Available online at www.sciencedirect.com
ScienceDirect
Palaeogeography, Palaeoclimatology, Palaeoecology 250 (2007) 68 – 88
PALAEO
www.elsevier.com/locate/palaeo

Early Jurassic shell beds from marginal marine environments in southern Mendoza, Argentina

S.E. Damborenea [a,*], S. Lanés [b]

[a] *Departamento Paleontología Invertebrados, Museo de Ciencias Naturales La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina*
[b] *Av. Estado de Israel 4740, 3er. piso dto. 9, 1185 Buenos Aires, Argentina*

Received 28 October 2006; received in revised form 14 February 2007; accepted 3 March 2007

Abstract

External estuarine facies in Late Sinemurian beds from the base of the Puesto Araya Formation in the Atuel river region, Mendoza Province, Argentina, contain concentrations of a new species of *Cardinioides* (a shallow burrowing suspension-feeding Pachycardiidae bivalve) and a low diversity benthic fauna. These bivalves appear in tidal inlet facies of a wave-dominated estuary (environment similar to lagoon-barrier island systems), forming bioclastic lags at the channel bases. The taphonomic attributes (such as shell articulation, degree of fragmentation and abrasion, bioclast size, orientation) change from North to South, from monospecific concentrations of nearly complete large *Cardinioides* shells with low degree of fragmentation and abrasion, through beds with smaller *Cardinioides* shells associated with a few bivalves from marine environments, to only isolated fragmented specimens associated with a fully marine biota including not only other bivalves but also brachiopods and ammonoids. This, together with different palaeoecologic, sedimentologic and stratigraphic attributes at the studied localities are evidence of southwards changing environmental conditions from marginal marine (brackish) to fully marine on the eastern margin of the Neuquén basin at that time. From detailed analysis of taphonomic features, size distribution of shells, and the associated fauna at the different localities, the new species is regarded as a brackish water endemic, possibly a low salinity euryhaline species, which inhabited well oxygenated waters. Salinity, turbulence levels and food supply were the main limiting factors in the distribution of the species.

Keywords: Sinemurian; Neuquén Basin; Argentina; Marginal marine environment; Estuary; Bivalvia, *Cardinioides*

1. Introduction

Marginal marine environments comprise a variety of settings, such as estuaries, deltas, lagoons and tidal flats, which are characterised by frequent fluctuations in salinity levels. In such environments, bivalves, and particularly shallow burrowing infaunal suspension feeders, are usually the dominant macrofauna. Another feature shared by marginal marine faunas is the contrast between the low species richness *versus* the great individual abundance.

Jurassic marginal marine environments and their faunas are known from many places around the world, most of them from the northern hemisphere. The better known examples are from the Hettangian of Germany (Huckriede, 1967) and France (Freneix and Cubaynes, 1984); Hettangian, Pliensbachian and Bajocian of Japan (Sugawara and Kondo, 2004; Kondo et al., 2006);

---

* Corresponding author. Tel./fax: +54 221 4721676.
E-mail addresses: sdambore@fcnym.unlp.edu.ar (S.E. Damborenea), lucero_sil@yahoo.com.ar (S. Lanés).

0031-0182/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2007.03.002

Bathonian of Scotland (Hudson, 1963a,b; Tan and Hudson, 1974; Hudson, 1980; Andrews and Walton, 1990; Hudson et al., 1995), France (Fürsich et al., 1995) and Morocco (Mongin, 1967); Late Jurassic of Germany (Huckriede, 1967) and Portugal (Fürsich et al., 1980; Fürsich, 1981; Fürsich and Werner, 1984, 1986), and Latest Jurassic–Early Cretaceous of England (Morter, 1984) and Tanzania (Aberhan et al., 2002). Although a number of salinity-controlled mollusc assemblages have been pointed out in Aberhan's model (1993, 1994b) for the South American Jurassic and Cretaceous, none has been reported from Sinemurian beds.

The Neuquén Basin is a Mesozoic back-arc basin placed in the western convergent margin of the South American Plate (Legarreta and Gulisano, 1989) attributed to the extension that fragmented Gondwana and opened the South Atlantic Ocean (Uliana and Biddle, 1988). Its infill exceeds 6000 m of marine and non-marine sedimentary rocks (epiclastics, carbonates, evaporites and volcaniclastics) of Late Triassic to Eocene age (Riccardi et al., 1988; Legarreta and Gulisano, 1989; Riccardi et al., 1991; Gulisano and Gutiérrez Pleimling, 1994; Riccardi et al., 1997, 2004). The study area is located to the North of the so-called "Neuquén embayment" of the basin, in one of the original depocenters of the first rifting episode, where a wave-dominated estuary developed during Sinemurian times (Lanés, 2002, 2005).

Marine Early Jurassic bivalves from the Neuquén Basin are relatively well-known from Argentina and Chile (Damborenea, 1987a,b, 1993; Aberhan, 1994a; Damborenea, 2002; Damborenea and Manceñido, 2005), but no species restricted to marginal marine deposits has been described so far. A new species of Pachycardiidae (see Appendix A), a mainly Mesozoic family that comprises conspicuously euryhaline genera ranging from brackish to marine, even freshwater habitats (Cox et al., 1969), has been found in early Jurassic beds of the upper Atuel river area, Mendoza Province, Argentina (Damborenea and Lanés, 2003; Lanés, 2005; Damborenea and Manceñido, 2005; Fig. 1). Excellently preserved representatives of this species are locally very abundant in the north-eastern sections here considered (Codo del Blanco, La Horqueta), where they form densely packed shell beds suggestive of stressful conditions. Litho-, tapho- and biofacies analysis of these deposits indicate a marginal marine setting (Lanés, 2002, 2005; Damborenea and Manceñido, 2005). The purpose of this paper is to provide a detailed analysis of these beds using an integrated sedimentological and palaeoecological approach, including faunal composition and species richness, shell morphology and taphonomy.

2. Materials and methods

Several stratigraphic sections were measured and their geometry, lithology, sedimentary structures and fauna were used to recognise the contemporaneous depositional systems and to propose a tectosedimentary interpretation of this part of the Neuquén Basin (Lanés, 2002, 2005), which is supported by stratigraphic correlations provided by ammonites and other invertebrates (Riccardi et al., 1991, 1993; Riccardi and Iglesia Llanos, 1999; Riccardi et al., 2000, 2004). Three of these sections contain *Cardinioides* beds and are referred to here: La Horqueta, logged by S. Lanés in 2003 (Fig. 2A; Lanés et al., in press, Fig. 2), Las Chilcas, logged by S. Damborenea and M. Manceñido in 1986 (Damborenea, 2004, Fig. 1; Lanés, 2005, Fig. 6; Lanés et al., in press, Fig. 2) and Codo del Blanco, logged by S. Lanés in 2000 (Lanés, 2005, Fig. 7; Lanés et al., in press, Fig. 2). *Cardinioides* beds were very recently found also at the western margin of Las Chilcas creek.

The fossil material described here was collected by the authors and colleagues during several field trips. Fossil specimens are housed in the collections of the Invertebrate Palaeontology Department at Museo de Ciencias Naturales La Plata, Argentina (MLP). Qualitative macroinvertebrate data were obtained in the field, together with relevant taphonomic observations (such as shell articulation, degree of fragmentation and abrasion, bioclast size, orientation, encrustation and bioerosion). Descriptions of the taphonomic features follow the semi-quantitative criteria published by Kidwell (1991) and Kidwell and Holland (1991). The systematic, palaeoecologic and palaeobiogeographic analysis forms part of a comprehensive research programme on Early Jurassic bivalves from Argentina (S.D.).

3. Geological setting

The Neuquén basin originated from a series of unconnected asymmetric north–south trending halfgrabens (Riccardi, 1983; Uliana and Biddle, 1988; Manceda and Figueroa, 1993, 1995; Vergani et al., 1995; Tankard et al., 1995) after the first rifting occurred during the Middle Triassic–Sinemurian (Ramos, 1992; Manceda and Figueroa, 1995), when non-marine siliciclastics and volcanics filled the unconnected halfgrabens at the basin margins while the basin center was rapidly transgressed by nearshore sandstones and offshore shales (Legarreta and Gulisano, 1989). The former topography of faulted blocks led to a partial synchroneity between the non-marine and marine transgressive successions and locally controlled the precise start of the transgression (Gulisano, 1981).

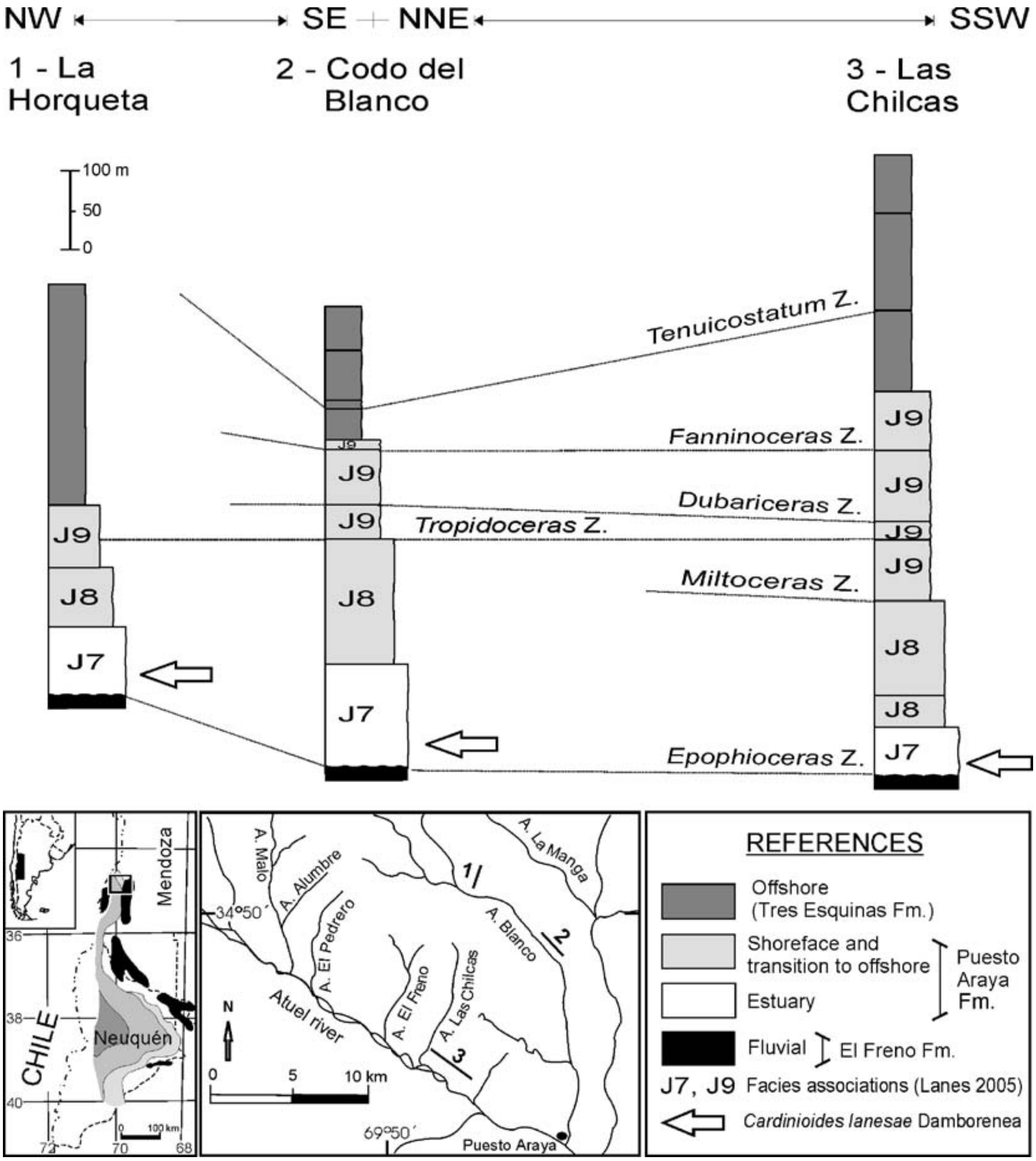


Fig. 1. Location map within the Neuquén Basin (palaeogeographic map for Hettangian–Early Pliensbachian simplified from Legarreta and Uliana, 2000) and general stratigraphic sections at the three main localities, levelled to the base of the *Tropidoceras* Zone, showing the distribution of broad facies associations, data from S. Lanés. Arrows point to beds containing *Cardinioides lanesae* Damborenea. See Table 1 for the local zonation.

The study area (S 34°39′ to 34°56′; W 69°41′ to 69°54′, Fig. 1) lies in the northern margin of the Atuel river valley, northern Neuquén Basin, in the Atuel–Valenciana halfgraben (Manceda and Figueroa, 1995), one of the initial depocenters of the first rifting episode. Here the transgression began in the Late Triassic (Riccardi et al., 1997, 2004) though most of the basin was transgressed later, during the Latest Sinemurian to Early Pliensbachian (Damborenea, 2002), when the unconnected halfgrabens coalesced due to the combined regional sag and eustatic sea level rise (Legarreta et al., 1993). In the study area the well-bedded transgressive succession comprises two units (Table 1). The basal one is a coarsening- and thickening-upwards succession of fan delta shales, sandstones and minor conglomerates of Rhaetian to Late Early Sinemurian age, outcropping only at the western localities of Malo and El Pedrero creeks (Arroyo Malo Formation and lower Puesto Araya Formation, synrift phase). The top unit (Late Early Sinemurian–Toarcian) is a fining- and thinning-upwards

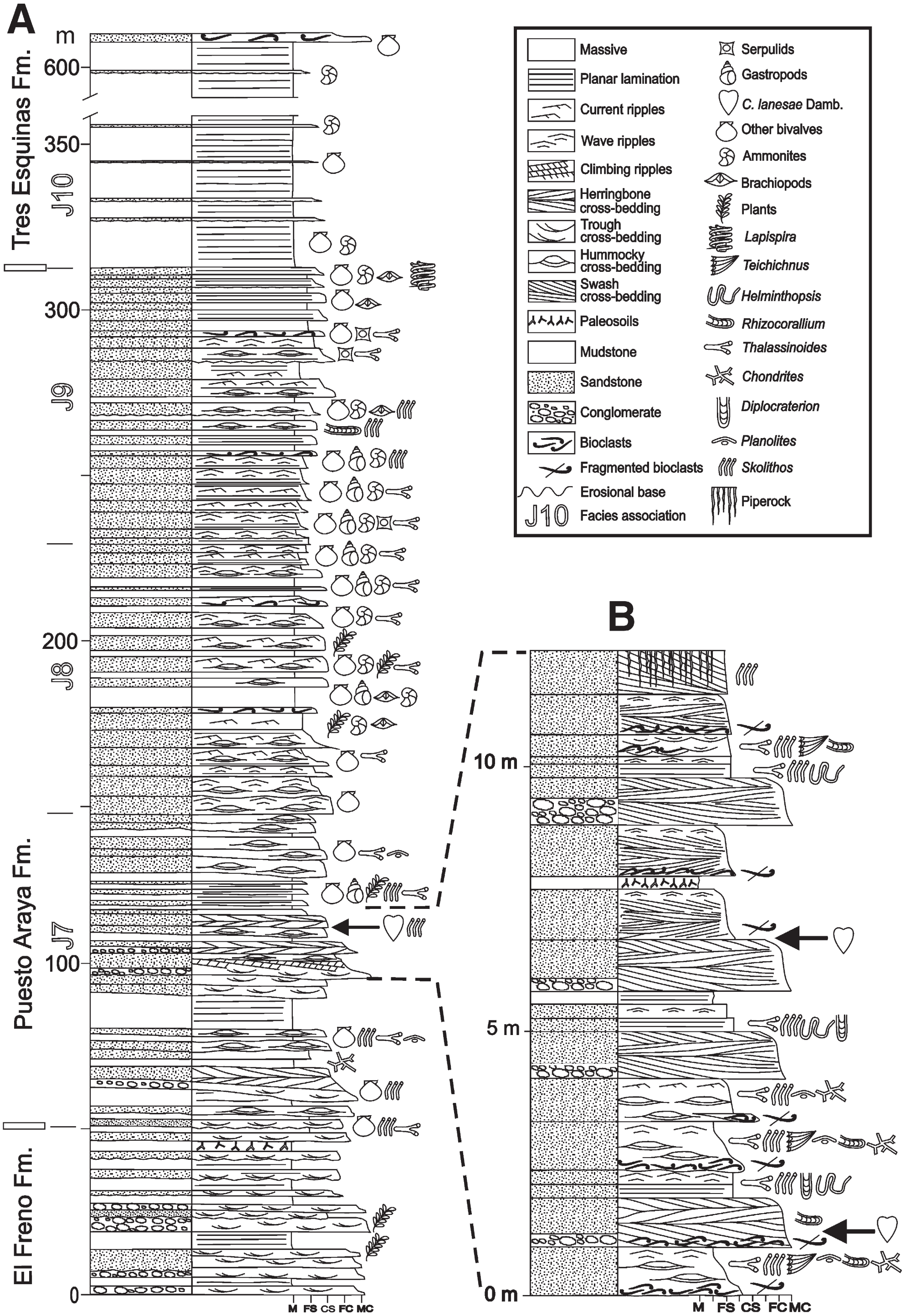
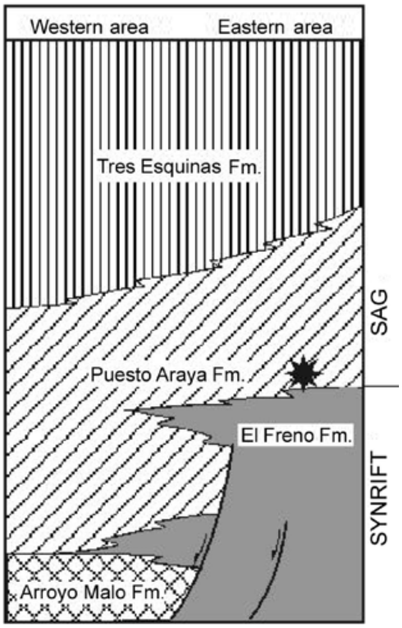


Fig. 2. A: Simplified section of the Early Sinemurian–Toarcian cycle in La Horqueta, data from S. Lanés. J7, J8, J9 and J10: facies associations of Fig. 1. B: Close-up of facies association J7, arrows point to *Cardinioides lanesae* shell-lags (hosted in taphofacies LC2 in Lanés, 2002).

succession of sandstones and shales. According to Lanés (2002) these were deposited in a wave-dominated estuary and a deepening-upwards storm-dominated shelf, showing a retrogradational pattern and a wider depositional area (upper Puesto Araya Formation, sag phase).

Table 1
Local biostratigraphic framework (adapted from Riccardi et al., 2000) and general stratigraphic arrangement of early Jurassic lithostratigraphic units in western and eastern areas of the Atuel river region (modified from Lanés, 2002; Bechis et al., 2005)

Stage	Ammonites		Bivalves	Brachiopods
Toarcian	*Dumortieria*		*Meleagrinella* ⇧	*Rhynchonelloidea* cf. *ruthenensis* ⇧
	Phlyseogrammoceras tenuicostatum			
	Phymatoceras		*Parvamussium* cf. *pumilum*	*Prionorhynchia*? cf. *rubrisaxensis*
	Collina chilensis			*Rhynchonelloidea lamberti*
	Peronoceras pacificum			
	Peronoceras largaense			
	Dactylioceras hoelderi			
	Tenuicostatum		*Posidonotis cancellata*	
Pliensbachian	*Fanninoceras*	*disciforme*	*Radulonectites sosneadoensis*	*Rhynchonelloidea cuyana*
		fannini		*Rhynchonelloidea burckhardti*
		behrendseni	*Otapiria neuquensis*	
	Dubariceras			
	Tropidoceras			
	Miltoceras			
Sinemurian	*Epophioceras*		*Cardinia* cf. *listen*	*Gibbirhynchia dereki*
	?		*Otapiria pacifica*	
	"Agassiceras"			
Hettangian	*"Vermiceras"*			
	Badouxia canadensis			*Furcirhynchia* cf. *trechmanni*
	"Waehneroceras-Schlotheimia"		*Palmoxytoma* cf. *cygnipes*	
	"Psiloceras"			
	Psiloceras rectocostatum			
	?			



The western area comprises the Arroyo Malo and El Pedrero creeks, see map in Fig. 1. The asterisk marks the position of the beds described in this paper.

Considering the Upper Triassic–Lower Jurassic transgressive succession of the study area as a whole, it shows an abrupt eastwards lateral change of facies and age (Riccardi et al., 1988, 1991; Reijenstein, 1967). In particular, its base becomes younger eastwards from Late Triassic at Malo creek (Riccardi et al., 1997) to Late Early Sinemurian at Las Chilcas creek (Riccardi et al., 1988, 1991) and Early Pliensbachian at Puesto Araya (type locality, Fig. 1). Simultaneously the marine fine-grained siliciclastics coarsen and the underlying fluvial conglomerates become thicker and coarser eastwards. These trends and the areal distribution of contemporaneous depositional systems show the influence of two ancient normal faults located near the present Alumbre and El Freno creeks (Fig. 1), which limited several faulted blocks downstepping westwards and northwards (Lanés, 2002, 2005; Giambiagi et al., 2005; Bechis et al., 2005; Table 1 here).

The bivalves reported here (*Cardinioides lanesae* Damborenea n. sp., see Appendix A) appear only in the estuarine deposits (facies association J7, Figs. 1 and 2A–B; lithofacies Stb and taphofacies LC2 in Lanés, 2005). The interpreted estuary at the study area is of the wave-dominated type (Dalrymple et al., 1992) with types and distribution pattern of facies that resemble those of lagoon-barrier island systems. It includes deposits of multiepisodic tidal inlets, subtidal sand waves, minor washover fans, shales of the central lagoon together with sandstones and amalgamated tempestites deposited above fair-weather wave-base (Lanés, 2002, 2005). Among the three studied localities (Las Chilcas, Codo del Blanco and La Horqueta sections) a preferential distribution of the estuarine facies exists with lagoonal shales and washover fan deposits developed in La Horqueta and Codo del Blanco sections but lacking in Las Chilcas section; while fair-weather wave and storm deposits of the outer estuary sandy complex predominate in the Codo del Blanco section. Evidence from detailed biostratigraphic correlation and facies distribution of the contemporaneous depositional systems supports an estuary opening to the north and west, dipping gently northwards.

Beds containing *C. lanesae* (Figs. 1 and 2) are Late Sinemurian in age, corresponding to the *Epophioceras* Zone of the local ammonite zonation, and the approximately equivalent *Cardinia* cf. *listeri* faunule and *Gibbirhynchia dereki* Zone of the local bivalve and brachiopod zonations (Table 1; Riccardi et al., 2000).

4. Taphonomy

C. lanesae is found in the lower part of the Puesto Araya Formation forming basal shelly lags in the tidal inlet deposits, but showing different palaeoecologic, taphonomic and sedimentologic attributes among the three localities, as is shown below (see also Table 2, Fig. 3).

These shell lags are lensoidal, with erosive bases and gradational tops, up to 20 m wide and up to 0.5 m thick but showing different dimensions among the sections (Table 2). They are always placed at the base of medium-grained sandstone lenses with herringbone trough-cross bedding successively overlain by planar lamination, parting lineation and swash cross-stratification at the top (Fig. 4B and C), which were interpreted as tidal inlet fillings of the outer part of a wave-dominated estuary (Lanés, 2002, 2005, see Fig. 2B here). Lensoidal shell lags have simple organization appearing as massive or normally graded shell beds, with a varying packing density ranging from dense to dispersed (bioclast- to matrix-supported, respectively). They also show different degrees of articulation, fragmentation and abrasion among the different localities. Incrustation is almost absent, only occurring in some specimens in the Las Chilcas section. Variation of the taphonomic features amongst the studied localities is detailed below.

1. At La Horqueta section (Figs. 2 and 4A) *Cardinioides* specimens form almost monospecific (monotypic *sensu* Kidwell et al., 1986) bioclast-supported, normally graded shell lenses, 0.3 to 0.5 m thick and

Table 2
Palaeoecologic, sedimentologic, taphonomic and stratigraphic features of the *Cardinioides* beds at the three localities (criteria modified from Kidwell, 1991)

Features		La Horqueta	Codo del Blanco	Las Chilcas
Palaeoecologic	Taxonomic composition (see also Table 3)	*Cardinioides lanesae, Gervillella araucana* and oysters	*Cardinioides lanesae*, a few bivalves and *Spiriferina*	*Cardinioides lanesae*, stenohaline bivalves, brachiopods, ammonoids, gastropods
	Life habits	Shallow burrowers, epibyssate and cemented forms	Shallow and deep burrowers, cemented, epibyssate and reclining forms	Shallow and deep burrowers, cemented, reclining, epibyssate, endobyssate, nektobenthic forms
	Trophic groups	Suspension feeders	Suspension feeders	Suspension feeders, carnivores, herbivores
	Age spectrum	Complete	Complete	Complete
Sedimentologic	Matrix	Fine-grained sand, scarce	Fine- to medium-grained sand	Fine- to medium-grained sand
	Hydraulic behaviour of matrix	More mobile than shells	More mobile than shells	More mobile than shells
	Shell packing	Dense, bioclast-supported	Dense, bioclast-supported	Bioclasts dispersed, matrix-supported
	Matrix size sorting	Good	Moderate	Moderate
	Associated structures	Grading	Grading	Massive
Taphonomic	Articulation	High	Medium	Low
	Fragmentation	Low	Moderate	High
	Orientation (on plane)	None	None	None
	Orientation (on section)	Concordant, sometimes in life position	Convex-up or -down shells, sometimes nested	Convex-up or -down, edgewise shells
	Abrasion	Low	Low	High
	Encrustation	Absent	Absent	Present
	Bioerosion	Absent	Absent	Present
	Shell size	Large	Medium to small	Small
	Bioclast size sorting	Poor	Poor	Poor
Stratigraphic	Thickness	0.3 to 0.5 m	Up to 0.35 m	Up to 0.3 m
	Lateral extension	15 to 20 m	5 to 20 m	5 to 10 m
	Geometry	Lenses	Lenses	Lenses
	Stratigraphic contacts	Erosional base, gradational top	Erosional base, gradational top	Erosional base, gradational top
	Internal complexity	Simple (graded)	Simple (graded)	None (homogeneous)
	Host lithofacies	Lenses of herringbone cross-bedded, medium-grained sandstones where the shell beds drape the base	Lenses of herringbone cross-bedded, medium-grained sandstones where the shell beds drape the base	Lenses of herringbone cross-bedded, medium-grained sandstones where the shell beds drape the base

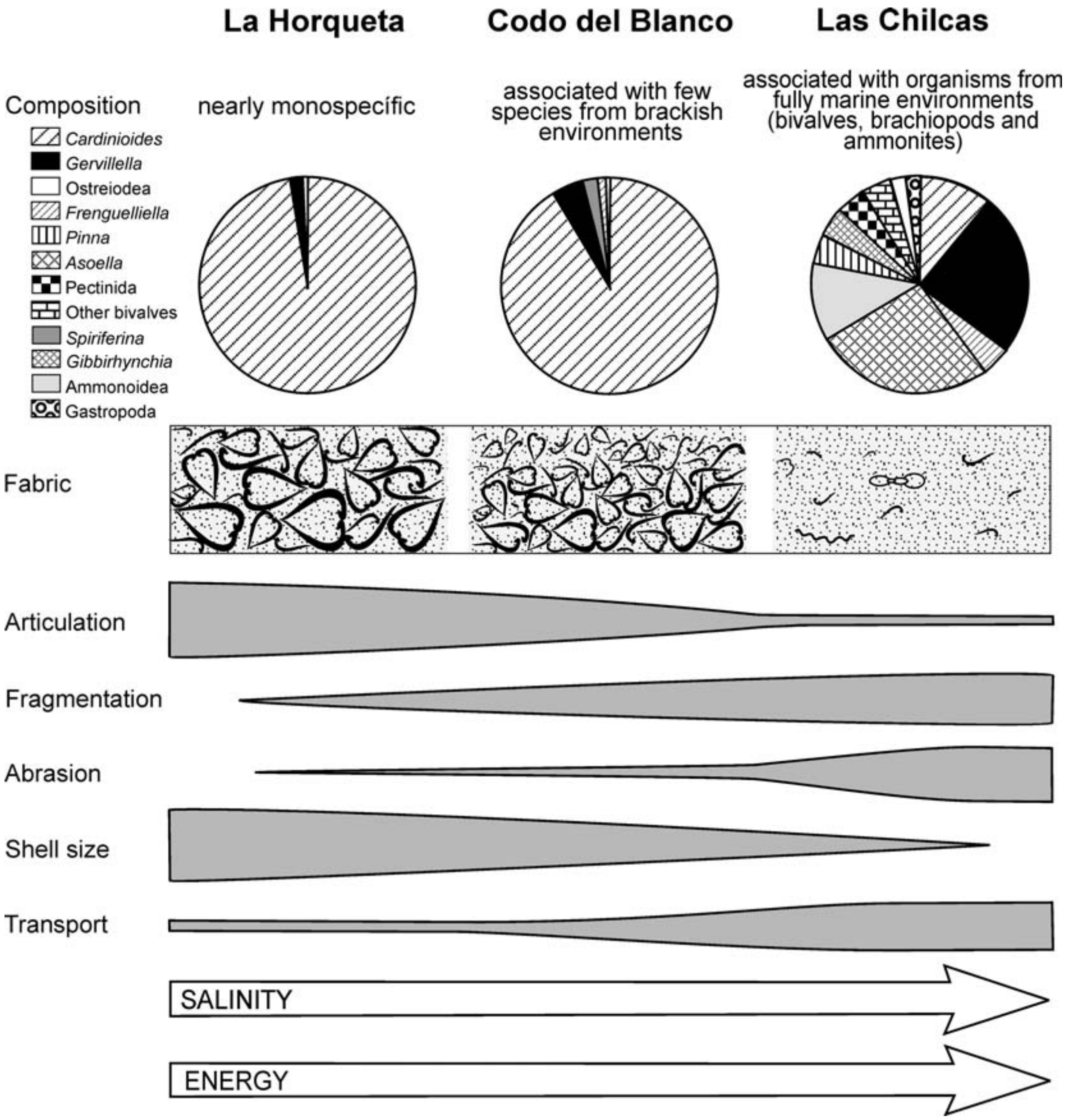


Fig. 3. Diagram summarising some of the palaeoecological, taphonomic, and sedimentologic features of *Cardinioides* beds at the three localities, and the inferred possible relations with energy and salinity levels. The faunal composition is given at generic level in the pie diagrams (percentage of specimens). See Table 3 for complete species list.

15 to 20 m wide. They are exclusively composed of *C. lanesae* that are usually articulated and with low levels of fragmentation and abrasion, and with poor size-sorting. In addition, locally one can find scarce complete valves of *Gervillella araucana* Damborenea and a few shell fragments possibly belonging to an ostreoid bivalve (Table 3A, Fig. 4A). Shells are randomly oriented, laying concordant (either convex-up or -down) and are poorly size-sorted, ranging between 20 and 74 mm (Fig. 5). The biofabric is densely-packed, the very scarce fine-sandy matrix is also graded, becoming siltier towards the top.

2. *Cardinioides*-shell beds at Codo del Blanco (Fig. 4B–D) consist of several nearly monospecific bioclast-supported shell lenses up to 0.35 m thick and 5 to 20 m wide, made up of medium- to small-sized *C. lanesae*, sometimes articulated, moderately fragmented and unabraded occurring together with a few euryhaline bivalves (Table 3B). *Cardinioides* shells are both articulated and disarticulated but mostly complete, poorly size-sorted, and ranging from 8 to 45 mm long (Fig. 5). Articulated shells are not current-oriented, usually concordant to bedding, and are seldom oriented with the commissural plane

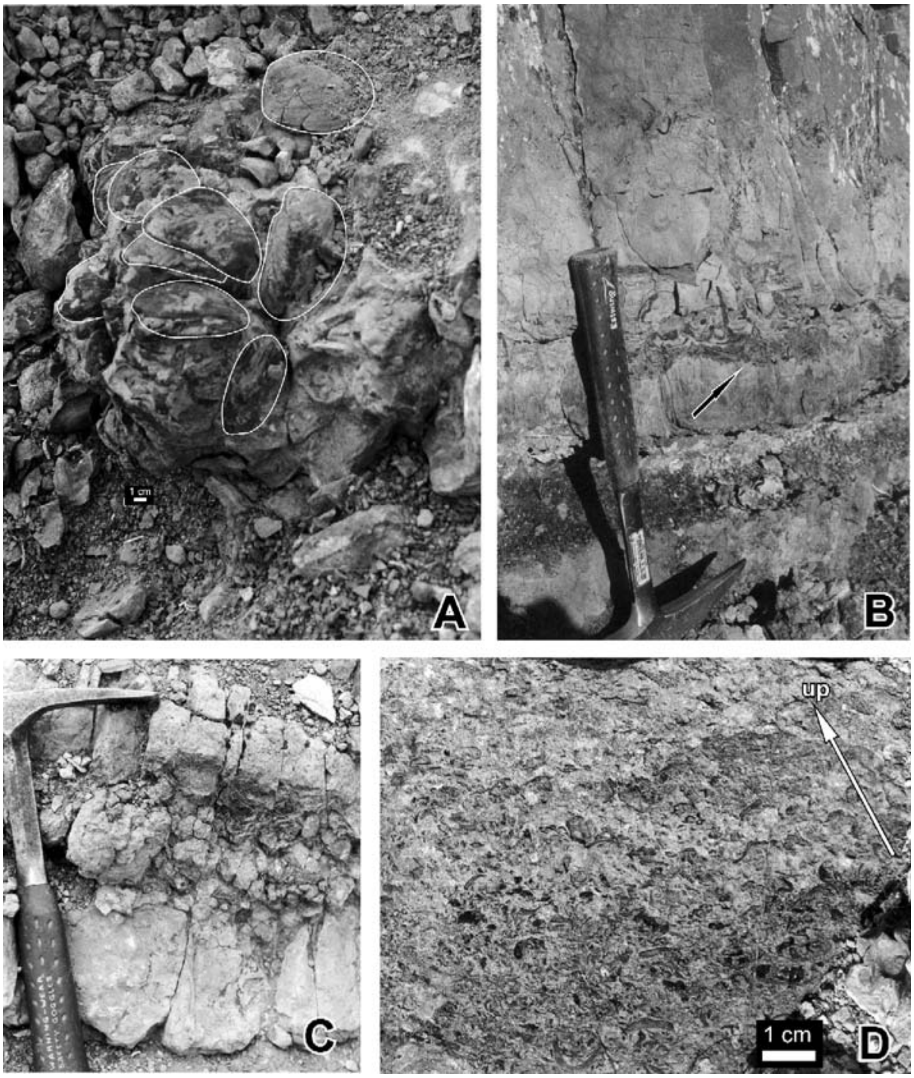


Fig. 4. A: Densely packed *Cardinioides* beds at La Horqueta, note abundance of complete articulated, large specimens (white line contours). B–D: Codo del Blanco section: B, shell-lag concentrations at the base of tidal inlets, arrow points to lag base, hammer length 40 cm; C, detail of one of the thin shell lags; D, detail of a graded and poorly sorted *Cardionioides lanesae* concentration (A, B and D: photographs S. Lanés; C: photograph S. Damborenea).

vertical (edgewise *sensu* Kidwell and Holland, 1991). Disarticulated shells lie either convex-up or -down and are occasionally nested. Biofabric is densely-packed, and skeletal elements are graded (Fig. 4D) but poorly size-sorted. The very scarce fine- to medium-grained sandy matrix is also fining towards the top.

3. At Las Chilcas only very small, isolated specimens of *C. lanesae* are associated with a fully marine biota including not only other stenohaline bivalves but also brachiopods and ammonoids (Table 3C). All of them form massive, matrix-supported shell lenses up to 0.3 m thick and 5 to 10 m wide. There *C. lanesae* occurs as dispersed, minute specimens predominantly disarticulated, fragmentated and abraded. Biofabric is massive, loosely-packed to dispersed, with abundant fine–sandy matrix. Only few fully marine shells are incrusted.

Increase of disarticulation, fragmentation, abrasion and successive replacement of densely-packed monospecific shell beds at La Horqueta with densely-packed almost monospecific ones at Codo del Blanco and then with loosely-packed poly-specific shell lags at Las Chilcas evidence increasing hydrodynamic transport (Fig. 3).

Table 3

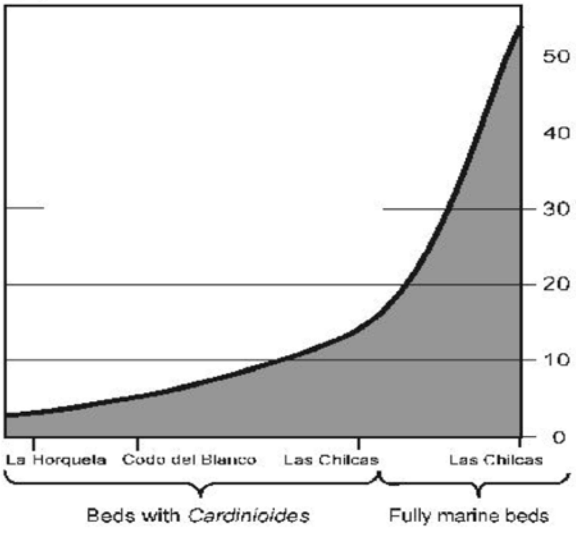
A–D: Faunal composition of early Late Sinemurian beds (*Epophioceras* Zone) at different localities of the Atuel river region, taxa arranged by relative abundance. To the right of the locality name, the total number of specimens is indicated

A **La Horqueta**	**233**
Cardinioides lanesae Damborenea	97%
Gervillella araucana Damborenea	2%
Fragments of Ostreoidea indet.	1%

B **Codo del Blanco**	**165**
Cardinioides lanesae Damborenea	92%
Gervillella araucana Damborenea	4%
Spiriferina? sp. indet.	2%
Frenguelliella cf. *poultoni* Leanza	1%
Fragments of Ostreoidea indet.	1%

C **Las Chilcas**	**45**
Asoella asapha (Leanza)	28%
Gervillella araucana Damborenea	25%
Cardinioides lanesae Damborenea	12%
Epophioceras? sp.	9%
Pinna cf. *folium* Y. and B.	4%
Frenguelliella cf. *poultoni* Leanza	4%
Gibbirhynchia dereki Manceñido	4%
Gryphaea aff. *cymbium* Lamarck	2%
Entolium cf. *lunare* (Roemer)	2%
Praechlamys cf. *valoniensis* (Defr.)	2%
Groeberella neuquensis (Groeber)	2%
Goniomya sp.	2%
Ammonitina indet.	2%
Gastropoda indet. A	2%

E



D **Fully marine beds (Las Chilcas)**	**374**
Entolium cf. *lunare* (Roemer)	13%
Peristerothyris reijensteini Manceñido	9%
Gibbirhynchia dereki Manceñido	8%
Weyla alata alata (von Buch)	7%
Gryphaea aff. *cymbium* Lamarck	6%
Asoella asapha (Leanza)	6%
Gryphaea darwini Forbes	5%
Epophioceras cf. *cognitum* Gu.Fr.	5%
Lywea unca (Philippi)	4%
Frenguelliella cf. *poultoni* Leanza	3%
Protocardia? sp.	3%
Pholadomya sp. C	2%
Pleuromya sp.	2%
Cardinia cf. *listeri* (J. Sowerby)	2%
Entolium sp.	1%
Lycettia sp.	1%
Grammatodon sp.	1%
Pseudolimea sp.	1%
Lucinoidea indet.	1%
Goniomya sp.	1%
Groeberella neuquensis (Groeber)	1%
Pholadomya sp. B	1%
Gastropoda sp. indet. C	1%
Ammonitina indet. A	1%
Praechlamys cf. *valoniensis* (Defr.)	1%
"Chlamys" textoria (Schlotheim)	1%
Kolymonectes sp.	1%
Lithotrochus humboldti (von Buch)	1%
cf. *Amberleya americana* Möricke	1%
Spiriferina cf. *ongleyi* Marwick	1%
cf. Lobothyris sp.	1%
Cosmetodon sp.	↑ less than 1% ↓
Pholadomya sp. A	
Gresslya? sp.	
Liostrea aff. *hisingeri* (Nilsson)	
Camptonectes? subulatus (Münster)	
Modiolus cf. *thiollierei* (Dumortier)	
Pinna cf. *folium* Y. and B.	
Antiquilima succincta (Schlotheim)	
Antiquilima n. sp.	
Ctenostreon sp.	
Plagiostoma? sp.	
Jaworskiella? sp.	
Astartidae indet.	
Gastropoda sp. indet. A	
Gastropoda sp. indet. B	
Gastropoda sp. indet. E	
Gastropoda sp. indet. F	
Gastropoda sp. indet. G	
Zeilleria ex. gr. *perforata* (Piette)	
Ammonitina indet. B	
Cnidaria indet. (*Stylophyllopsis*? sp.)	
Tetraserpula ? sp.	

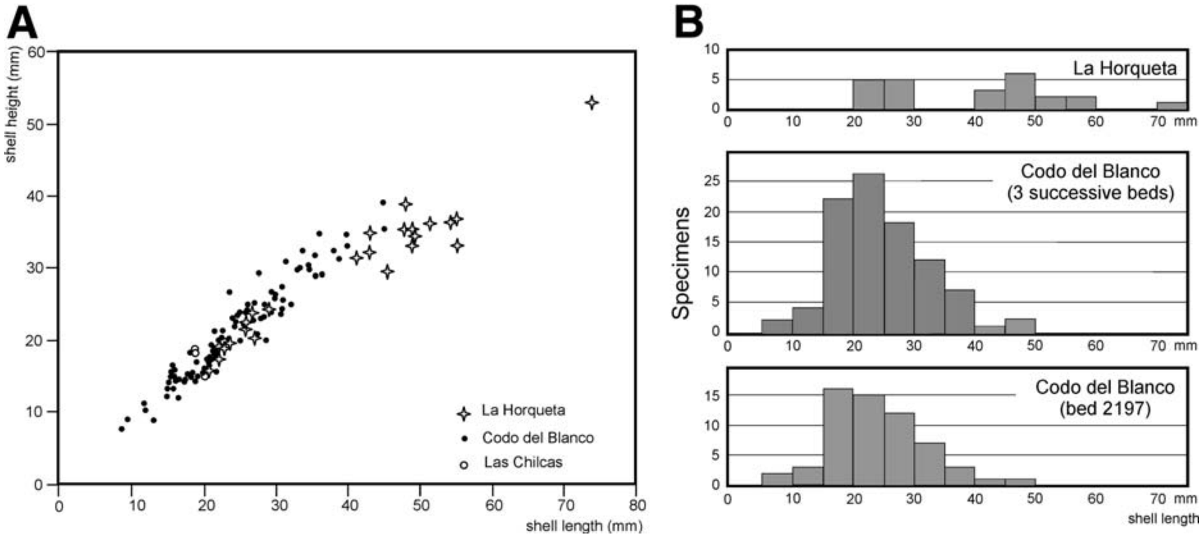


Fig. 5. A: Shell length *versus* shell height relationships of specimens of *Cardinioides lanesae* Damborenea n. sp. from the three studied localities. B: Distribution of shell size at La Horqueta and Codo del Blanco.

Dense packing of *Cardinioides*-shell lags in La Horqueta and Codo del Blanco suggests winnowing of the sandy matrix by current flows unable to redistribute the shells (in the case of La Horqueta near-monospecific shell beds) or transport the shells for long distances (as in the non-monospecific shell lags of Codo del Blanco). The loosely-packed, matrix-supported biofabric and small sizes of *C. lanesae* shells at Las Chilcas section evidence currents strong enough to transport the shells together with the medium to fine-grained sand (Fig. 3).

Originally aragonitic bivalve shells at La Horqueta and Codo del Blanco show replacement and almost complete destruction of original shell microstructure. This mode of preservation significantly differs from the usual preservation of aragonitic shells at other localities of the Atuel river region, where only internal, external and composite moulds are present. In normal marine facies of this region only some calcitic shells (oysters, some pectinids, brachiopods) are preserved with a slightly altered shell microstructure. The possible causes of this phenomenon are discussed below.

5. Palaeoecology

The shallow infaunal suspension-feeding habit of *C. lanesae* suggests its preference for stable sandy bottoms and agrees well with the interpretation of the sediment as part of the outer sandy complex at the mouth of a wave-dominated estuary (Fig. 6). The mixture of *C. lanesae* with stenohaline benthic fauna typical of normal marine shoreface in the shell beds of the Codo del Blanco section correlates with the increased thickness of outer estuary sandstone beds at that locality (Fig. 1).

The low diversity together with great individual abundances in the molluscan assemblages are features characteristic of brackish water faunas (Schmidt, 1951; Ekman, 1953; Parker, 1959; Hallam, 1976). Possible alternative causes to explain these conditions, such as biological stress due to oxygen deficiency, or extreme water turbulence or temperature, can be dismissed by the analysis of the regional geological setting. Other palaeoecological indicators of brackish-water biota are the absence of marine stenohaline species, the systematic composition of the fauna (belonging to families with freshwater or brackish water representatives) and the presence of certain characteristic morphotypes. All these conditions are met by the *Cardinioides* concentrations, as discussed below.

5.1. Low species richness and high abundance

Damborenea and Manceñido (2005) recognised a low diversity faunal association, the *Cardinioides* association in these sediments, which has a very simple structure, such as those typical of high-stress environments. It is interesting to note that epi- and endobionts

---

Notes to Table 3:
Total number of specimens to the right of the locality name. See also discussion in text. A–C: Beds with *Cardinioides* at the three localities, D: fauna from fully marine beds at Las Chilcas. E: Species richness curve for beds of the *Epophioceras* Zone at the three localities.

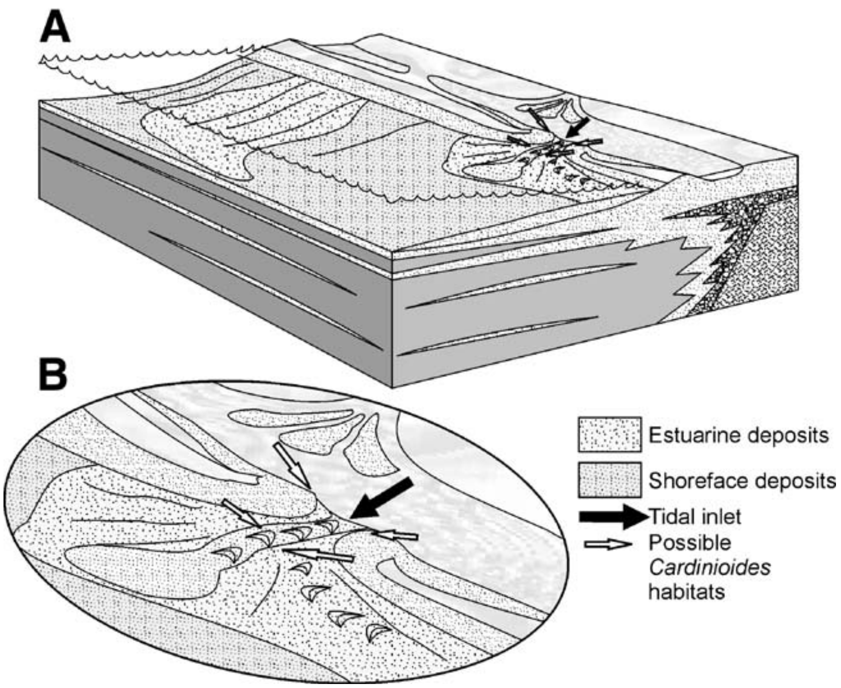


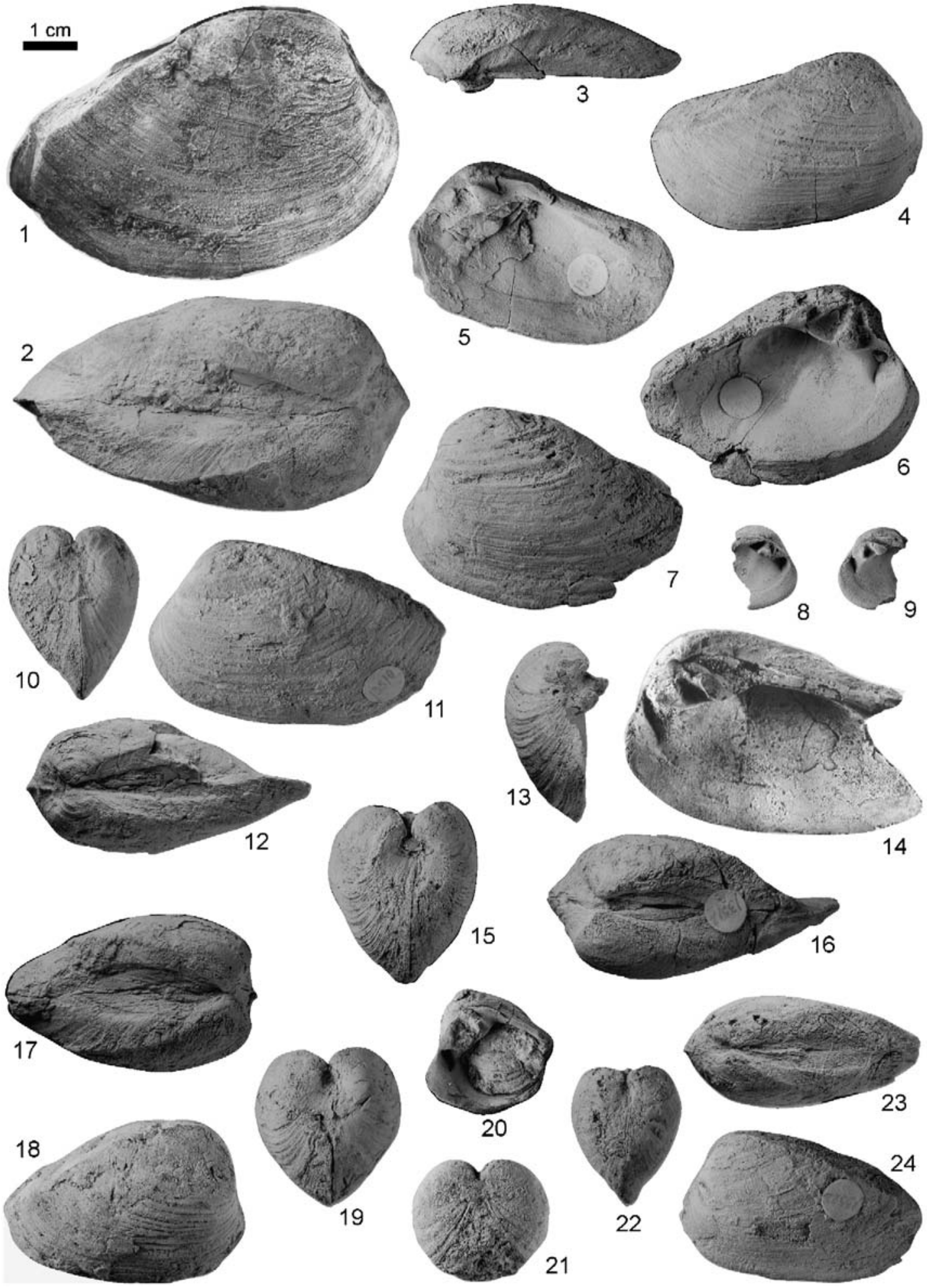
Fig. 6. A: Palaeoenvironmental framework of the *Cardinioides* beds of the Atuel river region, based on data from S. Lanés (2002). B: Detail of possible *Cardinioides* habitats.

are lacking altogether. Species richness increases from a minimum at La Horqueta, to low values at Codo del Blanco, and to slightly higher values at Las Chilcas (Table 3; Fig. 3). One of the beds with *C. lanesae* at La Horqueta contains also few but well-preserved, large specimens of *G. araucana* Damborenea and fragments of oysters, both epifaunal taxa. At Codo del Blanco at least three of the *Cardinioides* beds bear a few scattered but nearly complete, small specimens of *G. araucana* and oyster fragments, and one of them also contains *Frenguelliella* cf. *poultoni* Leanza, and *Spiriferina?* sp. indet. At Las Chilcas no *Cardinioides*-dominated beds have been recognised, and this bivalve occurs scattered in beds with a variety of benthic fauna. Fully marine beds of the same age and from neighbouring areas have a much greater species richness (Table 3).

The *Cardinioides* association, which only occurs in estuarine deposits (Damborenea and Manceñido, 2005) interpreted through facies analysis (J7 in Lanés, 2002, 2005), has thus a high facies fidelity. As discussed below, some preservational features of the shells point to frequent marine conditions in the outer part of the estuary, probably with cyclic (?) and significant changes of salinity. Although the coeval freshwater biota of the region is still unknown, the monospecific *Cardinioides* beds at La Horqueta most likely represent the diversity minimum in Remane's (1958) salinity gradient curve (Table 3E), and can be referred to the oligohaline salinity regime (according to Oertli, 1964, classification of marine waters based on salinity). This setting is similar to that proposed for the *Neomiodon* association of the Bathonian Great Estuarine Group of Scotland, assigned to the "species minimum" salinity range (5‰ to 9‰)

Fig. 7. *Cardinioides lanesae* Damborenea n. sp. All specimens figured at natural size. Graphic scale at the upper left corner. All specimens from La Horqueta except where otherwise indicated. 1–2, right valve and dorsal view of complete large specimen, paratype MLP 13507; 3–5, dorsal, external and internal views of complete right valve, holotype, MLP 13505; 6–7, external and internal views of complete left valve, paratype MLP 13503; 8–9, left and right valve internal views of a young specimen, paratype MLP 28973, Codo del Blanco; 10–12, anterior, left valve and dorsal views of complete specimen, MLP 13510; 13–14, anterior and internal views of nearly complete right valve, paratype MLP 13504; 15, anterior view of complete specimen, paratype MLP 13508; 16, dorsal view of complete specimen, showing long strong nymphs, paratype MLP 13512; 17–19, dorsal, right lateral and anterior views of complete specimen, MLP 13511; 20, internal view of a nearly complete young right valve, paratype MLP 28967, Codo del Blanco; 21, anterior view of small specimen with valves widely gaping, paratype MLP 13530, Las Chilcas; 22–24, anterior, dorsal and left valve external views, MLP 13522.

by Hudson (1963a,b, 1980; Hudson et al., 1995), and to the *Eomiodon angulatus* and *Neomiodon ruthenensis* associations from the Bathonian of the Causses, France (Fürsich et al., 1995). Similarly, nearly monospecific beds with the anthracosiid *Unionites brevis* (von Schauroth) in the Ladinian of southwest Germany are



interpreted as short-term, brackish intervals (Geyer et al., 2005). The nearly monospecific shell-beds of the late Triassic *Trigonodus–Isocyprina* assemblage from the Lhasa block (Tibet) described by Yin and Grant-Mackie (2005) have been interpreted as deposited in brackish to shallow marine environments with fluctuating salinity.

5.2. Absence of marine stenohaline species

Marine stenohaline higher taxa such as diverse brachiopods, ammonites and corals, which are common at other, nearby localities of the same age (Table 3D), are absent at La Horqueta, limited to one bed at Codo del Blanco, and scarce in the Las Chilcas *Cardinioides*-bearing beds. This pronounced impoverishment and eventual exclusion of marine stenohaline taxa is, in itself, a strong indication of at least temporary salinity reductions or fluctuations (Hallam and El Shaarawy, 1982; Fürsich and Werner, 1984; Hudson, 1990).

5.3. Systematic composition of the fauna

The Pachycardiidae is a mainly Mesozoic family that comprises conspicuously euryhaline genera ranging from brackish to marine, even freshwater habitats (Cox et al., 1969). According to Hayami (1961), in Japan *Cardinioides* appears in lagoonal facies with fine- to medium-grained sand in local shell concentrations with almost no other accompanying fauna. They have been interpreted as environmental stress-controlled faunas (Kobayashi and Ichikawa, 1952).

The accompanying bivalves at La Horqueta and Codo del Blanco (Table 3), namely *G. araucana*, *Frenguelliella* cf. *poultoni* and ostreoids, all belong to groups which have well-known euryhaline members that tolerate salinity fluctuations and are common in mixed marine/brackish environments (e.g., Huckriede, 1967; Tamura, 1980; Freneix and Cubaynes, 1984; Fürsich and Werner, 1984; Fürsich and Kauffman, 1984; Yin, 1989; Fürsich et al., 1995; Sugawara and Kondo, 2004; Geyer et al., 2005; Kondo et al., 2006). But on the whole, this cannot be regarded as merely an impoverished marine fauna, since it contains taxa which are absent from fully marine beds of the same region and age. It is interesting to note that the torted pterioid *G. araucana* has not yet been found at Las Chilcas or other Sinemurian fully marine beds of the region, but occurs in marine facies in the Pliensbachian of Argentina (Damborenea, 1987b) and Chile (Aberhan, 1994a). This was probably a euryhaline taxon which was able to extend its distribution to brackish environments. In the study area the relative abundance of *G. araucana* increases towards the West and South (see pie diagrams in Fig. 3).

The assemblage at Codo del Blanco contains a few small specimens of *Spiriferina*? sp. indet. Although articulate brachiopods are usually regarded as strictly stenoeuhaline, several examples from brackish environments are known from the Palaeozoic fossil record (Fürsich and Hurst, 1980) and experiments with living species have shown that some tolerate salinity fluctuations (Thayer, 1981). Nevertheless, very little is known about Mesozoic brachiopods in this context. Brachiopod diversity increases considerably towards fully marine facies in the area, which contain at least four species but where the same species of *Spiriferina*? was not found (Table 3D).

5.4. Characteristic morphotypes

The type of high stress environment, suggested by the sedimentological analysis and these broad palaeoecological indicators, is usually colonised by organisms which can cope with frequent changes in salinity. The known history of such environments has shown that these faunas are long-ranging and conservative, morphologically generalized. *C. lanesae* has a trapezoidal globose shell with posterior umbonal carina and a truncated posterior margin. These characters, together with the strong dentition, external parivincular ligament supported by nymphs, and presence of lunule, indicate that this suspension-feeder was an active shallow burrower, which is the most common guild present in marginal marine environments. Fürsich (1994) recognised six morphotypes characteristic of salinity-controlled environments, which remained constant since the Mesozoic, although species composition changed through time. *C. lanesae* clearly belongs to one of these morphotypes, represented by medium-sized to large, smooth and thick-shelled bivalves, trapezoidal–triangular in outline with external parivincular ligament and robust dentition (Figs. 7 and 8). According to Fürsich (1994, Fig. 24), this morphotype is mainly represented by Anthracosiidae in the Triassic, Neomiodontidae in the Jurassic, Corbiculidae in the Cretaceous to Recent, and Mactridae in Tertiary to Recent biotas. Added to this list should be Pachycardiidae in the Late Triassic–Early Jurassic (see Discussion below), and Pachydontinae corbulids in the Tertiary (cf. Nuttall, 1990). Many marginal marine Mesozoic communities are dominated by bivalves belonging to this morphotype, such as the Neomiodontidae *Neomiodon* in the Bathonian of Scotland (Hudson, 1963a,b, 1980; Hudson et al., 1995), *Eomiodon* and bakevelliids in brachyhaline and mesohaline environments in Portugal (Fürsich and Werner, 1984) and in tidal flat and coastal

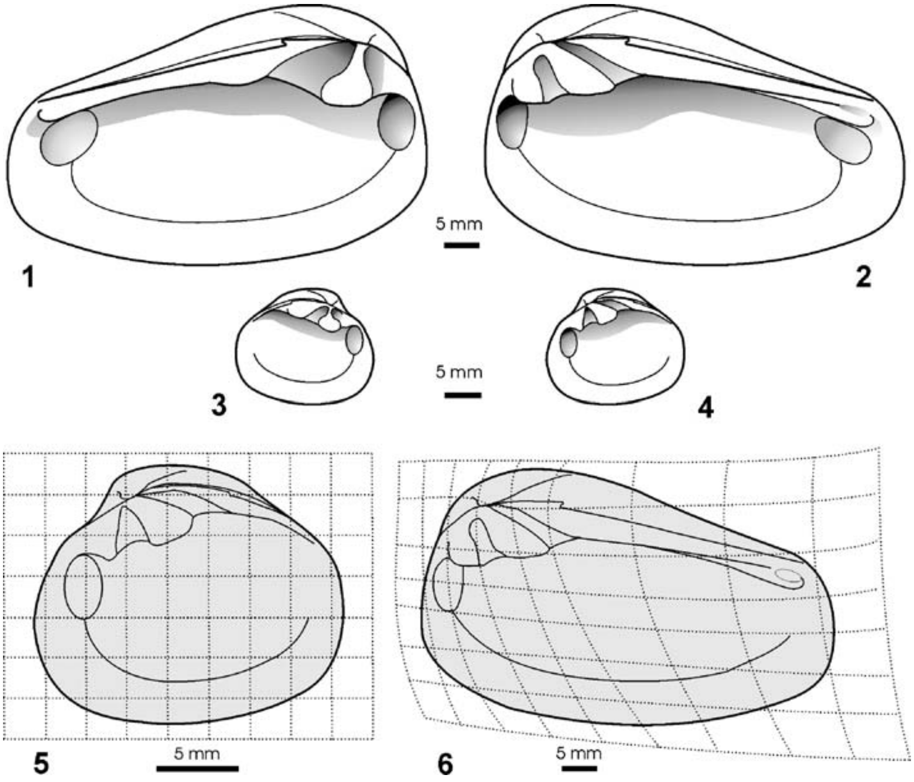


Fig. 8. *Cardinioides lanesae* Damborenea n. sp. Left and right valve hinges of adult (1–2, 6) and young specimens (3–5). 1–4 sketched to the same scale; 5–6 with grid to show different growing rates at different parts of the shell.

plain communities in the Late Jurassic of Tanzania (Aberhan et al., 2002), the corbiculid *Veloritina* in the Albian of Wyoming (Fürsich and Kauffman, 1984), and *Unionites* in monospecific mass-occurrences, which are interpreted as short-term brackish intervals, in the Ladinian of Germany (Geyer et al., 2005).

6. Discussion

The main stress factors in marginal marine environments are salinity, temperature, oxygen content, grain-size and water turbulence. As all these factors are highly variable, it is commonly difficult to evaluate which of them had the greatest influence on the faunal distribution (Hudson, 1990; Fürsich et al., 1995).

Teske and Wooldridge (2003) argued that the nature of sediment is more important than salinity in limiting the distribution of macrobenthos in South African estuaries, but sedimentary similarities of the *Cardinioides*-bearing beds among the studied sections enable us to discard the nature of the host sediment as a major control on bivalve distribution in this case.

The sedimentologic and taphonomic analysis indicates that the studied estuary was well oxygenated, and thus this factor can be dismissed as well. It is more difficult to single out the possible influence of temperature changes, which may have had a secondary role. Ample food supply is suggested by the high local abundance and large size of *C. lanesae*, which together with sedimentologic features of these deposits indicate high energy levels and deposition in tidal inlets (Fig. 6). Estuaries are usually nutrient traps and thus show high fertility despite the environmental stress. Estuary tidal inlets are known to be migrating routes for larvae of species which use low energy central estuary waters as breeding places (Smith, 1988; Eggleston et al., 1998) and this may be a source of abundant food supply for these suspension-feeding bivalves.

Salinity and water turbulence were probably the main factors controlling the distribution of this species. Fresh-water bivalves, such as unionids, are absent. Solution pits on the shell surface, clear indicators of long exposure to freshwater, even during the bivalve's lifetime (Fürsich, 1994), were not observed. Lacking dissolution features together with the preservation of the aragonitic shells at La Horqueta and Codo del Blanco sections are evidence of a long-term contact with normal marine pore waters. Ion concentration of shallow tropical marine waters makes them supersaturated with respect to, and prevents the dissolution of, aragonite (Canfield and Raiswell, 1991). Conversely, the shallow temperate marine waters of mid and high latitudes are undersaturated with respect to all carbonates, which are totally dissolved (Tucker and Wright, 1990). Then a freshwater environment at the La Horqueta and Codo del Blanco sections can be ruled out. This is consistent with the interpretation of *Cardinioides*-bearing deposits as tidal inlet facies of the outer part of a wave-dominated estuary. On the other hand, such type of estuary usually has a stratified water column resulting from the formation of a "salt wedge" (*sensu* Pritchard, 1955; Cameron and Pritchard, 1963) whereby fluvial freshwater, less dense, usually flows over the denser marine water. The development of this estuarine circulation pattern may vary depending on fluvial discharge, climate, tidal range and geometry of the estuary, among other factors. The possible development of a salt wedge can also explain the absence of a freshwater environment at La Horqueta and Codo del Blanco sections; and it also points to a possible marine environment with cyclical (?) and significant changes of salinity, possibly related to tides and/or climatic-induced fluctuations of the fluvial discharge.

Among the three localities (Las Chilcas, Codo del Blanco and La Horqueta sections) a preferential facies distribution exists showing mudstones of the central estuary at the La Horqueta and Codo del Blanco sections but not at Las Chilcas. In contrast, the fair-weather wave and storm deposits of the outer estuary sandy complex predominate at the Codo del Blanco section. Detailed biostratigraphic correlation and facies distribution of the contemporaneous depositional systems point to an estuary open to the north and west, dipping more gently northwards than westwards.

Precise salinity regimes (such as those proposed by Yin, 1989 for the Middle Jurassic of Qinghai; or by Fürsich et al., 1995 for the Middle Jurassic of France) cannot yet be proposed, as the detailed study of the lateral and stratigraphic relationships of these faunas is still pending. Further studies in the area will probably enable this to be explored, considering that the *Cardinioides* association is most probably a brackish-water fauna and its distribution was controlled mainly by salinity variations.

In variable salinity environments, the conditions under which individuals attain their species maximum size are an indication of optimal living conditions (Hallam, 1965; Fürsich and Kauffman, 1984; Powell and Stanton, 1996). For this reason, when dealing with marine euryhaline species, size and thickness of shells decrease towards brackish or hypersaline conditions (see examples in Fürsich, 1994), i.e., towards decreasing diversity of the biota. The opposite applies to the *Cardinioides* assemblage studied here. Not enough quantitative data are yet available to study in detail the size frequency distribution. However, from a broad analysis of shell sizes and species richness at the different localities (Figs. 3 and 5), together with other evidence, it is clear that the ecological optimum for *C. lanesae* was within the low salinity range of the estuarine environments. This is a strong indication that this species was a "brackish water endemic" (in the sense of Boesch, 1977), which grew to maximum size in oligo- or mesohaline environments, and became scarce and small-sized where fully marine conditions were prevailing, as attested by the presence of brachiopods, ammonites and other marine stenohaline bivalves.

This seems to apply largely to *G. araucana* too, though probably this species had somewhat different ecological requirements, as shown by its distribution in the sections (Fig. 3), which suggests that it thrived in a slightly higher salinity range than *Cardinioides*.

C. lanesae is also occasionally found in the shallow-water *Weyla–Gryphaea* association (Damborenea and Manceñido, 2005), yet it remains to be ascertained whether such occurrences may represent an extreme position within the broad range of salinity tolerance of the species, and/or to transport or to time-averaging within an environmental setting subject to strong, short-term, salinity fluctuations. In either case, *C. lanesae* can be regarded as a low-salinity euryhaline opportunist. The species is not known from other localities of the extensive Neuquén Basin.

The precise biostratigraphic position of the *Cardinioides* beds can be inferred by the accompanying fauna as Late Sinemurian. At Las Chilcas the beds contain a few ammonites of the *Epophioceras* Zone (Late Sinemurian), but there are no ammonites in the *Cardinioides* beds at La Horqueta and Codo del Arroyo Blanco outcrops, as one would expect from such environments. In these last two localities, though, the *Cardinioides* beds are overlain by marine facies containing ammonites and other fauna of the *Epophioceras* Zone.

7. Conclusions

We use a combined interdisciplinary approach (including sedimentology, taphonomy, palaeoecology and systematic palaeontology) to propose an environmental model for the lower part of the Puesto Araya Formation in the Atuel river region, northern Neuquén basin. The faunal assemblages discussed here provide evidence of environmental conditions changing from marginal marine (brackish) to fully marine on the eastern margin of the Neuquén Basin during Sinemurian times. These changes can be followed laterally for beds of the same age and also vertically in some sections. Jurassic marginal marine environments were previously poorly known in this basin.

C. lanesae Damborenea was an endemic brackish species, probably living in oligo- to mesohaline environments, but occasionally present in euhaline habitats as well. It can also be characterised as a low salinity euryhaline species.

Salinity and turbulence (together with food supply) were the main limiting factors in the distribution of the species in this marginal marine setting, and we suggest that its ecological optimum was near tidal inlets in a wave-dominated estuary.

Since sediments do not usually reflect subtle salinity fluctuations, brackish environments are very difficult to recognise on sedimentary features alone, and faunal characters are sometimes the only reliable source of evidence. Data on the salinity range of bivalves can be useful to complete the facies and basin analysis of the Neuquén Basin, providing an extra tool to study in detail the distribution of marginal marine environments.

One of the issues still pending is to separate the influence of absolute salinity levels from that of salinity fluctuations, which depend largely on the particular environment. Using fossils is a promising tool, because detailed enough palaeoecological data can help distinguish between estuary (with rapid and frequent salinity changes) and lagoonal settings (with more stable salinity).

Acknowledgements

We thank A.C. Riccardi for determining the ammonites and for commenting on an earlier version of the manuscript. M.O. Manceñido, A.C. Riccardi, G. Robles and S. Ros Franch participated in field trips directly related to this paper and their help is greatly acknowledged. We are very grateful to M. Manceñido and Jingeng Sha for fruitful discussions, to Y. Kondo for help with Japanese literature, and to J. Grant-Mackie and an anonymous reviewer for their thoughtful suggestions to improve the original text. The research was partly funded by CONICET PIP grants 2702/00 and 5635/05. This is a contribution to IGCP Project 506, “Marine and non-marine Jurassic”.

Appendix A. Systematic palaeontology (by S. Damborenea)

A.1.

Order Unionoida Stoliczka, 1870
Superfamily Unionoidea Fleming, 1828
Family Pachycardiidae Cox, 1961
Genus *Cardinioides* Kobayashi and Ichikawa, 1952

Type species. Cardinioides japonicus Kobayashi and Ichikawa, 1952, by original designation, Carnian, Japan.

The affinities of the genus *Cardinioides* are not yet clear. It was first described from the Late Triassic (Carnian) of Japan by Kobayashi and Ichikawa (1952). Later on Hayami (1957) described some species from the Early Jurassic (Pliensbachian or thereabouts) also from Japan. The genus was initially referred to the Cardiniidae by these authors, but subsequently Hayami (1961, p. 258) transferred it to the Pachycardiidae, and it was placed in this last family with a query by Cox et al. (1969) and later authors (Hayami, 1975; Kondo et al., 2006). The genus differs from the externally similar Jurassic–Cretaceous Neomiodontidae (Casey, 1955) by the absence of true lateral teeth, a different hinge formula and presence of lunule and escutcheon in some species.

Hayami (1975) provided an extended diagnosis of the genus and confirmed its reference to the Pachycardiidae. External homoeomorphism is common within this family and also among other smooth, trapezoidal globose bivalves (such as the Neomiodontidae), which makes taxonomic treatment and proper comparisons very difficult when internal features cannot be observed. Fortunately, the Argentine material is very well preserved and thus the hinge can be studied in detail.

Cardinioides is known from Carnian to lower Jurassic beds from circum-Pacific localities. It was regarded as an endemic genus during the Late Triassic and Early Jurassic, restricted to the NW palaeoPacific (mainly Japan). Furthermore, Hayami (1961, p. 291) regarded it as endemic to the Kuruma faunal province during the Early Jurassic and to the Japanese Inner Zone in Late Triassic times. It is interesting to note that the other bivalve genus regarded by Hayami as endemic to Kuruma was *Radulonectites*, which is also abundantly present in the Atuel river region and many other Argentine localities (Damborenea, 1993, 2002). Since its first description, the genus *Cardinioides* was recorded from late Triassic beds in eastern Siberia (Kurushin, 1990), western USA (Newton et al., 1987), northern Mexico (McRoberts, 1998), and early Jurassic beds from Thailand (Kobayashi et al., 1963) and now in western Argentina (Damborenea and Manceñido, 2005).

The genera referred to this family are very similar in external appearance, and thus identification is almost impossible if hinge details are not observable. *Cardinioides* can be distinguished from *Pachycardia* Hauer by the presence of an escutcheon and only an ill-defined lunule, a right valve with two cardinal teeth instead of one, and weaker lateral "teeth" (hinges illustrated, among others, by Broili, 1904; Waagen, 1907). Some species of *Trigonodus* Sandberger have also a similar shell shape but have stronger posterior lateral teeth and a right valve with only one cardinal tooth (see hinge illustrations in Wöhrmann, 1893; Waagen, 1907; Schmidt, 1928; Chen, 1976).

A.2. *Cardinioides lanesae* Damborenea n. sp.

Figs. 7 and 8 (figured as *Cardinioides* n. sp. in Damborenea and Manceñido, 2005, Fig. 9.B–E).

A.2.1. Material

Holotype: Complete right valve, MLP13505 (Fig. 7.3–5) from La Horqueta. *Paratypes*: one nearly complete specimen, with both valves showing internal characters (MLP 28973), three closed complete specimens (MLP 18371, 18372), five left valves (MLP 18362, 18364, 18366, 18368, 28966) and five right valves (MLP 18361, 18363, 18365, 28967), from Codo del Blanco; one right valve (MLP 13504), one left valve (MLP 13503), three complete specimens with the valves closed (MLP 13507, 13508, 13512) from La Horqueta, and one complete specimen with the valves slightly open (MLP 13530) from Arroyo Las Chilcas. *Other material*: 118 specimens with both valves, 25 right valves, 30 left valves, 1 steinkern and some fragments, all from upper Sinemurian beds (*Epophioceras* Zone) of the river Atuel area (Arroyo Las Chilcas, west of Arroyo Las Chilcas, Codo del Blanco and La Horqueta), MLP 13351, 13506, 13509 to 13511, 13513 to 13529, 13531, 13532, 18367, 18369, 18370, 18373 to 18381, 18447 to 18459, 28968 to 28972, 28974 to 28982.

A.2.2. Derivation of name

The species name is dedicated to Dr. Silvia Lanés, who collected the first specimens and studied the geology of the river Atuel region.

A.2.3. Diagnosis

Large, globose, thick shelled *Cardinioides* with ovoid to trapezoidal outline and variably developed umbonal carina. Nymphs short and deeply impressed, escutcheon long and narrow, limited by carina, lunule ill-defined. Right valve with two strong cardinal teeth, the anterior wide and flat, the posterior more prominent. Left valve with one strong cardinal tooth below umbo and a marginal thickening or second tooth below the nymph. Ridge-like posterior lateral "tooth" on each valve above the posterior muscle scar. Anterior adductor muscle scar small, deeply impressed and supported by short myophoric buttress, posterior one larger but not impressed. Pallial line continuous.

A.2.4. Description

Large, thick, equivalve shells of ovoid (in young valves) to trapezoidal outline, very globose. There is a great intraspecific variation of shell outline which is not correlated to size. Umbones wide and prosogyrous, placed at about 1/3 of total shell length or less from the anterior margin. Shell length nearly equal to height in young specimens, exceeding height in large ones. Umbonal carina well developed and sharp in some specimens (Fig. 7.1–3, 7.12, 7.17), rounded in others (Fig. 7.7, 7.23–24). Posterodorsal margin straight, joining the ventral margin in a rounded or bluntly angular corner at the postero-ventral part of the shell, which is longer in large specimens. Ventral margin evenly rounded, anterior margin rounded and narrow.

Deeply impressed nymphs extending about half of posterior dorsal length (Fig. 7.3, 7.12, 7.16–17). Some specimens have traces of ligament preserved (Fig. 7.23).

Shell exterior with well marked growth lines only, some well-preserved specimens also show a few concentric shallow folds near the umbonal region (Fig. 7.12). Interior of shell smooth, internal margin smooth, occasionally with a bevelled narrow platform (Fig. 7.6). Lunule smooth, ill-defined (Fig. 7.15); escutcheon long and narrow, limited by a blunt carina (Fig. 7.12) in well-preserved specimens. Lunule and escutcheon appear to be absent in poorly preserved specimens.

Anterior adductor muscle scar small, subcircular in outline, very deeply impressed, placed very near the dorsal margin (Fig. 7.6), just anterior to the cardinal plate and supported by short myophoric buttress. Small pedal retractor muscle scar just above it. Posterior adductor muscle scar larger than anterior one but not impressed on shell inner surface. Pallial line clearly marked, continuous between adductor muscle scars.

Right valve with two strong "cardinal" teeth radiating from umbo, the anterior one wide and flattened, anterior to umbo, the posterior one much more prominent, dorsally arched; and two large triangular sockets, one posterior to each tooth (Fig. 7.5, 7.9, 7.14, 7.20, 8.2, 8.4).

Left valve with one very strong pivotal "cardinal" tooth just below umbo, a posterior triangular marginal thickening (or second tooth) below the nymph, and two triangular deep sockets to each side of the strong "cardinal", the posterior one broader (Fig. 7.6, 7.8, 8.1, 8.3).

A radial internal ridge extends from the umbonal cavity to near the postero-dorsal corner of the shell in the right valve, becoming broader some distance from the margin above the posterior muscle scar (Fig. 7.5, 8.2). This ridge is nearly parallel to the dorsal margin of the shell and does not belong to the cardinal platform, being at the level of the commissure plane only at its posterior end. This structure corresponds to the "ridge-like posterior lateral tooth of *Cardinia*-type" described by Hayami (1957), and although it is not a proper tooth its posterior end may have aided in shell articulation. It limits ventrally a shallow ovoid depression corresponding to a similar structure in the left valve (Fig. 8.1).

A wide radial thickening extending from the cardinal platform to mid-ventral margin divides the shell interior into two areas, the posterior one deeper and containing the umbonal cavity (Fig. 7.6).

A.2.5. Measurements

See Fig. 5. Largest specimen (paratype MLP 13707, Fig. 7.1–2) is 73.95 mm long, 53.55 mm high and 39.20 mm thick.

A.2.6. Remarks

The species here described is referred to *Cardinioides* mainly on account of details of the hinge, muscle scars, and shell shape. The species has an ill-defined lunule and a well-marked escutcheon, these characters are clearly stated to be absent in the extended diagnosis of the genus provided by Hayami (1957, 1975). These features are only clearly visible, however, in well-preserved specimens of *C. lanesae* n. sp., appearing to be absent in other specimens.

The type species *C. japonicus* Kobayashi and Ichikawa (1952) has a wide variability of shell shape which was interpreted originally as representing different species, but the hinge details are not properly preserved to establish a detailed comparison.

Shell shape is closest to *C. varidus* Hayami (1957, pl. 12, Figs. 1–6; 1975, pl. 4, Fig. 9), from the Early Jurassic (Pliensbachian?) of Japan, but this species lacks lunule and escutcheon and the two cardinal teeth on the right valve are weaker than in *C. lanesae*. The other Early Jurassic Japanese species, *C. ovatus* Hayami (1957, pl. 12, Figs. 7–12) lacks an umbonal carina and adults are smaller than *C. lanesae* n. sp. *Cardinioides magnus* Kobayashi and Hayami (in Kobayashi et al., 1963), from Thailand is only known from internal moulds and thus cannot be compared in detail.

Cardinioides fidus Kurushin (1990, pl. 2, Fig. 5), and *Cardinioides tolli* Kurushin (1990, pl. 2, Fig. 6–8), both from the upper Triassic of eastern Siberia have very elongated shells, at least twice as long as high.

Cardinioides josephus Newton et al. (1987, Fig. 45), from Norian beds of Oregon, USA, is smaller, more elongated and less inflated than the specimens from Argentina. The specimen from Rhaetian beds of Sonora, Mexico, referred by McRoberts (1998, Fig. 3.12) to *Cardinioides* sp. is less inflated and has the umbones more posteriorly placed than *C. lanesae* n. sp., but its hinge region is unknown.

The shells of some species of *Hayamina* Ohta, from the Early Cretaceous of Japan, are externally very similar to those of the new species, but hinge characters are different (Kozai and Ishida, 2003; Kozai et al., 2005).

Trigonodus xiaobolangensis Yin and Grant-Mackie (2005), from late Triassic beds of Tibet, has a well-developed umbonal ridge, smaller size, and a less robust dentition with the anterior cardinal in the right valve larger than in *C. lanesae*.

From the scarce record of Mesozoic Unionidae from South America, the genus *Tacuaremboia* Martínez et al. (1993), from freshwater deposits of Uruguay (age undefined between late Triassic and late Jurassic) is quite different: its shells are very large (more than 30 cm long) and edentulous.

External appearance of *C. lanesae* is very similar to some species from the Triassic of Europe referred to *Unionites*, such as *Unionites donaciformis* (von Schlotheim), but the hinge characters are completely different (see for instance material figured by Geyer et al., 2005) and the new species has much thicker shell. The external similarity applies also to species of *Neomiodon* Fischer and *Eomiodon* Cox, which all have lucinoid hinges with well developed anterior teeth (see Casey, 1955; Huckriede, 1967).

References

Aberhan, M., 1993. Benthic macroinvertebrate associations on a carbonate-clastic ramp in segments of the Early Jurassic back-arc basin of northern Chile (26–29°S). Revista Geológica de Chile 20, 105–136.

Aberhan, M., 1994a. Early Jurassic Bivalvia of northern Chile. Part I. Subclasses Palaeotaxodonta, Pteriomorphia, and Isofilibranchia. Beringeria 13, 1–115.

Aberhan, M., 1994b. Guild-structure and evolution of Mesozoic benthic shelf communities. Palaios 9, 516–545.

Aberhan, M., Bussert, R., Heinrich, W.D., Schrank, E., Schultka, S., Sames, B., Kriwet, J., Kapilima, S., 2002. Palaeoecology and depositional environments of the Tendaguru Beds (Late Jurassic to Early Cretaceous, Tanzania). Mitteilungen aus dem Museum für Naturkunde, Berlin, Geowissenschaftliche Reihe, vol. 5, pp. 19–44.

Andrews, J.E., Walton, W., 1990. Depositional environments within Middle Jurassic oyster-dominated lagoons: an integrated litho, bio- and palynofacies study of the Duntulm Formation (Great Estuarine Group, Inner Hebrides). Transactions of the Royal Society of Edinburgh 81, 1–22.

Bechis, F., Giambiagi, L.B., García, V.H., 2005. Fallamiento normal de pequeña y mediana escala asociado a la extensión Triásica tardía — Jurásica temprana en el depocentro Atuel de la Cuenca Neuquina. 16° Congreso Geológico Argentino, Actas, vol. 2, pp. 87–94.

Boesch, D.F., 1977. A new look at the zonation of benthos along the estuarine gradient. In: Coull, B.C. (Ed.), Ecology of Marine Benthos. The Belle W. Baruch Library in Marine Sciences, vol. 6, pp. 245–266.

Broili, F., 1904. Die Fauna der Pachycardientuffe der Seiser Alp (Mit Ausschluss der Gastropoden und Cephalopoden). Palaeontographica 50, 145–227 (Taf. 17–27).

Cameron, W.M., Pritchard, D.W., 1963. Estuaries. In: Hill, M.N. (Ed.), The Sea, vol. 2. John Wiley and Sons, New York, pp. 306–324.

Canfield, D.E., Raiswell, R., 1991. Carbonate precipitation and dissolution, its relevance to fossil preservation. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy: Releasing the Data Locked in the Fossil Record. Topics in Geobiology, vol. 9. Plenum Press, New York, pp. 411–453.

Casey, R., 1955. The Neomiodontidae. A new family of the Arcticacea (Pelecypoda). Proceedings of the Malacological Society of London, vol. 31, pp. 208–222.

Chen, J., 1976. Triassic and Jurassic Lamellibranchia. In: Nanjing Institute of Geology and Palaeontology, Academia Sinica (Ed.), Mesozoic Lamellibranchia of Yunnan, Vol. A. Beijing, Science press, 161–386.

Cox, L.R., Newell, N.D., Boyd, D.W., Branson, C.C., Casey, R., Chavan, A., Coogan, A.H., Dechaseaux, C., Fleming, C.A., Haas, F., Hertlein, L.G., Fauffnab, E.G., Keen, A.M., Larocque, A., McAlester, A.L., Moore, R.C., Nuttall, C.P., Perkins, B.F., Puri, H.S., Smith, L.A., Soot-Ryen, T., Stenzel, H.B., Trueman, E.R., Turner, R.D., Weir, J., 1969. Mollusca 6. Bivalvia. In: Moore, R.C. (Ed.): Treatise on Invertebrate Paleontology. Part N. University of Kansas Press and Geological Society of America. Kansas. I, 1–489, II, 490–952.

Dalrymple, R.W., Zaitlin, B.A., Boyd, R., 1992. Estuarine facies models: conceptual basis and stratigraphic implications. Journal of Sedimentary Petrology 62 (6), 1130–1146.

Damborenea, S.E., 1987a. Early Jurassic Bivalvia of Argentina. Part I: Stratigraphical Introduction and Superfamilies Nuculanacea, Arcacea, Mytilacea and Pinnacea. Palaeontographica A 99 (1–3), 23–111.

Damborenea, S.E., 1987b. Early Jurassic Bivalvia of Argentina. Part II: Superfamilies Pteriacea. Buchiacea and part of Pectinacea. Palaeontographica A 99 (4–6), 113–216.

Damborenea, S.E., 1993. Early Jurassic South American pectinaceans and circum-Pacific palaeobiogeography. Palaeogeography, Palaeoclimatology, Palaeoecology 100 (1–2), 109–123.

Damborenea, S.E., 2002. Early Jurassic bivalves from Argentina. Part 3: Superfamilies Monotoidea, Pectinoidea, Plicatuloidea and Dimyoidea. Palaeontographica A 265 (1–4), 1–119.

Damborenea, S.E., 2004. Early Jurassic *Kalentera* (Bivalvia) from Argentina and its palaeobiogeographical significance. Ameghiniana 41 (2), 185–198.

Damborenea, S.E., Lanés, S., 2003. Bivalvos eurihalinos en depósitos de estuario del Jurásico temprano del sur de Mendoza, Argentina. Ameghiniana 40, 100R–101R (Suplemento Resúmenes).

Damborenea, S.E., Manceñido, M.O., 2005. Biofacies analysis of Hettangian–Sinemurian bivalve/brachiopod associations from the Neuquén Basin (Argentina). Geologica Acta 3 (2), 163–178.

Eggleston, D.B., Armstrong, D.A., Elis, W.E., Patton, W.S., 1998. Estuarine fronts as conduits for larval transport: hydrodynamics and spatial distribution of Dungeness crab postlarvae. Marine Ecology Progress Series 164, 73–82.

Ekman, S., 1953. Zoogeography of the Sea. Sidgwick & Jackson, London. 417 pp.

Freneix, S., Cubaynes, R., 1984. Biofaciès à *Cuneigervillia–Pteromya* et biofaciès á *Eomiodon* dans l'Hettangien du Quercy (Aquitaine orientale). Geobios 17, 5–17 (pl. 1).

Fürsich, F.T., 1981. Salinity-controlled benthic associations from the Upper Jurassic of Portugal. Lethaia 14, 203–223.

Fürsich, F.T., 1994. Palaeoecology and evolution of Mesozoic salinity controlled benthic macroinvertebrate associations. Lethaia 26, 327–346.

Fürsich, F.T., Hurst, J.M., 1980. Euryhalinity of Palaeozoic articulate brachiopods. Lethaia 13, 303–312.

Fürsich, F.T., Kauffman, E.G., 1984. Palaeoecology of marginal marine sedimentary cycles in the Albian Bear River Formation of south-western Wyoming. Palaeontology 27, 501–536.

Fürsich, F.T., Werner, W., 1984. Salinity zonation of benthic associations in the Upper Jurassic of the Lusitanian Basin (Portugal). Géobios, Mémoire Spécial 8, 85–92.

Fürsich, F.T., Werner, W., 1986. Benthic associations and their environmental significance in the Lusitanian Basin (Upper Jurassic, Portugal). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 172, 271–329.

Fürsich, F.T., Schmidt-Kittler, N., Ramalho, M., 1980. Biofacies analysis of Upper Jurassic marginally marine environments of Portugal, I. The carbonate-dominated facies at Cabo Espichel, Estremadura. Geologische Rundschau 69, 943–981.

Fürsich, F.T., Freytag, S., Röhl, J., Schmid, A., 1995. Palaeoecology of benthic associations in salinity-controlled marginal marine environments: examples from the Lower Bathonian (Jurassic) of the Causses (southern France). Palaeogeography, Palaeoclimatology, Palaeoecology 113, 135–172.

Geyer, G., Hautmann, M., Hagdorn, H., Ockert, W., Streng, M., 2005. Well-preserved mollusks from the Lower Keuper (Ladinian) of Hohenlohe (Southwest Germany). Paläontologische Zeitschrift 79, 429–460.

Giambiagi, L., Alvarez, P.P., Tunik, M., 2005. Relación entre las estructuras de rift triásicas–jurásicas y el estilo de deformación en las fajas plegadas y corridas Aconcagua y Malargüe. 16° Congreso Geológico Argentino, Actas, vol. 2, pp. 81–86.

Gulisano, C.A., 1981. El ciclo Cuyano en el norte de Neuquén y sur de Mendoza. 8^{a} Congreso Geológico Argentino, Actas, vol. 3, pp. 579–592.

Gulisano, C.A., Gutiérrez Pleimling, A.R., 1994. The Jurassic of the Neuquén Basin, b) Mendoza Province — Field Guide. Asociación Geológica Argentina, Serie E 3 (103 pp).

Hallam, A., 1965. Environmental causes of stunting in living and fossil marine benthonic invertebrates. Palaeontology 8, 132–155.

Hallam, A., 1976. Stratigraphic distribution and ecology of European Jurassic bivalves. Lethaia 9, 245–259.

Hallam, A., El Shaarawy, Z., 1982. Salinity reduction of the end-Triassic sea from the Alpine region into northwestern Europe. Lethaia 15, 169–178.

Hayami, I., 1957. On the occurrence of *Cardinioides* from the Liassic Kuruma Group in central Japan (Studies on the Jurassic Pelecypods in Japan, 3). Transactions and Proceedings of the Paleontological Society of Japan, n.s. 26, 69–73.

Hayami, I., 1961. On the Jurassic pelecypod faunas in Japan. Journal of the Faculty of Sciences, University of Tokyo, Sec. 2, Geology, Mineralogy, Geography and Geophysics 13 (2), 243–343.

Hayami, I., 1975. A systematic survey of the Mesozoic Bivalvia from Japan. Bulletin, The University Museum, The University of Tokyo 10, 1–249 (Tokyo).

Huckriede, R., 1967. Molluskenfaunen mit limnischen und brackischen Elementen aus Jura, Serpulit und Wealden NW-Deutschlands und ihre paläogeographische Bedeutung. Beihefte zum Geologischen Jahrbuch 67, 1–263.

Hudson, J.D., 1963a. The recognition of salinity-controlled mollusc assemblages in the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. Palaeontology 6, 318–326.

Hudson, J.D., 1963b. The ecology and stratigraphical distribution of the invertebrate fauna of the Great Estuarine Series. Palaeontology 6, 327–348.

Hudson, J.D., 1980. Aspects of brackish-water facies and faunas from the Jurassic of north-west Scotland. Proceedings of the Geologists' Association 91, 99–105.

Hudson, J.D., 1990. Salinity from faunal analysis and geochemistry. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Palaeobiology — A Synthesis. Blackwell Scientific Publications, Cambridge, pp. 406–408.

Hudson, J.D., Clemens, R.G., Riding, J.B., Wakefield, M.I., Walton, W., 1995. Jurassic paleosalinities and brackish-water communities — a case study. Palaios 10, 392–407.

Kidwell, S.M., 1991. The stratigraphy of shell concentrations. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy — Releasing the Data Locked in the Fossil Record. Topics in Geobiology, vol. 9. Plenum Press, New York, pp. 211–290.

Kidwell, S.M., Holland, S.M., 1991. Field description of coarse bioclastic fabrics. Palaios 6, 426–434.

Kidwell, S.M., Fürsich, F.T., Aigner, T., 1986. Conceptual framework for the analysis and classification of fossil concentrations. Palaios 1, 228–238.

Kobayashi, T., Ichikawa, K., 1952. The Triassic fauna of the Heki Formation in the Province of Tamba (Kyoto Prefecture), Japan. Japanese Journal of Geology and Geography 22, 55–96.

Kobayashi, T., Takai, F., Hayami, I., 1963. Contributions to the geology and palaeontology of Southeast Asia, VII. On some Mesozoic fossils from the Khorat Series of East Thailand and a note on the Khorat Series. Japanese Journal Geology and Geography 34, 181–192.

Kondo, Y., Kozai, T., Kikuchi, N., Sugawara, K., 2006. Ecologic and taxonomic diversification in the Mesozoic brackish-water bivalve faunas in Japan, with emphasis on infaunalization of heterodonts. Gondwana Research 10, 316–327.

Kozai, T., Ishida, K., 2003. Early Cretaceous non-marine bivalve faunal groups from central and East Shikoku, Japan. Memoir of the Fukui Prefectural Dinosaur Museum 2, 133–148.

Kozai, T., Ishida, K., Hirsch, F., Park, S.-O., Chang, K.-H., 2005. Early Cretaceous non-marine mollusc faunas of Japan and Korea. Cretaceous Research 26, 97–112.

Kurushin, N.I., 1990. Nobye i redkie vidy dvustvorchatykh mollyuskov iz triasovykh otlozhenyj severa srednej Sibiri. In: Dagis, A.S., Dubatolov, V.N. (Eds.), Trias Sibiri. Trudy Instituta Geologii i Geofiziki, Vypusk, vol. 767, pp. 13–28 (Novosibirsk).

Lanés, S., 2002. Paleoambientes y paleogeografía de la primera transgresión en Cuenca Neuquina, Sur de Mendoza. Tesis Doctoral, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales. 403 pp. Unpublished.

Lanés, S., 2005. Late Triassic to Early Jurassic sedimentation in northern Neuquén Basin, Argentina: tectosedimentary evolution of the first transgression. Geologica Acta 3 (2), 81–106.

Lanés, S., Manceñido, M., Damborenea, S., in press. *Lapispira*: a double helicoidal burrow from Jurassic marine nearshore environments. In: R. Bromley, L. A. Buatois, M.G. Mángano, J. Genise, R. Melchor (Eds.), Sediments–organism Interactions: A Multifaceted Ichnology. SEPM Special Publication 88.

Legarreta, L., Gulisano, C.A., 1989. Análisis estratigráfico de la cuenca Neuquina (Triásico superior–Terciario inferior). In: Chebli, G.A., Spalletti, L.A. (Eds.), Cuencas Sedimentarias Argentinas. Serie de Correlación Geológica (Tucumán), vol. 6, pp. 221–244.

Legarreta, L., Uliana, M.A., 2000. El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. 1. Facies sedimentarias. In: Caminos, R. (Ed.), Geología Argentina. Instituto de Geología y Recursos Minerales (Argentina) Anales, vol. 29, pp. 399–416.

Legarreta, L., Gulisano, C.A., Uliana, M.A., 1993. Las secuencias sedimentarias Jurásico–Cretácicas. In: Ramos, V.A. (Ed.), Geología y Recursos naturales de Mendoza. Mendoza, 12ª Congreso Geológico Argentino y 2ª Congreso de Exploración de Hidrocarburos, Relatorio, pp. 87–114.

Manceda, R., Figueroa, D., 1993. La inversión del rift mesozoico en la Faja Fallada y Plegada de Malargüe, provincia de Mendoza. 12ª Congreso Geológico Argentino y 2ª Congreso de Exploración de Hidrocarburos. Actas, vol. 3, pp. 219–232.

Manceda, R., Figueroa, D., 1995. Inversion of the Mesozoic Neuquén Rift in the Malargüe Fold and Thrust Belt, Mendoza, Argentina. In: Tankard, A.J., Suárez Soruco, R., Welsink, H.J. (Eds.), Petroleum Basins of South America. American Association of Petroleum Geologists, Memoir, vol. 62, pp. 369–382.

Martínez, S., Figueiras, A., Da Silva, J.S., 1993. A new Unionidae (Mollusca, Bivalvia) from the Tacuarembó Formation (Upper Triassic–Upper Jurassic), Uruguay. Journal of Paleontology 67 (6), 962–965.

McRoberts, C.A., 1998. Late Triassic (Norian–Rhaetian) bivalves from the Antimonio Formation, northwestern Sonora, Mexico. Revista Mexicana de Ciencias Geológicas 14 (2), 167–177 (1997).

Mongin, D., 1967. Les mollusques du Bathonien sâumatre du Moyen Atlas. Notes et Mémoires du Service Géologique du Maroc 200, 37–94.

Morter, A.A., 1984. Purbeck–Wealden Beds Mollusca and their relationship to ostracod biostratigraphy, stratigraphical correlation and palaeoecology in the Weald and adjacent areas. Proceedings of the Geologists' Association 95, 217–234.

Newton, C.R., Whalen, M.T., Thompson, J.B., Prins, N., Delalla, D., 1987. Systematics and Paleoecology of Norian (Late Triassic) Bivalves from a Tropical Island Arc: Walowa Terrane, Oregon. Paleontological Society Memoir 22. Journal of Paleontology 61 (4), 1–83 (Supplement).

Nuttall, C.P., 1990. A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. Bulletin, British Museum of Natural History (Geology) 45, 165–371.

Oertli, H.J., 1964. The Venice System for the classification of marine waters according to salinity. Publicazioni della Stazienoe Zoologica di Napoli 33, 611 (Supplement).

Parker, R.H., 1959. Macro-invertebrate assemblages of central Texas coastal bays and Laguna Madre. Bulletin of the American Association of Petroleum Geologists 43, 2100–2166.

Powell, E.N., Stanton Jr., R.J., 1996. The application of size–frequency distribution and energy flow in paleoecologic analysis: an example using parautochthonous death assemblages from a variable salinity bay. Palaeogeography, Palaeoclimatology, Palaeoecology 124, 195–231.

Pritchard, D.W., 1955. Estuarine circulation patterns. Proceedings of the American Society of Civil Engineers 81 (717), 1–11.

Ramos, V.A., 1992. Geología de la Alta Cordillera de San Juan. Revista de la Asociación Geológica Argentina 47 (3), 268–269.

Reijenstein, C., 1967. Estratigrafía y tectónica de la zona al norte del río Atuel entre los arroyos Blanco y Malo (Provincia de Mendoza). Trabajo Final de Licenciatura. Universidad de Buenos Aires. 97 pp. (Unpublished).

Remane, A., 1958. Ökologie des Brackwassers. In: Remane, A., Schlieper, C. (Eds.), Die Biologie des Brackwassers. Schweizerbart, Stuttgart. 216 pp.

Riccardi, A., 1983. The Jurassic of Argentina and Chile. In: Moullade, M., Nairn, A.E.M. (Eds.), The Phanerozoic Geology of the World II. The Mesozoic, B. Elsevier Sci. Publ., pp. 201–263.

Riccardi, A., Iglesia Llanos, M.P., 1999. Primer hallazgo de amonites en el Triásico de la Argentina. Revista de la Asociación Geológica Argentina 54, 298–300.

Riccardi, A., Damborenea, S., Manceñido, M.O., Ballent, S.C., 1988. Hettangiano y Sinemuriano marinos en Argentina. 5^{a} Congreso Geológico Chileno, Actas, vol. 2, pp. 359–377.

Riccardi, A.C., Damborenea, S.E., Manceñido, M.O., Ballent, S.C., 1991. Hettangian and Sinemurian biostratigraphy of Argentina. Journal of South American Earth Sciences 4, 159–170.

Riccardi, A.C., Damborenea, S.E., Manceñido, M.O., 1993. Invertebrados mesozoicos. In: Ramos, V. (Ed.), Geología y Recursos Naturales de la Provincia de Mendoza. Relatorio 12° Congreso Geológico Argentino, vol. II-12, pp. 329–339.

Riccardi, A., Damborenea, S.E., Manceñido, M.O., Scasso, R., Lanés, S., Iglesia Llanos, P., Stipanicic, P.N., 1997. Primer registro de Triásico marino fosilífero de la Argentina. Revista de la Asociación Geológica Argentina 52 (2), 228–234.

Riccardi, A.C., Damborenea, S.E., Manceñido, M.O., Ballent, S.C., 2000 [1999]. El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. 3. Bioestratigrafía. In: Caminos, R. (Ed.), Geología Argentina, Instituto de Geología y Recursos Minerales (Buenos Aires), Anales, vol. 29, pp. 419–432.

Riccardi, A.C., Damborenea, S.E., Manceñido, M.O., Iglesia Llanos, M.P., 2004. The Triassic/Jurassic boundary in the Andes of Argentina. Rivista Italiana di Paleontologia e Stratigrafia 110, 69–76.

Schmidt, H., 1951. Erkennbarkeit fossiler Brackwasserabsätze. Zeitschrift der Deutschen Geologischen Gessellschaft 103, 9–16.

Schmidt, M., 1928. Die Lebewelt unserer Trias. Hohenlohe'sche Buchhandlung, Öhringen. 143 pp.

Smith, L., 1988. Natural Communities of Louisiana. Louisiana Department of Wildlife and Fisheries, Baton Rouge. 45 pp.

Stoliczka, F., 1870–1871. Cretaceous fauna of southern India. V. 3. The Pelecypoda, with a review of all known genera of this class, fossil and Recent Geological Survey of India. Palaeontologia Indica. Series 6 (3), 1–537.

Sugawara, K., Kondo, Y., 2004. Brackish and shallow-marine benthic associations of the Lower Jurassic Niranohama Formation in the Shizugawa area, South Kitakami Belt, northeast Japan. Research Report of the Kochi University (Natural Science) 53, 21–40.

Tamura, M., 1980. A summary of the Cretaceous bivalves of fresh and brackish waters in Japan. Journal of the Geological Society of Korea 16, 223–238.

Tan, F.C., Hudson, J.D., 1974. Isotopic studies on the palaeoecology and diagenesis of the Great Estuarine Series (Jurassic) of Scotland. Scottish Journal of Geology 10, 9–128.

Tankard, A.J., Uliana, M.A., Welsink, H.J., Ramos, V.A., Turic, M., França, A.B., Milani, E.J., Brito Neves, B.B., Eyles, N., Skarmeta, J., Santa Ana, H., Wiens, F., Cirbián, M., López Paulsen, O., Germs, G.J.B., De Wit, M.J., Machacha, T., Miller, R., 1995. Structural and tectonic controls of basin evolution in southwestern Gondwana during the Phanerozoic. In: Tankard, A.J., Suárez Soruco, R., Welsink, H. (Eds.), Petroleum Basins of South America. American Association of Petroleum Geologists, Memoir, vol. 62, pp. 5–52.

Teske, P.R., Wooldridge, T., 2003. What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs. sediment particle size. Estuarine, Coastal and Shelf Science 57, 225–238.

Thayer, C.W., 1981. Ecology of living brachiopods. In: Dutro, J.T., Boardman, R.S. (Eds.), Lophophorates, Notes for a Short Course. University of Tennessee Department of Geological Sciences, Studies in Geology, vol. 5, pp. 110–126.

Tucker, M.E., Wright, V.P., 1990. Carbonate Sedimentology. Blackwell Science, Oxford. 482 pp.

Uliana, M.A., Biddle, K.T., 1988. Mesozoic–Cenozoic paleogeographical and geodynamic evolution of southern South America. Revista Brasileira de Geociências 18, 172–190.

Vergani, G.D., Tankard, A.J., Belotti, H.J., Welsink, H.J., 1995. Tectonic evolution and paleogeography of the Neuquén Basin, Argentina. In: Tankard, A.J., Suárez Soruco, R., Welsink, H.J. (Eds.), Petroleum Basins of South America. American Association of Petroleum Geologists, Memoir, vol. 62, pp. 383–402.

Waagen, L., 1907. Die Lamellibranchiaten der Pachycardientuffe der Seiser Alm nebst vergleichend paläontologischen und phylogenetischen Studien, Abhandlungen der k.k. Geologischen Reichsanstalt 18, 1–180 (Taf. 25–34).

Wöhrmann, S.F.v., 1893. Ueber die systematische Stellung der Trigoniden und die Abstammung der Nayaden, Jahrbuch k.k. Geologische Reichsanstalt 43, 1–12.

Yin, Jiarun, 1989. Brackish water bivalve fauna in Jurassic Yanshiping Group of southern Qinghai and its paleosalinity analysis. Acta Palaeontologica Sinica 28 (4), 415–434 (Pl. I–IV).

Yin, Jiarun, Grant-Mackie, J.A., 2005. Late Triassic–Jurassic bivalves from volcanic sediments of the Lhasa block, Tibet. New Zealand Journal of Geology and Geophysics 48, 555–576.