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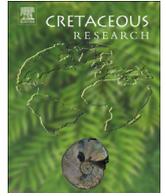
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Late Cretaceous reptilian biota of the La Colonia Formation, central Patagonia, Argentina: Occurrences, preservation and paleoenvironments



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ABSTRACT

Cropping out on the southeastern margin of the Somún Curá Plateau, the La Colonia Formation (Campanian–Maastrichtian) has yielded, over the last several decades, a varied fossil tetrapod fauna (mammals, ophidians, turtles, dinosaurs, plesiosaurs, anurans). For this study several field trips were carried out specifically to recover reptile remains. Three sections, located on the southeastern slope of the Sierra de La Colonia and in the vicinity of Cerro Bayo, Chubut Province (Argentina), were selected for particular attention. The prospected sections are composed of massive, laminated or heterolithic siltstones and claystones, with scarce and thin intercalations of massive, heterolithic or cross-bedded fine sandstones and of fossiliferous conglomerates. The most abundantly recovered reptiles are terrestrial and freshwater turtles, followed by plesiosaurs and dinosaurs. Among the chelonians, more than 16 specimens of *Patagoniaemys gasparinae* (Meiolaniformes), three specimens of *Yaminuechelys* aff. *Y. gasparinii* (Chelidae), and the remains of a new genus of Chelidae were identified. Among the dinosaurs, theropod metatarsal fragments, an incomplete abelisaurid theropod skeleton, sauropod vertebrae, ankylosaur osteoderms and appendicular fragments of hadrosaurs were found. Among the plesiosaurs there are several well preserved elasmosaurids (including two with associated gastroliths) and a polycotyloid (*Sulcusuchus erraini*). Except for the plesiosaurs, all the reptiles are terrestrial or freshwater taxa. However, analysis of the elasmosaurids indicates they are adult specimens of small body size, which could be related to forms that lived in restricted aquatic environments. Likewise, the polycotyloid possesses deep rostral and mandibular grooves, and a conspicuous vascularization and/or innervation, that is consistent with the presence of some associated special sensory structures similar to those known in some cetaceans that inhabit modern rivers and estuaries. Sedimentological analysis suggests that deposition would have been mostly in low-energy restricted environments, like muddy plains, marshes and ponds cut by meandering channels, probably in the central mixed-energy zone within an estuary. This interpretation is consistent with the habitat inferred for the recovered reptiles, as well as with associated foraminifers and with the probable origin of gastroliths found associate with the plesiosaurs.

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1. Introduction

During the Late Cretaceous and up into the Danian, wide areas of extra Andean Patagonia were covered by the Atlantic Ocean. This transgression, the first Atlantic transgression recognized in Patagonia, exceeded the extent reached by subsequent Atlantic

transgressions that occurred during the Cenozoic. However, it did not achieve great depth, giving rise to various marginal marine and shallow marine shelf environments (Náñez and Malumián, 2008).

The maximum extension of the coast line toward the continent in north and central Patagonia occurred during the Maastrichtian, producing the connection among the Colorado, Neuquén, Cañadón Asfalto, and Golfo de San Jorge basins, extending marine influence up to the foot of the Andes (Parras et al., 1998; Náñez and Malumián, 2008; Malumián and Náñez, 2011). At the beginning, this transgression (Campanian–Maastrichtian) reached the south of Mendoza, central-east and north of Neuquén, southwest of La Pampa, Río Negro and north of Chubut provinces (Fig. 1A). These deposits are included in different, partly correlatable, lithostratigraphic units that have yielded numerous tetrapod remains such as mammals, dinosaurs, turtles, snakes, sphenodonts and plesiosaurs (e.g., Bonaparte, 1987; Albino, 2000, 2011; Gasparini and de la Fuente, 2000; Gasparini and Salgado, 2000; Pascual et al., 2000; Gasparini et al., 2001; Rougier et al., 2009a, 2009b; Apesteguía and Jones, 2012). In the south of Mendoza and north of Neuquén provinces, the deposits are included in the Loncoche Formation, whereas in the eastern area, they are included in the Allen Formation. In the area of the Somún Curá Plateau they form the Allen, Coli Toro, Los Alamitos, Paso del Sapo and La Colonia formations (Page et al., 1999). The last is widely exposed along the southeastern margin of the Somún Curá Plateau, in Chubut Province (Fig. 1A–B) and has been explored and studied from stratigraphic and sedimentological approaches for more than 30 years (e.g., Pesce, 1979; Ardolino and Delpino, 1987), and particularly for its biotic content (e.g., Bonaparte, 1985; Archangelsky et al., 1999; Albino, 2000, 2011; Gasparini and de la Fuente, 2000; Pascual et al., 2000; Gasparini et al., 2001; Archangelsky and Zamalao, 2003; Gandolfo and Cúneo, 2005; Kielan-Jaworowska et al., 2007; Rougier et al., 2009b; Sterli and de la Fuente, 2011; O’Gorman and Gasparini, 2013; O’Gorman et al., 2013a, 2013b; Hermsen et al., 2014).

In this paper we present the first results of a project focused specifically on the prospection of reptiles in the Campanian–Maastrichtian interval of the La Colonia Formation. The aim

of this project is to increase the knowledge of the herpetofauna that inhabited Patagonia during this period, as well as to infer the sedimentary environments that would explain the presence of plesiosaurs, generally considered as marine (see Kear, 2006; Benson et al., 2013), but associated in this case with exclusively continental reptiles. For this purpose, the authors carried out three field projects (2011–2012) prospecting and collecting macrovertebrates with precise sedimentological and stratigraphic control. The results have two aspects of particular importance. First, numerous reptile specimens were recovered from terrestrial and aquatic environments, including dinosaurs of various clades (Theropoda, Sauropoda, Ankylosauria and Hadrosauria), terrestrial (Meiolaniformes) and freshwater turtles (Chelidae), and small-sized plesiosaurs (Elasmosauridae) and peculiar polycotylids (Polycotylidae). Second, this is the first study focused specifically on reptiles as a whole, performed in Campanian–Maastrichtian localities of the south of the Somún Curá Plateau. In this sense, it enables comparison with the reptile fauna from deposits of equivalent ages exposed farther north, within the area of the Plateau (Coli Toro and Los Alamitos formations) as well as in the Neuquén Basin (Loncoche and Allen formations).

2. Geological setting

The La Colonia Formation (Pesce, 1979) crops out along the southeastern margin of the Somún Curá Plateau, Chubut Province, Argentina (Fig. 1A–B). In the Sierra de La Colonia area, the sedimentary rocks of this unit are separated from the subjacent rocks of the Chubut Group (Barremian–Cenomanian) by a low angle unconformity (Pascual et al., 2000). The top of the succession is covered by the basalts of the El Buitre Formation (upper Paleocene–Eocene) or by the pyroclastic rocks of the Sarmiento Group (upper Oligocene–lower Miocene).

Pascual et al. (2000) recognized in this area three facies associations for the La Colonia Formation. The lowermost facies association is characterized by cross-bedded sandstones and conglomerates deposited in a moderate to low sinuosity fluvial

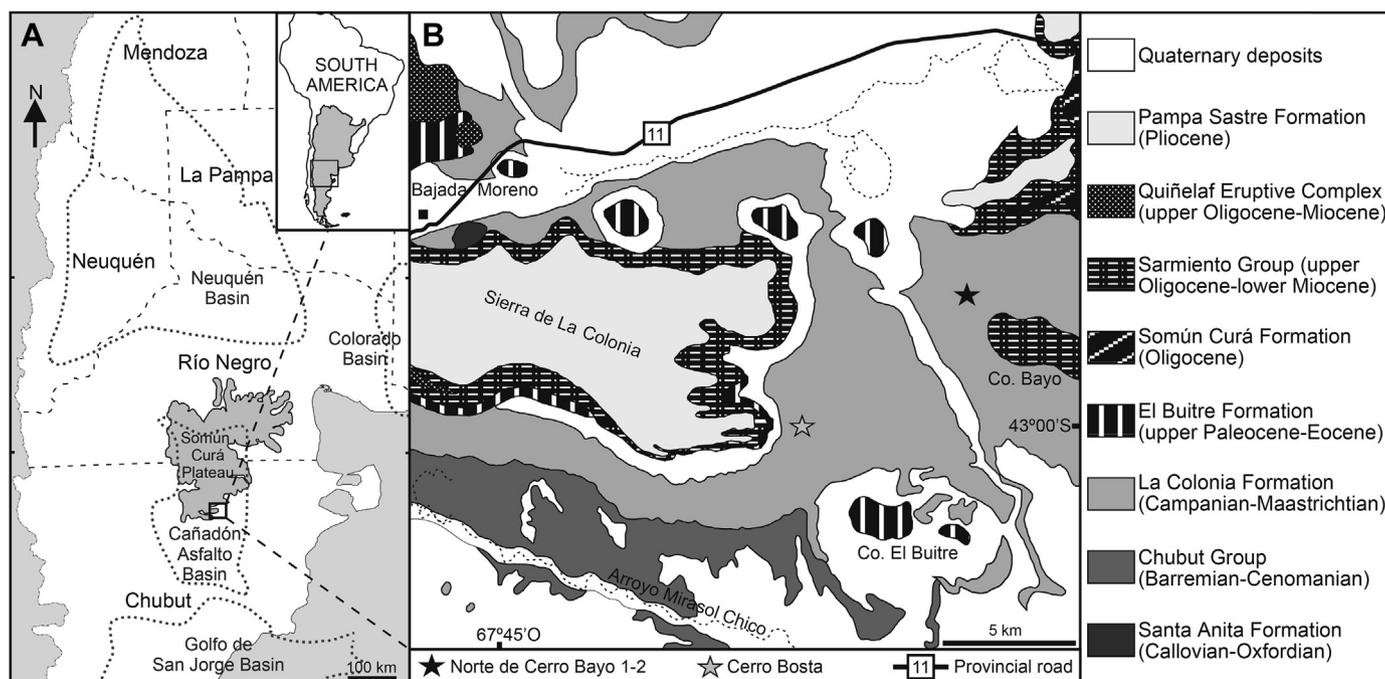


Fig. 1. Study area. A, Boundaries of the main sedimentary basins with Late Cretaceous deposits in central and northern Patagonia (taken from Náñez and Malumián, 2008) and location of the study area. B, Geologic map of the area of Sierra de La Colonia with location of the studied sections (modified from Anselmi et al., 2004; Ardolino et al., 2011).

environment. This facies association is considered by some authors (e.g., [Pesce, 1979](#)) to be a different lithostratigraphic unit, named the Puntudo Chico Formation. The second facies association is the thickest and most representative of the La Colonia Formation, and contains most of the vertebrate remains so far collected. It is composed mostly of laminated mudstones, pelitic fine sandstones, and banded siltstones and claystones deposited in an estuary, tidal flat or coastal plain environment, influenced by occasional high freshwater stream flow from the continent and tidal currents from the sea ([Pascual et al., 2000](#)). This facies association has been deposited under a seasonal climate with alternating periods of humidity and aridity ([Ardolino and Delpino, 1987](#); [Ardolino et al., 1995](#)). The uppermost facies association is composed of laminated pelites containing the remains of bivalves and was interpreted as having been deposited in the upper part of an intertidal flat environment ([Pascual et al., 2000](#)).

The age of the La Colonia Formation is not yet well established. The base is marked by the unconformity that separates this unit from the subjacent rocks of the Cerro Barcino Formation of the Chubut Group, which could be of Cenomanian age ([Codignoto et al., 1979](#)). Therefore, the age of the base of the La Colonia Formation depends on the time span encompassed by the unconformity below, but could not be older than Cenomanian. On the other hand, [Ardolino and Franchi \(1996\)](#), based on micropaleontological data, regarded the upper part of this unit as Campanian–Maastrichtian in age. These authors indicated that the top of the succession in some localities is covered by pelites with microfossils of Danian age that could probably be assigned to the Salamanca Formation. Later, [Pascual et al. \(2000\)](#), based on stratigraphic relations, proposed that quite probably the uppermost part of the La Colonia Formation represents the earliest part of the Paleocene. Recently, [Guler et al. \(2014\)](#), based on palynological data, suggested an age not older than Paleocene for the uppermost part of the unit in the Telsen area. In short, as noted by [Pascual et al. \(2000\)](#), the La Colonia Formation was deposited, at least, during the Campanian–Maastrichtian, beginning probably some time earlier than the Campanian and extending some time later than the Maastrichtian. [Page et al. \(1999\)](#) considered that the lower and middle sections of the La Colonia Formation could be correlated, at least in part, with the Allen Formation from the Neuquén Basin, whereas its upper part could be correlated with the Jagüel Formation from this basin. [Rougier et al. \(2009a\)](#) suggested, based on the mammalian fauna, a slightly younger age for the La Colonia Formation with respect to either the Allen or Los Alamitos formations, with the latter two closer to each other in age.

3. Methods and institutional abbreviations

Detailed vertical stratigraphic–sedimentological profiles were drawn for three localities (Figs. 1, 2) with exposures of the middle strata of the La Colonia Formation (second facies association of the Sierra de La Colonia, the Cerro Bosta section (S 43° 0' 29.5"; W 67° 36' 51"), and north of Cerro Bayo, the sections Norte de Cerro Bayo 1 (S 42° 57' 39.4"; W 67° 33' 17.1") and Norte de Cerro Bayo 2 (S 42° 57' 21.54"; W 67° 32' 58.92")) were measured. Lithology, sedimentary structures and geometry of the layers were observed in each section. Vertebrate remains were collected, recording taphonomic and sedimentological features as well as the stratigraphic position of each specimen with respect to the measured sections.

The collected materials are housed in the collection of the Museo Paleontológico "Egidio Feruglio", Chubut, as MPEF-PV. Specimens were compared with materials deposited in the collections of the Museo Argentino de Ciencias Naturales (MACN),

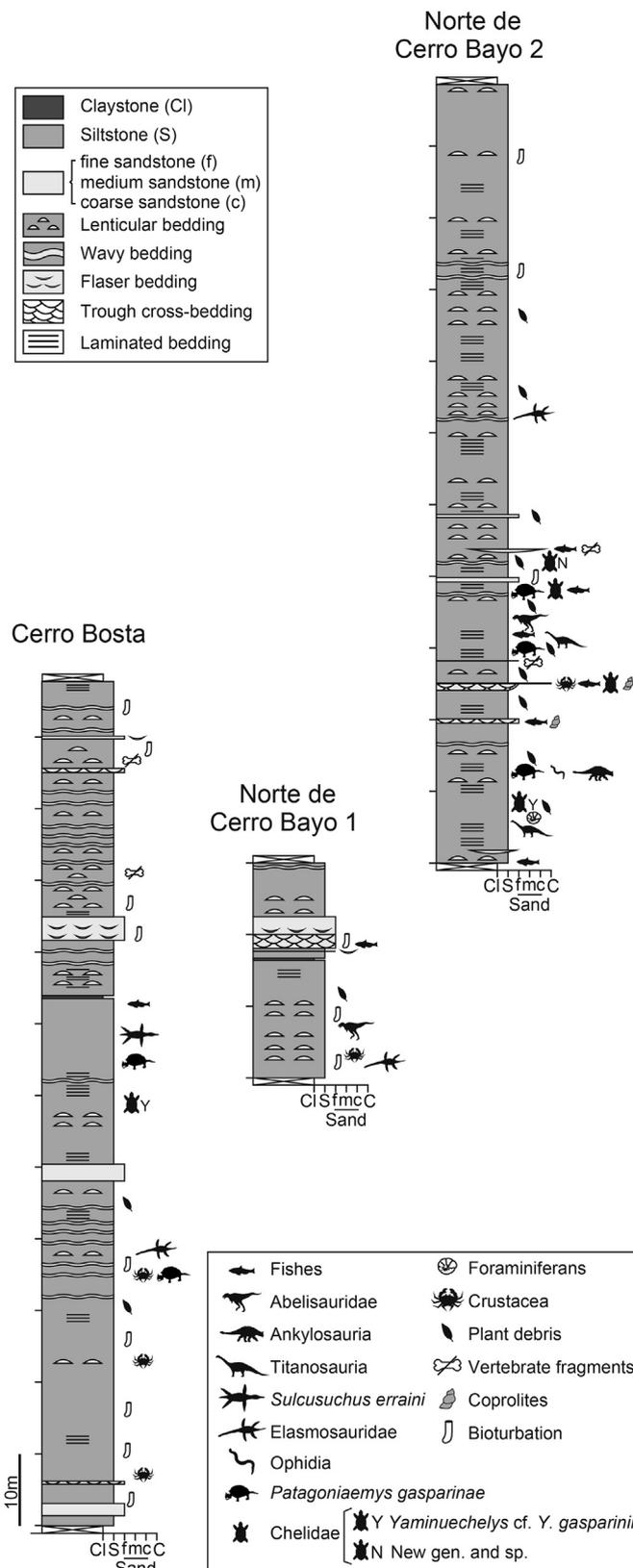


Fig. 2. Stratigraphic sections showing the levels bearing fossil material.

Buenos Aires; Museo de La Plata (MLP), Buenos Aires; Museo de Cinco Saltos (MCS), Río Negro, and Museo de la Universidad del Comahue (MUC), Neuquén.

4. Summary of the reptile-bearing facies: sedimentology and preservation

Six sedimentary facies were recognized in the studied sections (Cerro Bosta, Norte de Cerro Bayo 1 and Norte de Cerro Bayo 2) mainly based on lithology and sedimentary structures: laminated sandy to clayey siltstones and very fine-grained sandstones, heterolithic (lenticular-, wavy- and flaser-bedded) siltstones and fine-grained sandstones, massive clayey to sandy siltstones and very fine-grained sandstones, trough-cross-bedded fine-grained sandstones and matrix and clast-supported fossiliferous conglomerates. The color of the pelitic facies varies between light gray and olive green to yellowish, whereas the coarser facies are mostly gray. Ellipsoidal concretions with diameters between a few centimeters to one meter are frequent in the pelitic and fine-grained sandy facies. These concretions stand out in the profile because of their different cementation and dark gray to reddish color. They usually have cone-in-cone structure and bear well preserved fossil remains both of vertebrates (reptiles) and invertebrates (crustaceans). Likewise, levels with abundant plant debris and carbonaceous remains are also frequent, mainly in the Norte de Cerro Bayo 2 section. Fossil traces can be observed in the three localities, although the greatest abundance occurs in Cerro Bosta and consists of diffuse or mottled bioturbation or simple subvertical tubes. Crystals and thin gypsum layers are frequent in the three sections.

The Cerro Bosta section, 118 m thick (Figs. 2, 3A) is characterized by massive, laminated or heterolithic pelites with intercalations of beds, no more than 3.3 m thick, of massive, heterolithic (flaser) or

trough-cross-bedded fine-grained sandstones. Associated with pelitic sectors, mainly between 30 m and 70 m from the base of the section (Fig. 2), remains of dipnoans, turtles, plesiosaurs and fragments of other indeterminate vertebrates were found. Among the turtles, remains of *Patagoniaemys gasparinae* Sterli and de la Fuente, 2011 (MPEF-PV 10564), as well as one specimen of Chelidae, *Yaminuechelys* aff. *Y. gasparinii* de la Fuente, Lapparent de Broin and Manera de Bianco, 2001 (MPEF-PV 10567), were identified. Skull and mandibular remains of the polycotyloid plesiosaur *Sulcusuchus erraini* Gasparini and Spalletti, 1990 (MPEF-PV 650) were also found in this locality, as well as three vertebrae of elasmosaurid plesiosaurs.

North of Cerro Bayo, two correlatable stratigraphic sections are described. The Norte de Cerro Bayo 1 (Fig. 2), 30 m thick, is composed of massive, laminated or heterolithic siltstones and clayey siltstones. Towards the top, there are intercalations of massive, trough-cross-bedded or heterolithic (flaser) sandstones, containing fish vertebrae. In the basal pelitic levels, three specimens of elasmosaurid plesiosaurs were found (MPEF-PV 10601–10603), two of which have associated gastroliths. Likewise, in one concretion of 1.6 m in diameter, at 8 m from the base, were found the partially articulated remains of a theropod dinosaur.

The section Norte de Cerro Bayo 2 (Figs. 2, 3B) is 700 m north-east from the previous one, and is 108.6 m thick. It is characterized by the predominance of pelitic facies with intercalations, between 20 m and 50 m, of massive, laminated or with cross-bedded sandstones, as well as thin layers and lenses of fossiliferous conglomerates. Most recovered vertebrates come from this sector. The

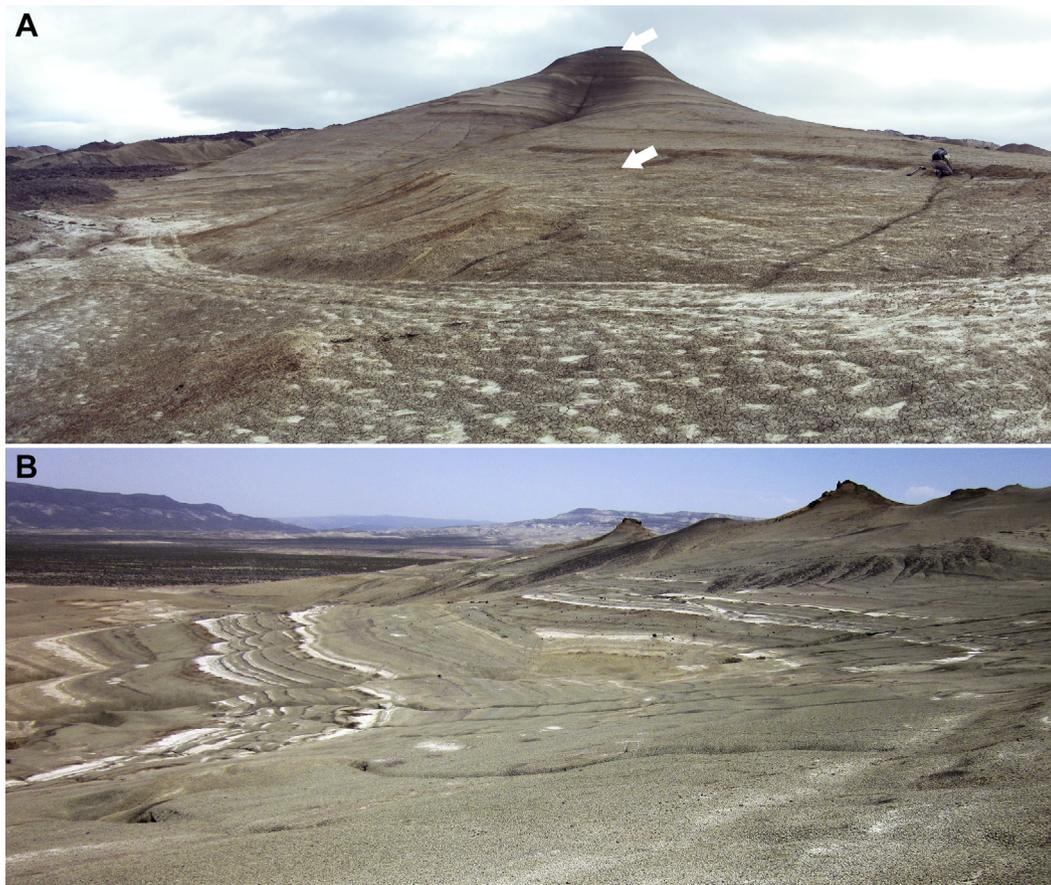


Fig. 3. View of the studied sections. A, Cerro Bosta section, pelitic facies of the first 70 m of the section, showing the provenance of the studied material (between the two white arrows). B, Norte de Cerro Bayo 2 section, pelitic facies bearing the studied materials, between 10 and 60 m from the base of the section, with thin intercalations (white beds) of massive, heterolithic and cross-bedded sandy facies.

remains associated with the pelitic facies are the most abundant and generally the best preserved, including fishes, turtles, dinosaurs, snakes and plesiosaurs. Among the turtles from this locality, ten specimens of *Patagoniaemys gasparinae* were found (MPEF-PV 10541–10543; 10545; 10548–10550; 10552–10554). Another five were collected in nearby areas (MPEF-PV 10544; 10546–10547; 10551; 10555), and the level bearing most of them could be placed in the measured section. MPEF-PV 10544 was found in the slopes of Cerro Bayo some 1.4 km south, and MPEF-PV 10546–10547 and MPEF-PV 10555 were collected between 1.3 km and 1.7 km northwest. On the contrary, the exact stratigraphic position with respect to the measured section of MPEF-PV 10551, collected 24 km southwest of the locality, could not be determined. Among the Chelidae of the Norte de Cerro Bayo 2, two specimens of *Yaminuechelys* aff. *Y. gasparinii* (MPEF-PV 10568–10569) and two of a new genus and species (MPEF-PV 10570 and 10830) were found. Among the dinosaurs, associated remains of theropods, sauropod vertebrae, ankylosaur osteoderms and appendicular fragments of hadrosaurs were found.

The studied remains that come from the pelitic facies are generally of centimeter scale and, most of them, show no evidence of prolonged transport or reworking. They appear commonly as disarticulated bone assemblages, except for the theropod dinosaur of Norte de Cerro Bayo 1, which was found partially articulated within a concretion. On the contrary the remains found in sandy and conglomerate facies have more varied taxonomic composition, as well as different taphonomic features. They mostly consist of millimeter-scale remains of fish (vertebrae, spines, teeth and scales) and to a lesser extent, amphibians, reptile remains (turtles, plesiosaurs, dinosaurs) and mammals, chaotically oriented. Most of them are fragmented with rounded and polished breakage surfaces showing high degree of alteration (Varela and Parras, 2013), probably due to hydraulic transport prior to their deposition. In particular, the remains from conglomerates are abundant but concentrated in thin lenses of little lateral extent.

5. Paleontology

5.1. Turtles

In the La Colonia Formation three species of continental turtles were recognized with certainty. These three species belong to two different clades of turtles, Meiolaniformes and Chelidae. Meiolaniformes is a recently named clade (Sterli and de la Fuente, 2013) that includes all turtles more related to *Meiolania platyceps* (Owen, 1886) (terrestrial, horned turtles from the Pleistocene of Australia of the clade Meiolaniidae) than to modern turtles (Pleurodira and Cryptodira). Meiolaniforms are continental, probably terrestrial, turtles (e.g., presence of osteoderms in the skin as in extant testudinids), that lived from the Early Cretaceous to the Holocene in South America, Australasia, Asia, and Europe (Gaffney, 1996; Sterli and de la Fuente, 2013). The meiolaniform record of the La Colonia Formation includes a single species, *Patagoniaemys gasparinae*. Thanks to these recent discoveries, *P. gasparinae* is the most complete turtle from the Late Cretaceous recovered in Argentina to date, represented by cranial and postcranial remains.

The other clade present in the La Colonia Formation is Chelidae. This is an extant clade of freshwater turtles belonging to the Pleurodira (side-necked turtles), which has lived in South America and Australasia since the Early Cretaceous (Smith, 2010; de la Fuente et al., 2011). Two well-differentiated species were recognized in the La Colonia Formation: *Yaminuechelys* aff. *Y. gasparinii*, represented by three well-preserved shells and some fragmentary material, and a new genus and species. All these new findings will bring valuable information to understand the anatomy and ecology

of the turtle biota from the Late Cretaceous of Patagonia and to explore the recently proposed association between chelids and meiolaniforms (Sterli and de la Fuente, 2013).

Testudinata Klein, 1760

Meiolaniformes Sterli and de la Fuente, 2013

Patagoniaemys gasparinae Sterli and de la Fuente, 2011 (figs. 3–10)

Fig. 4A–F

Holotype. MPEF-PV 3283, carapace and plastron remains, almost complete vertebral column, pelvic girdle, and the left postorbital (Sterli and de la Fuente, 2011; figs. 3–10).

Referred material. Sixteen specimens (MPEF-PV 10541–10555 and MPEF-PV 10564) representing cranial and postcranial remains (Fig. 4A–F).

Locality. Buitre Chico (MPEF-PV 3283), Norte de Cerro Bayo 2 (MPEF-PV 10541–10543; 10545; 10548–10550; 10552–10554), around Norte de Cerro Bayo 2 (MPEF-PV 10544; 10546–10547; 10551; 10555), and Cerro Bosta (MPEF-PV 10564) (Figs. 1, 2).

Remarks. *Patagoniaemys gasparinae* is the only named species of non-meiolaniid meiolaniforms from the La Colonia Formation. The original description was based on a single specimen represented by carapace remains, an almost complete vertebral column, a complete pelvic girdle, and small fragments of the plastron (Sterli and de la Fuente, 2011; figs. 3–10). The new findings include more than 16 specimens of *P. gasparinae* represented not only by known portions of the postcranium but also by skull remains and previously unknown portions of the shell, pectoral and pelvic girdles, and limbs. The discovery of cranial remains of *P. gasparinae* are very helpful in making comparisons with another meiolaniform from the Paleocene of Chubut, *Peligrochelys walshae* Sterli and de la Fuente, 2013 (fig. 10) that is only known from skull remains. Some features of the cranial anatomy of *P. gasparinae* resemble those of *Pe. walshae*. For example, the general cranial scute pattern (e.g., presence of several F scutes) and the carotid circulation pattern (e.g., foramen posterius canalis carotici cerebralis piercing the basisphenoid) found in *P. gasparinae* are similar to those described for *Pe. walshae* (Sterli and de la Fuente, 2013). The new postcranial remains of *P. gasparinae* show elongated femora, suggesting slender hindlimbs comparable to those of *Meiolania platyceps*. As in other meiolaniforms, osteoderms have been recovered for *P. gasparinae*. The presence of osteoderms is regarded as evidence for terrestrial habits for turtles because osteoderms are usually present in the highly terrestrial clade Testudinidae.

Patagonia has one of the most complete (around six species) and continuous record of Meiolaniformes in the world, from the Early Cretaceous (*Chubutemys copelloi* Gaffney, Rich, Vickers-Rich, Constantine, Vacca, and Kool, 2007) to the Eocene (*Niolamia argentina* Ameghino, 1899). All these new discoveries make *Patagoniaemys gasparinae* one of the most completely known meiolaniforms, allowing a better understanding of the morphology and evolution of this clade of turtles.

Testudines Batsch, 1788

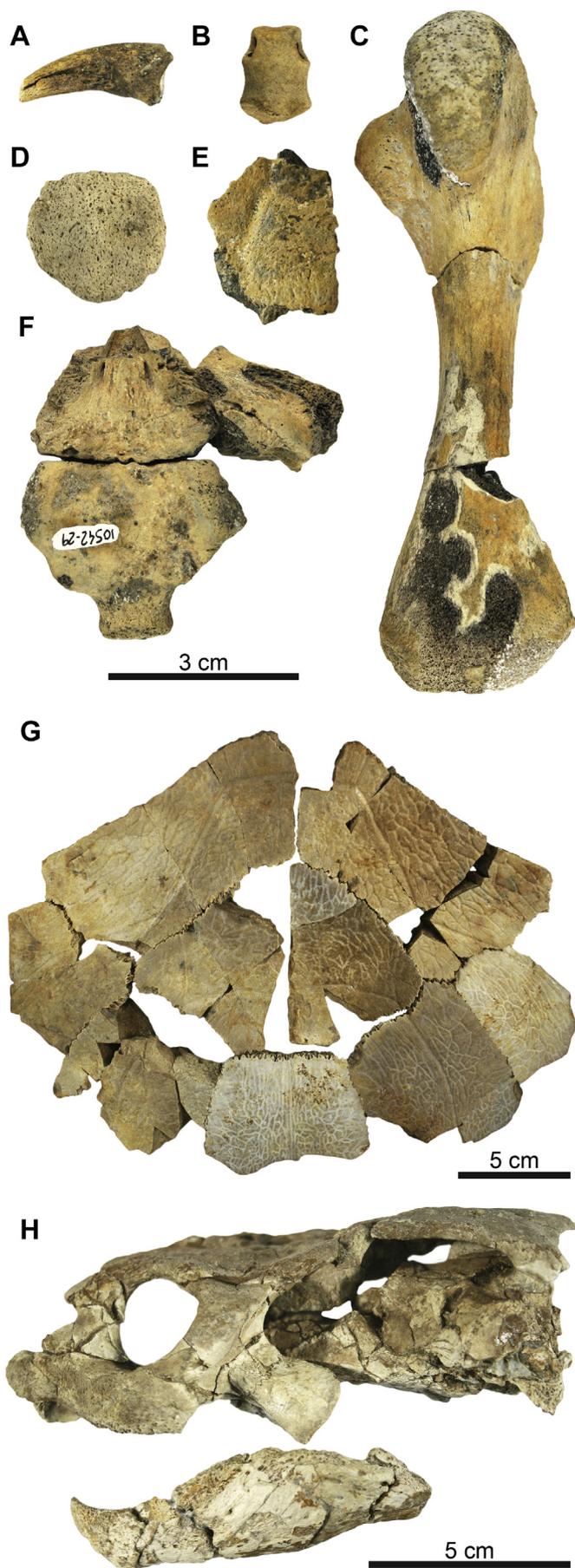
Pleurodira Cope, 1865

Chelidae Lindholm, 1929

Yaminuechelys aff. *Y. gasparinii* de la Fuente, Lapparent de Broin and Manera de Bianco, 2001 (figs. 1A–B, 2A–G)

Fig. 4G

Referred material. Three specimens (MPEF-PV 10567–10569; Fig. 4G) formed only by postcranial remains (mainly shell fragments).



Locality. Norte de Cerro Bayo 2 (MPEF-PV 10568–10569) and Cerro Bosta (MPEF-PV 10567) (Figs. 1, 2).

Remarks. *Yaminuechelys* de la Fuente, Lapparent de Broin and Manera de Bianco, 2001 is a long-necked chelid that survived the K–P boundary event and it is represented by at least two named species, *Y. gasparinii* from the Campanian–Maastrichtian of the Allen Formation (Río Negro Province, Argentina) and *Y. maior* (Staesche, 1929) from the Danian of the Salamanca Formation (Chubut Province, Argentina) (de la Fuente et al., 2001; Bona and de la Fuente, 2005).

Three new specimens comprising by shell remains and some postcranial elements (e.g., cervical vertebrae, limb bones) are recognized as *Yaminuechelys* aff. *Y. gasparinii*. These specimens are big turtles (carapace length around 60 cm) and the shell remains are thick and strongly ornamented with irregular polygons as in the extant *Hydromedusa* Wagler, 1830. The preserved cervical vertebrae are very long anteroposteriorly and short dorsoventrally, suggesting the presence of a long neck as in *Hydromedusa*. Due to the peculiar ornamentation of the shell of *Y. aff. gasparinii* also dozens of isolated plates and the remains recognized as Chelidae gen. et sp. indet. 1 by Gasparini and de la Fuente (2000) can also be assigned to this species.

More detailed studies will help to understand whether *Yaminuechelys* aff. *Y. gasparinii* from the La Colonia Formation represents a new species or if it belongs to one of the two named species. In a recent cladistic analysis (Bona and de la Fuente, 2005) all long-necked chelids (the South American *Chelus* Duméril, 1806, *Yaminuechelys*, *Hydromedusa*, and the Australasian *Chelodina* Fitzinger, 1826) are recovered as a monophyletic group. This hypothesis is contradicted by the molecular hypothesis (e.g., Seddon et al., 1997; Georges et al., 1998) where Australasian and South American chelids form two monophyletic assemblages, showing that the long-neck could have evolved independently in separate lineages. The new extinct chelids from the La Colonia Formation bring more information on the evolutionary history and biogeography of long-necked chelids.

New genus and species

Fig. 4H

Referred material. MPEF-PV 10570, skull, and lower jaw; MPEF-PV 10830, postcranial remains (e.g., shell remains, girdle fragments, limb bones).

Locality. Norte de Cerro Bayo 2 (MPEF-PV 10570 and 10830) (Figs. 1, 2).

Description. The skull (MPEF-PV 10570) is almost complete, only lacking the posterolateral portion and the basioccipital. The lower jaw is complete. The postcranial remains (MPEF-PV 10830) comprise by shell fragments (e.g., nuchal, peripherals, neurals), girdles (pectoral and pelvic remains), and limb bones (e.g., long bones, phalanges, metapods). This new species found in the La Colonia Formation is also a large chelid (carapace length 70 cm approximately), however the shell has no evident ornamentation. The skull is anteroposteriorly elongated, more than 10 cm long, and has a well-developed processus trochlearis pterygoidei (Gaffney, 1979). It has a marked cheek emargination

Fig. 4. A–F, *Patagoniaemys gasparinae* Sterli and de la Fuente 2011. A–D, MPEF-PV 10541; A, ungual phalange; B, phalange; C, right femur; D, osteoderm. E–F, MPEF-PV 10542; E, left frontal; F, basicranium: basisphenoid, basioccipital, and left prootic; G, *Yaminuechelys* aff. *Y. gasparinii* de la Fuente, Lapparent de Broin and Manera de Bianco 2001, MPEF-PV 10567, posterior part of the carapace; H, Chelidae, new genus and new species, MPEF-PV 10570, skull and lower jaw (the lower jaw is the mirror image of the right ramus).

and an almost non-existent temporal emargination. The posterior bridge separating both emarginations is thicker than in the extant *Phrynops* spp., *Acanthochelys* spp., and *Hydromedusa* spp. The morphology of the skull and lower jaw suggests MPEF-PV 10570 represents a new genus and species of chelid.

Remarks. Highly decorated chelids (e.g., *Yaminuechelys*) are more abundant in Upper Cretaceous outcrops than non-decorated chelids (e.g., this new genus and species). This specimen represents the first published find of cranial remains of chelid turtles not belonging to the clade *Yaminuechelys-Hydromedusa*. Consequently, MPEF-PV 10570 will bring valuable information on the diversification and evolution of chelid turtles in the Late Cretaceous of South America and on the origin of modern taxa.

5.2. Dinosaurs

Non-avian dinosaurs are a paraphyletic group of continental archosauriforms widely distributed from the Late Triassic to the Late Cretaceous. The single dinosaur recorded so far in the La Colonia Formation was *Carnotaurus sastrei* Bonaparte, 1985, represented by a very complete skeleton of a theropod abelisaurid characterized by the presence of frontal horns and an extreme reduction of the anterior limbs (Bonaparte et al., 1990). The new dinosaur remains found in this unit, among which there are two new theropod specimens, belong at least in the higher categories, to those known in other Patagonian units of equivalent ages, especially the Allen Formation (Gasparini et al., 2007).

Theropoda [Marsh, 1881](#)

Ceratosauria [Marsh, 1884](#)

Abelisauroidea Bonaparte and Novas, 1985

Abelosauridae Bonaparte and [Novas, 1985](#)

Gen. et sp. indet.

[Fig. 5A–C](#)

Referred material. MPEF-PV 10826, quite complete and partially articulated skeleton, of which only a few cranial (postorbital, nasal and maxilla) and postcranial fragments (pedal phalanges including unguals, metatarsal remains including a complete III metatarsal) are available for study at this time.

Locality. Norte de Cerro Bayo 1 ([Figs. 1, 2](#)).

Remarks. Characteristics of these remains allow inclusion of the specimen in the Abelosauridae: 1) nasal and maxillary ornamentation; 2) ungual phalanx with lateral groove bifurcated proximally and ventral side with a very conspicuous circular depression. In turn, some characteristics of this specimen differentiate it from *Carnotaurus sastrei* Bonaparte, 1985 because in the latter, the ornamentation of nasal and maxillary is composed of subcircular depressions, while in MPEF-PV 10826 this ornamentation is as slight elongated grooves. In addition, the postorbital of MPEF-PV 10826 differs from the particular morphology of *C. sastrei*, because the dorsal surface is anteroposteriorly elongated and less curved.

Theropoda [Marsh, 1881](#)

Gen. et sp. indet.

[Fig. 5D–H](#)

Referred material. MPEF-PV 10829, metatarsal fragments of a single individual.

Locality. Norte de Cerro Bayo 2 ([Figs. 1, 2](#)).

Remarks. The preserved elements include a metatarsal III ([Fig. 5D–E](#)), a probable left metatarsal IV ([Fig. 5F–G](#)), and distal fragments of two metatarsals. The surface of metatarsal IV for metatarsal III is concave, and it has proximally a flange that extends slightly on the posterior surface of metatarsal III, when

articulated. The plantar surface of the proximal part of metatarsal IV is flat. Neither the proximal nor the distal ends of metatarsal III have been preserved. One of the distal ends preserved probably corresponds to a metatarsal III because it is symmetrical and has a deep extensor depression on the anterior face ([Fig. 5H](#)).

Sauropoda [Marsh, 1878](#)

Macronaria [Wilson and Sereno, 1998](#)

Titanosauriformes [Salgado, Coria and Calvo, 1997](#)

Somphospondyli [Wilson and Sereno, 1998](#)

Titanosauria [Bonaparte and Coria, 1993](#)

[Fig. 5I–L](#)

Referred material. MPEF-PV 10827 and MPEF-PV 10828, two fragmentary caudal vertebrae.

Locality. Norte de Cerro Bayo 2 ([Figs. 1, 2](#)).

Remarks. MPEF-PV 10827 ([Fig. 5I–J](#)) probably pertains to the middle sector of the caudal region and only the anterior two-thirds of the centrum have been preserved. The anterior articular surface is a little wider (11.4 cm) than high (10 cm). The posterior condyle is broken, which permits observation of the camellate internal tissue and some major cavities, as commonly found in titanosaurs. The ventral face of the vertebral centrum is transversally concave (width of the ventral face of the centrum = 5.7 cm). On this face, there is a pathological growth of the bone extending on the right lateral surface. The lateral surfaces are flat and somewhat inclined laterally. There is a series of foraminae on the lateral and ventral surfaces. The floor of the neural canal is broad and expands transversely backwards. The base of the left neural arch has been preserved. The articular face of the anterior vertebra is deeply concave, suggesting the material belongs to Titanosauria ([Powell, 2003](#)). Additionally, the lateral faces of the vertebral centrum are slightly inclined, which also supports the identification of the material as Titanosauria ([Salgado and García, 2002](#)).

MPEF-PV 10828 ([Fig. 5K–L](#)) is a very fragmentary posterior caudal centrum. The left lateral face has been preserved, as well as part of the dorsal face posterior to the neural arch. The centrum is clearly wider than high (posterior height of the centrum = 3.7 cm; estimated width of the posterior centrum = 5 cm). The preserved part of the posterior face is slightly convex, as in titanosaurs ([Powell, 2003](#)), with a small depression on the central part of the articular face, which is slightly dorsally displaced. The lateral face is divided into two portions, ventral and dorsal. The dorsal one is medially inclined, similar to that observed in some titanosaurs ([Salgado and García, 2002](#)). Internally, the bone is camellate, as seen in some titanosaurs ([Salgado et al., 1997](#)). The length of the preserved portion of the centrum is 6 cm.

Ornithischia [Seeley, 1888](#)

Ankylosauria [Osborn, 1923](#)

Ankylosauria indet.

[Fig. 5M](#)

Referred material. MPEF-PV 10871, osteoderm.

Locality. Norte de Cerro Bayo 2 ([Figs. 1, 2](#)).

Remarks. The preserved portion of the osteoderm (MPEF-PV 10871) is 5.6 cm long, 3.9 cm wide, and 2.5 cm high, but it seems to be broken at one end ([Fig. 5M](#)). The scute has an oval shape in dorso-ventral view, with slightly pointed ends. A dorsal keel runs the length of the scute. On both sides of the keel it has slightly concave surfaces. The ventral face of the scute is concave and very rugose. This osteoderm belongs to a scute, according to the terminology proposed by [Blows \(2001\)](#), or shield-shaped osteoderm, with a smooth dorsal keel, according to the

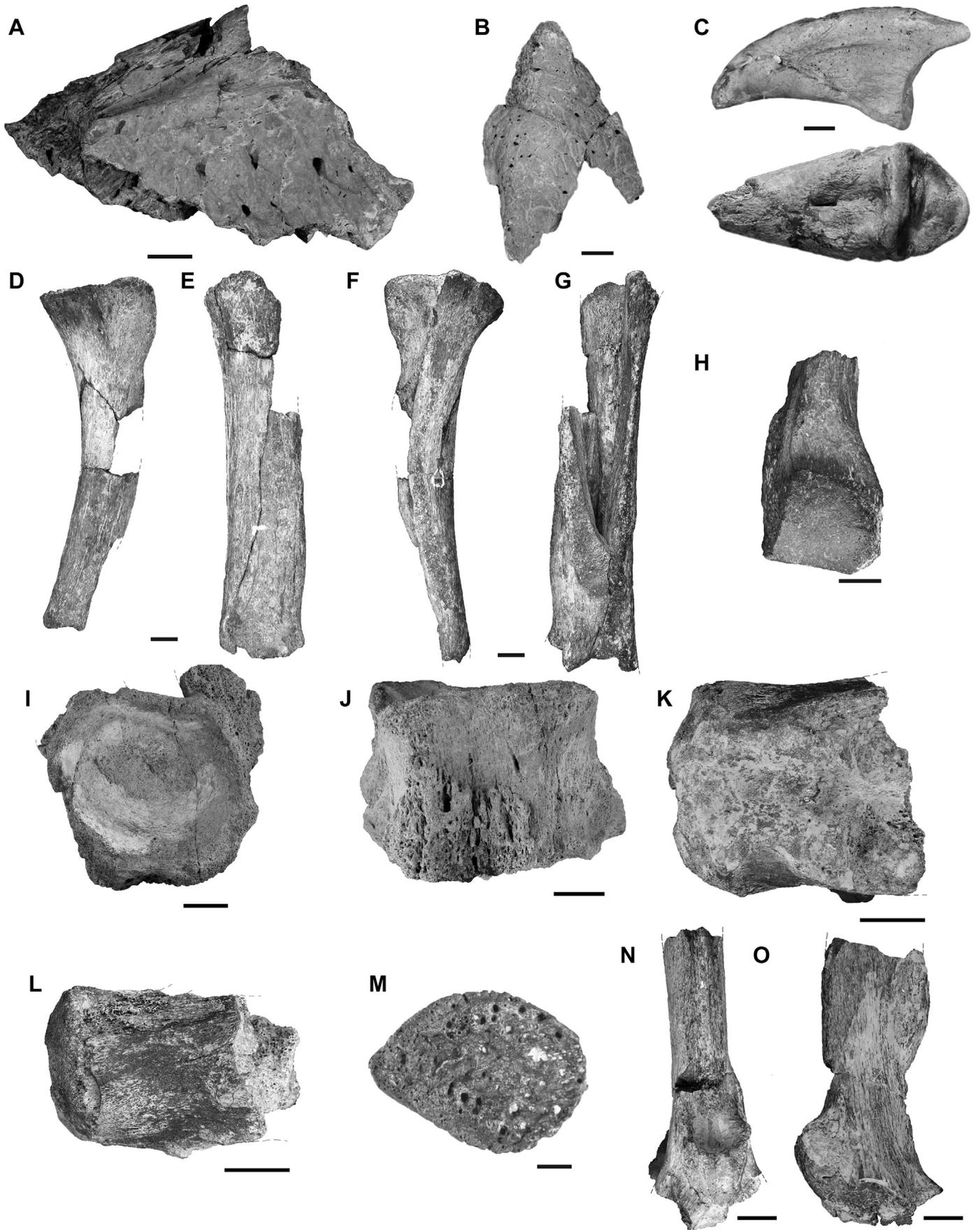


Fig. 5. A–C, MPEF-PV 10826 *Abelisauridae* indet. A, maxilla in lateral left lateral view; B, left nasal in lateral view; C, pedal ungual in lateral and ventral views. D–H, Theropoda indet. MPEF-PV 10829, metatarsal III in D, lateral, E, dorsal views, metatarsal IV in F, medial and G, plantar view, and H, distal end of metatarsal III in dorsal view. I–L Titanosauria indet. MPEF-PV 10827 mid caudal vertebra in J, anterior, and K, dorsal views. MPEF-PV 10828 posterior caudal vertebrae in K, dorsal, L, ventral views. M, Ankylosauria osteoderm MPEF-PV 10871. N–O, Hadrosauridae indet. MPEF-PV 10872. Caudal neural spine in N, posterior and O, lateral views. Scale bars = 10 mm (A–H, K–M) and 20 mm (I–J, N–O).

characterization of [Salgado and Gasparini \(2006\)](#). The osteoderm is similar to those found in Campanian–Maastrichtian levels of the Allen Formation, in the Patagonian locality Salitral Moreno ([Coria and Salgado, 2001](#), fig.8.5).

Hadrosauroidea [Sereno, 1986](#)

gen. et sp. indet.

Fig. 5N–O

Referred material. MPEF-PV 10872 and 10873, vertebral fragments; MPEF-PV 10875, metatarsal fragment.

Locality. Norte de Cerro Bayo 2 ([Figs. 1, 2](#)).

Remarks. MPEF-PV 10872 ([Fig. 5N–O](#)) is a fragment of neural spine of an anterior? caudal vertebra of a large hadrosaur. Both zygapophyses have been preserved (approximately 3.8 cm maximum length and 2.3 cm width). The anteroposterior length of the spine is 5.8 cm and the width at this level is 2.7 cm. The anterior margin of the spine has a wide transversal flange developed above the level of the postzygapophyses. The postzygapophyses diverge at an angle of approximately 30°, which is commonly found in caudal vertebrae of hadrosaurs ([Coria, 2009](#)).

MPEF-PV 10873 is a fragment of caudal neural spine, smaller than but similar to the previous one. Neural spines are laterally compressed, without a strong development of the spinal laminae. This remains match with the typical morphology of the caudal vertebrae of hadrosaurs, the single large-sized ornithischians of the Late Cretaceous of Patagonia ([Gasparini et al., 2007](#)).

The metatarsian fragment MPEF-PV 10875 probably belongs to a metatarsal III, which lacks the proximal and distal ends. On the anterior face, there is an important roughness, perhaps an insertion area. The bone is generally lateromedially compressed, and is identical to the metatarsians of hadrosaurids ([Coria, 2009](#)), although it has no diagnostic features.

5.3. Plesiosaurs

Plesiosaurs are a monophyletic group of cosmopolitan aquatic reptiles ([Ketchum and Benson, 2010, 2011](#)) characterized by extreme adaptation to aquatic life, which had even developed viviparity ([O'Keefe and Chiappe, 2011](#)). By the Late Cretaceous plesiosaurs are represented by only two families: Polycotylidae and Elasmosauridae, both recorded in the La Colonia Formation. Polycotylids are short necked longirostrine plesiosaurs mostly recorded in the Northern Hemisphere, with scarce records from Patagonia, Antarctica, New Zealand and Australia ([Welles and Gregg, 1971](#); [Gasparini and de la Fuente, 2000](#); [Kear, 2005](#); [D'Angelo et al., 2008](#)). Elasmosaurids represent an extreme degree of neck elongation with necks composed of more than 43 cervical vertebrae ([Welles, 1943](#)). Elasmosaurids are the most commonly recorded plesiosaurs from the Upper Cretaceous of South America ([Gasparini et al., 2001](#); [O'Gorman et al., 2013b](#); [Otero and O'Gorman, 2013](#); [Otero et al., 2014](#)).

Plesiosaurs from the La Colonia Formation comprise two species, one polycotylid, *Sulcusuchus erraini* [Gasparini and Spalletti, 1990](#), and one undescribed elasmosaurid known informally as “small-sized elasmosaurid from the La Colonia and Allen formations”.

Sauropterygia [Owen, 1860](#)

Plesiosauria de [Blainville, 1835](#)

Plesiosauroidea [Welles, 1943](#)

Polycotylidae [Cope, 1869](#)

Sulcusuchus erraini [Gasparini and Spalletti, 1990](#)

Fig. 6A–C

Holotype. MLP 88-IV-10-1, fragment of mandibular symphysis (Laguna Cari-Laufquen Grande, Río Negro Province) ([Gasparini and Spalletti, 1990](#), pl. 1).

Referred material. MPEF-PV 650, part of skull and mandible ([Fig. 6A–C](#)).

Locality. Cerro Bosta ([Figs. 1, 2](#)).

Remarks. *Sulcusuchus erraini*, the first polycotylid with skull and mandible discovered in South America, has been previously described by [Gasparini and Spalletti \(1990\)](#), [Gasparini and de la Fuente \(2000\)](#) and [O'Gorman and Gasparini \(2013\)](#). *S. erraini* is a polycotylid with a comparatively narrow rostrum formed by the premaxillary and maxillary, homodont gracile striated teeth, characterized by the following autapomorphies: (1) deep and broad rostral and mandibular grooves and (2) a wide notch on the posterior margin of the pterygoids that are combined with part of the body of the basioccipital, forming a flat plate together with the posteromedial processes of the pterygoids. The rostral and mandibular grooves of *S. erraini* are excavated in the maxilla (rostral groove) and dentary (mandibular). Their inner surface is smooth and there are several neurovascular foramina. This indicates that this grooves housed a soft structure.

[O'Gorman and Gasparini \(2013\)](#) considered several hypotheses about the nature of this soft structure but they concluded that only two of these were viable: either the soft tissue served a glandular structure or it was some sort of sensory organ. The position of the rostral and mandibular grooves in the anterior area of the skull, and their conspicuous vascularization and/or innervation is consistent with the presence of some associated special sensory structures. In extant cetaceans, areas with high skin sensitivity can be detected through concentrated vascularization. This technique was employed to infer the sensory function of rostral follicles in the dolphin *Sotalia guianensis* ([Mauck et al., 2000](#)). Recently, [Foffa et al. \(2014\)](#) proposed a sensory function for a complex system of neurovascular channels that end in foramina in the anterior tip of the rostrum of *Pliosaurus kevani* [Benson et al., 2013](#) and for the rostral pitting in pliosaurus. The possible best extant analogy of this is the electro-sensitivity detected in follicles of the rostrum of the river dolphin *S. guianensis*, which are probably used to detect fish buried in the soft sediments ([Wilkins and Hofmann, 2008](#)). A similar feeding behavior has been observed in the marine dolphin *Tursiops truncatus* ([Rossbach and Herzing, 1997](#)). Although the presence of electroreceptors and mechanoreceptors in *Sulcusuchus erraini* is difficult to confirm, a possible analogy with dolphins cannot be discarded at this stage. A system of high sensitivity could have been related to the capacity to detect prey hidden in soft bottoms. The use of infaunal or semi-infaunal prey as food by plesiosaurs has been previously recorded in marine elasmosaurid plesiosaurs ([McHenry et al., 2005](#)). This particular kind of feeding behavior could be consistent with the tidal estuarine depositional environment interpreted for the La Colonia Formation.

Elasmosauridae [Cope 1869](#)

Gen. and sp. indet.

Fig. 6D–K

Referred material. MPEF-PV 10601-3, three postcranial specimens that preserve cervical, dorsal and caudal vertebrae, ribs and gastroliths ([Fig. 6D–H](#)); and three vertebrae without collection number.

Locality. Norte de Cerro Bayo 1 (MPEF-PV 10601-3) and Cerro Bosta ([Figs. 1, 2](#)).

Remarks. The cervical centra of the specimens MPEF-PV 10601-3 are longer than high with lateral ridges and a dumbbell-shaped articular faces. These are the usual features that permit referring the described specimens to the Elasmosauridae ([Werner and Bardet, 1996](#); [Gasparini and Salgado, 2000](#); [Ketchum and Benson, 2011](#)). [Gasparini and Salgado \(2000\)](#) referred three specimens (MLP 71-II-13-1, MCS PV 4 and MUC Pv 92) from the

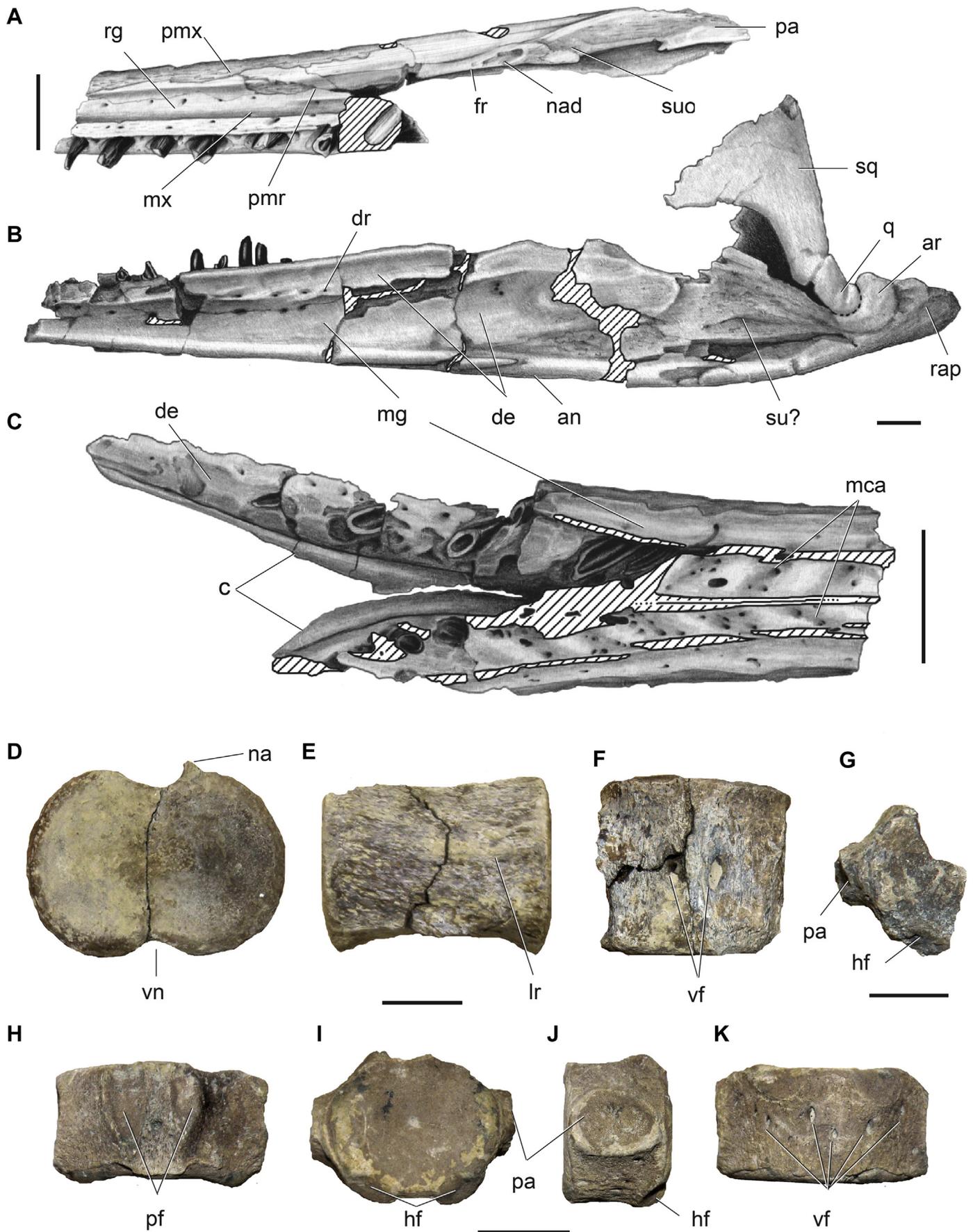


Fig. 6. A–C, MPEF-PV 650 *Sulcusuchus erraini*. Interpretative drawings. A, rostrum and skull roof in left lateral view; B, left mandibular ramus in lateral view; C, mandibular symphysis in ventral view. D–F, Elasmosauridae indet. MPEF-PV 10601, cervical vertebra in D, anterior, E, right lateral and F, ventral views. MPEF-PV 10602, G, caudal vertebra in anterior view. MPEF-PV 10603 caudal vertebrae in H, dorsal, I, anterior, J, left lateral and K, ventral views. Abbreviations: an, angular; ar, articular; c, coronoid; de, dentary; dr, dentary ridge; fr, frontal; mca, Meckelian canal; hf, haemal facets; lr, lateral ridge; mg, mandibular groove; mx, maxilla; na, neural arch; nad, nasal duct; pa, parapophysis; pa, parietal; pf, pedicular facets; pmr, posterior maxillar ridge; pmx, premaxilla; q, quadrate; rap, retroarticular process; rg, rostral groove; sq, squamosal; su, surangular; suo, supraorbital; vf, ventral foramina; vn, ventral notch. Scale bars = 20 mm.

Allen Formation, Río Negro, to Elasmosauridae indet. which share features with the specimen here described: 1) moderately elongated cervical centra with a ratio between the length and the average of the width and height (Vertebral Length Index – VLI – proposed by [Brown, 1981](#)) less than 130 (Fig. 6D–F); 2) broader than high vertebral centra; and 3) caudal vertebrae with distinctive parapophyses strongly projected laterally (Fig. 6G–K). A similar caudal morphology, with strongly projected parapophyses, has also been recorded in specimens from the Allen Formation but from the area of Salitral de Santa Rosa, Río Negro Province ([O’Gorman et al., 2011](#), fig. 3).

A preliminary comparison of the body size based on the size of the dorsal vertebrae indicates that the specimens MPEF-PV 10601-3 (La Colonia Formation) and MLP 71-II-13-1, MCS PV 4 and MUC PV 92 (Allen Formation) are smaller than other Late Cretaceous elasmosaurids ([O’Gorman et al., 2013b](#)). Although these plesiosaurs are small sized, they are adults because most of the specimens show no trace of the neuro-central suture ([Brown, 1981](#)). [Sato et al. \(2005\)](#) recorded small-sized elasmosaurs from the Campanian marine marginal to non-marine Dinosaur Park Formation (Alberta, Canada). These similar cases could indicate a relationship between the small body size of the specimens and this distinctive type of environment.

6. Discussion

6.1. Paleoenvironments and paleoecology of the reptiles from the La Colonia Formation

The middle strata of the La Colonia Formation (second facies association of [Pascual et al., 2000](#)) were interpreted as having been deposited in an estuary, tidal flat or coastal plain environment ([Page et al., 1999](#); [Pascual et al., 2000](#)), as well as in a lacustrine or littoral lagoon ([Ardolino and Delpino, 1987](#); [Page et al., 1999](#); [Gandolfo and Cúneo, 2005](#)). The retrogradational stacking pattern of the complete succession of this unit indicates relative sea-level rise exceeding the rate of sedimentary supply, in an area of low terrestrial gradient. In this context and on embayed coasts the transgression with deposition results in the generation of estuaries and lagoons ([Boyd et al., 2006](#)).

The studied sections are characterized by a dominance of massive, laminated and heterolithic mudstones, with scarce intercalated beds of massive, heterolithic or trough-cross stratified fine sandstones and fossiliferous conglomerates with mud intraclasts. The dominance of fine grained facies indicates low energy depositional conditions ([Boggs, 2009](#)), as well as the existence of a geomorphic setting that traps the fine-grained deposits. The preferred sedimentological settings for heterolithic bedding are tidally influenced environments, where a change takes place between slack water and turbulent water and where the corresponding sediments exist ([Reineck and Wunderlich, 1968](#)). These sedimentological characteristics (e.g., dominance of fine-grained sediments and scarce, mostly fine, cross-stratified sand intercalated beds, and heterolithic lamination) together with the ecological requirements of the well preserved fauna (mostly terrestrial, fresh and brackish water taxa), suggest deposition in muddy flood plains, marshes and ponds cut by meandering channels, probably at the mixed-energy central zone (sensu [Boyd et al., 2006](#)) of an estuary. This zone is the lowest-energy portion of the system, with mixed, and approximately equal in strength conditions in the long term, of marine energy (generally tidal currents) and river current energy. This is the position of net bedload convergence and typically contains the finest-grained sediments in the estuary. There the studied vertebrate remains have accumulated in situ or with

little transport and underwent rapid burial and fossilization. The intercalated fine sandy facies are no more than 3 m thick, although their lateral extent is usually tens of meters, and the fossiliferous conglomerates are restricted to decimeter thick layers and a few meters of lateral extension. Within estuarine environments, fine sandstone beds can be associated with the lateral accretion of meandering tidal fluvial channels ([Dalrymple and Choi, 2007](#)), whereas coarser beds can be produced by erosion of cut banks and adjacent muddy plains and salt marshes in the active margin of meandering. These sandier and conglomeratic beds, particularly the latter, contain mostly aquatic vertebrate remains, mainly fish, but also terrestrial vertebrates in very low proportion, such as neobatrachian anurans, all of them disarticulated and with clear evidence of transport ([Varela and Parras, 2013](#); [Muzzopappa and Varela, 2014](#)). Estuaries are considered biologically stressed environments in which ichnofossil associations have low diversity and individual traces are small, a feature observed in traces found in the studied sections. The trochamminid agglutinating foraminifers recovered from the base of the Norte de Cerro Bayo 2 section are common in marshes and mangroves as well as in hypersaline estuaries (A. Carignano, pers. comm. 2013).

Comparing the herpetofauna of the study area with closely related extant taxa, the species of *Hydromedusa* (sister clade of the extinct *Yaminuechelys*, see [Bona and de la Fuente, 2005](#)) are aquatic turtles mostly feeding on crustaceans, insect and snail larvae, among other invertebrates, as well as tadpoles and small fish ([Bonin et al., 2006](#)). Following the preferred habitats for chelids, and in particular for the extant *Hydromedusa*, the suggested preferred habitat for *Yaminuechelys* aff. *Y. gasparinii* would be swamps, ponds, and muddy streams. The general morphology of the limbs, the shape of the carapace, and the triturating surface of Meiolaniidae (the most derived group of meiolaniforms) resemble those of modern testudinids, which are terrestrial forms, mainly herbivorous. In the La Colonia Formation specimens of both groups (chelids and meiolaniforms) are associated in the same level and proximity (within a single square meter). This association is common in modern turtles, for example in the warmest and most humid areas of South America testudinids are distributed in the same areas as chelids ([Bonin et al., 2006](#)). The well-preserved and little-abraded turtle remains, often spatially associated, indicate minimal transport, suggesting that both groups could have coevally inhabited areas outside and inside the same water bodies.

The record of non-avian dinosaurs suggests clear continental conditions. Some taxa recorded in the La Colonia Formation, particularly hadrosaurs, are typical inhabitants of coastal environments; however, hadrosaurs are also recorded in diverse biotopes, such as intermontane and terrestrial foredeep basins in other regions, as in North America and Asia ([Horner et al., 2004](#)). In North America, some hadrosaur genera such as *Edmontosaurus* [Lambe, 1920](#) are found in near-marine environments, whereas others such as *Saurolophus* [Brown, 1912](#) and *Hypacrosaurus* [Brown, 1913](#), are found in marginally more continental lowlands ([Horner et al., 2004](#)). Unlike turtles, and like plesiosaurs, the lack of living examples of non-avian dinosaurs and the impossibility so far to identify them to species level prevents making paleoenvironmental inferences. The unabraded and partially articulated remains of the theropod were found associated inside a concretion, suggesting that at least this specimen was deposited in a low energy restricted environment with little to no transport. Besides the continental reptile groups here studied, snakes complete the taxonomic diversity of reptiles of the La Colonia Formation. The small madtsoiid *Alamitophis argentinus* [Albino, 1986](#), a large-sized madtsoiid, a probable booid and a snake *incertae sedis* ([Albino, 2000](#)) were also present in the same levels of the unit where the reptiles studied here were found.

The presence of well-preserved plesiosaur remains showing no evidence of transportation among the vertebrates from the La Colonia Formation has been traditionally considered an indication of a strong marine influence. However the records of plesiosaurs from brackish water to non-marine environments are not uncommon around the world. Early–Middle Jurassic plesiosaurs were collected from lacustrine deposits in China (Sato et al., 2003) and in the Early Cretaceous plesiosaurs were found also in non-marine environments from Australia (Kear, 2006, 2012). Moreover, an Early Cretaceous association, probably comprising two species has been recorded from the non-marine Eumeralla Formation in Australia (Benson et al., 2013). Younger elasmosaurids have been recorded in the Horseshoe Canyon Formation, in Canada (Sato et al., 2005; Sato and Wu, 2006). These discoveries increase the records of plesiosaurs in this kind of environment and suggest that the invasion of environments such as estuaries could have occurred more than once in plesiosaur evolution and probably in different clades within the Plesiosauria (Sato et al., 2003; Benson et al., 2013; O’Gorman and Gasparini, 2013). However, until now the specimens are fragmentary making difficult a complete study (Sato et al., 2005; Kear, 2012; Benson et al., 2013). Therefore the presence of two types of plesiosaurs (elasmosaurids and polycotyliids) among the fauna of the La Colonia Formation is compatible with an estuarine environment. Additionally, it is an important record that confirms the presence of multispecific plesiosaur associations in marginal marine to non-marine environments as mentioned by Benson et al. (2013). O’Gorman et al. (2013b) suggested that a preliminary comparison of the body size based on the size of the dorsal vertebrae indicates that the adult specimens from the La Colonia Formation and others from the Allen Formation are smaller than other Late Cretaceous elasmosaurids. Sato et al. (2005) recorded small-sized elasmosaurids from the Campanian marginal marine to non-marine Dinosaur Park Formation. These similar cases suggest a relationship between the small body size of the specimens and this distinctive type of environment. Likewise, the presence of deep rostral and mandibular grooves denoting a conspicuous vascularization and/or innervation in the polycotyliid, is consistent with the presence of associated special sensory structures that are analogously present in some extant cetaceans that inhabit estuarine and river environments (Wilkens and Hofmann, 2008). Additionally, based on the analysis of the gastrolith set of the specimen MPEF-PV 10602, O’Gorman et al. (2013a) inferred a fluvial or estuarine origin of the gastroliths based on shape features. This result is congruent with the one obtained by Cerda and Salgado (2008) in the specimen MCS PV 4 from the Allen Formation, Lago Pellegrini locality, Río Negro Province, and with all the other cases of elasmosaurid gastroliths analyzed using shape features (Darbi and Ojakangas, 1980; Cicimurri and Everhart, 2001; O’Gorman et al., 2013a).

6.2. Faunal comparison among Campanian–Maastrichtian reptile bearing localities from northern Patagonia

The taxonomic groups of reptiles represented in the La Colonia Formation are also recorded in other units of the Campanian–Maastrichtian of north Patagonia. Leanza et al. (2004) recognized different tetrapod assemblages for the Cretaceous terrestrial sediments of the Neuquén Basin. For the Campanian–Maastrichtian they recognized the Allenian assemblage characterized by the presence of saltasaurine titanosaurs, abelisaurid theropods, hadrosaurid ornithomorphs, ankylosaurian ornithischians, ornithure and non-ornithure birds, crocodyliforms, “madtsoiid” snakes, lizards, non-eilenodontine sphenodontians, chelid and meiolaniform turtles, pipoid and “leptodactylid” frogs, and dryolestoid and gondwanather mammals (see Leanza et al., 2004 for further citations).

The authors recognized this assemblage in the Angostura Colorada, Loncoche, Los Alamitos, La Colonia and Allen formations. In this contribution we enlarge the knowledge of the already known reptiles from the La Colonia Formation and corroborate the presence of the Allenian assemblage in the mentioned stratigraphic unit.

The association of Meiolaniformes and Chelidae is recorded from the Early Cretaceous (Cerro Barcino Formation, Chubut Group) to the Eocene (Sarmiento Formation) in Patagonia, and from the Eocene to the Holocene in Australia (Sterli and de la Fuente, 2013). Particularly during the Late Cretaceous in Patagonia, Chelidae and Meiolaniformes are associated in the La Colonia, Allen, Los Alamitos and Loncoche formations (de Broin, 1987; de Broin and de la Fuente, 1993; González Riga, 1999; Gasparini and de la Fuente, 2000; Martinelli and Forasiepi, 2004; Previtera and González Riga, 2008; Sterli and de la Fuente, 2013; Sterli et al., 2013). In the Allen Formation, the large and decorated chelid *Yaminuechelys gasparinii* and indeterminate chelids together with the large meiolaniform *Trapalcochelys sulcata* Sterli, de la Fuente and Cerda, 2013, and fragmentary remains of meiolaniforms have been recognized (de Broin and de la Fuente, 1993; de la Fuente et al., 2001; Martinelli and Forasiepi, 2004; Sterli et al., 2013). In the Los Alamitos Formation, the chelid *Palaeophrynops patagonicus* Lapparent de Broin and de la Fuente 2001, and other indeterminate chelids as well as fragmentary remains assigned to meiolaniforms have been identified (de Broin, 1987; de Broin and de la Fuente, 1993; Lapparent de Broin and de la Fuente, 2001; Sterli et al., 2013). For the Loncoche Formation, several chelids have been mentioned (e.g., decorated, not decorated and large) as well as indeterminate meiolaniforms (de Broin and de la Fuente, 1993; González Riga, 1999; Previtera and González Riga, 2008; Sterli et al., 2013). In all the known Campanian–Maastrichtian localities with remains of extinct turtles, the association of decorated chelids of medium to large size, undecorated large chelids, and meiolaniforms is repeated. The recovery of more complete specimens, their detailed study, and their comparative analyses are essential to establish its alpha taxonomy and to base interpretative analyses on the ecology and plausible interactions among those groups not only in the Late Cretaceous, but from the Early Cretaceous to the Eocene in Patagonia.

Concerning dinosaurs, the record of the La Colonia Formation is similar with that of other Campanian–Maastrichtian localities from northern Patagonia (Gasparini et al., 2007). The new records from Chubut described in this paper reveal that the composition of the dinosaur faunas of the Late Cretaceous of northern Patagonia extended at least to central Patagonia. The taxonomic similarity has to be restricted so far to the large suprageneric groups (abelisaurids, titanosaurs, ankylosaurs, hadrosaurs), since it is not currently possible to establish finer differences at the generic or specific level. Abelisaurids are also recorded in the Anacleto (Bonaparte and Novas, 1985; Coria et al., 2002) and Allen (Coria, 2001) formations. The theropod remains described herein demonstrate that the abelisaurid diversity in the La Colonia Formation is greater than previously known because at least two taxa (*Carnotaurus sastrei* and other species closely related) are present. Titanosaur sauropods are widely documented in most continental localities of the Late Cretaceous of Patagonia, particularly in the Anacleto, Allen and Los Alamitos Formations (Salgado and Bonaparte, 2007 and literature therein). To date, titanosaur remains are scarce in the La Colonia Formation. Those described in this paper are only enough to confirm the presence of the group in this unit. The described remains cannot be classified within any titanosaur group. The record of ornithischian dinosaurs of the Campanian–Maastrichtian of central Patagonia was limited to fragments of Hadrosauridae reported from the Paso del Sapo Formation (Apesteguía et al., 2012), exposed to the west of the study area. In a broader geographic

framework, ankylosaurs and hadrosaurs have an important record in the Late Cretaceous of northern Patagonia (Coria and Salgado, 2001). Particularly hadrosaurs are among the most abundant dinosaurs in certain Campanian–Maastrichtian localities (e.g., Allen Formation at Salitral Moreno). Likely, the entrance of this ornithischian group of North American lineage had no significant impact on the autochthonous populations of other species of herbivorous dinosaurs (mostly titanosaurs), because in several localities, among them, Salitral Moreno (north of Patagonia) and in the vicinity of Cerro Bayo (central Patagonia), hadrosaurs co-existed with titanosaurs (Coria, 2009), being numerically significant to the same degree. There are records of hadrosaurs and ankylosaurs in Late Cretaceous localities of the northeast of the Antarctic Peninsula, therefore the discovery of these forms in Central Patagonia was expected.

Among the plesiosaurs, the elasmosaurids recovered from the La Colonia Formation share features with the specimen from the Allen Formation described by Gasparini and Salgado (2000). Furthermore, the polycotylid *Sulcusuchus erraini* is also recorded in the Coli Toro Formation from northern Patagonia (Gasparini and Spalletti, 1990; Gasparini and de la Fuente, 2000; O’Gorman and Gasparini, 2013). These similarities could indicate affinities between the elasmosaurs and polycotylids recorded in the northern and southern slopes of the Somún Curá Plateau, which agrees with the supposed common age of these formations. Albino (2000, 2011) also stated affinities among the snakes recorded in Patagonia in the Campanian–Maastrichtian interval.

7. Concluding remarks

Sedimentological analyses of the La Colonia Formation suggest that the deposition occurred in the mixed-energy central zone of an estuary. The specimens recently recovered were preserved in situ or with minimal transportation and underwent rapid burial and fossilization processes. During the fieldwork carried out by the authors, three groups of reptiles (turtles, dinosaurs and plesiosaurs) have been recovered from the La Colonia Formation. Considering also previous works, the herpetofauna from the La Colonia Formation is represented by at least 12 taxa (at least three species of turtles, two species of theropods, one ankylosaur, one hadrosaurid, two taxa of plesiosaurs and at least three taxa of snakes). The most frequent tetrapod fossils collected are turtles, followed by plesiosaurs. Among dinosaurs, theropods are the most frequent taxon. Besides the mentioned diversity of reptiles, freshwater fishes, anurans, and mammals can also be included. These vertebrates document diverse terrestrial, fresh-water, and marginal marine associations. All of them are characteristic components of the Campanian–Maastrichtian terrestrial Allenian assemblage proposed by Leanza et al. (2004) for Patagonia.

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