

Description of ichthyosaur remains from the Lower Cretaceous Agrio Formation (Neuquén Basin, west-central Argentina) and their paleobiological implications

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ABSTRACT

Ichthyosaur remains from the Lower Cretaceous of the Neuquén Basin, west-central Argentina, are herein described and put into the broader context of their mode of occurrence and facies relationships. The ichthyosaur material was collected from six stratigraphic levels within the Agrio Formation. Five records come from upper Valanginian black and dark-gray shales, and one comes from upper Hauterivian fine-grained grayish sandstones. According to current paleogeographic schemes, all the studied ichthyosaur localities had a distal position on the marine shelf of the Agrio Formation, i.e., towards the offshore and basin. Ichthyosaurs were recorded in second-order TST and HST deposits, being better preserved in black shales of the TST. The best preserved material is a series of seven partially articulated posterior thoracic vertebral centra along with an ischiopubis (plus femur?) of an adult individual found in close association with a partially articulated fin and phalanges of a perinatal specimen. This finding might provide evidence of viviparity and also would indicate that at least some ichthyosaurs were able to pass through the volcanic arc from the Pacific Ocean to reproduce and give birth in an epeiric sea (the Neuquén Basin), similarly to what some large marine mammals do in the present. Given that the upper Valanginian–Hauterivian is particularly devoid of ichthyosaur records worldwide, the remains herein presented can shed light on the Early Cretaceous distribution of these marine reptiles in the Southern Hemisphere. The apparent local absence of ichthyosaurs from Berriasian–middle Valanginian deposits may be due to the overall prevalence of shallower settings in the Neuquén Basin in this time window that deterred the entrance of ichthyosaurs from the open ocean.

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1. Introduction

Ichthyosaurs were a highly successful group of reptiles that evolved an obligatory aquatic mode of life. Among Mesozoic marine reptiles, fish-shaped ichthyosaurs were the group that acquired the

highest level of aquatic adaptation. Anatomical traits associated with these adaptations include streamlined bodies with lunate tail and dorsal fin. The arrangement of limb bones is also strongly modified, forming fins (Motani, 1999; McGowan and Motani, 2003). Their evolutionary history spans most of the Mesozoic, from the Olenekian (Early Triassic) to the Cenomanian (Late Cretaceous) (Bardet, 1994; Fischer et al., 2011a,b, 2014). The youngest and most derived clade, the Ophthalmosauridae, dominated soon after its appearance in the early Bajocian, becoming diverse and geographically widespread (Fernández, 2003; Bardet et al., 2014; Druckenmiller and Maxwell, 2014). Knowledge about ophthalmosaurids increased significantly during the last decade

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(e.g., Fernández and Campos, 2015). However, hiatuses in their fossil record and scarcity of well-preserved materials from certain time intervals and/or geographic regions prove that further sampling is necessary to achieve a better understanding of the evolution of the group. In particular, records from the Valanginian–Hauterivian time lapse are still comparatively scant, with most studies alluding to undetermined remains due to an overall low completeness of records. Some exceptional records in this time interval include a rostrum of *Aegirosaurus* sp. from the late Valanginian of France (Fischer et al., 2011a), the type materials of *Acamptonectes densus* Fischer et al., 2012 from the Hauterivian of England and paratype and associated specimens from Germany. A recent completeness metric analysis shows that there are significant drops in species diversity and number of collections after the Jurassic/Cretaceous (J/K) boundary until a relatively small spike in the Albian (Cleary et al., 2015). However, new findings from the J/K boundary of Svalbard, Norway, have challenged this proposal (Delsett et al., 2017).

Reports of South American ichthyosaurs have been considered as rare (Stinnesbeck et al., 2014). However, there are significant findings from the Middle and Upper Jurassic of the Neuquén Basin. Although not abundant, early Middle Jurassic ichthyosaurs have been recovered that can be considered as outstanding as they represent the only ichthyopterygian records of this epoch from the Eastern Pacific including also the oldest diagnostic record of an ophthalmosaurid worldwide (Fernández, 2003) and some of the few diagnostic Aalenian–Bajocian ichthyosaurs: *Stenopterygius cayi* (= *Chacaicosaurus cayi* Fernández, 1994) and *Mollesaurus periallus* Fernández, 1999. Perhaps the most abundant and diverse ichthyosaur assemblage is the one recovered from Tithonian beds of the Vaca Muerta Formation (Neuquén Basin, Argentina), including at least three nominal taxa: *Arthropterygius* sp., *Aegirosaurus* sp. and *Caypullisaurus bonapartei* (Fernández, 2007; Fernández and Maxwell, 2012). Further south there are records of Early Cretaceous ichthyosaurs from Argentina and Chile. On the one hand, “*Platypterygius*” *hauthali* (von Huene, 1927) is known from the Barremian Río Belgrano Formation, Santa Cruz Province, Austral Basin of Argentina (Fernández and Aguirre-Urreta, 2005). On the other hand, a unique concentration of ophthalmosaurid skeletons has been recently recovered from bathyal to abyssal deposits of Valanginian–Hauterivian age (Stinnesbeck et al., 2014) in the Torres del Paine National Park of Chile. This assemblage comprises a total of 46 articulated and virtually complete adult, juvenile, embryonic, and neonate specimens (see also Pardo Pérez et al., 2015).

In this paper, new records of Lower Cretaceous ichthyosaurs from the Agrio Formation (Neuquén Basin) are studied. The Agrio Formation is a thick unit encompassing relatively shallow-marine deposits accumulated in a large epeiric sea connected to the Pacific Ocean during the Valanginian–Hauterivian. The ichthyosaur remains herein presented were collected from six stratigraphic levels that were accurately dated using the associated ammonoid fauna. Disarticulated but associated vertebral centra comprise most of the findings, but more complete postcranial remains, including one ischiopubis (plus femur?) and perinatal fin remains, were also recovered.

The study material was obtained while sampling for mollusks and other invertebrates in the Agrio Formation. It may not therefore be representative of the true diversity of ichthyosaurs present during the Valanginian–Hauterivian in the Neuquén Basin, but it is important to note that they resulted from more than 20 years of exploration and research in the unit and thus they are likely the best approximation to the actual diversity because of the intensive exploration and many years of collecting effort. Despite skeletal incompleteness and poor preservation, these records are important because they partially fill a significant gap in the ichthyosaur evolutionary history, since there are just a few records of this time

interval worldwide. Moreover, they also bear importance in terms of local sedimentary evolution, paleoenvironments and paleoecology of the Neuquén Basin through the Valanginian–Hauterivian. The new findings are herein discussed in a sequence stratigraphy framework for the Agrio Formation, comparing their distribution with that of previous plesiosaurian records from the same unit (O’Gorman et al., 2015).

Therefore, the objectives of the present contribution are as follows: 1) to describe and identify to the lowest possible taxonomic rank the new ichthyosaur material; 2) to provide accurate chronostratigraphic ages for these remains based on a refined ammonoid zonation; 3) to describe and interpret the taphonomic mode and the facies relationships of the fossil-bearing beds; and 4) to discuss the distribution of the ichthyosaur records in a sequence stratigraphy framework and compare it with that of local plesiosaur records.

2. Geological setting

2.1. The Neuquén Basin and the Agrio Formation

The Neuquén Basin is located near the present international Argentine–Chilean border along the Andes, roughly between 32° and 40°S. The basin covers an area of over 120,000 km², being represented by a narrow belt of outcrops with a trend parallel to the Andes mainly in Mendoza, and by an eastern expansion known as the Neuquén Embayment developed in the homonymous province (Fig. 1; Howell et al., 2005).

The basin was a back-arc depocenter during Early Jurassic–Early Cretaceous times, developed under active convergence in the western margin of South America. Deposition progressed under the influence of a well-developed volcanic arc. The subsidence regime was rather constant, suggestive of thermal drive. The paleoceanographic connection was towards the Pacific Ocean. Alternating marine and continental deposits accumulated in the basin driven by periodic transgressions. A broadly triangular epeiric sea embayment was formed during times of high relative sea level.

The studied ichthyosaur remains were recovered from the Agrio Formation, a unit defined by Weaver (1931) in the Río Agrio section (Neuquén Province), where it reaches more than 1000 m in thickness and includes three members. The lower or Pilmatué Member is mainly composed of massive clayey shales interbedded with thin layers of sandstones and shell beds, and has been interpreted mainly as a marine shelf (or ramp) with storm influence to a basinal setting towards the west and north (Fig. 1). The middle or Avilé Member, a thin continental unit, is represented by yellowish-brown cross-bedded sandstones of aeolian and fluvial origin, representing a second-order sea-level fall. The upper or Agua de la Mula Member is composed largely of massive shales in the lower part and gray calcareous shales interbedded with sandstones, sandy limestones and shell beds in the upper part, and represents a new marine transgression (Leanza et al., 2005; Spalletti et al., 2011). Comprehensive accounts of the lithofacies, paleoecology and paleoenvironments of the Agrio Formation can be found in Lazo (2006, 2007) and Spalletti et al. (2011).

The Agrio Formation has a rich and abundant fossil record, first described in detail by Weaver (1931), mainly comprising invertebrates such as bivalves, gastropods, nautiloids, ammonites, corals, crustaceans, echinoderms, bryozoans, brachiopods, and serpulids (Aguirre-Urreta et al., 2011). The invertebrate fauna as a whole has mainly Tethyan affinity, but some taxa have Andean affinity and even endemic taxa are present (Aguirre-Urreta et al., 2008; Cataldo, 2017). The invertebrates also indicate shallow warm-temperate waters (Lazo et al., 2005).

Marine reptiles have been scarcely recorded in the unit, corresponding to mainly disarticulated postcranial remains of plesiosaurs.

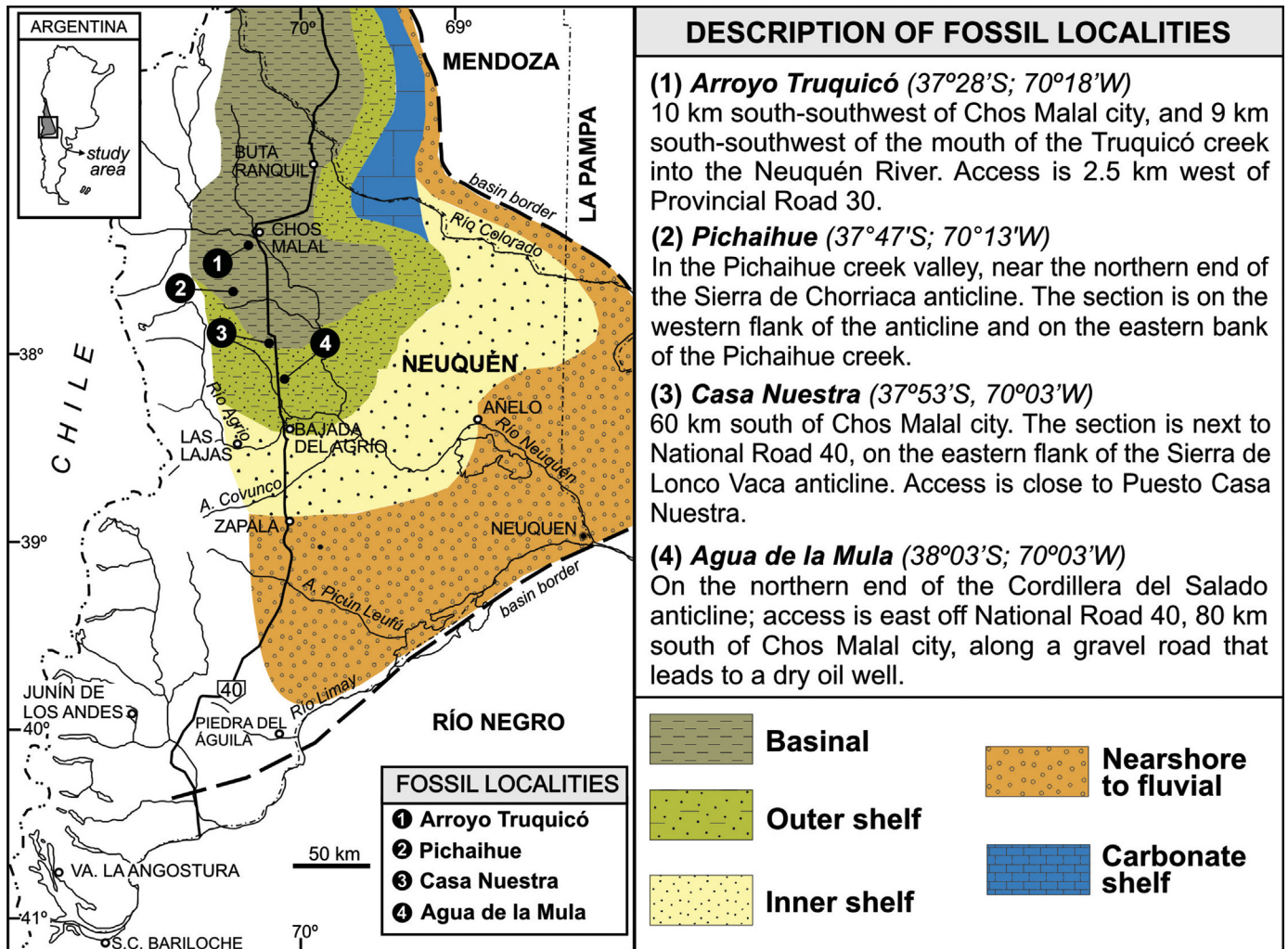


Fig. 1. Map of west-central Argentina showing fossil localities bearing Lower Cretaceous ichthyosaur remains from the Agrio Formation. Note that the studied localities belong to the distal sector of the basin, from outer shelf to basin. Paleogeography and facies from Legarreta and Uliana (1991).

Most of these findings belong to long-necked elasmosaurids recorded in both marine members of the Agrio Formation encompassing the Valanginian-Hauterivian interval (O'Gorman et al., 2015). Ichthyosaur remains are extremely rare in the unit, so far represented by disarticulated, isolated and fragmented vertebral centra only (see Cichowolski and Lazo, 2000). In the present study, however, more complete and partially articulated postcranial remains are described along with several isolated vertebral centra. A preliminary report of these records was published by Fernández et al. (2015). The studied materials come from both marine members of the Agrio Formation, i.e., the Pilmatué and the Agua de la Mula members (Fig. 2, Table 1).

Integrated studies on ammonoids, nannofossils and paly-nomorphs from the Agrio Formation have provided an excellent biostratigraphic framework for the unit that can be easily followed from one locality to another (see Aguirre-Urreta and Rawson, 2010, 2012; Aguirre-Urreta et al., 2005, 2007). The zonation is also correlated with the Standard Ammonoid Zonation of the Mediterranean Region of Western Europe (Aguirre-Urreta et al., 2007). The whole unit has been assigned a late early Valanginian to late Hauterivian age based on integrated biostratigraphy calibrated with U–Pb zircon ages (e.g., Aguirre-Urreta et al., 2015, 2017).

The studied ichthyosaur remains were collected at four localities. From north to south these are: 1) Arroyo Truquicó, 2) Pichaihue, 3)

Casa Nuestra, and 4) Agua de la Mula (Fig. 1). These sections are located towards the northern part of Neuquén and thus more distally placed on the marine shelf of the Agrio Formation, belonging to basinal (Arroyo Truquicó and Pichaihue) and outer shelf (Casa Nuestra and Agua de la Mula) settings, respectively (Fig. 1).

2.2. Sequence stratigraphy framework

Legarreta and Gulisano (1989) published the first attempt of an analysis of the sedimentary record of the Neuquén Basin using a sequence stratigraphy approach. The framework they proposed, which remains valid (see Veiga et al., 2005 and references therein), included three first-order sequences (also called super sequences) encompassing latest Triassic to Paleocene deposits. The Agrio Formation is included in the middle supersequence, previously referred to as Andean Cycle by Groeber (1946). This cycle is characterized by the overall presence of marine sedimentary deposits, especially black and dark-gray shales, but also by a continuous sedimentation through the Tithonian/Berriasian boundary that resulted in a transitional pass with no obvious contrast between Tithonian and Berriasian sedimentary facies.

The Andean cycle was in turn subdivided into five second-order sequences (also called mesosequences). The Mulichinco Formation and the Pilmatué Member of the Agrio Formation constitute the

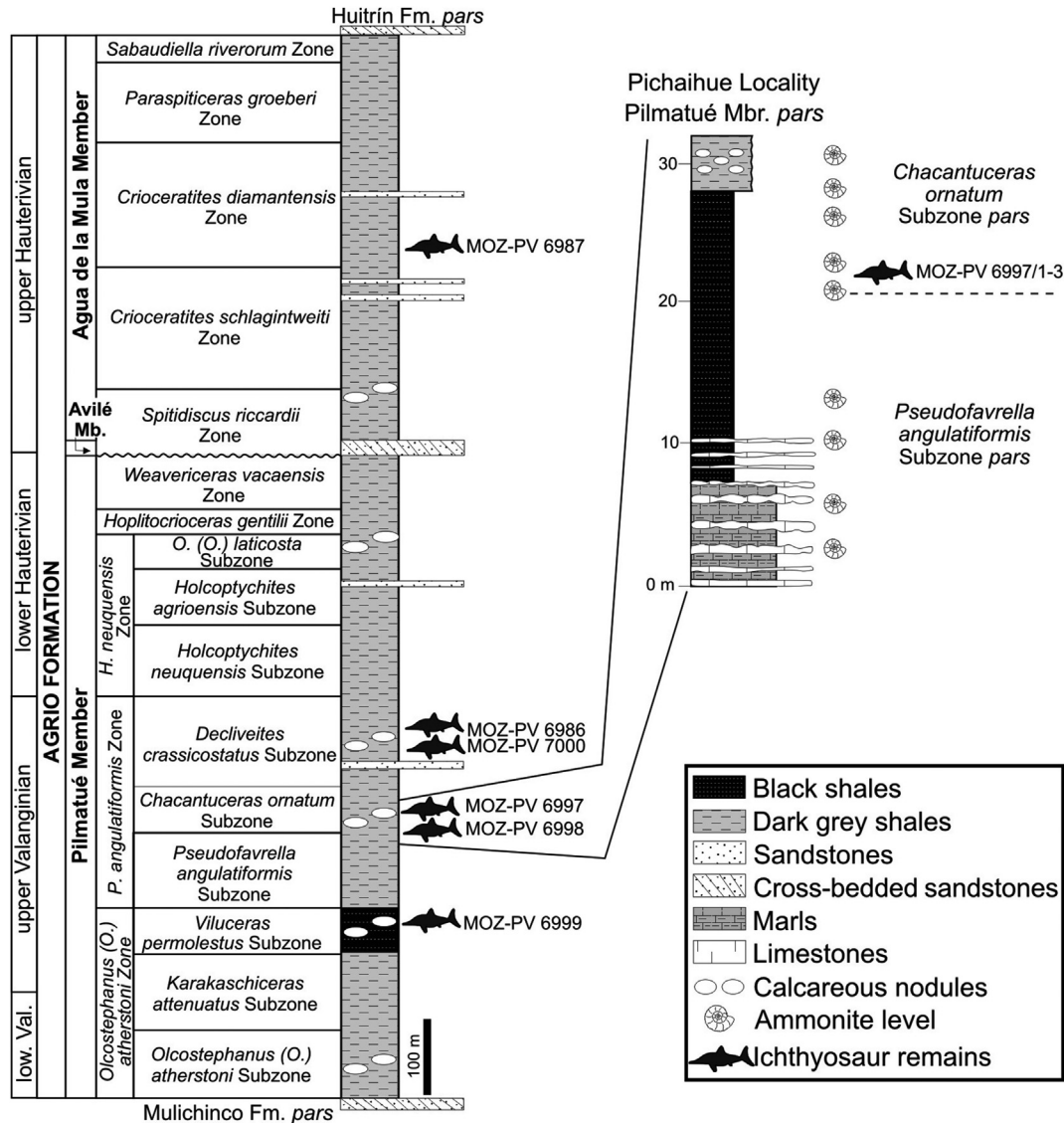


Fig. 2. Compiled section of the Agrio Formation showing the stratigraphic position and age of the recorded ichthyosaur remains and detail of the ichthyosaur-bearing beds at the Pichaihue locality. Ammonoid zonation and ages from Aguirre-Urreta et al. (2007) and Aguirre-Urreta and Rawson (2010).

middle Mendoza mesosequence, while the Avilé and Agua de la Mula members compose the upper Mendoza mesosequence. Two regional sequence boundaries depict the base of each mesosequence (Fig. 3): the older one is called the Intravalanginian Discontinuity (Gulisano et al., 1984) while the younger one is called Intrahauterivian Discontinuity (Legarreta and Kozłowski, 1984). Further details on the Intravalanginian Discontinuity and associated systems tracts can be found in Schwarz and Buatois (2012). Each mesosequence has been subdivided, from base to top, into second-order lowstand systems tract (LST), transgressive systems tract (TST) and highstand systems tract (HST). The base of each LST is depicted by the mentioned regional unconformities, which developed during major sea level falls. The LST includes mainly continental deposits in central parts of the basin while the TST and HST deposits are mainly of marine origin. Both the middle and upper Mendoza mesosequences and their division into LST, TST and HST are depicted in Fig. 3. This is the sequence stratigraphy framework used to evaluate the local ichthyosaur records.

The studied ichthyosaur materials and previously published plesiosaur remains from the Agrio Formation are placed in this

sequence stratigraphy framework to test for a correlation between sea level, accommodation space and the occurrence of marine reptiles (Fig. 3). The placement of each ichthyosaur/plesiosaur record was easily done by means of the associated ammonoid faunas and the current biostratigraphic zonation scheme. This type of analysis can be useful to interpret the paleoecological traits of ichthyosaurs, but also to evaluate biases in the ichthyosaur fossil record and determine the best localities for further prospection.

3. Systematic paleontology

The studied ichthyosaur materials are housed in the following collection under the catalogue numbers listed in the text: MOZ, Museo Juan Olsacher, Zapala, Neuquén, Argentina. Specimens were mechanically prepared. Five of the isolated phalanges of the MOZ-PV-6997/1, found in association with the articulated fin, were sectioned in order to explore the microstructural and histological pattern. The phalanges (1.2–2.3 cm in length) are roughly rounded and herein identified as belonging to the more distal portion of the fin. Thin sections were prepared using standard paleohistological

Table 1
Ichthyosaur materials from the Lower Cretaceous Agrio Formation (Neuquén Basin, west-central Argentina) discussed in this paper. TM1 = taphonomic mode 1, TM2 = taphonomic mode 2.

Rep. number MOZ-PV	Taxonomic revision	Material	Member	Locality and Province	Ammonoid Zone	Ammonoid Subzone	Stage	Lithology and Taphonomic mode
6986	Ichthyosauria incertae sedis	1 fragmented vertebral centrum	Pilmatué	Agua de la Mula, Neuquén	<i>Pseudofavrella angulatiformis</i>	<i>Declivites crassicostratus</i>	Upper Valanginian	Dark-gray shales (TM2)
6987	Ichthyosauria incertae sedis	1 posterior thoracic vertebral centrum	Agua de la Mula		<i>Crioceratites diamantensis</i>		upper Hauterivian	Fine-grained grayish sandstones (TM2)
6997/1	Ophthalmosauridae, Platypterygiinae indet.	Partially articulated fin and isolated phalanges of a perinatal individual	Pilmatué	Pichalhue, Neuquén	<i>Pseudofavrella angulatiformis</i>	<i>Chacantuceras ornatum</i>	upper Valanginian	Black shales (TM1)
6997/2	Ophthalmosauridae, Platypterygiinae indet.	1 ischiopubis and fragment of long bone (femur?) of an adult						
6997/3	Ichthyosauria incertae sedis	7 partially articulated posterior thoracic vertebral centra						
6998	Ichthyosauria incertae sedis	1 fragmented vertebral centrum		Casa Nuestra, Neuquén		<i>Chacantuceras ornatum</i>	upper Valanginian	Dark-gray shales (TM2)
7000	Ichthyosauria incertae sedis	1 posterior thoracic vertebral centrum				<i>Declivites crassicostratus</i>	upper Valanginian	
6999	Ichthyosauria incertae sedis	3 disarticulated but associated anterior thoracic (?) vertebral centra		Arroyo Truquicó, Neuquén	<i>Olcostephanus athersthoni</i>	<i>Viluceras permolestus</i>	lower Valanginian	Black shales (TM1)

techniques and examined with light microscopy (Chinsamy and Raath, 1992). Nomenclature and definitions of structures used in this study are derived from Chinsamy-Turan (2005) and Francillon-Vieillot et al. (1990). Identification of vertebral centra follows Kear (2006), Maisch and Matzke (2000), and Maxwell and Caldwell (2006). All described materials represent adult specimens, except material MOZ-PV-6997/1 that corresponds to a newborn or unborn specimen (= perinatal).

Order Ichthyosauria De Blainville, 1835.

Family Ophthalmosauridae Baur, 1887.

Subfamily Platypterygiinae Arkhangelsky, 2001 sensu Fischer et al., 2012

Platypterygiinae indet.

Figs. 4,5

Material. MOZ-PV-6997/1, partially articulated fin and phalanges of a perinatal specimen (Table 1).

Geographic and stratigraphic provenance. This material was recovered from the Pilmatué Member of the Agrio Formation at Pichalhue locality, Neuquén, Argentina. It was found loose but associated within a single stratigraphic level of black shales in close association with materials MOZ-PV-6997/2 and MOZ-PV-6997/3. All from the *Chacantuceras ornatum* Subzone of late Valanginian age (Table 1, Fig. 2).

Description. Eight articulated and several isolated fin elements have been studied. The articulated fin portion consists of three elements not anatomically displaced and mesopodials and phalanges *post-mortem* proximally displaced (Fig. 4). All the elements are plastically deformed. There is a conspicuous difference in the thickness of articulated and isolated elements. All fin elements are relatively small, the largest element (tentatively identified as carpal 3) reaching 30 mm antero-posteriorly and 23 mm proximo-distally. Some of them, tentatively interpreted as mesopodials, are as thick dorso-ventrally as they are long proximo-distally. The other elements, interpreted as phalanges, are longer than thick, being the most distal phalanges twice as long as thick. As the epipodium and zeugopodium are not preserved it is difficult to determine the dorso-ventral orientation of the articulated fin fragment. The most proximal element, interpreted as the intermedium, has a roughly hexagonal dorsal or ventral surface and bears two almost straight distal articular facets forming an obtuse angle between them. Distal to it, and naturally articulated with it, there is a pentagonal element that could belong, based on its topological relationship with the intermedium and its outline, to the distal carpal 3. Three elements, almost rectangular in outline, have been preserved articulated and, based on their morphology, are herein interpreted as phalanges. On one side a small round phalange has been preserved partially overlying two of the more proximal articulated phalanges. Isolated elements recovered in association with the articulated fragment comprise five dorso-ventrally thick elements that could correspond to counter lateral mesopodium and phalanges (Fig. 4). Two of them (one with the typical brick-like outline and the other smaller and with a slightly rounder profile) were sectioned for microstructure analysis.

Histology and microstructure of phalanges. Phalangeal sections depict the same internal pattern, so the description and figures correspond to only one of them, i.e., the most proximal one. The inner organization is cancellous and has a thick compact external layer of articular calcified cartilage (Fig. 5A, 5C). There is no open medullary cavity. The medullary region is cancellous, with few cavities separated by relatively thin trabeculae (Fig. 5B, 5D). The trabeculae contain globular shaped osteocyte lacunae with few canaliculi. The trabecular bone, in the inner part of the section, consists of primary bone with woven matrix and contains few




Stage		MEDITERRANEAN REGION	NEUQUÉN BASIN	SEQUENCE STRATIGRAPHY FRAMEWORK	PLESIOSAUR RECORDS	ICHTHYOSAUR RECORDS	
Hauterivian	upper	Standard Ammonoid zonation	Ammonoid Zonation	2nd order sequence (Upper Mendoza Mesosequence)	2nd order HST	 MOZ-PV 6987	
		"Pseudothurmannia ohmi"	Sabaudiella riverorum				
		Balearites balearis	Paraspiticeras groeberi				
		Plesiospidiscus ligatus	Crioceratites diamantensis				
		Subsaynella sayni	Crioceratites schlagintweiti				
	lower	Lyticoceras nodosoplicatum	Weavericeras vacaense	2nd order TST	2nd order LST	Intrahauterivian unconformity	
			Hoplitocrioceras gentilii				
		Crioceratites loryi	Holcoptychites neuquensis				2nd order HST
		Acanthodiscus radiatus	O. (O.) laticosta				
			Holcoptychites agrioensis				
Valanginian	upper	Criosarasinella furcillata	Decliveites crassicosatus	2nd order sequence (Middle Mendoza Mesosequence)		MOZ-PV 6986 MOZ-PV 7000	
			Chacantuceras ornatum				
			Pseudofavrella angulatiformis				
		Neocomites peregrinus	Viluceras permolestus				2nd order TST
		Saynoceras verrucosum	Karakaschiceras attenuatus				
	lower	Karakaschiceras inostranzewi	Olcostephanus (O.) atherstoni	2nd order LST		MOZ-PV 6999 MOZ-PV 6998 MOZ-PV 6997	
			O. (O.) atherstoni				
		Neocomites neocomiensiformis	Lissonia riveroi				2nd order HST pars
		Thurmanniceras pertransiens	Neocomites wichmanni				
		LMM pars					
Intravalanginian unconformity							

Fig. 3. Stratigraphic distribution of Valanginian–Hauterivian ichthyosaur and plesiosaur remains from the Agrio Formation in the studied second-order sequence stratigraphy framework and its correlation with the local ammonoid zonation of the Neuquén Basin and the Mediterranean Standard Zonation. Biostratigraphy, correlations and ages from Aguirre-Urreta et al. (2007), Aguirre-Urreta and Rawson (2012) and Reboulet et al. (2014). Sequence stratigraphy framework from Legarreta and Gulisano (1989). Sequence boundaries (regional unconformities) from Gulisano et al. (1984) and Legarreta and Kozłowski (1984). Previous plesiosaur records from O’Gorman et al. (2015). Abbreviation: LMM = lower Mendoza mesosequence.

simple vascular canals. This matrix remains monorefringent in polarized light. This feature reflects the absence of highly orderly spatial organization of the once present collagenous framework of bone tissue. Also in the trabeculae there are remnants of calcified cartilage (Fig. 5D). The calcified cartilage forms 82.63% of the total area (Fig. 5B). It is not possible to distinguish any sign of remodeling in the bone tissue.

Discussion. The genus *Platypterygius* von Huene is in need of a major revision. Species included within this genus share the typical

“brick-like” phalanges (McGowan and Motani, 2003; Kolb and Sander, 2009; Fischer, 2012), condition also present in other Platypterygiinae such as *Caypullisaurus* Fernández and *Sveltonectes* Fischer et al. Fischer (2016) in a revision of European forms assigned to *Platypterygius* stated that this genus should be restricted to the type species *P. platydictylus* (Broili, 1907). In this context, the studied MOZ-PV-6997/1 material is referred as *Platypterygiinae* indet. Even though it is not possible to give a more precise taxonomic identification, it is interesting to note the

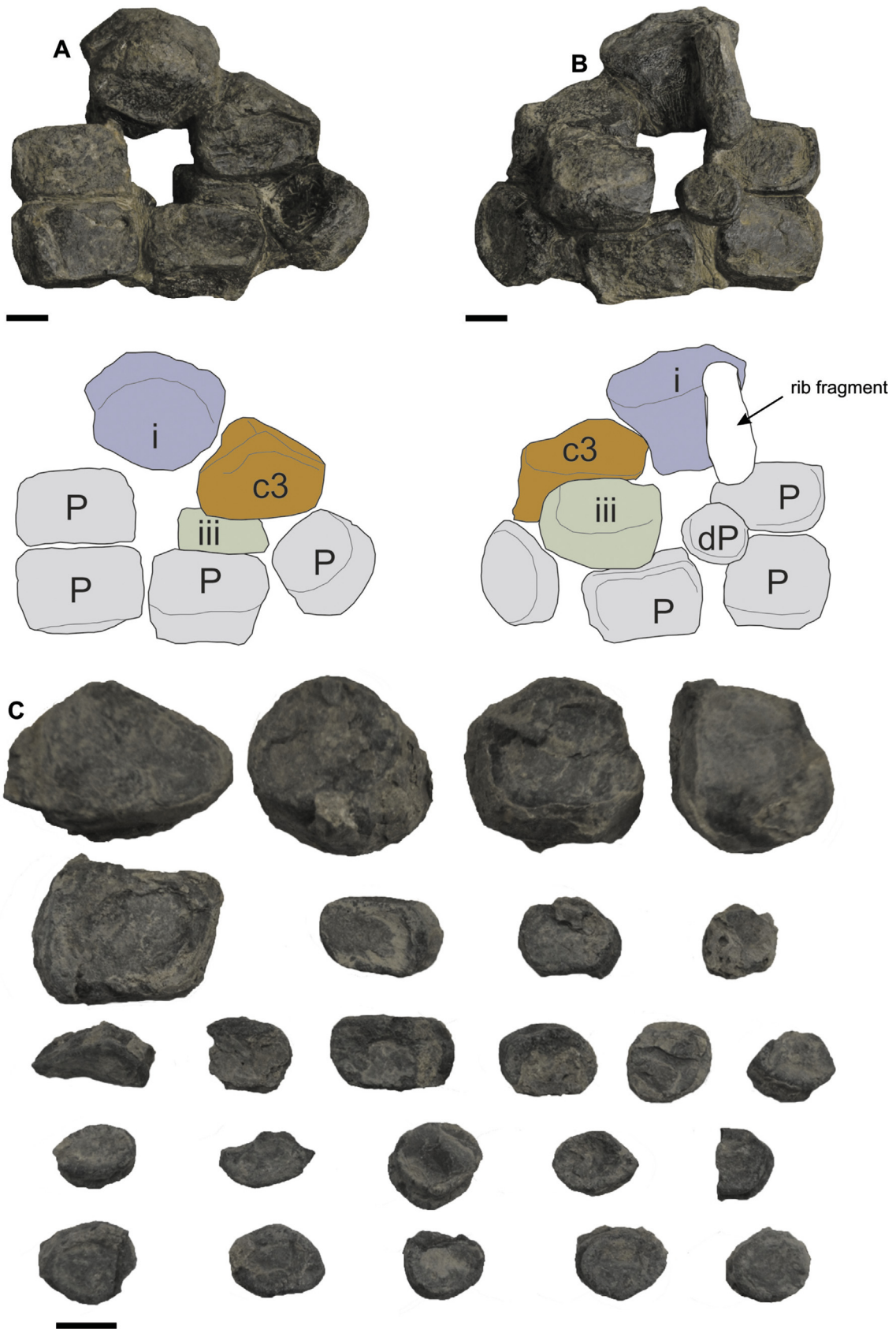


Fig. 4. Platypterygiinae indet (MOZ-PV 6997/1). A–B, partially articulated fin. C, isolated phalanges. Abbreviations: i = intermedium; c3 = distal carpal 3; dP = distal phalanges; P = phalanges, iii = metacarpal 3. In color: natural articulated elements; in gray: displaced phalanges. Scale bars are 10 mm. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

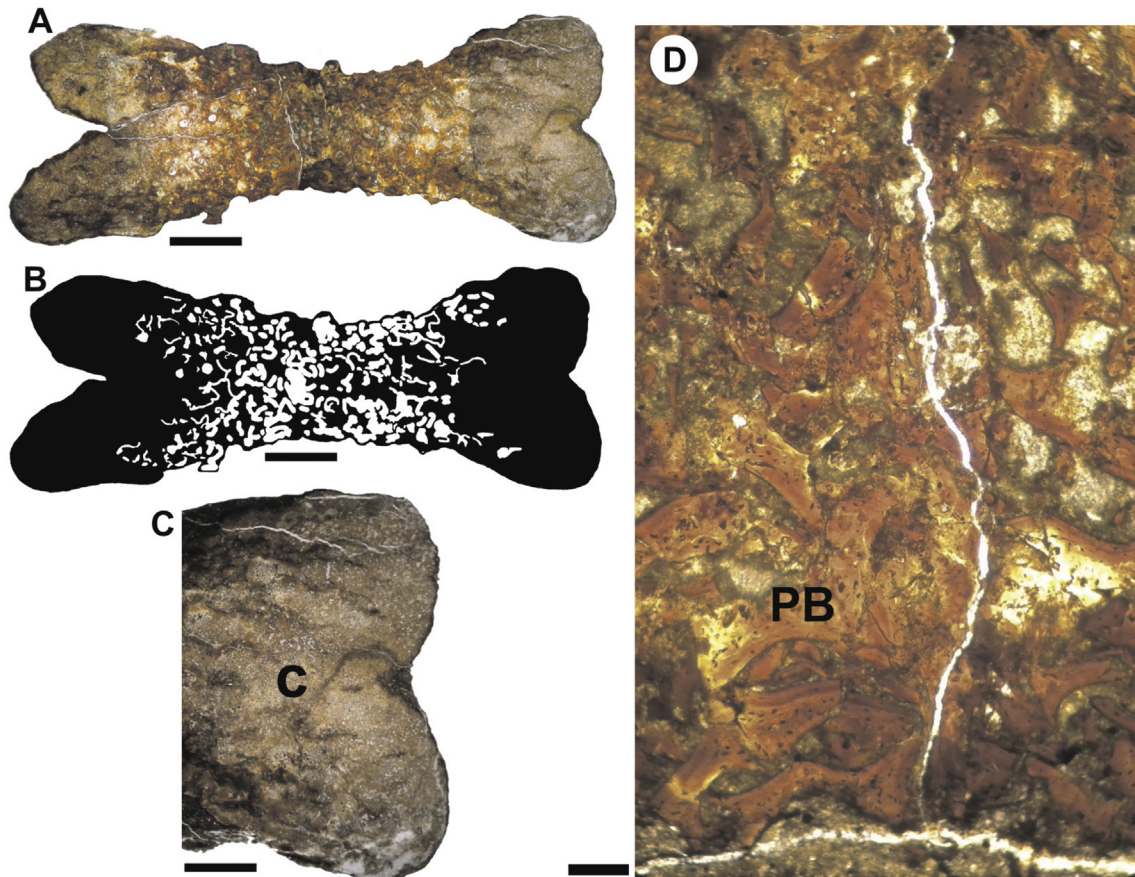


Fig. 5. Platypterygiinae indet. Histological sections. A–B, general view of the phalanx in cross section, scale bars are 10 mm. C, cortical section showing calcified cartilage, scale bar is 10 mm. D, medullary region with trabecular formed of primary bone, scale bar is 250 μ m. Abbreviations: C = calcified cartilage; Pb = primary bone.

hexagonal and diamond-shaped intermedium similar to the one described as diagnostic of “*Platypterygius*” *hauthali* von Huene, 1927 depicted by Fernández and Aguirre-Urreta (2005).

The most conspicuous feature of the fin is its reduced size. This fact could be interpreted as evidence of small-sized adults or a juvenile. Moreover, bone histology characterized by the predominance of cartilage, primary bone tissue without remodeling signs, the pattern of medullar tissue (i.e., globular shaped osteocyte lacunae, woven fibered bone) and few simple vascular canals, indicates that the bones correspond to a perinatal specimen (sensu Horner et al., 2001). As the bones were not found exactly within the presumed mother rib cage it cannot be determined if they belong to an unborn or a newborn (perinatal) specimen. However, as it is associated with a string of partially articulated posterior thoracic vertebral centra (MOZ-PV-6997/3) it is probably an unborn specimen. Among higher vertebrates, in embryos and in very fast growing young individuals, bone tissue is exclusively formed of a woven matrix (Francillon-Vieillot et al., 1990). The perinatal bone tissue is characterized by a lower organization of tissue and the presence of simple vascular canals (Klein et al., 2015). Woven fibered bone is unambiguously considered as indicative of a high absolute rate (expressed in microns/day) of periosteal accretion. Indeed, this bone tissue is accreted during the embryonic stage in numerous tetrapods (Francillon-Vieillot et al., 1990).

This finding shows some similarity with the case study of Maxwell and Caldwell (2003), who described articulated though only partially preserved remains of embryonic ichthyosaurs located within the body cavity of an adult, presumably the mother, from the Loon River Formation, Albian of Northwest Territories, Canada. It is

worth noting that these authors found the embryos attached to a string of eight mid-thoracic vertebrae (height of 6 cm, width of 2.5 cm) from a large adult ichthyosaur, which is very similar to the finding presented herein (i.e., several posterior thoracic vertebral centra—MOZ-PV-6997/3—of an adult individual associated with phalanx elements of a newborn or unborn specimen—MOZ-PV-6997/1). In spite of its relatively poor preservation, the finding presented here is considered an evidence of ichthyosaur viviparity and it raises an interesting hypothesis related to ichthyosaur reproductive habits implying that oceanic ichthyosaurs were able to enter a back-arc basin from the Eastern Pacific Ocean to reproduce and give birth in epeiric seas, closer to the coast, in a similar way to what some large marine mammals do in the present. However, more evidence on juvenile versus adult specimens is needed to test if the Neuquén Basin was a true reproductive area for ichthyosaurs.

Embryos of *P. hauthali* von Huene have also been found in the Valanginian-Hauterivian of southern Chile (Stinnesbeck et al., 2014, Table 1: specimen TY56), as well as neonates (Stinnesbeck et al., 2014, Table 1: specimens: TY01, TY36 and CPAP0002) among a total of 46 articulated ichthyosaurs, supporting the hypothesis of ichthyosaur viviparity and the use of a back-arc basin to reproduce. The Chilean locality at Tyndall (Rocas Verdes Basin) was also suggested as an ichthyosaur reproductive area (Stinnesbeck et al., 2014). These findings altogether reinforce the hypothesis that ichthyosaurs used protected areas for reproduction.

Platypterygiinae indet.

Fig. 6



Fig. 6. Platypterygiinae indet (MOZ-PV 6997/2). A–B, ischium and pubis completely fused, forming an ischiopubis, note distal portion strongly compressed. C, fragment of a long bone (femur?). Scale bars are 10 mm.

Material. MOZ-PV-6997/2, an isolated ischiopubis and a fragment of long bone (femur?) (Table 1).

Geographic and stratigraphic provenance. This material comes from the Pilmatué Member of the Agrio Formation at Pichaihue locality, Neuquén, Argentina. It was found loose in black shales of the *Chacantuceras ornatum* Subzone of late Valanginian age (Fig. 2), closely associated with materials MOZ-PV 6997/1 and MOZ-PV-6997/3.

Description. The ischium and pubis are completely fused, forming an ischiopubis with no trace of an obturator foramen. Its proximodistal length is 124 mm. As in all other platypterygiines, this ischiopubis is a rod-like structure for most of its length. Its anterior edge is slightly thicker than the posterior one. Both the acetabular and medial ends are almost equally antero-posteriorly expanded (maximum antero-posterior acetabular length = 45 mm; maximum antero-posterior medial length = 43 mm). Its proximal portion is thickened, ending in an ovoid rugose acetabular facet. Its distal portion is strongly compressed (Fig. 6A, B). There is an isolated fragment of a long bone poorly preserved (Fig. 6C) that could correspond to a femur fragment.

Discussion. The MOZ-PV-6997/2 shares the fused ischiopubis with the rest of the Baracromia clade (Fischer et al., 2013). Within this clade, it shares with the Platypterygiinae one of its unambiguous synapomorphies: the lack of an obturator foramen (Fischer et al., 2012, character 45). Morphology of the pelvic girdle is not known and/or described in ophthalmosaurids. In a recent contribution on the evolution of the Ichthyopterygian pelvic girdle, information on the ischiopubis is only available for 11 taxa among 23 ophthalmosaurids (Delsett et al., 2017). Although the information on the pelvic girdle is incomplete, a striking feature of the MOZ-PV-6997/2 is that, contrary to the condition known in all other ophthalmosaurids, the medial and acetabular ends of the ischiopubis are almost equally antero-posteriorly expanded.

Ichthyosauria incertae sedis

Fig. 7

Material. MOZ-PV-6986, one fragmented vertebral centrum; MOZ-PV-6987, one posterior thoracic vertebral centrum; MOZ-PV-6997/3, seven partially articulated posterior thoracic vertebral centra; MOZ-PV-6998, one fragmented vertebral centrum; MOZ-PV-6999, three disarticulated but associated anterior thoracic (?) vertebral centra; and MOZ-PV-7000, one posterior thoracic vertebral centrum (Table 1). MOZ-PV-6997/3 was found in close association with MOZ-PV-6997/1 (partially articulated fin) and MOZ-PV-6997/2 (ischiopubis) in a single interval of black shales of the Pilmatué Member at Pichaihue locality, Neuquén, Argentina.

Geographic and stratigraphic provenance. These vertebral centra come from a variety of facies of the Pilmatué and Agua de la Mula members of the Agrio Formation at Arroyo Truquicó, Casa Nuestra and Agua de la Mula localities, Neuquén, Argentina. They were found in the *Olcostephanus (O.) atherstoni*, *Pseudofavrella angulatiformis* and *Crioceratites diamantensis* zones, encompassing the lower Valanginian to upper Hauterivian (for further details see Table 1 and Fig. 2).

Description. MOZ-PV-6986 and MOZ-PV-6998 are two poorly preserved fragmented vertebral centra and thus difficult to identify. They are round and biconcave (amphicœlous). In particular, MOZ-PV-6986 shows diapophyses and parapophyses located low on the centrum, near the ventral region and thus it possibly represents a posterior thoracic or an anterior caudal vertebra.

MOZ-PV-6987 (Fig. 7C) probably represents a single posterior thoracic vertebral centrum (sensu Maisch and Matzke, 2000, fig. 19). It is a narrow, biconcave (amphicœlous), ovoid centrum; diapophyses and parapophyses are not distinguishable from each other, but placed close to the ventral margin.

MOZ-PV-6997/3 represents a series of seven partially articulated posterior thoracic vertebral centra (sensu Maisch and Matzke, 2000, fig. 19). These vertebral centra are narrow, biconcave discs (amphicœlous), slightly elongated in dorsoventral direction; diapophyses and parapophyses, small and subcircular, are located low on the centrum near the ventral region, close to each other, but still separated and close to the anterior face of the centrum (Fig. 7A–B, E–F). The ventral surface is smooth and round; the dorsal surface shows two straight, deep ovoid notches for articulation of the neural arch; the anterior and posterior surface margins form a low angle with the lateral centrum sides; neural arches and spines are lost but dorsal articulation face is noticeable and subrectangular. On two of the centra there is a phalange and a rib fragment still attached (Fig. 7A–B).

MOZ-PV-6999 comprises three vertebral centra; all of them are narrow, biconcave discs (amphicœlous); one of them shows diapophyses close to the articulation of the neural arch and parapophyses placed lower on the centrum and thus it could represent an anterior thoracic vertebra; the anterior and posterior surface margins form a low angle with the lateral centrum sides; neural arches and spines are lost.

MOZ-PV-7000 is an isolated posterior thoracic vertebral centrum (sensu Maisch and Matzke, 2000, fig. 19). It is a narrow, biconcave disc (amphicœlous), slightly elongated in dorsoventral direction; diapophyses and parapophyses are located low on the centrum near the ventral region; neural arches and spines are lost. **Discussion.** All of the vertebral features observed in the studied materials are compatible with those observed on vertebrae from post-Triassic ichthyosaurs. Unfortunately, poorly preserved isolated vertebrae preclude a more precise identification, which would be very interesting from an evolutionary point of view, given the overall scarcity of Early Cretaceous ichthyosaur remains worldwide (Fischer et al., 2011a,b).

The most informative material is MOZ-PV-6997/3, which was found partially articulated and in close association with MOZ-PV-6997/1 and 6997/2 and thus may be referred to Platypterygiinae.

4. Mode of occurrence and facies relationships

4.1. Methods

A general stratigraphic section of the Agrio Formation, approximately 1200 m in thickness, was measured at the Agua de la Mula locality (Fig. 2). This section along with partial ones from Arroyo Truquicó and Pichaihue localities (Fig. 2) were used to plot all

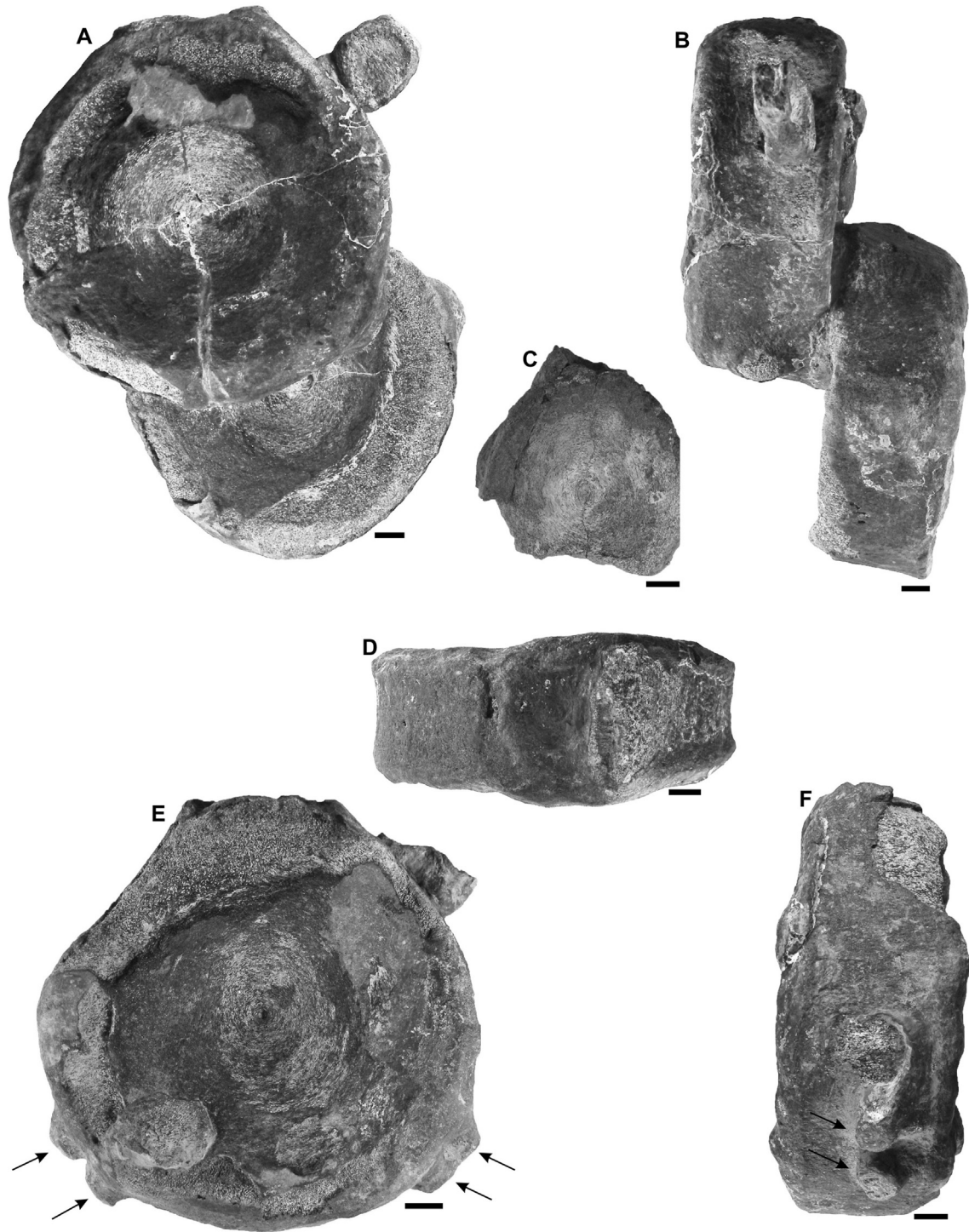


Fig. 7. *Ichthyosauria incertae sedis*. Vertebral centra. A–B, two articulated posterior thoracic vertebral centra in anterior and left lateral views, note attached phalanx (MOZ-PV-6997/3). C, posterior view of isolated posterior thoracic vertebral centrum (MOZ-PV-6987). D–F, posterior thoracic vertebral centrum in dorsal, anterior, and right lateral views (MOZ-PV-6997/3). Arrows point to diapophyses and parapophyses. Scale bars are 10 mm.

ichthyosaur records of the Agrio Formation from the studied localities corresponding to the upper Valanginian–upper Hauterivian. In particular, a bed-by-bed log of MOZ-PV-6997/1–3 bearing beds was performed at Pichaihue locality to study facies relationships and taphonomic modes of the recorded ichthyosaur remains. This locality was selected because it yielded the best-preserved material including the perinatal specimen. The studied ichthyosaur remains can be divided into two taphonomic modes

taking into account taphonomic observations and the fossil-bearing facies (see 4.2 and 4.3).

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 the general taphonomic guidelines proposed by Behrensmeier (1991). Cyclicity of deposits and sequence stratigraphy framework of the

Mulichinco and Agrio formations follow the proposals of Legarreta and Gulisano (1989), Schwarz and Howell (2005), Schwarz and Buatois (2012) and Spalletti et al. (2001).

4.2. Taphonomic mode 1: partially articulated ichthyosaur remains embedded in black shales

Description. MOZ-PV-6997/1–3 was found in a 20 m-thick interval dominated by tabular monotonous black shales, including paper and massive shales, with subordinated thin levels of tabular black marls and black concretionary mudstones (Fig. 8A–B). Parallel lamination is present with no evidence of bioturbation. Orientation of bones in cross-section is parallel to bedding. The interval has scattered thin levels of calcareous nodules of up to 15 cm of maximum length oriented parallel to bedding. Ammonites are abundantly recorded, laterally crushed and oriented parallel to the bedding plane (Fig. 8C). Body chambers are usually filled with sedimentary matrix while phragmocones are empty. There are no records of benthic macroinvertebrates.

Ichthyosaur remains MOZ-PV-6997/1–3 were found partially disarticulated but closely associated in a small outcrop area in the mentioned interval of monotonous black shales. It is difficult to say if they belonged to more than two individuals, but at least they belonged to one adult individual and one perinatal individual. MOZ-PV-6997/1 includes a partially articulated fin and several phalanges of a perinatal specimen, whilst MOZ-PV-6997/2 is an isolated adult ischiopubis plus a fragmentary long bone (femur?). MOZ-PV-6997/3 belongs to seven partially articulated thoracic vertebral centra of an adult individual. Only isolated rib fragments were recovered, which were left in the field. MOZ-PV-

6999 belongs to three disarticulated but associated anterior thoracic (?) vertebral centra found in black shales at Arroyo Truquicó locality.

Interpretation. This mode of preservation probably resulted from the floating and eventually sinking of carcasses to a muddy and calm seafloor under anoxic conditions, resulting in *in situ* (autochthonous) preservation without significant transport or physical reworking, except for modern weathering and disarticulation. Carcasses were rapidly embedded by the soft anoxic mud and thus preserved articulated. This allowed the preservation of the delicate remains of a perinatal specimen. The fossil-bearing facies can be interpreted as deposited in a basinal setting with water column stratification and stagnant seafloor. The absence of benthic fauna and bioturbation support the anoxic condition of the basin seafloor. Seafloor anoxia has a significant role in exceptional preservations, however, a combination of anoxia and rapid burial (obration) is better as anoxia on itself does not prevent decay on the long term (Seilacher et al., 1985; Allison, 1988). This ichthyosaur-bearing facies is very similar to the black shales recorded at the base of the Vaca Muerta Formation (basal transgressive deposits) where abundant Tithonian ichthyosaur material has been collected from different localities. It is also similar to the stagnant basin deposits of the Toarcian bituminous *Posidonia* Shales of Holzmaden where abundant complete ichthyosaur skeletons have been recovered (Seilacher et al., 1985). This taphonomic mode is consistent with the findings of Cleary et al. (2015) which showed that ichthyosaurs from predominantly fine-grained clastic deposits were the best preserved, followed by those from mixed clastic/carbonate facies and being those from predominantly carbonate units the worst preserved ichthyosaurs.

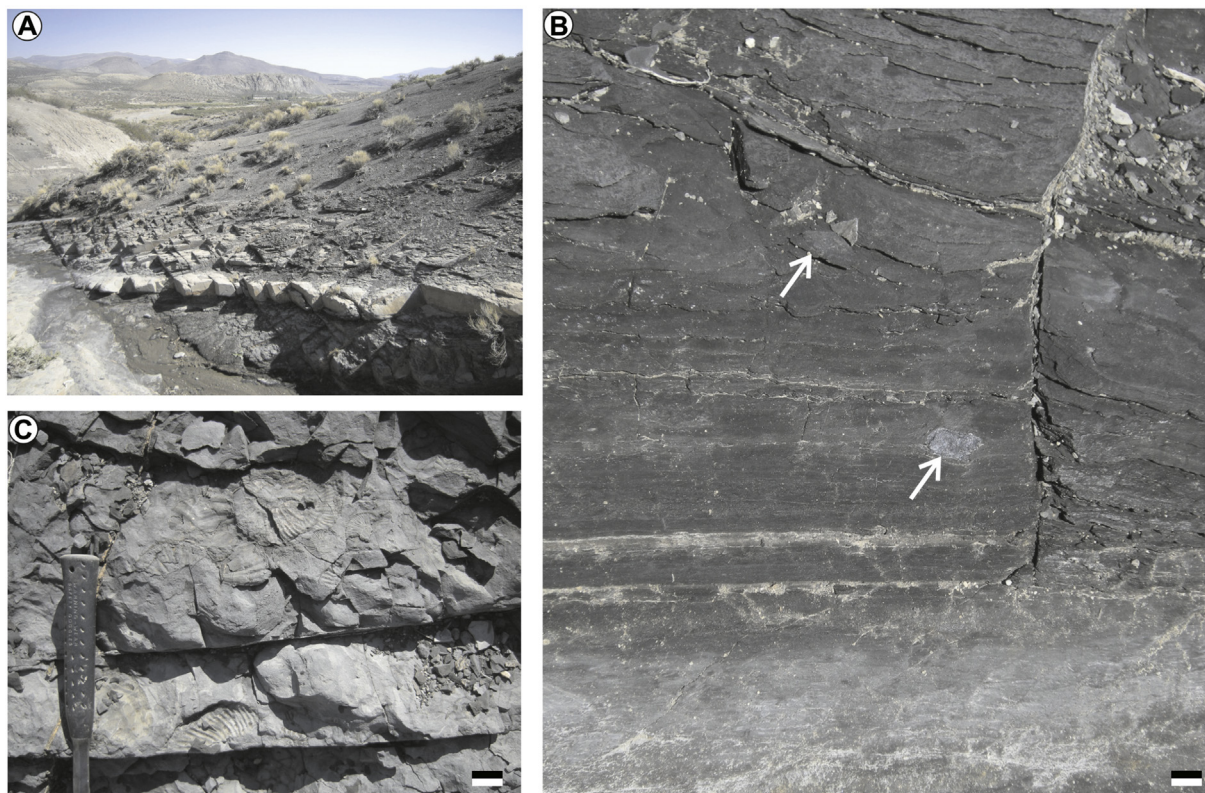


Fig. 8. Ichthyosaur-bearing facies at Pichaihue locality. A, general view of the measured section of the basal beds of the Pilmatué Member of the Agrio Formation (see Fig. 2). B, cross-section view of black shales containing ichthyosaur skeletal elements (white arrows). C, top plan view of ammonoid specimens recorded parallel to bedding. Scale bars are 1 cm.

4.3. *Taphonomic mode 2: isolated ichthyosaur vertebral centra in dark-gray shales and fine-grained sandstones*

Description. These records involve isolated vertebral centra (without neural arches), which are usually externally weathered and abraded, and also show some degree of fragmentation. Isolated ichthyosaur vertebral centra (MOZ-PV-6986, MOZ-PV-6998, and MOZ-PV-7000) were found embedded in tabular dark-gray shales, while MOZ-PV-6987 was found loose in a 10-cm thick bed of fine-grained grayish sandstones interbedded within a thick shale interval (Table 1). Fine bioturbation is recorded in shales while sandstones are usually highly bioturbated. Orientation of bones both in cross-section and plan-view is random. Associated fossils usually include isolated ammonoid and bivalve shells parallel to the bedding plane and small cementing oysters forming nests of aggregated specimens up to 40 cm-thick and 1 m in lateral extension.

Interpretation. This mode of preservation probably resulted from the floating and eventually sinking of carcasses to a muddy or fine sandy seafloor under oxic to suboxic benthic conditions, resulting in parautochthonous preservation, with some degree of physical and biological reworking resulting in vertebral centra only. However, postmortem transport and disarticulation via drifting of bloated carcasses cannot be discarded in addition to decay and disarticulation after sinking on the seafloor. Scavenging and decomposition would result in the dispersal of skeletal elements, especially those from the periphery of the carcass (e.g., skull, neck, distal limbs). The torso would then undergo further decomposition and disarticulation on the sea floor. The fossil-bearing facies can be interpreted as deposited in proximal to distal offshore settings.

4.4. *Ichthyosaur occurrence in the second-order sequence stratigraphy framework*

Ichthyosaurs from the Agrio Formation were recorded in second-order TST and HST deposits (Fig. 3). The best preserved and most abundant specimens, including articulated remains, come from black shales of the TST of the Pilmatué Member of the Agrio Formation.

The base of the Pilmatué Member is characterized by a regional transgressive surface that covers most of the basin. The rising sea level from the Pacific Ocean flooded the basin from west to east (surpassing the volcanic arc of islands) creating new marine habitats towards the continent and enlarging the epeiric engulfment area. Thanks to the rising sea level, open-ocean dwelling fauna, especially nektonic and planktonic species, could easily pass through the volcanic arc of islands entering the back-arc basin and thus finding access to new niches and resources within the basin boundaries. This situation benefited not only ichthyosaurs, but probably also ammonoids, as most (though not all) of their immigration horizons coincided with sea-level transgressive intervals (Rawson, 2007), providing access to new niches and resources within the basin boundaries.

The TST is also linked with the best preservation of ichthyosaur remains among the studied records, including skeletal elements of a perinatal specimen. This is connected to the paleoenvironment and type of facies deposited during this interval. The TST is characterized, in the studied localities, by a basinal setting and black shale deposition which boosted the preservation of partially articulated skeletons. It would be desirable that these beds were prospected in detail in the future to look for more and better-preserved ichthyosaur specimens.

Poorly preserved ichthyosaur materials, i.e., isolated vertebral centra, were recorded in HST intervals in the Pilmatué and Agua de la Mula members, especially in the basal third of each HST (Fig. 3).

The HST forms when sediment accumulation rates exceed the rate of increase in accommodation space during high sea level stillstand. The stacking patterns exhibit prograding and aggrading clinofolds and shallower settings are progressively recorded from base to top. The fact that ichthyosaurs are restricted to the base of each HST is probably related to the presence of more distal settings at the onset of the tract, but disappearing rapidly due to the shallowing-upwards trend. The poor preservation of these skeletal elements is due to physical and biological reworking on the seafloor, but lateral transport was probably low and thus they can be considered parautochthonous, as it is the case for benthic invertebrates of the unit (e.g., Lazo, 2006).

In contrast to ichthyosaurs, local plesiosaurians are present all along the second-order sequence composed by the Mulichinco and Agrio formations, including the LST, TST and HST (i.e., the middle Mendoza mesosequence). The fact that these reptiles were recorded throughout the depositional sequence is in line with the traditional, functional morphology-based life habit interpretation of long-necked plesiosaurs that suggests that they probably preferred shallower coastal habitats (Massare, 1988,1997a,b). Indeed, long-necked elasmosaurs are generally recorded in association 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 (Hornung et al., 2013; Kear et al., 2006; Lazo and Cichowolski, 2003; O'Gorman et al., 2011, 2013; Sato et al., 2005). However, most findings in the Agrio Formation are associated with dark-gray shales that have been interpreted as proximal to distal offshore deposits (O'Gorman et al., 2015).

Therefore, it is clear that the Lower Cretaceous ichthyosaurs and plesiosaurs from the Neuquén Basin overlap their habitats, but only partially. Both groups inhabited the basinal and offshore settings, while the proximal outer shelf and inner shelf settings were inhabited by plesiosaurs only.

Another important issue to be considered relates to a recent finding by Cleary et al. (2015) suggesting that ichthyosaur completeness is highest during times of low sea level and deteriorates as sea level rises. In our case study, LST intervals did not provide any ichthyosaur records, despite intense collecting efforts. The difference between Cleary's et al. (2015) study and ours may be due to the fact that eustatic sea level changes, even when strong, can be counterbalanced by local or regional tectonic processes (e.g., Haq, 2014). For instance, a global high sea level may be locally compensated in a particular basin by tectonic uplift resulting in a local LST and, vice versa, a global low sea level could be counterbalanced by local subsidence of the basin floor. Indeed, during the mid Valanginian there is a trough in the global sea level curve (Haq, 2014, fig. 1), but in the Neuquén Basin a local rise in sea level is recorded as a TST followed by a HST. The study by Cleary et al. (2015) did not take into account these local or regional sea level changes and considered global (eustatic) sea level changes only. This is possibly why they had the unexpected result that ichthyosaur completeness is highest during times of low sea level and deteriorates as sea level rises.

5. Conclusions

Ichthyosaur remains from the Lower Cretaceous Agrio Formation, west-central Argentina, are systematically described and put in the broader context of their mode of occurrence and facies relationships. The studied records, encompassing the Valanginian–Hauterivian time-interval, are significant because this interval is particularly devoid of records worldwide and thus can be useful to understand how the ichthyosaurs were distributed in the

Southern Hemisphere. Most records are incomplete and belong to isolated vertebral centra. The best preserved material (MOZ-PV-6997/1–3) is represented by a series of seven partially articulated posterior thoracic vertebral centra of an adult individual found in close association with an ischiopubis (plus femur?) of an adult and a partially articulated fin and phalange elements of a perinatal specimen. This finding is important because it provides evidence of viviparity, suggesting the idea that ichthyosaurs would have been able to enter a back-arc basin from the Pacific Ocean to reproduce and give birth in epeiric seas, in a similar way to some modern large marine mammals, e.g., whales in Peninsula de Valdés (Patagonia, Argentina).

In the Neuquén Basin there are abundant records of ichthyosaurs from the Tithonian of the Vaca Muerta Formation and now the present evidence shows the occurrence of ichthyosaurs in the Valanginian–Hauterivian of the Agrio Formation. The apparent local absence of ichthyosaurs from Berriasian and early–middle Valanginian deposits may be due to the overall prevalence of shallower settings, especially associated with the top of the Vaca Muerta Formation and the Mulichinco Formation, that deterred the entrance of ichthyosaurs from the open ocean through the Andean volcanic arc.

The studied remains resulted from more than 20 years of collecting efforts; however, more prospection is needed in the black shales of distal localities such as Pichaihue and Arroyo Truquicó, where the best preserved specimens were found. The recovered specimens show a clear preservation bias: best-preserved specimens were collected from black shales while isolated bone elements and fragments were recorded from dark-gray shales and fine sandstones. Ichthyosaur records are also biased positively towards distally placed localities in the marine shelf of the Agrio Formation, being proximal (more coastal) localities negatively biased and devoid of records.

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