

# A new record of an aristonectine elasmosaurid (Sauropterygia, Plesiosauria) from the Upper Cretaceous of New Zealand: implications for the *Mauisaurus haasti* Hector, 1874 hypodigm

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O'GORMAN, J.P., OTERO, R.A. & HILLER, N., 2014. A new record of an aristonectine elasmosaurid (Sauropterygia, Plesiosauria) from the Upper Cretaceous of New Zealand: implications for the *Mauisaurus haasti* Hector, 1874 hypodigm. *Alcheringa* 38. ISSN 0311-5518

An indeterminate aristonectine elasmosaurid is recorded from a lower Maastrichtian bed of the Conway Formation, Waipara River, South Island, New Zealand. The described specimen (CM Zfr 104), previously considered part of the hypodigm of *Mauisaurus haasti*, came from the upper part of the *Alterbidinium acutululum* biozone, the same zone from which the only well-known aristonectine from New Zealand, *Kaiwhekea katiki*, is recorded. The cervical vertebrae of CM Zfr 104 have the same distinctive features (i.e., with extremely broad rather than long centra) as those from previously recorded juvenile aristonectines from Argentina, Chile and Antarctica. This new record is congruent with the biogeographic relationships of Cretaceous marine amniotes from the Weddellian Palaeobiogeographic Province (i.e., Patagonia, western Antarctica, New Zealand and southeastern Australia). Therefore, this type of vertebra is regarded as a distinctive feature of the Weddellian aristonectine elasmosaurids.

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Key words: Aristonectinae, *Aristonectes*, *Kaiwhekea*, Conway Formation, Upper Cretaceous, Weddellian Province

ELASMOSAURIDS (Sauropterygia, Plesiosauria) are a monophyletic group of cosmopolitan long-necked plesiosaurs that flourished during the Late Cretaceous until the mass extinction at the end of the period (Vincent *et al.* 2011, Benson & Druckenmiller 2013).

Elasmosaurids from the Weddellian Province (*sensu* Zinsmeister 1979) have been collected since the 19th century (Gay 1848, Hector 1874, Ameghino 1893), but the systematic affinities of the first discoveries remained obscure until recent revisions (Welles & Gregg 1971, Gasparini & Goñi 1985, O'Gorman & Varela 2010). Even more recent discoveries have usually been identified only to family level (Hiller & Mannering 2004, 2005, Gasparini *et al.* 2007, Kellner *et al.* 2011, Otero *et al.* 2012a, b, O'Gorman 2012, O'Gorman *et al.* 2013a, b).

The first elasmosaurid specimens from New Zealand were also collected in the 19th century from several Upper Cretaceous deposits in North Canterbury in the South Island (see Welles & Gregg 1971; Fig. 1B). Later

finds included those from Mangahouanga Stream in the Hawkes Bay region of the North Island (Wiffen & Moislely 1986) and from Shag Point, north of Dunedin, on the South Island (Cruickshank & Fordyce 2002; Fig. 1B). To date, New Zealand's elasmosaurids that are identifiable to genus and species level have been classified into three species, *Mauisaurus haasti* Hector, 1874, *Tuarangisaurus keyesi* Wiffen & Moislely, 1986 and *Kaiwhekea katiki* Cruickshank & Fordyce, 2002, the last described originally as a cryptoclidid (Cruickshank & Fordyce 2002) but recently referred to the Elasmosauridae (Ketchum & Benson 2011, Benson & Druckenmiller 2013).

After the pioneering works of the 19th century (Owen 1861, Hector 1874), the affinities of several New Zealand plesiosaur taxa have remained uncertain, mostly because of the fragmentary nature of the type materials, which are in most cases difficult to diagnose. Welles & Gregg (1971) made the first systematic attempt to clarify this situation. In the case of *M. haasti*, the original description did not designate any formal type material; thus Welles (1962) assigned DM R 1529, comprising a fragmentary pelvic girdle and a hindlimb, as the lectotype of the species. An additional seven

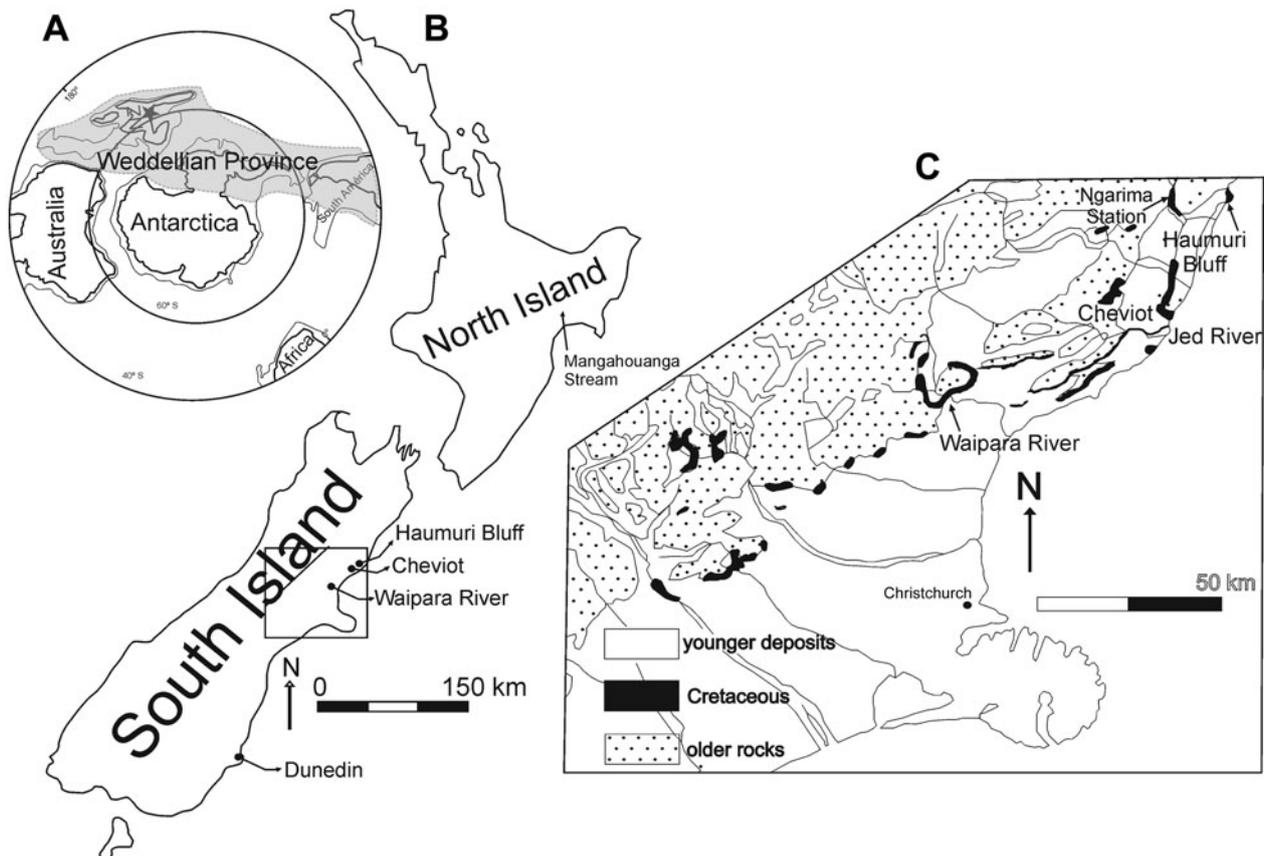


Fig. 1. Maps. A, New Zealand's geographic position during the latest Cretaceous. B–C, Location where CM Zfr 104 was collected, B, general; C, detail (modified after Cruickshank & Fordyce 2002, Hiller *et al.* 2005).

specimens included in the original description by Hector (1874) were designated paralectotypes, and their taxonomic affinities were discussed by Welles & Gregg (1971). The morphological features of the lectotype included the presence of a distinctively large, hemispherical articular head (capitulum) on the femur, which was considered unique among elasmosaurids at that time and used to define the species. This proposal was subsequently used as the basis for further studies on Late Cretaceous plesiosaurs from the Southern Hemisphere (Gasparini *et al.* 2003a, Hiller *et al.* 2005, Martin *et al.* 2007, Otero *et al.* 2010). Welles & Gregg (1971) concluded that most of the morphological diversity among the Late Cretaceous elasmosaurid fossils from New Zealand reflected differing growth stages of *M. haasti* individuals. More recently, Hiller *et al.* (2005) described a new, fairly complete skeleton of this taxon from New Zealand (CM Zfr 115). Together with this, Hiller *et al.* (2005) also made a critical review of the previously referred materials and provided an emended diagnosis based on a composite of the existing specimens.

The status of other plesiosaurs from New Zealand, particularly *Kaiwhekea katiki*, has been discussed by several authors (Cruickshank & Fordyce 2002, Hiller *et al.* 2005). O'Keefe & Street (2009) proposed the 'Aristonectidae' as a new family of cryptocleoidids,

which includes *Kimmerosaurus* from the Kimmeridgian of England (Brown 1981), *Tatenectes* from the Oxfordian of Wyoming (O'Keefe & Wahl 2003), together with Weddellian genera *Aristonectes* from the upper Maastrichtian of southern South America and Antarctica (Gasparini *et al.* 2003b, Otero *et al.* 2014) and *Kaiwhekea* from the Maastrichtian of New Zealand (Cruickshank & Fordyce 2002). Later, Ketchum & Benson (2011) and Benson & Druckenmiller (2013) in competing phylogenetic analyses of Plesiosauria recovered *Kaiwhekea katiki* as an elasmosaurid rather than a cryptocleiid as originally proposed by Cruickshank & Fordyce (2002), or alternatively a leptocleiid (Ketchum & Benson 2010, Druckenmiller & Knutsen 2012). Berezin (2011) conversely retained 'Aristonectidae' as a family-level grouping. Irrespectively, these results suggest a close relationship between *K. katiki* and *Aristonectes parvidens* Cabrera, 1941. Gasparini *et al.* (2003b) likewise recovered *Aristonectes* within the Elasmosauridae. In addition, Otero *et al.* (2012a) utilized the original data-set of O'Keefe & Street (2009) to obtain both *Aristonectes* and *Kaiwhekea* within the Elasmosauridae and listed the Aristonectinae as a subfamily within the Elasmosauridae but excluded both *Kimmerosaurus* and *Tatenectes* from this new clade.

O'Gorman *et al.* (2013a) identified, for the first time, juvenile aristonectine specimens from Patagonia

and the Antarctic Peninsula based on the distinctive proportions of their cervical centra. These are characterized by a high B/L ratio, especially in the middle and caudal part of the neck. Similar cervical vertebra morphotypes have been recovered from Chile (Otero & O’Gorman 2013), Argentina (O’Gorman *et al.* 2014) and Antarctica (O’Gorman 2012), and are consistent with the inferred distributional record of *Aristonectes* (i.e., Argentina, Chile and the Antarctic Peninsula; Gasparini *et al.* 2003b).

The main goals of this paper are therefore: to document the presence of ‘aristonectine-type’ cervical vertebrae in an osteologically immature plesiosaurian postcranial skeleton (CM Zfr104) from the Upper Cretaceous of New Zealand; and to provide critical comments and taxonomical clarification to part of the hypodigm of *Mauisaurus*.

## Geological setting

Plesiosaurs from New Zealand have been recorded from the Haumurian Stage (Santonian–Maastrichtian) of the Mata Series (Crampton *et al.* 2000). The specimen described herein was collected in the Middle Waipara River section of the Conway Formation (South Island). This comprises a succession of poorly consolidated dark grey, massive siltstones or silty sandstones, largely without preserved primary sedimentary structures. The unit was deposited under marine conditions with restricted bottom circulation (Warren & Speden 1978).

Other than marine amniotes (plesiosaurs and mosasaurs), the Conway Formation has yielded only scattered remains of calcareous-shelled invertebrates, linguloid brachiopods, fish and sparse plant fragments (Hiller *et al.* 2005). Among the microfossils, foraminiferans are generally rare and poorly preserved, but rich dinoflagellate assemblages are present (Roncaglia *et al.* 1999). CM Zfr 104 is dated to the early Maastrichtian using associated dinoflagellate cysts indicative of the *Alterbidinium acutulum* Zone (Wilson *et al.* 2005).

*Institutional abbreviations.* **AMNH**, American Museum of Natural History, New York, USA; **AM**, Australian Museum, Sydney, Australia; **CIT**, California Institute of Technology, California (the specimens of the CIT were moved to the Los Angeles Natural History Museum, California), USA; **CM**, Canterbury Museum, Christchurch, New Zealand; **MLP**, Museo de La Plata, Buenos Aires Province, Argentina; **MML**, Museo Municipal de Lamarque, Río Negro Province, Argentina; **MUC**, Museo de la Universidad del Comahue, Neuquén Province, Argentina; **OU**, Geology Museum, University of Otago, Dunedin, New Zealand; **SGO**, **PV**, Área Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; **TTU**, Museum of Texas Tech University, Texas, USA.

*Anatomical abbreviations.* **cap**, coracoid anterior process; **cpp**, coracoid posterior process; **d**, distal carpal/tarsal **ep**, epipodial element; **gf**, glenoid facet; **gr**, groove; **hf**, hemal facets; **mt**, metapodial element; **mvp**, mid-ventral process; **par**, parapophyses; **pf**, pedicellar facets; **pr**, proximal carpal/tarsal; **sf**, scapular facet; **tr**, transverse ridge; **vf**, ventral foramina; **vn**, ventral notch.

## Methods

Linear measurements were taken using a calliper that allows a precision of 0.1 mm. The indices used are those proposed by Welles (1952) and applied following O’Gorman *et al.* (2013a) and Otero & O’Gorman (2013), taking into account the centrum length ( $L$ ), the ratio between maximum height ( $H$ ) and length of the centrum ( $100 \times H / L$ ), and the ratio between maximum breadth ( $B$ ) and length of the centrum ( $100 \times B / L$ ). In addition, the ratio between the breadth and height ( $100 \times B / H$ ) was also considered. Both breadth and height were measured in this work on the posterior articular face. The vertebral length index  $\{VLI = L / [0.5 \times (H + B)]\}$  (Brown 1981) was used. Furthermore, the categories of ontogenetic development proposed by Brown (1981) based on the fusion of the neural arch to the cervical vertebral centrum were employed to differentiate the ‘adult’ and ‘juvenile’ morphotypes.

## Systematic palaeontology

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA de Blainville, 1835

PLESIOSAUROIDEA Welles, 1943

ELASMOSAURIDAE Cope, 1869

ARISTONECTINAE O’Keefe & Street, 2009 (*sensu* Otero *et al.* 2012a)

Aristonectinae indet. (Figs 2, 3)

1971 *Mauisaurus haasti* Welles & Gregg, fig. 13a–d.

2005 *Mauisaurus haasti* Hiller *et al.*, fig. 18A.

*Materials.* CM Zfr 104, nine cervical vertebrae, one pectoral vertebra, eight posteriormost caudal vertebrae, rib fragments, anterior part of the right coracoid, four elements from a limb (see Discussion for identity) and other indeterminate fragments.

*Locality and bed.* Weka Creek, Waipara River (Fig. 1C); New Zealand Fossil Record File Number M34/f7322. Lower Maastrichtian level of the Conway Formation (according to Welles & Gregg 1971).

## Description

*Axial skeleton.* The cervical series is incomplete, with at least one important gap between the first and second

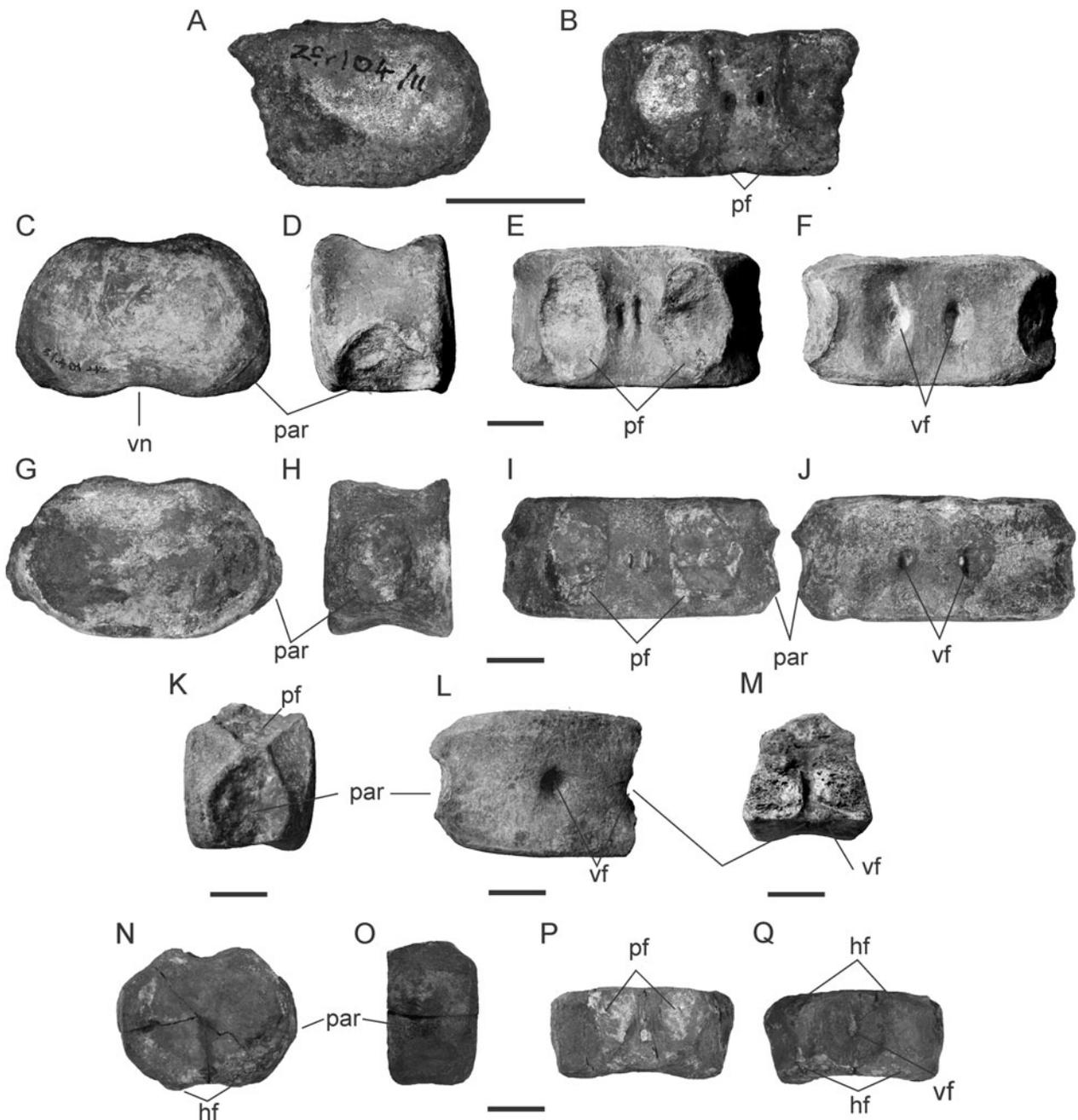


Fig. 2. Aristonectinae indet. CM Zfr 104. A–B, Anteriormost cervical centrum in A, anterior and B, posterior views. C–F, cervical centrum in C, anterior, D, right lateral, E, dorsal and F, ventral views. G–J, posterior cervical centrum in G, anterior, H, right lateral, I, dorsal and J, ventral views. K–M, pectoral centrum in K, left lateral view, L, ventral and M, medial cross-section. N–Q, caudal vertebra in N, anterior, O, left lateral, P, dorsal and Q, ventral views. Scale bars = 20 mm.

preserved cervical vertebra (inferred based on the evident size difference; Table 1). All the cervical centra are higher than long and broader than high (Fig. 2A–J, Table 1). In dorsal view, the pedicellar facets of the neural arches occupy more than 2/3 of the transverse width of the centra and are elliptical with a craniocaudal long-axis. The pedicellar facets are slightly depressed and covered by foramina (Fig. 2B, E, I). The pedicellar facets are almost as long as the centrum and enclose the neural canal, which is slightly concave and bears two craniocaudally elongate foramina (Fig. 2B, E, I). The

articular faces are dumbbell shaped (bilobed) due to the presence, in some vertebrae, of a dorsal and ventral notch (Fig. 2C). In contrast, the articular faces of the cranial-most centrum, and those of the last three cervical centra, are elliptical and lack a ventral notch (Fig. 2A, G). The articular faces are almost flat in transverse plane. The lateral sides of the centra are antero-posteriorly slightly concave and lack a lateral ridge. The parapophyses are elliptical to subcircular and are latero-ventrally located in the middle cervical centra (Fig. 2D). The dorsal margin of the parapophyses

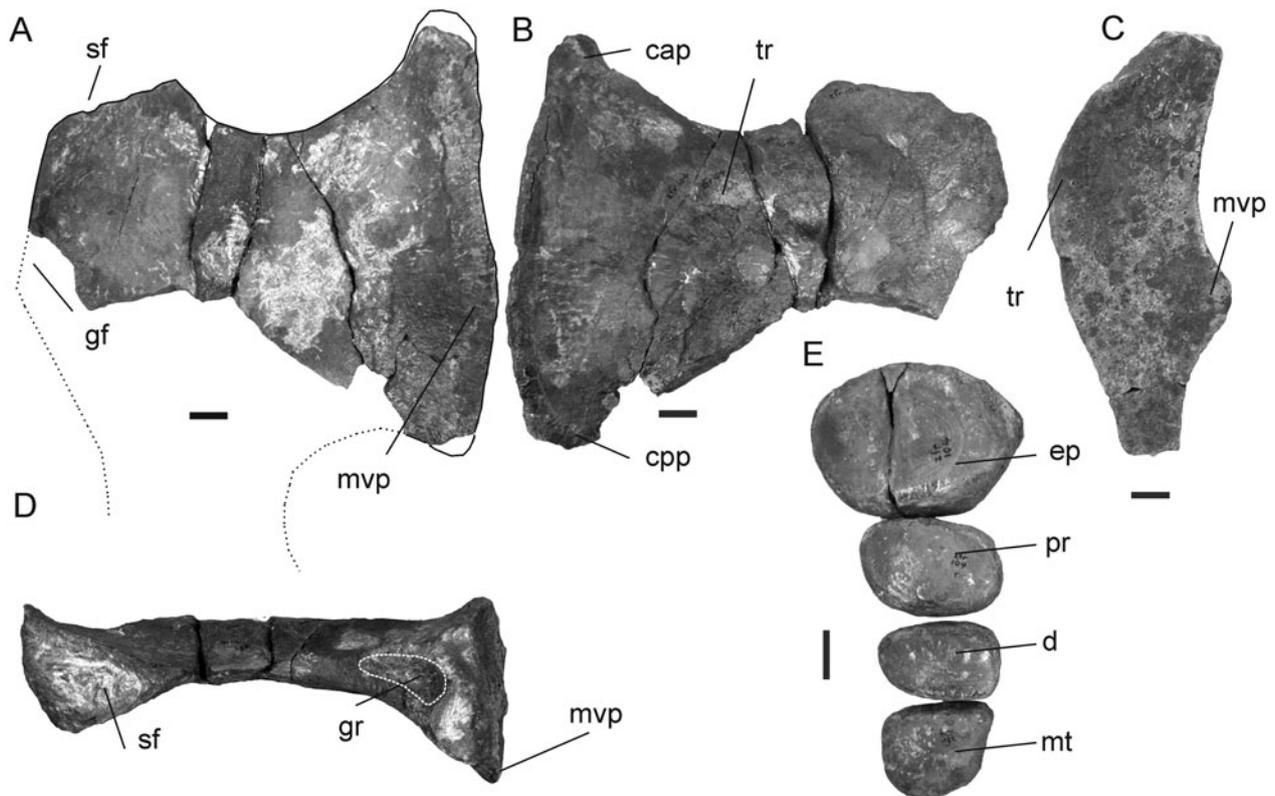


Fig. 3. Aristonectinae indet. CM Zfr 104. A–D, coracoid in A, ventral, B, dorsal, C, symphyisial and D, anterior views. E, epipodial, proximal element, distal element and metacarpal/tarsal. Scale bars = 20 mm.

	L	H	B	HI	BI	BHI	VLI
Cervical	23	26	42	113	183	162	67.7
	40	49	74	123	185	151	65.0
	40	49	73	123	183	149	65.6
	42	51	84	121	200	165	62
	42	54	80	129	190	148	62.7
	42	52	81	124	193	156	63.2
	41	55	87	134	212	158	57.8
	43	58	89	135	207	153	58.5
	42	56	87	133	207	155	58.7
Pectoral	44		88		200		
Caudal	32	47	59	147	184	126	60.4
	28	42		150			
	25	36	45	144	180	125	61.8
	25	35	42	140	168	120	65
	23	33	35	143	152	106	67.6
	21	27	35	129	167	130	67.7
	20	23	27	115	135	117	80
	17	23	26	135	153	113	69.3

Table 1. Measures L, H and B and indexes HI, BI, BHI and VLI of the vertebrae CM Zfr 104 (approximate values in italics). Lineal measures in mm.

extends progressively dorsally in the caudad cervical centra (Fig. 2H). On the ventral surfaces of each centrum, there are two foramina subcentralia separated by a broad, transversely convex ridge (Fig. 2F, J). Only the cranial-most pectoral vertebra is identifiable by its contribution of the parapophysis to the rib facet (Fig. 2K). There are two ventral foramina (Fig. 2L).

Only eight distal caudal centra are preserved. These are broader than high and higher than long (Fig. 2N–O). In dorsal view, the pedicellar facets are triangular with their broadest portion near the proximal articular facet (Fig. 2P). The articular face is subcircular, with a concave ventral margin between the hemal facets (Fig. 2N). A single foramen is situated between the pedicellar facets (Fig. 2P). The left distal and right proximal hemal facets of each vertebra are subtriangular, whereas the right distal and left proximal hemal facets are reduced (Fig. 2Q). A single ventral foramen is evident between the hemal facets (Fig. 2Q). The lateral parapophyses are proximally located (Fig. 2O), suggesting placement of the recovered vertebrae within the distal caudal series.

**Pectoral girdle.** Only the cranial part of the right coracoid is preserved (Fig. 3A–B). The margin between the tip of the pectoral anterior process and the scapular facet is deeply concave. The pectoral anterior process is broad and triangular in outline (Fig. 3A–B); it is also curved ventrally (Fig. 3C). In cranial view, there is a deep groove on the disto-lateral margin of the pectoral anterior process (Fig. 3D). The scapular and glenoid facets are clearly differentiated and offset relative to each other. The scapular facet is subtriangular and rugose, whereas the glenoid facet is subcircular with a smoother bone surface. The ventral surface of the coracoid has a well-developed mid-ventral process (Fig. 3C, D), and dorsally

bears a transverse ridge between the glenoid ramus and the intercoracoid symphysis (Fig. 3C). Caudally, the coracoid has a posterior process (Fig. 3A), and the remaining caudal margin indicates the presence of a cordiform fenestra.

*Limb elements.* Four limb elements are preserved. All have incompletely ossified articular surfaces, consistent with osteological immaturity. Based on the general proportions of elasmosaurid distal limb components depicted by Welles (1952), we identify the larger bone in CM Zfr 104 as an epipodial; the others represent a possible radiale/tibiale, distal carpal/tarsal I and metapodial I (Fig. 3E).

## Discussion

*Systematic affinities.* CM Zfr 104 is interpreted to be a 'juvenile' *sensu* Brown (1981) because its neural arches are not fused to the vertebral centra (Fig. 2B, E, I); likewise, those of the ribs (Fig. 2D, H), and the epipodial, basipodials and metapodial lack well-defined articular facets (Fig. 3E). The presence of dumbbell-shaped articular faces on some of the cervical centra, together with a cordiform intercoracoid fenestra, indicates elasmosaurid affinities (see Hiller *et al.* 2005). Our vertebral index plots (Fig. 4A–C) suggest closest

proportional similarity to the cervical centra of a 'juvenile' elasmosaurid from the upper Maastrichtian of Seymour Island, Antarctica, TTU P 9219, which was originally referred to '*Morturneria seymourensis*' by Chatterjee & Small (1989), but later attributed to *Aristonectes parvidens* by Gasparini *et al.* (2003b). O'Gorman *et al.* (2013a) and Otero & O'Gorman (2013) considered proportions of the middle and caudal cervical centra to be differential discriminators of *Aristonectes*. However, comparable dimensions also occur in *Kaiwhekea* from the uppermost Cretaceous of New Zealand, casting doubt on the diagnostic utility of this trait beyond the subfamilial level (O'Gorman *et al.* 2014). Indeed, CM Zfr 104 was recovered from the same dinoflagellate zone (*Alterbidinium acutulum* Zone), and probably the same subzone (*Palaeocystodinium granulatum* Subzone; Wilson *et al.* 2005) as the holotype of *Kaiwhekea* (OU 12649), implying potential synonymy. The coracoid CM Zfr 104 shows features implying particular affinities with 'juvenile' aristonectines described by Otero *et al.* (2012a) and O'Gorman *et al.* (2013a, 2014) prompting our referral to Aristonectinae indet.

### Comments on the hypodigm of *Mauisaurus haasti*

CM Zfr 104 was not among the specimens originally assigned to *Mauisaurus haasti* by Hector (1874). Welles & Gregg (1971) referred the coracoid (CM Zfr 104) to

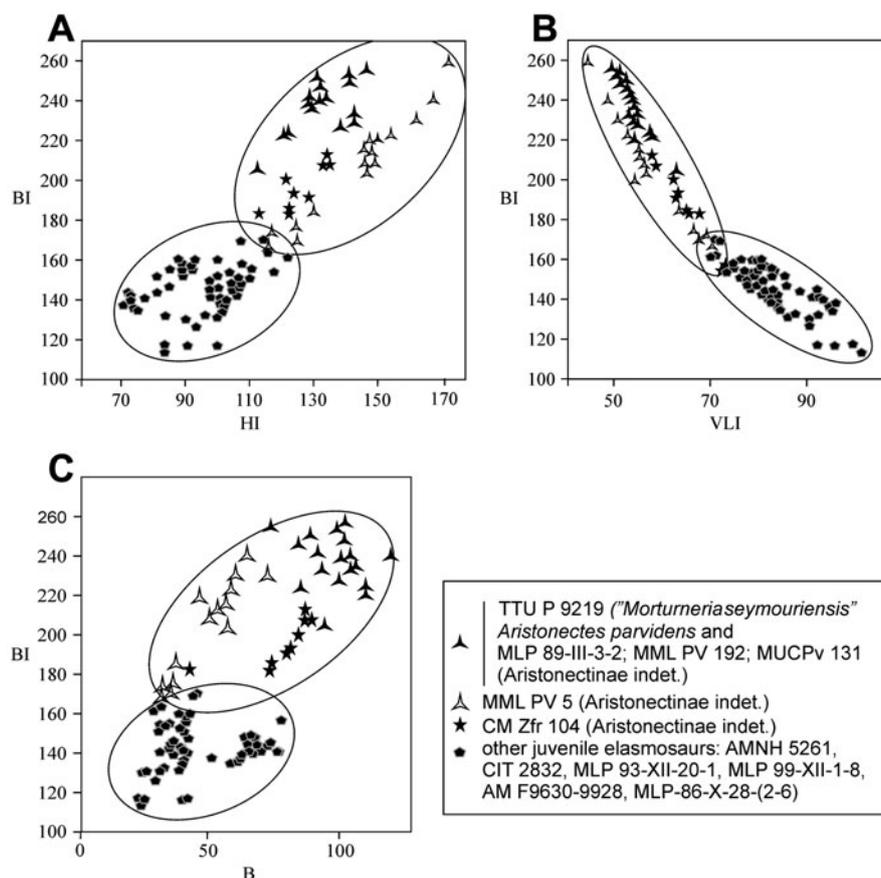


Fig. 4. Bivariate diagrams of cervical centrum values of juvenile aristonectines and juvenile non-aristonectines elasmosaurids (modified from O'Gorman *et al.* 2014). A, HI-BI; B, VLI-BI; and C, B-BI plots.

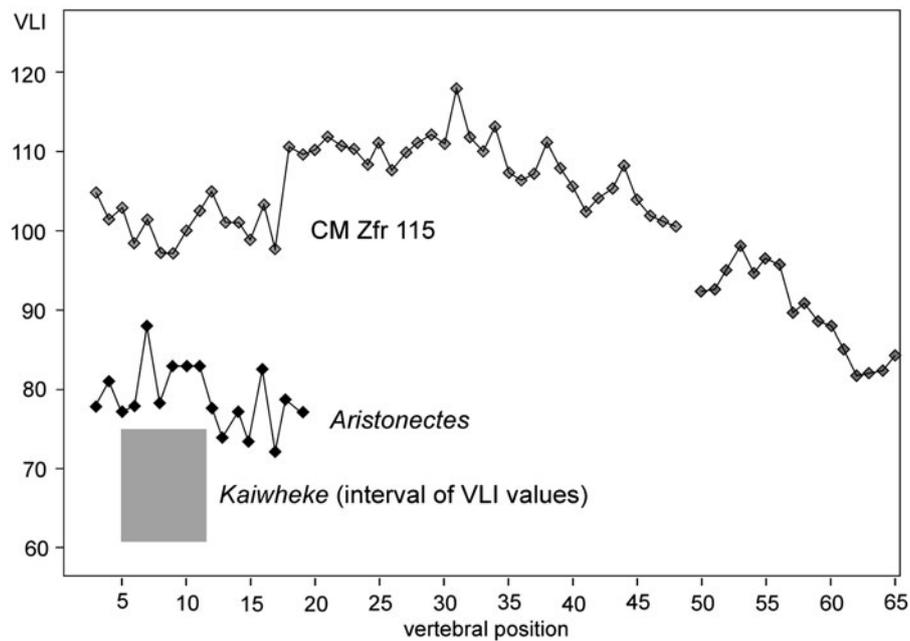


Fig. 5. VLI index of the cervical vertebrae of CM Zfr 115 (referred to *Mauisaurus haasti*, total cervical account estimated), *Aristonectes parvidens* (MLP 40-XI-14-6) and *Kaiwheke katiki* (OU 12649). Data from O'Keefe & Hiller (2006); Cruickshank & Fordyce (2002) and J.O.P. pers obs.

*M. haasti*, but they did not mention the other associated elements registered under the same number. This study has shown that the CM Zfr 104 vertebrae series belongs to a taxon that is structurally compatible with *Kaiwheke* and *Aristonectes*. The *Mauisaurus haasti* hypodigm, as considered by Hiller *et al.* (2005), was defined using CM Zfr 115. This specimen has elongate cervical centra that proportionally differ from *Aristonectes parvidens* (MLP 40-XI-14-6) and *Kaiwhwkea katiki* (OU 12649) when comparing their respective VLIs (Fig. 5). Therefore, given the closer compatibility of CM Zfr 104 (based on its vertebrae and coracoid) with these taxa, we suggest that the traditional hypodigm of *Mauisaurus haasti* probably includes a composite of at least two phylogenetically distinct elasmosaurid plesiosaurians. It is beyond the scope of this paper to discuss the taxonomical status of the lectotype, DM R1529, but our results suggest that this material also needs to be reviewed. Irrespectively, however, CM Zfr 115, which comprises a fairly complete skeleton described by Hiller *et al.* (2005), unequivocally belongs to a non-aristonectine elasmosaurid, is characterized by a very long neck and is substantially different to CM Zfr 104 as studied here.

#### Palaeobiogeography

Zinsmeister (1979) first proposed the existence of a Late Cretaceous–early Paleogene, biogeographic unit called the Weddellian Province. This extended over the shallow shelf regions from Australia and New Zealand along the Pacific margin of Antarctica and southern South America (Fig. 1A). The relatively isolated conditions of the southern Pacific during the Late Cretaceous are evidenced by endemic invertebrate assemblages

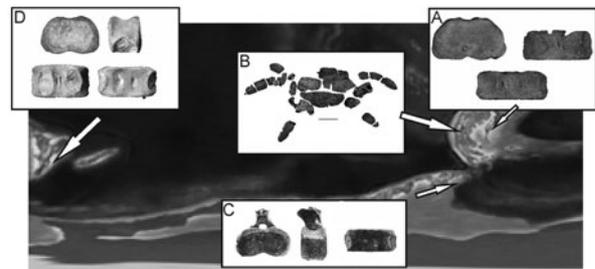


Fig. 6. Weddellian records of juvenile Aristonectinae. A, MML PV 192, northern Patagonia, Argentina; B, SGO PV 260 (scale bar = 100 mm), Central Chile; C, TTU P 9219, Seymour Island (Marambio Is.), Antarctica; D, CM Zfr 104, South Island, New Zealand (Chatterjee & Small 1989, Otero *et al.* 2012a, O'Gorman *et al.* 2013a, map of the southern Pacific modified after Blakey 2013).

(Zinsmeister 1982, Zinsmeister & Griffin 1995), a pattern that is also beginning to emerge among the coeval marine amniotes (Novas *et al.* 2002; Martin & Fernández 2007, Otero *et al.* 2012b).

Despite this, the biogeographical relationships of at least the Weddellian plesiosaurians remain obscured by a scarcity of diagnostic material, and especially cranial elements. Based on the current specimens, though, it is clear that the interpreted palaeobiogeographical distribution is based mainly on osteologically immature aristonectines (Fig. 6) and that further assessment of ontogenetic trajectories and species boundaries is needed to bolster this current radiation hypothesis.

#### Acknowledgements

This research was supported by projects PICT 2008-0261, PICT 2012-0748; PICTO 2010-0093; UNLP N 677, UNLP N607 and PIP 0433. The authors thank

E. Fordyce (Otago University, New Zealand); P. Scofield (Canterbury Museum) and J. Simes (National Paleontology Collection, GNS Science Avalon, New Zealand), for allowing us to review the elasmosaurs from those institutions, and Kyle Davis (Canterbury Museum), for taking some of the photographs. RAO was initially supported by the Antarctic Ring Project (Anillos de Ciencia Antártica ACT-105, Conicyt-Chile) and is currently supported by the Domeyko II UR-C12/1 grant 'Red Paleontológica U-Chile' of the Universidad de Chile.

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