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Late Cretaceous (Campanian/Maastrichtian) freshwater to restricted marine mollusc fauna from the Loncoche Formation, Neuquén Basin, west-central Argentina

Ana Parras [a,*], Miguel Griffin [b]

[a] INCITAP (CONICET-UNLPam), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina
[b] CONICET, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

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ABSTRACT

This study is the first detailed account of freshwater to restricted marine molluscs from the Upper Cretaceous sedimentary rocks in the northern sector of the Neuquén Basin. The fossils are from the Campanian–Maastrichtian Loncoche Formation in southern Mendoza, west-central Argentina, which records the initial connection of the Neuquén Basin to the Atlantic Ocean. Six species of bivalves (*Diplodon bodenbenderi*, *Pleiodon*? sp., *Isognomon*? *mechanquilensis*, Mactridae? indet., *Panopea*? sp., and *Laternula* sp.) and three of gastropods (*Paleoanculosa macrochilinoides*, *Paleoanculosa ameghiniana*, and a possible cerithioidean) are described. Specimens were collected from fine to coarse sandstones, which may be massive or with planar stratification, planar-cross stratification or trough-cross stratification, and a few from bioclastic limestones and mudstones. Although the sections are from 50 to 300 m thick, the specimens are found only in the lower 120 m. Molluscs represent autochthonous/parautochthonous assemblages composed of mostly non-broken gastropods and articulated bivalve specimens, some of which show signs of postmortem transport; however, they were not removed far from their original habitat. Review of the habitats of living genera supports the inference of dominantly freshwater palaeoenvironments in the lower and middle part of the Loncoche Formation, with restricted marine influence in the southernmost localities studied where there are a few samples that contain specimens belonging to predominantly marine groups (e.g., *Laternula*, *Panopea*).

1. Introduction

Scarce taxonomic information is available on mainly freshwater and brackish molluscs from the Late Cretaceous (Campanian–Maastrichtian) in the Neuquén Basin. This is true notwithstanding the fact that these molluscs occur at many localities and in different beds, showing a considerable diversity. The earliest papers recording their presence in the rocks considered were published during the first decades of the last century, with others following during the second half of it (Fritzsche, 1919; Doello-Jurado, 1927; Wichmann, 1927; Weaver, 1927, 1931; Groeber, 1929, 1933, 1946, 1947a, b; Mühlmann, 1937; Camacho, 1969; Parodiz, 1969; Dessanti, 1973, 1978; González Díaz, 1979; Manceñido and Damborenea, 1984; Parras et al., 1996, 1998). However, only a few of these provide detailed descriptions and illustrations of the fossils present, and most referred to fossils from localities in the southeastern sector (Neuquén Embayment) of the basin (Doello-Jurado, 1927; Parodiz, 1969; Manceñido and Damborenea, 1984).

The aim of this article is to fully document, for the first time, the mollusc fauna of the Loncoche Formation exposed in the northern sector of the Neuquén Basin, and to provide details of their stratigraphic distribution. Extensive collections made over the years with detailed stratigraphic data have allowed correct identification of the fauna and detailed knowledge on the stratigraphic range of the different taxa. Taxonomic identification and a study of the taphonomic features of the material dealt with herein are important for correlation among rocks exposed at different localities within the Neuquén Basin, allowing refinement of the palaeoenvironmental and palaeogeographic reconstructions for the Campanian–Maastrichtian in west-central Argentina. All of the material studied comes from the lower and middle section of the Loncoche Formation at the following localities: Puesto La

* Corresponding author.
E-mail addresses: aparras@exactas.unlpam.edu.ar (A. Parras), miguelgriffin@aol.com (M. Griffin).

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Bebida (=Arroyo Agua del Choique, 69° 44′ W, 35° 27′ S), Arroyo Brea (69° 43′ W, 35° 31′ S), Arroyo Loncoche (69° 40′ W, 35° 41′ S), Cerro Butaló (69° 40′ W, 35° 50′ S), Ranquil-Có (69° 30′ W, 36° 12′ S), Malal Vaca (69° 48′ W, 36° 12′ S), El Alambrado (69° 51′ W, 36° 14′ S), Arroyo Calmu-Có (69° 50′ W, 36° 30′ S), Bordo Alto del Payún (69° 27′ W, 36° 31′ S), and Cañadas Coloradas (69° 40′ W, 36° 32′ S). All lie within the Malargüe Department in southern Mendoza (Fig. 1), occurring along approximately 120 km in a N–S direction. The fossil-bearing beds range from fine to coarse sandstones and to a lesser degree limestones and mudstones; the logged sections are shown in Fig. 2. The taxonomic composition of the mollusc faunas, including the number of specimens recovered from each locality, and a synthesis of lithology, structures and associated fauna of the mollusc-bearing beds, are presented in Table 1.

2. Stratigraphy and age

The Neuquén Basin lies in west-central Argentina, including part of the present provinces of Río Negro, Neuquén, La Pampa and Mendoza. It contains marine and continental sedimentary rocks over 7000 m thick that reflect deposition during the Mesozoic and early Palaeogene. It opened along the western edge of the South American plate between the western volcanic arc and the highlands of the North Patagonian Massif in the southeast and the Piedra Pintada System in the northeast (Fig. 1). The basin is broadly triangular in shape and two main regions are commonly recognized: the Neuquén Andes to the west and the Neuquén Embayment to the east and southeast (Howell et al., 2005).

The sedimentary infill of this basin was divided by Groeber (1946) into three sedimentary cycles, which he called "Jurásico" (Hettangian–Kimmeridgian), "Ándico" (Tithonian–Coniacian) and "Riográndico" (Santonian–Danian). This contribution focuses on the upper part of the "Ciclo Riográndico" (Groeber, 1946), which was subdivided into a lower subcycle comprising the Neuquén Group (Digregorio, 1972) and an upper subcycle comprising the Malargüe Group (Uliana and Dellapé, 1981). These two units are separated by an unconformity (Andreis et al., 1974).

The Malargüe Group encompasses the late Campanian–Palaeocene and is characterized by the record of the first marine transgression from the Atlantic Ocean into the Neuquén Basin (Windhausen, 1914, 1926; Wichmann, 1927; Bertels, 1979; Uliana and Dellapé, 1981). These deposits accumulated in a foreland basin along a belt less than 120 km wide and running in a NNW–SSE direction, to the east of the magmatic arc (Malumián et al., 1983; Uliana and Biddle, 1988).

In the northwestern sector of the basin, the Malargüe Group is exposed over a wide area along the foothills of the Andes, where it is over 500 m thick and composed from bottom to top of the

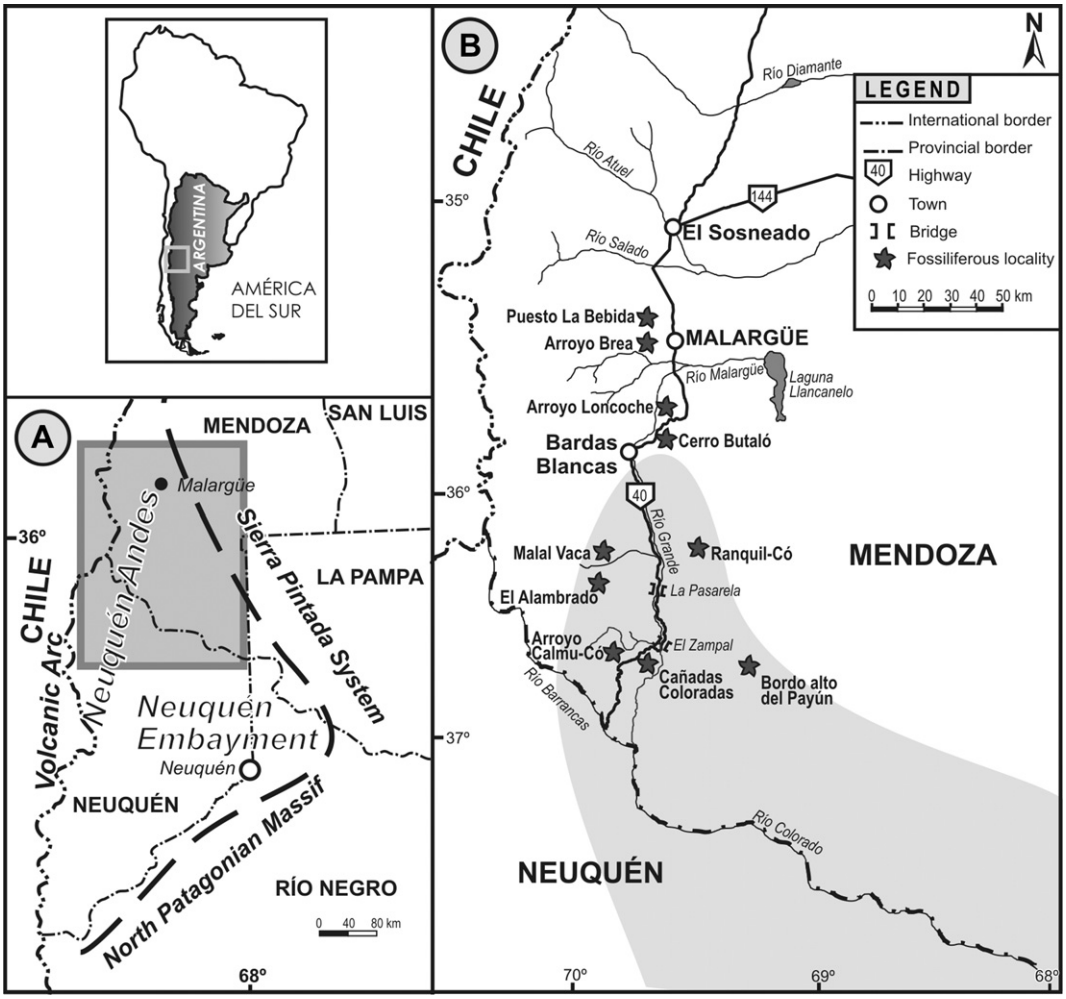

Fig. 1. A, general location of area studied within the Neuquén Basin in southern Mendoza. B, detailed map of shaded area in A, showing fossil localities studied along the foothills of the Andes, northern Patagonia, west-central Argentina. Probable extent of marine influence (based on mollusc content) during the beginning of the Atlantic (SE) transgression shown as shaded area.

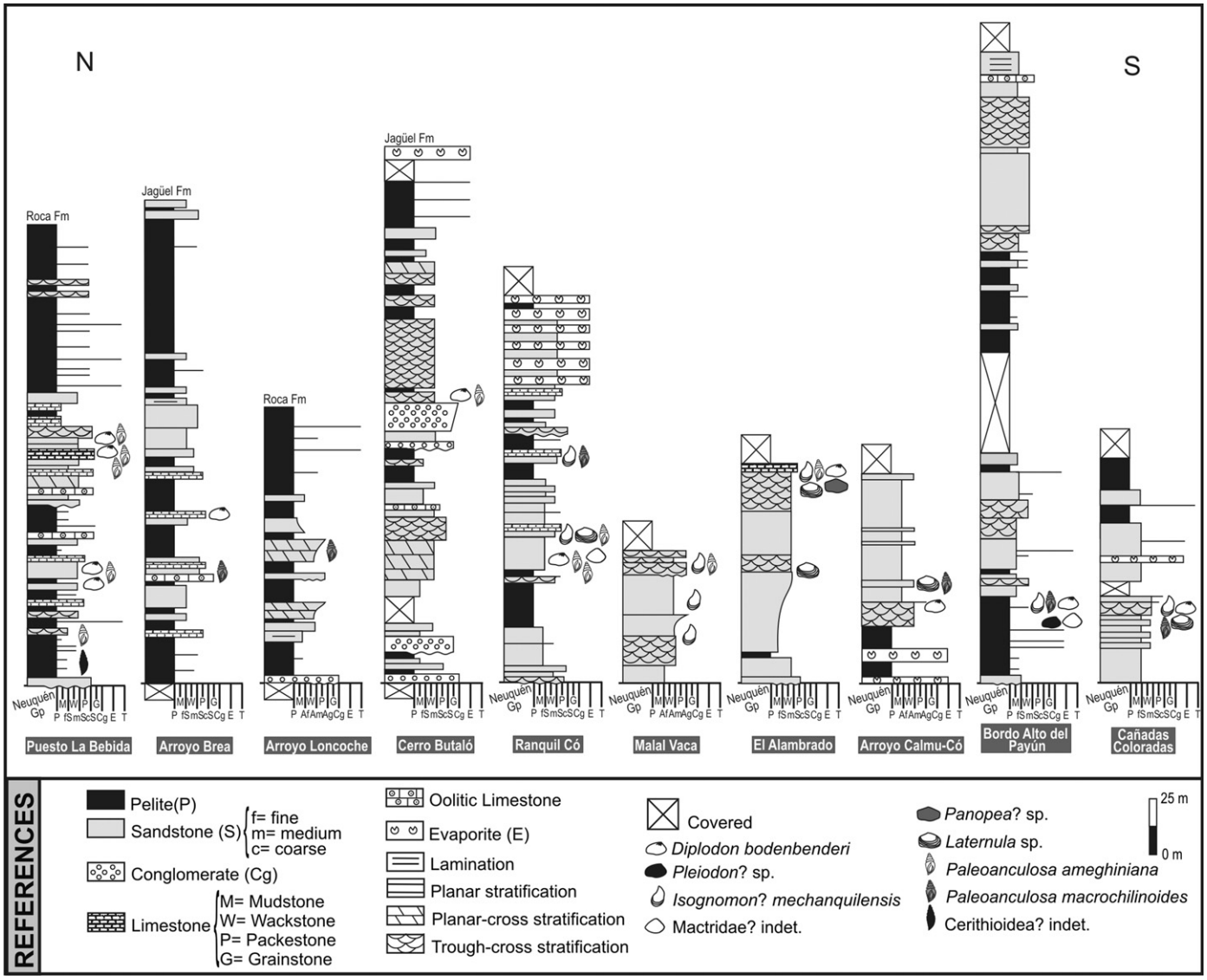

Fig. 2. Stratigraphic sections of the Loncoche Formation in all ten localities from which material was collected, showing precise stratigraphic provenance of specimens.

Loncoche, Jagüel, Roca, and Pircala formations. Its thickness in the southeastern sector is less than 200 m, and the units involved are the Allen, Jagüel, Roca, and El Carrizo formations.

The molluscs described herein come from the Loncoche Formation ("Loncochense", Groeber, 1946). This comprises the lower beds of the Malargüe Group, which consist of over 200 m of siltstones and sandstones, and subordinate fine conglomerates, limestones, evaporites and tuffs, containing ostracods, charophytes, spores, pollen, algae, forams, wood, vertebrates and molluscs (Mühlmann, 1937; Groeber, 1946; Dessanti, 1973; Uliana and Musacchio, 1978; Volkheimer, 1978; Papú, 1990, 1993, 1997; Zavattieri and Papú, 1993; Parras et al., 1998; González Riga, 1999; Parras and Casadío, 1999; Previtera and González Riga, 2008). Dessanti (1973), Legarreta et al. (1989), and Cruz et al. (1990) inferred that these rocks reflect deposition of sediments in a mixed marine-continental environment. Parras et al. (1998) interpreted the depositional environment of the area surrounding Malargüe as fluvial to deltaic under fluvial influence, with a few lacustrine episodes for the lower and middle part of this unit; the upper part was interpreted as tide-influenced delta environments. The equivalent unit in the southeastern area of the basin is the Allen Formation (Roll, 1939), known previously as the "Senoniano Lacustre" (lacustrine Senonian; Wichmann, 1927) because of the freshwater and brackish faunas it contains. Uliana and Dellapé (1981) interpreted this formation as having been deposited in a littoral to restricted marine environment. Barrio (1989) pointed out that in the eastern part of the basin the facies association could be attributed to intertidal deposits whereas in the western part the unit shows features that agree better with a tide-dominated estuarine environment. He attributed this asymmetry to tide-range differences directly related to basin geometry.

In the deeper parts of the basin, the Loncoche Formation and its equivalents are overlain by marine shales of the Jagüel Formation (Bertels, 1969), which grade transitionally into the very fossiliferous limestones of the regressive and diachronous Roca Formation (Weaver, 1927). In the eastern sector, the Roca Formation is overlain by claystones, sandstones and evaporites of the El Carrizo Formation (Uliana and Dellapé, 1981), whereas in the western area it gradually gives way to the continental sandstones and mudstones of the Pircala Formation ("Estratos de Pircala", Bohem in Fossa Mancini, 1938; "Pircaliano", Groeber, 1946).

Table 1
Taxonomic composition (including number of specimens at each locality), lithology and sedimentary structures of the mollusc-bearing beds in the Loncoche Formation at each of the reported localities. PLB, Puesto La Bebida; AB, Arroyo Brea; AL, Arroyo Loncoche; CB, Cerro Butaló; RC, Ranquil-Có; MV, Malal Vaca; EA, El Alambrado; AC, Arroyo Calmu-Có; BAP, Bordo Alto del Payún; CC, Cañadas Coloradas.

Species	Locality from north to south										Associated Fauna	Lithology and sedimentary structures
	PLB	AB	AL	CB	RC	MV	EA	AC	BAP	CC		
Isognomon? mechanquilensis	–	–	–	–	12	43	39	–	2	2	*Diplodon bodenbenderi*, *Pleiodon*? sp., Mactridae? indet., *Panopea*? sp., *Laternula* sp., *Paleoanculosa ameghiniana*, *P. macrochilinoides*, and vertebrate remains	Medium to coarse sandstones. Massive, with planar or trough-cross stratification, channelized bottoms and intraclasts. Also massive packstones
Diplodon bodenbenderi	16	9	–	2							*Paleoanculosa ameghiniana*, *P. macrochilinoides*, and vertebrate remains	Fine to coarse sandstones. Massive or with planar stratification. Also massive packstones and grainstones
					45	–	1	44	5	11	*Pleiodon*? sp., *Isognomon? mechanquilensis*, Mactridae? indet., *Panopea*? sp., *Laternula* sp., *Paleoanculosa ameghiniana*, *P. macrochilinoides*, coprolites, and vertebrate remains	Medium to coarse sandstones and packstones. Massive or with trough-cross stratification, channelized bottoms and intraclasts
Pleiodon? sp.	–	–	–	–	–	–	–	–	1	–	*Diplodon bodenbenderi*, *Isognomon? mechanquilensis*, Mactridae? indet., *Paleoanculosa macrochilinoides*, and vertebrate remains	Medium sandstones, with channelized bottom and intraclasts
Mactridae? indet.	–	–	–	–	3	–	–	–	1	–	*Diplodon bodenbenderi*, *Pleiodon*? sp., *Isognomon? mechanquilensis*, *Laternula* sp., *Paleoanculosa ameghiniana*, *P. macrochilinoides*, and vertebrate remains	Medium to coarse sandstones. Massive or with trough-cross stratification, channelized bottoms and intraclasts. Also massive packstones
Panopea? sp.	–	–	–	–	–	–	5	–	–	–	*Diplodon bodenbenderi*, *Isognomon? mechanquilensis*, *Laternula* sp., *Paleoanculosa ameghiniana*, and vertebrate remains	Medium sandstones massive, and packstones with trough-cross stratification
Laternula sp.	–	–	–	–	7	–	1	14	–	9	*Diplodon bodenbenderi*, *Isognomon? mechanquilensis*, Mactridae? indet., *Panopea*? sp., *Paleoanculosa ameghiniana*, *P. macrochilinoides*, coprolites, and vertebrate remains	Medium to coarse sandstones. Massive, with planar or trough-cross stratification, channelized bottoms and intraclasts
Paleoanculosa macrochilinoides	–	43	31	–	7	–	–	123	32	145	*Diplodon bodenbenderi*, *Pleiodon*? sp., *Isognomon? mechanquilensis*, Mactridae? indet., *Laternula* sp., and vertebrate remains	Medium to coarse sandstones. Massive, or with planar-cross and trough-cross stratification, frequent channelized bottoms and intraclasts. Also massive packstones
Paleoanculosa ameghiniana	69	–	–	46	114	152	73	–	–	–	*Diplodon bodenbenderi*, *Isognomon? mechanquilensis*, Mactridae? indet., *Panopea*? sp., *Laternula* sp., and vertebrate remains	Medium to coarse sandstones. Massive, or with planar or trough-cross stratification. Also fine laminated sandstones and massive or trough-cross stratified packstones and grainstones
Cerithioidea? indet.	6	–	–	–	–	–	–	–	–	–	Vertebrate remains	Laminated mudstones and fine sandstones

The differences in depositional environments recorded from the Malargüe Group between the Andes and Embayment sectors, apparent from the dominance of continental and deltaic facies, as well as from the abundance of pyroclastic material in the Andes sector, suggest the proximity of an emergent and volcanically active zone (Digregorio, 1978; Parras et al., 1998). On the other hand, the eastern area is dominated by marine deposits, comprising mainly shales, limestones and evaporites, suggesting a distal location with respect to the source areas and close oceanic links.

At the top of this group there is an important regional unconformity, and in the entire western (Andes) part of the basin there is evidence of deformation and erosion of the units, linked to the Andean Orogeny (Legarreta et al., 1989).

The age of the Loncoche Formation providing the specimens described here is difficult to establish accurately. It apparently lacks microfossils that may aid in pinpointing an acceptable age-bracket. Thus, all inferences on the age of this unit are based on indirect evidence provided datings of the strata under- and overlying the laterally equivalent Allen Formation. The age of the Allen Formation is constrained between the early–mid Campanian and late Maastrichtian, according to the ages based on magnetostratigraphical data on the underlying Anacleto Formation (Dingus et al., 2000) and by micropalaeontological data on the overlying Jagüel Formation (Náñez and Concheyro, 1997; Concheyro et al., 2002) respectively. In Mendoza, the age of the Loncoche Formation as revealed by massulae of the water-fern family Salvinaceae (Papú et al., 1988) and megaspores referred to *Grapnelispora* Stover and Partridge 1984 (Sepúlveda et al., 1989) appears to be restricted to the Campanian–Maastrichtian, although further accuracy is not possible because of the nature of the taxa used in these datings.

3. Previous palaeontological references to molluscs in the Loncoche Formation

The mollusc fossil record from the Loncoche Formation has been poorly studied even though it is very abundant and distributed across the northern sector of the Neuquén Basin. Detailed palaeontological studies are scarce and, except for those of Camacho (1969) and Doello-Jurado (1927), all mentioned the presence of molluscs but no illustrations of new specimens of the reported bivalves and gastropods were provided. Fritzsche (1919) published the results of his study on the fauna collected by Gerth in the environs of Malargüe (Arroyo Pequenco, Paso Loncoche, Arroyo de la Ventana and Arroyo Chacay) and El Sosneado (Arroyo Las Aucas). He mentioned the presence of five new species of molluscs belonging to *Paludina* (*Campeloma*?), *Paludina* (*Vivipara*), *Hydrobia*, *Melania* and *Cerithium*, and also *Planorbis* sp. and *Goniobasis*? sp. for the lower part of the sections (Loncoche Formation). However, he did not include either detailed descriptions or illustrations of the new species, thus introducing numerous doubts leading to

confusion when attempts are made to compare his material with other specimens collected later. In any event, the names introduced by him for this material are all "nomina nuda".

Doello-Jurado (1927) described a fauna from what was then known as "Senoniano Lacustre" and now referred to as Allen Formation exposed in the provinces of Río Negro and Neuquén. In this paper, he described the new species *Melania pehuenchensis* and *Melania macrochilinoides* from equivalent beds exposed in southern Mendoza Province (e.g., Arroyo Calmu Có and Río Grande at its junction with Río Barrancas) and there known as the Loncoche Formation.

Weaver (1927, 1931) mentioned the presence of *Hydrobia* sp. and *Paludina malarguana* Fritzsche in the Malargüe area.

Groeber (1929, 1933, 1946, 1947a, b) recorded the presence of *Modiola*, *Paludina*, *Hydrobia*, *Cerithium*, *Corbicula*, *Mya*, *Unio*, *Viviparus*, *Melania*, *Diplodon*, *Perna*, *Ceratodus*, and crocodile and turtle remains for the "Loncochense". However, such diversity is misleading. Most of Groeber's material came from the area surrounding Calmu-Có. Changing generic assignations of his specimens over the years resulted in this apparent high diversity.

Mühlmann (1937) studied exposures at Arroyo Pequenco, Pampa Amarilla, and Cerro Chachao, all in the environs of Malargüe. At these localities she was able to identify *Hydrobia*? sp., *Melania macrochilinoides* Doello Jurado, *Melania ameghineana* Doello Jurado [sic], *Diplodon* cf. *bodenbenderi* Doello Jurado, *Diplodon*? sp., and *Paludina malarguana* Fritzsche, for the "Malargüe inferior" (=lower Malargüe; i.e., Loncoche Formation).

Camacho (1969) described and illustrated *Acteonina* sp. and the new species *Inoceramus mechanquilensis*, both from Arroyo Mechanquil (south of Bardas Blancas).

Dessanti (1973, 1978), in his description of the Bardas Blancas and Malargüe quadrangles (29b and 28b), recorded the presence of crabs and freshwater gastropods and bivalves (*Melania* sp. and *Diplodon* sp.) in the lower section of the Malargüe Formation.

González Díaz (1979), in his description of the La Matancilla quadrangle (31d), mentioned the presence of *Actaeonina*? sp. [sic] in the Malargüe Formation of the Liu Malal river area of southern Mendoza. He also referred to isolated exposures in the northeastern corner of the quadrangle bearing molluscs belonging in *Actaeonina* sp.

Parras et al. (1996, 1998) studied the Loncoche Formation in the Malargüe area (Puesto La Bebida, Arroyo Loncoche, Arroyo Brea and Cerro Butaló) and reported the presence of the following taxa in the lower and middle part: *Diplodon* aff. *D. bodenbenderi* Doello-Jurado, 1927; *Diplodon* aff. *D. pehuenchensis* (Doello-Jurado, 1927); a probable new species of *Diplodon*; *Neocorbicula*? sp. (=*Cyanocyclas*? sp.); *Paleoanculosa patagonica* Parodiz, 1969; *Paleoanculosa bullia* (Ihering, 1907); a probable new species of *Paleoanculosa*; *Hydrobia* sp.; and *Potamides* sp. Although at the time this fauna was not studied from a systematic point of view, it was recognized as palaeoenvironmentally important for understanding the sedimentary setting in which this unit was deposited.

4. Systematic palaeontology

Preservation of most specimens is adequate for identification. In some cases, specimens are deformed, but enough morphological details are preserved to enable description and comparisons with similar taxa.

The material studied was collected from the Loncoche Formation at ten localities and comprises 1113 specimens, 272 of which are bivalves and 841 gastropods (Table 1). All specimens are housed in the collection at the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (GHUNLPam). Type material of *Inoceramus mechanquilensis* is housed in the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (CPBA).

The systematics broadly follows the "Treatise on Invertebrate Paleontology" (Cox et al., 1969), although with modifications (Parodiz, 1969; Graf and Cummings, 2006, 2007). The synonymy lists include only references to illustrated material or references to material seen by us. Measurements were taken on each specimen using a caliper and recorded in millimetres. For bivalves the measurements and abbreviations are: L, length: total shell length measured parallel to the hinge axis; Lavg, average length; Lmax, maximum length; H, height: total shell height perpendicular to length; Havg, average height; Hmax, maximum height; W, width: maximum width of articulated shell; Wavg, average width; Wmax, maximum width; H/L, elongation. For gastropods the measurements and abbreviations are: H, height: height of spire; Havg, average height of spire; Hmax, maximum height of spire; W, width: width of last whorl; Wavg, average width of last whorl; Wmax, maximum width of last whorl; HLW, height of last whorl; HLWavg, average height of last whorl; HLWmax, maximum height of last whorl; AH, aperture height; AHavg, average aperture height; AHmax, maximum aperture height; AW, aperture width; AWavg, average aperture width; AWmax, maximum aperture width; H/W, elongation; AH/AW, aperture elongation.

Phylum Mollusca Linné, 1758
Class Bivalvia Linné, 1758
Subclass Pteriomorphia Beurlen, 1944
Order Pterioida Newell, 1965
Suborder Pteriina Newell, 1965
Superfamily Pterioidea Gray, 1847
Family Isognomonidae Woodring, 1925
Genus *Isognomon* Lightfoot, 1786
Type species. *Ostrea perna* Linné, 1767; by monotypy.

Isognomon? *mechanquilensis* (Camacho, 1969)
Fig. 3

1969 *Inoceramus mechanquilensis* Camacho, p. 221, fig. 1A
2006 "*Inoceramus*" *mechanquilensis* Camacho, 1969: Lazo, p. 1113 (=*Isognomon*)

Material. 98 specimens, most univalved or fragmentary, a few bivalved (no interior features available). Of these, 12 come from Ranquil-Có (GHUNLPam 15601–15605, 15626, 15627, 15765–15769), 43 from Malal Vaca (GHUNLPam 16051–16093), 39 from El Alambrado (GHUNLPam 16254–16292), two from Bordo Alto del Payún (GHUNLPam 16566, 16567), and two from Cañadas Coloradas (GHUNLPam 16511, 16512). All are from the Loncoche Formation.

Description. Shell ovate, of medium size (Havg, 44.8 mm; Hmax, 59 mm; Lavg, 33.4 mm; Lmax, 55 mm; H/L, 1.34), anteriorly inflated (Wavg, 14.7 mm; Wmax, 21 mm), and compressed near posterior dorsal and posterior ventral margins; umbones terminal, prosogyrous and pointed; dorsal margin short, joining posterior margin to form a wide angle; ventral margin rounded; anterior margin concave under umbones, and gently convex posteriorly; outer ornamentation of commarginal growth lines and, in some specimens, slightly lamellose growth ledges. Subumbonal cavity deep.

Discussion. The presence of this species in Mendoza was recorded by Camacho (1969, p. 221) at Mechanquil, along Mechanquil stream. He placed his specimen (CPBA-8051) in *Inoceramus* Sowerby, 1814 (type species *Inoceramus cuvierii* Sowerby, 1814)

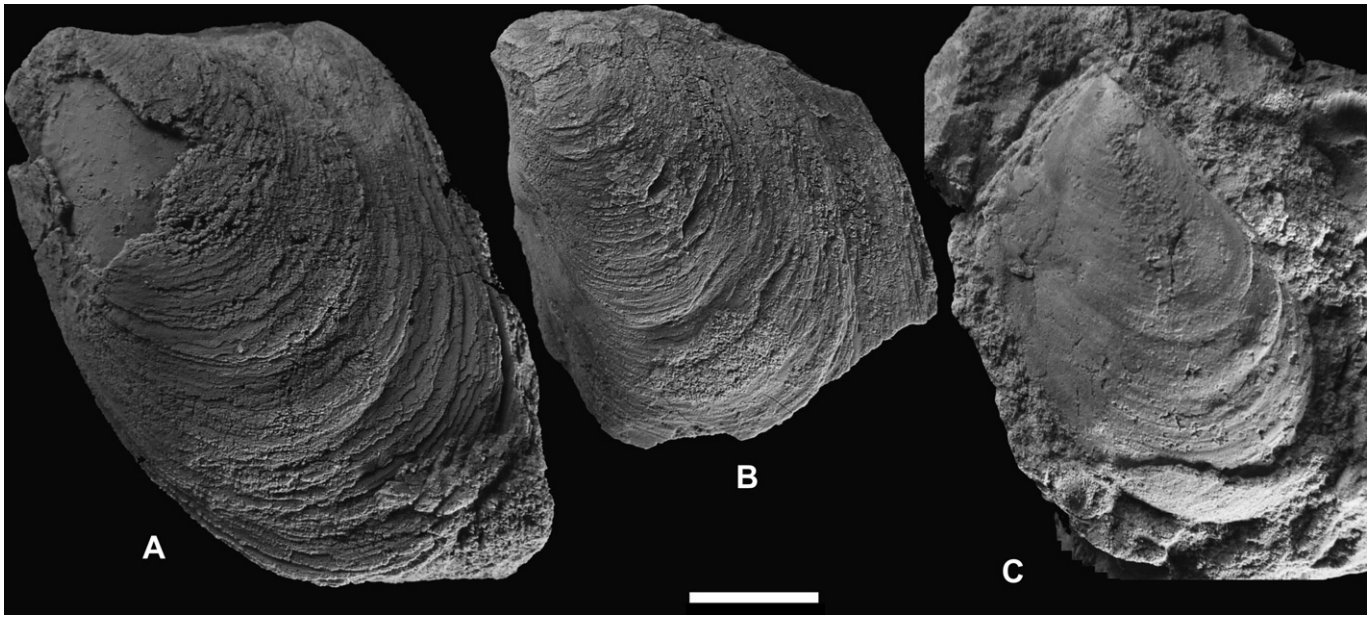

Fig. 3. *Isognomon? mechanquilensis* (Camacho, 1969). A, GHUNLPam 16080, left valve, external view. B, GHUNLPam 16079, left valve, external view. C, GHUNLPam 15765, right valve, internal mould, shell partly preserved. A and B from Malal Vaca; C from Ranquil-Có. Scale bar represents 1 cm.

even though some characters such as its outline and lamellose ornamentation suggested otherwise. This was acknowledged later by Lazo (2006, p. 1113) who suggested that it would fit better in *Isognomon* Lightfoot, 1786. Although no internal features are clearly visible in the specimens from Mendoza, there are characters that point towards a generic placement other than in *Inoceramus*. In the first place, the shell, especially in some of the better preserved specimens, is clearly mytiliform with a terminal pointed umbo. The ligament is not preserved, but the ligament plate appears to be inclined at an angle of 45° to the commissure plane similar to the inclination observed in many species of *Isognomon*. No trace of a pitted ligament platform is visible to suggest definite affinities either with inoceramids or isognomonids. It seems very likely that it belongs in a different group, but exactly into which genus or even family it can be fitted with certainty remains uncertain until better specimens are collected.

Localities. Ranquil-Có, Arroyo Mechanquil, Malal Vaca, El Alambrado, Bordo Alto del Payún, and Cañadas Coloradas, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation; Campanian–Maastrichtian.

Subclass Palaeoheterodonta Newell, 1965
Order Unionoida Stoliczka, 1870–1871
Superfamily Etherioidea Deshayes, 1830
Family Hyriidae Swainson, 1840

Remarks. The taxonomic arrangement of the South American hyriids, and especially species of *Diplodon* Spix in Spix and Wagner, 1827, has been always controversial. Parodiz and Bonetto (1963) stated that the Family Hyriidae, which can also be found living today in Australia and New Zealand but is absent from the rest of the world, belonged in the Superfamily Unionoidea. Graf (2000) and Graf and Cummings (2006, 2007), based on phylogenetic analyses, placed it within the Superfamily Etherioidea stating that such an arrangement was supported by the biogeography of the clade. South American hyriids belong in the Subfamily Hyriinae, comprising mainly the species of *Diplodon* but also other genera living in South America and Australasia. According to Graf and Cummings (2006) this subfamily is characterized by a single morphological synapomorphy: the presence of radial umbonal scupulture.

Subfamily Hyriinae Swainson, 1840
Tribe Rhipidodontini Starobogatov, 1970
Genus *Diplodon* Spix in Spix and Wagner, 1827

Type species. *Diplodon ellypticum* Spix in Spix and Wagner, 1827; subsequent designation by Simpson, 1900.

Diplodon bodenbenderi Doello-Jurado, 1927
Figs. 4, 5A

1927 *Diplodon*: Wichmann, pp. 391–393, pl. 3, figs. 14–16, pl. 4, fig. 18 (as *Diplodon Bodenbenderi* Doello-Jurado n. sp. in figure captions)
1927 *Diplodon*: Wichmann, p. 394, pl. 3, fig. 13, pl. 4, fig. 20 (as *Diplodon colhuapensis* Ih. var. *pehuenchensis* Doello-Jurado, n. var. in figure captions)
1927 *Diplodon colhuapensis* Ih., var. *pehuenchensis*, n. var.: Doello-Jurado, pp. 410, 411, pl. 3, fig 13, pl. 4, fig. 20
1927 *Diplodon bodenbenderi*, n. sp.: Doello-Jurado, p. 411, pl. 3, figs. 14–16, pl. 4, fig. 18
1969 *Diplodon bondenbenderi* Doello-Jurado (*sic*): Parodiz, p. 56, pl. 1, fig. 6, pl. 2, figs. 4–7
1969 *Diplodon pehuenchensis* Doello-Jurado: Parodiz, pp. 56, 57, pl. 1, fig. 5, pl. 2, figs. 1–3
1984 *Diplodon* (*Antediplodon*?) *bodenbenderi* Doello Jurado: Manceñido and Damborenea, pp. 436, 437, pl. 4, figs. 9–11, 14
1984 *Diplodon pehuenchensis* Doello Jurado: Manceñido and Damborenea, p. 437, pl. 4, figs. 12, 13
1996 *Diplodon* aff. *D. bodenbenderi* Doello-Jurado, 1927: Parras, Casadío and Pires, p. 47
1996 *Diplodon* aff. *D. pehuenchensis* (Doello-Jurado, 1927): Parras, Casadío and Pires, p. 47
1996 *Diplodon* n. sp.: Parras, Casadío and Pires, p. 47
1998 *Diplodon* aff. *D. pehuenchensis* (Doello-Jurado, 1927): Parras, Casadío and Pires, p. 64
1998 *Diplodon* sp.: Parras, Casadío and Pires, p. 64

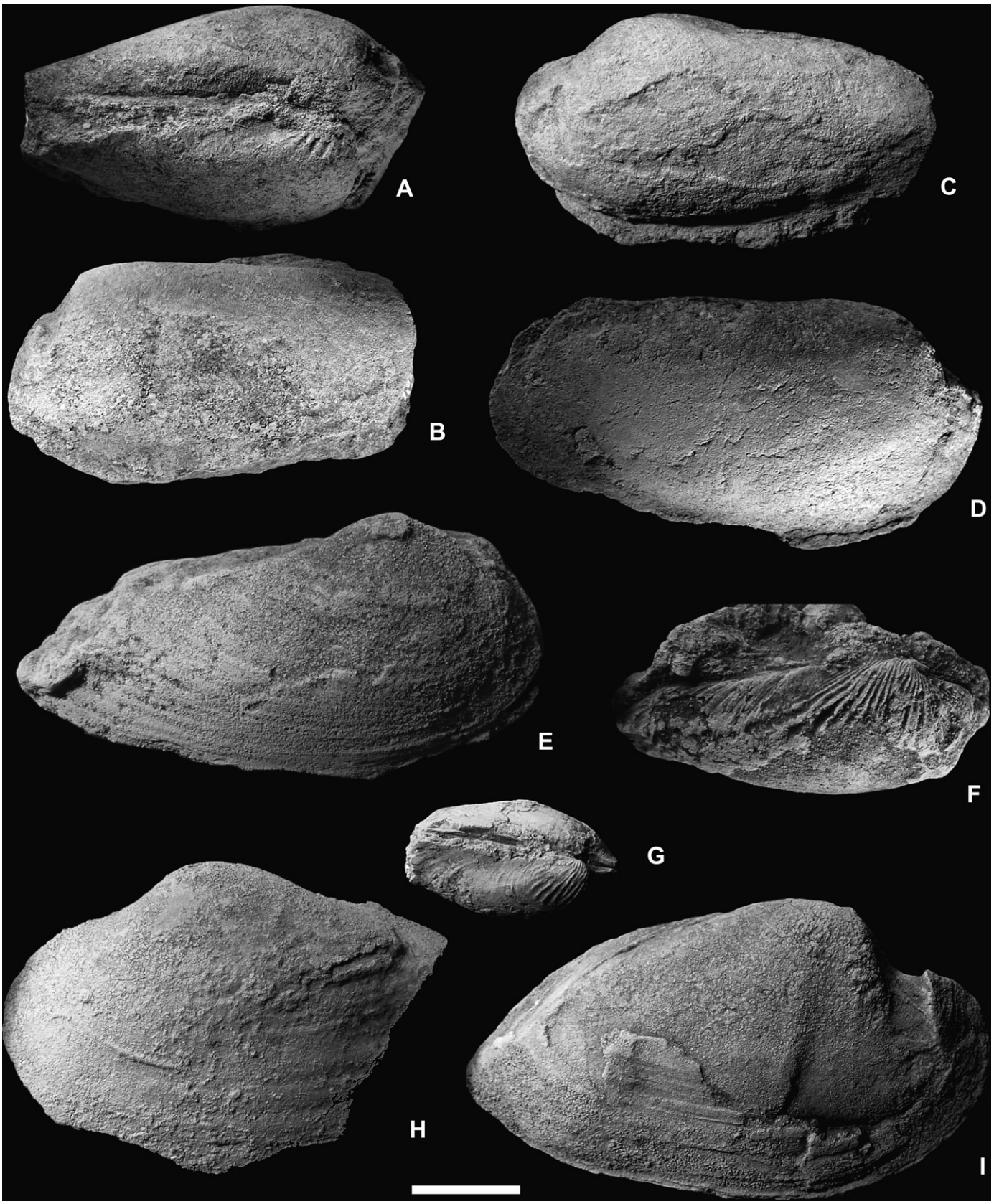

Fig. 4. *Diplodon bodenbenderi* Doello-Jurado, 1927. A, B, GHUNLPam 10389, internal mould. A, dorsal view showing early ornamentation of umbonal area. B, left valve view. C, GHUNLPam 10388, internal mould, left valve view. D, GHUNLPam 10376, internal mould, right valve view. E, GHUNLPam 11089, internal mould of right valve. F, GHUNLPam 11076, umbonal area of right valve showing early ornamentation and postumbonal keel. G, GHUNLPam 10255, juvenile bivalve specimen showing early ornamentation, dorsal view. H, GHUNLPam 16248, internal mould, left valve view. I, GHUNLPam 11082, internal mould of right valve with partly preserved shell showing large anterior muscle scar impression. A–D from Puesto La Bebida; E, F and I from Arroyo Calmu-Có; G from Cerro Butaló; H from El Alambrado. Scale bar represents 1 cm.

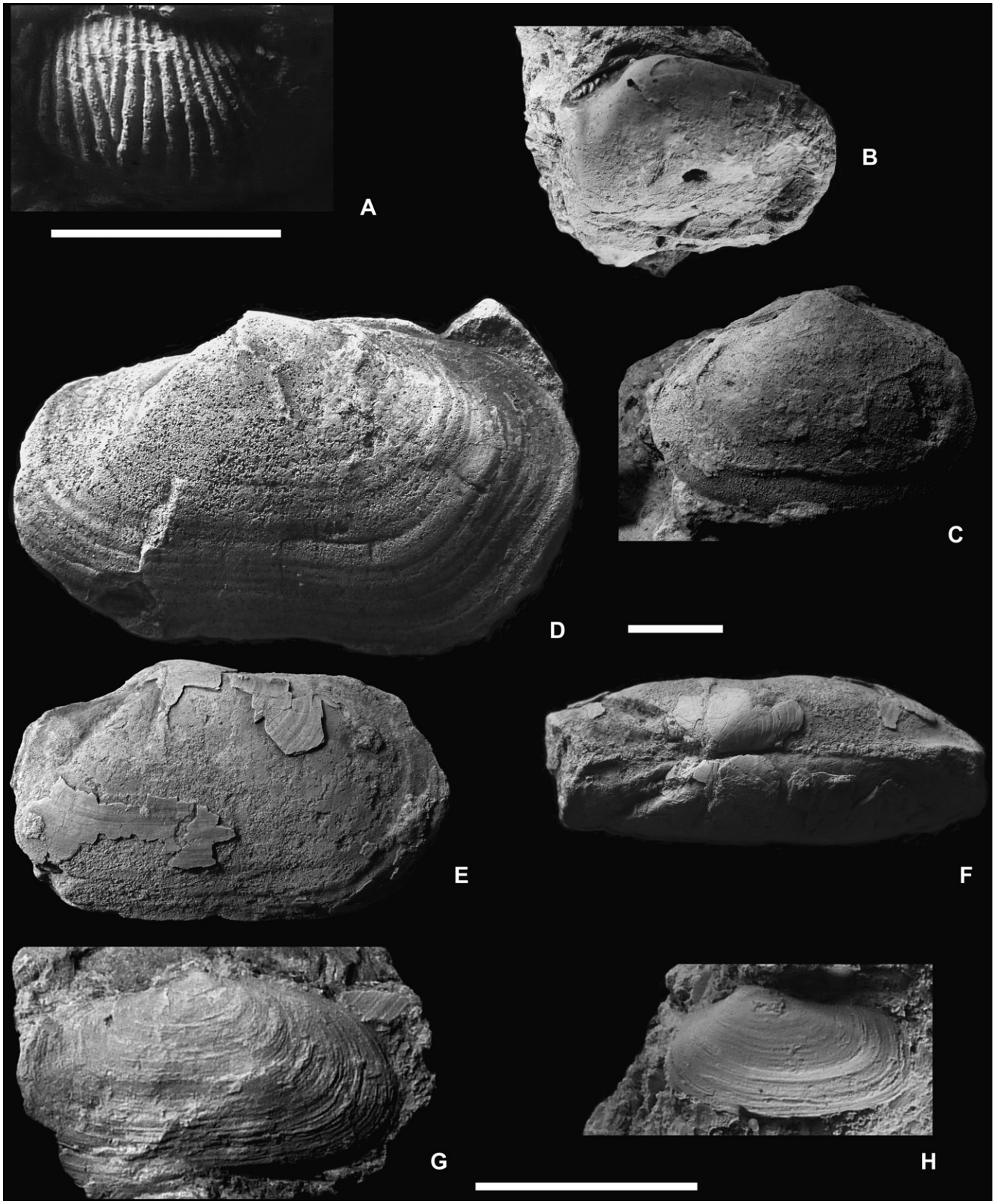

Fig. 5. A, *Diplodon bodenbenderi* Doello-Jurado, 1927, GHUNLPam 16572, mould of umbonal area showing V ornamentation. B, *Pleiodon*? sp., GHUNLPam 16574, internal mould showing hinge teeth, slightly tilted. C, Mactridae? indet., GHUNLPam 15763, internal mould, left valve view. D–F, *Laternula* sp. D, GHUNLPam 11101, internal mould, right valve view. E, F, GHUNLPam 15617, internal mould with part of shell preserved. E, right valve view. F, dorsal view. G, H, *Panopea*? sp. G, GHUNLPam 11231, right valve. H, GHUNLPam 11230, left valve. A and B from Bordo Alto del Payún; C, E and F from Ranquil-Có; D from Arroyo Calmu-Có; G and H from El Alambrado. Scale bars represent 1 cm.

Material. 133 specimens, mostly internal moulds, very few still retaining part of the preserved shell. Of these, 16 come from Puesto La Bebida (GHUNLPam 10357–10359, 10372–10376, 10388–10395), nine from Arroyo Brea (GHUNLPam 10081, 10082, 10160–10166), two from Cerro Butaló (GHUNLPam 10254, 10255), 45 from Ranquil-Có (GHUNLPam 15432–15463, 15748–15760), one from El Alambrado (GHUNLPam 16248), 44 from Arroyo Calmu-Có (GHUNLPam 11049–11092), five from Bordo Alto del Payún (GHUNLPam 16568–16572), and 11 from Cañadas Coloradas (GHUNLPam 16514–16524). All are from the Loncoche Formation.

Description. Shell strongly inequilateral, elongated, trapezoidal to oval-elongate with pointed posterior end, and small to medium in size (Havg, 24.3 mm; Hmax, 36 mm; Lavg, 40.8 mm; Lmax, 65 mm); height more than half of length (H/L, 0.6); shell inflated anteriorly (Wavg, 16.9 mm; Wmax, 24.8 mm); umbones prosogyrous and prominent; lunule cordiform, concave and well defined; weak postumbonal keel running from umbo to posteroventral margin, rendering some shells slightly winged in outline; anterior margin rounded; posterior margin acuminate, slightly truncated; dorsal margin straight, inclined; ventral margin gently convex; outer surface with well-marked commarginal growth lines; well-preserved specimens with umbonal area carrying radial ribs, the central ones V-shaped and the lateral ones approximately parallel.

Discussion. Two species of *Diplodon* have been described from rocks similar in age to that of the Loncoche Formation. *Diplodon pehuenchensis* (Doello-Jurado, 1927, pp. 410, 411, pl. 3, fig. 13, pl. 4, fig. 20) was based on material from the Allen Formation (Campanian–Maastrichtian) exposed in Lenza Niyeu, province of Río Negro. It was distinguished from *Diplodon bodenbenderi* Doello-Jurado, 1927 (p. 411, pl. 3, figs. 14–16, pl. 4, fig. 18) from the same unit exposed in Aguada de Trapalcó and Bajo de Santa Rosa, province of Río Negro, by its smaller size, its very distinct postumbonal ridge, different ornamentation, and well-developed lower lateral teeth. However, study of a large suite of specimens of *Diplodon* from the Loncoche and Allen formations reveals that these differences are not significant and in general are a result of preservational biases, because the taphonomic attributes of the material are just as varied as the types of rocks in which the different specimens are found. Most specimens are compressed/deformed in different directions, which accounts for the wide variation in shape. Whenever ornamentation is preserved, specimens of different shapes show the same kind of early ribbing on the umbonal area. In the figures provided by Parodiz (1969) some specimens of *Diplodon bodenbenderi* show ribs behind as well as in front of the umbones, a feature that was supposedly exclusive of *Diplodon pehuenchensis*. Teeth are rarely preserved, and then only as moulds. In these cases it is possible to observe specimens in which two posterior lateral teeth are preserved and others in the same sample in which only one or none is visible. Thus, two of the main characters that allowed them to be identified as different species, early ornamentation and dentition, appear to be an unsatisfactory basis upon which to separate them. Likewise, there are gradations and a great variation in shell outline, inflation, and size.

The size and outline of some specimens referred herein to *Diplodon bodenbenderi* are similar to that of *Diplodon esperanzaensis* Camacho, 1957 (as figured in Herbst and Camacho, 1970, p. 340, fig. 3), from the Jurassic of Antarctica. However, the specimens from Mendoza can be separated by their straighter dorsal margin and more clearly angulate posteroventral end of the shell. Other South American Mesozoic species include *Diplodon simplex* Morton, in Morton and Herbst, 2001, and *Diplodon matildensis* Morton, in Morton and Herbst, 2001, from the Middle Jurassic La Matilde Formation in Santa Cruz Province. These two species are based on small specimens (up to 12 mm long) in which only shell outline and part of the surface ornamentation are preserved. No traces of umbonal ribs are present. However, these species can be easily distinguished from *Diplodon bodenbenderi* by their small size and less conspicuous umbones. *Diplodon baqueroensis* Morton, 1984, from the middle Cretaceous Baqueró Formation in Santa Cruz Province was based on small, highly deformed specimens also lacking any trace of umbonal ornamentation. This species is also smaller and with more compressed valves and better marked growth lines than our specimens. Likewise *Diplodon bodenbenderi* can be distinguished from *Diplodon batoviensis* Martínez and Figueiras, 1991, from the Mesozoic Tacuarembó Formation of Uruguay because the latter has a convex posterodorsal shell margin joining the posterior margin in a gentle curve.

Diplodon bodenbenderi is similar to *Diplodon colhuapiensis* Ihering, 1903, from the Late Cretaceous of Chubut, although this southern species shows a more rounded anterior margin, with a sinus-like depression in front of the umbo. *Diplodon* (*Prodiplodon*) *amphitheatri* Manceñido and Damborenea, 1984, from the Upper Cretaceous Neuquén Group is based on specimens from Río Negro Province that bear a relatively large umbonal area with strong V-shaped ribs. While this character is shared with *Diplodon bodenbenderi*, the latter has generally more inflated shells. The umbonal ornamentation of *Diplodon* (*Prodiplodon*) *amphitheatri* is stronger, with the central ribs adopting a more open V-shaped configuration. In *Diplodon bodenbenderi* the V-shaped ribs are closed more narrowly and the lateral ones are more subparallel. Thus, when worn, shells appear to have umbonal areas with parallel radial ribs, because only the ends of the ribs nearer the umbones generally remain obvious.

Localities. Puesto La Bebida, Arroyo Brea, Cerro Butaló, Ranquil-Có, El Alambrado, Arroyo Calmu-Có, Bordo Alto del Payún, and Cañadas Coloradas, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation in Mendoza (this paper), and Allen and Coli Toro formations in Río Negro (Doello-Jurado, 1927; Wichmann, 1927; Parodiz, 1969; Manceñido and Damborenea, 1984); Campanian–Maastrichtian.

Unioniformea indet.
Genus *Pleiodon* Conrad, 1834.

Type species. *Pleiodon macmurtriei* Conrad, 1834 (=*Iridina ovata* Swainson, 1823); by monotypy.

Pleiodon? sp.
Fig. 5B

Material. One specimen, including the external and internal mould from Bordo Alto del Payún (GHUNLPam 16574).

Discussion. The only specimen preserved is a fragment of a mould, but enough of the hinge is available for the unusual secondarily taxodont teeth arrangement can be observed. This hinge morphology is common in the Iridinidae, a family of freshwater mussels presently living in west, east and central Africa. This character was included in a phylogenetic analysis of freshwater mussels of the world by Graf and Cummings (2006), because it is present in one of the species they analysed, namely *Mutela dubia* Gmelin, 1791. Other Iridinidae from Africa with similar hinges are well documented in the fossil record. Such is the case of *Pleiodon moharensis* (Gautier, 1965), *P. tavernieri* (Gautier, 1965), *P. lanceolatum* Kat, 1987 and *P. rusingae* Kat, 1987.

Although the family Iridinidae is known only from Africa, Morris and Williamson (1988) described a few hinges from the Hell Creek Formation, a Maastrichtian unit in Montana, USA. These hinges are

poorly preserved, but clearly show the pseudotaxodont character seen in some African Iridinidae, which led to their inclusion in *Pleiodon*. Hartman et al. (2006) contested such a taxonomic assignment and commented on the puzzling distribution of these pseudotaxodont freshwater bivalves. They stated that the most parsimonious explanation for the appearance of these shells during the Late Cretaceous in the Western Interior of North America and Africa was probably the independent radiation of the American forms at the end of the Cretaceous.

The specimen from the Loncoche Formation adds an intriguing new record to the already disjunct distribution of this kind of hinge morphology. There are two possible explanations for this record. On the one hand, it could have an independent origin, as the North American one probably does according to Hartman et al. (2006). On the other hand, it may represent a Late Cretaceous relict of a group that had a more widespread pre-Cretaceous Gondwanic distribution. Both hypotheses will, however, need further testing when more and better preserved material from South America becomes available. In the meantime, the specimens from Bordo Alto del Payún are provisionally referred to *Pleiodon*.

Locality. Bordo Alto del Payún, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation; Campanian–Maastrichtian.

Subclass Heteroconchia Hertwig, 1895
Order Veneroida H. Adams and A. Adams, 1856
Superfamily Mactroidea Lamarck, 1809
Family Mactridae Lamarck, 1809

Mactridae? indet.
Fig. 5C

Material. Four specimens preserved as internal moulds. Of these, three are from Ranquil-Có (GHUNLPam 15761, 15763, 15764), and one from Bordo Alto del Payún (GHUNLPam 16573). All specimens were collected from the Loncoche Formation.

Description. Shells small (Havg, 23.5 mm; Hmax, 24 mm; Lavg, 32.8 mm; Lmax, 36 mm; Wavg, 13 mm; H/L, 0.72), mactriform, with a wide pallial sinus; small mould of chondrophore present in one specimen.

Discussion. The specimens are all internal moulds. They are all fairly tall, almost equilateral shells, with a faint postumbonal keel. Moulds of the hinge are preserved in two of the specimens and one of them shows a slightly forwardly directed chondrophore immediately under the umbone. Lateral ends of the hinge are obliterated by recrystallization. The muscle scars are well marked and the pallial line shows a shallow, broadly ovate and almost horizontally directed sinus. The sinus does not reach the midline perpendicular to the hinge and passing through the umbones. Because the shell and most hinge features are missing, further precision in the identification of this material is not possible.

Localities. Ranquil-Có and Bordo Alto del Payún, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation; Campanian–Maastrichtian.

Order Myoida Goldfuss, 1820
Superfamily Hiatelloidea Gray, 1824
Family Hiatellidae Gray, 1824

Genus *Panopea* Ménard de la Groye, 1807

Type species. *Panopea aldrovandi* Ménard de la Groye, 1807 (=*Mya glycymeris* Born, 1778); ICZN Opinion 1414, 1986

Panopea? sp.
Fig. 5G, H

Material. Five specimens from El Alambrado (GHUNLPam 11230–11234).

Description. Shells small (Havg, 6 mm; Hmax, 8 mm; Lavg, 12 mm; Lmax, 16 mm), relatively thick, ornamented with comparatively well-developed commarginal ribs; ventral margin straight and posterior truncated end provided with a fairly well-developed siphonal gap.

Discussion. These features suggest that the shell may fit in *Panopea*, although no hinges are exposed that would allow a more definite identification. Because of this and the small size of the shells, we place them questionably in *Panopea*. The potential significance that these shells may have in the interpretation of the environment they inhabited is presently limited.

Locality. El Alambrado, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation; Campanian–Maastrichtian.

Subclass Anomalodesmata Dall, 1889
Order Pholadomyoida Newell, 1965
Superfamily Pandoroidea Rafinesque, 1815
Family Laternulidae Hedley, 1918
Genus *Laternula* Röding, 1798

Type species. *Laternula anatina* (=*Solen anatinus* Linné, 1758); subsequent designation by Gray, 1847

Laternula sp.
Fig. 5D–F

Material. 31 specimens, most are internal moulds but a few still have some shell matter preserved. Seven of these moulds come from Ranquil-Có (GHUNLPam 15612–15618), one from El Alambrado (GHUNLPam 16250), 14 from Arroyo Calmu-Có (GHUNLPam 11093–11106), and nine from Cañadas Coloradas (GHUNLPam 16525–16533). All of the material was collected from the Loncoche Formation.

Description. Shell ovoid to trapezoidal and of medium size (Havg, 31.4 mm; Hmax, 40 mm; Lavg, 56.5 mm; Lmax, 66 mm; Wavg, 17.1 mm; Wmax, 22.2 mm); greatest height slightly in front of umbones (approximately 0.55 of total length from anterior end); umbones small and opisthogyrous; umbonal slit narrow and running posteriorly for about 0.2 of total height; interior of umbones split by mould left behind by buttress supporting chondrophores on both valves; chondrophores also preserved as moulds; anterior margin rounded to slightly truncate anteroventrally; posterior margin truncated; dorsal margin concave in front of and behind umbones; ventral margin straight to slightly concave; outer surface ornamented with weak commarginal ribs, defined better anteriorly.

Discussion. This taxon is represented by internal moulds, but a few specimens have some shell matter preserved. No shell interiors are

preserved, but the slit dividing the umbones, reflecting the presence of a subumbonal buttress, leaves no doubt as to its inclusion in the Anomalodesmata and more precisely in the Laternulidae. Bivalves of this family are known to occur in normal marine to somewhat restricted marine environments, and occur in Cretaceous rocks in different parts of the world. The specimens in our collections may be conspecific with those referred to as Myas [sic] by Groeber (1929, p. 38).

Localities. Ranquil-Có, El Alambrado, Arroyo Calmu-có, and Cañadas Coloradas, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation; Campanian–Maastrichtian.

Class Gastropoda Cuvier, 1797
Superfamily Cerithioidea Férussac, 1819
Family uncertain
Genus *Paleoanculosa* Parodiz, 1969

Type species. *Paleoanculosa patagonica* Parodiz, 1969; original designation.

Remarks. Parodiz (1969, pp. 123, 124) proposed *Paleoanculosa* for a group of extinct gastropods resembling "the living North American subquadrate species of Pleuroceridae". He designated as type species the Cretaceous (Palaeocene, according to Parodiz, 1969) *Paleoanculosa patagonica* Parodiz, 1969 (p. 124, pl. 14, figs. 3, 4), from Lenza Niyeu in northern Patagonia. His proposal of a new genus followed Doello-Jurado's (1927) belief that the fossil species of melaniids from Patagonia should be placed in a new genus. *Paleoanculosa* was included by Parodiz (1969) in the Pleuroceridae based on the similarity of the Patagonian species to some of the North American members of the family. Unfortunately, no soft body anatomical characters are reflected on the shell. In addition, many of the North American Pleuroceridae shows different shells. Therefore, the taxonomic placement of *Paleoanculosa* within Pleuroceridae appears to be unwarranted. However, this generic name has since been used extensively in the literature and, to avoid further confusion, we prefer to maintain its usage until an in-depth review of these fossil gastropods is undertaken, a task that is beyond the scope of this study.

Paleoanculosa macrochilinoides (Doello-Jurado, 1927)
Fig. 6A–F

1927 Gasterópodos: Wichmann, pp. 386, 387, pl. 11, fig. 75 (as *Melania macrochilinoides* Doello-Jurado, n. sp. in the figure captions) and fig. 77 (as *Melania pehuenchensis* Doello-Jurado, n. sp. in the figure captions)
1927 *Viviparus wichmanni* Doello-Jurado: Doello-Jurado, pp. 412, 413 (non pl. 11, figs. 72, 73)
1927 *Melania pehuenchensis*, n. sp.: Doello-Jurado, pp. 415, 416, pl. 11, fig. 77
1927 *Melania macrochilinoides*, n. sp.: Doello-Jurado, p. 416, pl. 11, fig. 75
1969 *Paleoanculosa patagonica* n. sp.: Parodiz, p. 124, pl. 14, figs. 3, 4
1969 *Paleoanculosa macrochilinoides* (Doello-Jurado): Parodiz, pp. 124, 125, pl. 14, fig. 5, pl. 15, fig. 11
1969 *Paleoanculosa bullia* (Ihering): Parodiz, pp. 125–128, pl. 12, figs. 7–9 (non pl. 14, fig. 2 and pl. 15, figs. 2–6)
1984 *Paleoanculosa patagonica* Parodiz: Manceñido and Damborenea, p. 440, pl. 3, fig. 18 only
1996 *Paleoanculosa patagonica* Parodiz: Parras, Casadío and Pires, p. 47
1996 *Paleoanculosa* n. sp.: Parras, Casadío and Pires, p. 47
1998 *Paleoanculosa* sp.: Parras, Casadío and Pires, p. 64

Material. 381 specimens. Of these, 43 come from Arroyo Brea (GHUNLPam 10078–10080, 10167–10206), 31 from Arroyo Loncoche (GHUNLPam 10000–10018, 10020–10031), seven from Ranquil-Có (GHUNLPam 15619–15625), 123 from Arroyo Calmu-Có (GHUNLPam 11107–11229), 32 from Bordo Alto del Payún (GHUNLPam 16534–16565) and 145 from Cañadas Coloradas (GHUNLPam 16366–16500, 16501–16510). All were collected from beds within the Loncoche Formation.

Description. Shell relatively large (Hmax, 33 mm; Havg, 22.4 mm; Wmax, 19 mm; Wavg, 13.7 mm; H/W, 1.63), outline subquadrate, anomphalous, last whorl about 0.8 of total height (HLWmax, 25 mm; HLWavg, 18.1 mm), with a shallow depression below shoulder and decidedly convex below that; aperture large (AHmax, 17 mm; AHavg, 12.2 mm; AWmax, 12 mm; AWavg, 8.1 mm; AH/AW, 1.51), angulate posteriorly and rounded anteriorly; columellar callus 1–1.5 mm wide; sutures well impressed; outer surface with sinuous and conspicuous growth lines; few very faint spirals on shoulder of some specimens.

Discussion. The first specimens of this species collected were those found by Wichmann in Lenza Niyeu, province of Río Negro. These were described by Doello-Jurado (1927, pp. 412, 413) and included in his *Viviparus wichmanni* Doello-Jurado, 1922 (original material from near General Roca). At the same time, Doello-Jurado (1927) described three species of *Melania*, i.e., *Melania ameghiniana* (pp. 413–415, pl. 10, figs. 61–71, pl. 11, fig. 74), *Melania pehuenchensis* (pp. 415, 416, pl. 11, fig. 77) and *Melania macrochilinoides* (p. 416, pl. 11, fig. 75).

Parodiz (1969, p. 124) described *Paleoanculosa patagonica* as new and designated it as the type species of *Paleoanculosa*. The type material of *P. patagonica* consists of the specimens of *Viviparus wichmanni* that were collected by Wichmann in Lenza Niyeu. Parodiz excluded from *P. patagonica*, the type specimens of *V. wichmanni*, which came from General Roca, also in the province of Río Negro. He did not include any additional material in his new species. At the same time, he (Parodiz 1969, pp. 124, 125) transferred *Melania macrochilinoides* to *Paleoanculosa*. He included in this species the holotype and only known specimen, originally illustrated by Doello-Jurado (pl. 11, fig. 75).

Manceñido and Damborenea (1984) realized that *Paleoanculosa macrochilinoides* differed from *P. patagonica* only by its larger size. However, as it was known only from the holotype, they did not synonymize the two species until the range of variation of *P. macrochilinoides* was properly assessed. The type locality of *P. macrochilinoides* is, according to Doello-Jurado (1927, p. 416), Puente Río Grande. However, Parodiz (1969, p. 125) stated that this was a mistake and that instead the type specimen was collected by Groeber at Cerro Bayo de la Esperanza, also in southern Mendoza (Groeber, 1939, p. 74). The holotype of *P. macrochilinoides* is a large specimen (38 mm high), but the shell outline and all other characters agree well with the rest of the specimens traditionally referred to *P. patagonica*.

A third species of *Paleoanculosa* described by Parodiz is *Paleoanculosa bullia* (Ihering, 1907). In this species he (Parodiz, 1969, pp. 125–128) included *Melania ameghiniana* and *M. pehuenchensis*. According to Parodiz (1969, p. 126), the type locality of *M. pehuenchensis* was also an error: it was not Camu-Có in southern Mendoza as stated by Doello-Jurado (1927, pp. 415, 416), but instead was Aguada de Trapalcó, in the province of Río Negro (according to the collector's label, Wichmann, fide Parodiz). The

Fig. 6. A–F, *Paleoanculosa macrochilinoides* (Doello-Jurado, 1927). A, B, GHUNLPam 11131. A, abapertural view. B, apertural view. C, GHUNLPam 11126, abapertural view. D, GHUNLPam 16387, apertural view. E, GHUNLPam 11132, apertural view. F, GHUNLPam16454, apertural view. G–L, *Paleoanculosa ameghiniana* (Doello-Jurado, 1927). G, GHUNLPam 10218, apertural view. H, GHUNLPam 10211, apertural view. I, J, GHUNLPam 15569. I, apertural view. J, abapertural view. K, L, GHUNLPam 16325. K, apertural view. L, abapertural view. M, Cerithioidea? indet., GHUNLPam 10315, impression. A–C and E from Arroyo Calmu-Có; D and F from Cañadas Coloradas; G and H from Cerro Butaló; I and J from Ranquil-Có; K and L from El Alambrado; M, from Puesto La Bebida. Scale bar represents 1 cm.

illustration of the only specimen available to Wichmann is similar in shape, size and ornamentation to *Paleoanculosa patagonica* and to our specimens; it does not resemble the type material of *P. bullia*.

Unfortunately, the type material of *Melania pehuenchensis* and *M. macrochilinoides* was not available for study. However, all available information (descriptions, illustrations and additional data) indicate that these two taxa are synonyms of *Paleoanculosa patagonica*, as already hinted at in part by Manceñido and Damborenea (1984). Therefore, we select *P. macrochilinoides* (Doello-Jurado, 1927) as the valid name. *Paleoanculosa macrochilinoides* can be separated from *Paleoanculosa ameghiniana* by its larger size, higher spire, and more conspicuous growth lines.

Localities. Arroyo Brea, Arroyo Loncoche, Ranquil-Có, Arroyo Calmu-Có, Bordo Alto del Payún, and Cañadas Coloradas, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation in the province of Mendoza and Allen and Coli-Toro formations in the province of Río Negro (Doello-Jurado, 1927; Parodiz, 1969; Manceñido and Damborenea, 1984); Campanian–Maastrichtian.

Paleoanculosa ameghiniana (Doello-Jurado, 1927)
Fig. 6G–L

1927 Gasterópodos: Wichmann, pp. 391, 392, pl. 10, figs. 61–71, pl. 11, fig. 74 (as *Melania ameghiniana* Doello-Jurado, n. sp. in the figure captions)
1927 *Melania ameghiniana*, n. sp.; Doello Jurado, pp. 413–415, pl. 10, figs. 61–71, pl. 11, fig. 74
1969 *Paleoanculosa bullia* (Ihering); Parodiz, pp. 125–128, pl. 14, fig. 2, pl. 15, figs. 2–6 (non pl. 12, figs. 7–9)
1969 *Actaeonina* sp.: Camacho, p. 222, fig. 1B
1984 *Paleoanculosa patagonica* Parodiz: Manceñido and Damborenea, p. 440, pl. 3, figs. 16 and 17 only
1984 *Paleoanculosa ameghiniana* (Doello Jurado): Manceñido and Damborenea, pp. 440, 441, pl. 3, figs. 19–21
1996 *Paleoanculosa bullia* (Ihering): Parras, Casadío and Pires, p. 47
1998 *Paleoanculosa bullia* (Ihering): Parras, Casadío and Pires, p. 64

Material. 454 specimens. Of these, 69 come from Puesto La Bebida (GHUNLPam 10317–10346, 10354–10356, 10361–10371, 10380–10387, 10396–10410, 10888, 10889), 46 from Cerro Butaló (GHUNLPam 10208–10253), 114 from Ranquil-Có (GHUNLPam 15400–15416, 15464–15476, 15517–15600), 152 from Malal Vaca (GHUNLPam 16094–16245) and 73 from El Alambrado (GHUNLPam 16293–16365). All were collected from the Loncoche Formation.

Description. Shell relatively small (Hmax, 24.4 mm; Havg, 16.9 mm; Wmax, 18 mm; Wavg, 10.6 mm, H/W, 1.59), anomphalous, with a conical outline; at least five weakly convex whorls; last whorl about 0.8 of total spire height (HLWmax, 20.5 mm; HLWavg, 13.4 mm); surface ornamentation of very fine, inconspicuous, sinuous growth lines; aperture small, elongate, base narrowly rounded (AHmax, 12.8 mm; AHavg, 8.8 mm; AWmax, 10 mm; AWavg, 6.4 mm; AH/AW, 1.38), with slightly thickened basal lip; columellar lip excavated.

Discussion. This species was originally described as *Melania ameghiniana* by Doello-Jurado (1927, pp. 413–415) based on several specimens collected by Wichmann in Aguada Trapalcó and Cabeza de Potro, province of Río Negro. Doello-Jurado distinguished these specimens from *Melania pehuenchensis* (=*Paleoanculosa macrochilinoides*) by its less globose shape, more convex last whorl, its narrower spire, narrower aperture and smaller average size.

Doello-Jurado (1927, p. 415) compared his species with *Melania bullia* Ihering, 1907 (p. 464, pl. 18, fig. 127), because Wichmann (1927, p. 403) had commented on the similarity of these two species. According to Doello-Jurado, they are quite distinct, based on the absence of columellar callus in *Melania bullia*, which was erected on the basis of one broken specimen in which the aperture is not adequately preserved for comparison.

Parodiz (1969, pp. 125–128) synonymized *Melania ameghiniana* with *M. bullia*, and transcribed Ihering's description of the latter. However, he did not have any additional material of *M. bullia* available for study other than Ihering's type. As correctly pointed out by Doello-Jurado (1927), further comparisons must necessarily be based on more and better material of this species. Until such material becomes available, we prefer to use the specific epithet *ameghiniana* for the material from Río Negro described by Doello-Jurado and for our material from southern Mendoza.

Localities. Puesto La Bebida, Cerro Butaló, Ranquil-Có, Malal Vaca and El Alambrado, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation in the province of Mendoza (this paper) and Allen Formation in the province of Río Negro (Doello-Jurado, 1927; Parodiz, 1969; Manceñido and Damborenea, 1984); Campanian–Maastrichtian.

Superfamily Cerithioidea?

Genus and species indet.
Fig. 6M

1996 *Potamides* sp.: Parras, Casadío and Pires, p. 47
1998 *Potamides*? sp.: Parras, Casadío and Pires, p. 64

Material. Six specimens from Puesto La Bebida (GHUNLPam 10315), collected from the Loncoche Formation.

Discussion. The six specimens available are flattened impressions of a small, very high-spired cerithioid-like gastropod that cannot be assigned presently to a family or genus. The specimens occur in a claystone at the base of the Loncoche Formation. They are too poorly preserved to be positively identified, but the shell outline is reminiscent of some of the many species of gastropods described by Bonarelli (1927) from the Maastrichtian Yacoraite Formation in northern Argentina and traditionally assigned to such genera as *Zygopleura* Koken, 1892, or *Katosira* Koken, 1892, and lately reassigned to *Bonarelliella* Cónsole Gonella, 2011, and *Percossmannella* Cónsole Gonella, 2011. However, better material is needed in order to provide adequate comparisons.

Locality. Puesto La Bebida, Malargüe Department, province of Mendoza.

Stratigraphic distribution and age. Loncoche Formation; Campanian–Maastrichtian.

5. Stratigraphic, taphonomic and palaeoecological features of the studied mollusc fauna

Molluscs from the Loncoche Formation include freshwater and restricted marine species. The total species diversity is relatively low, comprising six species of bivalves belonging to six different families, and three species of gastropods (Table 1). Some of the fossil-bearing beds also contain vertebrate remains. Among these

are fish, amphibians, and reptiles (Gonzáles Riga, 1999; Previtera and González Riga, 2008). Preservation of the mollusc shells varies, but they are generally represented by internal moulds; only a few specimens show any trace of shell material.

In the following sections we analyse the stratigraphic and geographic distribution of the species identified, the preservation of the specimens, and the general environmental requirements of extant members in each of the groups represented in the fauna.

5.1. Diplodon bodenbenderi *Doello-Jurado, 1927*, Pleiodon? *sp.*

Unionoida is mostly represented by *Diplodon bodenbenderi*, which is recorded from almost all of the localities studied (Table 1). All specimens of this species come from the lower and middle parts of the Loncoche Formation, between 33 and 123 m above the unconformity separating the Malargüe Group from the underlying Neuquén Group (Fig. 2). The specimen identified as *Pleiodon*? sp. comes from Bordo Alto del Payún, in a bed 34 m above the underlying Neuquén Group (Table 1, Fig. 2).

Most of the specimens of Unionoidea are represented by internal moulds; only 5% (from Arroy Brea, El Alambrado and Cerro Butaló) have preserved shell-matter attached to the moulds. Orientation of the specimens is generally chaotic, except in one bed in the section at Ranquil-Có in which the specimens lie parallel to bedding-plane. Dissolution is almost complete. Fragmentation is low and in the specimens with preserved shells abrasion is low, and encrustation and bioerosion are absent. In the sections located in the more northern area (Puesto La Bebida, Arroyo Brea and Cerro Butaló; Table 1, Figs. 1, 2) specimens are preserved in a massive or planar-stratified fine- to coarse-grained sandstone; they also occur in massive packstones and grainstones. The associated fauna includes *Paleoanculosa ameghiniana*, *P. macrochilinoides* and vertebrate remains (Chelidae plates and fish bones). In the sections further south (Ranquil-Có, El Alambrado, Arroyo Calmu-Có, Bordo Alto del Payún, and Cañadas Coloradas; Table 1, Figs. 1, 2) the specimens occur in medium- to coarse-grained sandstones and packstones, both massive or with trough-cross stratification. These beds sometimes appear as channel deposits with erosional bases and carry intraclasts of the underlying beds. The associated fauna includes *Isognomon*? *mechanquilensis*, Mactridae? indet., *Panopea*? sp., *Laternula* sp., *Paleoanculosa ameghiniana* and *P. macrochilinoides*, together with coprolites and remains of fishes, amphibians and reptiles.

The recent species of the bivalve Order Unionoida, colloquially known as freshwater mussels, pearly mussels or nayades, are conspicuous inhabitants of rivers and lakes (Graf and Cummings, 2007). Adult freshwater mussels are sedentary, infaunal filter-feeders, and they disperse mainly by means of a larval stage (glochidium) which is a parasite of fish gills. More rarely, they can be also transported from one waterbody to another adhering to the feet of birds (Morgan, 1982). These two dispersal modes allow them to form new populations in a relatively short time.

5.2. Isognomon? mechanquilensis *(Camacho, 1969), Mactridae? indet.,* Panopea? *sp.,* Laternula *sp.*

All of these species were recorded from the base of the Loncoche Formation, between 15 and 102 m above its contact with the underlying Neuquén Group (Fig. 2). They are present only in the sections located south of 36°S (Fig. 1, Table 1). Specimens of *Isognomon*? *mechanquilensis* appear chaotically oriented, generally disarticulated and sometimes fragmented; only 8% of bivalved specimens were available. Abrasion is moderate and encrustation and bioerosion are absent. Specimens of Mactridae? indet. are all poorly preserved internal moulds, while *Panopea*? sp. is represented by small specimens with preserved shell attached. *Laternula* sp. is represented only by internal moulds of bivalved shells, some still showing vestiges of shell matter. In the case of the mactrids, *Panopea*? sp. and *Laternula* sp. orientation is also chaotic, and whenever shells are preserved they do not show signs of abrasion, bioerosion or encrustation. All specimens are preserved either in medium- to coarse-grained sandstones that may be massive or with planar or trough-cross stratification, or in massive or trough-cross stratified packstones. At some localities (e.g., Bordo Alto del Payún) the fossil-bearing sandstone shows a channelled base and silty intraclasts. The associated fauna includes *Diplodon bodenbenderi*, *Pleiodon*? sp., *Paleoanculosa ameghiniana*, *P. macrochilinoides* and vertebrate remains.

Isognomon is represented currently by species inhabiting shallow marine to marginal marine environments in which salinity fluctuates, such as lagoons, estuaries, and mangroves in tropical to subtropical regions (Yonge, 1968; Stanley, 1970). Mactrids are also a group of bivalves that tolerate low salinities and may live in the outer areas of estuaries (Aguirre, 1994). The species of Mactridae currently inhabiting the Patagonian coast live in sandy and muddy bottoms in the intertidal to shallow subtidal zone in large protected beaches of gulfs or bays (Signorelli and Pastorino, 2011). *Laternula* includes species that also live in brackish water (Prezant et al., 2008).

5.3. Paleoanculosa macrochilinoides *(Doello-Jurado, 1927),* Paleoanculosa ameghiniana *(Doello-Jurado, 1927)*

Specimens of these two species are preserved either as internal moulds or calcite shell replacements. They were recorded at all localities (Table 1) within the lower and middle parts of the Loncoche Formation, between 22 and 123 m above the underlying Neuquén Group (Fig. 2). They occur either in medium- to coarse-grained sandstones that may be massive, planar stratified, planar-cross stratified or trough-cross stratified, or else in massive or trough-cross stratified packstones and grainstones. *Paleoanculosa ameghiniana* also occurs in fine-grained laminated sandstones. At the southernmost localities (Cañadas Coloradas, Arroyo Calmu-Có and Bordo Alto del Payún) the sandstones contain silty intraclasts and show channelled bases. These gastropods occur together with *Diplodon bodenbenderi*, *Isognomon*? *mechanquilensis*, *Laternula* sp. and vertebrate remains. At Bordo Alto del Payún they are also recorded with *Pleiodon*? sp. and Mactridae? indet. and at El Alambrado they co-occur with *Panopea*? sp.

The palaeoecological requirements of *Paleoanculosa* cannot be inferred from analogy with any extant group. Parodiz (1969) included this genus in the Family Pleuroceridae, a group living today only in eastern North America. This affinity was apparently based on shells resemblance. However, the simple shell of pleurocerids and *Paleoanculosa* are so generalized and devoid of distinctive features that they may easily be mistaken for shells of other unrelated groups if soft anatomy is not available. Because of this, the inclusion of *Paleoanculosa* in Pleuroceridae is unwarranted; hence, no palaeoenvironmental requirement drawn on the basis of such a taxonomic placement can be supported. The presence of *Paleoanculosa* in Upper Cretaceous rocks in southern South America has generally been considered to indicate freshwater to brackish environmental settings for the deposition of the sediments that formed these rocks (e.g., Parras et al., 1996; Salgado et al., 2007). However, this line of argument cannot be sustained any longer. Other evidence in these rocks, fossil or sedimentological, has to be used to infer the palaeoenvironmental requirements of *Paleoanculosa*. The fauna with which it is generally associated includes either freshwater (Unionoidea) or restricted marine (e.g., *Isgnomon*? *mechanquilensis*, *Laternula* sp.) groups, or both, for which ecological requirements are well-known on the basis of the ecological requirements of modern analogues.

5.4. Cerithioidea? indet.

The specimens of cerithioid-like gastropods come from the base of the Loncoche Formation at Puesto La Bebida. The deposits in which they were found consist of finely laminated claystones and siltstones, with a few intercalations of fine sandstone. These are between 3 and 7 m above the contact with the underlying Neuquén Group (Fig. 2). They also contain vertebrate remains. The material remains unidentified and its affinity with the species common in the Maastrichtian Yacoraite Formation requires confirmation.

6. Discussion and conclusions

The invertebrate macrofauna from the Loncoche Formation at the localities studied includes bivalves and gastropods. The latter are dominant not in number of species but in number of specimens. Most of the molluscs occur as internal moulds, chaotically oriented in medium- to coarse-grained sandstones, which may be massive or with planar stratification, planar-cross stratification, or trough-cross stratification. Fragmentation and abrasion are generally low and encrustation and bioerosion are absent. Disarticulation is high only in *Isognomon*? *mechanquilensis*. Dissolution is the dominant taphonomic process for most of the species identified.

The overall sedimentologic and taphonomic signatures suggest the existence of moderate- to high-energy conditions of deposition with lateral transport for most of the localities. One exception is the very fine-grained, laminated beds with cerithioid-like gastropods at the base of the formation at Puesto La Bebida. These beds probably reflect a low-energy setting. However, the degree of time-averaging may be considered moderate to low; most specimens were probably buried relatively soon after death and remained articulated. The taxon with the highest taphonomic index is *Isognomon*? *mechanquilensis*, because the disarticulated condition of most of the specimens indicates that transport of the shells was significant prior to burial.

Molluscs contained in the Loncoche Formation can be classified in two distinct groups according to their ecological requirements: (1) an exclusively freshwater group including *Diplodon bodenbenderi* and *Pleiodon*? sp., which appear together with *Paleoanculosa* spp., and (2) a group of restricted marine taxa such as *Isognomon*? *mechanquilensis*, Mactridae? indet., *Panopea*? sp. and *Laternula* sp., which also occur with unionids and *Paleanculosa* species in the same beds.

Documentation of the distribution of the different taxa in the localities examined has revealed that sections located north of latitude 36°S (Fig. 1) contain low diversity assemblages with *Diplodon bodenbenderi*, *Paleoanculosa ameghiniana*, *P. macrochilinoides*, and cerithioid-like gastropods. This array is dominated by mussels, which are restricted to freshwater environments such as lakes and rivers (Graf and Cummings, 2007), and by *Paleoanculosa*. The habitats represented are rivers and lakes or ponds possibly associated with deltaic or estuarine complexes probably free of marine influence allowing the maintenance of limnic conditions.

Sections to the south of 36°S (Fig. 1) contain assemblages of *Diplodon bodenbenderi*, *Pleiodon*? sp., *Isognomon*? *mechanquilensis*, Mactridae? indet., *Panopea*? sp., *Laternula* sp. and the gastropods *Paleoanculosa ameghiniana* and *P. macrochilinoides*. This mixture of freshwater and restricted marine taxa is dominated by *Paleoanculosa*. Second in importance is *Isognomon*? *mechanquilensis*, the genus being an indicator of brackish to restricted-marine environments (Yonge, 1968; Stanley, 1970). This mixture is difficult to explain if the water-body in which the fauna lived was under constant or frequent marine influence, because it includes strictly freshwater elements and most of the specimens are either autochthonous or parautochthonous (having undergone little transport prior to burial). It may be attributed to occasional storm events that introduced marine taxa into adjacent non-marine water-bodies as has been reported for the Cretaceous Mata Amarilla fauna in southern Santa Cruz Province (Griffin and Varela, 2012).

Thus, the lower and middle parts of the Loncoche Formation contain species associated with more saline environments towards the south of the area studied (south of 36°S). The presence of restricted marine molluscs in the southernmost sections, might indicate sporadic marine influence of the Atlantic Ocean during deposition of the lower and middle parts of the formation in this region.

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