

A SMALL BODY SIZED NON-ARISTONECTINE ELASMOSAURID (SAUROPTERYGIA, PLESIOSAURIA) FROM THE LATE CRETACEOUS OF PATAGONIA WITH COMMENTS ON THE RELATIONSHIPS OF THE PATAGONIAN AND ANTARCTIC ELASMOSAURIDS

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Abstract. The systematics of the Late Cretaceous non-aristonectine elasmosaurids from Argentinean Patagonia are poorly known as there is no valid species currently recognized. Here a new non-aristonectine elasmosaurid: *Kawanectes lafquenianum* nov. comb. from the late Campanian–early Maastrichtian Allen Formation is diagnosed. *K. lafquenianum* is a distinctively small-body sized non-aristonectine elasmosaurid characterized by caudal vertebrae with marked laterally projected parapophyses, presence of pelvic bar, high ratio (~1.2) between humerus/femur length and a large posterodistal projection of the humerus which bears a posterior accessory articular facet. A phylogenetic analysis recovered *K. lafquenianum* closely related with *Morenosaurus stocki*, *Vegasaurus molyi*, and Aristonectinae, showing the relationships between the elasmosaurids from Patagonia, Western Antarctic, and the Pacific coast of the USA. *K. lafquenianum* is part of the fauna of the coeval Allen and La Colonia formations that also comprises indeterminate aristonectines and polycotylids. This relatively high diversity plesiosaur fauna includes the three main morphotypes (aristonectines, non-aristonectine elasmosaurids and polycotylids), which is remarkable because the depositional environments of the Allen Formation have been inferred as marginal marine to non-marine environments.

Key words. Elasmosauridae. Upper Cretaceous. Patagonia. Antarctic Peninsula.

Resumen. UN PEQUEÑO ELASMOSÁURIDO NO ARISTONECTINO (SAUROPTERYGIA, PLESIOSAURIA) DEL CRETÁCICO SUPERIOR DE PATAGONIA CON COMENTARIOS SOBRE LA RELACIÓN ENTRE LOS ELASMOSÁURIDOS DE ANTÁRTIDA Y PATAGONIA. La sistemática de los elasmosáuridos no aristonectinos del Cretácico de la Patagonia Argentina es poco conocida, no habiendo ninguna especie válida reconocida actualmente. En esta contribución un nuevo elasmosáurido no aristonectino: *Kawanectes lafquenianum* nov. comb. proveniente de la Formación Allen (Campaniano superior–Maastrichtiano inferior) es diagnosticado. *K. lafquenianum* es un elasmosáurido no aristonectino de pequeño tamaño corporal que se caracteriza por la presencia de vértebras caudales con parapófisis fuertemente proyectadas lateralmente, presencia de barra pélvica, elevada proporción longitud del húmero / longitud del fémur (~1,2) y una marcada proyección posterodistal del húmero que lleva una carilla articular accesoria. El análisis filogenético recupera a *K. lafquenianum*, estrechamente relacionado con *Morenosaurus stocki*, *Vegasaurus molyi* y los aristonectinos que muestran las relaciones entre los elasmosáuridos del norte de Patagonia, Antártida Occidental y la costa pacífica de USA. *K. lafquenianum* es parte de la fauna de las formaciones coetáneas Allen y La Colonia, que comprende aristonectinos indeterminados y policotílidos. Esta diversidad relativamente alta, con los tres morfotipos principales presentes (elasmaosáuridos aristonectinos, elasmaosáuridos no aristonectinos y policotílidos), es notable ya que el ambiente de deposición de la Formación Allen se ha inferido como marino marginal con intercalaciones de ambientes no marinos.

Palabras clave. Elasmosauridae. Cretácico Superior. Patagonia. Península Antártica.

ELASMOSAURID plesiosaurs form a monophyletic group of cosmopolitan diapsid marine reptiles that flourished during the Late Cretaceous (Vincent *et al.*, 2011; Benson and Druckenmiller, 2014). Elasmosaurids comprise the more typical non-aristonectine elasmosaurids, characterised by elongated

cervical centra and a relatively small cranium, and the aristonectines, with short cervical centra and a relatively large cranium, more numerous teeth (Gasparini *et al.*, 2003a; Otero *et al.*, 2012, 2014b).

Elasmosaurids have been collected in southern South

America since the XIX century (Gay, 1848; Ameghino, 1893; Gasparini *et al.*, 2007; Otero *et al.*, 2009; O’Gorman *et al.*, 2013b). Late Cretaceous elasmosaurids from southern South America have been collected from the lower levels of the Mata Amarilla Formation (Cenomanian), Allen and Loncoche formations (upper Campanian–lower Maastrichtian), La Colonia Formation (Campanian–Maastrichtian), Dorotea and Quiriquina formations (Maastrichtian–Danian), and the late Maastrichtian levels of the Lefipán and Jagüel formations (Gasparini and Salgado, 2000; Gasparini *et al.*, 2003a,b, 2007; Previtera and González Riga, 2008; Otero *et al.*, 2009; O’Gorman *et al.*, 2011; Varela *et al.*, 2012). In spite of these abundant records, only two elasmosaurid species from southern South America are currently considered valid: *Aristonectes parvidens* Cabrera, 1941, and *Aristonectes quiriquinensis* Otero, Soto-Acuña, O’Keefe, O’Gorman, Stinnesbeck, Suárez, Rubilar-Rogers, Salazar and Quinzio-Sinn, 2014. The absence of nominated non-aristonectine elasmosaurids from Patagonia is connected with the poor preservation of cranial material and the poorly understood postcranial morphology (Gasparini and Salgado, 2000; Gasparini *et al.*, 2003b).

Gasparini and Goñi (1985) nominated a new species “*Trinacromerum lafquenianum*” based on a well preserved postcranium from the late Campanian–early Maastrichtian Allen Formation exposed at Lago Pellegrini, Río Negro, Patagonia (Figs. 1–4). Later, Gasparini and Salgado (2000) described two additional specimens from the same locality and formation and referred them to *Elasmosauridae* indet. The three mentioned specimens are the holotype of “*T. lafquenianum*” (MLP 71-III-13-1, MLP refers to Museo de La Plata, La Plata, Argentina) and the two new specimens mentioned above, *i.e.*, MCS PV 4 and MUC Pv 92 (MCS refers to Museo de Cinco Saltos, Río Negro Province, Argentina; MUC refers to Museo de la Universidad del Comahue, Neuquén Province, Argentina). This taxonomic identification has been followed since then (Gasparini *et al.*, 2001, 2007; Cerda and Salgado, 2008; O’Gorman *et al.*, 2011). These three specimens were reviewed by the author (O’Gorman, 2013), who concluded they belong to the same elasmosaurid species. The aims of this paper are to name *Kawanectes* gen. nov., re-describe *Kawanectes lafquenianum* nov. comb., and discuss its relation with other elasmosaurids from the Weddellian Province *sensu* Zinsmeister, 1979 (*i.e.*, Patagonia, western Antarctica and New Zealand).

Institutional abbreviations. **AMNH**, American Museum of Natural History; **BRSMG**, Bristol City Museum and Art Gallery, Bristol, UK; **CIT**, California Institute of Technology, Pasadena now in the Natural History Museum of Los Angeles County, USA; **CM**, Canterbury Museum, Christchurch, New Zealand; **DM**, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; **MDNH**, Denver Museum Natural History, Colorado, USA; **MCS Pv**, Museo de Cinco Saltos, Río Negro Province, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MIWG**, ‘Dinosaur Isle’ Museum of Isle of Wight Geology, Sandown, UK; **MLP**, Museo de la Plata, Buenos Aires Province, Argentina; **MML**, Museo Municipal de Lamarque, Río Negro Province, Argentina; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **MPEF**, Museo Paleontológico Egidio Feruglio, Chubut Province, Argentina; **MUC Pv**, Museo de la Universidad del Comahue, Neuquén Province, Argentina; **CD NZGS**, Nuclear and Geological Science, Lower Hut, New Zealand; **OU**, Geology Museum, University of Otago, Dunedin, New Zealand; **QM**, Queensland Museum, Brisbane, Australia; **SGO.PV**, Museo Nacional de Historia Natural, Santiago, Chile; **UCMP**, University of California Paleontological Museum, San Francisco, USA.

Anatomical abbreviations. **act**, acetabulum; **af**, accessory facet; **cap**, capitulum; **cr**, cervical rib; **di**, diapophysis; **dlp**, dorsolateral process; **dr**, dorsal rib; **epf**, epipodial foramen; **f**, femur; **ff**, fibular facet; **fi**, fibula; **gr**, glenoid ramus; **hf**, hemal facets; **ivf**, intervertebral foramen; **is**, ischium; **lk**, lateral keel; **nc**, neural canal; **ns**, neural spine; **pu**, pubis; **par**, parapophysis; **pb**, pelvic bar; **pez**, prezygapophysis; **pf**, pedicellar facet; **poz**, postzygapophysis; **rf**, radial facet; **rpp**, rib posterior process; **t**, tibia; **tf**, tibial facet; **tp**, transverse process; **tro**, trochanter; **tub**, tubercle; **uf**, ulnar facet; **vf**, ventral foramina; **vn**, ventral notch.

GEOLOGICAL SETTING

The Allen Formation, where specimens MCS PV 4, MLP 71-III-13-1 and MUC Pv 92 were collected, crops out in the north of Patagonia (Fig. 1.1) (Río Negro, La Pampa and Neuquén provinces). It is a thick succession of sandstones and shales with interbedded carbonatic and evaporitic rocks in its upper section (Andreis *et al.*, 1974). The Allen Formation yielded vertebrates such as dipnoans, teleosts, elasmosaurids and polycotyloid plesiosaurs, ophidians, theropods,

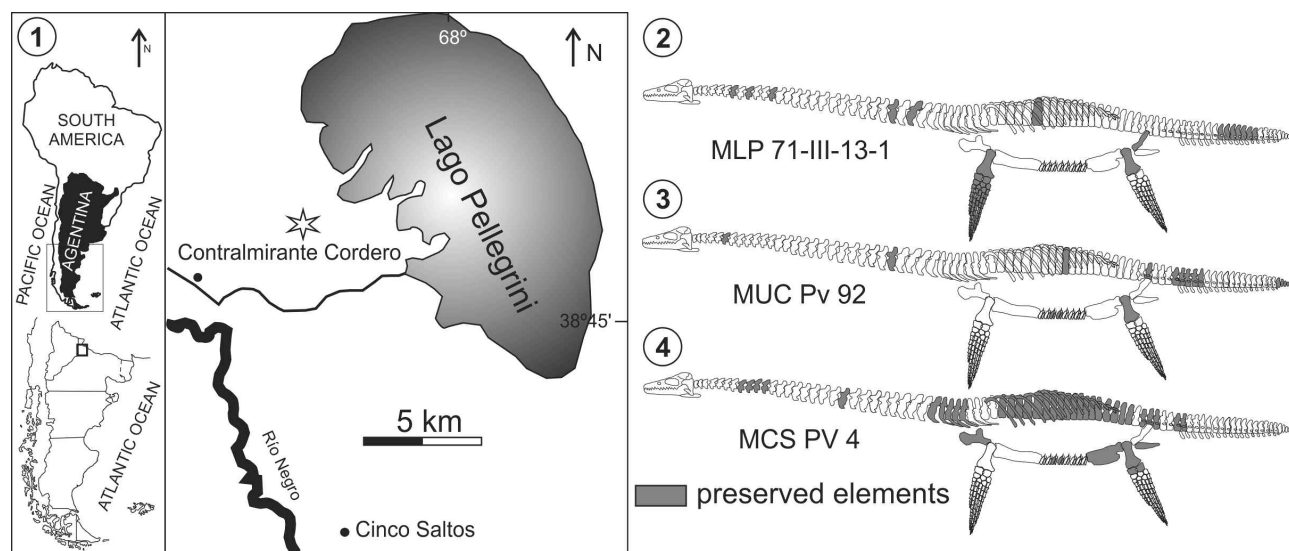


Figure 1. 1, Location map of the locality where the specimens (MLP 71-III-13-1, holotype, and MCS Pv 4) of *Kawaneptes lafquenianum* nov. comb. were collected; 2–4, preserved elements in each specimen of *K. lafquenianum*.

sauroptiles, hadrosaurs (Martinelli and Forasiepi, 2004; Salgado *et al.*, 2007; Novas *et al.*, 2009; O’Gorman *et al.*, 2011; García, 2013), mammals (Rougier *et al.*, 2009), and some mollusks (Gasparini *et al.*, 2007). This formation was deposited in a marginal marine environment (Barrio, 1990; Gasparini *et al.*, 2007). Based on ostracods and magnetostratigraphy, the Allen Formation is regarded as late Campanian–early Maastrichtian in age (Ballent, 1980; Dingus *et al.*, 2000).

MATERIALS AND METHODS

The linear measurements were taken using a digital caliper. The indices considered are those proposed by Welles (1952) for the description of vertebral centra, which take into account the length (L), the height (H), length-centrum ratio ($HL = 100 \times H / L$), and the breadth (B) length-centrum ratio ($BL = 100 \times B / L$); also, the breadth-height centrum ratio ($BH = 100 \times B / H$) was considered. Both the breadth and height were measured on the posterior articular face. Also, the degree of vertebral elongation, (vertebral length index (Brown, 1981) ($VLI = L / (0.5 \times (H + B))$)) was used. In the description of propodials, the B:L index ($B:L = 100 \times Bd / Lt$), which is the ratio between the distal antero-posterior breadth (Bd) and the total length (Lt) (Welles, 1952), was used.

The ontogenetic developmental categories proposed by

(Brown, 1981), based on the fusion of the neural arch to the vertebral centrum, were considered to differentiate the “adult” from the “juvenile” growth stages.

In order to clarify the phylogenetic position of *Kawaneptes lafquenianum* nov. comb. within Elasmosauridae, a phylogenetic analysis was performed. The data set is based on the data published by Benson and Druckenmiller (2014), and modified in order to include more Late Cretaceous elasmosaurids. The scoring of the Weddellian Elasmosauridae *Kaiwhekea katiki* Cruickshank and Fordyce, 2002 (OU 12649), *Aristonectes parvidens* (MLP 40-XI-14-6), *Aristonectes quiriquinensis* (holotype SGO.PV 957 and referred specimen SGO.PV 260), *Tuarangisaurus keyesi* Wiffen and Molesley, 1986 (CD NZGS CD 425 and NZGS CD 426), *Morenosaurus stocki* Welles, 1943 (CIT 2802), *Hydrotherosaurus alexandrae* Welles, 1943 (UCMP 33912), *Callawayasaurus colombiensis* Welles, 1962 (UCMP 38349), and *Thalassomedon haningtoni* Welles, 1943 (DMNH 1588) were modified based on personal observations. Additionally, *Elasmosaurus platyrus* Cope, 1869 and *Styxosaurus snowii* (Williston, 1890) Welles, 1943, were scored based on bibliography. The final data set comprises 89 taxa. Additionally, three characters were added to the character list of Benson and Druckenmiller (2014), rendering a total of 273 characters; additionally some characters were modified (see Supplementary Online Information 1 and 2). A data set was compiled using

Mezquite (Maddison and Maddison, 2011) and analysed using TNT (Goloboff *et al.*, 2008). All the characters are considered unordered. The data set was analysed using a heuristic search (tree bisection reconnection, with 1,000 random addition sequence replicates). Consistency (CI) and retention (RI) indexes (Farris, 1989) were calculated, and Bremer Support (Bremer, 1994) values were calculated for some nodes.

SYSTEMATIC PALEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLESIOSAUROIDEA Welles, 1943

Family ELASMOSAURIDAE Cope, 1869

Genus *Kawanectes* gen. nov.

Type species. *Trinacromerum lafquenianum* Gasparini and Goñi, 1985.

Derivation of name. *Kawa* for the “Kawas Sea” named given by (Casamiquela, 1978: 137) to the last Mesozoic marine transgression in Patagonia (late Campanian–Danian) and –*nectes*, meaning swimmer in Greek.

Diagnosis. Same as for species by monotypy.

Kawanectes lafquenianum nov. comb.

Figures 2–8; 9.1, 10

Trinacromerum lafquenianum: Gasparini and Goñi, 1985: 56.

Tricacromerum lafquenianum: Gasparini and Salgado, 2000:15 (incorrect spelling).

Derivation of name. “*lafquenianum*” as for the mapuche word for “sea” (Moesbach, 1984).

Diagnosis. Small sized elasmosaurid (*ca.* 3.8 m long, see Table 2 for comparison with other elasmosaurids) which belongs to the non-elongated group (*sensu* O’Keefe and Hiller, 2006) that differs from other elasmosaurids by the

following combination of characters: vertebral centra broader than long, marked laterally projected parapophyses of caudal vertebrae forming a lateral “knob”, presence of pelvic bar, high humerus/femur length ratio (~1.2) (a proportion only shared among elasmosaurids by *Callawayasaurus colombiensis*), large posterodistal projection of humerus which bears an accessory articular facet (a feature only shared among elasmosaurids by *Morenosaurus* Welles, 1943, *Vegasaurus* O’Gorman, Salgado, Olivero, and Marensi, 2015, and *Kaiwhekea* Cruickshank and Fordyce, 2002), and femur with strongly convex capitulum. It differs from *Vegasaurus molyi* by its non-elongate trochanter in the dorsal surface of the femur and from *Vegasaurus molyi* and *Morenosaurus stocki* by its small body size, laterally projected parapophyses of the caudal vertebrae, higher humerus/ femur length ratio (1.2), and presence of a pelvic bar.

Type material. MLP 71-II-13-1, six cervical vertebrae, three dorsal vertebrae, three sacral vertebrae, nine caudal vertebrae, right femur, right humerus, ilium, one mesopodial element, one caudal phalanx and one caudal rib (Gasparini and Goñi, 1985: lam I, II; Gasparini and Salgado, 2000: fig. 7).

Type locality and horizon. Quarry of the “Bentonitas Patagónicas” company, northeast of Lago Pellegrini, Río Negro Province, Argentina. Middle Member of the Allen Formation, late Campanian–early Maastrichtian (Ballent, 1980; Page *et al.*, 1999; Dingus *et al.*, 2000).

Referred specimens. MCS PV 4, fifteen cervical vertebrae, three pectoral vertebrae (*contra* O’Gorman, 2013), fifteen dorsal vertebrae, three caudals, right scapula, part of right coracoid, both pubes and ischia, distal part of a femur and epipodium, phalanges, rib fragments and 389 gastroliths (Gasparini and Salgado, 2000: fig. 1e, 2, 4, 5, 6a,b; Gasparini *et al.*, 2007: fig. 3a–e; Cerda and Salgado, 2008: fig. 2). MUC Pv 92, two cervical vertebrae, three dorsal vertebrae, one sacral and eight caudal vertebrae, fragments of girdles, right femur, two epipodial elements, ribs and phalanges (Gas-

Figure 2. *Kawanectes lafquenianum* nov. comb.: 1–4, MLP 71-III-13; 1, anterior and 2, left lateral views of anterior cervical vertebra; 3, anterior and 4, left views of posterior cervical vertebra; 5–12, MCS PV 4; 5, right lateral; 6, anterior, and 7, left lateral views of cervical vertebrae; 8, left lateral; 9, anterior; 10, posterior and 11, ventral views of posterior cervical vertebra; 12, left lateral view of posterior cervical vertebra. Scale bar= 20 mm.

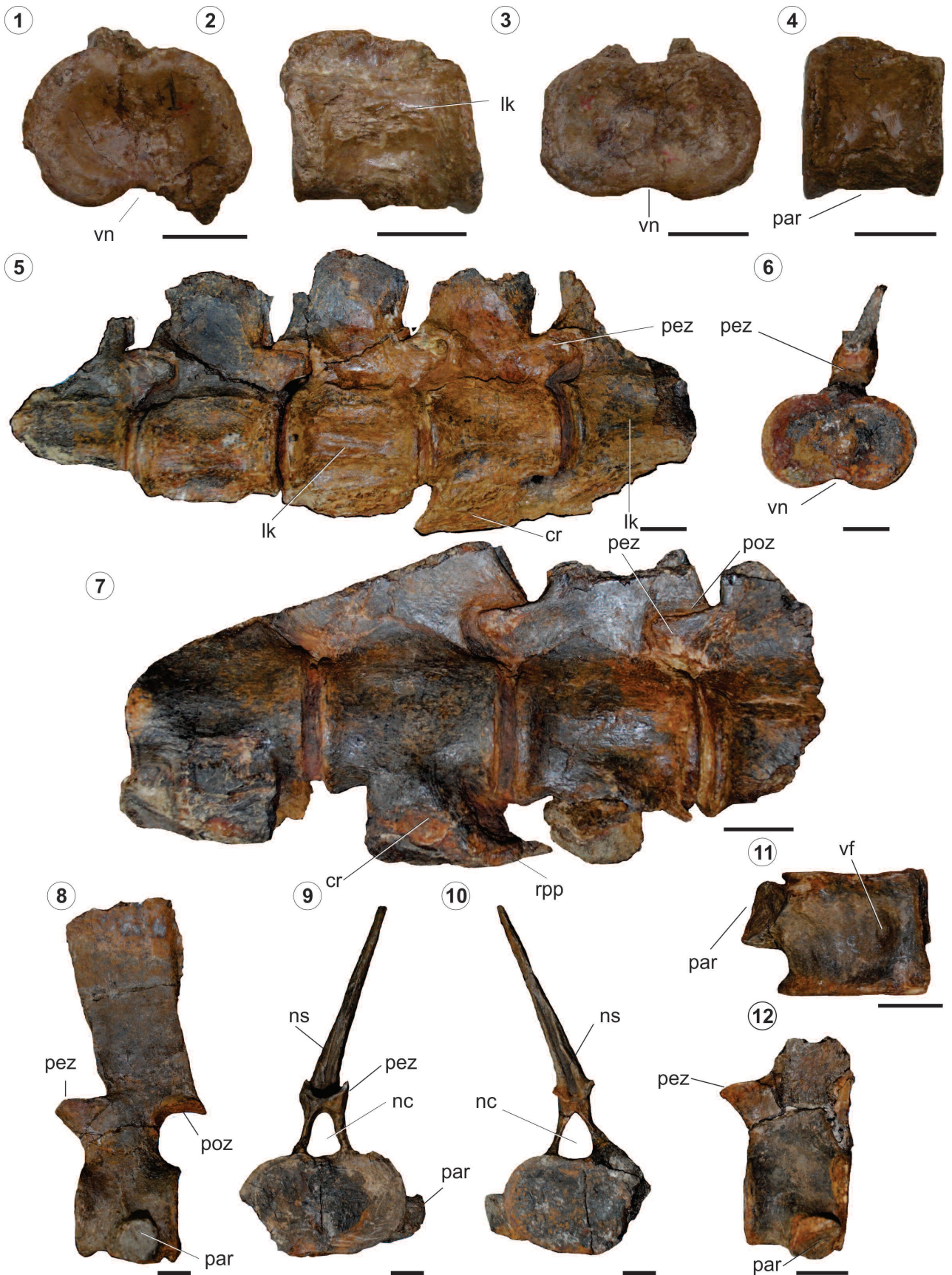


TABLE 1 – *Kawanectes lafquenianum nov. comb. Vertebral measurements of holotype and referred specimens (in mm).*

<i>vertebrae</i>	<i>L</i>	<i>H</i>	<i>B</i>	<i>HI</i>	<i>BI</i>	<i>BHI</i>	<i>VLI</i>
<i>MCS Pv 4</i>							
<i>C1</i>	49	32	52	65	106	163	117
<i>C2</i>	45	33	50	73	111	152	108
<i>C3</i>	-	-	-	-	-	-	-
<i>C4</i>	50	36	59	72	118	164	105
<i>C5</i>	48	37	57	77	119	154	102
<i>C6</i>	49	35	57	71	116	163	107
<i>C7</i>	50	36	58	72	116	161	106
<i>C8</i>	52	-	-	-	-	-	-
<i>C9</i>	50	36	60	72	120	167	104
<i>C10</i>	48	38	59	79	123	155	99
<i>C11</i>	48	38	60	79	125	158	98
<i>C12</i>	-	-	-	-	-	-	-
<i>C13</i>	39	37	59	95	151	159	81
<i>C14</i>	41	42	60	102	146	143	80
<i>C15</i>	45	44	66	98	147	150	82
<i>D1</i>	45	47	58	104	129	123	86
<i>D2</i>	47	45	56	96	119	124	93
<i>D3</i>	46	49	60	107	130	122	84
<i>D4</i>	42	50	55	119	131	110	80
<i>D5</i>	44	45	57	102	130	127	87
<i>D6</i>	44	45	55	102	125	122	88
<i>D7</i>	45	43	54	96	120	126	93
<i>D8</i>	48	44	56	92	117	127	96
<i>D9</i>	47	45	56	96	119	124	93
<i>D10</i>	47	-	55	-	117	-	-
<i>D11</i>	45	42	54	93	120	129	94
<i>D12</i>	43	40	50	93	116	125	96
<i>D13</i>	41	38	54	93	132	142	89
<i>D14</i>	40	38	55	95	138	145	86
<i>D15</i>	40	36	50	90	125	139	93
<i>S1</i>	38	36	52	94	136	144	86
<i>S2</i>	37	35	55	94	148	157	82
<i>Ca1</i>	32	34	54	106	169	159	73
<i>Ca2</i>	32	35	-	109	-	-	-
<i>Ca3</i>	31	35	50	113	161	143	73

TABLE 1 – Continuation.

<i>vertebrae</i>	<i>L</i>	<i>H</i>	<i>B</i>	<i>HI</i>	<i>BI</i>	<i>BHI</i>	<i>VLI</i>
<i>MLP 71-II 13-1</i>							
<i>C1</i>	43	36	49	84	114	136	101
<i>C2</i>	45	37	50	82	111	135	103
<i>C3</i>	42	38	48	90	114	126	98
<i>C4</i>	35	38	60	109	171	158	71
<i>C5</i>	34	37	57	109	168	154	72
<i>C6</i>	34	39	60	115	176	154	60
<i>D1</i>	33	33	46	100	139	139	83
<i>D2</i>	33	30	40	91	121	133	94
<i>D3</i>	35	34	48	97	137	141	86
<i>Ca1</i>	28	33	45	118	161	136	72
<i>Ca2</i>	28	32	43	114	154	134	75
<i>Ca3</i>	27	33	42	122	156	127	72
<i>Ca4</i>	27	32	41	119	152	128	74
<i>Ca5</i>	27	31	39	115	144	126	77
<i>Ca6</i>	28	32	42	114	150	131	77
<i>Ca7</i>	25	30	41	120	164	137	70
<i>Ca8</i>	24	30	40	125	167	133	69
<i>Ca9</i>	25	27	36	108	144	133	79
<i>Ca10</i>	24	28	34	117	142	121	77
<i>MUC Pv 92</i>							
<i>C1</i>	28	20	35	71	125	175	102
<i>C2</i>	33	-	-	-	-	-	-
<i>D1</i>	40	37	50	93	125	135	92
<i>D2</i>	42	41	59	98	140	144	84
<i>D3</i>	50	41	55	86	108	134	104
<i>S1</i>	35	33	48	94	137	145	86
<i>Ca1</i>	30	33	46	110	153	139	76
<i>Ca2</i>	32	34	46	106	144	135	80
<i>Ca3</i>	32	35	46	109	144	131	79
<i>Ca4</i>	32	34	42	106	131	124	84
<i>Ca5</i>	31	33	42	106	135	127	83
<i>Ca6</i>	29	32	40	110	138	125	80
<i>Ca7</i>	29	30	40	103	138	133	83
<i>Ca8</i>	31	30	37	97	119	123	93

L, length; *H*, height; *B*, breadth; indexes *HI*, height (*H*)/length (*L*) ratio ($HI = 100 \cdot H/L$); *BI*, breadth (*B*)/length (*L*) ratio ($BI = 100 \cdot B/L$); *BHI*, breadth/height ratio ($BHI = 100 \cdot B/H$); and *VLI*, Vertebral Length Index [$VLI = 100 \cdot L / (0.5 \cdot (H + B))$]. *C*, cervical, *D*, dorsal, *S*, sacral, *Ca*, caudal. In bold, articulated vertebrae.

TABLE 2 – Body length of several elasmosaurids.

Taxon	Length (m)	Ratio with <i>Kawanectes</i>	References
<i>Kawanectes lafquenianum</i>	ca. 3.8 (total)		O’Gorman, 2013
<i>Vegasaurus molyi</i>	6,5 (total)	1.7	O’Gorman, 2013
<i>Thalassomedon haningtoni</i>	10.86 (total)	3.9	Welles, 1952
<i>Elasmosaurus platyrus</i>	10.3 (total)	3.7	Welles, 1952
<i>Hydralmosaurus serpentinus</i>	9.44 (total)	3.4	Welles, 1952
<i>Mausaurus haasti</i> (based on CM Zfr 115)	+8	+2.9	Hiller et al., 2005
<i>Hydrotherosaurus alexandrae</i>	7.77 (total)	2.8	Welles, 1952
<i>Futabasaurus suzukii</i>	6.4-9.2	2.3-3.3	Sato et al., 2006
<i>Styxosaurus browni</i>	5.25 (neck)	-	Welles, 1952
<i>Libonectes morgani</i>	5.06 (neck)	-	Welles, 1952
<i>Morenosaurus stocki</i>	3.63 (trunk and tail)	-	Welles, 1952

parini and Salgado, 2000: fig. 1a–d, 3, 6c–e; Gasparini *et al.*, 2007: fig. 3f–k).

Locality and horizon of referred specimens. The specimen MCS 4 was collected at the northeast of the depression occupied by Lake Pellegrini, middle member of the Allen Formation (Gasparini and Salgado, 2000). The MUC Pv 92 specimen has no precise provenance but it probably comes from the nearby Lake Pellegrini.

Description

Axial skeleton

The cervical region of *K. lafquenianum* includes an unknown number of vertebrae. The anterior and middle cervical vertebrae are longer than high and broader than long. The VLI index reaches 110 in the longest preserved cervical centrum (Table 1). The articular facets are flat to slightly concave with dumbbell-shaped articular facets (Fig. 2.1, 3, 6). Additionally, the lateral surface shows a marked and sharp lateral keel (Fig. 2.2, 5). These three features are absent in the posteriormost vertebral centra, preserved in the

holotype (MLP 71-III-13-1) and MCS PV 4, where the vertebral centra are short (VLI ~85) with almost elliptical articular facets (slight or absent ventral notch) and without a lateral keel (Fig. 2.4, 7, 8, 12). All the vertebrae have two ventral foramina on the ventral surface (Fig. 2.11). The right and left prezygapophyses contact each other along the midline and the same is observed in the postzygapophyses, although its distal tip remains free (Fig. 2.6, 9, 10), a common feature in Late Cretaceous elasmosaurids (Hiller *et al.*, 2005; Sato, 2003). Most of the neural spines are not well preserved but the posteriormost vertebral centra of MCS PV 4 are complete. These neural spines are tall (about twice the height of the centra), they show a rectangular shape, and are slightly cranially inclined in lateral view (Fig. 2.8). In both the anterior and posterior margin the neural spine shows a groove extending until at least half of the total length (Fig. 2.10). The anterior and middle cervical ribs are relatively short with anterior and posterior processes; they are fused to the centra (Fig. 2.7). On the other side, the posterior cervical ribs are more elongated, bearing closer simi-

Figure 3. *Kawanectes lafquenianum* nov. comb.: 1–3, MLP 71-III-13-1; 1, anterior, 2, left lateral and 3, ventral views of dorsal vertebra; 4–9, MCS PV 4; 4, dorsal view of dorsal and sacral regions; 5, anterior, 6, right lateral and 7, ventral views of dorsal vertebra; 8, dorsal and 9, posterior views of 8th dorsal vertebra and rib. Scale bar= 20 mm.



larity to the dorsal ribs and they are not fused with the cervical centra, as revealed by the free parapophyses (Fig. 2.9, 11,12). This absence of fusion on the posterior cervical centra has been recorded in other elasmosaurids such as *Vegasaurus molyi* O’Gorman, Salgado, Olivero and Marenssi, 2015 and *Futabasaurus suzukii* Sato, Hasegawa and Manabe, 2006.

The pectoral region is well preserved in specimen MCS PV 4 but it is obscured by the matrix and scapula and therefore cannot be described (Fig. 6.1). The dorsal region, well preserved in specimen MCS PV 4, comprises fifteen vertebrae; one of it still articulated with the pectoral region (Fig. 3.4). The vertebral centra are broader than long and as long as high (Table 1). The articular facets are dorsoventrally



Figure 4. *Kawanectes lafquenianum* nov. comb.: 1–4, MLP 71-III-13-1; 1, anterior; 2, posterior; 3, dorsal and 4, ventral views of sacral vertebra; 5–6, MCS PV 4; 5, anterior and 6, dorsal views of sacral vertebrae; 7–14, MUC Pv 92; 7, anterior; 8, left lateral; 9, dorsal and 10, ventral views of sacral vertebra; 11, anterior; 12, posterior and 13, proximal views of sacral rib; 14, reconstruction of sacral vertebrae in position. Scale bar= 20 mm.

depressed to subcircular (Fig. 3.1, 5, 9). The ventral surface usually bears two foramina, and one of the vertebrae has a third smaller foramen (Fig. 3.3). The diapophyses are directed laterally, in an almost horizontal direction (Fig. 3.1, 9). Specimen MCS PV 4 preserves the complete sacral region, formed by three vertebrae (Fig. 3.4). The vertebral centra are broader than high and higher than long (Table 1). The articular facets are kidney-shaped (Fig. 4.1, 5, 7). The diapophyses and parapophyses are convergent as in all elasmosaurids, forming the transverse process that articulates with the sacral rib (Fig. 4.1, 5). Ventrally, there are one or two foramina (Fig. 4.4, 10). Only one sacral rib of the MUC PV 92 is preserved (Fig. 4.11–14). The proximal facet is divided in two parts, a smaller dorsal part and a large ventral one that form an angle of about 130° between them. In anterior

view, the proximal surface shows a concave zone (Fig. 4.13). The distal zone of the sacral rib is strongly rugose (Fig. 4.11, 12).

The caudal region is comprised of an unknown number of vertebrae. The caudal centra are broader than high and higher than long. The pedicellar facets are subtriangular and anteroposteriorly elongated (Fig. 5.3, 11). The parapophyses are strongly laterally projected (Fig. 5.1, 7, 9) with a rib facet varying from circular to elliptical (Fig. 5.2, 11). The hemal facets are well developed (Fig. 5.4, 8, 12). Specimens MLP 71-III-13-1 and MUC Pv 92 show a change in the relative development of the anterior and posterior hemal facets along the tail. Ventrally, there are two foramina in the anteriormost caudal vertebrae and one foramen and an almost flat ventral zone in the other vertebrae (Fig. 5.4, 8, 12).

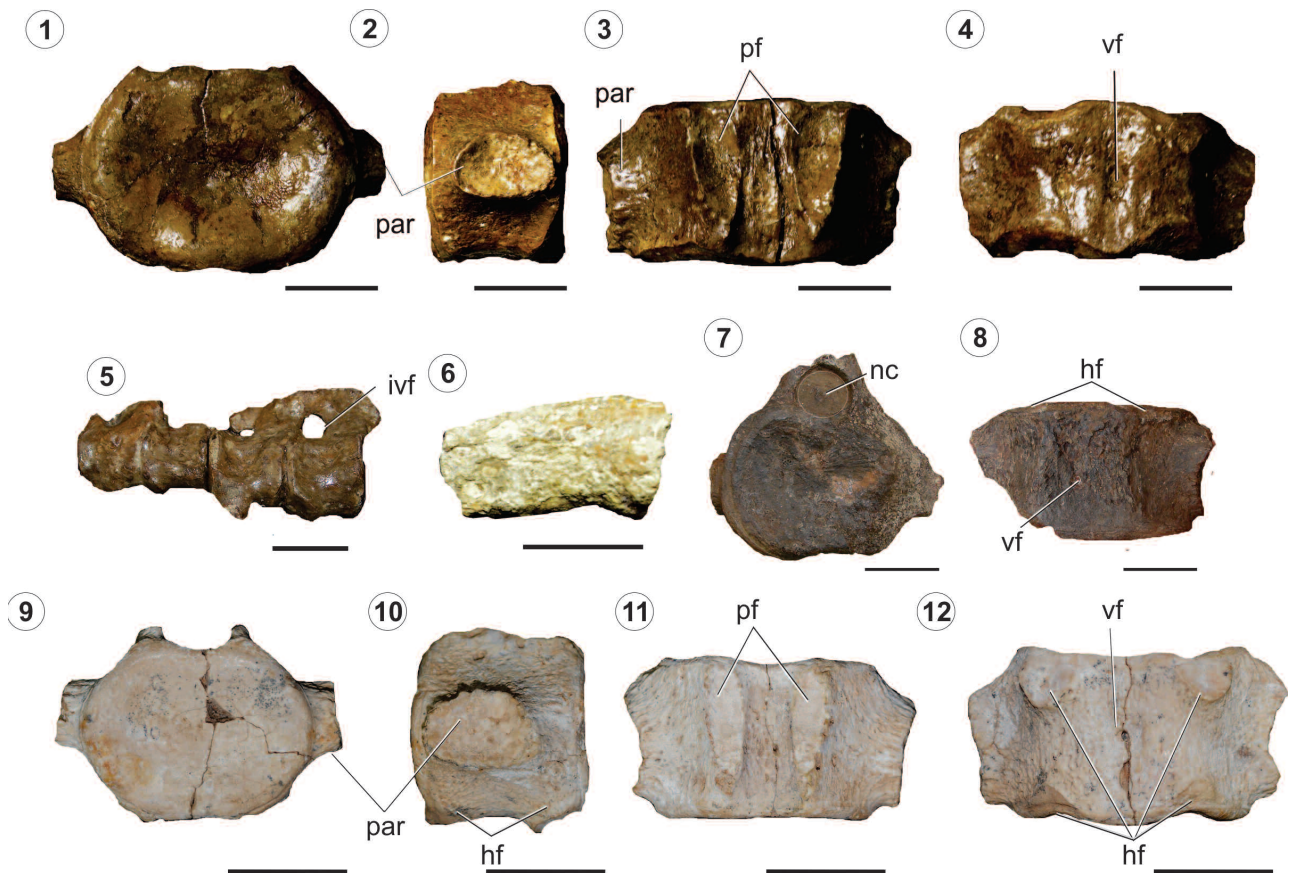
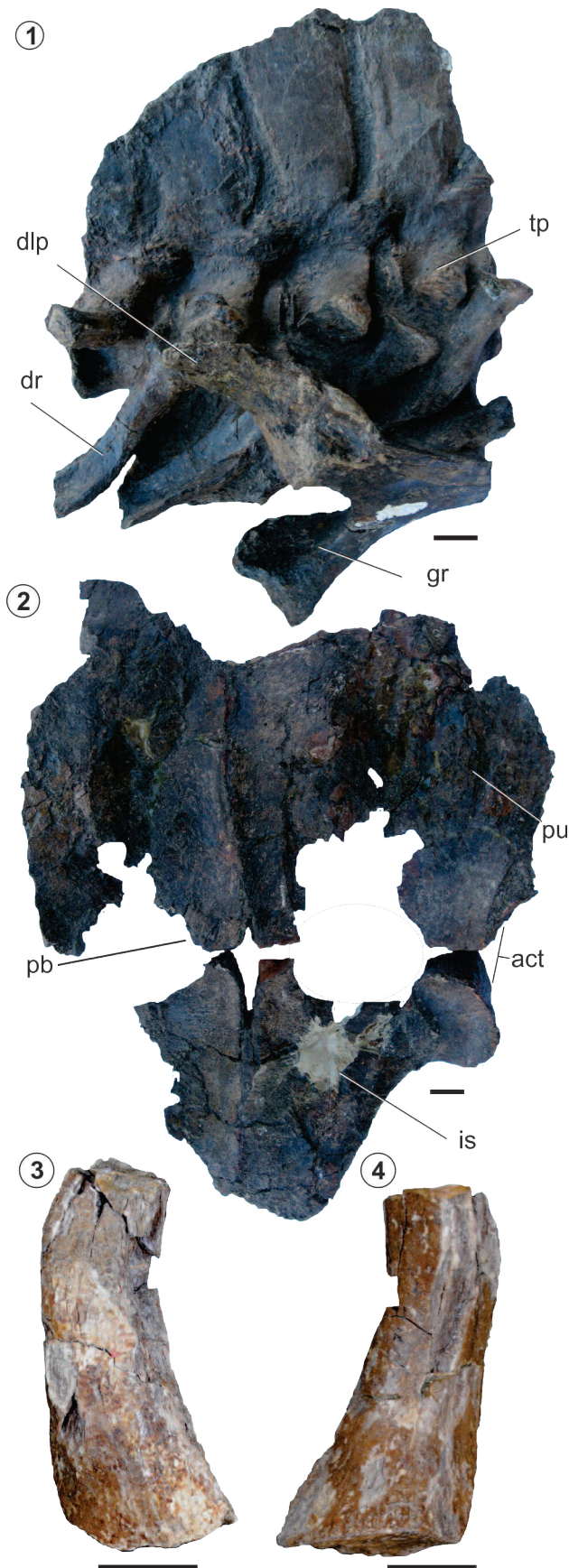


Figure 5. *Kawanectes lafquenianum* nov. comb.: 1–6, MLP 71-III-13-1; 1, anterior; 2, left lateral; 3, dorsal and 4, ventral views of caudal vertebra; 5, left lateral view of last caudal vertebrae; 6, caudal rib; 7–8, MCS PV 4, 7, anterior and 8, ventral views of caudal vertebrae; 9–12, MUC PV 92: 9, anterior; 10, left lateral; 11, dorsal and 12, ventral views of caudal vertebra. Scale bar = 20 mm.



Girdles

The pectoral girdle is not well preserved in any specimen. The scapula, preserved only in specimen MCS PV 4, shows the typical elasmosaurid morphology with a large ventral ramus and a dorsolateral process. It is not possible to determine whether the scapulae meet each other at the midline. The dorsolateral process is long and slender (Fig. 6.1). The coracoid is not preserved –other than fragments– in any specimen.

The pelvic girdle of MCS PV 4 is well preserved (Fig. 6.2). The anterior margin of the pubis is strongly convex and the posterior margin forms the anterior limit of the puboischiadic fenestra (Fig. 6.2). The ischia form an almost complete pelvic bar with its pubis, forming a diamond shaped fenestra between them (Fig. 6.2). The ilium is a dorsally tapering element with a bent shaft (Fig. 6.3, 4). The tip of the angle is marked by a posterior knob (Fig. 6.3, 4).

Limbs

The humerus of MLP 71-III-13-1 is 207 mm long and 141 mm in distal width (anteroposterior distal length), rendering a B:L index of 68%. The capitulum and the tuberosity are not completely convergent (Fig. 7.1, 3). In dorsal view, the tuberosity is slightly displaced towards the posterior margin (Fig. 7.1). This tuberosity shows a bone growth over its posterior margin that visible in ventral view (Fig. 7.2). In dorsal view, there is a slight but long depression in the anterior margin (arrow, Fig. 7.2). At the distal end, there is a developed posterior expansion holding much of the posterior ulnar facet. There are two slightly concave distal facets (Fig. 7.1, 2). A third facet, much shorter than the other two, possibly associated with an accessory element, is limiting the posterior expansion and it is almost perpendicular to the two epipodial articular facets (Fig. 7.1, 2).

The femur of MLP 71-III-13-1 is 171 mm long. The distal end is broken and, therefore, it is impossible to calculate the B:L index. At the proximal end, the femur has a strongly

Figure 6. *Kawanectes lafquenianum* nov. comb.: 1–2, MCS PV 4; 1, right lateral view of pectoral region and scapula; 2, dorsal views of pubis and ischia; 3–4, MLP 71-III-13-1; 3, lateral? and 4, medial? views of ilium. Scale bar= 20mm.



Figure 7. *Kawaneptes lafquenianum* nov. comb.: MLP 71-III-13-1: 1, dorsal; 2, ventral and 3, proximal views of humerus; 4, dorsal; 5, ventral and 6, proximal views of femur; 7, mesopodial element; 8, phalange. Arrow indicates depression on the ventral shaft. Scale bar = 20mm.

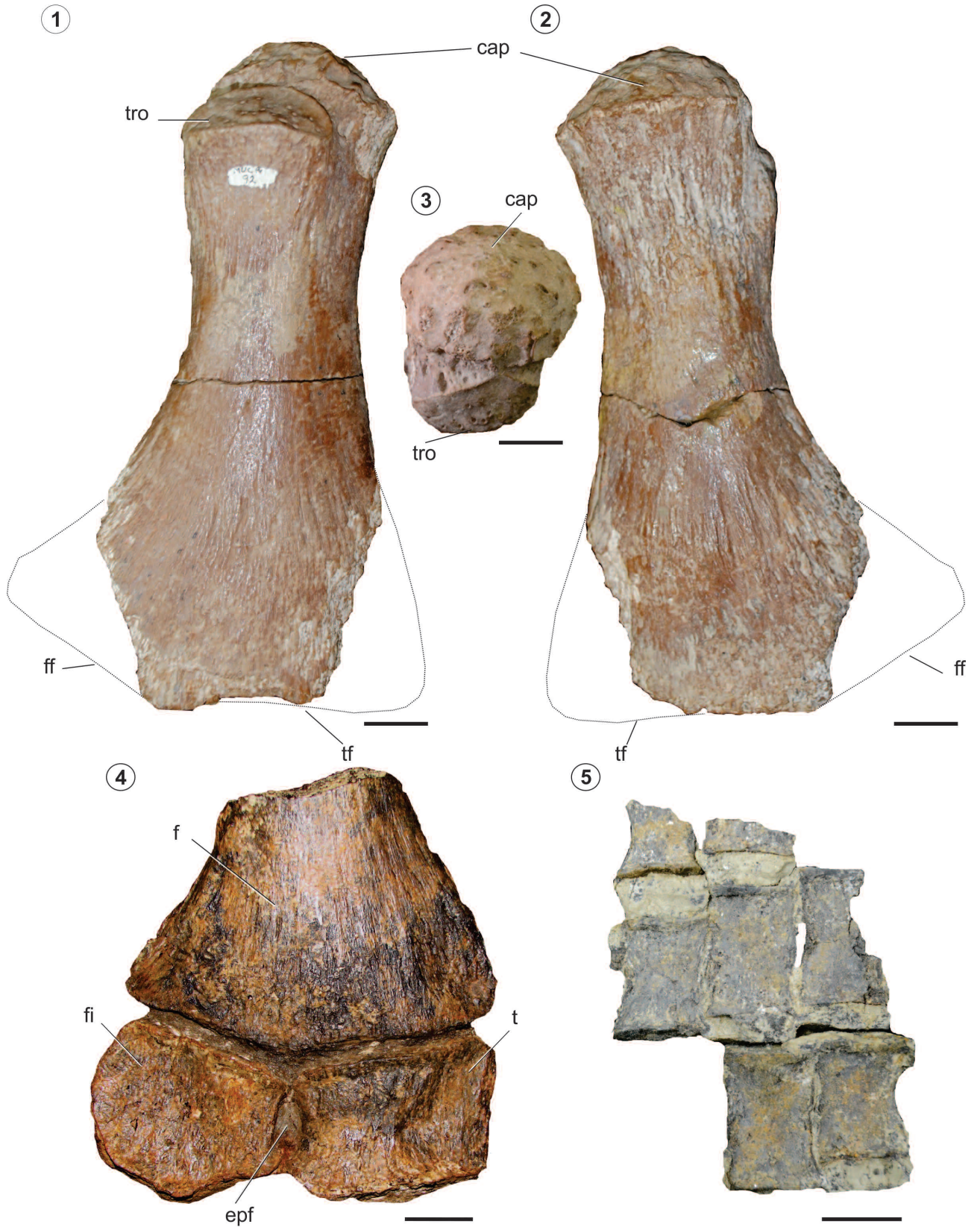


Figure 8. *Kawanectes lafquenianum* nov. comb.: 1–3, MUC Pv 92; 1, dorsal; 2, ventral and 3, proximal views of femur; MCS PV 4; 4, dorsal view of distal part of right femur and epipodials; 5, phalanges. Scale bar= 20 mm.

convex capitulum. The capitulum and trochanter are not completely confluent (Figs. 7.4, 5, 8.1–3) and both are surrounded by a rim that is more conspicuous in the capitulum (Fig. 7.4, 5). In dorsal view, the trochanter is displaced towards the posterior margin of the shaft (Fig. 7.4). In ventral view, it shows there is a prominent roughness associated with muscle attachment (Fig. 7.5). Most of the projection of the shaft coincides with the tibial facet, the only one almost completely preserved and it is posteriorly followed by a small portion of the fibular facet (Fig. 7.5). The specimen MCS PV 4 preserves the distal end of the femur in articulation with the tibia and fibula (Fig. 8.4). Both are broader than long and form a well-defined epipodial foramen (Fig. 8.4). The preserved phalanges are short and centrally slightly constricted (Figs. 7.8, 8, 5).

PHYLOGENETIC ANALYSIS

The phylogenetic analysis resulted in 250 trees of 1424 steps (CI=0.284 and RI= 0.673). The relationships outside Elasmosauridae are not the focus of this contribution and are not to be discussed here. Elasmosauridae is recovered as a monophyletic group sustained by ch. 179 (1→0), reduced number of dorsal centra 20–23 to 17–19; ch. 183

(0→1), strong constriction at the base of the dorsal neural spines; ch. 241 (1→2) ratio humerus to femur length >1. The internal resolution is relatively low, a feature consistent with previous analyses (Vincent *et al.*, 2011; Kubo *et al.*, 2012; O'Gorman *et al.*, 2015; Fig. 10). *Kawanectes lafquenianum* is recovered as part of a monophyletic group (*Kawanectes lafquenianum*; *Vegasaurus molyi*; *Morenosaurus stocki*; (*Kaiwehekea katiki*; *Aristonectes parvidens*; *Aristonectes quiriquinensis*)) sustained by ch. 23 (3→1), postaxial ossicles or articular face for it on propodials and ch. 248 (0→1) epipodial facets aligned in humerus. The aristonectine are sustained by ch. 154 (2→1), cervical centra as long as high; ch. 173 (1→2), ratio BI more than 130 in anterior half of the neck; ch. 203 (1→0), scapular dorsolateral process subequal to width at midlength; ch. 254 (2→1), radius longer than broad; ch. 255 (2→1), tibia longer than broad; ch. 261 (1→0) long epipodial foramen.

DISCUSSION

Taxonomic comparisons

Kawanectes lafquenianum shows diagnostic features of Elasmosauridae, such as lateral keel on the cervical vertebrae, cervical vertebrae with dumbbell-shaped articular

TABLE 3 – Characters used to differentiate *Kawanectes* from other Weddellian and Pacific Taxa. 1, cervical centrum proportions; 2, caudal prapophysis laterally projected; 3, ilium dorsal end; 4, pelvic bar; 5, humerus posterior accessory facet; 6, trochanter widely expanded in dorsal view; 7, ratio humerus length/femur length; 8, body length.

	1	2	3	4	5	6	7	8
<i>Kawanectes lafquenianum</i>	L>H	present	tapering	present	present	absent	1.2	3.8 m
<i>Vegasaurus molyi</i>	L>H	absent	expanded	absent	present	present	1.08	6.5 m
<i>Morenosaurus stocki</i>		absent	expanded	absent	present	present	1.08	3.63 m (trunk and tail)
<i>Hydrotherosaurus alexandrae</i>	L>H	absent	expanded	?	absent	absent	1.14	7.77 m (total)
<i>Aristonectes parvidens</i>	L≤H	absent	?	?	absent	?		?
<i>Mausaurus haasti</i> (DM R1529, holotype)	?	?	?	?		present		?
CM Zfr 115, referred)	L>H		?	?	?	absent		+ 8 meters
<i>Kaiwehekea katiki</i>	L≤H	absent	?	?	present	present		6 m

Data taken from Welles, 1943; Cruickshank and Fordyce, 2002; Hiller *et al.*, 2005; O'Gorman *et al.*, 2015).

facets produced by the presence of a ventral notch; cervical centra longer than high; epipodials broader than long (Gasparini *et al.*, 2003a; Kubo *et al.*, 2012; Benson and Druckenmiller, 2014). Specimens MUC Pv 92, MCS PV 4 are clearly adults *sensu* Brown (1981) due to the fusion between the neural arches and the vertebral centra in the cervical and dorsal centra, whereas specimen MLP 71-II-13-1 shows some neural arches free in the posteriormost cervical centra indicating a less advanced degree of fusion. However, a close observation of the pedicellar facets indicates that the neuro-central closure had started. Specimens MUC Pv 92 and MLP 71-II-13-1 shows the neural arches and caudal centra unfused, a feature usually observed in adult specimens (Gasparini *et al.*, 2003a; Hiller *et al.*, 2005; O’Gorman *et al.*, 2015). A detailed comparison of *K. lafquenianum* with other elasmosaurids has been conducted focusing on the features that allow distinguishing them and summarized in Table 3 for differences with other Weddellian and Pacific elasmosaurids.

The axial skeleton contains useful information, such as the cervical vertebrae with dumbbell-shaped articular facets that are present in all Late Cretaceous elasmosaurids, but absent in the Aptian *Callawayasaurus colombiensis* and other Early Cretaceous elasmosaurids (Kear, 2005; Druckenmiller and Russell, 2006; O’Gorman *et al.*, 2015). *K. lafquenianum* has cervical vertebrae with a VLI that differs from the extreme elongated condition of the genera *Elasmosaurus* Cope, 1869 and *Styxosaurus* Welles, 1943 (O’Keefe and Hiller, 2006) and from the aristonectines *Aristonectes* Cabrera, 1941, *Kaiwhekea* (characterized by a cervical centra shorter than other elasmosaurids; Gasparini *et al.*, 2003a; Cruickshank and Fordyce, 2002; Otero *et al.*, 2014b). Other Late Cretaceous elasmosaurids also differ from *K. lafquenianum* in their cervical proportions and dorsal vertebral count. For instance, the Cenomanian *Libonectes morgani* (Welles) Carpenter, 1997 (for Cenomanian age of *Libonectes* see Sachs and Kear, 2014) and the Santonian *Hydralmosaurus serpentinus* (Cope) Welles, 1943 have mid-cervical vertebral centra longer than broad (Welles, 1952), unlike those of *K. lafquenianum*, that are always broader than long (Table 1). Additionally, the dorsal region of *K. lafquenianum* comprises fifteen dorsal vertebrae, less than the 25 vertebrae in the Cenomanian *Thalassomedon haningtoni* Welles, 1943. The caudal vertebrae of *K. lafquenianum* show strongly laterally

projected parapophyses (Fig. 5.1, 7, 10). A similar morphology has been recorded in some elasmosaurids (Leidy, 1865: pl V.12; O’Gorman *et al.*, 2011: fig. 3.3, 4; O’Gorman *et al.*, 2013b: fig. 2.K, L) but it is absent in the closely related *Vegasaurus molyi* and *Morenosaurus stocki* (pers. obs.).

The anatomy of the girdles also distinguishes *K. lafquenianum* from other taxa. The dorsolateral process of *K. lafquenianum* is long and gracile differing from the anteroposteriorly long and stocky dorsolateral process of the Albian *Wapuskaneetes betsynichollsae* Druckenmiller and Russell, 2006 and the Maastrichtian *M. stocki*. The presence of pelvic bar is ontogenetically variable but it is useful to compare adult specimens (Carpenter, 1999). *Hydrotherosaurus serpentinus* Welles, 1943 (AMNH 1495), *M. stocki* and *V. molyi* lack a pelvic bar (Welles, 1943, 1952: fig. 21; Carpenter, 1999: fig. 6C), unlike *K. lafquenianum* (Fig. 6.2). This difference cannot be explained by ontogenetic variation since *Hydralmosaurus serpentinus* and *M. stocki* are also adult specimens and larger than *K. lafquenianum* (Table 2). In addition, the pubis of *Terminonatator ponteixensis* Sato, 2003, has a strong concavity in the outer margin (Sato, 2003: fig. 12), unlike that of *K. lafquenianum* (Fig. 6.2). The ilium of *K. lafquenianum* has a well-developed posterior knob which differs from that of *Futabasaurus suzukii* (Sato *et al.*, 2006: fig.7 E, F) and *Zarafasaura oceanis* Vincent, Bardet, Suberbiola, Bouya, Amaghazaz, Meslouh, 2011 (Lomax and Wahl, 2013: fig. 12), where it is absent. The circular cross section of the dorsal part of the ilium of *K. lafquenianum*, differs from that of *M. stocki*, which is strongly laterally compressed (Welles, 1943, J. P. O’Gorman per. obs.). Additionally, the dorsal end of the ilium, although damaged, seems to be unexpanded, differing thus from *Hydrotherosaurus alexandrae* (Welles, 1943; J. P. O’Gorman per. obs.), *Thalassomedon haningtoni* (Welles, 1943: fig. 16) and *Vegasaurus molyi* (O’Gorman *et al.*, 2015: fig. 10 C, D).

The ratio between humerus and femur in *K. lafquenianum* (1.2) differs from that of *Hydralmosaurus* Welles, 1943; *Terminonatator* Sato, 2003; and CM Zfr 145, in which the femur is longer than the humerus (an uncommon feature among elasmosaurids; Welles, 1943; Sato, 2003; Hiller and Mantering, 2005). In most elasmosaurid genera the humerus is longer than the femur, such as *Morenosaurus stocki* (1.08) and *Hydrotherosaurus alexandrae* (1.14) (Welles, 1943). The humerus of *Futabasaurus* Sato, Hasegawa and Manabe, 2006,

is 18% longer than the femur, a difference regarded as diagnostic of *Futabasaurus suzukii* (Sato *et al.*, 2006). In *K. lafquenianum*, the humerus is 21% longer than the femur, so this character is shared with *Futabasaurus suzukii*. Interestingly, the posterior expansion of the humerus of *K. lafquenianum* is similar to that of *Hydralmosaurus serpentinus*, although in the latter there is no accessory articular face (Carpenter, 1999). The only non-aristonectine elasmosaurids that share with *K. lafquenianum* the relatively unusual humerus with a posterior expansion and an accessory articular facet are *Wapuskanectes betsynichollsae*, *Vegasaurus molyi* and *Morenosaurus stocki* (Druckenmiller and Russell, 2006; Welles, 1943; O'Gorman *et al.*, 2015). The femur of *K. lafquenianum* has a trochanter that is not dorsally expanded, contrasting with *Vegasaurus molyi*, *Mauisaurus haasti* Hector, 1874, and the aristonectine *Aristonectes* sp. and *Kaiwhekea*, where the trochanter has a long posterodistal development (Cruikshank and Fordyce, 2002; Hiller *et al.*, 2005; O'Gorman, 2013; O'Gorman *et al.*, 2015). *Mauisaurus haasti* is currently under revision; however, due to the importance of this taxon among the Weddellian elasmosaurids, a special comparison is made to differentiate the two main specimens of *Mauisaurus haasti* (the lectotype DM R1529 and CM Zfr 115 referred by Hiller *et al.*, 2005) from *K. lafquenianum*. The first difference between *M. haasti* and *K. lafquenianum* is the body size. Hiller *et al.* (2005) indicate a body length in excess of 8 meters for specimen CM Zfr 115 and, although the body size of *K. lafquenianum* is not directly known, it is much smaller and has been inferred to be approximately 3.8 meters (Table 2) by comparing it with the proportions of *V. molyi* (O'Gorman, 2013). Additionally, the femur of *K. lafquenianum* differs from that of the lectotype of *Mauisaurus* because the latter has a long posterior expansion that is absent in *K. lafquenianum*.

The lack of differences between *Tuarangisaurus keyesi* and *Kawanectes lafquenianum* in the data set is because the former is known only from cranial material and scarce postcranial elements. This problem cannot be resolved at the moment. However, the phylogenetic analysis did not recover *Tuarangisaurus keyesi* close to *Kawanectes lafquenianum*, providing at least some evidence against the synonymy of *K. lafquenianum* and *Tuarangisaurus keyesi*.

Ontogenetic comparisons

In order to show that *K. lafquenianum* does not represent a juvenile stage of *V. molyi* (which is morphologically similar but larger in body size), an analysis of the relationship between size and proportions of the elements was performed. In particular, three bits of evidence were used to show this: (1) *K. lafquenianum* shows anatomical evidence that is usually related with an adult condition, as was previously mentioned; (2) it is well recorded that during the ontogenetic development of elasmosaurids there is a trend of the cervical vertebrae to increase the HI and BI due to the relative elongation of the cervical centra (O'Keefe and Hiller, 2006). Figure 9.11 shows that the cervical vertebrae of *K. lafquenianum* have higher or similar HI and BI values than the cervical vertebrae of *V. molyi* and (3) the pelvic bar is usually absent in juvenile specimens but is present in *K. lafquenianum* and absent in the holotype of *V. molyi* (whose pelvic girdle is larger than the one of *K. lafquenianum*). This evidence indicates that a putative ontogenetic sequence including the *Kawanectes lafquenianum* materials (holotype and referred specimens) and the *Vegasaurus molyi* holotype would not be consistent with current knowledge on ontogenetic changes in elasmosaurids.

Neck elongation pattern

Three groups of elasmosaurids can be recognised based on the neck elongation patterns (two of them with cervical centra longer than high): the "elongated group" (*Elasmosaurus* and *Styxosaurus*), the non-elongate group (*i.e.*, the "plesiomorphic group" *sensu* Otero *et al.* 2015; *Hydrotherosaurus*; *Hydralmosaurus*; *Vegasaurus*) and the aristonectines characterized by cervical centra higher than long (O'Keefe and Hiller, 2006; Otero *et al.*, 2015). Out of these three groups only aristonectines are currently considered to be monophyletic. The definition of the two former groups was given by O'Keefe and Hiller (2006), who defined the elongated group based on the following features: average VLI (125–138), and presence of some mid-cervical vertebrae with VLI between 150 to 200 and, with some exception, the middle cervical centra has VLI higher than 130. Additionally, O'Keefe and Hiller (2006) pointed out that a single mid-cervical centra with VLI higher than 135 is a strong indication of an elongated pattern. On the other hand, the "non-elongated" group has an average VLI much lower than (125–

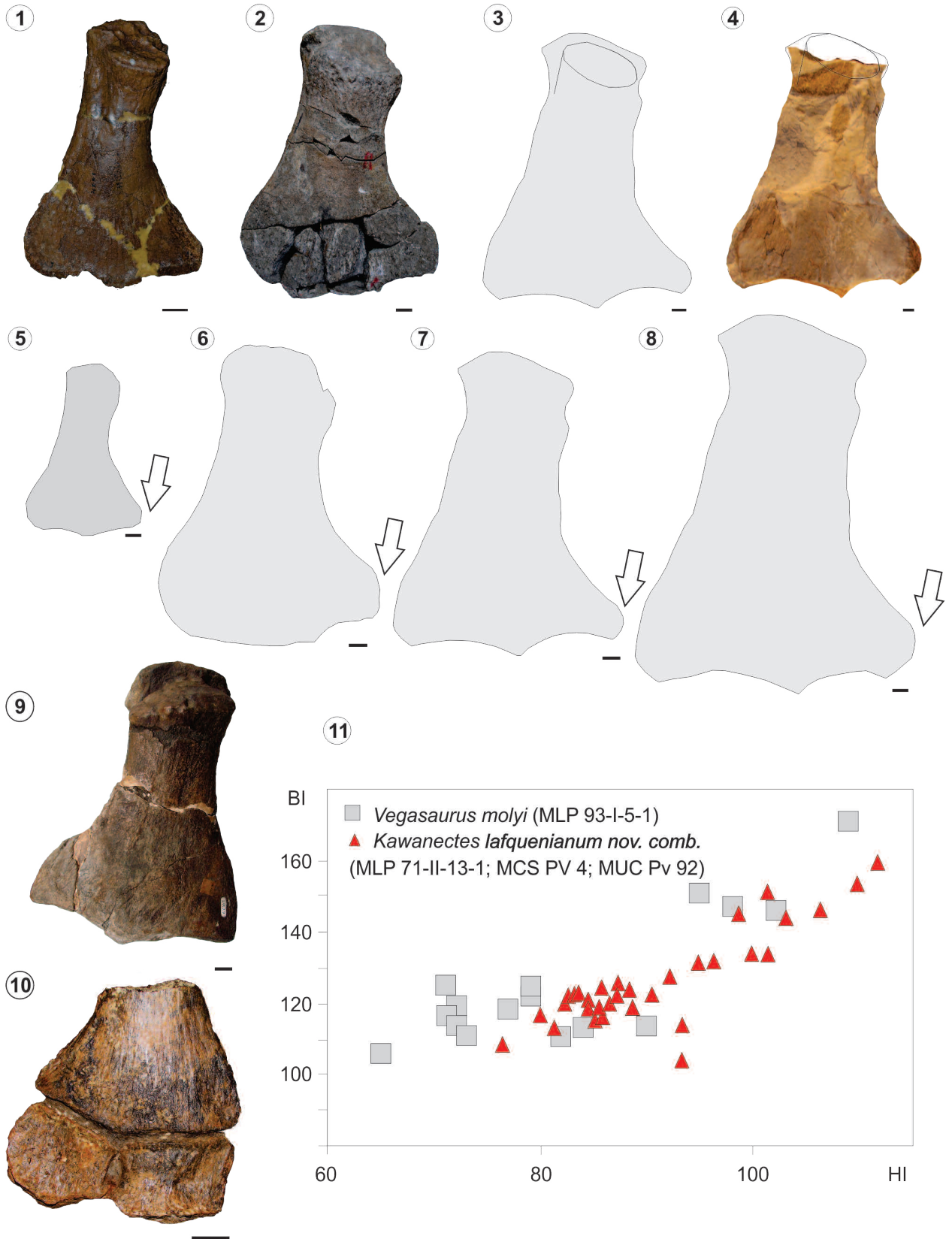


Figure 9. Comparison among the humeri of Weddellian elasmosaurids: 1–4, same size and 5–8, same scale; 1 and 5, *Kawanectes lafquenianum* nov. comb.; 2 and 6, *Vegasauru molyi*; 3 and 7, *Morenosaurus stocki*; 4 and 8, *Kaiwehekea katiki*. White arrows indicate the posterior expansion and accessory facet; 9–10, Comparison between femur of 9, *Maisaurus haasti* lectotype (DM R1529) and 10, *Kawanectes lafquenianum* nov. comb. Arrows indicate posterior accessory facet. Scale bar = 20 mm; 11, plot of the BI vs. HI indexes of *Vegasaurus molyi* and *Kawanectes lafquenianum*.

138) and usually about 100 but the middle cervical centra are nonetheless longer than high. Finally, the aristonectine are characterized by cervical centra higher than long and average VLI lower than 80. One of the main biogeographical patterns indicated by O'Keefe and Hiller (2006) restricts the "elongated group" to the Western Interior Sea.

Following the definition of the three mentioned groups, the cervical centra of *Kawanectes lafquenianum* clearly belong to the non-elongated group. Previously, Otero *et al.* (2015) inferred the presence of elasmosaurids of the "elongated group" (extreme elongated of Otero *et al.*, 2015) in Patagonia during the late Campanian–early Maastrichtian based on the specimens MUC Pv 92, MCS PV 4 and MLP 71-II-13-1 (*i.e.*, holotype and referred specimens of *Kawanectes lafquenianum*). Their inference was based on the assumption that specimens MLP 71-II-13-1, MCS PV 4, and MUC Pv 92 were juveniles and therefore, the centra were not considered to have adult proportions. However, the neural arches of the cervical and dorsal vertebrae of these specimens are fused to the centra indicating their adult condition and, additionally, the pelvic bar of MCS PV 4 is almost formed, showing another adult feature. Furthermore, Otero *et al.* (2015) indicate that the specimen MPEF s/n. (Gasparini *et al.*, 2001: fig. 3-4) from La Colonia Formation (not Allen Formation as indicated by Otero *et al.*, 2015) has a VLI of ca. 110 and belongs to the "elongated group". However, this value does not indicate they belong to the elongated group of O'Keefe and Hiller (2006). Therefore, at least the specimens mentioned here do not provide evidence of the presence of the "elongated group" outside de WIS during the Late Cretaceous.

Phylogenetic relationships

The result of the phylogenetic analysis (Fig. 10) is mostly congruent with previous analyses, but some differences are present. Elasmosauridae is recovered as a monophyletic group, as in previous studies (O'Keefe, 2001; Druckenmiller and Russell, 2008; Benson and Druckenmiller, 2014). The resolution of Elasmosauridae is relatively low, showing the necessity of further work. Nevertheless, Aristonectinae is recovered as monophyletic and well supported (Bremer support = 3) within Elasmosauridae, following the results of other studies (Gasparini *et al.*, 2003a; Otero *et al.*, 2012; Benson and Druckenmiller, 2014). Three other species are

recovered forming a well-supported monophyletic group (Bremer Support = 3) along with Aristonectinae: the Antarctic early Maastrichtian *Vegasaurus molyi* (O'Gorman *et al.*, 2015), the Maastrichtian *Morenosaurus stocki* from the Pacific Coast of California, and the late Campanian–early Maastrichtian *Kawanectes lafquenianum* described in this contribution. This result is congruent and reinforces those of O'Gorman (2013) and O'Gorman *et al.*, (2015), which indicated a phylogenetic relationship between Weddellian and Pacific non-aristonectine elasmosaurids and Aristonectinae.

Kawanectes and aristonectine elasmosaurids

The classical questions about the origin of Aristonectinae are: "Within which clade?"; "How?"; "When?" and "Where?". The first point has produced several difficulties because for many years the elasmosaurid affinity of Aristonectinae was not considered the most probable hypothesis (Welles, 1962; Cruickshank and Fordyce, 2002; O'Keefe and Street, 2009 but see Cabrera, 1941). Aristonectines have been only recently considered a clade within Elasmosauridae (Gasparini *et al.*, 2003a; Otero *et al.*, 2012, 2014b). The recent consensus about their phylogenetic affinities allows answering the other questions mentioned. The appearance of aristonectine (*Aristonectes*, *Kaiwhekea*) features such as short cervical vertebrae, large skulls and high number of teeth probably involved a poorly understood complex sequence of character acquisition; however, this process probably involved some paedomorphic events (O'Gorman, 2013, O'Gorman *et al.*, 2014; Araújo *et al.*, 2015). The question of the time of appearance should be answered by the age of the oldest aristonectine record which is, until now, late Campanian–early Maastrichtian (O'Gorman *et al.*, 2013a) and comes from Patagonia (Río Negro Province). Additionally, a fragmentary postcranial specimen from the upper Campanian Herbert Sound Member of the Snow Hill Island Formation (James Ross, Antarctica) was referred to the aristonectines by Otero *et al.* (2014a: fig 6). Therefore, until now the oldest record of Aristonectinae seems to be late Campanian in age. However, the Santonian *Futabasaurus suzukii* was recovered within Aristonectinae by Otero *et al.* (2014b) but not by O'Gorman *et al.* (2015) and thus the possibility of an older (at least Santonian) origin has been proposed. Finally, the previous absence of aristonectines outside the Weddellian Province, with the only and controversial possibility of the



Japanese *F. suzukii* and the presence of non-aristonectine elasmosaurids closely related with them in the Weddellian Province, was considered as strong support of a Weddellian origin of aristonectines (O'Gorman *et al.*, 2015). Nonetheless, a recent record from the lower Maastrichtian of Angola (Araújo *et al.*, 2015) generates some doubts as they are now not endemic from the Weddellian Province. The internal relationships between *Kawanectes*, *Vegasaurus*, and *Morenosaurus* are important in order to answer the question about the geographical origin of aristonectines because if *Kawanectes* and *Vegasaurus* are more closely connected with aristonectines than *Morenosaurus* or *Futabasaurus*, a Weddellian origin can still be considered as more likely. Still, the results of the analysis are not conclusive on this point because the relationships of these taxa are not clear because they are depicted as part of a polytomy in the phylogenetic analysis. Also, the results show an internal relationship between some aristonectines and some non-aristonectine elasmosaurids from the Weddellian Province and California, a relation previously commented by O'Gorman *et al.* (2015).

The Kawas plesiosaur assemblage

The Kawas plesiosaur fauna (included in the upper Campanian–lower Maastrichtian Allen, Los Alamitos [“Coli Toro Inferior”], and La Colonia formations) is a remarkable association for several reasons. It comprises the three major groups of Late Cretaceous plesiosaurs: polycotylids, aristonectines, and non-aristonectine elasmosaurids (Gasparini and Spalletti, 1990; Gasparini and Salgado, 2000; O'Gorman *et al.*, 2013a, b; O'Gorman and Gasparini, 2013). Each of the three groups are represented by more than one specimen and in particular *Kawanectes* is represented by at least three specimens. The depositional environment of the Allen, La Colonia and Coli Toro formations has been inferred as a marine marginal to non-marine environment (Barrio, 1990; Gasparini and Salgado, 2000; Pascual *et al.*, 2000; Gasparini *et al.*, 2015). Thus, it is remarkable that plesiosaurs are almost the unique faunal elements with strict marine affini-

ties. Therefore, this indicates the occupation of a non-marine normal environment by the three groups of plesiosaurs in the Weddellian Province, similar to that inferred by Benson *et al.* (2013) in early–middle Albian deposits of Australia. Another particular feature of *Kawanectes*, probably related to the particular environment of the Allen Formation, is its strikingly small size compared to other adult elasmosaurids. A similar case was recorded by Sato *et al.* (2005) at the Dinosaur Park Formation (late Campanian) where sub-adult specimens were smaller than those recorded in nearby marine formations. Similarly, elasmosaurs from the Allen and La Colonia formations have a smaller body size compared with those from the marine Jagüel Formation (O'Gorman *et al.*, 2013b; Gasparini *et al.*, 2015).

ACKNOWLEDGMENTS

This research was supported by projects PICT 2012-0748, UNLP N 677, UNLP N 607 and PIP 0433. The author thanks Z. Gasparini and M. Fernández for reading an earlier version of the manuscript and Z. Gasparini, L. Salgado, I. Cerda and Y. Herrera for the fieldwork and L. Acosta Burrelle for the preparation of some specimens. Thanks P. Arregui for improving the English of this contribution. The author also thanks the curators of Museo de La Plata (M. Reguero), Museo Paleontológico Egidio Feruglio (E. Ruigómez), Museo Municipal de Lamarque (D. Cabaza), Museo de Cinco Saltos (I. Cerda), Museo de la Universidad del Comahue (L. Salgado), University of California, Museum of Paleontology (P. Holroy), Natural History Museum of Los Angeles (M. Walsh), Geology Museum, University of Otago (E. Fordyce), Museum of New Zealand Te Papa Tongarewa (A. J. D. Tennyson) for providing access to the material. Finally, the author thanks R. Otero (Laboratorio de Ontogenia y Filogenia, Departamento de Biología, Facultad de Ciencias, Universidad de Chile) and an anonymous reviewer for its comment that improve this contribution.

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Figure 10. Strict consensus of 250 most parsimonious trees (1424 steps, CI = 0.284 and RI = 0.673). Bremer support values are given below selected nodes.

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doi: 10.5710/AMGH.29.11.2015.2928

Submitted: June 11th, 2015

Accepted: November 29th, 2015