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Biofacies analysis of Hettangian-Sinemurian bivalve/brachiopod associations from the Neuquén Basin (Argentina)

S.E. DAMBORENEA and M.O. MANCEÑIDO

CONICET. Departamento de Paleontología de Invertebrados, Museo de Ciencias Naturales de La Plata
Paseo del Bosque s/n, 1900 La Plata, Argentina. Damborenea E-mail: sdambore@museo.fcnym.unlp.edu.ar
Manceñido E-mail: mmanceni@museo.fcnym.unlp.edu.ar

---| **A B S T R A C T** |---

Based upon extensive sampling with strict stratigraphical control on Hettangian and Sinemurian deposits cropping out at the river Atuel region (southwest Mendoza Province), the presence of all bivalve and brachiopod genera was recorded. Data gathered from the analysed interval were processed by multivariate analysis and the resulting Q-mode dendrogram was used to discriminate five associations (i.e. *Entolium*-limoids, *Pholadomya-Pinna-Pleuromya*, *Weyla-Gryphaea*, *Lywea* and *Cardinioides*). These are not in simple stratigraphical succession but are recurrent, reflecting palaeosynecological and biofacies influences. The palaeoenvironmental implications of these associations are analysed, as well as their geographical and stratigraphical distributions in the studied sections (Arroyo Malo, El Pedrero and Las Chilcas). The *Cardinioides* association is controlled by palaeosalinity and corresponds to a paralic/estuarine environment, of restricted geographical and stratigraphical distribution, whereas the remaining associations correspond to normal marine shelf to littoral environments. The *Lywea* association is interpreted as allochthonous and probably an impoverished subset derived from the diverse *Weyla-Gryphaea* association. On the basis of the palaeoautecological characteristics of the taxa involved in terms of guilds represented in these benthonic associations, it is concluded that most of the associations were dominated by the epifauna, whereas in the *Pholadomya-Pinna-Pleuromya* association the infauna and semi-infauna were particularly conspicuous and diverse, and the *Cardinioides* association was characterized by shallow infauna. Typical basinal biofacies from deeper, off-shore environments, and fresh-water biofacies, are both missing.

KEYWORDS | Hettangian. Sinemurian. Bivalvia. Brachiopoda. Palaeoecology.

INTRODUCTION

Early Jurassic benthonic invertebrate faunas from western Argentina are diverse, geographically widespread, and their systematics are relatively well-known. Bivalves and brachiopods are the most diverse and abundant groups. A sizeable part of their systematic description has already been published (Manceñido, 1990; Pérez et al., 1995; Damborenea, 1998, 2002, 2004), and the remaining are in progress. Local studies on the distribution and palaeoecology of benthonic faunas from the marine Lower Jurassic of southern South America have been published by Damborenea et al. (1975) for Pliensbachian beds of the Piedra Pintada area, southern

Neuquén, Argentina, and by Aberhan (1992, 1993a, 1993b) for Sinemurian to Toarcian carbonate ramp deposits in northern Chile.

The aim of this paper is to present a synthesis of a general palaeoecological interpretation dealing with the bivalve and brachiopod distribution in the Neuquén Basin during earliest Jurassic times. The Hettangian-Sinemurian succession chosen for the present analysis represents not only a key stage in the Mesozoic evolution of the basin, just preceding the widespread oceanic flooding of the Neuquén embayment (Legarreta and Uliana, 1996, 2000), but is also interesting in the context of the global faunal recovery after the end-Triassic mass extinction event (cf. Sandy, 1995; McRoberts et al., 1997; Hallam and Wignall, 2000; Dulai, 2001).

GEOLOGICAL SETTING

Marine sediments of Hettangian-Sinemurian age in Argentina are limited to the southern Mendoza region, very well exposed in the Atuel River area (Figs. 1 and 2) (Riccardi et al., 1988, 1991, 2004). These sediments, referred to El Cholo (or Puesto Araya) Formation, were deposited during early rifting episodes in the northern part of the Neuquén Basin, a back-arc basin developed in the western margin of the South American Plate, and generally overlie conglomerates and sandstones, mostly of fluvial origin (El Freno Formation; Riccardi and Damborenea, 1993). The Rhaetian-Hettangian marine deposits
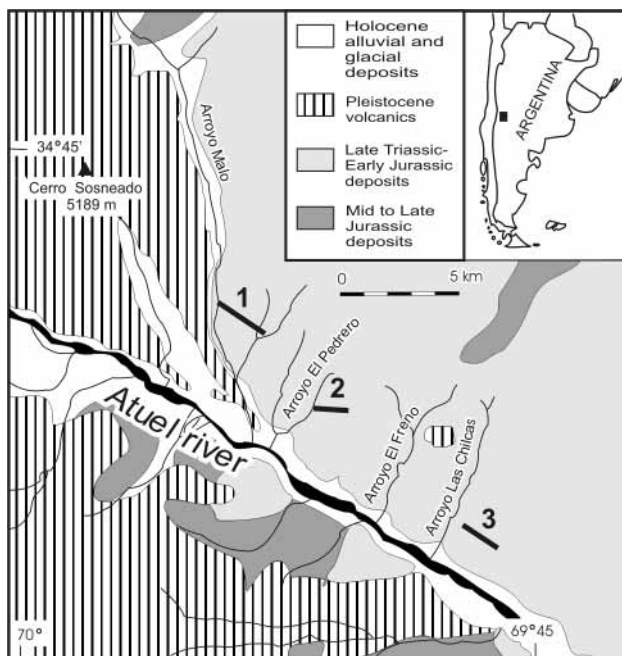

FIGURE 1 | **Location map of the study area in southern Mendoza Province, Argentina. Geological sketch adapted from Volkheimer, 1978. 1. Arroyo Malo section. 2. Arroyo El Pedrero section. 3. Arroyo Las Chilcas section.**

FIGURE 2 | **Photographs of the main sections. A) Arroyo Malo section. B) Arroyo El Pedrero section. C) Arroyo Las Chilcas section.**

of the Atuel River region indicate that the initial system of unconnected halfgrabens was only locally covered by the sea, preceding the following phase (late Sinemurian-Pliensbachian) which involved the coalescence of the depocentres and enlargement of the area under marine influence, thus developing the Neuquén embayment (Legarreta and Uliana, 1996, figs. 8 and 9; 2000, Figs. 3 and 5).

The most recent regional interpretation of the Atuel River area was done by Lanés (2002, 2005) in a detailed and comprehensive study that substantially improves previous knowledge on the sedimentological and basinal evolution of the area. She recognized two regions with different tectosedimentary histories, to the West and East of El Freno creek, respectively. Three sections to the

north of the Atuel River are here analysed (Fig. 3). Two of them (Arroyo Malo and Arroyo El Pedrero) are located in Lanés western region, which records well bedded,

coarsening- and thickening upwards mudstones, sandstones and conglomerates deposited by fluvio-dominated, slope-type and intermediate shelf fan deltas. The Arroyo
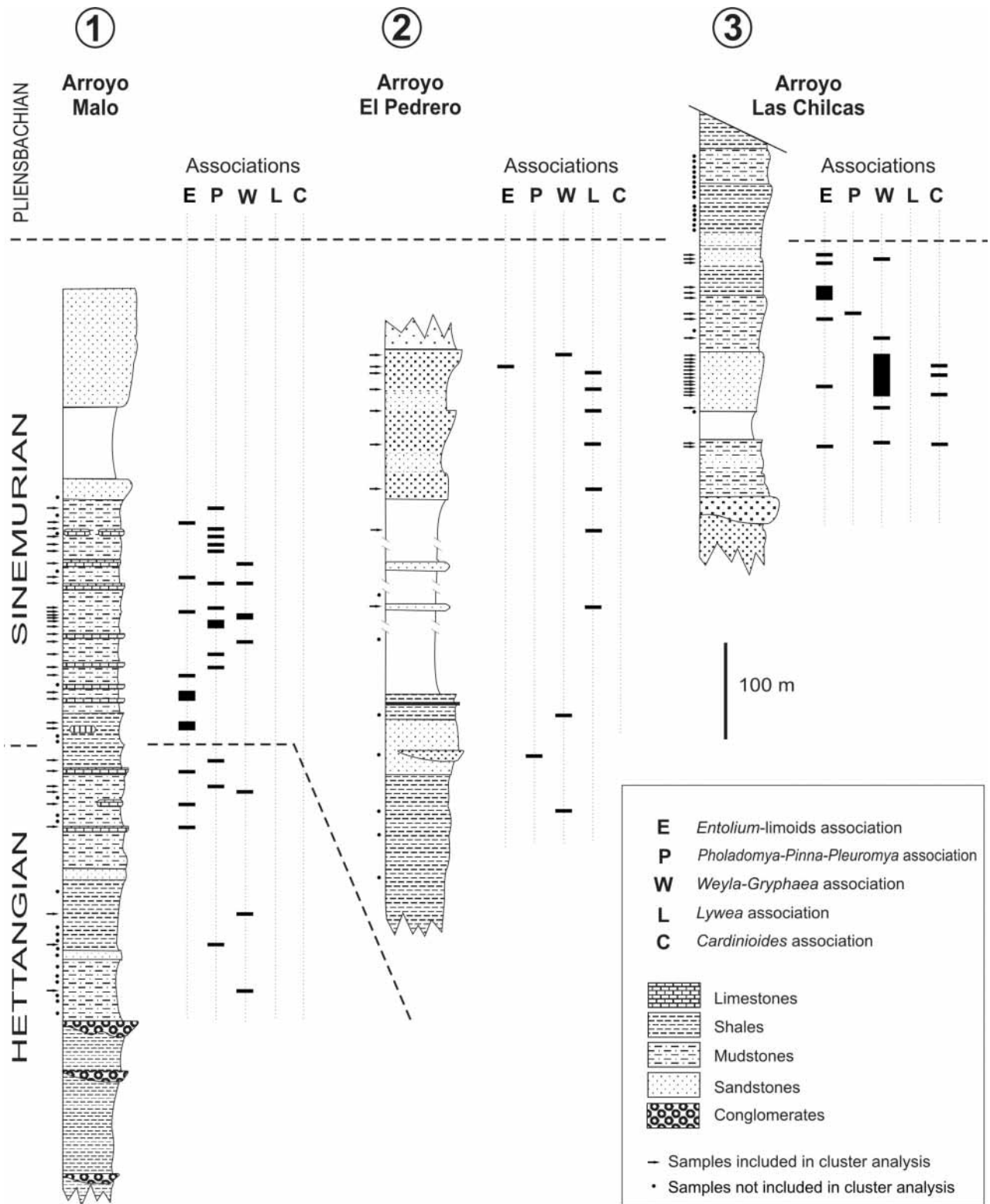

FIGURE 3 | **General lithologic sketch of the logged sections (located in Fig. 1), with stratigraphic position of samples and distribution of the recognized associations. Horizontal distances not to scale.**

Las Chilcas section belongs to the eastern region, with well bedded, fining- and thinning-upwards sandstones and shales corresponding to transgressive siliciclastic storm-dominated shelf deposits (Lanés, 2005). As seen below, these different depositional environments also affect the composition and distribution of the faunal associations.

Significant lateral changes in the age of the earliest transgressive marine deposits are evident in this area (Fig. 3), their base being progressively younger towards the East (Riccardi et al., 1988, 1991, 1997; Riccardi and Iglesia Llanos, 1999) in agreement with a fast initial drowning advancing from NNW to SSE over the underlying dominant rifting fabric (Legarreta and Uliana, 1996). For this reason, Hettangian beds reflecting the initial marine encroachment are confined to the Arroyo Malo section.

Biostratigraphy

The biostratigraphical framework of this analysis is the zonation for the Neuquén Basin based on various macroinvertebrate groups (Riccardi et al., 1988, 1991, 2000a, 2000b; Manceñido, 1990). Whenever possible, samples were dated according to ammonite occurrences, or otherwise, by their bivalve or brachiopod content. The analysed interval corresponds to the following units: *Palmoxytoma* cf. *cygnipes, Otapiria pacifica* and *Cardinia* cf. *listeri* bivalve Association Zones, and the *Furcirhynchia* cf. *trechmanni* and *Gibbirhynchia dereki* brachiopod Association Zones, spanning Hettangian and Sinemurian times (Fig. 4).

MATERIAL AND METHODS

This research is based on the samples collected from three main field sections and other supplementary localities in the river Atuel region (Figs. 1 and 2), northern bank, southwest Mendoza province, Argentina. Most of the samples were collected by the authors and colleagues during several field trips between 1973 and 2003. Material from other collectors was also occasionally included, as a means for independent checking (collected by Reijenstein in 1967; and by Lanés between 1997 and 2003). Location of samples in each section is shown on Fig. 3.

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*		*Rhynchonelloidea cuyana*	
PLIENSBACHIAN	*Fanninoceras*	*disciforme*	*Radulonectites sosneadoensis*		*Rhynchonelloidea burckhardti*	
		fannini				
		behrendseni	*Otapiria neuquensis*			
	Dubariceras					
	Tropidoceras					
	Miltoceras					
SINEMURIAN	*Epophioceras*		*Cardinia cf. listeri*		*Gibbirhynchia dereki*	
	?		*Otapiria pacifica*			
	"*Agassiceras*"					
	"*Vermiceras*"					
HETTANGIAN	*Badouxia canadensis*		*Palmoxytoma cf. cygnipes*		*Furcirhynchia cf. trechmanni*	
	"*Waehneroceras-Schlotheimia*"					
	"*Psiloceras*"					
	Psiloceras rectocostatum					
	?					

FIGURE 4 | **Biostratigraphic zonation for the Early Jurassic of the Neuquén Basin based on ammonites, bivalves and brachiopods. Time span included in this study is shaded.**

All bivalves and brachiopods were identified in every sample at species level, although data are used at the genus level (as already discussed in Damborenea et al., 1975). The use of genera instead of species helps to minimize the risk of bias due to overweighing stratigraphically restricted species in the clustering process. Conversely, the possible discrimination of so-called "parallel associations" (Fürsich, 1984; Aberhan, 1993a) becomes impractical as similar congeneric groupings would tend to be pooled through time. Only complete specimens or large identifiable fragments were considered, since these attributes of death assemblages have been shown to yield high life/death fidelity (Kowalewski et al., 2003).

The composition of each sample is regarded as representative of the faunal content of each sampled bed and amenable to qualitative treatment. Our data cannot be used quantitatively because sampling sites were not randomly chosen and sample size was not uniform. Besides, it is long known that qualitative characteristics, such as taxonomic composition and spatial-temporal distribution are most likely to be accurately preserved in the fossil record, and presence-absence patterns are usually adequate for palaeosynecological identifications, whereas quantitative aspects (like diversity, equitability, homogeneity, trophic relationships) are often not, as pointed out by Macdonald (1976).

Data were initially plotted in a presence-absence matrix 66 genera x 104 samples. Taxa present in only one sample, and most samples with a single taxon were omitted. Nevertheless, all the taxa were taken into account for the palaeoecological interpretation. The cluster analysis was carried out considering the distribution of the remaining 44 genera in 85 samples. The resulting data matrix was processed with several clustering techniques, using the NTSYSpc program version 2.0 (Rohlf, 1997; for the methodological rationale chosen see Damborenea et al., 1975; Jones, 1990; Shi, 1993). Dice similarity coefficient was applied:

$$D_{i\text{-}j} = 2C_{i\text{-}j}/(N_i+N_j)$$

$C_{i\text{-}j}$: number of genera in common between samples I and J
N_i: total number of genera in sample I
N_j: total number of genera in sample J

The results using unweighted paired group clustering technique using arithmetic averages (UPGMA) are presented here.

Rather than attempting a detailed reconstruction of fossil food chains, which may become unreliable due to intrinsic problems involved (Stanton, 1976), the preferable alternative followed for the present analysis is to characterize the units in terms of taxonomic composition and guild content of the preserved shelly fauna (Aberhan, 1994; Brenchley and Harper, 1998; with distinction between detritus and deposit feeders as in Bromley, 1990). Molluscan death assemblages are thought to provide a reliable means of assessing community composition (see Kidwell, 2001).

The taxonomic diversity index (TDI) of each association was estimated in the same way as in Damborenea et al. (1975, p. 190) for the reasons discussed there.

All the fossil material analysed for this study is deposited in the Invertebrate Palaeontology collection, La Plata Natural Sciences Museum, La Plata, Argentina (MLP).

RESULTS

Five groups can be recognized in the Q-mode dendrogram (Fig. 5): *Entolium*-limoids (E, samples 1397 to 1953), *Weyla-Gryphaea* (W, samples 1694 to Re50), *Pholadomya-Pinna-Pleuromya* (P, samples 1895 to 1474), *Lywea* (L, samples 1453 to AP13) and *Cardinioides* (C, sample CB2-12) associations. These are statistically recurrent groupings, which are regarded as associations, a term here used in the meaning recommended by Kauffman and Scott (1976). The first three associations have a wide geographical and stratigraphical distribution, the last two are somewhat restricted. The alternating stratigraphic relationships and marked overlap of the faunal associations (Fig. 3) demonstrate that they should not be regarded as biochronological units. Rather, their stratigraphic distributional pattern indicates clearly that they are ecological units which bear biofacial and palaeoecological significance (cf. Scott, 1974; Damborenea et al., 1975; Warme et al., 1976). The faunal contents of each recognized association is provided in the Appendix.

Entolium-limoids association (E)

This is a diverse association both regarding the taxonomic composition (TDI = 53.1) and the guilds represented (Figs. 6 and 10A). It is dominated by pectinoid (*Entolium, Praechlamys, Eopecten, Camptonectes, Agerchlamys, Pseudopecten*), limoid (*Plagiostoma, Pseudolimea, Antiquilima, Ctenostreon*) and buchioid genera (*Otapiria, Asoella*). Therefore, epifaunal, byssate, suspension feeding bivalves are well represented. The suspension feeding infauna appears as subordinate elements, comprising burrowers, mainly shallow (*Groeberella*, Astartidae, *Lingularia*) and some deep (*Pholadomya, Pleuromya*), endobyssate (*Myoconcha, Pinna*), and even some deposit feeding shallow burrowers (*Palaeoneilo*?). Pedunculate taxa include rhynchonelloids (*Gibbirhynchia*) and terebratuloids (*Peristerothyris*?). The associated
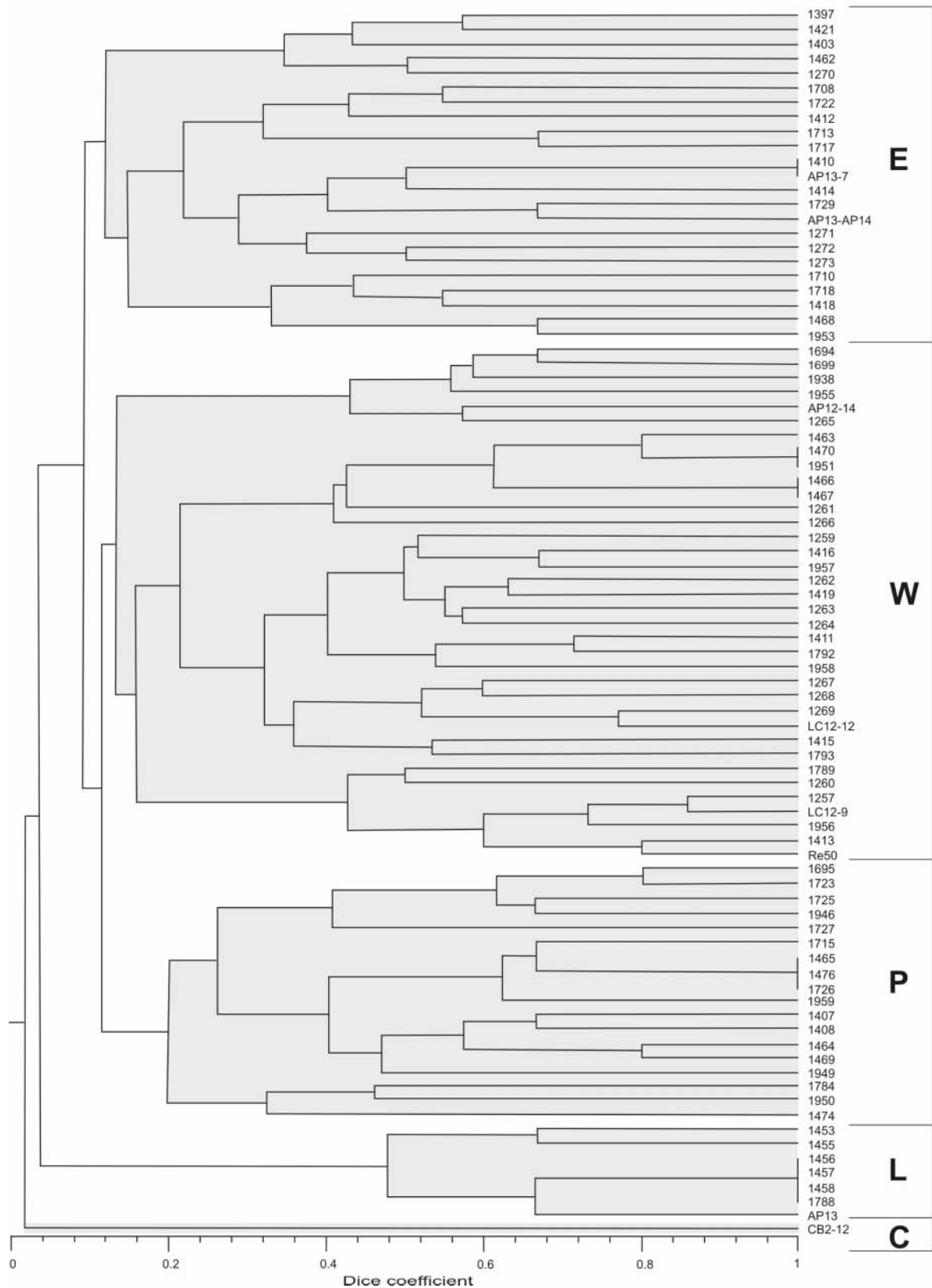
FIGURE 5 | **Q-mode dendrogram of the Hettangian-Sinemurian associations of bivalve/brachiopod using Dice coefficient. Numbers correspond to field sample numbers (most located in sections published by Riccardi et al. (1988, 1991); see also Fig. 3 here). E: *Entolium*-limoids association; W: *Wey-la-Gryphaea* association; P: *Pholadomya-Pinna-Pleuromya* association; L: *Lywea* association; C: *Cardinioides* association.**

fauna includes ammonoids and gastropods (common), and occasionally scaphopods, echinoderms and solitary corals.

This association has a very wide stratigraphical distribution in the study area, and is well represented throughout the middle and upper parts of the Arroyo Malo and Las Chilcas sections, where it occurs in a recurrent alternating pattern with both the *Pholadomya-Pinna-Pleuromya* and the *Weyla-Gryphaea* associations (Fig. 3). The whole fauna, which includes stenohaline brachiopods, ammonoids, bivalves and corals, is indicative of euhaline sea-water.

There are local variations of the faunal contents of this association. Both smooth shelled and ribbed limoids preserved with their valves closed or gaping are conspicuous locally, in sediments spanning Hettangian to late Sinemurian age, and a subordinate or independent unit characterized by these bivalves may even deserve a more formal recognition eventually. *Entolium* is dominant at some levels forming widespread pavements of almost complete valves of nearly equal (and usually large) size, as already pointed out by Damborenea (2002). Similar *Entolium* concentrations as shell-pavements have been recognized elsewhere, for instance, in Pliensbachian outcrops of East Greenland by Rosenkrantz (1942, fig. 15), in Early and Middle Jurassic deposits of Germany (Staesche, 1926), and more recently, for the lower and upper Pliensbachian of Chile, where they appear in assemblages linked to middle carbonate ramp depositional settings, located rather away from the shore (depth zone 2 of Aberhan, 1992, 1993b).

This is the only association in which certain peculiar shallow infauna has been recorded. According to Sellwood (1972), presence of linguloid brachiopods as well as detritus/deposit feeders (here represented by both protobranchs and dentaliids), may suggest a local regime with relatively turbid waters and little current action; nekto-benthonic, thin-shelled pectinids would also point to outer-shelf settings. On the other hand, the presence of pedunculate articulate brachiopods indicates normal, sublittoral sea floors, and in no way would they fit into any deep water category, within the scheme for Mesozoic environments recognized by Ager (1965, 1993). At genus level articulate brachiopods resemble those of sublittoral biotopes with muddy bottoms recognized by Tchoumatchenco (1972, 1996) for the Hettangian-Sinemurian of Bulgaria, thus corresponding to an outer shelf brachiopod biofacies in the scheme compiled by Sandy (1995).

Certain resemblance to sub-biofacies A4 recognized for the Pliensbachian of Neuquén Province (Damborenea et al., 1975) may be worth recording. It should be also
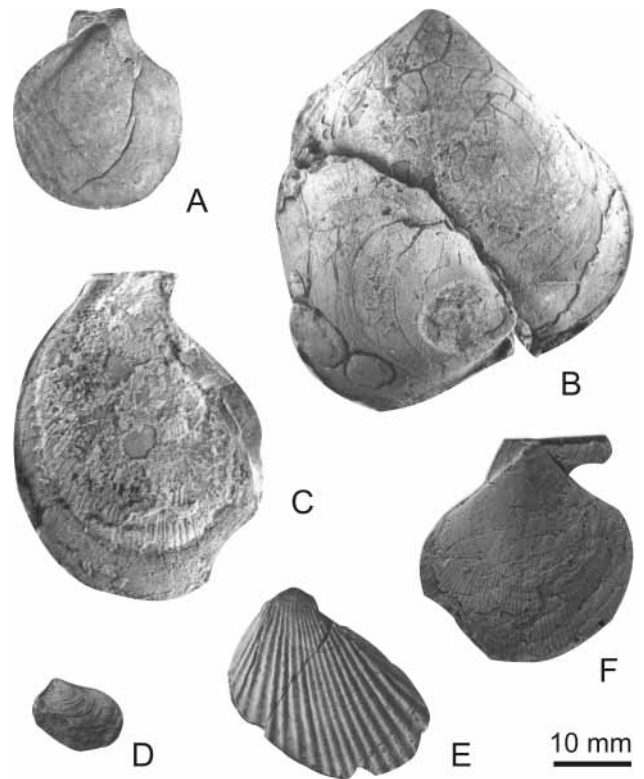

FIGURE 6 | **Some elements of the *Entolium*-limoids association. A) *Entolium (Entolium)* cf. *lunare* (RÖMER), MLP 24950, Arroyo Las Chilcas, Sinemurian. B) *Plagiostoma cf. giganteum* J. SOWERBY, MLP 31154, Arroyo Malo, Sinemurian. C) *Antiquilima* sp., MLP 28423, Arroyo Malo, Sinemurian. D) *Otapiria pacifica* COVACEVICH and ESCOBAR, MLP 22379, Arroyo Malo, Hettangian. E) *Pseudolimea* cf. *duplicata* (J. de C. SOWERBY), MLP 31156, Arroyo Las Chilcas, Sinemurian. F) *Praechlamys* cf. *valoniensis* (DEFRANCE), MLP 25010-a, Arroyo Malo, early Sinemurian.**

recalled that an assemblage characterized by *Plagiostoma* has been reported for the upper Sinemurian of Chile and interpreted as a para-autochthonous relict in a shallow siliciclastic ramp by Aberhan, but without locating it in his detailed scheme; yet *Plagiostoma* is further present in other associations of his depth zones 1 and 2, and thus regarded as an overall indicator of shallow shelves (Aberhan, 1992, 1993a, 1993b). Likewise, *Plagiostoma* and *Entolium* co-occur in the epeiric carbonate mud community reconstructed for the Sinemurian-Pliensbachian of Dorset (England) by Sellwood (1978, fig. 72). Considering the *Entolium*-limoids association as a whole, it shows a close correspondence with composite assemblage C2 within the integrated environmental model developed for Early and Middle Jurassic faunas of western USA by Taylor (1982) and Taylor et al. (1983).

Pholadomya-Pinna-Pleuromya association (P)

This is a moderately diverse (TDI = 35.9) association (Figs. 7 and 10B), characterized by the deep burrowers *Pholadomya* and *Pleuromya* and the semi-infaunal
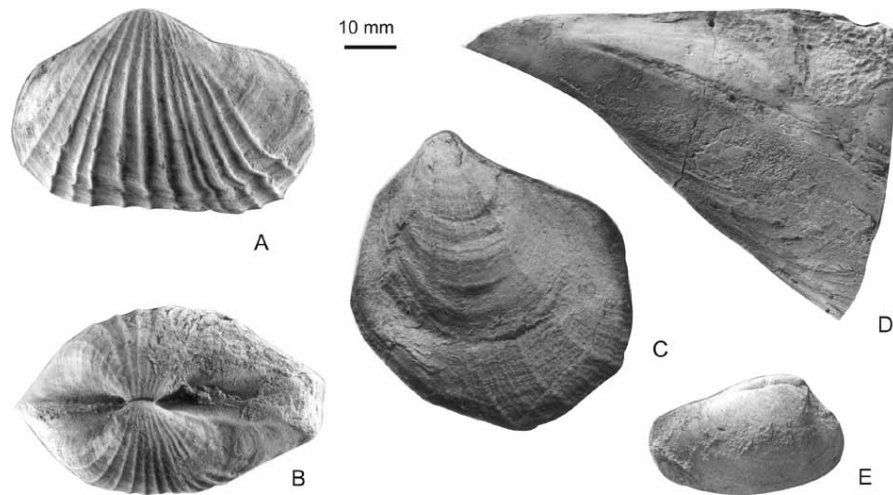
FIGURE 7 |Some elements of the *Pholadomya-Pinna-Pleuromya* association. A and B) *Pholadomya* sp., MLP 31158, arroyo Malo, early Sinemurian. C) *Eopecten* cf. *velatus* (GOLDFUSS), MLP 22256, Arroyo Malo, Hettangian. D) *Pinna cf. folium* YOUNG and BIRD MLP 31160, arroyo Malo, early Sinemurian. E) *Pleuromya* sp., MLP 31159, arroyo Malo, early Sinemurian.

endobyssate *Pinna*. There are scarce rhynchonelloid brachiopods (*Furcirhynchia*, *Calcirhynchia*?), other infaunal suspension feeding bivalves, including deep and shallow burrowers (Astartidae, Trigoniidae, *Sphaeriola*?) and endobyssate semi-infaunal forms (*Inoperna*), many of them can be found in life position. Nevertheless, a variety of epifauna is also present: epibyssate (*Eopecten, Camptonectes, Chlamys, Pseudolimea, Plagiostoma, Palmoxytoma*), recliners (*Kolymonectes*?, *Entolium, Gryphaea*), pedunculate bra-

chiopods and cemented oysters, suggesting local availability of firm substrates (and/or benthonic islands), within an overall soft-bottom environmental setting. The overall faunal composition suggests a euhaline environment.

This association is well represented along the Arroyo Malo section, spanning Hettangian and Sinemurian times. It occurs also occasionally at the El Pedrero and Las Chilcas sections (Fig. 3).
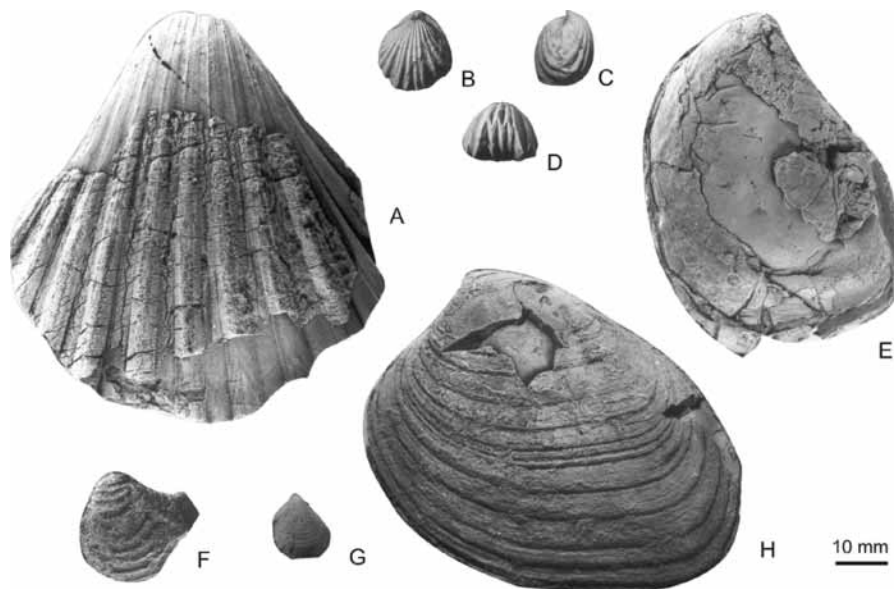

FIGURE 8 |Some elements of the *Weyla-Gryphaea* association. A) *Weyla alata* (v. BUCH), MLP 31127, La Horqueta, arroyo Blanco, late Sinemurian. B to D) *Gibbirhynchia dereki* MANCEÑIDO, MLP 24413, arroyo Las Chilcas, late Sinemurian. E) *Gryphaea* aff. *cymbium* LAMARCK, MLP 28075, arroyo Las Chilcas, late Sinemurian. F) *Frenguelliela* sp., MLP 31153, arroyo Las Chilcas, late Sinemurian. G) *Asoella asapha* (LEANZA), MLP 28024-a, arroyo Las Chilcas, late Sinemurian. H) *Cardinia cf. listeri* (J. SOWERBY), arroyo Las Chilcas, late Sinemurian.

In the Early Jurassic of Chile Aberhan (1992, 1993a, 1993b) recognized a number of broadly comparable associations such as *Pleuromya uniformis*, *Pachymya rotundocaudata*, and *Pholadomya hemicardia*, all of them referred to shallow shelf mixed siliciclastic-carbonate bottoms of his bathymetric zone 1. A tenuous resemblance to sub-biofacies A1, reported from the Pliensbachian of Neuquén (Damborenea et al., 1975) is also perceivable, albeit without strict matching in every detail. Likewise, a broad similarity is evident with the silty clay and muddy sand subtidal communities reconstructed for the Lower Lias of Yorkshire (England) by Sellwood (1972; 1978, figs. 65-66). Concerning the environmental model developed for Early and Middle Jurassic faunas of western USA (Taylor, 1982; Taylor et al., 1983), the *Pholadomya-Pinna-Pleuromya* association compares favourably with their composite assemblage C1.

Weyla-Gryphaea association (W)

This is the most diverse (TDI = 65.6) association (Figs. 8 and 10C), dominated by free-lying reclining bivalves (*Gryphaea*, *Weyla*, *Entolium*, *Lywea*) together with burrowing bivalves, both shallow (*Frenguelliella*, *Grammatodon*, *Cardinia*, *Groeberella*, *Jaworskiella*, astartids) and deep (*Pholadomya*, *Goniomya*, *Pleuromya*, *Gresslya*). Also well represented are epifaunal pedunculate brachiopods (*Gibbirhynchia*, *Spiriferina*, *Zeilleria*), epifaunal bivalves (*Asoella*, *Lycettia*, a variety of pectinoids), semi-infaunal endobyssate bivalves (*Modiolus*, *Pinna*, *Myoconcha*) and an assortment of other ancillary taxa. Ammonoids are sometimes common as accompanying fauna; some samples contain also gastropods and plant remains.

This association has a wide geographical and stratigraphical distribution and is represented in the three sections (Figs. 1 and 3). At Arroyo Malo and El Pedrero it is intercalated with other associations but at Las Chilcas it is conspicuously present at the lower part of the El Cholo Formation and less common towards the top.

The environmental range inferred for this association spans from littoral to shallow shelf normal euhaline marine settings, with predominant siliciclastic soft-bottoms and local availability of benthonic islands and/or firmer substrates. Brachiopods represented clearly fit into the category of normal, sublittoral sand-grade sea floors within the classical comprehensive scheme developed for Mesozoic environments by Ager (1965, 1993). They are comparable to those of the sublittoral biotope with sand-grade floor and agitated water recognized for the Hettangian-Sinemurian of Bulgaria by Tchoumatchenco (1972, 1996), corresponding to a shallow water brachiopod biofacies (Sandy, 1995). The occasional occurrence of the

bivalve *Cardinioides* appears to be positively correlated with specimens of this genus having small adult size (see discussion below, under *Cardinioides* association).

The *Weyla-Gryphaea* association shows a remarkably close correspondence to sub-biofacies A2 recognized in Pliensbachian deposits from southern Neuquén (Damborenea et al., 1975), although the latter displays an even richer array in terms of taxa and guilds represented. With regard to the integrated environmental model developed by Taylor (1982; Taylor et al., 1983) for Early and Middle Jurassic faunas of western USA, this association agrees quite well with their composite assemblage B, which bears distinctive elements like *Weyla*, *Cardinia*, *Pho-*
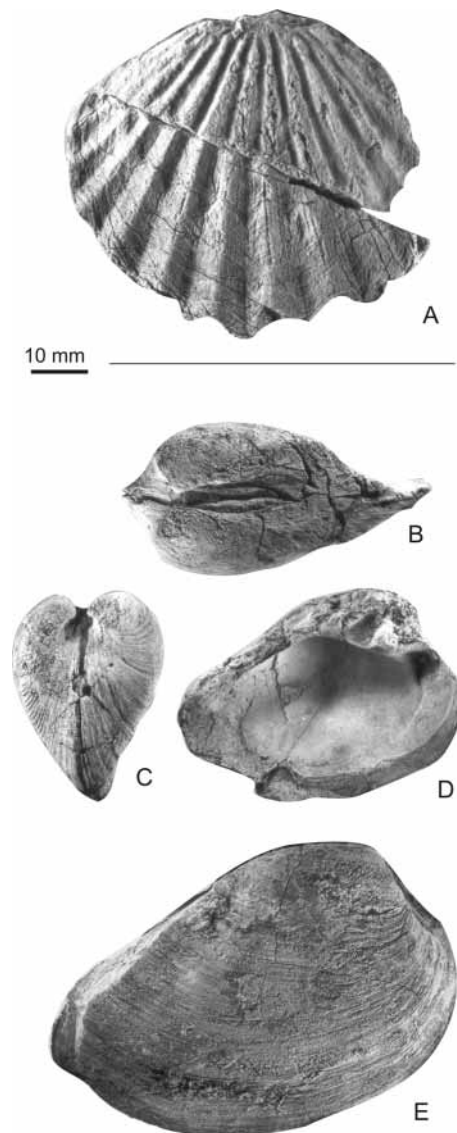

FIGURE 9 | Some elements of the *Lywea* (A) and *Cardinioides* (B to E) associations. A) *Lywea* cf. *unca* (PHILIPPI), MLP 31161, arroyo El Pedrero, early Sinemurian, left valve. B to E) *Cardinioides* n. sp., early Sinemurian, La Horqueta, Arroyo Blanco; B and C) MLP 13512; D) MLP 13503; E) MLP 13507.

ladomya, Gresslya in Lower Jurassic formations from California and Nevada. On the other hand, for the Early Jurassic of Chile, a number of associations characterized by *Weyla* and/or *Gryphaea* have been pointed out by Aberhan (1992, 1993a, 1993b), which were attributed mostly to his onshore zones 1 and 2. Nevertheless, the fact that his model was based mainly upon carbonate ramp deposits, hinders more detailed comparisons.

Lywea association (L)

This is a low-diversity (TDI = 7.8) association (Figs. 9A and 10D), dominated by the coarsely costate pectinoid *Lywea*, escorted by the oyster *Gryphaea* and a few other pectinoids, trigoniids and astartids.

In the study area, the geographical distribution of this association is restricted to the Arroyo Pedrero section (Figs. 1 and 3). At this locality it accompanies a local shallowing upward trend of the fossil-bearing deposits. These sediments show an increase of flow deposits towards the top of El Pedrero section.

This association leans towards a lethal-lipostratal biofacies (*sensu* Schäfer, 1972; as lethal-heterostratal in Schäfer, 1962), as the coarse-grained sediments show evidence of recurrent erosion. The benthonic fauna probably derives from neighbouring biocenosis and shares the common feature of containing loose inhabitants of the few upper centimetres of substrate. Since the few elements occurring in this association are all present also in the *Weyla-Gryphaea* association described above, it may be regarded as an impoverished version of the latter.

All these characteristics, in addition to the notorious absence of any firmly attached or deeply embedded taxon, is reminiscent of sub-biofacies A3 from Pliensbachian beds in southern Neuquén (Damborenea et al., 1975). Both the *Lywea* and A3 associations show low diversity levels and even their taxonomic and guild contents are almost the same. However, it should be pointed out that the *Lywea* association did not result from transport by turbiditic/tempestitic currents, the mechanism implicitly suggested by Damborenea et al. (1975) for sub-biofacies A3. The delta front scenario put forward by Lanés (2002, 2005) appears as an interesting interpretation which accounts for the short lateral allochthony of this association.

Cardinioides association (C)

This is the least diverse (TDI = 1.5) association (Figs. 9B-9E), dominated by the shallow-infaunal suspension-feeding bivalve *Cardinioides* which belongs to the Pachycardiidae, a mainly Mesozoic family that comprises conspicuously euryhaline genera ranging from brackish to marine, even freshwater habitats (Cox et al., 1969). Representatives of this genus

are locally very abundant at some localities to the northeast of the sections here considered (Codo del Arroyo Blanco, La Horqueta, see Lanés, 2002, for location), where they form closely packed monospecific shell beds, suggestive of stressful conditions. These monotypic beds form bioclastic lags at the base of tidal channel deposits (Damborenea and Lanés, 2003). The low diversity, high abundance, systematic composition of the fauna (lacking marine stenohaline species) and the dominant bivalve morphotype (characteristic of marginal marine environments) may be taken collectively as reliable indicators of brackish-water biotas. On the basis of the taphonomic analysis and faunal composition, the environment was possibly oligo- to mesohaline in the northern localities and polyhaline (or brachyhaline) near the base of the marine succession at Las Chilcas.

The geographical distribution of this association in the study area is limited to the lower part of the El Cholo Formation at Arroyo Las Chilcas section (Figs. 1 and 3) and other north-eastern localities in beds referred by Lanés (2002) to estuarine or lagoonal environments. Therefore, this is highly consistent with the salinity controlled environment interpretation based on faunal considerations alone.

Admittedly, *Cardinioides* is also occasionally found (as isolated small valves, usually broken and abraded) in the shallow-water *Weyla-Gryphaea* association, but it remains to be ascertained whether such ancillary occurrence may be due to extreme marginal location in a broad range of salinity tolerance, and/or to time-averaging effects within an environmental setting subject to strong, short term, salinity fluctuations.

Also in Late Triassic beds of SW Japan the genus *Cardinioides* appears in local shell concentrations with almost no other accompanying fauna, interpreted as depending largely on environmental factors (Kobayashi and Ichikawa, 1952). Furthermore, Hayami (1961, fig. 2.2) indicates that in the Early Jurassic of Japan, *Cardinioides* is confined to lagoonal restricted environments, on the basis of independent (mainly sedimentological) evidence. Although a number of salinity-controlled molluscan assemblages have been pointed out in Aberhan's model (1993a, 1994) for the Late Jurassic and Cretaceous, none of them is strictly comparable to this one, and none has been reported from the Sinemurian of Chile.

CONCLUDING REMARKS

The five benthonic associations here recognized are recurrent in time and most of them show broad geographical distribution as well. It should be emphasized that these groups are independent, and have a different meaning from the successive, non overlapping, zonal units known from the same interval (Fig. 4), which have been
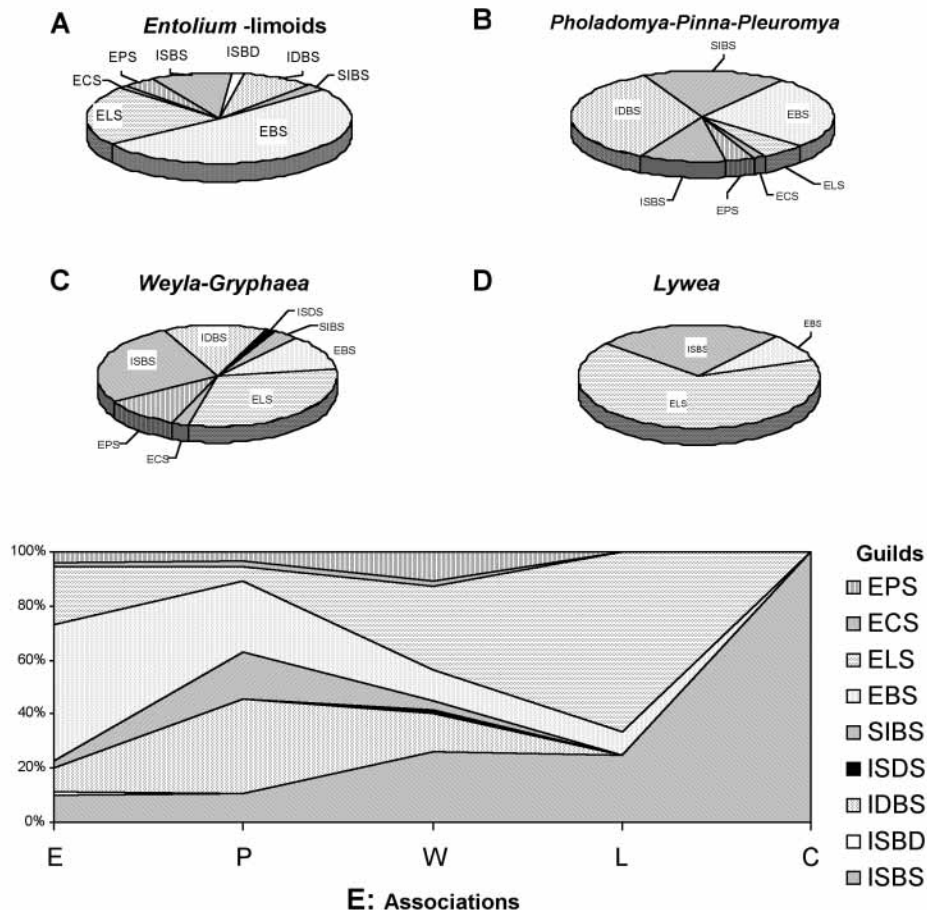
FIGURE 10 | **Percentage composition of guilds in the recognized associations. Data in Appendix. A to D) Pie diagrams. E) Comparison of all the associations. Abbreviations: EBS: epifaunal byssate suspension feeders; ECS: epifaunal cemented suspension feeders; ELS: epifaunal free lying suspension feeders; EPS: epifaunal pedunculate suspension feeders; IDBS: infaunal deep burrowing suspension feeders; ISBD: infaunal shallow burrowing deposit feeders; ISBS: infaunal shallow burrowing suspension feeders; ISDS: infaunal shallow burrowing detritus/suspension feeders; SIBS: semi-infaunal endobyssate suspension feeders.**

established on the basis of vertical ranges of biostratigraphically significant species.

Most of such benthonic associations have developed chiefly "in situ" in well bedded sediments, and may thus be assigned to vital-pantostratal biofacies in Schäfer's (1972) scheme (as vital-isostratal in Schäfer, 1962). The *Lywea* association is interpreted as allochthonous and probably derived from the diverse *Weyla-Gryphaea* association, and it is linked with a local shallowing up of the Early Sinemurian sequence at some western localities.

Pectinoid bivalve species are common elements in most associations. The distribution of pectinoids is heavily substrate-related throughout the history of this group (Aguirre et al., 1996). The general rule of strongly-ribbed, inflated shells being related to coarse-grained deposits, while smooth, flat-shelled species being common in fine-grained lithofacies, is evident also from this analysis. Strongly ribbed and inflated *Lywea* and *Weyla* appear in coarse and medium-grained sands respectively, while densely ribbed

(*Praechlamys, Eopecten, Camptonectes, Agerchlamys, Pseudopecten*) and smooth flat (*Entolium*) pectinoids are usually found in fine-grained sandstones and mudstones.

Concerning their mutual relationships (Fig. 10E), these associations are interpreted as the result of a combined interplay of natural gradients in physical factors, such as bathymetry, nature of substrate, and salinity. The *Cardinioides* association was clearly controlled by palaeosalinity. It corresponds to a wave-dominated estuarine environment, and occurs only at the base of the marine transgression in north-eastern localities. The other associations developed in normal marine shelf to littoral environments and are thus more widely distributed. Their recurrent alternation within a single section (well displayed in the upper part of the Arroyo Malo column, see Fig. 3) may be a response to slight environmental fluctuations, such as a series of successive shifts involving small-scale changes in water-depth or in substrate texture and consistency. A similar explanation has been invoked for Lower Jurassic rhythmic deposits of Great Britain (Sellwood, 1972).

The present results are in good general agreement with the interpretation of depositional environments proposed on sedimentological grounds by Lanés (2002, 2005) for the Early Jurassic succession of the upper Atuel river region. Several of the biofacial associations now characterized from the Hettangian-Sinemurian interval of southwest Mendoza seem to herald some of those recorded from Pliensbachian deposits of southeast Neuquén (A2, A3, possibly A1 and A4, too), except for the notable absence of any deep-water biofacies (like B, in Damborenea et al., 1975).

As already suggested, certain noticeable differences with Aberhan´s model for the Early Jurassic of Chile may be a consequence of the obvious influence of a carbonate ramp developed there. In contrast, the lithofacies in SW Mendoza are dominantly siliciclastic with the whole spectrum of benthonic associations falling roughly within depth zones 1 and 2 of Aberhan's scheme (1992, fig. 52; 1993b, fig. 5), whereas the deeper water zone 3 is not represented.

Approximate correspondence to the composite assemblage environmental model developed by Taylor (1982) and Taylor et al. (1983) for Early and Middle Jurassic shelly faunas of western USA, is relatively more straightforward to establish, especially for the inshore, epeiric suites (B-C1-C2), with the proviso that their shallowest assemblage A, may be partly equivalent to, or replaced by, the low-salinity *Cardinioides* association. In addition, no biofacies strictly comparable to their offshore suites (D1-D2) have been recognized in Hettangian-Sinemurian deposits cropping out to the north of the Atuel River.

Consequently, on the basis of the distribution of shelfal biofacies reported herein, one would predict that genuine basinal association(s) of this age, if present, would occur to the south of the Atuel River. Likewise, fresh-water faunas might be found towards the northeast of the study area.

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APPENDIX

Faunal contents of associations here recognized

Faunal contents of associations here recognized. (1): Sample relative abundance. (2) Sample presence percentage (parameters 1 and 2 as used by Aberhan, 1992, 1993b and Fürsich et al., 2001). * Not included in the cluster analysis. Guilds: EBS: epifaunal epibyssate suspension feeders; ECS: epifaunal cemented suspension feeders; ELS: epifaunal free lying suspension feeders; EPS: epifaunal pedunculate suspension feeders; IDBS: infaunal deep burrowing suspension feeders; ISBD: infaunal shallow burrowing deposit feeders; ISBS: infaunal shallow burrowing suspension feeders; ISDS: infaunal shallow burrowing detritus/suspension feeders; SIBS: semi-infaunal endobyssate suspension feeders.

Entolium-limoids association (23 samples)

	(1)	(2)	Guild
Entolium	15	52	ELS
Pectinoidea	9	30	EBS
Praechlamys	6	22	EBS
Pseudolimea	5	17	EBS
Plagiostoma	5	17	EBS
Pholadomya	5	17	IDBS
Otapiria	4	13	EBS
Asoella	4	13	EBS
Eopecten	4	13	EBS
Antiquilima	4	13	EBS
Limoidea	4	13	EBS
Astartidae	4	13	ISBS
Pleuromya	4	13	IDBS
Weyla	2.25	9	ELS
Gryphaea	2.25	9	ELS
Grammatodon	1.25	4	ISBS
Pinna	1.25	4	SIBS
Kolymonectes?	1.25	4	ELS
Camptonectes	1.25	4	EBS
Chlamys	1.25	4	EBS
Ostreoidea	1.25	4	ECS
Groeberella	1.25	4	ISBS
Trigoniidae	1.25	4	ISBS
Myoconcha	1.25	4	SIBS
Gibbirhynchia	1.25	4	EPS
Peristerothyris?	1.25	4	EPS
Terebratuloidea	1.25	4	EPS
Palaeoneilo? *	1.25	4	ISBD
Agerchlamys *	1.25	4	EBS
Pseudopecten *	1.25	4	EBS
Ctenostreon *	1.25	4	EBS
Arcticoidea *	1.25	4	ISBS
Lingularia *	1.25	4	ISBS

Pholadomya-Pinna -Pleuromya association (18 samples)

	(1)	(2)	Guild
Pholadomya	23.5	72	IDBS
Pinna	16	50	SIBS
Pleuromya	12.7	39	IDBS
Astartidae	7	22	ISBS
Eopecten	5.1	16	EBS
Camptonectes	3.4	11	EBS
Chlamys	3.4	11	EBS
Pectinoidea	3.4	11	EBS
Pseudolimea	3.4	11	EBS
Plagiostoma	3.4	11	EBS
Palmoxytoma	1.7	6	EBS
Kolymonectes?	1.7	6	ELS
Entolium	1.7	6	ELS
Gryphaea	1.7	6	ELS
Ostreoidea	1.7	6	ECS
Limoidea	1.7	6	EBS
Trigoniidae	1.7	6	ISBS
Sphaeriola?	1.7	6	ISBS
Calcirhynchia?	1.7	6	EPS
Inoperna *	1.7	6	SIBS
Furcirhynchia *	1.7	6	EPS

Weyla-Gryphaea association (36 samples)

	(1)	(2)	Guild
Gryphaea	11	50	ELS
Frenguelliella	11	50	ISBS
Entolium	9	44	ELS
Weyla	8.5	39	ELS
Pholadomya	8	36	IDBS
Gibbirhynchia	7	33	EPS

Asoella	3.5	16	EBS		*Otapiria*	0.5	3	EBS
Cardinia	3.5	16	ISBS		*Camptonectes*	0.5	3	EBS
Goniomya	3.5	14	IDBS		Limoidea	0.5	3	EBS
Cardinioides	2.5	11	ISBS		Trigoniidae	0.5	3	ISBS
Astartidae	2.5	11	ISBS		*Sphaeriola*?	0.5	3	ISBS
Peristerothyris?	2.5	11	EPS		*Myoconcha*	0.5	3	SIBS
Lywea	2	8	ELS		*Spiriferina*	0.5	3	EPS
Ostreoidea	2	8	ECS		*Zeilleria* *	0.5	3	EPS
Pleuromya	2	8	IDBS		*Gervillaria* *	0.5	3	SIBS
Grammatodon	1	5	ISBS		*Liostrea* *	0.5	3	ECS
Modiolus	1	5	SIBS		*Jurassicardium*? *	0.5	3	ISBS
Lycettia	1	5	EBS		*Tancredia* *	0.5	3	ISBS
Pinna	1	5	SIBS		*Gresslya* *	0.5	3	IDBS
Kolymonectes	1	5	ELS		*Gastrochaenolites* *	0.5	3	ISBS
Praechlamys	1	5	EBS					
Chlamys	1	5	EBS					
Antiquilima	1	5	EBS					

Lywea association (7 samples)

Pseudolimea	1	5	EBS
Groeberella	1	5	ISBS

	(1)	**(2)**	**Guild**
Jaworskiella	1	5	ISBS
Lucinoidea	1	5	ISDS
Protocardia?	1	5	ISBS
Pholadomyidae	1	5	IDBS
Parallelodon	0.5	3	EBS

	(1)	**(2)**	**Guild**
Lywea	59	100	ELS
Astartidae	17	28	ISBS
Pectinoidea	8	14	EBS
Gryphaea	8	14	ELS
Trigoniidae	8	14	ISBS