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Reappraisal of *Fresnosaurus drescheri* (Plesiosauria; Elasmosauridae) from the Maastrichtian Moreno Formation, California, USA

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ABSTRACT

The elasmosaurid *Fresnosaurus drescheri*, Welles from the contact between the Tierra Loma/Marca members of the Moreno Formation (Maastrichtian), California, USA is reviewed. Most of the features included in Welles's original diagnosis are considered related only to the juvenile ontogenetic stage of the holotype and only specimen. The new diagnosis is based on diagnostic characters of the ilia, including long rectangular shaped sacral facets located in the dorsal part of the shaft, two gentle knobs in the shafts and unexpanded dorsal end. Additional material from the Moreno Formation (numbered under the same number as the *F. drescheri* holotype but not mentioned by Welles and therefore considered part of a different specimen) are described for the first time. The latter are referred to the aristonectine, being the first evidence of aristonectines from the North Hemisphere.

1. Introduction

Elasmosaurids were successful cosmopolitan Cretaceous plesiosaurs that reached the Cretaceous/Paleogene (K/Pg) boundary without any evidence of diversity decrease prior to the extinction (Gasparini et al., 2003, 2007; Vincent et al., 2011). The knowledge of the North American Late Cretaceous elasmosaurids is mostly based on records from the Western Interior Seaway (WIS) which expands from the Cenomanian to Campanian stages (Welles, 1962; Carpenter, 1999). Additionally, the final part of the Cretaceous is well recorded in the Pacific Coast, where a rich assemblage of elasmosaurids occur in the Maastrichtian Moreno Formation, Fresno County, California (Welles, 1943; Workman Ford, 2006; Fig.1).

The Maastrichtian elasmosaurids from California were first mentioned by Stock (1939), and later described by (Welles, 1943) in his now classical contribution where he erected four monotypic genera: *Hydrotherosaurus alexandrae*, *Morenosaurus stocki*, *Aphrosaurus furlongi* and *Fresnosaurus drescheri*. Welles (1943:181) described *F. drescheri* based on the holotype and only specimen originally cataloged as CIT 2758, CIT (California Institute of Technology), now housed in the LACM (Natural History Museum of Los Angeles County) as LACM 2758. Later Welles (1952) pointed out that although the holotype of *F. drescheri* belong to a juvenile specimen it is distinguishable from other known juvenile elasmosaurids. After the work of Welles little attention was paid to *F. drescheri* or the plesiosaurs from the Moreno Formation, probably due to the absence of well preserved cranial material. However, the mosasaur fauna from the Moreno Formation has been recently reviewed (Lindgren & Schulp, 2010) and additional work related to the stratigraphical position of the marine reptiles along the sections has been performed (Workman Ford, 2006). At the same time, the classical elements of the plesiosaur fauna from the Paleobiogeograohic Weddellian Province (i.e. South of South America; Western Antarctica and New Zealand) were also reviewed (Hiller et al., 2014; Otero et al., 2014; O'Gorman et al., 2015; O'Gorman, 2016). The new results indicate a possible close phylogenetical relationships between some elasmosaurids from the Weddellian Province (i.e. the aristonectine and the non aristonectine*Vegasaurus molyi* and *Kawanectes lafquenianum*) and some from California (Moreno Formation) such as *Morenosaurus stocki* (O'Gorman et al., 2015; O'Gorman, 2016). Additionally aristonectine were recently recorded in Angola, extending its previous known geographic range outside the Weddellian Province (Araujo et al., 2015). Therefore, the revision of the elasmosaurids from the Moreno Formation is necessarily in order to complete the general view of the

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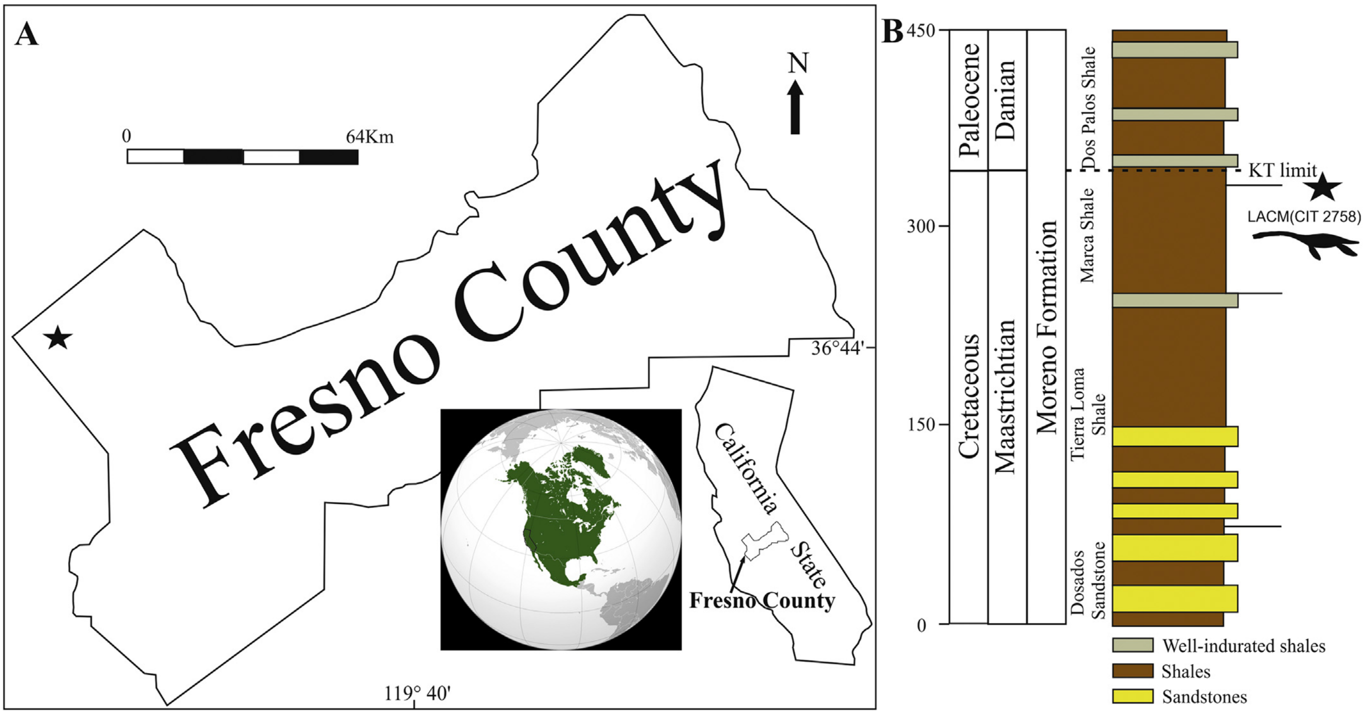

Fig. 1. **A**, locality where the LACM 2758, *Fresnosaurus drescheri* holotype, was collected (black star). **B**, generalized column of the Moreno Formation showing the level where the LACM 2758 was collected (Adapted from Worman Ford, 2006).

elasmosaurid diversity of the final stage of the marine reptiles in the Pacific coast of North America and to clarify the relation between those of the Weddellian Province.

The aim of this paper is to redescribe *Fresnosaurus drescheri*, describe material previously not mentioned from the Moreno Formation, discuss the validity of *F. drescheri* and the significance of the plesiosaur fauna of the Moreno Formation among the Pacific elasmosaurids.

2. Geological setting

The Moreno Formation is a classic sedimentary sequence that represents a continuous deposition of marine sediments across the K/Pg boundary (McGuire, 1988; Workman Ford, 2006). The sequence records the shoaling of the central San Joaquin basin to shelf depths during the middle Maastrichtian and late Danian interval (McGuire, 1988). The Moreno Formation is divided into four conformable members: Dosados, Tierra Loma, Marca and Dos Palos members (Fig. 1B). The sequence records the transitions among base of slope turbidite facies (Dosados Member and lower Tierra Loma Member); an oxygen-deficient lower to middle slope shale facies (Tierra loma Member); an upwelling-related anoxic upper slope shale facies (Marca Member); upper slope to shelf-edge shale and mudstone facies (lower Dos Palos Member) and a sediment starved outer shelf glauconite shale facies of the upper Dos Palos Member (McGuire, 1988).

The K/Pg boundary is within the Moreno Formation, inferred where the benthic foraminifera *Siphogenerinoides whitei* disappears from the record, 6.7 m above the Marca Member/Dos Palos Member contact (Worman Ford, 2006). This placement coincides with McGuire's (1988), just above the top of the Marca Shale.

The Moreno Formation has a rich fauna of marine reptiles including the turtle *Basilemys*, elasmosaurids such as *Morenosaurus stocki* and *Hydrotherosaurus alexandrae* (Welles, 1943), mosasaurids such as *Plotosaurus*, *Plesiotylosaurus*, *Prognathodon*, cf. *Mosasaurus* and *Halisaurus* (Lindgren & Schulp, 2010) and hadrosaurids (Morris, 1973).

3. Material and methods

All the linear measurements of the material were taken using an electronic caliper that allows accuracy of 0.01 mm. Following Welles (1952), the indices taken into account the ratio between height (H) and length (L) of the vertebral centrum ($HI = 100*H/L$), and the ratio between breadth (B) and length of the centrum ($BI = 100*B/L$). In addition, the ratio between the breadth and height ($BHI = 100*B/H$) was considered. Both breadth and height were measured in this work on the posterior articular face of the vertebra. Additionally, the vertebral length index [$VLI = L/(0.5*(H + B))$] was also used. Furthermore, the categories of ontogenetic development proposed by Brown (1981) based on the fusion of the neural arch to the vertebral centrum were considered to differentiate the “adult” and “juvenile” conditions. The specimens considered for the comparison are indicated in Table 2.

Institutional Abbreviations—**AMNH**: American Museum Natural History, New York, USA; **CM**, Canterbury Museum, Christchurch, New Zealand, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles County, USA (previously housed on the **CIT**, California Institute of Technology, California); **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; **NZGS**, Nuclear and Geological Science, Lower Hut, New Zealand; **SGO PV**, Área Paleontologia, Museo Nacional de Historia Natural, Santiago de Chile, Chile; **TTU P**, Museum of Texas Tech University, Texas, USA; **UCMP**, Museum of Paleontology, University of California, Berkeley, California, USA.
Anatomical Abbreviations—**af**, acetabular facet; **ak**, anterior knob; **pez**, prezygapophysis; **poz**, postzygapophysis; **mvp**, mid

Table 1
Juvenile elasmosaurid specimens considered for comparison, data taken from Brown, 1913; Sato and Wu, 2006[1]; Otero et al., 2014[2]; O'Gorman et al., 2014[3]; O'Gorman et al., 2013, 2014[4]; Araujo et al., 2015[5].

Material	Locality and age
Juveniles specimens	
AMNH 5261: *Leurospondylus ultimus* (nomen dubium) Elasmosauridae indet.[1]	Red Deer River, Canada. Horseshoe Canyon Formation of the Edmonton Group. Upper Campanian?-Maastrichtian
SGO. PV. 260: *Aristonectes quiriquinensis*.[2]	Las Tablas Bay, Biobío Region, Chile. Quiriquina Formation. Maastrichtian
MML PV 5: Aristonectinae indet.[3]	Salinas de Trapalcó, Río Negro Argentina. Upper part of the Jagüel Formation. Upper Maastrichtian
MLP 89-III-3-2: Aristonectinae indet.[4]	Seymour Island (*I. Marambio*), Antarctic Península. López de Bertodano Formation, Klb 9. Upper Maastrichtian
NZGS, CD 428: Aristonectinae indet.[5] and NZGS, CD 429: Aristonectinae indet.[5]	Mangaouanga Streem. New Zealand. Maungataniwha Sandstone Member of the Tahora Formation. Upper Campanian-lower Maastrichtian
Adult specimens	
LACM 2802: *Morenosaurus stocki* holotype	Panoche Hills, California, Tierra Loma Member of Moreno Formation. Upper Maastrichtian
LACM 2748 *Aphrosaurus furlongi* holotype	Panoche Hills. California, Moreno Formation (unknown member). Upper Maastrichtian
UCMP 33912 *Hydrotherosaurus alexandrae* holotype	Panoche Hills. California, Tierra Loma Member of Moreno Formation. Upper Maastrichtian

Table 2
Aristonectinae? indet. Vertebral measurements of LACM 2758, additional material (in mm): L, length; H, height and B, breadth, indexes HI, (HI = 100*H/L), BI, (BI = 1 0*B/L), BHI, (BHI = 100*B/H) and VLI, [VLI = 100*L/(0.5*(H + B))]. d, dorsal, s, sacral, ca, caudal.

Vertebrae	L	H	B	HI	BI	BHI	VLI	Num. for, ventrales
1p	32.62	48.55	73.6	149	226	152	53	2?
1d	32.4	41.8	64.4	129	199	154	61	2?
2d	31.5	41.8	61.2	133	194	146	61	2
3d	36.1	48.9	68.3	135	189	140	62	3?
4d	34.1	49.2	68.3	144	200	139	58	2
5d	36.6	50	67.6	137	185	135	62	2
6d	34.9	52.1	68.2	149	195	131	58	2?
7d	37.2	53.1	69.2	143	186	130	61	2
8d	35.3	51.7	66.55	146	189	129	60	–
9d	35.28	50.58	68.8	143	195	136	59	4?
10d	41.6	51.6	64.04	124	154	124	72	2?
11d	34.2	51.6	66.08	151	193	128	58	2
12d	34.6	50.4	71.6	146	207	142	57	2
13d	35.1	43.7	67.9	125	193	155	63	–
14d	35.2	47.08	65.8	134	187	140	62	–
15d	35.2	49.26	71.7	140	204	146	58	2
16d	34.6	42.8	64.3	124	186	150	65	2
17d	35.8	43.8	63.2	122	177	144	67	2
18d	32.7	42.8	61.69	131	189	144	63	2
1s	32.4	42.5	64.07	131	198	151	61	2?
2s	33.37	45.5	65.49	136	196	144	60	2
3s	33.05	42.7	63.24	129	191	148	62	1
4s	27.4	43.7	57.1	159	208	131	54	–
1ca	28.4	42.3	60.1	149	212	142	55	1?

ventral process; **pa**, parapophyses; **pf** pedicellar facets; **pk**, posterior knob; **sf**, sacral facet; **vf**, ventral foramina.

4. Systematic paleontology

Sauropterygia Owen, 1860
Plesiosauria de Blainville, 1835
Plesiosauroidea Welles, 1943
Elasmosauridae Cope, 1869
Fresnosaurus Welles, 1943

Fresnosaurus drescheri Welles, 1943
Figs. 2–3

Fresnosaurus drescheri: Camp, Welles, Green, 1949: 279
Fresnosaurus drescheri: Welles, 1952: 103 fig. 24
Fresnosaurus drescheri: Welles, 1962: 73 fig. 19

Holotype and only specimen. LACM 2758, coracoids, humerus, pelvic girdle, femora and disarticulated paddle elements (Welles 1943: fig 27).
Type locality and horizon. CIT locality 346, Panoche Hills, Fresno County, California, USA. Contact levels between the Tierra Loma and Marca members of the Moreno Formation, Maastrichtian (McGuire, 1988; Workman Ford, 2006).
Revised diagnosis. ilium with dorsal rectangular shaped sacral facets; one anterior knob in the ventral area of the sacral facet; posterior knob in the posterior margin of the middle shaft. Additional useful features: ilium distally unexpanded.

Holotype statement. During the revision of the LACM 2758 several vertebral centra and neural arches labeled in the same way as the holotype material were discovered. This represents a problem regarding the constitution of the *Fresnosaurus drescheri* holotype (See Discussion). Three elements must be taken in to account 1) Welles did not mentioned any vertebra or neural arch or describe them (Welles, 1943). 2) Welles (1943: Table 14) stated that the vertebrae of *F. drescheri* are "unknown" and 3) the ICZN art 73.1.3 stipulates that "the holotype of a new nominal species-group taxon can only be fixed in the original publication and by the original authors". Additionally a deep research into the collection records did not provide evidence that prove that the vertebrae belong to the holotype specimen. Therefore although the additional material could be part of the same specimen (shared ontogenetical stage, color and other taphonomical features) is here described as a different specimen, although all are numbered under LACM 2758.
Description
LACM 2758 (*Fresnosaurus drescheri* holotype)
Appendicular skeleton. The elements of the holotype of *Fresnosaurus drescheri* LACM 2758 were carefully described by Welles (1943) and there are only a few remarks and new figures added.

Both coracoids are preserved. The main features recorded are the presence of mid-ventral process, dorsal ridge and posterior ramus that embrace a cordiform fenestra (Fig. 2A, B). The distal expansion shows a laterally and medially expanded distal end (Fig. 2A, B).

The other elements of the pelvic girdle also have remarkable features. The pubes are anteroposteriorly short (Fig. 2C). The right ischium is relatively gracile, particularly near the glenoid (Fig. 2C). Additionally, the symphyseal surface is thickened only near the anterior limit and the iliac facet is well defined.

The most distinctive element represented in LACM 2748 is the ilium. Welles described the ilia (Welles, 1943:182), incorrectly

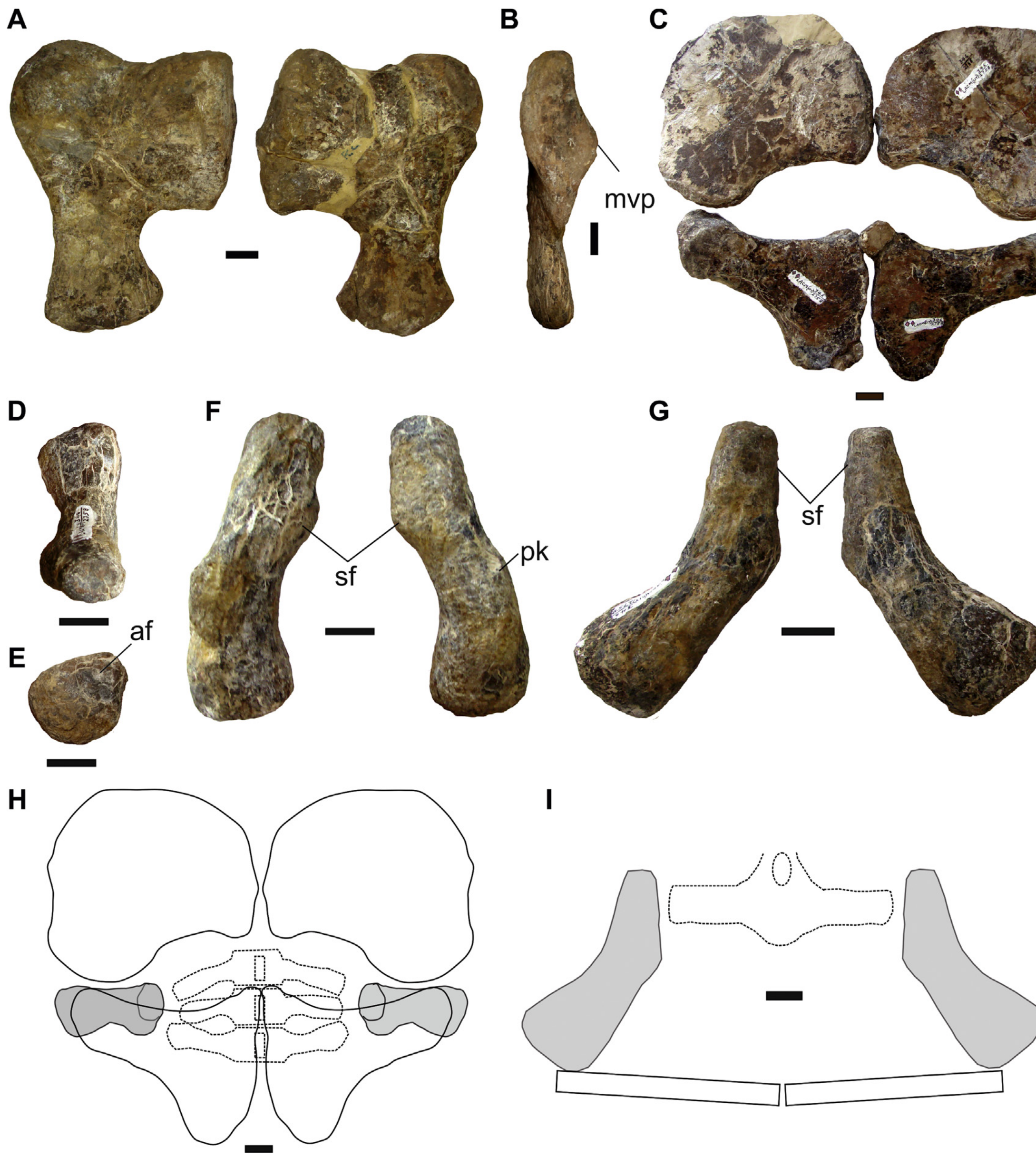

Fig. 2. LACM 2758 *Fresnosaurus drescheri* holotype. **A-B** coracoids in **A**, ventral and **B**, symphysial views. **C**, pelvic girdle in dorsal view; **D**–**G**, ilium in **D**, dorsal **E**, ventral, **F**, medial and **G**, anterior views; **H**–**I**, diagrams showing the position of the ilia, pelvic girdle and sacral region in **H**, dorsal and **I**, anterior views. Scale bars represent 20 mm.

describing them as "ischia" at the beginning of the paragraph: "*Pelvis and femur* {sic} The Ischia are arched laterally and have a large rugosity on the posterior margin about one-third the distance …". This elements are now included in the revised diagnosis of *Fresnosaurus drescheri*.

The ilia were described by Welles (1943) but because they are considered essential in the diagnosis, they are re-described here. Both ilia are preserved (Fig. 2D–G). The ilia have a dorsal unexpanded end (Fig. 2G). The distal end is lateromedially compressed, with elliptic cross section (Fig. 2D). The medial surface bears a rectangular facet interpreted as the sacral facet (Fig. 2F). The anteroventral limit of the sacral facet generates a convex region, better preserved in the right ilium (Fig. 2F). The middle zone shows a marked posterior curvature that generates a posterior knob (Fig. 2F). The ventral region has the largest cross section and has a larger ischial facet and a smaller, not well defined anterodorsal acetabular facet (Fig. 2E). The inferred position of the ilia and pelvic girdle is given in Fig. 2H, I.

The femur is longer than the humerus, an interesting feature when compared with the usual condition among adult elasmosaurids that show a humerus longer than the femur (Fig. 3A–D; Welles, 1943; Sato, 2002; Kubo et al., 2012; O'Gorman et al., 2015). Additionally, other limbs elements are preserved but it is not possible to be sure about its identity (Fig. 3D) but based on their relative size epipodial, mesopodial and basipodial elements are probably represented.

LACM 2758 (Additional material)
Aristonectinae? indet.
Figs. 4–5

Material. LACM 2758 (Additional material), postcranial skeleton consisting of vertebral centra (one pectoral, eighteen dorsals, three to four sacrals and one caudal);
Type locality and horizon. CIT locality 346, Panoche Hills, Fresno County, California, USA. Contact levels between the Tierra Loma

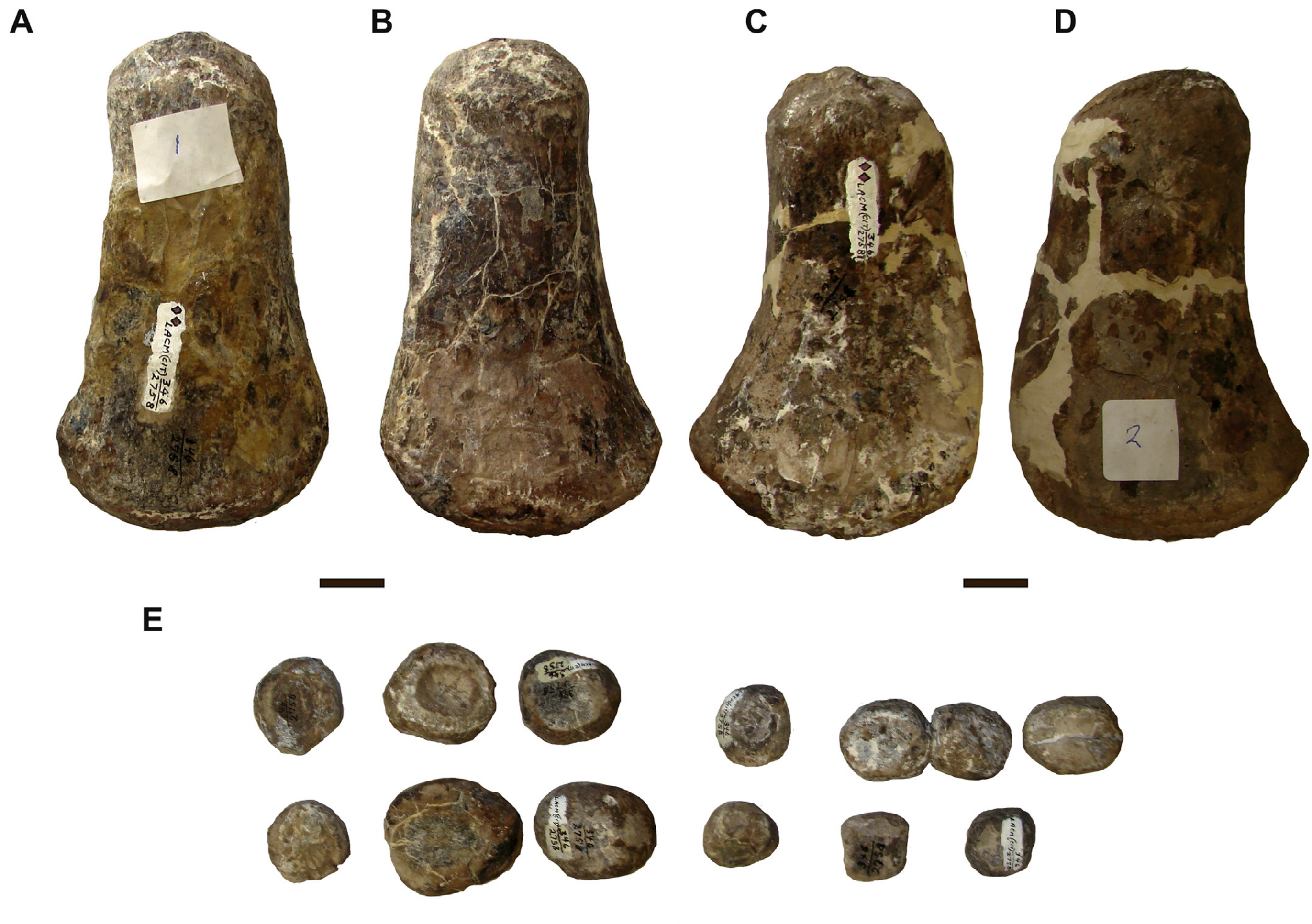

Fig. 3. C.I.T 2758 *Fresnosaurus drescheri* holotype. **A**–**B**, femur; **C**, **D**, humerus; **E**, epipodial and mesopodial and basipodial elements. Scale bar represents 20 mm.

and Marca members of the Moreno Formation. Maastrichtian (McGuire, 1988; Workman Ford, 2006).

Description

Axial skeleton. Welles (1943, 1952, 1962) did not describe or mention the presence of vertebral centra and neural arches among the elements of the holotype (Welles, 1943:181). It is not clear why these vertebral elements are labeled under the same number as the holotype (Fig. 4A–C)

The only pectoral centrum is higher than long and broader than high (Fig. 4D–G; Table 1). The pedicellar facets have a rectangular shape and are strongly laterally inclined (Fig. 4D). The ventral surface is pierced by two ventral foramina (Fig. 4F). The dorsal centra are broader than high and higher than long (Fig. 4H–J; Table 1). The pedicellar facets are rectangularly shaped and laterally inclined (Fig. 4H). Ventrally, there are two or three ventral foramina (Fig. 4J). Three to four sacral vertebrae are preserved. The number of sacrals cannot be well established due to the poor preservation of the material. The sacral centrum is broader than high and higher than long with one ventral foramina (Fig. 4K–N). The caudal centrum is distinctively high and bears a poorly defined parapophysis laterally (Fig. 4O–R).

Eighteen neural arches were preserved. The pedicels of the dorsal neural arches are rectangularly shaped with the articular faces inclined laterally. The diapophyses are rounded and are slightly dorsally directed. The neural spine is anteriorly broad and rectangularly shaped in dorsal view. The left and right prezygapophyses do not contact in the midline and the same is observed in the postzygoapophyses (Fig. 5A–D).

The sacral neural arch shows a neural spine more laterally compressed than the dorsal ones but relatively higher. The pedicellar facets are relatively larger and confluent with the diapophyseal part of the transverse process (Fig. 5E–G). The caudal neural arch shows the zygapophyses not meeting in the midline (Fig. 5H–J)

5. Discussion

5.1. Holotype, juvenile condition and diagnosis

The first problem that emerges when the holotype is reviewed is the existence of material not mentioned by Welles (1943) under the same collection number of the holotype of *Fresnosaurus drescheri*. This is a central issue because the type specimen is of considerable importance as the holotype is a name–bearing entity in zoological taxonomy (ICZN) and to avoid nomenclatural confusion the holotype must be a single individual. The observations about the identical labeling and additional color, preservation and ontogenetic stage, congruent with the elements mentioned by Welles (1943, 1952, 1962) indicate the same origin and curatorial history. Additionally Welles commented "The California Institute of Technology has collected additional reptilian remains from the Moreno

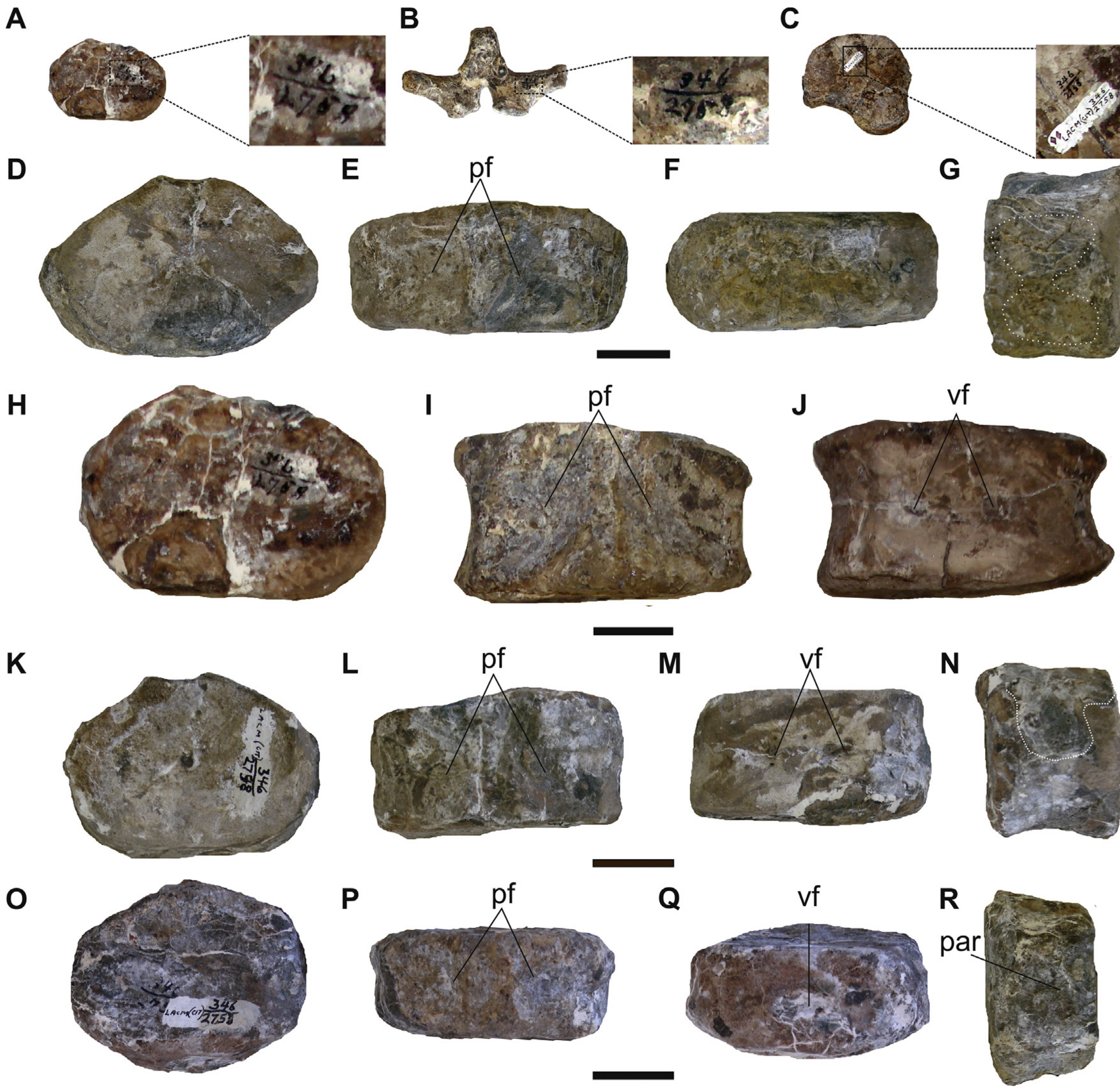

Fig. 4. Aristonectinae? indet. LACM 2758 (Additional material). **A**–**C**, labeling of material of the material **A**, dorsal centrum, **B**, dorsal neural arch and **C**, pubis (LACM 2758 holotype). **D**–**G**, pectoral centrum in **D**, anterior, **E**, dorsal, **F**, ventral and **G**, left lateral view; **H**–**J**, dorsal centrum in **H**, anterior, **I**, dorsal and **J**, ventral views; **K**–**N**, sacral centra in **K**, anterior, **J**, dorsal, **M**, ventral and **N** left lateral views; **O**–**R**, caudal vertebrae in **O**, anterior, **P**, dorsal, **Q**, ventral and **R**, left lateral views. Scale bars represent 20 mm.

formation near the *Hydrotherosaurus* locality (Stock, 1939). This material consist of parts of six skeletons; four are relatively complete, the other two are fragmentary. Three are juveniles" Welles 1943:165. The three juveniles form part of the collection of the CIT (now in the LACM) but Welles did not mention any additional juvenile specimen. However Welles did not mention vertebral material among the holotype of *Fresnosaurus drescheri* and even stated that the vertebral material of *Fresnosaurus drescheri* was "unknown" (Welles, 1943: table 14) Therefore in order to resolve this problem here we considered as part of the holotype only the material mentioned and described by Welles and the additional vertebral material is considered part of a different specimen (also numbered under LACM 2758) but here indicate as LACM 2758 (additional material).

Due the juvenile stage of the holotype LACM 2758, some features mentioned in the diagnosis by Welles (1943) are probably related to the juvenile condition of the specimen. Therefore, these features are probably not useful in diagnosing *Fresnosaurus drescheri* because they vary with ontogeny and are likely to be shared by other elasmosaurids. Welles (1943) took note of that and skillfully dealt with this problem comparing *F. descheri* with other North American genera based on juvenile specimens: *Ogmodirus* Williston and Moodie, 1913 and *Leurospondilus* Brown, 1913 both currently considered nomen dubium (Welles, 1962; Sato and Wu, 2006).

The second step in our analysis is to determine which features of *F. drescheri* are probably only related to its ontogenetic stage and which could be used to diagnose it. This issue is difficult to discuss and it is not possible to be sure due to the absence of complete growth series of most of the elasmosaurid genera. Additionally, this is an issue not resolved in other plesiosaurid groups (O'Keefe and Byrd, 2012). In order to determine which features are related to the juvenile stage of LACM 2758 a comparison with other juvenile elasmosaurids specimens from the Late Cretaceous was performed (Table 2) looking for the features used by Welles (1943) to diagnose *F. drescheri*.

"Coracoid short, broad and thick, weakly concave anteriorly, not projecting in front of the glenoid in midline [i.e. without coracoid

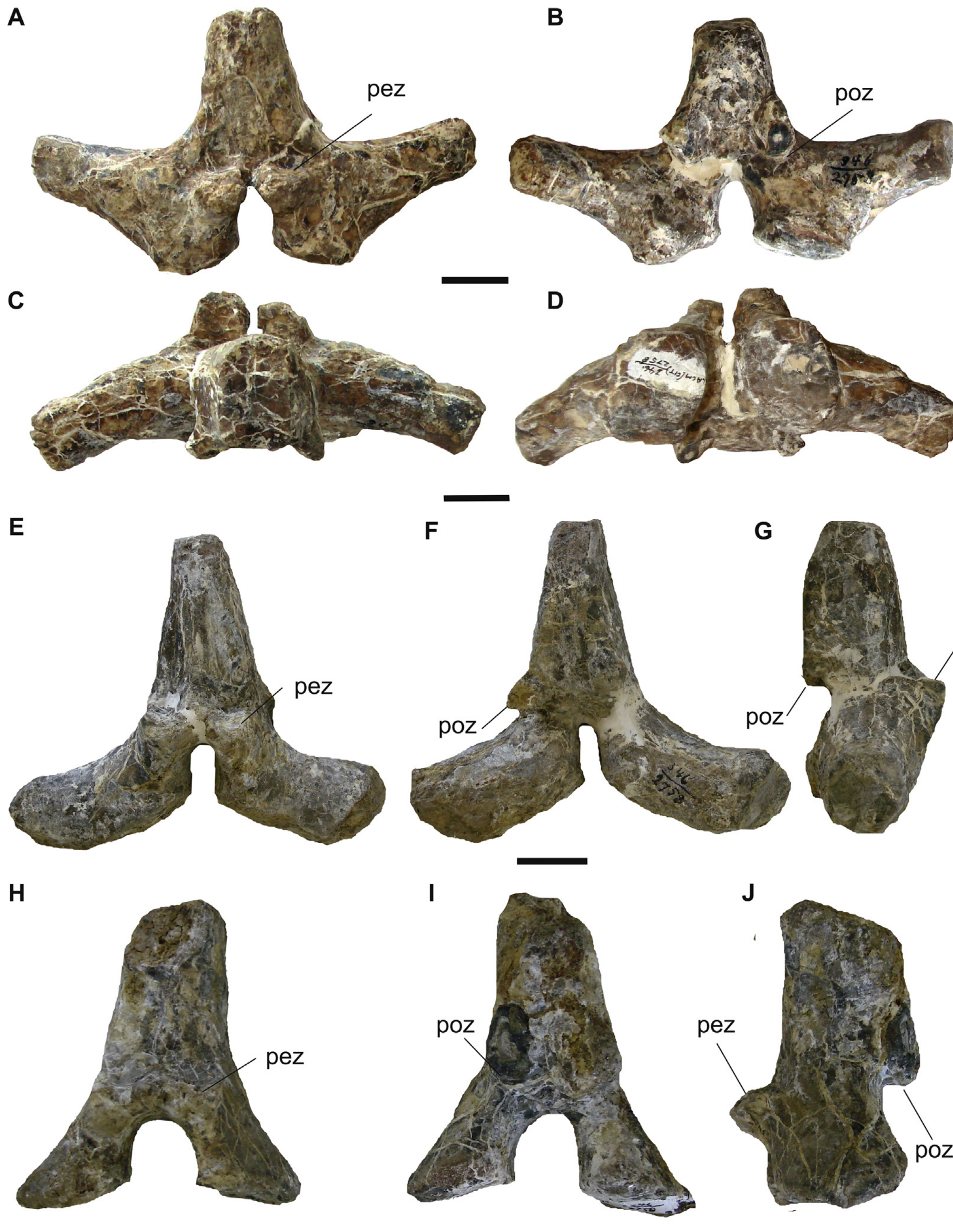

Fig. 5. Aristonectinae? indet. LACN 2758 (Additional material). **A**–**D**, neural arch of dorsal vertebrae in **A**, anterior, **B**, posterior, **C**, dorsal and **D**, ventral views; **E**–**G** neural arch of pectoral vertebrae in **E**, anterior, **F**, posterior and **G** right lateral views; **H**–**J**, neural arch of caudal vertebrae in **H**, anterior, **I**, posterior and **J**, left lateral view. Scale bars represent 20 mm.

anterior process], and with short posterior shaft only slightly expanded posteriorly. Inter-coracoid cordiform vacuity broad". Coracoid "short and broad" is a feature observed in all the juvenile specimens of elasmosaurids available (Fig. 6A–F), independently of the real size of the coracoid and its thickness, and therefore it is probably related to the general stocky morphology of juvenile elasmosaurids. The slightly concave anterior margin is observed also in the juveniles MML PV 5 and SGO PV 260 (Fig. 6B, C) and is at least partially related to the absence of development of both the anterior process, which is short and blunt in juveniles, and also to the lack of development of the anterior margin of the glenoid facet (Fig. 6A–F). Finally, the cordiform fenestra is shared by all elasmosaurids and the broad condition is directly linked with the broadness of the entire coracoid. To compare these with a more adult condition (Figs. 6G, 7A, B, D, E).

"Femur with only slight posterior expansion and no constriction in the shaft. Humerus with slight development of shaft and round anterodistal and distal border". The presence of undifferentiated or only slightly differentiated shaft and distal end unexpanded is also observed in other juvenile elasmosaurids and it is connected with the lack of differentiation of the distal end (Moodie, 1911; Wiffen and Moisley, 1986:fig. 18; O'Gorman et al., 2014:fig. 4A–H).

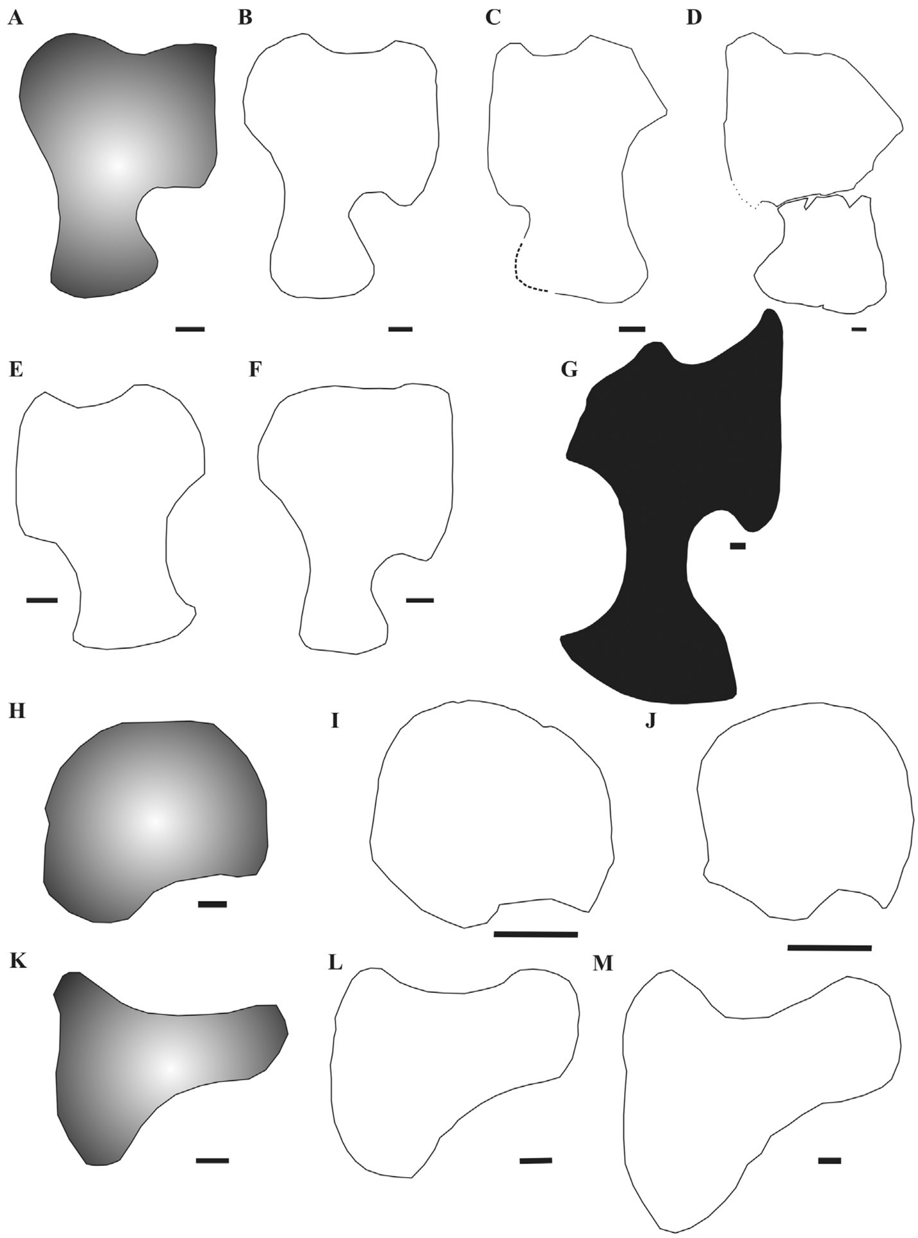

Fig. 6. Generalized diagrams for comparisons. **A**–**G**, coracoids of juvenile (**A**–**F**) and adult (**G**). **A**, *Fresnosaurus drescheri* holotype: LACM 2758, **B**, MML PV 5: Aristonectinae indet., **C**, SGO PV 260: *Aristonectes quiriquinensis*, **D**, MLP 89-III-3-2: Aristonectinae indet., **E**, AMNH 5261: Elasmosauridae indet. **F**, NZGS, CD 428 elasmosauridae indet. **G**, LACM 2748: *Afrosaurus furlongi*. **H**–**J**, diagram of pubes, **H**, LACM 2758: *Fresnosaurus drescheri* holotype, **I**, MML PV 5, Aristonectinae indet. **J**, SGO PV 260, Aristonectinae indet. **K**–**M** diagram of different Ischia. **K**, LACM (C.I.T 2758) *Fresnosaurus drescheri*. **L**, MML PV 5 Aristonectinae indet. **M**, SGO PV 260 *Aristonectes quiriquinensis*. (**A**–**H**, **K**, **M**) Scale bars represent 20 mm; **I** and **J** Scale bars represent100 mm.

"Femur longer than humerus": This is not common among elasmosaurids, however allometric growth of propodials has been recorded among Sauropterygia Caldwell (1997), Sanders (1989), Kear (2007), and Vincent (2010) and therefore it is not useful to diagnose *F. drescheri*.

"Pubes convex anteriorly, with posterodistal concavity much longer than postero-external, not projecting posteriorly in midline to form pelvic bar" (Fig. 6H). The convexity of the pubes is shared by all the juvenile specimens considered for comparison (MML PV 5, SGO PV 260, CMN 9454 and GNS CD 429; Fig. 6I, J; Brown, 1913:fig. 6; Araujo et al., 2015) and the absence of lateral concavity is probably also a feature probably connected with the juvenile ontogenetic stage due the lack of complete development of the glenoid area and the anterior margin. The only feature that seems to be distinctive because it is not shared by the comparison material (MML PV 5 and SGO PV 260) is the lateral elongation related to the anteroposterior length.

"Ischium short anteroposteriorly" (Fig. 6K). The shortness of the ischium is also a feature observed in other juvenile elasmosaurids (Otero et al., 2012; O'Gorman et al., 2014) due to the progressive extension of the posterior ramus during ontogeny (Fig. 6L, M).

"Ilium not compressed anteroposteriorly at proximal end, with large posterior rugosity one-third the way down the shaft". The ilium of *F. drescheri* is distinctive because it has three remarkable features: planar subrectangular "sacral facet", anterior and

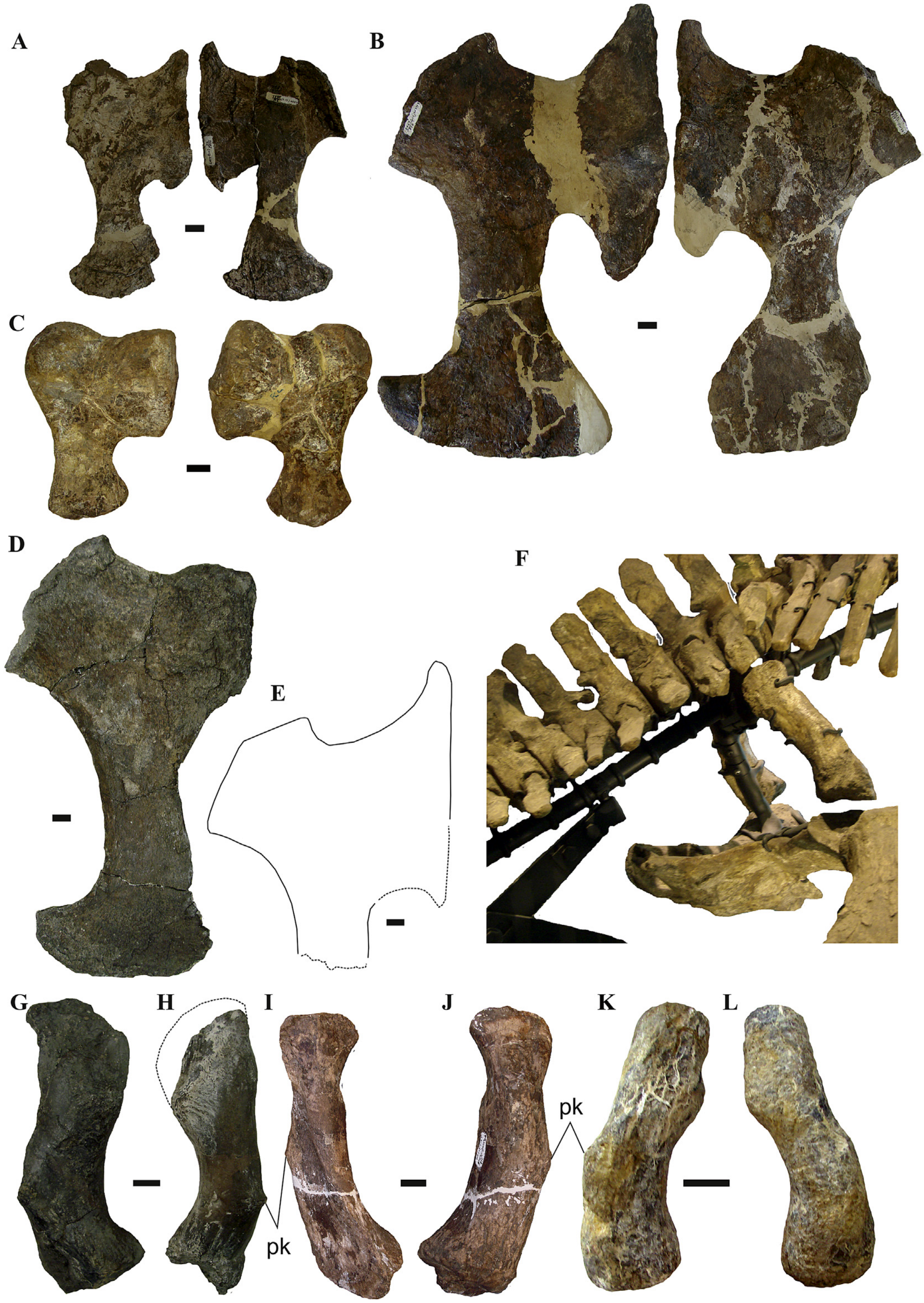

Fig. 7. Comparison of elasmosaurids from the Moreno Formation. **A**–**E**, coracoids of **A**, LACM 2758: *Fresnosaurus drescheri* (dorsal view), **B**, LACM 2748: *Afrosaurus furlongi* holotype (ventral view), **C**, LACM 2832: *Afrosaurus furlongi* referred (ventral view). **D**, UCMP 33912: *Hydrotherosaurus alexandrae* holotype ventral view, **E**, LACM 2802: *Morenosaurus stocki* diagram taken from Welles, 1943. **F**–**L**, ilia. **F**, LACM 2802: *Morenosaurus stocki* **G-H**, UCMP 33912: *Hydrotherosaurus alexandrae* in ventral view, **G**, left and **H**, right. **I**–**J**, LACM 2748: *Afrosaurus furlongi*, right ilium in **I**, medial and **J**, lateral view, **K**–**L**, LACM 2758: *Fresnosaurus drescheri*: **K**, left and **L**, right ilia in medial views. **A**–**D**; **G**–**L** scale bars represent 20 mm. E, scale bar represents 40 mm. F, not to scale.

posterior convex zones (Fig. 2F) and an unexpanded distal end (Fig. 2D–G). No other elasmosaurid shares this combination of features and therefore they are useful to diagnose *Fresnosaurus drescheri* until more specimens allow better knowledge of its morphology.

5.2. Comparison of Fresnosaurus *with other elasmosaurids from the Moreno Formation*

The juvenile condition of *Fresnosaurus drescheri* has always generated some doubts about its validity. However, Welles

(1952, 1962) considered that the analysis of the proportions allows discarding the possibility that *Fresnosaurus drescheri* is a juvenile of other elasmosaurid from the Moreno Formation such as *Aphrosaurus furlongi*, *Hydrotherosaurus alexandrae* and *Morenosaurus stocki*. The only elements that can be compared are the coracoids and ilia. Welles (1943) considered two specimens as part of the hypodigm of *Aphosaurus furlongi*: LACM 2748, holotype specimen, and LACM 2832 referred specimen (Fig. 7A, B). If both specimens belong to the same species it is clear that the coracoid of *Aphrosaurus furlongi* achieved a more gracile condition at smaller sizes than *F. drescheri*, and therefore the coracoid of *Fresnosaurus drescheri* (Fig. 7C) did not fit well in a growth series of *Aphrosaurus furlongi*. Additionally, the ilium of *Aphrosaurus furlongi* does not show a square sacral facet and it is straighter than that of *F. drescheri* (Fig. 7I, J). The coracoids of the holotypes of *Hydrotherosaurus alexandrae* and *Morenosaurus stocki* are compatible with the growth of *Fresnosaurus drescheri* and the only other elements that could be compared are the ilia. The ilia of *Morenosaurus stocki* and *Hydrotherosaurus alexandrae* are known only by the holotype material. The ilium of *H. alexandrae* is strongly arched with a distal expanded area; a square sacral facet is absent (Fig. 7G–H). On the other hand, the ilium of *Morenosaurus stocki* is not strongly arched, instead its shaft changes direction roughly at the level of the articulation with the ischium (Fig. 7F). Thus, none of these two seem to be similar to the ilia of *F. drescheri* (Fig. 7K, L). The possibility of complete morphological change cannot be completely discarded but, until more complete growth series of the elasmosaurids from the Moreno Formation are available, this question cannot be answered.

5.3. LACM 2758 (additional material)

The LACM 2758 (additional material; LACM 2758A hereafter) shows interesting features mostly related with the proportions of the vertebral centra. It is knows that the cervical vertebrae of juveniles aristonectines shows distinctive proportions that differed from the proportions of non aristonectine elasmosaurids (O'Gorman et al., 2013). The main problem is that the LACM 2758A does not preserve cervical vertebrae. However the later does preserve a pectoral centrum (Fig. 4D) that could be considered an accurate proxy of the proportions of the posteriormost cervical centra. Fig. 8 shows the plot of the HI and BI indexes (see Methods) showing that LACM 2758A is among the plots of the aristonectine specimens. Therefore this evidence indicate aristonectine affinities of the LACM 2758A but without more evidence (cervical series, skull material) this is a weak determination and open nomenclature is used.

5.4. The American Pacific elasmosaurids and the Wedellian marine reptiles

The revision of *Fresnosaurus* and the other members of the plesiosaur fauna from the Moreno Formation not only has local importance but also biogeographical implications related to Circum-Pacific marine reptiles (mostly mosasaurids and elasmosaurids). Over the past several years, several contributions have shown the biogeographical connection along the Weddellian Province (WMRF) [Patagonia, Western Antarctica and New Zealand] (Novas et al., 2002; Gasparini et al., 2003; Otero et al., 2014; O'Gorman et al., 2015, O'Gorman, 2016). Additionally, a

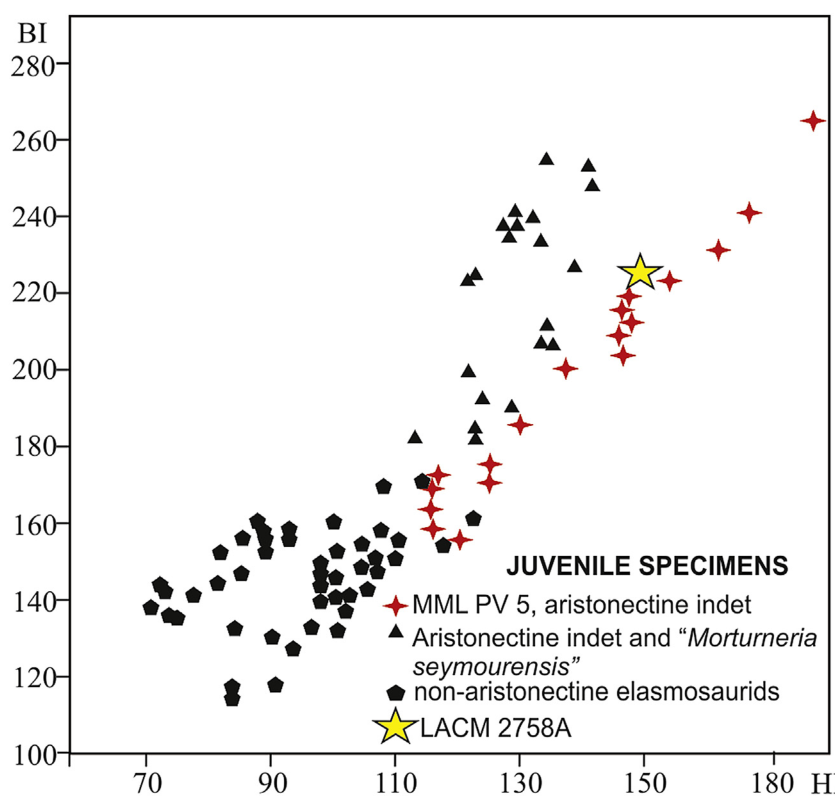

Fig. 8. Bivariate diagrams (HI-BI) of cervical centrum values of juvenile aristonectines and non-aristonectine elasmosaurids and posterior cervical centrum values of adult *Aristonectes* sp. and the non-elasmosaurid *Vegasaurus molyi* (Data taken from Welles, 1943, O'Gorman, 2013, O'Gorman et al., 2013, 2014, 2015); ✦, MML PV 5 (Aristonectinae indet.); ▲, CM Z fr 104; MLP 89-III-3-2; MML PV 192; MUC PV 131 (Aristonectinae indet.) and TTUP 9219 ("*Morturneria seymourensis*"); ⬟, AMNH 5261; CIT 2832; MLP 93-XII-20-1; MLP 99-XII-1-8; AM F9630-9928; MLP-86-X-28-(2-6) (non-aristonectine elasmosaurid). ☆, LACM 2758A. Modified from O'Gorman et al. (2014).

relationship between WMRF and the marine reptile from the Maastrichtian of California has been suggested due to the presence of a specimen referred to as *Prognathodon* cf. *waparaensis* and the recent record of cf. *Plotosaurus* in Chile (Lindgren and Schulp, 2010; Frey et al., 2016) and the phylogenetic relation between *Morenosaurus* and the Aristonectinae (O'Gorman et al., 2015). The recognition of the possible aristonectine affinities of the LACM 2758A is consistent wit this general pattern.

Recently, it has been proposed that the aristonectine retain morphological features related to the juvenile condition, reaching larger sizes until the final acquisition of more adult osteological features (O'Gorman, 2013; O'Gorman et al., 2014; Araujo et al., 2015). Therefore, it is possible that *F. drescheri* has aristonectine affinities but, because it is almost impossible to determine the aristonectine affinities based only on the morphology of girdles and appendicular material (O'Gorman et al., 2013), the affinities of the elasmosaurid *F. drescheri* remain unknown.

6. Conclusions

A new diagnosis of *Fresnosaurus drescheri* based on its ilium with dorsal rectangular shaped sacral facets; one anterior knob in the ventral area of the sacral facet and posterior knob in the posterior margin of the middle shaft is given. Additional material comprising vertebrael centra and neural arches (also labeled as LACM 2758) is described but until new evidence arise is considered a separate specimen. The later is considered a probably aristonectine. This reinforces the similarities between the plesiosaur fauna from the Weddellian Biogeograpical province and the one of the Moreno Formation and it is the first evidence of aristonectines from the North Hemisphere.

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