New plesiosaur records from the Lower Cretaceous of the Neuquén Basin, west-central Argentina, with an updated picture of occurrences and facies relationships

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ABSTRACT

In this work new records of elasmosaurid plesiosaurs are described from the Lower Cretaceous Agrio Formation of the Neuquén Basin (west-central Argentina) and their bearing facies and taphonomic modes are analyzed. New records from both members of the upper Valanginian—Hauterivian Agrio Formation are described along with a careful revision of previous records from the Pilmatué Member. These records include the first elasmosaurids reported from the upper Hauterivian of South America. Even though the studied materials comprise solely fragmentary postcranial elements, they suggest the presence of at least two different elasmosaurid taxa. Additionally, the rarity of cervical centra with a ventral notch in the articular faces among pre-Cenomanian elasmosaurids is confirmed. In terms of plesiosaur taphonomy and bearingfacies the studied plesiosaurs from the Agrio Formation were recorded in two different taphonomic modes, 1) preservation of disarticulated but closely associated postcranial elements within dark-grey shales, that probably resulted from bloating, drifting and eventually sinking of carcasses to a muddy and calm seafloor under oxic to suboxic conditions, without further transport or physical reworking; and 2) preservation of isolated plesiosaur bones in shell beds, including mostly weathered and encrusted isolated vertebrae. These taphonomic modes are not randomly distributed in the studied marine succession, but closely follow cycles of changes in the relative sea level and can be linked to fourth-order high frequency cycles. Taphonomic mode 1 includes better preserved specimens deposited in highstand systems tract intervals subjected to higher sedimentation rate while taphonomic mode 2 is related to transgressive systems tract intervals subjected to a reduced sedimentation rate and higher time of exposure of remains on the seafloor, resulting in poorly preserved specimens.

1. Introduction

Plesiosaurs constitute a monophyletic group of cosmopolitan marine reptiles encompassing the Late Triassic—Late Cretaceous time interval (Ketchum and Benson, 2010). The most extensive plesiosaur records are known from the Jurassic of Europe and Upper Cretaceous of USA, while Lower Cretaceous plesiosaurs are far less common worldwide (Benson et al., 2010; Ketchum and Benson, 2010; Vincent et al., 2011). Recently, Early Cretaceous plesiosaurs have received more attention; a few new species have been described while revisions were performed on classic specimens (Druckenmiller, 2002; Druckenmiller and Russell, 2006, 2008; Kear, 2005; Kear et al., 2006a; Kear and Barret, 2011; Ketchum, 2011; Benson et al., 2013a,b; Hampe, 2013), but their systematics and diversity are still poorly understood when compared to those of other time periods.

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Early Cretaceous plesiosaur records are very informative, as apparently there was a faunal turnover at the end of the Jurassic caused by a decreasing diversity of Late Jurassic cryptoclidids and pliosaurids and their replacement by a Cretaceous plesiosaur fauna dominated by polycotylids, elasmosaurids, leptocleidids and brachauchenines (Benson and Druckenmiller, 2014). Therefore, new plesiosaur records from the Lower Cretaceous are important to improve an overall poor fossil record of the group, and to clarify their evolutionary history just after the faunal turnover.

Previous occurences of Lower Cretaceous plesiosaurs of the Southern Hemisphere comprise abundant materials from Australia (Kear, 2003, 2005; Kear et al., 2006a,b) and other records from South America. The latter comprise only undetermined elasmosaurids from the upper Valanginian–lower Hauterivian Pilmatué Member of the Agrio Formation of the Neuquén Basin of west-central Argentina (Lazo and Cichowolski, 2003; revised herein) and the elasmosaurid *Callawayasaurus colombiensis* (Welles, 1962) from the upper Aptian "Leiva Shale", Paja Formation, of Colombia (Welles, 1962; Goñi and Gasparini, 1983; Carpenter, 1999). However, this paucity of records probably reflects a collection bias rather than a true low abundance, since new field work performed recently in the Agrio Formation provided the new materials studied herein.

The main goals of this article are as follows, 1) to describe new plesiosaur specimens and to revise previously described ones from the Lower Cretaceous Agrio Formation of the Neuquén Basin, west-central Argentina; 2) to date the study materials using a refined biostratigraphic framework based on ammonoids and calcareous nannofossils; 3) to discuss the affinities and diversity of the studied plesiosaurs; and 4) to describe and interpret the plesiosaur bearing-facies, taphonomic modes and paleoecological traits in the Agrio Formation.

Institutional abbreviations: **GWWU**, Geomuseum der West-faelischen Wilhems-Universitaet, Münster, Germany; **LEICT**, New Walk Museum, Leicester, UK; **MOZ**, Museo Juan Olsacher, Zapala, Neuquén Province, Argentina; **NHMUK**, Natural History Museum, London, UK; **SCARB**, Rotunda Museum, Scarborough, UK.

Anatomical abbreviations: **azyg**, anterior zygapophyses; **cap**, capitulum; **cf**, coracoids facet; **cr**, cervical rib; **di**, diapophyses; **gf**, glenoid facet; **lr**, lateral longitudinal ridge; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pa**, parapophyses; **pez**, pre-zygapophyses; **pg**, posterior groove; **poz**, postzygapophyses; **sf**, scapular facet; **tr**, transverse ridge; **tub/troch**, tuberosity/trochanter; **vf**, ventral foramina.

2. Geological setting

The Neuquén Basin, located in west-central Argentina along the Andean foothills, extends through most of the Neuquén Province and part of the Mendoza, Río Negro and La Pampa provinces (Fig. 1). During the Early Cretaceous the basin was located not far from its
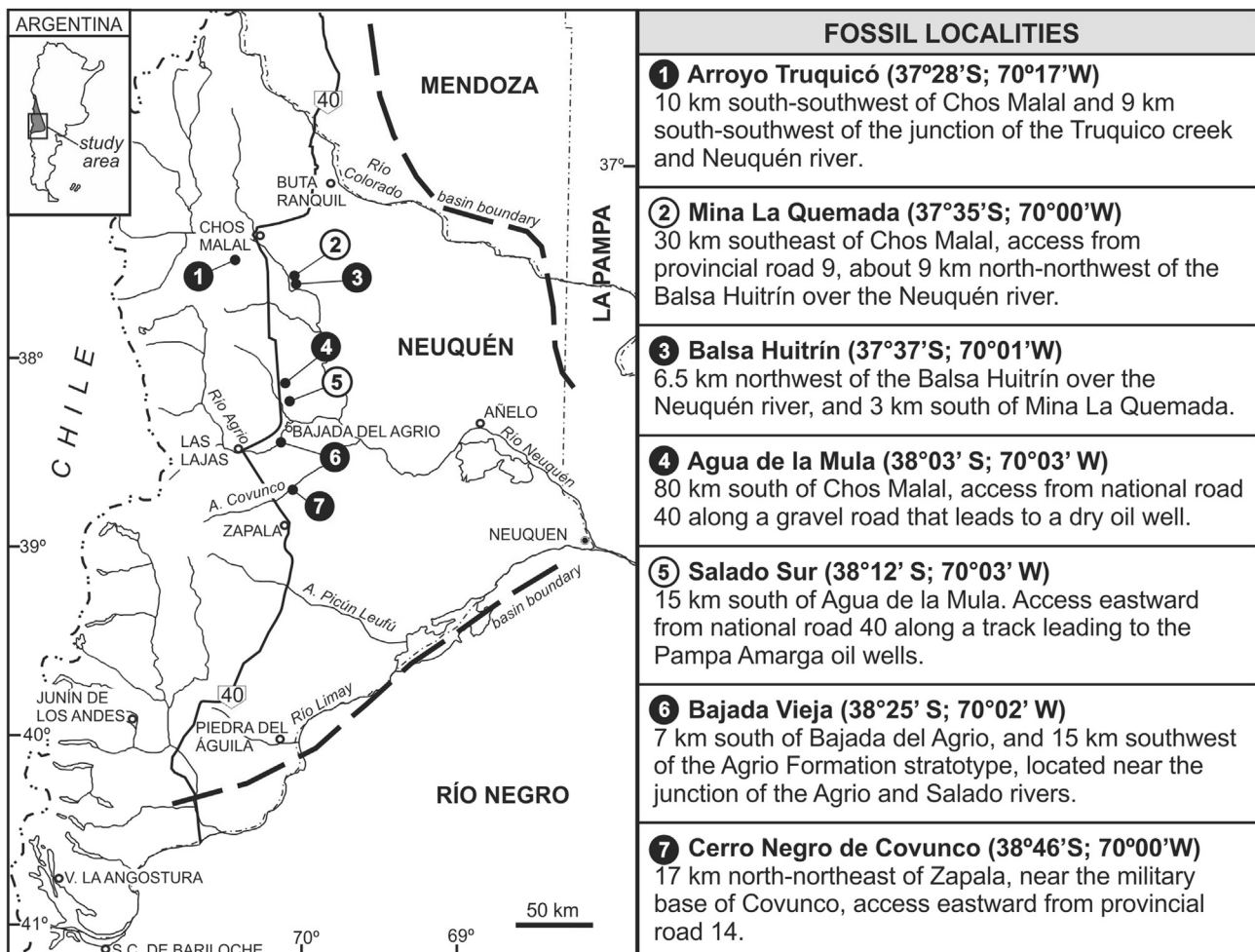

Fig. 1. Map of west-central Argentina showing the fossil localities with Early Cretaceous plesiosaur remains from the Agrio Formation. Localities with black circle and white number correspond to the Pilmatué Member; localities with white circle and black number correspond to the Agua de la Mula Member.

current latitudinal position, approximately between 28° and 36° SL (Somoza, 2011), at the boundary between the tropical and subtropical regions.

The Neuquén Basin had a complex tectono-sedimentary evolution controlled by changes in the subduction system of the western margin of South America. Three consecutive tectonic regimes are generally considered: rift, retroarc and foreland stages (Howell et al., 2005). The basin was opened to the proto-Pacific Ocean during the first two stages. In particular, the Mendoza Group was deposited from the Kimmeridgian to the early Barremian, in the retroarc stage of the basin, which was characterized by an active subduction associated with the development of a magmatic arc along its western border (Howell et al., 2005; Ramos and Folguera, 2005).

The Mendoza Group comprises continental and marine sedimentary rocks that may exceed 3000 m of total thickness (Leanza et al., 2001). This group encompasses the Tordillo, Vaca Muerta, Mulichinco and Agrio formations and their lateral equivalents. The marine deposits, present in the entire unit except the Tordillo Formation, are typically composed of low to high-frequency sedimentary cycles, which reflect the interplay between eustacy, clastic input, climatic oscillations and thermal subsidence (Legarreta and Uliana, 1991).

In particular, the Agrio Formation, defined by Weaver (1931), crops out from central Mendoza Province to southern Neuquén Province and encompasses the early Valanginian to earliest Barremian time interval. The unit comprises three members, the lower Pilmatué Member, the middle Avilé Member and the upper Agua de la Mula Member (Weaver, 1931; Leanza et al., 2001). Both the Pilmatué and Agua de la Mula members are mainly composed of black to dark-grey shales and calcareous shales, with intercalation of thin sandstones and shell beds that were deposited in a mixed clastic-carbonate ramp under an overall storm influence (Spalletti et al., 2001; Lazo et al., 2005). The marine sediments of the Agrio Formation were deposited within a shallow sea, which was partially connected to the proto-Pacific ocean through sea corridors across the Andean magmatic arc. The modern Java Sea, an epeiric semi-closed sea with abundant clastic input in a warm climate region, may be considered a good analogous setting for the Agrio Formation, on the basis of recent paleoecological studies of coral biostromes (Garberoglio et al., 2013). A paleosalinity analysis of the unit, based on carbonate oxygen isotopes, recorded some temporal and spatial variations, mostly within the euhaline range, reflecting shallow paleoenvironmental conditions (Lazo et al., 2008). In general, water temperatures were probably warm to warm-temperate as indicated by the presence of thick-shelled bivalves, oolites and coral patch-reefs (Lazo et al., 2005).

The typical macrofauna of the Agrio Formation comprises mainly invertebrates, including mollusks, corals, serpulids, decapods and echinoderms. In particular, bivalves, gastropods, ammonoids, and nautilids are abundant and are usually recorded in shell beds. Paleobiogeographic affinities of the invertebrate fauna are mainly tethyan, but a number of taxa are endemic or have Andean affinities (Aguirre-Urreta et al., 2008). Calcareous nannofossils from several sections of the Agrio Formation have cosmopolitan features. The presence of nannofossil species with tethyan, boreal and bipolar distribution in the Neuquén Basin suggests the existence of marine connections with the Tethys region and northwestern Europe (Bown and Concheyro, 2004). Vertebrate remains have been scarcely recorded and include fragmentary remains of pycnodontiform fishes, ichthyosaurs and plesiosaurs (Bocchino, 1977; Cione and Pereira, 1986; Cichowolski and Lazo, 2000; Lazo and Cichowolski, 2003).

3. Material and methods

3.1. Material

All study material, including newly and previously collected specimens, along with repository number, unit, ammonoid zone, age, taphonomic mode, and notes are summarized in Table 1.

3.2. Methods

The ages of the plesiosaur fossils described here have been determined by means of the associated calcareous nannofossils and ammonoids, following the proposals of Applegate and Bergen (1988) and Aguirre-Urreta et al. (2005, 2007), respectively. Integrated studies on ammonoids, nannofossils and palynomorphs from the Agrio Formation have provided an accurate biostratigraphic zonation that allows precise correlation to the Mediterranean Standard Zonation and therefore permits to correlate the studied plesiosaurs with those from the Northern Hemisphere (Fig. 2; Aguirre-Urreta et al., 2007). Particularly, the Valanginian–Barremian interval has been calibrated using the standard nannofossil markers and can be correlated with the known CC Mediterranean zonation (Sissingh, 1977; Applegate and Bergen, 1988). Based on those markers, the interval has been correlated to the CC3B, CC4 and CC5 nannofossil zones (Aguirre-Urreta et al., 2005; Concheyro et al., 2009).

A general stratigraphic section of the Agrio Formation, approximately 1200 m in thickness, was measured at the Agua de la Mula locality in central Neuquén Province (Figs. 1 and 3). This section along with a basal one from Arroyo Truquicó locality (Figs. 1 and 3) were used to plot all plesiosaur records of the Agrio Formation from localities corresponding to the upper Valanginian up to the lowermost Barremian, including the newly described records. In particular, a bed-by-bed log of each plesiosaur bearing facies was performed to study in detail the facies relationships and taphonomic modes in the Agrio Formation. In all cases, lithofacies and sedimentary cycles were characterized in the field taking into account geometry, lithology, sedimentary structures and fossil content. In addition, taphonomic features were qualitatively described in the field based on general taphonomic guidelines proposed by Behrensmeyer (1991) including sample size, number of individuals, age spectrum, bone articulation, sorting, size of the accumulation, orientation in plan view and in cross-section, fragmentation, and weathering. Definition of taphonomic modes follows Behrensmeyer and Hook (1992). Taphonomic modes are here interpreted in terms of the sedimentary cyclicity of the marine deposits of the Agrio Formation. Cyclicity and sequence stratigraphy framework and definition of high-frequency cycles follow the proposal of Spalletti et al. (2001) for the Agua de la Mula Member of the Agrio Formation.

Micro Jack and ME 9100 model jackhammers were used in fossil preparation. The recorded linear measurements were taken using a caliper that allows an accuracy of 0.01 mm. The studied indices are those originally proposed by Welles (1952), which take into account the centrum length (L), the ratio between maximum height (H) and length of the centrum (100*H/L), and the ratio between breadth (B) and length of the centrum (100*B/L). In addition, the ratio between the breadth and height (100*B/H) was also considered. Both breadth and height were measured in this work on the posterior articular face. The vertebral length index [VLI = 100*L/(0.5*(H + B))] (Brown, 1981) was also estimated. In order to consider the absolute measures, the mean diameter of the articular face 0.5*(H + B) is also used. Furthermore, the categories of ontogenetic development proposed by Brown (1981), which are based on the fusion between the neural arch and vertebral centrum (neuro-central closure without visible suture) were considered to differentiate the "adult" and "juvenile" growth stages.

Table 1
Specimens from the Agrio Formation (Nequén Basin, Argentina) discussed in this paper.

Rep. number MOZ-PV	Taxonomic revision	Material	Member of the Agrio Fm.	Locality and province	Ammonoid zone	Ammonoid subzone	Age	Facies and taphonomic mode	Notes
6890	Elasmosauridae indet.	10 cervical vertebrae	Pilmatué	Arroyo Truquicó, Neuquén	*Olcostephanus (O.) atherstoni*	*Karakaschiceras attenuatus*	Late Valanginian	Shales/Taph. mode 1	Revision of material published by Lazo and Cichowolski (2003).
6891	Plesiosauria indet.	1 cervical vertebra	Pilmatué	Cerro Negro de Convunco, Neuquén	*Pseudofavrella angulatiformis*	*Decliveites crassicostatus*	Late Valanginian	Shales/Taph. mode 1	Revision of material published by Lazo and Cichowolski (2003).
6892	Elasmosauridae indet.	1 Cervical vertebra and undetermined postcranial fragments	Pilmatué	Agua de la Mula, Neuquén	*Pseudofavrella angulatiformis*	*Decliveites crassicostatus*	Late Valanginian	Shales/Taph. mode 1	Revision of material published by Lazo and Cichowolski (2003).
6893	Elasmosauridae indet.	18 cervical, 4 dorsal and 1 caudal vertebrae and undetermined postcranial fragments	Pilmatué	Agua de la Mula, Neuquén	*Hoplitocrioceras gentilii*	*Hoplitocrioceras gentilii*	Early Hauterivian	Shales/Taph. mode 1	Revision of material published by Lazo and Cichowolski (2003).
6894	Elasmosauridae indet.	2 cervical vertebrae and undetermined postcranial fragments	Pilmatué	Bajada Vieja, Neuquén	*Weavericeras vacaense*		Early Hauterivian	Shell bed/Taph. mode 2	Revision of material published by Lazo and Cichowolski (2003).
6990	Plesiosauria indet.	1 dorsal vertebra and undetermined centra	Agua de la Mula	La Mina La Quemada, Neuquén	*Crioceratites schlagintweiti*		Late Hauterivian	Shales/Taph. mode 1	Newly collected material
6991	Elasmosauridae indet.	12 cervical vertebrae, 2 dorsal vertebrae, several neural spines, 1 propodium, 2 coracoids and undetermined postcranial fragments	Agua de la Mula	Salado Sur, Neuquén	*Crioceratites schlagintweiti*		Late Hauterivian	Shales/Taph. mode 1	Newly collected material
6992	Elasmosauridae indet.	1 cervical vertebra	Pilmatué	Bajada Vieja, Neuquén	*Pseudofavrella angulatiformis*	*Pseudofavrella angulatiformis*	Late Valanginian	Shell bed/Taph. mode 2	Newly collected material
6993	Plesiosauria indet.	1 dorsal vertebra	Pilmatué	Balsa Huitrín, Neuquén	*Hoplitocrioceras gentilii*		Early Hauterivian	Shell bed/Taph. mode 2	Newly collected material

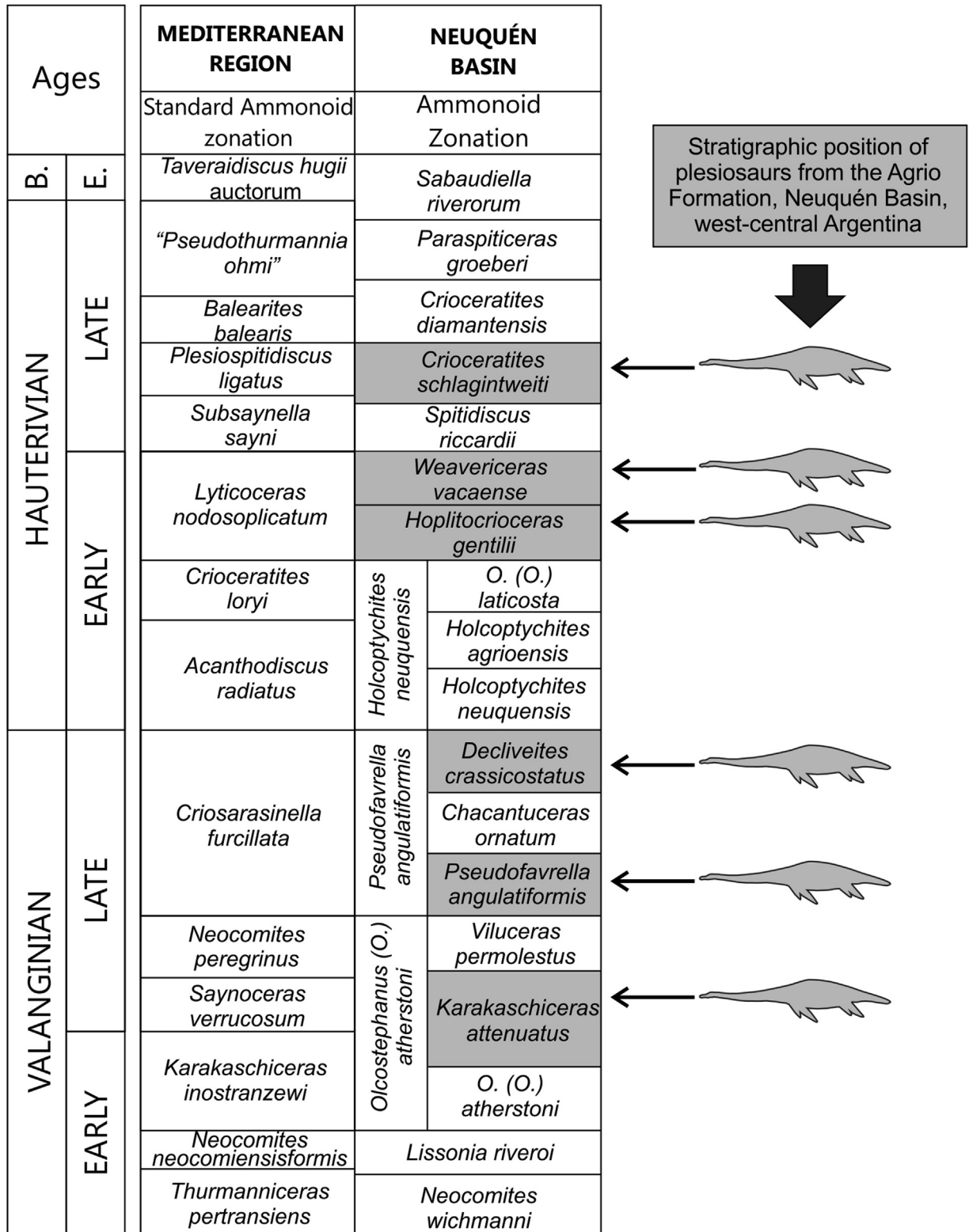| Ages		MEDITERRANEAN REGION	NEUQUÉN BASIN	
		Standard Ammonoid zonation	Ammonoid Zonation	
B.	E.	*Taveraidiscus hugii auctorum*	*Sabaudiella riverorum*	
HAUTERIVIAN	LATE	*"Pseudothurmannia ohmi"*	*Paraspiticeras groeberi*	
		Balearites balearis	*Crioceratites diamantensis*	
		Plesiospitidiscus ligatus	*Crioceratites schlagintweiti*	
		Subsaynella sayni	*Spitidiscus riccardii*	
	EARLY	*Lyticoceras nodosoplicatum*	*Weavericeras vacaense*	
			Hoplitocrioceras gentilii	
		Crioceratites loryi	*Holcoptychites neuquensis*	*O. (O.) laticosta*
		Acanthodiscus radiatus		*Holcoptychites agrioensis*
				Holcoptychites neuquensis
VALANGINIAN	LATE	*Criosarasinella furcillata*	*Pseudofavrella angulatiformis*	*Decliveites crassicostatus*
				Chacantuceras ornatum
				Pseudofavrella angulatiformis
		Neocomites peregrinus	*Olcostephanus (O.) atherstoni*	*Viluceras permolestus*
		Saynoceras verrucosum		*Karakaschiceras attenuatus*
	EARLY	*Karakaschiceras inostranzewi*		*O. (O.) atherstoni*
		Neocomites neocomiensisformis	*Lissonia riveroi*	
		Thurmanniceras pertransiens	*Neocomites wichmanni*	

Fig. 2. Stratigraphic distribution of Valanginian–Hauterivian plesiosaurs from the Agrio Formation in grey and correlation to the local ammonoid zonation of the Neuquén Basin and to the Mediterranean Standard Zonation. Biostratigraphy, correlations and ages from Aguirre Urreta et al. (2007), Aguirre-Urreta and Rawson (2012) and Reboulet et al. (2014).

4. Systematic paleontology

Sauropterygia Owen, 1860
Plesiosauria de Blainville, 1835
Plesiosauroidea Welles, 1943
Elasmosauridae Cope, 1869
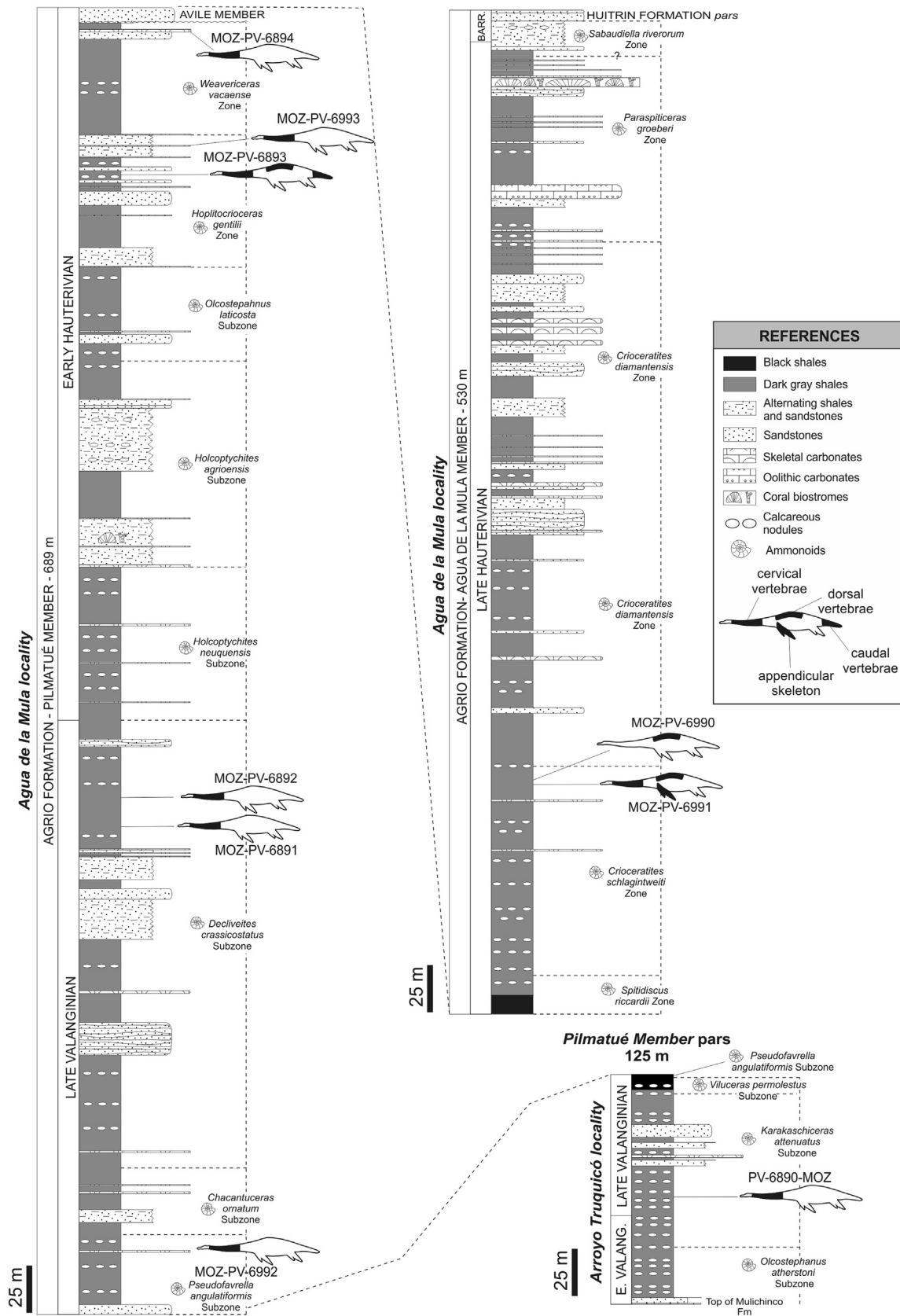Elasmosauridae indet.
Figures 4, 5A, B

Fig. 3. Stratigraphic sections of the Agrio Formation showing in the stratigraphic position of studied plesiosaur remains. Biostratigraphy and ages from Aguirre-Urreta et al. (2007).
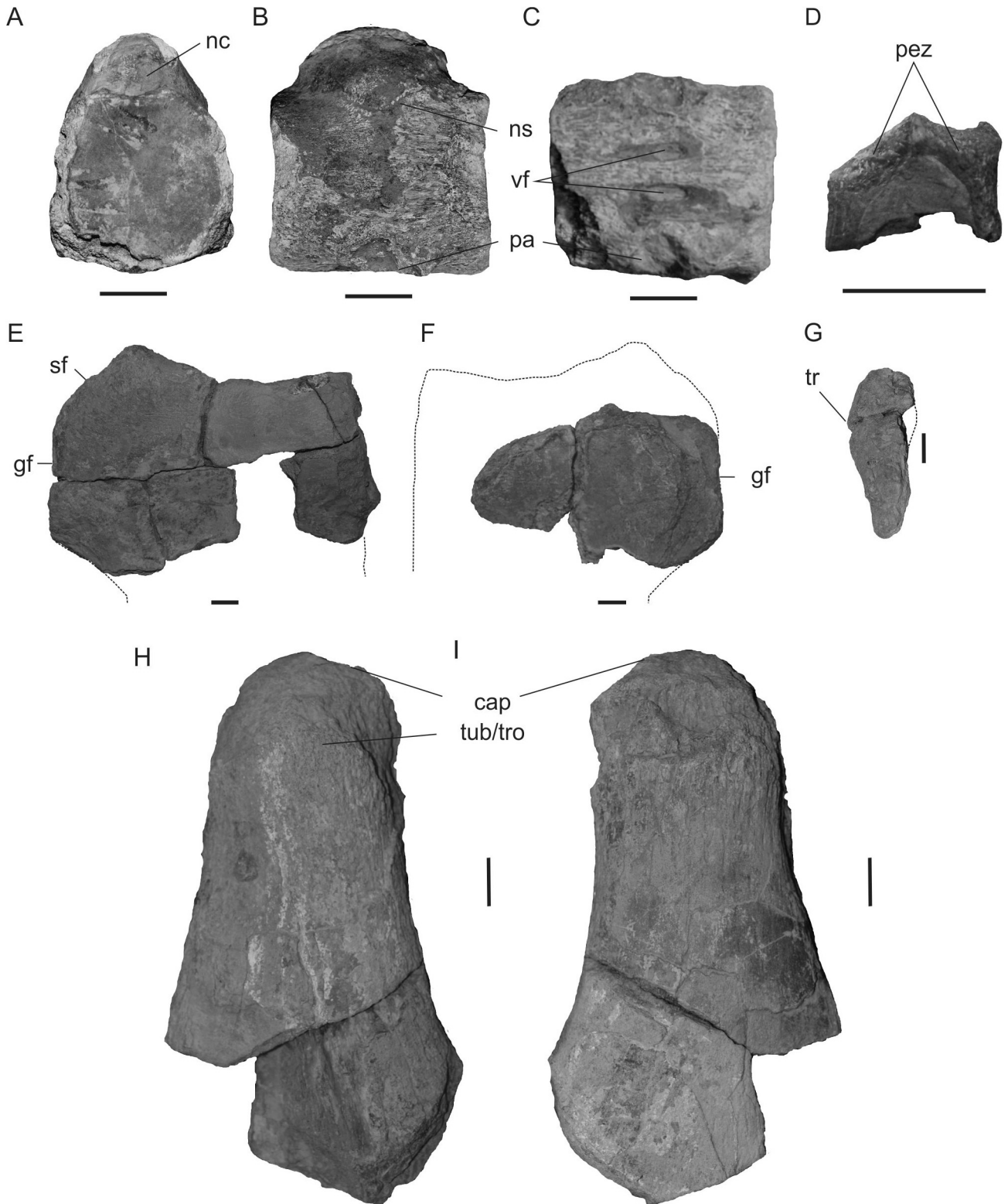
Fig. 4. Elasmosauridae gen. et sp. indet. MOZ-PV-6991. A—C, cervical vertebra in A, anterior, B, left lateral, and C, ventral views. D, prezygapophyses. E—F, coracoid in dorsal view. G, coracoid in symphysial view. H—I, propodium in H, dorsal, and I, ventral views. Scale bars = 20 mm.

Material: MOZ-PV-6890/1—10, ten cervical vertebrae (Lazo and Cichowolski, 2003, fig 3.5—8); MOZ-PV-6892, one cervical vertebra, and a few other bone fragments; MOZ-PV-6893/1—23, twenty three vertebrae, comprising eighteen cervical, four dorsal, and one caudal, and other undetermined bone fragments (Lazo and Cichowolski, 2003, fig 3.1—4, 3.9—12); MOZ-PV-6894/1—2, two disarticulated cervical vertebrae and other bone fragments; MOZ-PV-6991, twelve cervical vertebrae, two dorsal
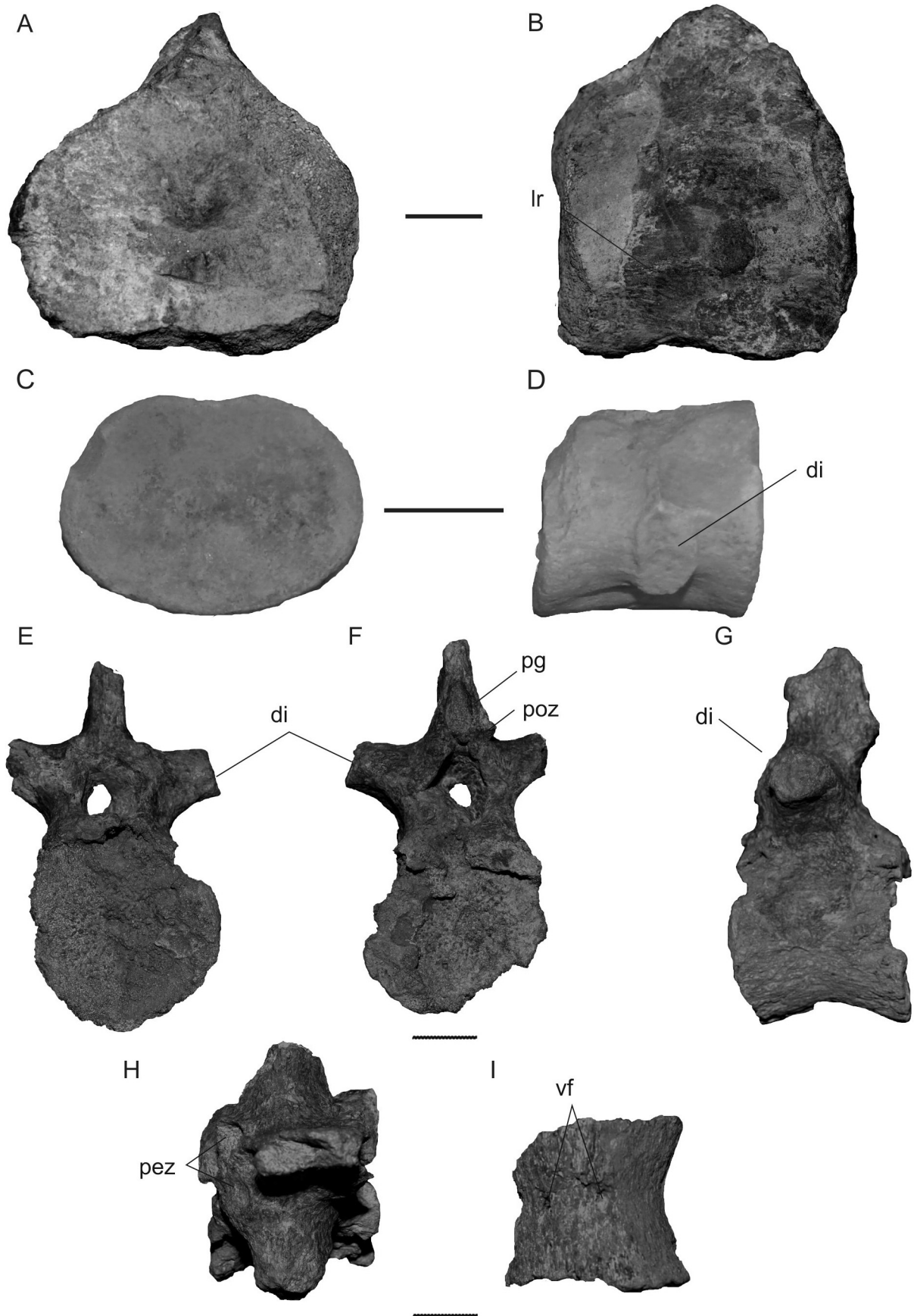
Fig. 5. Elasmosauridae gen. et sp. indet. MOZ-PV-6992. A–B, cervical vertebra in A, anterior view and B, left lateral. MOZ-PV-6891. C–D, cervical vertebrae in C, posterior and D, left lateral views. Plesiosauria indet. MOZ-PV-6993. E–I, dorsal vertebra in E, anterior, F, posterior, G, left lateral, H, dorsal, and I, ventral views. Scale bars = 20 mm.

Table 2
Measurements L (length), H (height), B (breadth) as well as the HI, BI, BHI and VLI indices of the studied vertebrae (measurements which are approximated are expressed in italics, Ce, cervical; Do., dorsal; Ca., caudal). Lineal measurements in mm.

		L	H	B	HI	BI	BHI	VLI
MOZ-PV-6893	Ce.1	26	20	24	77	92	120	118
	Ce.2	26	23	27	88	104	117	104
	Ce.3	32	25	27	78	84	108	123
	Ce.4	42	34	–	81	–	–	–
	Ce.5	45	37	–	82	–	–	–
	Ce.6	42	35	*40*	83	95	114	112
	Ce.7	42	33	*48*	79	114	145	104
	Ce.8	–	–	–	–	–	–	–
	Ce.9	–	42	*50*	–	–	119	–
	Ce.10	45	42	–	93	–	–	–
	Ce.11	40	–	*40*	–	100	–	–
	Ce.12	40	–	–	–	–	–	–
	Ce.13	48	41	–	85	–	–	–
	Ce.14	45	37	–	82	–	–	–
	Ce.15	45	39	*50*	87	111	128	101
	Ce.16	45	37	50	82	111	135	103
	Ce.17	45	40	53	89	118	133	97
	Ce.18	41	40		98	–	–	205
	Do.19	–	–	45	–	–	–	–
	Do.20	40	42	–	105	–	–	–
	Do.21	–	–	–	–	–	–	–
	Do.22	40	45	52	113	–	–	–
	Ca.23	25	30	40	120	160	133	71
MOZ-PV-6890	Ce.1	46	36	43	78	93	119	116
	Ce.2	49	40	44	82	90	110	117
	Ce.3	48	39	42	81	88	108	119
	Ce.4	50	42	46	84	92	110	114
	Ce.5	49	41	46	84	94	112	113
	Ce.6	53	45	49	85	92	109	113
	Ce.7	54	45	50	83	93	111	114
	Ce.8	57	45	50	79	88	111	120
	Ce.9	60	46	51	77	85	111	124
	Ce.10	59	47	52	80	88	111	119
MOZ-PV-6892	Ce.1	55	–	49	–	89	–	–
MOZ-PV-6891	Ce.1	37	37	50	100	135	135	85
MOZ-PV-6991	Ce.1	59	–	–	–	–	–	–
	Ce.2	60	–	–	–	–	–	–
	Ce.3	60	–	–	–	–	–	–
	Ce.4	61	51	*52*	84	85	102	118
	Ce.5	60	52	*61*	87	102	117	106
	Ce.6	63	52	*50*	83	79	96	124
	Ce.7	61	55	*54*	90	89	98	112
	Ce.8	60	59	*70*	98	117	119	93
	Ce.9	69	60	–	87	–	–	–
MOZ-PV-6993	Do.	50	61	*54*	122	108	89	87

vertebrae, neural spines, one propodium, both coracoids, other bone fragments (Fig. 4); MOZ-PV-6992, one isolated cervical vertebra (Fig. 5A, B).

Locality and horizon: all specimens from the Agrio Formation.

From the Pilmatué Member: MOZ-PV-6890/1–10, Arroyo Truquicó, *Karakaschiceras attenuatus* Subzone, *Olcostephanus* (*O.*) *atherstoni* Zone, upper Valanginian; MOZ-PV-6892 and MOZ-PV-6893/1–23, Agua de la Mula, *Decliveites crassicostatus* Subzone, *Pseudofavrella angulatiformis* Zone, upper Valanginian, and *Hoplitocrioceras gentilii* Subzone, *Hoplitocrioceras gentilii* Zone, lower Hauterivian, respectively; MOZ-PV-6894/1–2, Bajada del Agrio, *Weavericeras vacaense* Zone, lower Hauterivian; MOZ-PV-6992, Bajada Vieja, *Pseudofavrella angulatiformis* Subzone, *Pseudofavrella angulatiformis* Zone, upper Valanginian.

From the Agua de La Mula Member; MOZ-PV-6991, El Salado, *Crioceratites schlagintweiti* Zone, upper Hauterivian.

Description

Specimens MOZ-PV-6890/1–10, MOZ-PV-6892, MOZ-PV-6893/1–23 and MOZ-PV-6894/1–2 were described in detail by Lazo and Cichowolski (2003) and thus only a table with vertebral measurements (Table 2) and a few new observations are added further on in this work. The newly collected specimens MOZ-PV-6991 and MOZ-PV-6992 are described in the following lines for the first time.

MOZ-PV-6991: There are twelve preserved cervical vertebrae. The cervical vertebral centra are longer than high or broad. The cervical centra are as dorsoventrally high as laterally broad, thus, the articular surfaces are circular, without ventral notch (Table 2, Fig. 4A, C). The anterior and posterior articular faces are nearly flat, without strongly marked marginal rim (Fig. 4A). The lateral surface is slightly concave (Fig. 4B), but in some cervical vertebrae there is a slightly convex zone that corresponds to a lateral longitudinal ridge. The elliptical (anterior vertebrae) to circular (posterior vertebrae) parapophyses are always free from the ribs (Fig. 4B, C). On the ventral surface, the cervical centra have two elongated foramina separated by a transversely rounded craniocaudal keel (Fig. 4C). However, the general ventral surface tends to be flat, a feature more clearly observed in the posterior cervical. The prezygapophyses contact each other along the midline (Fig. 4D). The centra of the two dorsal vertebrae are higher than long and broader than high. The dorsal centra are spool-shaped. In the ventral surface there are two foramina.

Only the anterior part of the left coracoid is preserved (Fig. 4E, F). The symphyseal surface is thick but a mid ventral process is not observed, although this area is damaged and it is not possible to determine the original morphology. On the dorsal surface there is a transverse thickening (Fig. 4G) called transverse ridge (Hiller et al., 2005). The coracoid cranial margin is concave (Fig. 4E), and the glenoid ramus bears a scapular facet, which is shorter than the glenoid facet (Fig. 4E). The general dorsoventral thickness decreases to the caudal margin; however, it is not possible to determine the shape of the coracoids. Only one incomplete propodium is preserved. The tuberosity/trochanter is displaced to the caudal margin in relation with the shaft axis and confluent with the capitulum. In dorsal view a strongly rugose area is observed on the caudal margin and coalesces with the capitulum (Fig. 4H, I). The propodium is not complete therefore it is not possible to ascertain the shape of its distal expansion, however the general morphology indicate that the distal expansion was probably larger, giving a stocky morphology.

MOZ-PV-6992: Represented by one isolated cervical vertebra with the neural arch and ribs fused to the centrum (Fig. 4A, B). The vertebral centrum is not well preserved and therefore measurements are precluded. On the lateral surface there is a well-developed lateral ridge separated from the rib by a concave area (Fig. 4A). At least one foramen is present ventrally.

Plesiosauria indet.
Fig. 5C–I
Material: MOZ-PV-6990, one dorsal vertebra and three indeterminate centra; MOZ-PV-6891, one cervical vertebra; MOZ-PV-6993, one dorsal vertebra.

Locality and horizon: all specimens from the Agrio Formation (Fig. 2).

From the Pilmatué Member: MOZ-PV-6891, Cerro Negro de Covunco, *Decliveites crassicostatus* Subzone, *Pseudofavrella angulatiformis* Zone, upper Valanginian; MOZ-PV-6993, Balsa Huitrín, *Hoplitocrioceras gentilii* Zone, lower Hauterivian.

From the Agua de la Mula Member: MOZ-PV-6990, Mina La Quemada, *Crioceratites schlagintweiti* Zone, upper Hauterivian.

Description

Although it was studied by Lazo and Cichowolski (2003), specimen MOZ-PV-6891 is redescribed here. Additionally, the specimen MOZ-PV-6993 is described for the first time. MOZ-PV-6990 is poorly preserved and lacks relevant information; therefore, it will not be described herein.

MOZ-PV-6891: this cervical centrum is broader than high and as high as long (Table 2; Fig. 5C, D). The lateral surface bears a dorsoventrally elongated parapophysis (Fig. 5D). Two foramina are present ventrally, separated by a transversely rounded keel. The proportions and size of the parapophysis indicate that it is a posterior cervical vertebra.

MOZ-PV-6993: the dorsal centrum (Fig. 5D–I) is higher than long and as high as broad (Table 2, Fig. 5E–G). The articular face is subcircular (Fig. 4E, F). The lateral surface of the vertebral centrum is anteroposteriorly concave (Fig. 5G). Ventrally, there are two foramina (Fig. 5I). The neural canal is elliptical, with the long axis vertical (Fig. 5E, F). The neural spine is laterally compressed and shows a deep groove in the lower part of the posterior margin (Fig. 5I). There is no medial contact between the right and left zygapophyses (Fig. 5E, F).

5. Systematic discussion and comparisons

MOZ-PV-6991 is a juvenile specimen *sensu* Brown (1981) because the neural arches are clearly unfused to the centra (Fig. 4B). Other features such as the absence of closure of the suture between ribs and cervical centra and the rounded morphology of the propodium are also congruent with a juvenile growth stage. However, the vertebrae shows well defined articular faces indicating that although this specimen is in the growth stage "juvenile" it is probably not extremely juvenile. Additionally, the neural arches attached to the centra in most of the cervical vertebrae indicate that the neural closure (but not the fusion) had started. Using the same criteria, MOZ-PV-6992 and MOZ-PV-6993 are considered as adults because of the closure of the neurocentral suture. Following Lazo and Cichowolski (2003), specimen MOZ-PV-6890/1–10 is interpreted as a juvenile while specimen MOZ-PV-6893/1–23 is thought to have been an adult.

The specimens described by Lazo and Cichowolski (2003) and those described here share some features that need to be discussed in order to clarify their systematic affinities. Elongated cervical centra (i.e. HI < 100 and usually VLI > 100; Table 2) are observed in the MOZ-PV-6890/1–10, MOZ-PV-6892, MOZ-PV-6893/1–23 and MOZ-PV-6991. This feature is associated with a plesiosauromorph morphotype (*sensu* O'Keefe, 2002). The elongation of cervical centra is extremely developed in elasmosaurids but is also present in the cryptoclidid *Muraenosaurus leedsii* Seeley, 1874 and the microcleidid *Microcleidus tournemirensis* (Sciau, Crochet and Mattei, 1990) also has this feature (Brown, 1981; Bardet et al., 1999). However, these features seem to be absent in the leptocleidids (Andrews, 1910, 1911; Druckenmiller and Russell, 2008; Kear and Barret, 2011; Benson et al., 2012, 2013b; Hampe, 2013).

All the cervical centra preserved are interpreted to have been associated with single headed ribs. This character is present in elasmosaurids (Welles, 1962; Gasparini et al., 2003; Ketchum and Benson, 2011), cryptoclydids (*Muraenosaurus leedsii*, *Cryptoclidus eurymerus* (Phillips, 1871) and *Abyssosaurus nataliae* Berezin, 2011), leptocleidids such as *Leptocleidus* spp., *Brancasaurus brancai* Wegner, 1914 and *Umoonasaurus demoscyllus* Kear, Schroeder and Lee, 2006a (Cruickshank and Long, 1997; Kear et al., 2006a; Ketchum and Benson, 2010, Ch. 125; Berezin, 2011; Kear and Barret, 2011; Benson and Druckenmiller, 2014) and the possibly Early Cretaceous *Opallionectes* (Kear, 2006a). This feature is also recorded for the latest Jurassic Svalbard cryptocleidoids *Spitrasaurus* Knutsen, Druckenmiller and Hurum, 2012a and *Djupedalia* Knutsen, Druckenmiller and Hurum, 2012b, polycotylids (Carpenter, 1996) and some pliosaurids such as *Brachauchenius lucasi* (Ketchum and Benson, 2010, Ch. 125). Therefore, the presence of single headed cervical ribs does not allow us to determine the specimen at family level.

Medially fused prezygapophyses, as observed in MOZ-PV-6893/1–23 and MOZ-PV-6991, are present in elasmosaurids (Welles, 1962), cryptoclidids such as *Muraenosaurus leedsii*, *Cryptoclidus eurymerus*, *Tricleidus seeleyi* Andrews, 1909 (Brown, 1981; Ketchum and Benson, 2010, Ch. 128) and some polycotylids such as *Dolichorhynchops* Williston, 1903, but this character is absent in leptocleidids such as *Leptocleidus* spp., *Brancasaurus brancai* and *Vectocleidus pastorum* Benson, Ketchum, Naish and Turner, 2013b (Hampe, 2013, Ch. 13; Benson et al., 2013b).

A lateral longitudinal ridge is completely absent in the specimens MOZ-PV-6890/1–10, MOZ-PV-6892 and MOZ-PV-6893/1–23, a faint ridge is recorded in MOZ-PV-6991, and a strong, sharp lateral longitudinal ridge is evident in MOZ-PV-6992. A poorly developed lateral longitudinal ridge is present in the late Aptian elasmosaurid *Callawayasaurus colombiensis* whereas well developed lateral longitudinal ridges are recorded in the Callovian cryptoclidid *Muraenosaurus*, the Toarcian microcleidid *Microcleidus tournemirensis* (Andrews, 1910; Welles, 1962; Brown, 1981; Bardet et al., 1999), the Toarcian plesiosaurid *Seeleyosaurus guilelmiimperatoris* (Dames, 1895) and the Tithonian *Spitrasaurus* and *Djupedalia* (Knutsen et al., 2012a,b).

A sharp ventral keel is present in MOZ-PV-6893/1–23 but absent in MOZ-PV-6890/1–10 and MOZ-PV-6991. This kind of ventral keel is present in leptocleidids (*Brancasaurus brancai*) but also in some centra of *Callawayasaurus colombiensis* and in the cranialmost cervical centra of other elasmosaurids (Welles, 1962; Hampe, 2013; J.P.O'G. pers. obs.).

The prezygapophyses of MOZ-PV-6991 are narrower than the cervical centra, as observed in elasmosaurids (Sato, 2003; Hiller et al., 2005). A similar but less marked condition was described for *Muraenosaurus* (Andrews, 1910) and *Spitrasaurus* and *Djupedalia* (Knutsen et al., 2012a,b).

The dorsal vertebra MOZ-PV-6993 show deep grooves along the anterior and caudal margins of the neural spine. These deep grooves are present in elasmosaurids but also in *Muraenosaurus* (Andrews, 1910; Welles, 1962; Hiller et al., 2005).

A well developed mid ventral process of the coracoid is commonly found in elasmosaurids, even in the most ancient ones, such as *Wapuskanectes betsinicollsae* Druckenmiller and Russell, 2006 and *Callawayasaurus colombiensis* (Welles, 1962; Druckenmiller and Russell, 2006, fig. 8B). However it is absent in some cases, e.g. *Hydrotherosaurus* (Sachs, 2005a). Additionally, a dorsal transverse ridge is also present in elasmosaurids (Welles, 1962; Hiller et al., 2005; O'Gorman et al., in press) and in the leptocleidids *Brancasaurus* and *Vectocleidus* (Benson et al., 2013b; Wegner, 1914).

In sum, the features recorded in the discussed specimens show that leptocleidid affinities of the specimens from the Agrio Formation are not likely, since leptocleidids do not have elongated cervical centra or medially fused prezygapophyses as recorded for the specimens MOZ-PV-6890/1–10, MOZ-PV-6892, MOZ-PV-6893/1–23 and MOZ-PV-6991.

Elongated cervical centra are present in the Callovian cryptoclidid *Muraenosaurus leedsii*. However, the VLI (vertebral length index) of the cervical vertebrae centra in juvenile specimens of *Muraenosaurus leedsii* is about 100, and always lower than 105 (Brown, 1981: 289), and therefore they are less elongated than the cervical vertebrae of MOZ-PV-6890 and MOZ-PV-6991 (Table 2). The cervical VLI values in adult specimens of *Muraenosaurus leedsii* may reach 110, and therefore they are less elongated than the cranialmost cervical vertebrae of the MOZ-PV-6893. Similarly, the Toarcian *Microcleidus tournemirensis* has strongly elongated cervical centra with transversely convex ventral surfaces, whereas in MOZ-PV-6890, MOZ-PV-6991 and MOZ-PV-6893 the centra have transversely almost flat ventral surfaces (even though their vertebrae bear a rounded keel between the foramina the general surface remains almost flat and is not transversely rounded), more similar to what is observed in elasmosaurids (Welles, 1943, 1952) and the recently considered sister group (*Spitrasaurus* and *Djupedalia*) of the Elasmosauridae (Knutsen et al., 2012a,b). However, the specimens MOZ-PV-6890/1–10, MOZ-PV-6893/1–23 and MOZ-PV-6992 differ from *Spitrasaurus*, *Djupedalia* and *M. tournemirensis* stocky propodial elements, unlike the gracile and elongated ones of the latter genera (Bardet et al., 1999; Knutsen et al., 2012a,b). Overall, the features present in the study material (such as single cervical ribs, fused prezygapophyses, transversely flat ventral surface of cervical vertebrae and stocky propodials element) indicate elasmosaurid affinities. Considering the results of recent phylogenetical analysis the composition of Elasmosauridae is an issue under discussion (Sato, 2002; Gasparini et al., 2003; Ketchum and Benson, 2010; Kubo et al., 2012; Druckenmiller and Knutsen, 2012). Ketchum and Benson (2010) recovered Elasmosauridae supported by six unambiguous sinapomorphyes including nearly flat articular face of the cervical centra (Ketchum and Benson, 2010:ch. 124.2). This feature is observed in most of the materials referred to Elasmosauridae here (MOZ-PV-6890/1–10; MOZ-PV-6893/1–23; MOZ-PV-6894/1–2; MOZ-PV-6991). Druckenmiller and Knutsen (2012) define the Elasmosauridae node by the presence of ventral notch on cervical vertebrae (Druckenmiller and Knutsen, 2012:122.1) and Kubo et al. (2012) and Sachs and Kear (2014) include this feature among in their diagnoses of Elasmosauridae. However, some well known elasmosaurids (ej. *Callawayasaurus colombiensis*) do not show this feature and therefore its absence is not enough motive to dismiss elasmosaurids affinities (see below) when other features are not known. Kubo et al. (2012) recovered Elasmosauridae sustained by fifteen sinapomorphies, most of them cannot be determined for the specimens described here but the presence of elongated cervical centra (previously discussed) and massive humerus or femur are present in the MOZ-PV-6991. Therefore, although incomplete we think that specimens MOZ-PV-6890/1–10, MOZ-PV-6892, MOZ-PV-6893/1–23, MOZ-PV-6894/1–2, MOZ-PV-6991 and MOZ-PV-6992 could be referred to Elasmosauridae.

6. Plesiosaur diversity in the Agrio Formation

Some features observed in specimens MOZ-PV-6893/1–23, MOZ-PV-6890/1–10 and MOZ-PV-6991 might suggest that more than one taxa is represented. Fig. 6 shows that the cervical vertebrae of MOZ-PV-6893/1–23 tend to be smaller than MOZ-PV-6890/1–10 and MOZ-PV-6991. Additionally, MOZ-PV-6893/1–23 preserves the anterior to middle and posterior cervical vertebrae (the cervical vertebra numbered as 18 has a dorsoventrally and laterally extended parapophysis, indicating that it belongs to the posteriormost vertebrae along the neck) and therefore the MOZ-PV-6893/1–23 gives information about the maximum height and breadth of the entire neck. Comparing ontogenetical stages and sizes, a striking feature of the materials becomes evident. The MOZ-PV-6893 is clearly an adult specimen lacking any evidence of the neuro-central sutures and cervical ribs fused to the centra, whilst MOZ-PV-6890/1–10 and MOZ-PV-6991 are juveniles, as neuro-central sutures are visible, and do not have the cervical ribs fused to the centra.
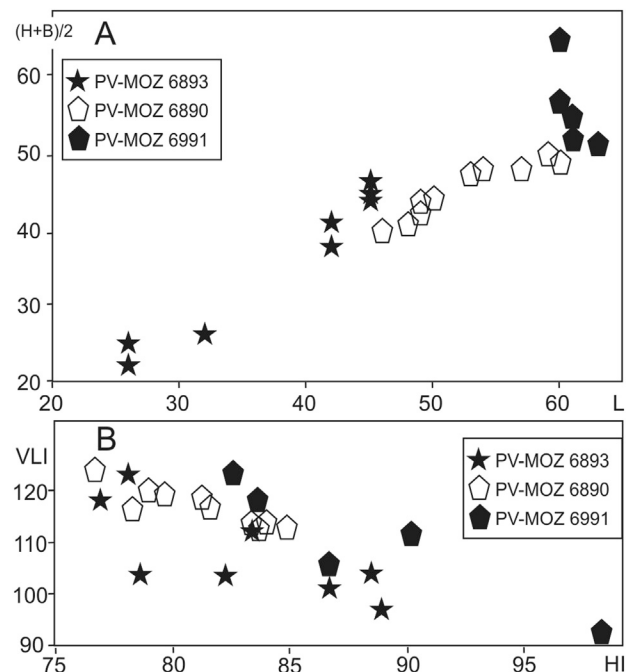

Fig. 6. Comparisons between MOZ-PV-6893, MOZ-PV-6890 and MOZ-PV-6991. A, absolute size [L; 0.5*(H + B)]. B, proportions [HI = 100*H/L; VLI = 100*L/(0.5*(H + B))].

Additionally, the VLI values of the cervical centra of MOZ-PV-6893/1–23 are similar or lower than those of MOZ-PV-6890/1–10 and MOZ-PV-6991, this is not consistent with the well recorded tendency of elongation of the cervical centra though ontogeny for elasmosaurids (O'Keefe and Hiller, 2006). In summary, we have identified an adult specimen (MOZ-PV-6893/1–23) with less elongated and smaller cervical centra than those of juvenile specimens (MOZ-PV-6890/1–10 and MOZ-PV-6991). Therefore, the specimen MOZ-PV-6893/1–23 could not belong to the same taxon as MOZ-PV-6890/1–10 and MOZ-PV-6991, indicating the presence of more than one elasmosaurid in the Agrio Formation.

As it was mentioned before the absence of some typical elasmosaurid features, such as articular faces with a ventral notch, is one of the most interesting features of the cervical centra of MOZ-PV-6890/1–10, MOZ-PV-6892, MOZ-PV-6893/1–23 and MOZ-PV-6991. Among Early Cretaceous elasmosaurids, the ventral notch of the articular facet of the cervical centra is also absent in the Berriasian GWWU A3.B2 holotype of *Gronausaurus wegneri* from Germany (see Benson and Druckenmiller, 2014, Ch. 155), in the preserved vertebrae of the Hauterivian "Speeton Clay Plesiosaur" (NHMUK R8623; SCARB 200751) (Benson and Druckenmiller, 2014, Ch. 155) and in the upper Aptian *Callawayasaurus colombiensis*, one of the oldest well known elasmosaurids (Welles, 1962). The mid to late Albian *Eromangasaurus australis* (Sachs, 2005b) Kear, 2007, from Australia, only preserves five cervical vertebrae with articular faces that are ovoid in outline (Kear, 2005, 2007). Other Early Cretaceous records referred to Elasmosauridae indet. from Australia also lack the ventral notch (Kear, 2002, 2005, 2006b; pers. comm. 2014). The elasmosaurids from the lower Albian Wabiskaw Member of the Clearwater Formation also lack a ventral notch (Druckenmiller, 2006; Druckenmiller pers. comm.). The only Early Cretaceous record with a ventral notch on the cervical centra (LEICT G1.2001.014) comes from the Tithonian–Valanginian, Spilsby Sandstone, England. The LEICT G1.2001.014 is a cervical vertebra that shows a slight depression in the middle of the ventral surface (Forrest and Oliver, 2003, fig. 8; for age see Hopson et al., 2008; Fisher et al., 2012). Then, although abundant elasmosaurid cervical vertebrae from the Lower Cretaceous have been recovered (Welles, 1962; Lazo and Cichowolski, 2003; Kear, 2005; Druckenmiller, 2006; Kear et al., 2006a; this work), the ventral notch is absent or scarcely represented. Additionally, two plesiosauroids from the Upper Jurassic of Spitsbergen, Norway, recovered as sister group of the Cretaceous elasmosaurids, lack the ventral notch (Knutsen et al., 2012a,b).

Therefore, the presence of a ventral notch on cervical centra remained uncommon until the Late Cretaceous, with the appearance of taxa with a deeply excavated ventral notch in both hemispheres probably during the Cenomanian stage, for example *Thalassomedon haningtoni* Welles, 1943 [Graneros Shale Formation, USA]; *Libonectes morgani* (Welles, 1949) [Britton Formation, USA; for Cenomanian age of *L. morgani* see Sachs and Kear, 2014] and an Elasmosauridae indet. [Mata Amarilla Formation, Argentina] all Cenomanian in age (Welles, 1943; O'Gorman and Varela, 2010, fig. 4; Varela et al., 2012).

7. Plesiosaur taphonomy and bearing facies

Taphonomic processes affecting terrestrial vertebrates are reasonably well known, but marine forms have been less studied in this respect, so current knowledge on their taphonomy is based on observations of decay and disintegration of recent fishes and marine mammals (Schäfer, 1972). In particular, some taphonomic studies of ichthyosaur skeletons have been reported (e.g. Martill, 1987) but little has been published about plesiosaurs (Barnes and Hiller, 2010) and thus it would be useful to begin implementing taphonomic studies, along with paleoecological analyses, to get a clearer picture of the postmortem processes and biases that affected this group of Mesozoic marine reptiles. A combined taphonomic and sedimentary facies study of the plesiosaurs recorded from the Agrio Formation (Fig. 7) is outlined below and two taphonomic modes are described and interpreted.

7.1. Taphonomic mode 1, plesiosaur remains embedded in dark-grey shales

Description: Most of the materials (MOZ-PV 6890, 6891, 6892, 6893, 6990 and 6991) were found in thick beds of dark-grey shales. This mode, in particular, includes one of the most complete plesiosaur skeletons yet found in the Agrio Formation (MOZ-PV 6991). This taphonomic mode consists of fragmentary skeletons found *in situ*. In general, skeletal elements are found disarticulated but closely associated in the field, presumably belonging to a single individual in each occurrence. Findings are scattered throughout the unit (Fig. 3). Records involve elements of the postcranial
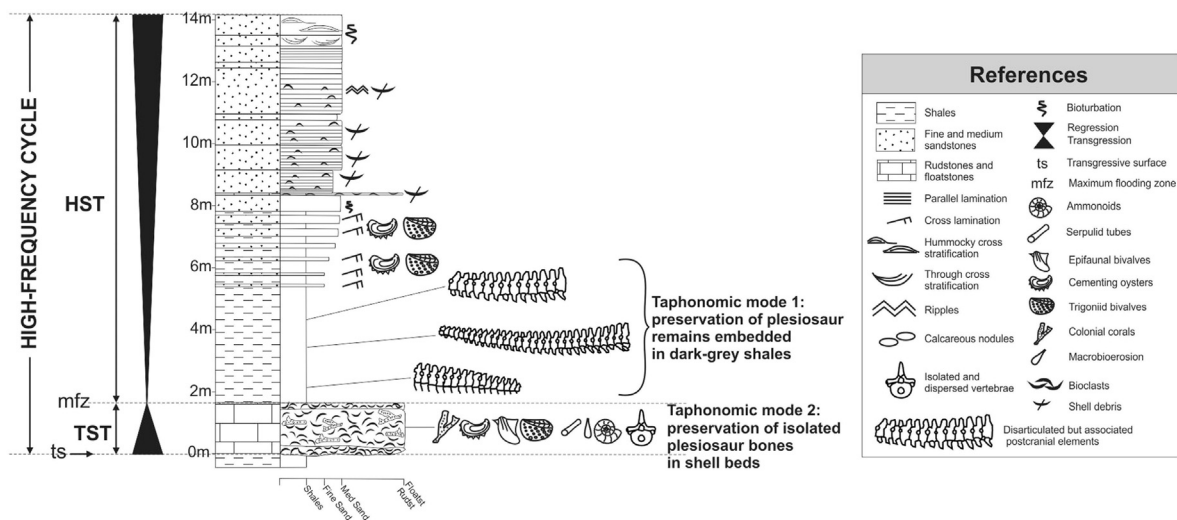

Fig. 7. Stratigraphic position in a generalized fourth-order high-frequency cycle of the two taphonomic modes described for plesiosaur records from the Agrio Formation, Neuquén Basin, west-central Argentina. High-frequency cycle modified from Spalletti et al. (2001) and Garberoglio et al. (2013).

skeleton and usually correspond to cervical, dorsal and/or caudal vertebrae plus autopodium elements. Skeletal parts are unsorted and usually occur in an area of 10 m^2 approximately. Orientation of elements in plan view is difficult to assess as bones usually appear scattered, but in cross-section view they are parallel to bedding. Bones show low degree of external weathering, but vertebrae usually do not show processes and some of the centra are externally encrusted by small cementing oysters. Associated fossils include isolated ammonoid and trigonioid shells oriented parallel to bedding and small cementing oysters conforming nests of aggregated specimens up to 40 cm thick and 1 m of lateral extension (Fig. 7).

Interpretation: This mode of preservation probably resulted from the floating and eventually sinking of carcasses to a muddy and calm seafloor under oxic to suboxic conditions, resulting in preservation *in situ* without significant transport or physical reworking. However, *postmortem* transport via drifting of bloated carcasses cannot be discarded. Scavenging and decomposition would result in the dispersal of some skeletal elements, especially from the periphery of the carcass (e.g. skull, neck, distal limbs). The torso would then undergo further decomposition and disarticulation on the seafloor after sinking. The bearing facies can be interpreted as deposited in a proximal to distal offshore setting, below the storm wave base, within a context of moderate to high sedimentation rate.

This mode of occurrence, recorded at different stratigraphic levels of the Agrio Formation, may be linked to the cyclicity of the unit that is in turn related to relative sea level changes. In terms of sequence stratigraphy it can be pointed out that fourth-order high-frequency cycles have been described for the Agua de la Mula Member of the Agrio Formation by Spalletti et al. (2001). These cycles are composed of a basal carbonate interval that is followed by a thick siliciclastic interval that coarsens upwards from shales at the base to sandstones at the top. The basal carbonate interval has been interpreted as transgressive systems tract deposits while the upper siliciclastic interval has been regarded as highstand systems tract deposits. These cycles have a maximum thickness of around 15 m and are equivalent to 10^5 years approximately. The shales bearing plesiosaur remains may be regarded as deposits of highstand systems tract within high-frequency cycles within "both marine members of" the Agrio Formation.

7.2. Taphonomic mode 2, preservation of isolated plesiosaur bones in shell beds

Description: A second taphonomic mode, which is less common, involves isolated and dispersed bone elements deposited in mollusk-dominated shell beds. This mode corresponds to three findings (MOZ-PV-6894, 6992 and 6993) from the Pilmatué Member. Bone elements belong to isolated vertebrae that are weathered, abraded and heavily encrusted by small cementing oysters. Orientation of bones both in cross-section and plan view is random. Shell beds are densely to loosely packed and range between 0.5 and 3.5 m in thickness. Thicker shell beds are tabular while thinner ones are lens-shaped. The matrix is carbonate mud. Lower boundaries are sharp, sometimes with evidence of erosion, whereas tops are sharp to transitional to dark-grey shales. The shell beds show a mixture of shells with different degrees of physical, biological or chemical alteration. Size-sorting of bioclasts is usually poor, with mixture of several-centimeters-long complete shells and small shell fragments. Macroinvertebrates include a diverse assemblage of bivalves, ammonoids, nautiloids and gastropods that form the bulk of the shell beds. At first sight, shells seem randomly oriented in cross-section, but concordant (shells convex-down and

convex-up), nested, and perpendicular orientations of shells and fragments dominate locally (Fig. 7).

Interpretation: This mode of preservation probably resulted from biogenic and possibly physical reworking of previously settled vertebrate carcasses on the seafloor. Skeletons were disarticulated and individual elements got dispersed, isolated and finally deposited along with a diverse assemblage of mollusks. Shell beds containing isolated bones are interpreted as deposited in the transition zone and upper offshore settings during reduced input of siliciclastic material and originated via gradual accumulation of bioclasts influenced by biogenic reworking and sometimes by storm waves and currents. Variable degrees of fragmentation, abrasion, encrustation and bioerosion are probably related to the time of residence of bioclasts on the seafloor and to the intensity of the processes of reworking.

In terms of sequence stratigraphy this mode of occurrence corresponds to the basal carbonate interval of the high-frequency cycles defined by Spalletti et al. (2001) in the Agua de la Mula Member of the Agrio Formation. This basal interval is interpreted as transgressive systems tract deposits in which exposition of skeletal elements prior to final burial and biogenic reworking is caused by a relatively low sedimentation rate during times of reduced clastic input.

8. Paleoecological remarks

Plesiosaurs were undoubtedly marine aquatic reptiles that reached a cosmopolitan distribution throughout the Jurassic and Cretaceous (Benson and Druckenmiller, 2014). It is apparent from previously described fossil occurrences that they inhabited a range of marine settings, from shallow coastal to deeper basinal ones (Welles, 1943; Kear, 2005; Sato et al., 2005; O'Gorman et al., 2013; Benson and Druckenmiller, 2014). In particular, elasmosaurid plesiosaurs have been generally recorded associated with shallow marine (offshore/shelf to shoreface) environments, such as epicontinental seas, but also associated with marginal-marine settings such as barrier-island systems, estuaries and deltaic environments, all of them being more or less connected to the open sea (Sato et al., 2005; Kear et al., 2006b; O'Gorman et al., 2011, 2013; Hornung et al., 2013). Some authors have also claimed that some Jurassic and Cretaceous plesiosaur taxa lived in fully freshwater continental environments as far as hundreds of kilometers away from the nearest coast (e.g., Russell, 1931; Sato et al., 2003; Kear, 2006b, 2012; Benson et al., 2013a). Many of these studies are based on scarce material or did not include a careful taphonomic analysis of the recorded specimens along with a detailed sedimentary facies analysis, which are generally necessary to detect highly reworked and/or time-averaged vertebrate assemblages. Therefore, although it is quite likely that some plesiosaurs had temporary incursions into the head of estuaries or deltaic plains, a completely freshwater habitat for some plesiosaurs has not yet been unmistakably proved. More studies of associated sedimentary facies and paleoenvironments along with updated stratigraphic schemes and careful taphonomic analyses are needed in order to shed light on various plesiosaurian habitats.

Preservation of the elasmosaurid remains studied here followed two different taphonomic modes that are interpreted in terms of high-frequency cycles of relative sea level. Most findings are associated with dark-grey shales that have been interpreted as proximal to distal offshore deposits in a context of moderate to high sedimentation rate within a highstand systems tract. Less frequently, elasmosaurids are recorded as isolated bones embedded in shell beds, implying major taphonomic alteration of carcasses; they are associated with transgressive episodes and lower net

sedimentation rates in a context of a transgressive systems tract. The elasmosaurid record of the Agrio Formation is thus biased in terms of sequence stratigraphy and changes in relative sea level. More and better preserved specimens should be expected to turn up in fine-grained sediments deposited during highstand systems tracts and badly preserved specimens in shell beds of transgressive systems tracts.

9. Conclusions

New elasmosaurid records are reported from the Valanginian–Hauterivian Agrio Formation of the Neuquén Basin, west-central Argentina, including the first late Hauterivian records from South America and demonstrating the presence of elasmosaurids in both the Pilmatué and Agua de la Mula members of the Agrio Formation. The relationship between growth stages and size indicates the presence of at least two elasmosaurid taxa, while additional morphological differences could be indicative of a third one. Additionally, the Agrio Formation elasmosaurids confirm the scarcity of pre-Cenomanian elasmosaurids with a ventral notch in the cervical vertebrae, a feature that will become widespread among Late Cretaceous elasmosaurids.

The taphonomic analysis shows two modes of preservation, 1) disarticulated but closely associated plesiosaur postcranial skeletons embedded in dark-grey shales, and 2) isolated plesiosaur bones in shell beds. Elasmosaurid records from the Agrio Formation are biased in terms of preservation; the bias is related to changes in relative sea level. Well-preserved specimens are expected to be found in shales deposited during highstand systems tracts, whilst badly-preserved ones are expected to be found in shell beds deposited during transgressive systems tracts of fourth-order high-frequency sedimentary cycles.

Elasmosaurids from the Agrio Formation indicate that they were related to shallow marine settings since the early stages of its evolutionary history.

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