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Coexistence of brachiopod and bivalves in the Late Paleozoic of Western Argentina

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ABSTRACT

The relationship between brachiopods and bivalves has been widely discussed in previous studies. Based on analyses at different temporal and spatial scales, several authors have argued either for the indifference or the interaction between the two clades. In this contribution we evaluate brachiopod and bivalve coexistence at two different spatial scales in a siliciclastic shelf developed during the Late Paleozoic in Western Argentina. At regional scale, bivalves were more diverse than brachiopods, although both had a similar total number and comparable distribution of occurrences. At local scale, however, multivariate analyses indicate that brachiopods and bivalves were segregated. Null models reinforce this pattern confirming the non-random co-occurrence pattern, and that the coexistence of brachiopods and bivalves was significantly low. In addition, multivariate analyses indicate that the biotic gradient neither followed the bathymetrical, nor a geographical or temporal gradient. The possibility that such segregation would have been caused by taphonomic (storm) reworking, was also disregarded considering multivariate analyses together with taphonomic evidence. The lack of environmental segregation between brachiopods and bivalves, coupled to analyses taking into account ecological guilds, indicates that possible factors controlling the segregation, such as turbidity, substrate or productivity were not relevant. As a whole, these results suggest a possible competitive interaction between brachiopods and bivalves at local scales. Interestingly, brachiopod–bivalve coexistence at regional scale did not foster local coexistence, indicating that the processes acting at these two scales are, at least partially, decoupled. Finally, the regional coexistence pattern suggests that the major transition between brachiopod and bivalve dominated communities was most probably related to processes acting at regional to biogeographic scales rather than to competition.

1. Introduction

The relationship between brachiopods and bivalves has been a matter of discussion for many years. While brachiopods were once the dominant clade in marine benthic communities during most of the Paleozoic (Thayer, 1979, 1985, 1986; Bambach, 1993; Peters, 2008), bivalves dominate such communities since the Mesozoic (Thayer, 1979; Valentine and Jablonski, 1983; Sepkoski, 1984). Because their Phanerozoic diversity trajectories appear to have opposite trends and both clades have similar life habits, some authors claimed that such pattern could have been the consequence of competitive interactions (Sepkoski, 1984, 1996). However, based also on global diversities and metabolic estimates, many authors concluded that brachiopods and bivalves were indifferent to each other (Gould and Calloway, 1980; Babin et al., 1992; Payne et al., 2014).

On the other hand, detailed paleoecological analyses have indicated that brachiopods and bivalves were not that indifferent. Several studies have shown that these groups tend to be segregated, often defining different biofacies or community types (Fürsich et al., 2001; Olszewski and Patzkowsky, 2001; Bonuso and Bottjer, 2006). These studies highlighted that brachiopods were more abundant in carbonate environments, while bivalves in siliciclastic settings (e.g., Tomašových, 2006b). Indeed, such differential environmental preference has been shown to explain large scale diversity trajectories of both clades (Peters, 2008). The preference for either environment, however, can be explained by different hypotheses because both settings differ in multiple characteristics such as productivity, turbidity and substrate stability (Peters, 2008; Nichols, 2009). In addition, all studies have been carried out in low latitude regions (e.g., Bonuso and Bottjer, 2006) and little is known from high latitude regions where carbonate environments do not commonly occur. Therefore, the analyses of brachiopod–bivalve co-occurrences in high latitudinal regions during intervals where both

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clades were numerically and taxonomically abundant might shed light on the underlying factors controlling their distributions.

In this contribution we study the coexistence of brachiopods and bivalves at two different spatial scales (regional and local) from west-central Argentina during the Late Paleozoic (Upper Carboniferous–Early Permian), particularly in the youngest terms of Pennsylvanian–Cisuralian transgression, where the glacial sediments are absent due to the glaciers' retreat. The presence of a siliciclastic shelf at high to intermediate latitudes, coupled to the good knowledge of its fauna, provides an ideal place to analyze brachiopod–bivalve coexistence in the southwestern Gondwana margin.

2. Geological setting

The Late Paleozoic marine ingression of Western Argentina was developed on retroarc and arc-related basins (Astini et al., 2005), located at intermediate to high latitudes (~40° South, Geuna et al., 2010). The region has been classically divided in different depocenters, although similarities in the tectono-sedimentary evolution indicate a shared evolution of the whole region (López Gamundí et al., 1994; Astini et al., 2005). The latest Carboniferous–earliest Permian interval in the studied area is associated to a Paleo-Pacific transgressive event that represents the transition from the glacial to postglacial condition, characterized by the establishment of lakes and fjord embayments with the posterior climatic amelioration (López Gamundí, 1989; Limarino et al., 2002).

The combined effect of glacioeustatic sea-level rise and subsidence along basin margins allowed the creation of space to accommodate a transgressive systems' tract (TST), that can be recognized all along the studied area (Limarino et al., 2002). The basins record a siliciclastic shelf with a broad array of sedimentary environments, ranging from offshore to shallow-marine storm-dominated and tide-dominated deposits, and estuaries and deltaic systems. The predominant marine facies basinward are interbedded with fluvial deposits to the east (Desjardins et al., 2009, 2010; Limarino et al., 2013 and references cited therein).

The chronostratigraphic issues are well resolved in this region (Lech, 2002; Gulbranson et al., 2010; Barredo et al., 2011; Césari et al., 2011) and paleontological data widely known (Césari et al., 2007 and references therein cited). Invertebrate faunas have been studied in several lithostratigraphic units in two main areas: Río Blanco–Western Paganzo basins in the north and Calingasta–Uspallata in the south (Fig. 1). The marine fauna is composed of brachiopods (rhynchonelliformeans and linguliformeans), bivalves, gastropods and ostracods. Brachiopods and bivalves considered in this analysis are well known by many contributions that have dealt with systematic (Manceñido et al., 1977; González, 1997; Taboada, 1998, 2006; Cisterna and Simanauskas, 2000; Sterren, 2000, 2004; Archbold and Simanauskas, 2001; Cisterna et al., 2002; Archbold et al., 2005; Cisterna and Sterren, 2007; Cisterna, 2011); In addition, information concerning the biostratigraphic (Cisterna et al., 2006; Cisterna, 2010) and taphonomic (Sterren, 2000, 2008) aspects are well known.

The marine invertebrates associated with this transgression belong to the *Tivertonia jachalensis–Streptorhynchus inaequiornatus* zone, originally considered Moscovian–Kasimovian (Sabattini et al., 1990) and Asselian by other authors (Cisterna et al., 2002; Archbold et al., 2004). However, the recent radiometric ages support a Late Carboniferous age for this zone (Gulbranson et al., 2010; Césari et al., 2011). To the south of the Calingasta–Uspallata Basin, the fauna integrates the *Costatumulus amosi* zone (Taboada, 1998), considered Early Permian by Cisterna (2010) and Late Sakmarian–Early Artinskian by Taboada (2010).

3. Data

3.1. Sampling and dataset

More than fifty samples coming from six different formations in two related basins were obtained for these analyses (Fig. 1, Supplementary information). Most of this dataset has been published elsewhere for taphonomic, biostratigraphic or systematic analysis. In previous contributions, many samples were lumped as single assemblages, however we here used the original samples.

Although all body fossils were collected, only brachiopods and bivalves are analyzed. Fossils were identified to the lowest taxonomic level possible but the analysis is performed at generic level. While relative abundances record important information for paleoecological studies (Ludvigsen et al., 1986), presence–absence datasets register similar information for multivariate paleoecological analyses (Olszewski and Patzkowsky, 2001; Balseiro et al., 2011). The final dataset consists of 55 samples and 247 occurrences of 26 brachiopod and 35 bivalve genera.

We modified the dataset two different ways. First, an exhaustive dataset was created by removing all monospecific samples. The exhaustive dataset contains 42 samples and 60 genera. Second, a restrictive

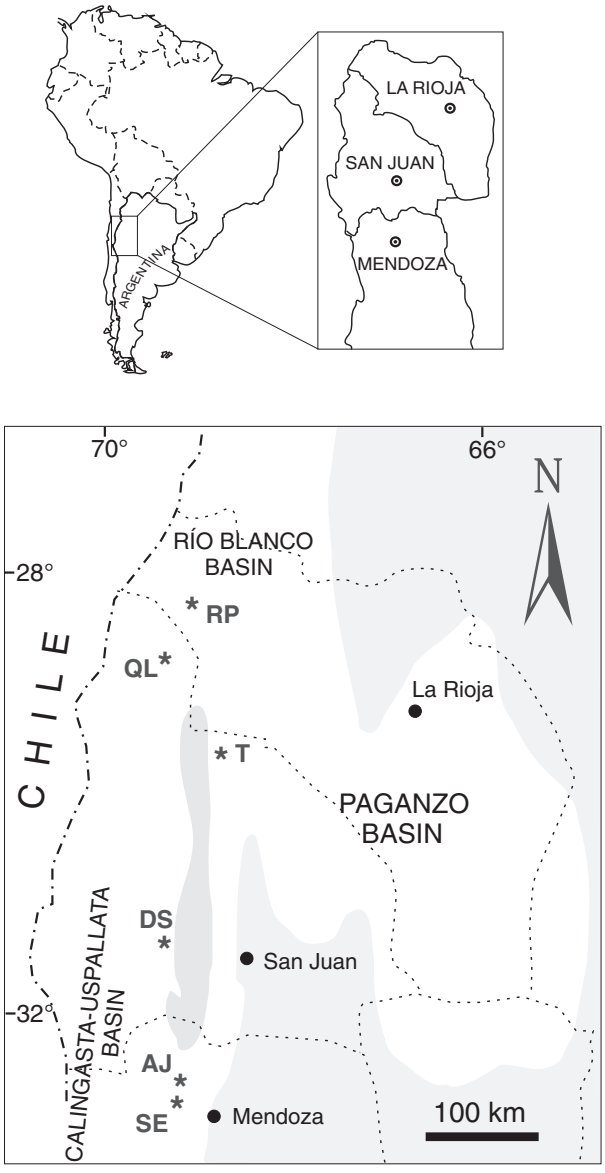

Fig. 1. Map of South America indicating the location of the studied region, and detailed map showing paleogeography of the basins and sampled formations (and localities). RP: Río del Peñon Formation (Anticlinal del Río Blanco), QL: Quebrada Larga Formation (Quebrada Larga), T: Tupe Formation (Quebrada de la Herradura and Quebrada de la Delfina), DS: Del Salto Formation (Quebrada del Salto), AJ: Agua del Jagüel Formation (Quebrada de Agua de Jagüel), SE: Santa Elena Formation (Quebrada de Santa Elena).