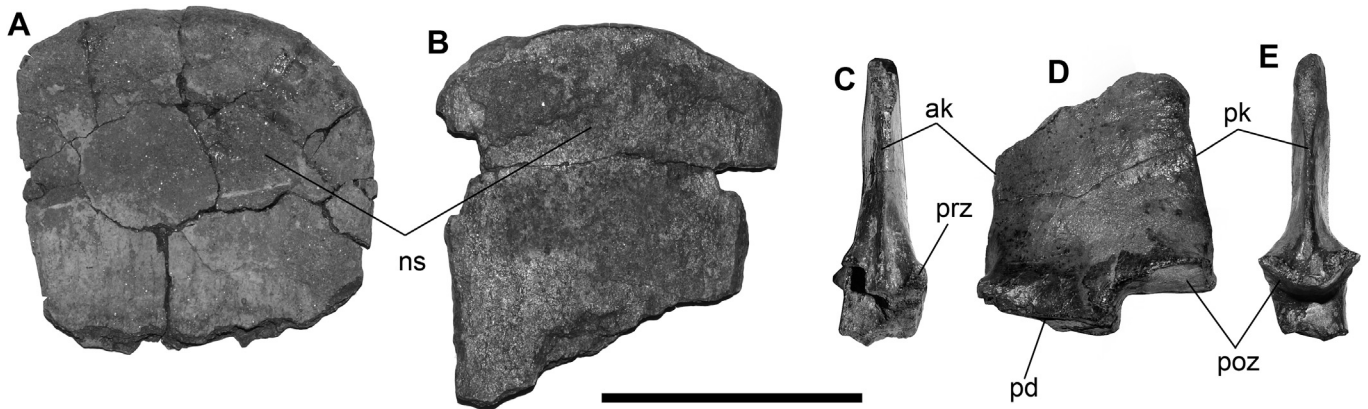
Fig. 7. Isolated neural spines referred as part of the SGO.PV.6506. A, B, putative dorsal neural spines in left lateral view; C, caudal neural spine in anterior view; D, same in left lateral view; E, posterior view. Scale bar equals 50 mm.

which allow their articulation in an intermediate position between two successive centra. Noteworthy, the sixth last centrum has pedicels fused to the posterior pair of facets, while in the third last centrum the pedicels remain fused to the anterior pair of facets. This suggests that in adult and old individuals, all the pedicels should be fused to the centra in a pygostyle-like structure that confers rigidity to the caudal end. Pygostyles are documented among elasmosaurids (Kubo et al., 2012) and it seems to be present in other elasmosaurids from the WBP (Gasparini and Goñi, 1985). They are also documented amongst other plesiosaurians. *Umoonasaurus demoscyllus* Kear et al. (2006) from the Aptian–Albian of Australia has a pygostyle-like caudal end comprising at least five fused centra. A similar condition is present in *Brancasaurus brancai* Wegner, 1914, from the Valanginian of Germany, showing that this structure appear in several different xenopsarians.

7. Comparison with other elasmosaurids from the WBP

SGO.PV.6506, although fragmentary, has morphologic features in the ilium and the anterior caudal centra that allow it to be differentially diagnosed from all known aristonectines, as well as from other non-Pacific Weddellian elasmosaurids with known ilia. It differs from *Aristonectes* sp. in the absence of anterior caudal centra with distinctive octagonal articular outline (determined by the two dorsal facets for the neural pedicels, each lateral facet for the ribs, and the flattened ventral surface of the centrum). This feature is recognized in the holotype of *Aristonectes parvidens* Cabrera, 1941 from the upper Maastrichtian of Chubut, Argentina (Gasparini et al., 2003b), in the juvenile postcranial skeleton (SGO.PV.260) from the upper Maastrichtian of central Chile referred to *Aristonectes* sp. (Otero et al., 2012; Otero and O'Gorman, 2013), and in the juvenile specimen MLP 89-III-3-2 from the late Maastrichtian of Antarctica referred to *Aristonectes* cf. *parvidens* (O'Gorman et al., 2013). On the other hand, the anterior caudals of SGO.PV.6506 have oval articular facets that are broader than high. Other postcranial differences between SGO.PV.6506 and SGO.PV.260 (referred to *Aristonectes* sp.) are present in the ilium, which is very slender, contrary to the massive distal end in the ilia of SGO.PV.260 (Fig. 9A, B).

Comparison with the lectotype of *Mauisaurus haasti* (DM R1529) from the upper Campanian of New Zealand designated by Welles (1962) shows that the ilium is very different to that of SGO.PV.6506 (see below). DM R1529 has a thick ilium (Fig. 9C) with a massive ventral end, while the rest of the shaft has a cross-section slightly different to the breadth of its ventral end. The dorsal end of DM R1529 is absent, making further comparisons impossible.

Despite this, the ilia of both taxa differ by presence of the internal groove on SGO.PV.6506, as well as by the more gracile shaft of SGO.PV.6506.

Hiller et al. (2005) described another relatively complete juvenile elasmosaurid, referred to *M. haasti* (CM Zfr 115), from the upper Campanian of New Zealand. Comparison of SGO.PV.6506 with CM Zfr 115 shows different proportions of the cervical vertebrae. CM Zfr 115 has centra that are more reduced in height, although this can be explained due its juvenile stage. Dorsal vertebrae as well as their neural arches are also similar in both specimens. The most remarkable differences are in the caudal vertebrae. In CM Zfr 115, the caudal centra have subtriangular facets for the neural arches which are slightly displaced anteriorly, although no evidence of a second pair of facets was observed in any caudal centra, not even in the smallest available (RAO, pers. obs., 2013). This strongly suggests that the presence of neural arches displaced between each pair of caudal-most centra is not present in CM Zfr 115. In addition, even though the anterior caudals of SGO.PV.6506 are slightly crushed, they differ from those of the CM Zfr 115 in having a more oval outline.

MML-PV4 is one of two specimens recovered from the upper Maastrichtian at Salinas de Trapalcó, Río Negro, Argentina (Gasparini et al., 2003a). This specimen was described as having an ilium and caudal vertebrae preserved, although the ilium was a misidentified pectoral rib (J.P. O'Gorman, pers. comm., 2013). In CM Zfr 115, the caudal vertebrae have a semi-oval articular outline, but they are comparatively higher in the mid portion (Gasparini et al., 2003a: fig. 3), which differs from the strongly oval outline of the same elements of SGO.PV.6506. The caudal vertebrae are enough different between MML-PV4 and SGO.PV.6506 to separate them (Fig. 9A, D).

Postcranial remains that probably belong to a single individual collected from the middle to upper Maastrichtian in Marambio (=Seymour) Island, Antarctica, were described by Fostowicz-Frelik and Gaździcki (2001). The specimen was considered to be related to *Mauisaurus* based on the presence of a femur with a prominent and hemispherical head. These remains include caudal vertebrae which are small, broader than high and high than long, and has octagonal articular outline (Fig. 9E), suggesting close affinities to aristonectines (Gasparini et al., 2003b; O'Gorman et al., 2013; Otero and O'Gorman, 2013). SGO.PV.6506 is different in having anterior caudal vertebrae with oval articular faces.

Another relevant postcranial specimen from late Maastrichtian levels of New Zealand was described by Hiller and Mannering (2005). This specimen (CM Zfr 145) includes most of the skeleton with the exception of the neck and the skull. CM Zfr 145 has distinctive caudal vertebrae with octagonal outline, equally broad
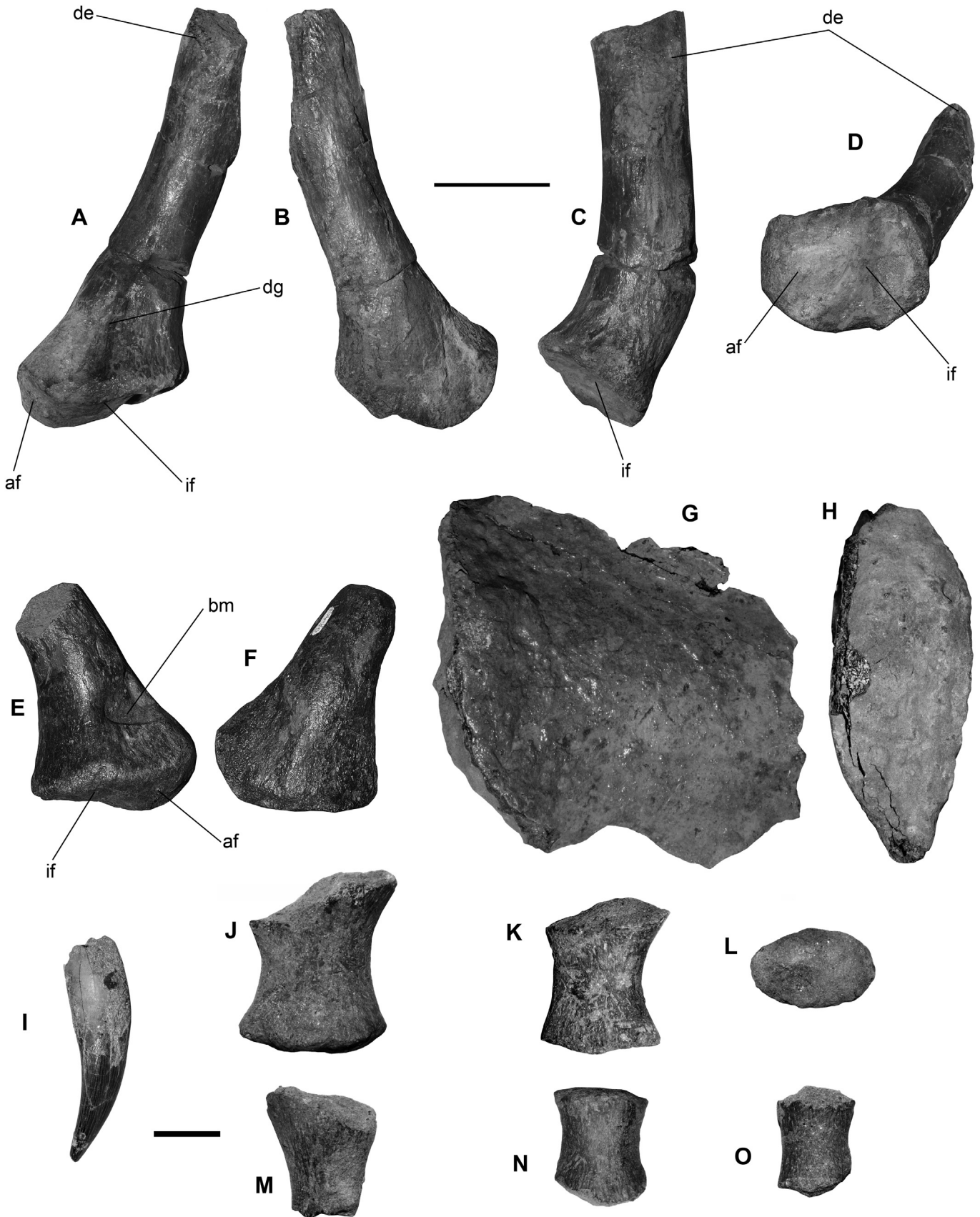
Fig. 8. Elasmosauridae gen. et sp. indet. SGO.PV.6506. A, right pubis in dorsal view. B, same in ventral view. C, internal view. D, articular view of the ventral end. E, fragmentary left ilium in dorsal view. F, ventral view. G, fragmentary right pubis in dorsal (internal) view. H, same in articular (acetabular) view. I, isolated tooth. J, large isolated phalanx in dorsoventral view. K, another phalanx in dorsoventral view. L, same in proximal articular view. M–O, different phalanges in dorsoventral view. Scale bar equals 100 mm in A,H; 10 mm in I–O.
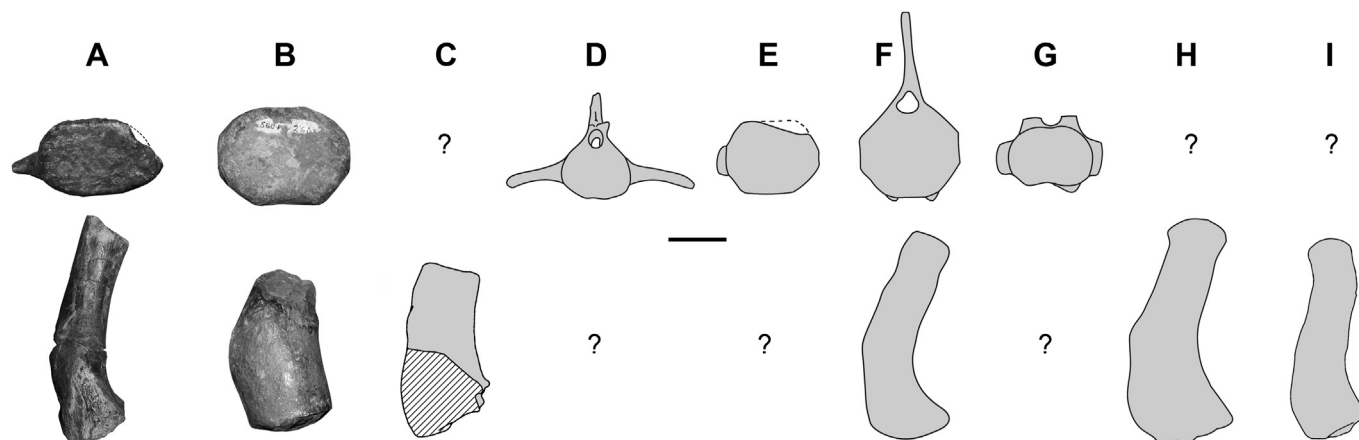
Fig. 9. Comparison of caudal vertebrae and ilia of different elasmosaurids from the Upper Cretaceous of the WBP. A, Elasmosauridae gen. et sp. indet. (SGO.PV.6506), near adult specimen. Pelluhue, central Chile, Quiriquina Formation, lower upper Maastrichtian. B, *Aristonectes* sp. (SGO.PV.260, referred), juvenile specimen. Quiriquina Island, central Chile, Quiriquina Formation, late Maastrichtian (modified from Otero et al., 2012). C, *Mauisaurus haasti* Hector, 1874 (DM R1529, lectotype designated by Welles, 1962). Jed River, Gore Bay, New Zealand, Conway Formation, middle Campanian. D, Elasmosauridae indet. (MML-Pv4), adult specimen. Salinas de Trapalcó, Río Negro, Argentina. Jagüel Formation, upper Maastrichtian (modified from Gasparini et al., 2003a). E, Elasmosauridae indet. (ZPAL R.8/1), sub-adult specimen. Seymour Island, Antarctica, López de Bertodano Formation (lower levels), middle to upper Maastrichtian (modified from Fostowicz-Frelik and Gaździcki, 2001). F, Elasmosauridae indet. (CM Zfr 145), young adult specimen. Waipara River, New Zealand. Conway Formation, upper Maastrichtian; G, Elasmosauridae indet. (MUCPv-92), adult specimen. Río Negro, Argentina, Allen Formation, upper Campanian to lower Maastrichtian (modified from Gasparini and Salgado, 2000); H, Elasmosauridae indet. (NZGS CD438), right ilium of an immature adult specimen. Mangahouanga Stream, New Zealand, Conway Formation, Campanian-Maastrichtian; I, Elasmosauridae indet. (NZGS 440), right ilium of a juvenile specimen. Mangahouanga Stream, New Zealand, Conway Formation, Campanian–Maastrichtian. All ilia are illustrated in lateral (external) view. Outlines of ilia on B, and I are mirrored for better comparison. Scale bar equals 50 mm.

as high, contrary to the broader than high caudal vertebrae of *Aristonectes*. Also, the CM Zfr 145 preserves the ilium, which is slender but comparatively more recurved than that of the SGO.PV.6506 (Fig. 9F).

The specimen MLP-71-II-13-1 from the upper Campanian–lower Maastrichtian of the Allen Formation, in Rio Negro, Argentina (Gasparini and Salgado, 2000) is an adult individual of small size. Interestingly, MLP-71-II-13-1 possesses caudal vertebrae with neural spines overlapping the immediately anterior centrum and facets for the haemal arches between each pair of successive caudal centra (Gasparini and Goñi, 1985). The same features are likely to be present in SGO.PV.6506, but in contrast the anterior caudal vertebrae of the MLP-71-II-13-1 have a distinctive bilobed articular outline (Gasparini and Salgado, 2000) that differs from the oval outline of the same elements in SGO.PV.6506 (Fig. 9F).

Finally, few fragmentary specimens from New Zealand can be distinguished from SGO.PV.6506. NZGS CD438 and NZGS CD440 from Maastrichtian beds of New Zealand were described by Wiffen and Moisley (1986) and referred to Elasmosauridae indet. These specimens comprise two different ilia, figured in different views. It is very probable that both specimens belong to a single taxon, and that the differences in size are consequence of different ontogenetic stages. None of them matches with SGO.PV.6506 (Fig. 9H, I).

8. Results of the graphic bivariate analysis

We have considered the SGO.PV.6506 as a near adult specimen, and therefore, cervical indices (Table 1) were compared with other adult elasmosaurid representatives instead of juveniles. The plot of the cervical indices of SGO.PV.6506 shows low dispersion in the three plots. The obtained indices exclude it from aristonectines, instead placing SGO.PV.6506 in the range of long-necked elasmosaurids, but distant from extreme forms such the genus *Elasmosaurus* (Fig. 10). Such separation becomes more evident when comparing young aristonectines and young long-necked elasmosaurids. In these cases the groups are completely separated in the

plots, and therefore, and so this technique is considered useful for distinguishing cervical vertebrae of young individuals of *Aristonectes* from young individuals belonging to other elasmosaurids (O'Gorman et al., 2013). The results of the present analysis support SGO.PV.6506 as different from *Aristonectes*, the latter being the most common marine reptile in the Quiriquina Formation, while long-necked elasmosaurids are so far scarce in the unit.

9. Affinities of the SGO.PV.6506 with the type material of "*Cimoliasaurus andium*" Deecke

Steinmann et al. (1895) provided detailed descriptions of elasmosaurid remains from the Upper Cretaceous Quiriquina Formation of central Chile made by Wilhelm Deecke. Deecke coined the species "*C. andium*" based on several different individuals. Four caudal series, mistakenly regarded as cervicals, were included within this taxon. One of the caudal series (Steinmann et al., 1895: plate III, fig. 1) belongs to the caudal-most elements and has neural arches overlapping the immediately anterior centrum, although no large, deep posterior pair of facets (neither the fusion of the half of any neural arch) is observed in any other centra as in SGO.PV.6506 (Fig. 11A–C). Moreover, Deecke's material (housed at the Geologisches und Mineralogisches Museum, Institut für Geowissenschaften, Christian-Albrechts-Universität, Kiel, Germany) shows neural arches that are well fused to the centra indicating an adult stage, whereas SGO.PV.6506 is a near adult individual. These

Table 1
Measurements of the cervical vertebral centra of the indeterminate elasmosaurid SGO.PV.6506.

Length	Height	Breadth	VLI	HI	BI
69.2	59.1	89.7	93.01	85.41	129.62
70.8	66.9	93.9	88.06	94.49	132.63
72.8	68.2	94.7	89.38	93.68	130.08
73.6	–	98.6	–	–	133.97
73.8	65.6	99.6	89.35	88.89	134.96
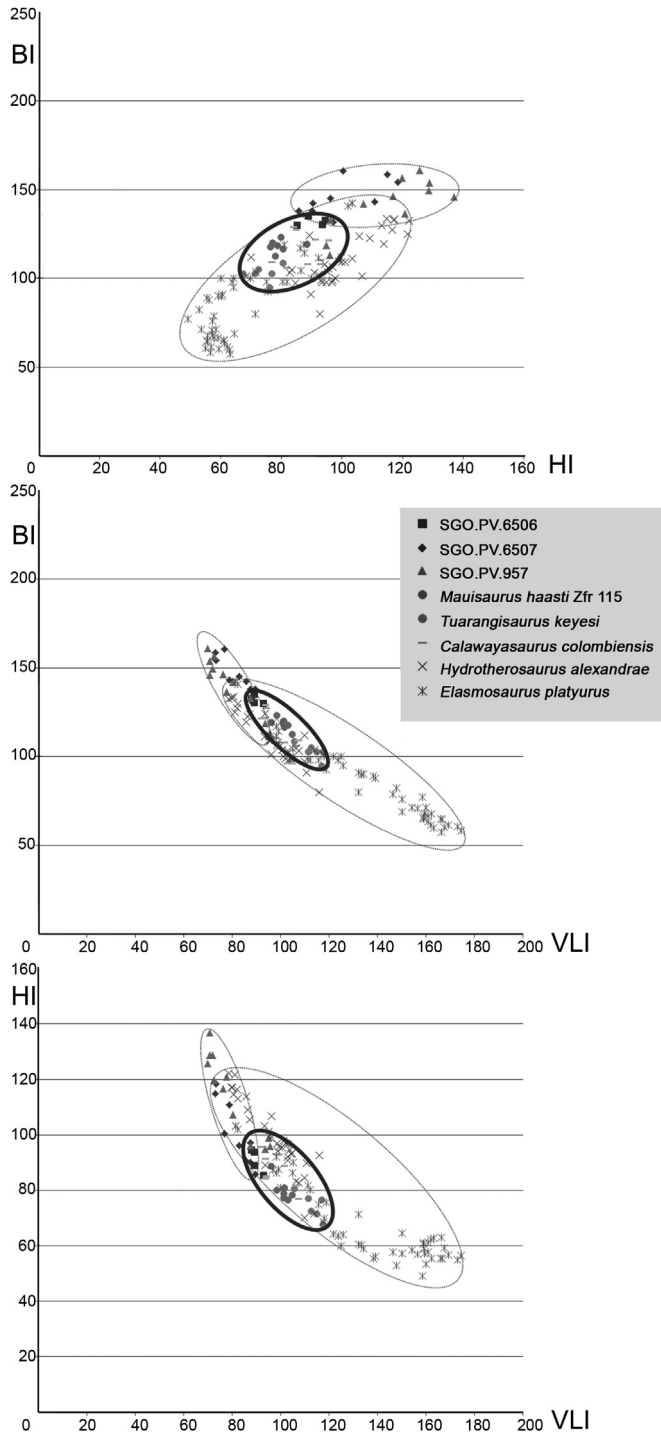
Fig. 10. Graphic bivariate analysis of the cervical vertebrae of the SGO.PV.6506. The dark oval includes all the long-necked elasmosaurids from the WBP which have scarce dispersion of their plots. Small light oval includes all the known adult aristonectines. Large light oval groups all the long-necked elasmosaurids (non-aristonectines) from the Upper Cretaceous of North America.

referred to "*C.*" *andium* Deecke 1895. The material includes anterior caudal vertebrae (originally regarded as cervicals by Broili), which are remarkably similar to those of SGO.PV.6506. Also, the short and dorso-ventrally compressed shape of the phalanges of the forelimb (Broili, 1930: fig. 1) matches the phalanges of SGO.PV.6506 (Fig. 11D).

Despite more than 160 years of plesiosaur finds in central Chile beginning with Gay (1848), the most informative specimens referable to non-aristonectine elasmosaurids are those of Steinmann et al. (1895), Broili (1930), and SGO.PV.6506. Most of the late Maastrichtian specimens from Chile that are identifiable to subfamily, genus, or species are referred to Aristonectinae (Casamiquela, 1969; Suárez and Fritis, 2002; Gasparini et al., 2003b; Otero et al., 2012: 2014) supporting that the latter were the most common elements of the marine herpetofauna along the southeastern Pacific during this lapse.

The morphologic affinities between the specimens of Steinmann, Broili and SGO.PV.6506 strongly suggest that these could belong to a single taxon or to closely related taxa. Because of this, we propose to reunite all of them under a same "*andium*" morphotype, although, any generic identification cannot be given by now due the lack of more complete specimens.
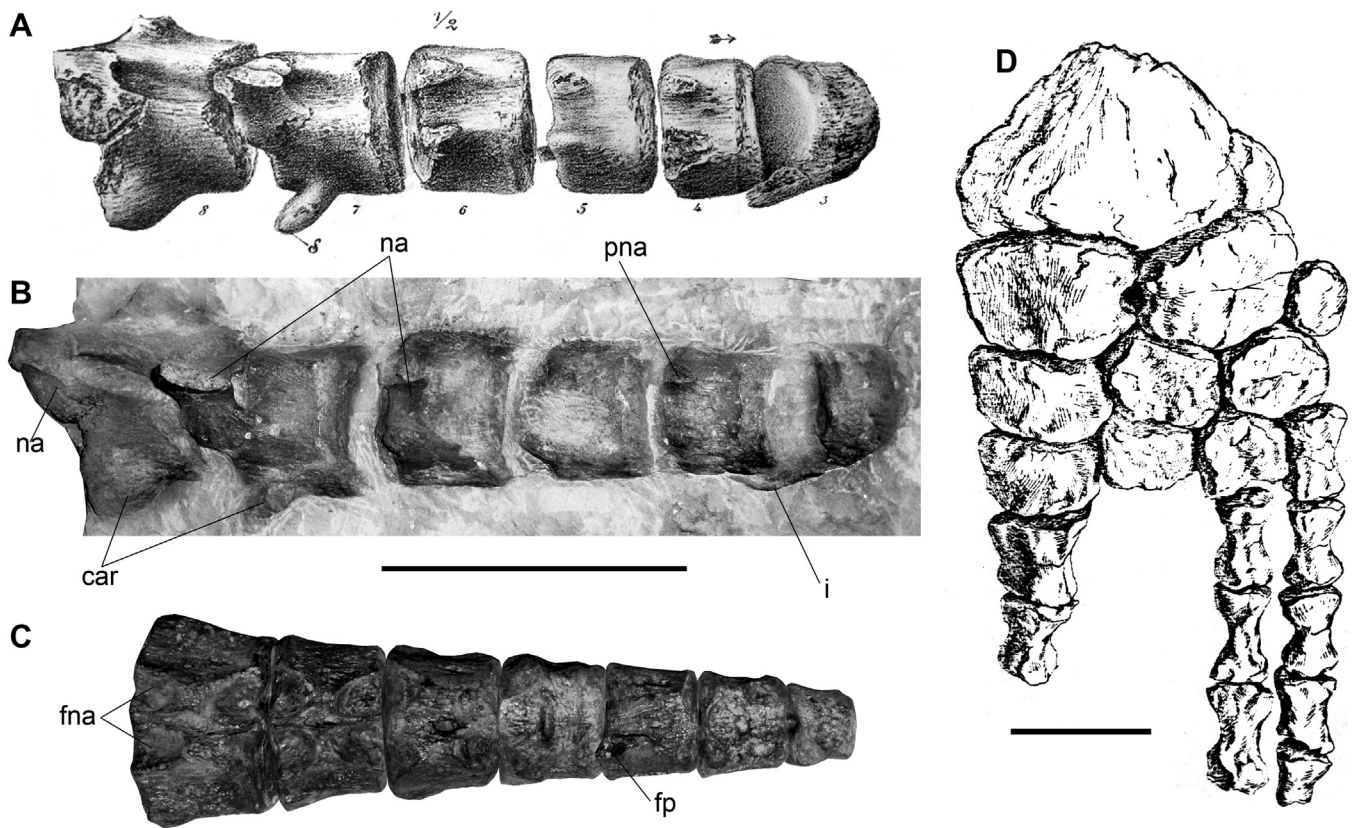
10. Functional considerations about the caudal end

Regarding to the rostral displacement of the neural arches with respect to the centra and the subsequent fusion of the vertebrae into a pygostyle-like structure, this caudal structure may have played an important role during the axial locomotion in life. Some osteological characters in the caudal vertebrae can be correlated with the presence of tail fin (Smith, 2013). A tail fluke has been described for a handful of plesiosaurs such as *Archaeonectrus rostratus* (Owen, 1865), *Seeleyosaurus guilelmiimperatoris* (Dames, 1895), some cryptocleidids (Wilhelm, 2010), and *Rhomaleosaurus zetlandicus* (Smith, 2013). Although there is no preservation of the neural and haemal arches in the SGO.PV.6506, the latero-medial compression of the last nine caudal centra, the ventral curvature of the distal end of the tail, and the interpreted presence of a pygostyle-like structure in the adult stage, support the existence of a caudal dermal fluke.

11. Taxonomic status of "*Cimoliasaurus andium*" Deecke 1895

Our study of SGO.PV.6506 shows that the 'cervical' vertebrae of "*C. andium*" (Steinmann et al., 1895: plate III, fig. 1) are indeed the caudal-most centra, and that this specimen belongs to a non-aristonectine elasmosaurid. Also, one vertebra regarded as cervical (Steinmann et al., 1895: plate I, fig. 3) unequivocally belong to an anterior caudal of *Aristonectes* sp. based on the distinctive octogonal outline in articular view. The presented evidence shows that the hypodigm of "*C. andium*" includes at least two different taxa. Besides the anterior caudal vertebra referable to *Aristonectes* sp. and the specimens of Steinmann et al. (1895: plate III, figs. 1–4) here discussed, to date the rest of the hypodigm is not diagnostic beyond family level and should remain as Elasmosauridae indet.

The genus "*Cimoliasaurus*" was recognized by O'Keefe and Street (2009) as an elasmosaurid. In addition, the family "Cimoliasauridae" sensu DeLair (1859) as well as the emended diagnosis by Persson (1962, 1963) were considered as junior synonym of the Elasmosauridae Cope, 1869 by O'Keefe and Street (2009) (because of the priority of Cimoliasauridae, this should be regarded as senior synonym). O'Keefe (2001) proposed an emended diagnosis of the "Cimoliasauridae" including *Morturneria*, *Kimmerosaurus* and their most recent common ancestor. This "Cimoliasauridae" sensu O'Keefe (2001) was later synonymized with the Aristonectidae. On the other hand, the Late Cretaceous genus *Aristonectes* Cabrera,

observations suggest that the '*andium*' taxon could be closely related to SGO.PV.6506, if they are not the same taxon on different ontogenetic stages.

In addition, the specimen from the Quiriquina Formation described by Broili (1930) (also housed at the Geologisches und Mineralogisches Museum, Institut für Geowissenschaften, Christian-Albrechts-Universität, Kiel, Germany) was tentatively

Fig. 11. A, original drawing in dorso-lateral view of the caudal portion of an elasmosaurid, regarded as the cervical vertebrae of 'Cimoliasaurus andium' Deecke by Steinmann et al. (1895: plate III, fig. 1); B, picture of the previous specimen in the same view. Specimen housed at the Geologisches und Mineralogisches Museum, Institut für Geowissenschaften, Christian-Albrechts-Universität, Kiel, Germany (picture courtesy of S. Nielsen); C, dorsal view of the last seven caudal centra of the SGO.PV.6506. D, forelimb of the specimen described by Broili (1930) and referred to 'Cimoliasaurus' andium Deecke. Scale bars equals 100 mm.

1941 from South America and Antarctica is currently demonstrated to be an elasmosaurid by the recent description of several informative specimens from the Southern Hemisphere (O'Gorman et al., 2013; Otero and O'Gorman, 2013; Otero et al., 2012, 2014; Benson and Druckenmiller, 2014). All these facts now allow the current consideration of the original "Cimoliasauridae" of DeLair, as well as all their posterior emended diagnoses, as senior synonyms of Elasmosauridae.

Regarding "C. andium", the validity of the taxon was first questioned by Colbert (1949), and subsequently considered as nomen vanum by Welles (1962) and then referred to an indeterminate elasmosaurid. Our research agrees with this, clarifying the determination of part of the specimens of the original description, although, the evidence here presented shows the existence of a likely single morphotype that can reunite most of the non-aristonectine elasmosaurids from central Chile.

12. Conclusions

SGO.PV.6506 sheds light on the still obscure hypodigm of "Cimoliasaurus andium" Deecke (in Steinmann et al., 1895). These new comparisons afford the recognition of a single morphotype of the caudal complex originally described by Steinmann et al. (1895: plate III, fig. 1) and regarded as part of the cervical vertebrae of "C. andium". The additional 'cervicals' (actually caudal vertebrae) referred to the same species (Steinmann et al., 1895: plate III, figs. 2—4) can be referred to the same morphotype. Also, the remains of a single individual described by Broili (1930) tentatively identified

as "C." andium (with doubts about the genus), comprising a forelimb, dorsal and caudal vertebrae (the latter originally regarded as cervicals), can be referred to the same morphotype by the diagnostic anterior caudal vertebrae and phalanges.

One anterior caudal vertebra referred to "C. andium" (Steinmann et al., 1895: plate I, fig. 3) is referable to Aristonectes sp., proving that at least two different taxa are included in the hypodigm. In addition, the remaining elements of the hypodigm are not diagnostic beyond family level and belong to the Elasmosauridae.

The known late Maastrichtian specimens from central Chile referable to non-aristonectine elasmosaurids are scarce. Based on the low morphologic disparity of the non-aristonectine elasmosaurids, studied here, there is reasonable evidence for referring them to a single morphotype, but for the moment, the incompleteness of the available specimens precludes formally naming this taxon. However, if further research could reveal such taxonomic determination, the "andium" species should be retained due nomenclatural priority. If this could be the case, we recommend to fix the "andium" name to the specimen comprising 6 caudal vertebrae described by Steinmann et al., 1895 (plate III, fig. 1).

pictures of the type material of '*C. andium*' hosted in Kiel, Germany. Thanks to Karina E. Buldrini and Jhonatan Alarcón (Museo Nacional de Historia Natural, Santiago, and Red Paleontológica U-Chile) for the remarkable work on the preparation of the specimen. Dr. Paul Scofield and Dr. Norton Hiller (Canterbury Museum, Christchurch, New Zealand) are especially acknowledged for the access to the specimen CM Zfr 115 and for valuable discussions about Weddellian plesiosaurs. James F. Parham (California State University, Fullerton) and Jacobus P. Le Roux (Universidad de Chile) helped to correct the English and provided valuable comments that improved the manuscript. Dr. Benjamin Kear (Uppsala University, Sweden) and Dr. Frank R. O'Keefe (Marshall University, US) are especially acknowledged for the critical review of the manuscript and valuable comments that helped to improve it.

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