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Bivalves and brachiopods in the Carboniferous - Early Permian of Argentine Precordillera: Diversification and faunal turnover in Southwestern Gondwana

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ABSTRACT

Diversification patterns and faunistic turnovers of bivalves and brachiopods through the Carboniferous - Early Permian interval in the central western Argentinian basins are analyzed and compared with the global events proposed in former studies. This study reveals a generalized increase of bivalves, at familiar and generic levels, through three time intervals, i.e., Early Carboniferous (Tournaisian-Visean), Late Carboniferous (Bashkirian-Kasimovian) and Early Permian (Asselian-Sakmarian), while the brachiopod diversity seems to remain stable from the Late Carboniferous to the Early Permian. The trends recognized in the faunistic diversity appear to be closely related to the palaeoclimatic, palaeogeographic and palaeotectonic evolution at the Southwestern Gondwana margin. Highly stressing environmental changes in the Early Carboniferous, resulting fundamentally from the development of glacial conditions, may account for the lowest faunistic diversity recorded. Particular stress conditions, such as the nutrient availability, temperature and oxygen level, would have mainly affected the brachiopod faunas that evidence the lowest diversity recognized in the interval studied. At the Visean-Serpukovian boundary, the Late Palaeozoic marine record of the Precordillera shows a major break linked to a globally recognized glacial maximum, whereas an important faunistic turnover is mainly identified in the brachiopod faunas at the beginning of the Late Carboniferous. The more stable, less stressing environmental situation developed during the Late Carboniferous-Early Permian postorogenic sedimentation is also reflected by the different faunal assemblages studied. The Late Carboniferous was characterized by postglacial transgressions. During this time local rebound, a continuous increase of the diversity and an important faunal turnover, which mainly affected the brachiopod faunas, were recorded. These faunal trends may be related to the Early Permian climatic amelioration that affected the central western Argentinian basins. The subsequent Permian transgressive events, which produced new areas of potential spreading for the benthic fauna, allowed its increase and diversification, much better reflected by the bivalve assemblages.

KEYWORDS **Diversification. Faunistic turnover. Bivalves. Brachiopods. Carboniferous-Permian. Argentine Precordillera.**

INTRODUCTION

The Late Palaeozoic marine biota from the Gondwanan regions shows a close relationship with the palaeogeographic and palaeoclimatic setting. In these areas, the diversification and extinction processes observed in several invertebrate groups would have been mainly controlled by the particular dynamic of the glacial event.

The beginning of the massive glaciation time interval has been placed at the Serpukovian age, and the biotic changes related are well documented in the south-western Gondwana margin where the glaciers were widespread throughout.

The Argentine Precordillera can be considered a classical study area of the Late Palaeozoic marine fossil assemblages in the particular palaeoenvironmental context where the glaciation was clearly recorded.

The general aim of this paper is the study of the distribution of bivalves and brachiopods through the Carboniferous-Permian interval in the central western Argentinian basins (Río Blanco, Calingasta-Uspallata and western Paganzo basins) and to analyse its relationship with the palaeogeographic and palaeoclimatic scenario.

Bivalves and brachiopods are abundant and important components in the Late Palaeozoic marine faunas of Argentina, and these groups have been the object of numerous taxonomy studies in recent years. The distribution analysis of these groups allows researchers to recognize diversification patterns and faunistic turnovers from the Early Carboniferous to the early Permian.

The global diversity study in the marine invertebrate faunas from the late Early Carboniferous to Early Permian (Early Sakmarian) allows for the recognition of the sluggish diversification and low taxonomic rates of evolutionary turnover (Powell, 2005). This interval of time with relatively stable diversity is known as the "late Palaeozoic ice age" (LPIA) (Stanley and Powell, 2003). Similar patterns, which appear to be relatively influenced by the local conditions, are observed in the fossil assemblages considered in this paper.

GEOLOGICAL AND PALAEOBIOLOGICAL SETTING

The Late Palaeozoic geological record in central-western Argentina shows a complex history of interaction among tectonism, sea-level changes and climatic conditions (Limarino et al., 2006). Carboniferous-earliest Permian marine sediments of the Precordillera appear disconnected, showing an irregular pattern along western Argentinian basins. This region was affected several times by diachronic Palaeo-Pacific transgressive events whose eastern extension was restricted by an important orogenic belt known as the Protoprecordillera (Amos and Rolleri, 1965) or the Acadian Precordillera (Baldis and Chebli, 1969). This north-trending upland would have controlled the sedimentation in these two areas: to the west, the Río Blanco (Amos, 1964) and Calingasta-Uspallata (Amos and Rolleri, 1965) basins, dominated by marine sedimentation and, to the east the Paganzo basin (Azcuy and Morelli, 1970) with continental sedimentation mainly (Figs. 1 and 2 and electronic Appendix I available at www.geologica-acta.com). However, the connection of the western Paganzo basin fluvial systems with the Carboniferous sea of the Río Blanco basin can be explained because the height of the Protoprecordillera would have decreased to the north (Archangelsky et al., 1987; López Gamundí et al., 1994).

The first marine transgressive episode was identified in two localities of the Río Blanco basin (Fig. 2): to the north

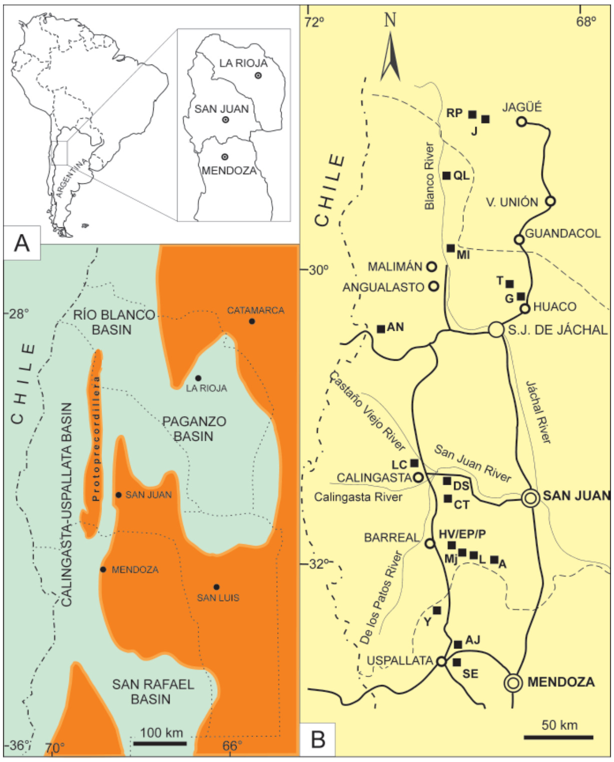

FIGURE 1 | **A) Maps showing the location of the study area and the paleogeography of the Paganzo, Río Blanco and Calingasta-Uspallata basins in western Argentina. B) Generalized geographic map showing the locations of outcrops sampled in these basins. RP: Río del Peñón Formation, J: Jagüé Formation, QL: Quebrada Larga Formation, MI: Malimán Formation, T: Tupe Formation, G: Guandacol Formation, AN: Agua Negra Formation, LC: La Capilla Formation, DS: Del Salto Formation, CT: Ciénaga Larga del Tontal Formation, HV: Hoyada Verde Formation, EP: El Paso Formation, P: Pituil Formation; Mj: Majaditas Formation, L: Leoncito Formation, A: Ansilta Formation, Y: Yalguaraz Formation, AJ: Agua del Jagüel Formation, SE: Santa Elena Formation.**

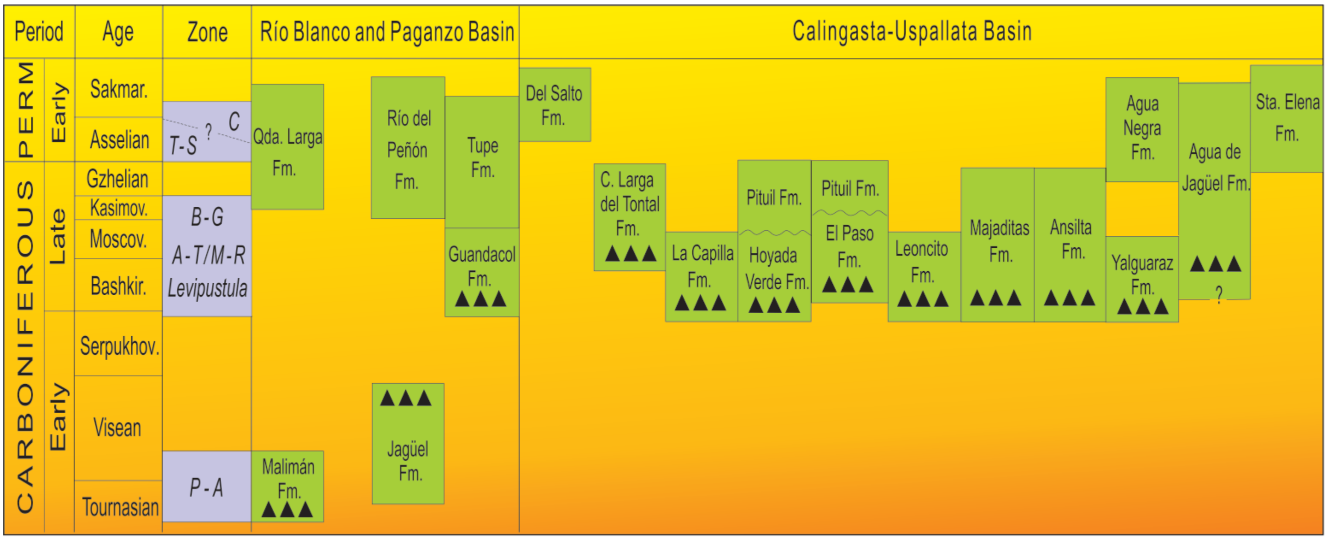

FIGURE 2 | **Chronostratigraphic chart of the formations studied in this paper. Invertebrate zones: *P-A= Protocanites-Azurduya*; *A-T/M-R= Aseptella-Tuberculatella/Micraphelia-Rhipidomella*; *T-S= Tivertonia-Streptorhynchus*, *C= Costatumulus.* Triangles indicate diamictitic horizons. Time scale after Gradstein et al. (2004). See explanation of the stratigraphy and general characteristics of these units these units in APPENDIX I in the electronic version of this paper available at www.geologica-acta.com.**

(Bolsón de Jagüel Area, La Rioja province), marine sediments with invertebrate faunas were included in the Jagüel Formation (Fauqué and Limarino, 1991), and to the south (Malimán Area, San Juan province), in the Malimán Formation (Scalabrini Ortiz, 1972), the lower part of the Angualasto Group (Limarino and Cesari, 1993). Early Carboniferous marine fauna from these units integrate the *Protocanites scalabrinii-Azurduya chavelensis* Zone (Sabattini et al., 2001), characterized by the brachiopods *Azurduya chavelensis* (Amos), *Azurduya cingolanii* Cisterna and Isaacson, *Chilenochonetes*? sp., *Pseudosyringothyris*? sp. and the bivalves *Palaeoneilo subquadratum* González, *Malimania triangularis* González, *Posidoniella malimanensis* González, *Sanguinolites punillanus* González. A Tournaisian-Visean age, based on the *Archaeosigillaria-Malimanium* and *Frenguellia-Paulophyton* (Carrizo and Azcuy, 1997) phytozones and on the associated palynological data (Césari and Limarino, 1995) was assigned to this biozone. The second marine transgressive event, identified in the Paganzo and Calingasta-Uspallata basins, has been related to an important postglacial transgression recognized in several outcrops of western Argentina (Limarino et al., 2002). In the Paganzo Basin (Figs. 1 and 2) this event is represented by black shales with marine invertebrates covering the diamictitic beds located in the base of the Guandacol Formation (Cuerda, 1965), the lower part of the Paganzo Group (Martínez, 1993). In the Calingasta-Uspallata Basin this transgressive event has a well-known palaeontological record in different localities, and the sea-level rise was attributed to glacioeustatic changes due to deglaciation processes (Limarino et al., 2002). Two invertebrate marine faunas have been associated with this episode: the typical *Levipustula* Fauna, included in the *Levipustula levis* Zone (Serpukhovian-Bashkirian, Taboada, 1997), recognized in different stratigraphical sections (i.e., Hoyada Verde, La Capilla, Leoncito, Yalguaraz, etc., Fig. 2), and a younger fauna that integrates the *Balakhonia peregrina-Geniculifera tenuiscostata* Zone, considered to be Moscovian-Kasimovian (Taboada, 1997), identified fundamentally in the Pituil Formation (Taboada, 1997) and the upper part of the Ansilta Formation (Harrington, 1971). The *Levipustula* Fauna is a relatively diversified fossil assemblage distinguished by the brachiopod species *Levipustula levis* Maxwell, *Costuloplica leoncitensis* (Harrington), *Beecheria* sp., *Spiriferellina octoplicata* (Sowerby), *Septosyringothyris keideli* (Harrington), *Kitakamithyris booralensis* (Campbell), *Kitakamithyris immensa* (Campbell), *Torynifer tigrensis* Taboada and Cisterna and the bivalves *Aviculopecten barrealensis* Reed, *Streblochondria sanjuanensis* Sterren and *Streblochondria stappenbecki* Reed.

The younger *Balakhonia-Geniculifera* fauna, restricted in area to the Barreal hill and mainly recognized in the Pituil Formation (Fig.2), can be considered of local significance, and it is characterized by the brachiopods *Balakhonia peregrina* Taboada, *Geniculifera tenuiscostata* Taboada, *Neochonetes granulifer* (Owen), *Reticularia notica* Reed, *Orbiculoidea* aff. *saltensis* Reed and the bivalves *Nuculanella camachoi* González and *Aviculopecten barrealensis* Reed.

Levipustula and *Balakhonia-Geniculifera* faunas and the marine fossil assemblages of the El Paso Formation (Mésigos, 1953; member El Paso, San Eduardo Formation, *sensu* Taboada 1997) could be included in the same transgressive event. In this formation (Fig. 2), the most typical brachiopod associations are *Aseptella-Tuberculatella* (*Tuberculatella peregrina* (Reed) and *Aseptella* aff. *patriciae* Simanauskas) and *Micraphelia-Rhipidomella* (*Rhipidomella*? sp., *Micraphelia indianae* Simanauskas and Cisterna), and these associations suggest Late Carboniferous biostratigraphical affinities (Simanauskas and Cisterna, 2001). Although the age of this fauna is being reviewed by the authors, recent palynological data have indicated a Pennsylvanian age (late Bashkirian) (Vergel et al., 2008). This fauna, composed of a particular invertebrate fossil assemblage, is clearly different than the *Levipustula* fauna and has also been recognized in the lower part of the Agua del Jagüel Formation, associated with diamictitic horizons that have also been related to the Late Carboniferous glacial event (Martínez et al., 2001; Simanauskas and Cisterna, 2001; Ciccioli et al., 2008).

The youngest transgressive marine event in the Precordillera was identified in three basins during the Late Carboniferous-Early Permian interval (Gzhelian-Sakamarian, Limarino et al., 2006 and references there herein). Widespread exposures of these marine sediments appear in the Río del Peñón Formation (Borrello, 1955) and Quebrada Larga Formation (Scalabrini Ortiz, 1972), in the Río Blanco Basin (Fig. 2). This event only reached the western area of Paganzo basin where it has been documented in different stratigraphical sections of the Tupe Formation. The marine invertebrates associated with this transgression belong to the *Tivertonia jachalensis-Streptorhynchus inaequiornatus* Zone (Sabattini et al., 1990), considered to be early Permian (Asselian) by Cisterna et al. (2002b) and Archbold et al. (2004), and the *Rhynchopora - Neochonetes pegnonensis* fossil assemblage (assemblage III, Cisterna and Simanauskas, 2000), considered to be Late Asselian- Sakmarian (Archbold et al., 2004). The brachiopods that characterize these zones are *Streptorhynchus inaequiornatus* Leanza, *Tivertonia jachalensis* (Amos), *Kochiproductus riojanus* (Leanza), *Kochiproductus* sp., *Costatumulus* sp., *Coronalosia argentinensis* Archbold and Simanauskas, *Tupelosia paganzoensis* Archbold and Simanauskas, *Pericospira pericoensis* (Leanza), *Pericospira riojanensis* (Lech), *Septosyringothyris* sp. aff. *S. jaguelensis* Lech, *Crurithyris*? sp., *Orbiculoidea* sp., *Neochonetes pegnonensis* Cisterna and Simanauskas, *Septosyringothyris jaguelensis* Lech and *Rhynchopora* sp., accompanied by the bivalves *Nuculavus levatiformis* (Walcott), *Ptychopteria (Ptychopteria) liagracielae* (Leanza), *Pterinopectinella ramacionii* González, *Heteropecten anteloi* González, *Septimyalina* sp., *Leptodesma (Leptodesma) potens* Hall, *Acanthopecten jaguelensis* González, *Wilkingia riojana* González, *Grammatodon* sp. and *Parallelodon* sp. (Manceñido et al., 1976; González, 1997; Sterren, 2000).

To the north of the Calingasta-Uspallata basin (Fig. 2), this transgressive episode has recently been recognized in the Del Salto Formation (Quartino et al., 1971) because of the occurrence of some brachiopod species that characterize the *Tivertonia jachalensis-Streptorhynchus inaequiornatus* Zone (Taboada, 2006). *Tivertonia jachalensis* appears in association with species of the genera *Septosyngothyris*, *Costatumulus* and *Etherilosia*? (Cisterna and Archbold, 2007) in a fossiliferous interval from the lower part of this Formation. *Pericospira sanjuanesis* (Lech and Aceñolaza) and *Saltospirifer guevarii* (Cisterna and Archbold) have also been described in this interval (Cisterna and Archbold, 2007). To the south of the Calingasta-Uspallata Basin, the Early Permian faunas associated with the transgression integrate the *Costatumulus amosi* Zone (Taboada, 1998), considered Late Asselian - Sakmarian by Taboada (2006) and recognized in the Santa Elena Formation and in the upper part of the Agua del Jagüel Formation (Harrington, 1971). The brachiopods *Costatumulus amosi* Taboada, *Coolkilella keideli* Taboada and *Crurithys* sp., accompanied by the representative bivalve *Oriocrassatella sanjuanina* González (González, 1982), appear to distinguish this biozone. However, the species *Tivertonia jachalensis* has also been described in association with the *Costatumulus* fauna (Lech, 1990, 2002; Taboada, 2006). Hence, the stratigraphical relationship between the *Costatumulus amosi* Zone and the *Tivertonia jachalensis-Streptorhynchus inaequiornatus* Zone is in review by the present authors.

This transgressive event has also been identified in the Cerro Agua Negra Formation (Polanski, 1970). Two faunal assemblages are recognized in the lower part of this unit (Coturel et al., 2006), i.e., the brachiopods *Rhynchopora* sp., *Costatumulus*? sp., Rugosochonetidae indet., Linoproductoidea indet., Productoidea indet. and Spiriferida indet. (Del Áspero Creek locality) and the bivalves *Oriocrassatella sanjuanina* González and *Stutchburia iglesiaensis* González, accompanied by the brachiopods *Neochonetes*? sp., with *Costatumulus*? sp. and *Orbiculoidea* sp. (Las Tranquitas de Abajo locality). This fauna was included in the *Costatumulus amosi* Biozone (González, 1976), but recent studies indicate that there are not diagnostic elements of this biozone, as well as preliminary brachiopod affinities with the youngest Early Permian fauna from the middle part of the Río del Peñón Formation (Coturel et al., 2006).

A summary of the lithostratigraphical units and the diagnostic components of the fossil assemblages studied are provided in Appendices I and II in the electronic version of this paper available at www.geologica-acta.com.

DATABASE AND METHODS

The distribution and abundance of the bivalves and brachiopods (rhynchonelliformeans and linguliformeans) of Argentine Precordillera are analyzed here in three time intervals: Early Carboniferous (Tournaisian-Visean), Late Carboniferous (Bashkirian-Kasimovian) and Early Permian (Asselian-Sakmarian).

The database includes taxa described and illustrated from different authors (Archbold et al., 2006; Cisterna, 1997; Cisterna and Taboada, 1997; Cisterna and Simanauskas, 1999, 2000; Cisterna et al., 2002a-b, 2006; Cisterna and Archbold, 2007; Cisterna and Sterren, 2007, 2008; González, 1982, 1992, 1994, 1997, 2002; Lech, 1986, 1993, 1995; Lech and Milana, 2006; Lech et al., 1998; Taboada, 1997, 1998; 2004, 2006; Taboada and Cisterna, 1996; Sterren, 2000, 2002, 2003, 2004, 2005) as well as bivalves and brachiopods recently reviewed by the present authors.

Familiar and generic data in each interval of time are presented in the appendices and various figures. Appendix III (Bivalves) and Appendix IV (Brachiopods) summarize all the information available for the database; Figures 3 to 7 show the variations of the groups studied at different scales along the Carboniferous-Early Permian interval.

BIODIVERSITY PATTERNS OF CARBONIFEROUS-EARLY PERMIAN BIVALVES AND BRACHIOPODS IN PRECORDILLERA

The study of the diversity of bivalves and brachiopods in the marine sequences of central western Argentina reveals in the first place that bivalves are relatively more diversified than the brachiopods; there is also a continuous increase, at familiar and generic levels, of the bivalves through the time intervals considered (Figure 3). However, in the brachiopods, this increase is significant from the Early to Late Carboniferous, but during the Early Permian, the diversity appears to be constant. The analysis of the faunistic turnover in both groups, along the three time intervals considered, also suggests a different behaviour. The bivalves exhibit a steady increase in the familiar and generic richness and show a relative persistence of the taxa with an important diversification of the epifaunal and infaunal groups (Figure 4). The brachiopods, on the contrary, show a significant turnover, fundamentally between the Early Carboniferous and the Late Carboniferous (Figure 5).

Early Carboniferous (Tournaisian - Visean)

In the Early Carboniferous, the fossil assemblages studied exhibit two characteristics: the record of lowest diversity in the Late Palaeozoic of Precordillera and a larger predominance of bivalves over brachiopods (Figure 3).

Bivalves. Six orders of bivalves, with one or two families each (Malletidae, Nuculanidae, Mytilidae, Myalinidae, Pterineidae, Myophoridae, Cardinidae, Edmondidae, Sanguinolitidae) and 11 genera, have been registered in this interval of time.

The auto-ecological analysis of the components that integrate bivalve assemblages for the Early Carboniferous clearly allows for the recognition of a predominance of infaunal mobile habitats concerning the semi-infaunal byssate forms and scarce records of the epifaunal bivalves. In addition, the detritivorous taxa (*Palaeoneilo subquadratum* González, *Malimania triangularis* González and *Phestia* sp.) included in the Nuculoids are dominant during this interval of time. This group can be considered a classical example of deposit feeders that inhabited slightly dysaerobic, muddy-silty and rich in organic matter substrates. Several *Phestia* species are relatively abundant in the Late Palaeozoic, and they are frequently present in opportunistic

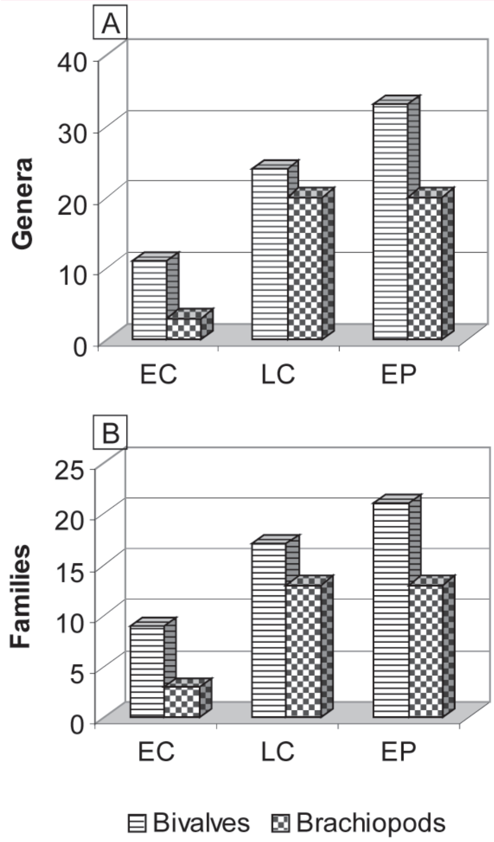

FIGURE 3 | **Histograms showing the diversity of bivalves and brachiopods in Precordillera and the number of genera and families in each time interval. A) Genus level. B) Family level. EC: Early Carboniferous, LC: Late Carboniferous, EP: Early Permian.**

assemblages, commonly associated with stress conditions (Sterren, 2000; Simanauskas and Cisterna, 2000; Lebold and Kammer, 2006). The genus *Malimania* appears associated with glacigenic sediments in Patagonia (*Malimania patagoniensis* González), perhaps because this genus can tolerate low temperatures. The other abundant element is *Posidoniella malimanensis* González, which belongs to the posidoniids group, considered to be markers of dysaerobic conditions in some environments of Triassic sequences (Aberhan, 1994; Schatz, 2005).

Brachiopods. In contrast with bivalves, the brachiopods document only 3 orders (Productida, Rhynchonellida and Spiriferinida), with one family in each (Chonetidae, Camarotoechiidae and Syringothirididae) and 3 genera. This is the lowest diversity of brachiopods recognized along the three time intervals studied.

Brachiopods that integrate the Early Carboniferous faunal assemblages are represented by components of epifaunal life habits with pedunculate (rhynchonellids) and liberosessile forms (productids and spiriferinids). The rhynchonellids, a group adapted to turbulent environments (ribs, strong pedicle, thick shell) and especially common in the Early Carboniferous, are dominant in these assemblages with the genus *Azurduya*. The productids that appear typically associated with *Azurduya* with the genus *Chilenochonetes*? display a free lying habit. This chonetid develops morphological adaptations for stability and support (i.e., concavo-convex thin-shelled, developing posteriorly directed spines along the ventral cardinal margin, adapted to the “ski effect” (Basset, 1984)) on soft bottoms. The Early Carboniferous chonetid species could also have developed some type of opportunistic strategy, such as the ones widely studied in other Late Palaeozoic chonetid species (Jacobs, 1976; Simanauskas and Muzón, 1990; Simanauskas and Cisterna, 2000), suggesting that palaeoenvironmental conditions were highly stressed.

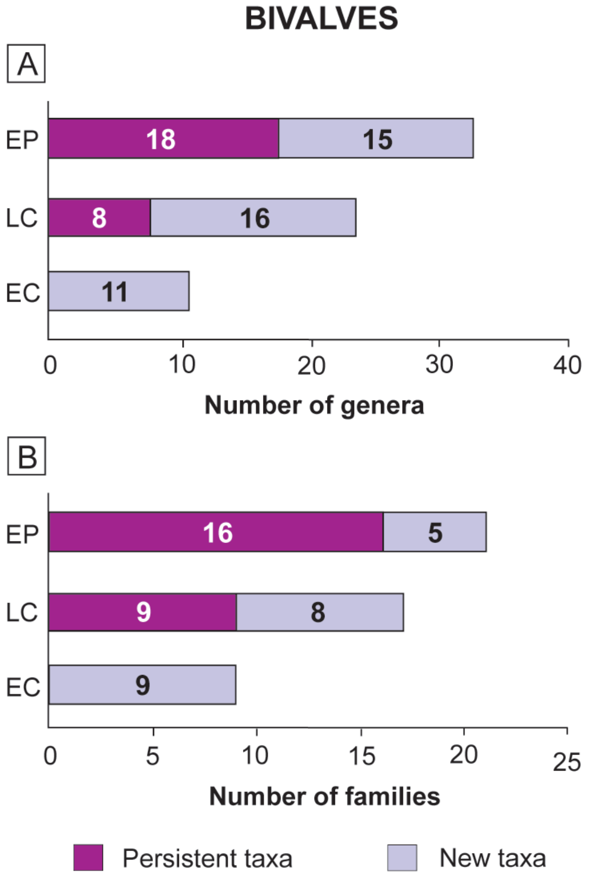

FIGURE 4 | **Histograms showing the number of genera and families of bivalves that appear in each time interval and the number of persistent taxa from the previous interval. A) Genus level. B) Family level.**

Interpretation. The bivalves and brachiopods studied in this interval of time integrate a marine faunal assemblage composed of ortoconic nautiloids, gastropods, hyoliths, conulariids and some trilobites (González, 1993; Sabattini et al., 2001; Cisterna and Isaacson, 2003), which occurs in the Malimán and Jagüel formations, previously mentioned in the geological setting paragraph. In the lower part of the Malimán Formation, the Early Carboniferous fauna is associated with a sequence of offshore shales and coastal fine-grained sandstones that gradually pass upward to the deltaic, fluvial and diamictitic deposits of the Cortaderas Formation (Limarino and Spalletti, 2006). Two glacial horizons in the basal interval of Malimán Formation have also been recognized by Pazos et al. (2005). The marine fauna in this unit appears distributed in an interval about 60 m thick, composed of littoral and shelf green mudstones and sandstones (Limarino et al., 2006). Bivalves and brachiopods are disperse or concentrated as nests in the mudstones, as well as in shell beds 1-5 cm thick in the sandstone horizons.

In the Jagüel Formation, the Early Carboniferous assemblage appears generally disperse and occasionally concentrated in two fossiliferous horizons (González, 1994). The taphonomic features of these deposits suggest a shoreface to offshore transition environment (Sterren, 2008). The recent identification of diamictitic glacial deposits in this formation (Las Minitas Range locality) could be considered evidence of a Late Devonian-Early Carboniferous glaciation (Ezpeleta and Astini, 2009).

In the Early Carboniferous (Tournaisian-Visean) successions two important aspects can be noted, i.e., the bivalves and brachiopods show the lowest diversity registered along the Late Palaeozoic interval, and the fossil assemblages studied exhibit a larger predominance of bivalves than brachiopods (Figure 3).

The recent glacial sedimentary records identified in the Malimán and Jagüel formations give an explanation of the low diversity of the Early Carboniferous fauna, which would have been exposed to the extreme temperatures related to glacial conditions. However, other types of restrictions, probably related to environmental conditions such as type of substrate, energy, turbidity and oxygen availability in the water, would also have controlled the Early Carboniferous assemblages. Thus, the predominance of opportunistic bivalves and brachiopods (*Palaeoneilo*, *Malimania, Posidoniella, Phestia* and chonetids) indicates highly stressed environments, related to dysaerobic conditions and unstable substrates.

These conditions would have facilitated the predominance of bivalves in relation to the brachiopods. Although the substrate features have usually been considered the most important restriction in the distribution of the brachiopods, variations in nutrient supply, temperature, oxygen levels and biotic interactions have been suggested for modern brachiopod distributions. The actualistic hypothesis suggests that bivalves and brachiopods have different metabolic demands in relation to the nutrient supply, temperature and oxygen (Tomasovych, 2006), which could explain the differential abundance of these groups for the interval of time studied. Environmental changes can affect the development and distribution of some groups of brachiopods in the fossil assemblages, considering the nutrient availability and the sedimentological setting (water depth and facies context) (Pérez-Huerta and Sheldon, 2006).

An equivalent low-diversity brachiopod assemblage mainly composed of *Azurduya chavelensis* (Amos), *Chilenochonetes anna* Isaacson and Dutro, *Septosyringothyris covacevichi* Isaacson and Dutro, *Septosyringothyris* sp. and *Pseudosyrinx* sp., which reflects a high-stressed environment in a clastic, nearshore setting, has also been described from the Early Carboniferous of northern Chile (Sierra de Almeida, Zorritas Formation) by Isaacson and Dutro (1999).

Late Carboniferous (Late Serpukovian - Kasimovian)

The Late Carboniferous marine fauna of the Precordillera is characterized by an important increase in bivalves and brachiopods, and it includes three different faunal assemblages (i.e., *Levipustula* fauna (Late Serpukhovian-Bashkirian); *Aseptella-Tuberculatella/Micraphelia-Rhipidomella* fauna (probably late Bashkirian-Moscovian?) and *Balakhonia-Geniculifera* fauna (Moscovian-Kasimovian)), which have temporal and biostratigraphical implications. A very important faunistic turnover can be identified in the brachiopods (Figure 5).

Bivalves. In this interval of time, the number of bivalve families increases to 16. The most important increase is related to the first records of the Order Pectinoida herein represented by the Aviculopectinidae, Deltopectinidae, Euchondriidae and Streblochondriidae families. The number of genera shows an important increase of 23 genera (8 persistent from the previous interval and 3 genera disappear). The increase in the diversity of the bivalves is mostly due to the occurrence of limids and several pectinoids represented by the genera *Palaeolima, Aviculopecten, Streblochondria, Streblopteria, Limipecten, Euchondria* and *Orbiculopecten*. These epifaunal and suspension feeding organisms appear more diversified displaying epibyssate, libero-sessil and pedunculate habits. The first record of the families Nuculidae (*Nuculopsis* and *Nuculanella* genera) and two Pholadomyids appears in this interval (*Pleurophorella* genus and *Myofossa* genus), increasing the infaunal number in relation to the Early Carboniferous interval. The morphological features of these infaunal bivalves suggest their inclusion in the rapid burrowing bivalves group, and a moderate depth of burial would be expected for the pholadomyids (Sterren, 2002).

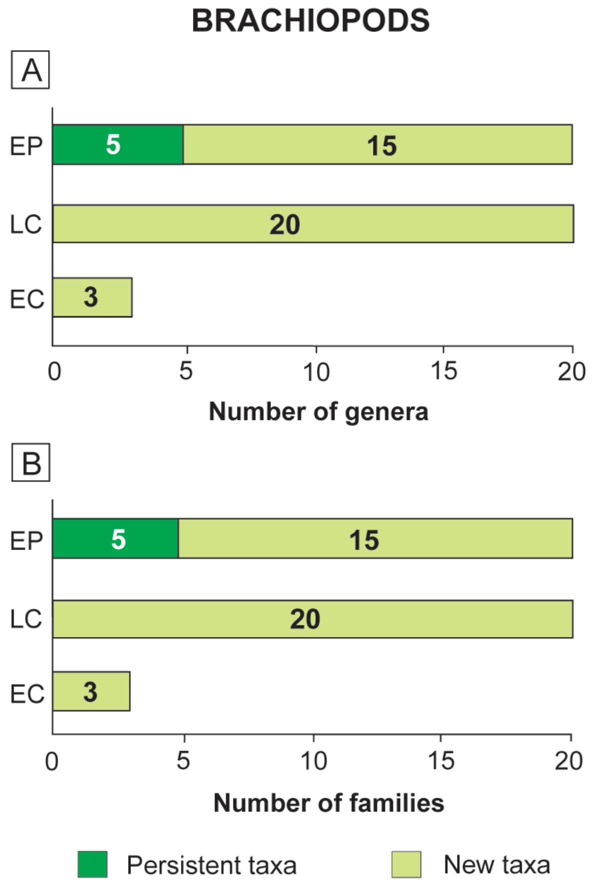

FIGURE 5 | **Histograms showing the number of genera and families of brachiopods that appear in each time interval and the number of persistent taxa from the previous interval. A) Genus level. B) Family level.**

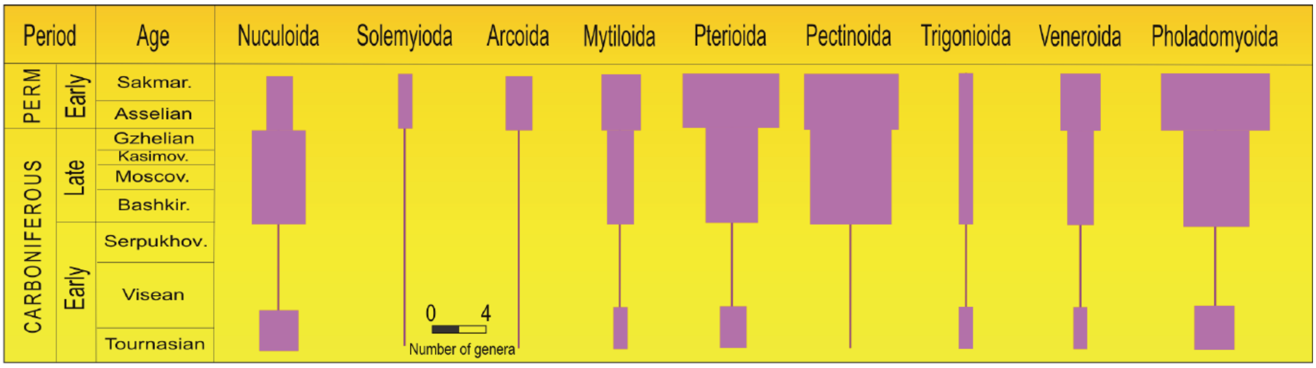

FIGURE 6 | **Temporal distribution of bivalve families in Precordillera during the time interval considered.**

Brachiopods. The faunal turnover in the Late Carboniferous is comparatively more significant in the brachiopods (Figure 5). The number of orders increases to 7 (Lingulida, Productida, Orthida, Rhynchonellida, Spiriferida, Spiriferinida and Terebratulida), with 13 families (Discinidae, Anopliidae, Rugosochonetidae, Productellidae, Linoproductidae, Rhipidomellidae, Paranorellidae, Trigonotretidae, Reticulariidae, Elythidae, Syringothyrididae, Crenispiriferidae, Beecheriidae) and 20 genera that appear for the first time in this interval. No brachiopod genera from the previous interval are present in the Late Carboniferous. Productida with the genera *Gonzalezius, Neochonetes, Rugosochonetes, Micraphelia, Tuberculatella, Aseptella, Levipustula, Geniculifera, Balakhonia* become the most dominant group of all the interval, followed by the Spiriferida (*Costuloplica, Reticularia, Kitakamithyris, Torynifer*) and Spiriferinida with the genera *Syringothyris, Septosyringothyris, Spiriferellina* (Figure 7). Orthids (*Rhipidomella*) and terebratulids (*Beecheria*) are restricted to this interval, and the brachiopod inarticulates documented herein are the first records. The epifaunal brachiopod forms are dominant in the interval, with pedunculate and free-sessile life strategies in some productids, spiriferids and spiriferinids. However, the productids that constitute the most highly diversified group also include endofaunal forms that develop a quasi- infaunal life strategy (i.e., genera *Tuberculatella*, *Levipustula*, *Geniculifera*, *Balakhonia*).

Interpretation. The faunal events at the Visean-Serpukovian boundary are difficult to evaluate due to the general scarcity of fauna related to the development of the glaciers during the Serpukovian and probably early Bashkirian, which represents the beginning of the "Late Palaeozoic Ice Age" (Stanley and Powell, 2003), recognized in this sector of Gondwana. By contrast, the faunal turnovers for the rest of the Late Carboniferous time interval (middle and late Bashkirian to Kasimovian), mainly related to the glacial retreat and the posterior climatic amelioration, are evident in the three faunal assemblages previously noted.

The increase of bivalves and brachiopods in this time is related to the postglacial interval.

The *Levipustula* Fauna is the most representative for the Late Carboniferous, and it is usually related to the most important glacial event that affected the south-western Gondwanan basins (Early Pennsylvanian, Limarino et al., 2006). The bivalves and brachiopods that characterize this fauna integrate an assemblage composed of bryozoans, gastropods, crinoids and scarce conularids that frequently appears associated with glaciomarine sequences. These sequences generally grade upward to postglacial open marine fine-grained clastics, which have been interpreted as the sedimentary response to a glacioeustatic sea level rise that occurred during the glacial retreat subsequent to a widespread glaciation (López Gamundí, 1989, 1990). The Hoyada Verde Formation encloses the most complete record of the *Levipustula* Fauna, where it has been studied widely (Cisterna and Sterren, 2003, 2004, 2010; Sterren and Cisterna, 2006). In this unit, compositional, taphonomic and palaeoecological features have allowed researchers to distinguish the "Intra-glacial *Levipustula* Fauna", a very low diversified fauna interbedded with diamictitic horizons in the lower part of the section, and a more highly diversified "Post-glacial *Levipustula* Fauna", associated with mudstones facies and easily identified above the glacial diamictitic deposits of the upper part (Cisterna and Sterren, 2008; Cisterna and Sterren, 2010). The communities of the "Post-glacial *Levipustula* Fauna" would have been developed in a stable marine environment, such as an open shelf with moderate bottom currents, and the variations would have been controlled by the substrate type and food supply, directly related to the postglacial transgressive event (Cisterna, 1999; Simanauskas et al., 2001; Cisterna and Sterren, 2010). The distribution of the fossil assemblages of the "Post-glacial *Levipustula* Fauna" shows a gradual deepening with water still cold and a continuous increase

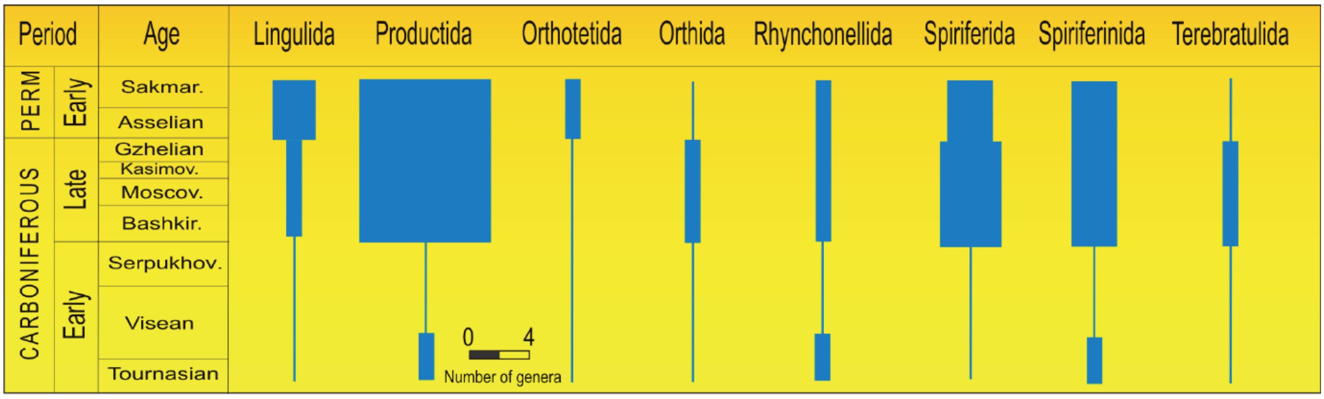

FIGURE 7 | **Temporal distribution of brachiopod families in Precordillera during the time interval considered.**

of nutrient availability, which is evidenced by a rise in biovolume and specific richness (Cisterna and Sterren, 2010). During the maximum flooding, in a more stable substratum, the suspension feeding and epifaunal organisms appear more diversified (epibyssate, libero-sessil and pedunculate habits). This local deepening event, well studied in the postglacial communities of the Hoyada Verde Formation (Cisterna, 1999), would have produced the important increase in the Late Carboniferous faunal diversity, related to a generalized transgressive episode in the basins of the Palaeo-Pacific margin (Sterren and Cisterna, 2008).

The horizons that contain the younger fossil assemblages appear physically disconnected from the oldest *Levipustula* fauna or, for some of them, succeeded by a fault or angular unconformity to the previous fauna. No significant lithofacies and palaeoenvironmental changes seem to have occurred between *Levipustula* fauna and the relatively younger *Aseptella-Tuberculatella/Micraphelia-Rhipidomella* faunal assemblage, which was affected by the glaciation as well. However, new brachiopod taxa have allowed researchers to identify a different fossil assemblage. Bivalves and brachiopods that integrate the *Aseptella-Tuberculatella/Micraphelia-Rhipidomella* fauna, identified in the El Paso Formation (Simanauskas and Cisterna, 2001) and the lower part of Agua del Jagüel Formation (Martínez et al., 2001), are accompanied by gastropods, ortoconic nautiloids, crinoids and solitary corals, which usually appear dispersed in mudstone and sandstone sequences and, occasionally, concentrated in shell beds formed in offshore to shoreface environments. This fauna can be linked to the transgressive episode related to last pulse of the Carboniferous glaciation (Martínez et al., 1998).

The youngest faunal assemblage *Balakhonia-Geniculifera*, recognized in the Pituil Formation and the upper part of the Ansilta Formation (Taboada, 1997, 2004, 2006), does not appear associated with glacial deposits, and it has been considered as a temperate fauna, an indicator of the end of the Carboniferous glaciation and the beginning of better palaeoclimatic conditions (Taboada, 2004). This fauna would have been linked to wave dominated shallow marine environments (Buatois and Limarino, 2003; Limarino and Buatois, 2003).

Early Permian (Asselian - Early Sakmarian)

In the Early Permian the diversity of bivalves and brachiopods exhibits a different pattern, i.e., the bivalves show a continuous increase at familiar and generic levels, and the brachiopods diversity appears to remain constant.

Bivalves. Twenty-one families of bivalves with 33 genera have been registered in this interval of time. The first record of the order Solemyioida, with the genus *Solemya*, appears during the Early Permian in the Precordilleran basins. In addition, there are two features that characterize this time: one of them is the first appearance of two quasi-infaunal genera of Arcoida (*Grammatodon*, *Parallelodon*), and the other is that the order Pterioida is the most diversified with a significant increase of genera (Figure 6). A large diversification of epibyssate bivalves are identified in the Early Permian, essentially in the Pterineidae and Mytilidae families. Moreover, the order Pectinoida is diversified at the generic and specific levels. These epifaunal and suspension feeding organisms are included in several typical genera: *Pterinopectinella, Aviculopecten, Acanthopecten, Streblopteria, Heteropecten, Euchondria,* and *Streblochondria*. The Order Pholadomyoida also shows an important diversification of the families Phermophoridae (*Netschajewia* and *Stutchburia* appear by the first time) and Sanguinolitidae with the genus *Wilkingia*. The morphological features of these organisms suggest the colonization of relatively deeper infaunal levels for the members of this group.

The groups of bivalvia diversified in the Early Permian would have participated in the large Ordovician radiation (with exception of Solemyoida, which has been well known from the Devonian), but the diversification to lower taxonomical hierarchies would have been going on to the end of the

Palaeozoic. The large diversification identified in the Early Permian, fundamentally in the Pterineidae and Mytilidae families (Sterren and Sánchez, 2007), can be considered as an example. This diversification is probably related to the important global development registered in the components of the subclass Pteriomorphia in the Late Palaeozoic (Babin et al., 1992). The increase of the diversity in the Permophoridae and Sanguinolitidae families (included in the Pholadomyoida) can be associated with the development of new morphological structures related to successful ecological strategies, i.e., the colonization of deeper infaunal levels that allows the differentiation into higher taxonomical hierarchies. This is also linked to the generalized increase to specific levels registered in the subclass Anomalodesmata in the Late Palaeozoic (Morris et al., 1991).

From the 23 genera of bivalves identified in the Late Carboniferous, 18 genera have persisted to the Early Permian.

Brachiopods. In the Early Permian the brachiopods show roughly the same diversity as the previous interval at the familiar level; seven families disappear (Anopliidae, Productellidae, Rhipidomellidae, Paranorellidae, Reticulariidae, Elythidae and Beecheriidae), and another 7 families appear (Lingulidae, Productidae, Monticuliferidae, Strophalosiidae, Streptorhynchidae, Rhynchoporidae, and Ambocoeliidae). The order Orthotetida appears in this interval with the genus *Streptorhynchus*; there is an increase of the generic richness in the order Lingulida (*Argentiella, Lingula* and *Orbiculoidea* genera) and a decrease of the generic richness in the order Spiriferida. As in the Late Carboniferous, Productida is the most dominant group in the entire interval, followed by Lingulida, Spiriferida and Spiriferinida (Figure 7). The productids show a higher diversification of the quasi-infaunal forms, with the genera *Kochiproductus*, *Coolkilella*, *Costatumulus*, *Coronalosia*, *Tupelosia* and *Etherilosia*. The orders Spiriferida are characterized in this interval by the dominance of epifaunal free-sessile forms with genera such as *Pericospira*, *Saltospirifer* and *Septosyringothyris*. The spiriferinid *Septosyringothyris*, a conspicuous element in the early Permian faunal assemblages of the Precordillera, can be considered a classical example of the free-sessile life strategy that indicates low energy environments, with a relatively firm substrate in which the sediment suspension predominates over sediment traction (Simanauskas and Cisterna, 2000).

Interpretation. The Early Permian (Asselian - Early Sakmarian) marine fauna is the most widely distributed and diversified of the Late Palaeozoic faunal assemblages of Precordillera, and it is well known from the Río Blanco, Paganzo and Calingasta-Uspallata basins. Bivalves and brachiopods that integrate these youngest assemblages belong essentially to the *Tivertonia - Streptorhynchus* fauna and the *Costatumulus* fauna.

The earliest Permian (Asselian) *Tivertonia-Streptorhynchus* fauna is composed of bivalves, brachiopods, gastropods and ostracods. This faunal assemblage characterizes the northernmost sector of the studied area (Río del Peñón and Quebrada Larga Formations in the Río Blanco Basin; Tupe Formation in the western Paganzo Basin; Del Salto Formation, to the north of the Calingasta-Uspallata Basin). Probably the youngest *Costatumulus* fauna (Late Asselian - Sakmarian, Taboada, 2006), characteristic of the southern Calingasta-Uspallata Basin (Agua del Jagüel and Santa Elena Formations), is composed fundamentally of bivalves and brachiopods, accompanied by gastropods, cephalopods, scaphopods and conularids. Early Permian sequences that contain these faunal assemblages are generally characterized by marine foreshore to offshore deposits (Sterren, 2008).

The development of these faunas is associated with an important climatic amelioration recorded in the western Argentinian basins, and it is better reflected in the behaviour of the bivalves. This amelioration of the climatic conditions has also been registered at a global level in Gondwana. Lithologic and palaeontological data suggest for this time a climatic amelioration with a relatively higher temperature than normal (Dickins, 1978, 1996). In this part of Gondwana, the onset of these temperate conditions would have occurred at the end of the Late Carboniferous (Kasimovian-Gzhelian, López Gamundí et al., 1993), and they are represented by significant coal horizons documented in the basins studied. On the other hand, towards the end of Carboniferous, Bahlburg and Hervé (1997) documented the first records of magmatic activity with the deposition of volcaniclastic sequences that indicate the occurrence of an active volcanic arc in the proto-Pacific margin. These evidences of volcanism contemporaneous with the sedimentations have been identified in Argentina in the Paganzo basin (Limarino et al., 1986) as well as in the Río Blanco, Calingasta-Uspallata and Arizaro basins (López Gamundí and Breitkreuz, 1997). In this context, the volcanic activity would have affected the development of the marine fauna. The increase of temperature, the transgressions, the increase of the nutrient supply and the carbon dioxide are extrinsic primary controls on the ecosystems, produced by submarine volcanism (Vermeij, 1995). Additionally, the volcanism would favour the warming of some areas, fundamentally those located in middle to high latitudes. This climatic amelioration would have been accentuated by the action of warm marine currents that produced localized variations in the gradient of temperature. This can explain the important participation of elements with palaeoequatorial affinities within the bivalve assemblages of the *Tivertonia-Streptorhynchus* fauna (Sterren, 2004).

The relative increase in temperature in the Early Permian, explained by different reasons, i.e., the palaeogeographical position of the central western Argentinian basins, volcanism and marine currents, was an important factor in the diversification of the bivalves.

DISCUSSION

The study of bivalve and brachiopod diversity patterns from the Early Carboniferous to the Early Permian in the Argentine Precordillera reveals a generalized increase, at the familiar and generic levels, of bivalves through the time intervals studied. However, although the brachiopod diversity increases during the Carboniferous, it seems to be stable from the Late Carboniferous to the Early Permian. Some tectonic, climatic and palaeogeographic features of the basins in this part of Gondwana would have controlled the behaviour noted in the bivalves and brachiopods analyzed.

The global bivalve and brachiopod diversity has been summarized by Babin et al. (1992), with data of the Treatise on Invertebrate Paleontology from the end of 1960's to the beginning of 1970. The accumulative abundance curves for brachiopods and bivalves carried out by these authors clearly show dissimilar trends for each group (Figure 8). Even if this information were not updated, it shows that the number of brachiopod genera decreases clearly from the Devonian, while the bivalves exhibit a small but continuous increase from the Ordovician, with a stable stage at the superfamiliar level in the Late Palaeozoic (Stanley, 1968). The data from the Precordillera analyzed here demonstrate a correspondence with the global bivalve diversity pattern but not with the brachiopod diversity patterns.

The important diversification of bivalves and the stability noted in the brachiopod diversity during the Late Carboniferous-Early Permian interval in the Precordillera can also be explained in the context of the "Evolutionary Faunas" suggested by Sepkoski (1981, 1990). From this viewpoint, the brachiopods are an important component of the Palaeozoic evolutionary fauna and the bivalves of the Modern evolutionary fauna. At the end of the Permian, one of the most important biotic events of the Phanerozoic has been documented. It can be considered the most significant taxonomical and palaeoecological crisis that produced the collapse of the existing ecosystems, their subsequent replacement and the substitution of the Palaeozoic evolutionary fauna (Mc Ghee et al., 2004; Sepkoski, 1984, 1990).

The trend of bivalve and brachiopod diversity from the Early Carboniferous to the Early Permian analyzed in the Argentine Precordillera, would be indicative of the evolutionary history of these faunal groups, closely related to the palaeogeographic-palaeotectonic evolution of the Southwestern Gondwanan basins. Thus, the evolution from the uplift of the Protoprecordillera orogen and coeval tectonic subsidence in the Early Carboniferous basins, to a more stable time characterized by postorogenic sedimentation

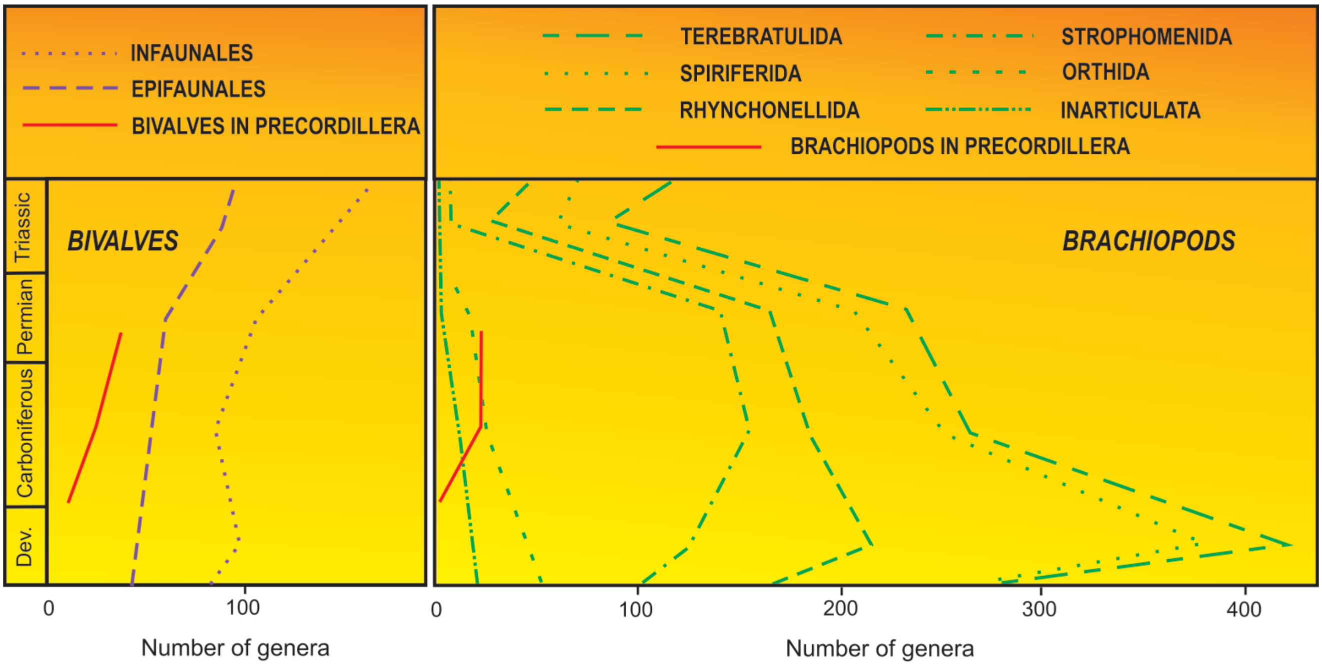

FIGURE 8 | **Curves showing the variation of the bivalve and brachiopod genera in Precordillera during Carboniferous and Permian times in comparison to the general change trends proposed by Babin et al., (1992).**

in the Late Carboniferous-Early Permian (Limarino et al., 2006), is also reflected in the different faunal assemblages of the Precordilleran basins.

The Late Palaeozoic marine record in Precordillera is discontinuous and shows the largest break, probably related to a maximum glacial recognized at the global and regional levels, during the Visean-Serpukovian boundary. Extreme palaeoenvironmental conditions could be the reason for the low faunal diversity in the Early Carboniferous. At this time, two important aspects can be noted, i.e., the bivalves and brachiopods show the lowest diversity registered along the Late Palaeozoic, and the fossil assemblages studied exhibit a larger predominance of bivalves over brachiopods (Figure 3). The configuration of the Carboniferous sea would have been controlled by an irregular topography resulting from the extensional dynamics (rifting) that produced isolated depocentres. Continental and littoral glacial sediments characterize the initial sedimentary infill (Tournaisian) of these depocentres. Accommodation space was reduced by the glacial onset, and the transgressive-regressive cycles seem to have been related to sea level fluctuations by glacial advances and retreats. A decrease in the accommodation spaces because of the strong aggradational to progradational wedges and the maximum Protoprecordillera uplift in the late Visean (Pazos et al., 2005; Limarino et al., 2006) would also have inhibited the development of the early Carboniferous marine faunas in these basins. The Early Carboniferous marine sedimentation that contains the fauna studied is restricted by sedimentary glacial records that suggest an important local palaeoclimatic control on its diversity.

A global mass extinction event has been recognized at the Devonian-Carboniferous boundary, and it represents one of the largest biotic disturbances of the Phanerozoic (Sepkoski, 1996; Caplan and Bustin, 1999). The Devonian-Carboniferous bio-event encloses significant faunal changes at various trophic levels throughout diverse environments, producing the loss of biodiversity in the Late Devonian (McGhee et al., 2004). The Late Devonian was characterized by global climatic changes that generated a devastating impact on the already stressed marine biota. Important lithologic, palaeontological and geochemical changes have been documented from the Upper Devonian stratigraphic record (Caplan and Bustin, 1999). The global cooling would have affected the ecosystems of Precordillera to the Devonian-Carboniferous boundary, and the lowest faunal diversity could be related to this global faunal crisis.

The central western Argentinian basins studied here were located at about 30° to 60° South latitude in the Carboniferous-Permian interval (Conti and Rapalini, 1993; Buggisch et al., 1994; Rapalini and Vilas, 1996). Considering the palaeogeographic position of this sector of Gondwana, which suggests temperate to moderately cold conditions, the low diversity of the Early Carboniferous assemblages can be explained by the extreme glacial temperatures. Other types of restrictions, probably associated with local environmental conditions, would have controlled this fauna. Thus, the low abundance of bivalves and brachiopods, which would have developed opportunistic strategies in these faunal assemblages, can indicate highly stressed environments related to dysaerobic conditions and unstable substrates.

The maximum glacial suggested for the Visean-Serpukovian boundary produced extreme temperatures as well as more reduced depositional areas, which would have generated faunistic isolation and stressed environmental conditions. Hence, the Visean-Serpukovian boundary is difficult to evaluate due to the general scarcity of fauna related to the onset of the glaciation ("late palaeozoic ice age") in Late Visean. The heavy faunal extinction appears to be concentrated in Early Serpukovian times (Stanley and Powell, 2003; Powell, 2005). Different authors have suggested that the Serpukovian glaciation event would have produced an extinction comparable to the "Big Five" (Sepkoski, 1986). However, the magnitude and duration of this event appear to vary greatly between the different fossil groups (Shen et al., 2006). In the Precordilleran faunal assemblages studied here, this event cannot be evaluated in the brachiopod faunas, but it is clearly documented in the bivalves. However, the aim of this paper is not to evaluate whether the magnitude of the Serpukovian extinction is comparable to the Sepkoski's "Big Five".

The Late Carboniferous interval in the Precordillera is characterized by the postglacial transgressions and the enlargement of the depositional areas accompanied by the beginning of temperate climatic conditions. Local rebounds, a continuous increase of the diversity and an important faunal turnover related to the postglacial conditions fundamentally expressed in the brachiopod faunas, have been recognized. The post-Serpukovian rebound can be considered diachronic in different areas (Stanley and Powell, 2003). In the Precordillera this diversification event begins in the Bashkirian with the *Levipustula* Fauna, and it remains until the early Permian with a constant increase and diversification of the mollusk faunas and the stability of brachiopods.

This faunistic tendency persists in the Latest Carboniferous-Early Permian, and it is associated with the subsequent Palaeo-Pacific transgressive events that produced new accommodation spaces. The climatic amelioration registered in the central western Argentinian basins, as well as the volcanic activity and the action of relatively warmer marine currents, would have been important local factors that controlled the bivalve and brachiopod distribution. The combination allowed for the increase and diversification of the fauna, much better reflected in the behaviour of the bivalves.

CONCLUSIONS

The diversification patterns of bivalves and brachiopods through the Carboniferous-Permian interval in the central western Argentinian basins reveal a generalized increase, at the familiar and generic levels, of bivalves through the Early Carboniferous (Tournaisian-Visean), Late Carboniferous (Bashkirian-Kasimovian) and Early Permian (Asselian-Sakmarian), while the brachiopod diversity seems to be stable from the Late Carboniferous to the Early Permian.

The faunistic turnover in the interval of time studied is more evident in the brachiopod faunas, fundamentally between the Early and Late Carboniferous.

The trend recognized in the faunistic diversity appears to be closely related to the palaeoclimatic and palaeogeographic/palaeotectonic evolution of the Southwestern Gondwana margin.

The lowest faunistic diversity registered in the Early Carboniferous, fundamentally in the brachiopod faunas, can be explained by the highly stressed palaeoenvironmental local conditions, associated mainly with a glacial episode, apart from the tectonic uplift apogee in Precordillera that occurred in the Late Visean. As a consequence of these events, a decrease in the accommodation space and consequently in the size of marine basins limited the normal development of the faunal assemblages.

At the Visean-Serpukovian boundary, the Late Palaeozoic faunal marine record in central West Gondwana shows the largest break linked to a globally recognized glacial maximum.

A more stable time, characterized by the Late Carboniferous-Early Permian, postorogenic sedimentation is also reflected in the different faunal assemblages studied. Towards the Late Carboniferous, distinguished by the postglacial transgressions, a local rebound, a continuous increase of the diversity, and an important faunal turnover, fundamentally expressed in the brachiopod faunas, have been recognized. This tendency is related to a climatic amelioration that seems to be continuous to the Early Permian. The subsequent transgressive events would have produced new accommodation spaces in this interval of time, allowing for the increase and diversification of the fauna, which are much better reflected in the behaviour of the bivalves.

The data from the Precordillera analyzed here demonstrated correspondence with the global bivalve diversity pattern but not with the brachiopod diversity patterns.

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APPENDIX I
Summary of lithostratigraphy and paleo-environmental features of the Late Paleozoic formations from the Argentine Precordillera
(See Fig. 2 in the main text)

RIO BLANCO AND PAGANZO BASINS

Malimán Formation (Scalabrini Ortiz, 1972)

A massive, muddy matrix-supported fine paraconglomerate with sub-rounded clasts of shales, mudstones and mesosilicic volcanic rocks characterizes the lower part of this formation. This interstratified succession of diamictites, conglomerates and plant-bearing mudstones has been interpreted as deposits in low-gradient fluvial plains close to the shoreline. This interval is overlain by the deposits of a retrogradational transgressive system track that consists of sandstones, bioturbated mudstones, and marine fauna bearing shales. Thin intercalations of massive diamictites and pebbly mudstones record sporadic gravity flow sedimentation. The upper part of the section (highstand) shows thickening and coarsening upward parasequence sets composed of medium sandstones and mudstones resulting from mouth bar and coastal deposit progradation.

Quebrada Larga Formation (Scalabrini Ortiz, 1972)

This unit is characterized by a predominance of white sandstones, occasionally interbedded with fine conglomerates and mudstones containing the remains of flora in the lower part. The marine fauna associated with green sandstones with thin limestone horizons is in the middle part of the section. The coarsening-upward sequences increase to the upper part with a major presence of sandstones. The sequence represents fluvial distributary channels and an interdistributary bay with a marine ingression in the middle part.

Jagüel Formation (Fauqué and Limarino, 1991)

This unit is a stratigraphical interval of alternating green sandstones and mudstones with paleofloristic assemblages. To the middle part, grey mudstones appear thinly stratified with fine to medium grained sandstones where the marine fauna is located. In some outcrops, an interstratified succession of diamictites, conglomerates and pebbly mudstones can be recognized. This sequence has been interpreted as a littoral marine environment, in some cases related to glaciomarine conditions.

Río del Peñón Formation (Borrello, 1955)

The lowest part of the section is characterized by the abundance of conglomerate facies with an agradational stacking pattern, interpreted as proximal facies of alluvial fans. Complexes of fluvial distributary channels and an interdistributary bay, identified by coal beds, and bioclastic sandstones-mudstones horizons with marine invertebrate fauna have been recognized from the lower to middle members. The middle-upper members of the section are characterized by coarsening-upward sequences that suggest mouth bar overlaying prodeltaic mudstones and represent the delta front with wave reworking and subordinated tidal action. Siliciclastic facies with a fine record of marine invertebrates have also been recognized in the middle part. This interval suggests a marginal marine environment, such as a tidal and subtidal flat with mixed sedimentation and a deltaic front. In the upper part of the section, complexes of fluvial distributary channels associated with overbank deposits have been identified.

Guandacol Formation (Cuerda, 1965)

This unit presents transgressive mudstones resting directly atop gravity-resedimented diamictites and probably terrestrial tillites. Marine fauna has been reported from the black shales covering the diamictitic levels near the base of this formation. This sequence is interpreted as glacial deposits, and the lower part grades to lacustrine and deltaic environments.

Tupe Formation (Cuerda, 1965)

Sandstones and mudstones with coal facies that have been interpreted as a deltaic swamp system containing a high proportions of organic matter characterize the lower part of this unit. The marine fossil assemblages appear in the middle part of the section in a stratigraphical interval of alternating sandstones and claystones with mudstones lenses. This formation illustrates the transition from a coastal-plain to a marine embayment.

CALINGASTA-USPALLATA BASIN

Del Salto Formation (Quartino et al., 1971)

This unit is composed of stratified conglomerates, sandstones and mudstones in upward coarsening sequences. The marine fauna have been found in the lower part of the section in a stratigraphical interval composed of alternating sandstones and mudstones with intercalated calcareous beds and lenses. This interval has been interpreted as a littoral to sub-littoral marine environment. The upper part of this section changes to a regime of alluvial fan deposition that suggests a progressive continental sedimentation.

Ciénaga Larga del Tontal Formation (Barredo and Ottone, 2003)

This formation is composed by glacimarine diamictites that grade upwards into mudstones and sandstones with marine fauna. The lower middle part is characterized by conglomeratic facies that represent a marine regression. In the upper part coarse sandstones lenses with shell beds have been recognized. At the top, stromatolitic limestones with sandstones and mudstones represent the middle-upper shoreface.

La Capilla Formation (Amos et al., 1963)

This sequence is essentially composed of sandstones, grey-greenish mudstones, shell beds and fine conglomerates subordinated. The marine fauna appears in the upper part of the section. In another stratigraphical section described, two members have been recognized: the lower, which contains the fauna, has been considered as a proximal glaciomarine and deltaic apron environment; the upper member, consisting fundamentally of brown-greenish sandstones and mudstones, is interpreted as a deltaic sequence.

Hoyada Verde Formation (Mésigos, 1953)

A glacigenic sequence (diamictite and pebbly shale facies) that grades upwards into fossiliferous shales that has been interpreted as the postglacial transgression. Associated with the diamictitic facies, a single bed of striated boulder pavement assumed to be of subglacial origin is present in the upper part of this formation. The marine invertebrate assemblages are associated with the postglacial shales. To the uppermost part of this section, the sequence is characterized by mudstones with fine sandstone interbedded that show a coarsening and thickening upward tends. This interval has been interpreted as the transition from the offshore with glacial influence to the lower shoreface.

Pituil Formation (Taboada, 1997)

This formation includes conglomeratic lenses and stratified sandstones with marine fauna. Coaly concretions have been recognized in the upper part, and megaflora are associated with a mudstones interval in the top of the section. This regressive sequence is considered as the transition from the offshore to the upper shoreface.

El Paso Formation (Mésigos, 1953)

Complex suite of glacigenic facies recording the advancing and retreating phases of the ice masses that ended with the flooding of the depositional site are associated with the installation of an open marine system. Two diamictitic packages occur in the lower and upper parts of the section, and vertical alternations of pebbly sandstones, boulder conglomerates, pebbly shales, sandstones, siltstones and shales occur elsewhere. The marine fauna is widespread in the upper part of the section.

Leoncito Formation (Baldis, 1964)

This section is dominated by sandstones facies and diamictite beds appearing to the top of the section, where a striated pavement has also been identified. This pavement is shaped on bioturbated fine-grained sandstones with fragment of plants, and the surface is covered by a massive diamictite. In this stratigraphical section the fauna occurs in sandstone and mudstone horizons, located below the glacial diamictitic horizons. This interval has been interpreted as shoreface sandstones and mudstones with glacial influence.

Majaditas Formation (Amos and Rolleri, 1965)

Glacigenic facies that grades upwards into mudstone and sandstone beds characterize this unit. To the top of the section sandstone and conglomerate horizons are present. This sequence has been interpreted as the transition from the offshore to the upper shoreface.

Ansilta Formation (Harrington, 1971)

This unit is dominated by diamictites and stratified sandstones and mudstones facies that contain the marine fauna. This section has been interpreted as a littoral marine environment, which includes the upper to lower shoreface with a glaciomarine sedimentation in the lower part of the sequence.

Yalguaraz Formation (Amos and Rolleri, 1965)

This unit includes diamictitic facies with mudstone and sandstone beds that increase to the upper part. An intertill striated pavement has also been suggested at the top of this section. The marine fossil assemblages are located in the middle part of the section, associated with mudstone and sandstone facies. This sequence has been interpreted as a submarine fan in the lower part and as a littoral to sub-littoral marine environment in the upper part.

Agua Negra Formation (Polanski, 1970)

This unit is composed of alternating sandstones, mudstones and occasionally limestone beds where the marine fauna has been mainly identified. Siltstones, sandstones and scarce beds and lens of conglomerates characterize the middle and upper part of the section. This sequence has been considered a littoral marine environment (upper shoreface) to deltaic environment at the top.

Agua del Jagüel Formation (Harrington, 1971)

This stratigraphical unit, characterized by a deglaciation succession up to fluvial a shallow marine deposit, is composed of three depositional sequences. The first of them characterizes the deglaciation phase and includes the marine fauna identified immediately above to the diamicitic horizons in the lower part of the section. The other two depositional sequences of this formation, distinguished by shoreface sandstones and offshore shales, contain several fossiliferous horizons with invertebrate faunas in the uppermost part of the section.

Santa Elena Formation (Yrigoyen, 1967)

This unit is characterized by a repetitive alternation of sandstone and mudstone facies and the marine fauna appears in the lower, middle and upper parts of the section. This formation is interpreted as a shelf sequence, represented by the stacking of successive upward coarsening parasequences that range from offshore-transitional to a shoreface.

APPENDIX II

Marine fossil assemblages identified in the Late Paleozoic sequences of Argentine Precordillera

CARBONIFEROUS FOSSIL ASSEMBLAGES

***Protocanites scalabrinii* - *Azurduya chavelensis* Zone (Sabattini et al., 2001)**

Late Tournaisian - Early Visean

Protocanites (cf. *Michiganites*) *scalabrinii* Antelo, *Azurduya chavelensis* (Amos), *Azurduya cingolanii* Cisterna and Isaacson, *Pseudosyringothyris*? sp., *Chilenochonetes*? sp., *Malimania triagularis* González, *Posidoniella malimanensis* González, *Palaeoneilo subquadratum* González, *Sanguinolites punillanus* Gon-zález, *Trepospira* (*Angyomphalus*) sp., *Bellerophon* (*Bellerophon*) sp., *Murlonia punillana* Sabattini et al., *Hyolithes malimanensis* Sabattini et al., *Paraconularia anteloi* Sabattini, *Pseudorthoceras* sp.

***Levipustula levis* Zone (Amos and Rolleri, 1965)**

Bashkirian - Moscovian

Levipustula levis Maxwell, *Costuloplica leoncitensis* (Harrington), *Kitakamithyris booralensis* (Campbell), *Kitakamithyris immensa* (Campbell), *Kitakamithyris* sp., *Torynifer tigrensis* Taboada and Cisterna, *Septosyringothyris keideli* (Harrington), *Spiriferellina octoplicata* (Sowerby), *Beecheria* sp., *Streblochondria sanjuanensis* Sterren, *Streblochondria stappenbecki* Reed, *Oriocrassatella andina* González, *Myofossa calingastensis* González, *Neoplatyteichum barrealense* (Reed), *Barrealispira mesigosi* Taboada and Sabattini, *Ptychomphalina striata* (Sowerby), *Ptychomphalina sabattinii* Taboada, *Ptychomphalina turgentis* Taboada, *Fenestella sanjuanesis* Sabattini, *Fenestella barrealensis* Sabattini, *Fenestella altispinosa* Sabattini, *Polypora neerkolensis* Crockfor, *Sphenotallus stubblefieldi* Schmidt and Teichmüller

***Aseptella* - *Tuberculatella* and *Micraphelia* - *Rhipidomella* fossil assemblage (Simanauskas and Cisterna, 2001)**

Moscovian

Tuberculatella peregrina (Reed), *Aseptella* aff. *A. patriciae* Simanauskas, *Micraphelia indianae* Simanauskas and Cisterna, *Rhipidomella*? sp., Meristelloidea indet., *Myofossa calingastensis* González

***Balakhonia peregrina* - *Geniculifera tenuiscostata* Zone (Taboada, 1997)**

Moscovian - Kasimovian

Balakhonia peregrina Taboada, *Geniculifera tenuiscostata* Taboada, *Neochonetes granulifer* (Owen), *Reticularia notica* Reed, *Orbiculoidea* aff. *saltensis* Reed, *Nuculanella camachoi* González, *Aviculopecten barrealensis* Reed, *Glabrocingulum (Stenozone) argentinus* (Reed), *Neoplatyteichum barrealensis* (Reed), *Straparollus (Euomphallus) subcircularis* (Mansuy), *Euphemites* sp., *Sphenotallus stubblefieldi* Schmidt and Teichmüller

PERMIAN FOSSIL ASSEMBLAGES

***Tivertonia jachalensis-Streptorhynchus inaequiornatus* Zone (Sabattini et al., 1990)**

Asselian

Streptorhynchus inaequiornatus Leanza, *Tivertonia jachalensis* (Amos), *Svalbardia* sp., *Kochiproductus riojanus* (Leanza), *Kochiproductus* sp., *Costatumulus* sp., *Coronalosia argentinensis* Archbold and Simanauskas, *Coronalosia* sp., *Tupelosia paganzoensis* Archbold and Simanauskas, *Septosyringothyris* sp. aff. *S. jaguelensis* Lech, *Septosyringothyris globosa* Lech, *Saltospirifer guevarii* (Cisterna and Archbold), *Pericospira sanjuanensis* (Lech and Aceñolaza), *Spiriferellina* sp., *Orbiculoidea* sp., *Lingula* sp., *Crurithyris*? sp., *Etherilosia*? sp., *Nuculavus levatiformis* (Walcott), *Heteropecten anteloi* González, *Modiolus (Modiolus)* sp., *Pterinopectinella ramaccionii* González, *Ptychopteria (Ptychopteria) liagracielae* (Leanza), *Septimyalina* sp., *Barrealispira tupensis* Sabattini et al., *Donaldina* sp., *Knightites* (*Cymatospira*) *montfortianus* (Norwood and Pratten), *Peruvispira* sp.

***Costatumulus amosi* Zone (Taboada, 1998)**

Late Asselian - Sakmarian

Costatumulus amosi Taboada, *Coolkilella keideli* Taboada, *Crurithys* sp., *Septosyringothyris jaguelensis* Lech, *Argentiella stappenbecki* Archbold et al., *Orbiculoidea* sp., *Oriocrassatella sanjuanina* González, *Cypricardinia*? sp., *Sanguinolites* sp., *Schizodus* sp., *Streblochondria*? sp.

***Rhynchopora* - *Neochonetes pegnonensis* fossil assemblage (Cisterna and Simanauskas, 2000)**

Late Asselian - Sakmarian

Neochonetes pegnonensis Cisterna and Simanauskas, *Rhynchopora* sp., *Septosyringothyris jaguelensis* Lech, *Orbiculoidea* sp., *Nuculavus levatiformis* (Walcott), *Parallelodon* sp., *Leptodesma (Leptodesma) potens* Hall, *Ptychopteria (Ptychopteria) liagracielae* (Leanza), *Palaeolima* cf. *P*. sp. Dickins, *Acanthopecten jaguelensis* González, *Aviculopecten* sp. nov., *Schizodus arrondoi* González, *Wilkingia riojana* González

APPENDIX III
Late Paleozoic bivalves identified in the Argentine Precordillera

Families	Genera	Early C	Later C	Early P
Malletiidae	*Palaeoneilo*	x	x	
	Malimania	x		
Nuculidae	*Nuculopsis*		x	
	Nuculanella		x	
	Nuculavus			x
Nuculanidae	*Phestia*	x	x	x
Solemyidae	*Solemya*			x
Parallelodontidae	*Grammatodon*			x
	Parallelodon			x
Mytilidae	*Litophaga*			x
	Modiolus		x	x
	Promytilus		x	x
	Volsellina	x		
Myalinidae	*Posidoniella*	x		
	Septimyalina			x
	Atomodesma		x	
Pterineidae	*Leptodesma*	x	x	x
	Leiopteria		x	x
	Ptychopteria			x
	Merismopteria			x
Limidae	*Palaeolima*		x	x
	Elimata			x
Pterinopectinidae	*Pterinopectinella*			x
Acanthopectinidae	*Acanthopecten*			x
Aviculopectinidae	*Aviculopecten*		x	x
	Limipecten		x	
Deltopectinidae	*Orbiculopecten*		x	
	Streblopteria		x	x
Etheripectinidae	*Heteropecten*			x
Euchondriidae	*Euchondria*		x	x
Streblochondriidae	*Streblochondria*		x	x
Myophoriidae	*Schizodus*	x	x	x
Crassatellidae	*Oriocrassatella*		x	x
Cardinidae	*Cypricardinia*	x	x	x
Permophoridae	*Pleurophorella*		x	x
	Netschajewia			x
	Stutchburia			x
Edmondiidae	*Edmondia*	x	x	x
Sanguinolitidae	*Myofossa*		x	x
	Sanguinolites	x	x	x
	Vacunella	x	x	x
	Wilkingia			x

APPENDIX IV
Late Paleozoic brachiopods identified in the Argentine Precordillera

Families	Genera	Early C	Later C	Early P
Lingulidae	*Argentiella*			x
	Lingula			x
Discinidae	*Orbiculoidea*		x	x
Anopliidae	*Gonzalezius*		x	
Chonetidae	*Chilenochonetes?*	x		
Rugosochonetidae	*Neochonetes*		x	x
	Rugosochonetes		x	
	Svalbardia			x
	Tivertonia			x
	Micraphelia		x	
Productellidae	*Tuberculatella*		x	
	Aseptella		x	
	Levipustula		x	
	Geniculifera		x	
Productidae	*Kochiproductus*			x
Linoproductidae	*Balakhonia*		x	
	Coolkilella			x
Monticuliferidae	*Costatumulus*			x
Strophalosiidae	*Coronalosia*			x
	Tupelosia			x
	Etherilosia			x
Streptorhynchidae	*Streptorhynchus*			x
Rhipidomellidae	*Rhipidomella*		x	
Camarotoechiidae	*Azurduya*	x		
Paranorellidae	*Sanjuania*		x	
Rhynchoporidae	*Rhynchopora*			x
Ambocoeliidae	*Crurithyris*			x
Trigonotretidae	*Pericospira*			x
	Saltospirifer			x
	Costuloplica		x	
Reticulariidae	*Reticularia*		x	
Elythidae	*Kitakamithyris*		x	
	Torynifer		x	
Syringothyrididae	*Syringothyris*		x	x
	Septosyringothyris		x	x
	Pseudosyringothyris?	x		
Crenispiriferidae	*Spiriferellina*		x	x
Beecheriidae	*Beecheria*		x	