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“Levipustula Fauna” in central-western Argentina and its relationships with the Carboniferous glacial event in the southwestern Gondwanan margin

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ABSTRACT

The *Levipustula* Fauna (included in the *Levipustula levis* Zone) is a relatively diversified fossil assemblage composed of brachiopods, bivalves, bryozoans, gastropods, and crinoids. This fauna usually is associated with glaciomarine sequences related to the Carboniferous glacial event that affected the southwestern Gondwanan margin. The *Levipustula* Fauna has been identified in different units (e.g., Hoyada Verde, La Capilla, Leoncito, and Yalguaraz Formations) exposed in the Calingasta-Uspallata Basin. The Hoyada Verde Formation, herein proposed as a key section, contains the most complete record of the *Levipustula* Fauna. A detailed compositional, taphonomic, and paleoecological study of this section allows us to propose two associations within the so-called *Levipustula* Zone: the “Intraglacial *Levipustula* Fauna,” present in the diamictite-dominated lower part, and the “Postglacial *Levipustula* Fauna,” dominant in the upper part of section. The fossils of the “Intraglacial *Levipustula* Fauna” are scarce and poorly diversified. These two features suggest environmentally stressed conditions, probably related to low temperatures in areas close to glaciers. In comparison, the “Postglacial *Levipustula* Fauna,” relatively more abundant and diverse, exhibits compositional variations that could be explained by paleoenvironmental changes associated with fluctuations in substratum and food supply, such as those identified in modern ecosystems. The identification of the “Intraglacial *Levipustula* Fauna” and the “Postglacial *Levipustula* Fauna” may constitute a new tool for understanding the particular relationship between faunal assemblages and climatic variations linked to the Gondwanan glaciation in the Calingasta-Uspallata Basin. Also, the new “Intraglacial *Levipustula* Fauna” identified in the Hoyada Verde Formation would have biostratigraphical and paleogeographical implications in intra- and inter-basinal correlations.

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INTRODUCTION

The marine invertebrates of the *Levipustula* Fauna constitute a relatively diversified fossil assemblage composed of brachiopods, bivalves, bryozoans, gastropods, and crinoids. This fauna can be considered the most conspicuous element in different localities in the Calingasta-Uspallata Basin (Fig. 1A), where it usually is associated with glaciomarine deposits. Previous studies (Taboada and Cisterna, 1996; Cisterna, 1999; Cisterna and Ster-

ren, 2004, 2008; Sterren, 2003, 2005) in the classical localities with *Levipustula* Fauna (Hoyada Verde, Leoncito, and La Capilla Formations) have recognized significant taxonomic, paleoecologic, and taphonomic variations. These variations, as well as the stratigraphic position of this fauna along the glacial sequence, suggest an important paleoenvironmental control.

This paper provides a review of the paleogeographic/paleoclimatic and biostratigraphical framework of the *Levipustula* Fauna in the Calingasta-Uspallata Basin. In particular, we

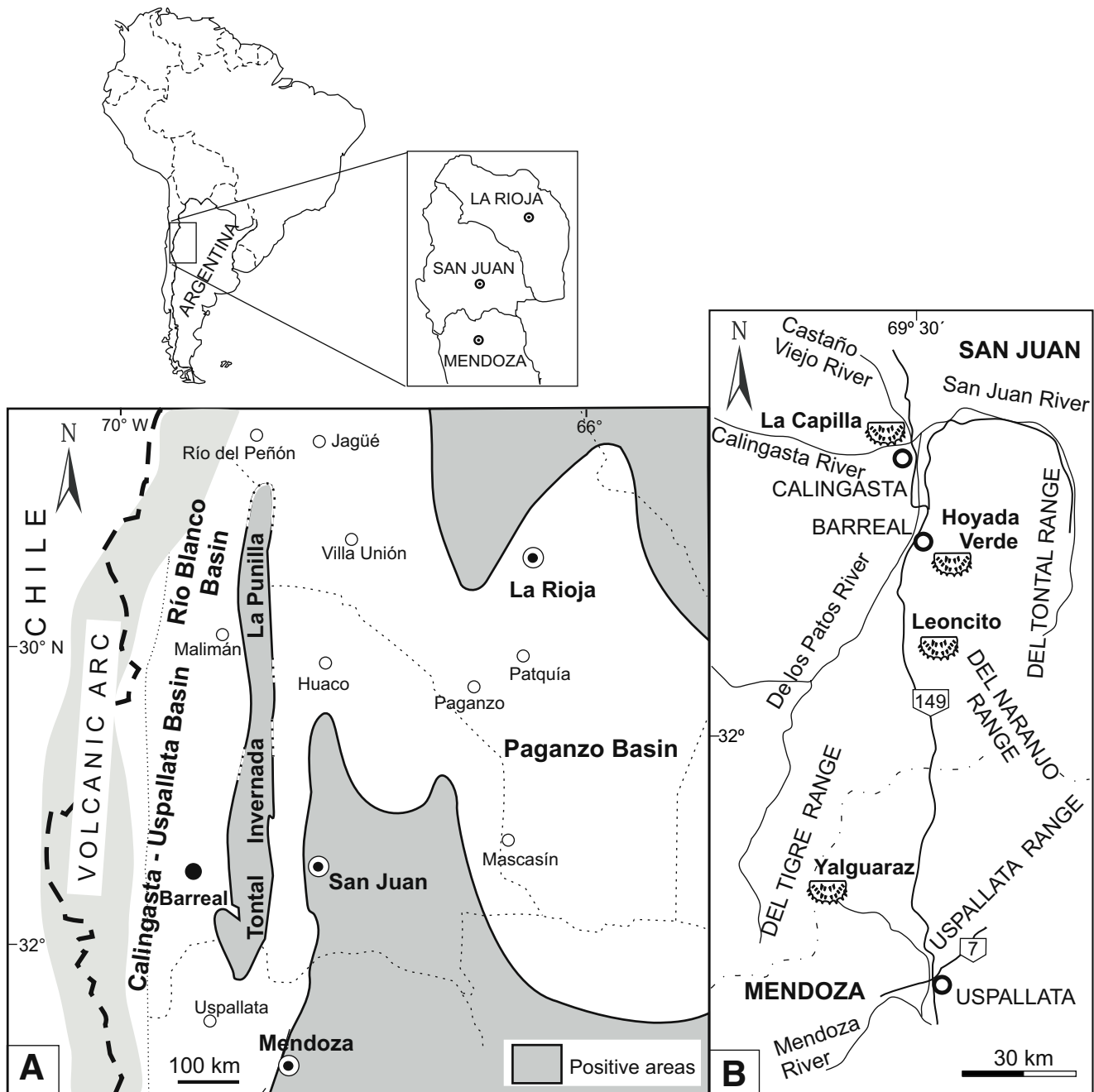


Figure 1. Location maps showing the paleogeography and geography of the Calingasta-Uspallata Basin with the *Levipustula* Fauna occurrences.

analyze the relationship of this fauna with the Carboniferous glacial event in the Hoyada Verde Formation, herein proposed as a key section. Because brachiopods and bivalves are the most abundant and diversified invertebrates in the *Levipustula* Fauna, the present study will be focused on these two groups.

PALEOGEOGRAPHIC AND PALEOCLIMATIC SETTING

During the late Paleozoic all the Gondwanan subcontinents were affected by an extensive glaciation (Hambrey and Harland, 1981). Paleomagnetic and paleoclimatic data suggest that the pole moved across South America, Southern Africa, Antarctica, and Australia throughout the Carboniferous-Permian transition as a result of the apparent path of polar wander (Crowell, 1983; Caputo and Crowell, 1985; Scotese and Barret, 1990; Scotese and McKerrow, 1990). Three glacial episodes have been suggested within this late Paleozoic paleoclimatic mega-event (López-Gamundí, 1997). In western Gondwana, the earliest glacial episode is recorded in sediments of latest Devonian–earliest Carboniferous exposed in the Solimões and Amazonas Basins of Brazil and the Titicaca Lake region of western Bolivia. The second glacial episode, identified in the Late Carboniferous sediments (Namurian-Westphalian) along the southwestern South American basins, is closely associated with the *Levipustula* Fauna herein studied. The latest episode has been identified in latest Carboniferous to earliest Permian sediments in basins of eastern South America (Paraná, Sauce Grande, and Malvinas Basins) and South Africa.

The late Carboniferous glacial episode is best documented along western Argentina, particularly in the Calingasta-Uspallata Basin, a back-arc basin formed behind an active magmatic arc (Ramos et al., 1986; Ramos and Palma, 1996). A combination of high latitude and altitude allowed the formation of ice centers along the margins of this basin (López-Gamundí, 1997). In this sense, a local north-trending high called the Proto-Precordillera (Amos and Roller, 1965), located to the east of the Calingasta-Uspallata Basin (Fig. 1A), might have exerted an important topographic control during this glacial stage (López-Gamundí and Rosello, 1995). Striated and boulder pavements within the Carboniferous glaciomarine sequences (e.g., Hoyada Verde and Leoncito Formations) have been recognized. Strong northward components in the paleo-ice flow indicators, as well as paleocurrents from the overlying shallow marine sandstones, suggest a common regional paleoslope for both glacial and early postglacial times (López-Gamundí and Martínez, 2000).

The Carboniferous glacial sequences of the Calingasta-Uspallata Basin are characterized by glaciomarine diamictites that grade upward to postglacial open-marine fine clastics. The presence of the marine fine clastics resting on diamictites has been interpreted as the sedimentary response to a glacio-eustatic sea-level rise, expressed as a transgression in stratigraphic terms, that occurred during the glacial retreat subsequent to a widespread glaciation (López-Gamundí, 1989, 1990, this volume).

The *Levipustula* Fauna is usually considered to be associated with the postglacial event (López-Gamundí, 1989, 1990; López-Gamundí and Espejo, 1993; López-Gamundí and Martínez, 2000). However, the position of this fauna in the glacial sequence of the Hoyada Verde Formation, as well as its taxonomic and paleoecological/taphonomic variations, suggests the presence of a recently identified “Intraglacial *Levipustula* Fauna” (Cisterna and Sterren, 2008), besides the typical *Levipustula* Fauna associated with the postglacial transgression.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION OF THE *LEVIPUSTULA* FAUNA

The *Levipustula* Fauna has been identified in different diamictite-bearing sections of the Calingasta-Uspallata Basin (Fig. 1B). Detailed studies on the brachiopods and bivalves of this fauna suggest significant taxonomic, taphonomic and paleoecological variations (Cisterna and Sterren, 2003, 2004, 2008; Sterren, 2005). The material studied in this contribution was collected from the classical localities of the *Levipustula* Fauna of the Hoyada Verde, La Capilla and Leoncito Formations (Table 1). We provide herein a review of the geographic, stratigraphic, and paleontological aspects of these units.

Hoyada Verde Formation. The Hoyada Verde Formation (Mésigos, 1953) is exposed in the eroded core of a broad north-south anticline (the Hoyada Verde anticline) located 3 km east of Barreal village (Fig. 2). The basal contact of the Hoyada Verde Formation is unknown and the top is overlain by the Tres Saltos Formation with an angular unconformity (Fig. 3). The Hoyada Verde section is characterized by a glaciogenic sequence (diamictite and pebbly [dropstone] shale facies) that grades upward into postglacial, dropstone-free shales that contain the typical *Levipustula* Fauna. An intertill boulder pavement, considered of subglacial origin (López Gamundí and Martínez, 2000), is present in the upper part of the Hoyada Verde Formation and is associated with the diamictic facies. To the uppermost part of the section (Fig. 3), the sequence is characterized by mudstones with interbedded fine sandstones arranged in coarsening and thickening-upward sequences. This interval has been interpreted as the transition from the offshore to the lower shoreface (Buatois and Limarino, 2003), and a succession of fossils traces composed of *Psammichnites implexus* (Rindsberg) and *Psammichnites plummeri* (Fenton and Fenton) has been recognized by Mángano et al. (2003). In the top of the Hoyada Verde Formation the uppermost fossiliferous horizon identified is located in a coquina with gastropods such as *Peruvispira reedi* Sabattini and *Mourlonia* sp. (Sabattini, 1980).

The marine invertebrate assemblage associated with the postglacial shales is composed of brachiopods, bivalves, bryozoans (the fenestellids *Fenestella sanjuanesis* Sabattini, *F. barrealensis* Sabattini, *F. altispinosa* Sabattini, and *Polypora neerkolensis* Crockfor, described by Sabattini [1972]) and scarce gastropods and crinoids. The brachiopods assemblage is dominated by the *Levipustula*-*Costuloplica*-*Kitakamithyrus* association with the

TABLE 1. TAXONOMIC COMPOSITION OF THE *LEVIPUSTULA* FAUNA IN THE CALINGASTA-USPALLATA BASIN

Taxon	HOYADA VERDE FM.		LA CAPILLA FM.		LEONCITO FM.
	Lower part	Upper part	South (LC)	North (LJ)	
<i>Levipustula levis</i> Maxwell	C	D	D	---	M
<i>Costuloplica leonicitensis</i> (Harrington)	C	D	D	M	D
<i>Kitakamithyris booralensis</i> (Campbell)	---	---	D	D	---
<i>Kitakamithyris</i> sp.	---	D	D	D	---
<i>Beecheria</i> sp.	---	D	D	M	D
<i>Spiriferellina octoplicata</i> (Sowerby)	C	D	M	M	D
<i>Spiriferellina</i> sp.	---	---	D	M	---
<i>Septosyringothyris keideli</i> (Harrington)	---	---	---	M	D
<i>Orthotetoidea</i> indet.	---	---	---	M	M
<i>Nuculopsis</i> sp.	C	---	---	---	M
<i>Phestia</i> sp. aff. <i>P. bellistriata</i> (Stevens)	---	D	---	---	---
<i>Phestia</i> sp.	C	---	D	---	M
<i>Palaeolima retifera</i> (Shumard)	C	D	---	---	---
<i>Streblochondria stappenbecki</i> Reed	---	D	---	---	---
<i>Streblochondria sanjuanensis</i> Sterren	---	D	---	---	---
<i>Aviculopecten barrealeensis</i> Reed	---	---	D	---	---
<i>Schizodus</i> sp.	---	---	D	M	M
<i>Oriocrassatella</i> ? sp.	---	---	D	---	---
<i>Pleurophorella</i> ? sp.	---	---	D	---	M
<i>Oriocrassatella andina</i> González	---	---	---	D	---
<i>Myofossa calingastensis</i> González	---	---	---	D	---
<i>Leptodesma (Leiopteria)</i> sp.	---	---	---	D	---
<i>Cypricardina</i> sp.	---	---	---	D	---
<i>Promytilus</i> sp.	---	---	---	D	---
<i>Pyramus</i> ? sp.	---	---	---	D	---
<i>Naiadites</i> sp.	---	---	---	---	D
<i>Barrealispira mesigosi</i> Taboada and Sabattini	D	---	---	---	M
<i>Murlonia striata</i> (Sowerby)	D	---	---	---	---
<i>Ptychomphalina sabattinii</i> Taboada	---	---	---	D	---
<i>Ptychomphalina turgentis</i> Taboada	---	---	---	D	---
<i>Ptychomphalina</i> cf. <i>kuttungensis</i> Taboada	---	---	---	D	---
<i>Peruvispira reedi</i> Sabattini	---	D	---	D	---
<i>Straparollus (Euomphalus)</i> sp.	---	---	---	M	---
<i>Leptoptygma</i> sp.	---	---	---	M	---
<i>Fenestella sanjuanensis</i> Sabattini	---	D	---	---	---
<i>Fenestella barrealeensis</i> Sabattini	---	D	---	---	---
<i>Fenestella altispinosa</i> Sabattini	---	D	---	---	---
<i>Fenestella</i> sp.	---	---	---	---	M
<i>Polypora neerkolensis</i> Crockford	---	D	---	---	---
<i>Cladochonus harringtoni</i> Sabattini	---	D	---	---	---
<i>Sphenotallus stubblefieldi</i> Schmidt and Teichmüller	D	---	---	---	---
Bryozoans indet.	C	---	M	M	M
Crinoids indet.	C	C	M	---	M
Ostracods indet.	C	---	---	---	M

C - Cited in this work

D - Described in previous work

M - Mentioned in previous work

species *Levipustula levis* Maxwell, *Costuloplica leonicitensis* (Harrington), and *Kitakamithyris* sp., usually accompanied by *Beecheria* sp. and “*Spiriferellina*” *octoplicata* (Sowerby). The bivalve fauna studied by Sterren (2003) is composed of *Phestia* sp. aff. *P. bellistriata* (Stevens), *Palaeolima retifera* (Shumard), *Streblochondria sanjuanensis* Sterren, and *S. stappenbecki* Reed. Although this is the main faunal assemblage in the Hoyada Verde

Formation, the gastropods *Neilsonia*? sp., *Neoplatyteichum barrealeense* (Reed), *Barrealispira mesigosi* Taboada and Sabattini, *Ptychomphalina striata* (Sowerby), the annelid *Sphenotallus stubblefieldi* Schmidt and Teichmüller, and the brachiopods *Levipustula levis* Maxwell and *Kitakamithyris* sp. have been identified in the lower part of the section (Sabattini, 1980; Taboada and Sabattini, 1987; Taboada, 1997). Taboada (1997) has also

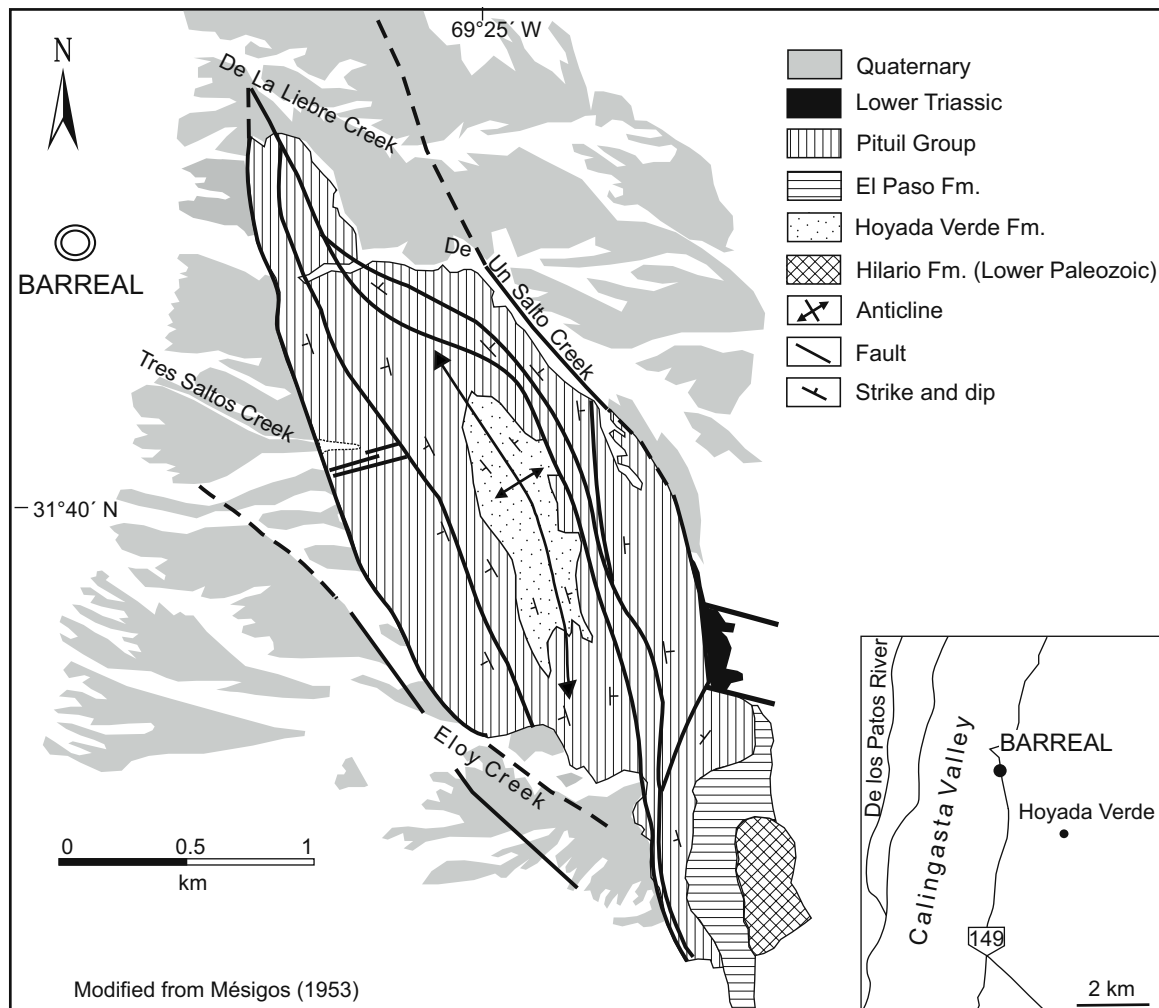


Figure 2. Generalized geological map showing the distribution of the Hoyada Verde Formation outcrops. Modified from Mésigos (1953).

suggested the presence of brachiopods, probably the species *Levipustula levis* Maxwell, associated with the diamictite-rich glacial section.

The Hoyada Verde Formation has been considered chronologically equivalent to the El Paso Formation (Amos and Rollet, 1965; Amos and López-Gamundi, 1981; González, 1990), a diamictite-rich section exposed in the southernmost part of the Barreal hill (Fig. 2). However, there no physical continuity between the two units, and the brachiopods identified in the El Paso Formation (*Micraphelia indianae* Simanaukas and Cisterna, *Tuberculatella peregrina* (Reed), *Aseptella* aff. *A. patriciae* Simanaukas, and *Rhipidomella?* sp.) would exhibit latest Carboniferous biostratigraphical affinities (Simanaukas and Cisterna, 2001).

La Capilla Formation. Outcrops of the La Capilla Formation (Amos et al., 1963) have been recognized in two sectors in the Calingasta area (Fig. 1B). One of these exposures

is located 1400 m north La Capilla village, along the road that connects Calingasta and the Castaño Viejo mines, ~300 m west of Las Cambachas. This 39-m-thick section is essentially composed of sandstones, gray-green mudstones, coquinoid lenticular beds, and scarce fine conglomerates (Amos et al., 1963). The *Levipustula* Fauna occurs in the upper part of the section and is taxonomically close to that present in the Hoyada Verde Formation. However, the taxonomic differences among bivalves (*Phestia* sp., *Aviculopecten barrealeensis* Reed, *Schizodus* sp., *Oriocrassatella?* sp., and *Pleurophorella?* sp.) are more important than those of the brachiopods (Cisterna and Sterren, 2003, 2004; Sterren, 2005).

Other outcrops of the La Capilla Formation are located ~5 km north of La Capilla village, in a locality known as Las Juntas. Sessarego and Amos (1987) recognized two members: a lower member, where the *Levipustula* Fauna occurs, has been interpreted as deposited in a proximal glaciomarine setting

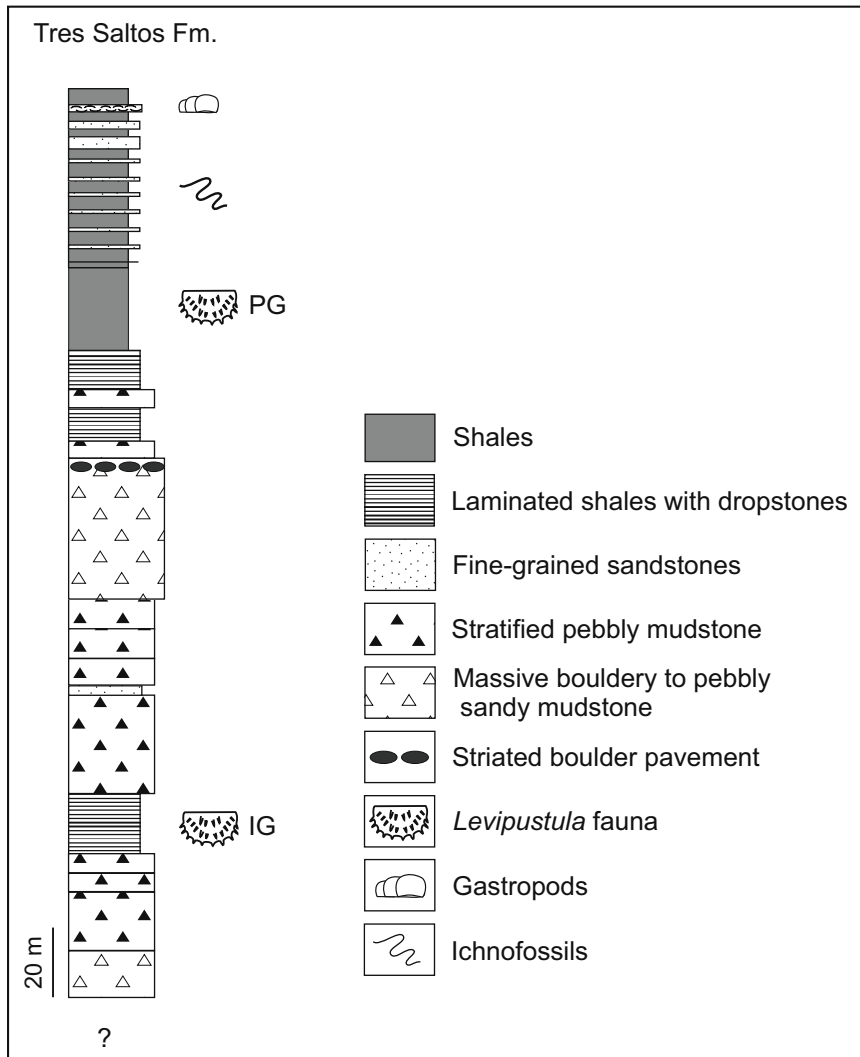


Figure 3. Stratigraphic section of the Hoyada Verde Formation (modified from López-Gamundí, 1983) and vertical distribution of the Intraglacial (IG) and Postglacial *Levipustula* Fauna (PG).

with deltaic influence (Sessarego and Amos, 1987), and an upper member, consisting of deltaic greenish brown sandstones and mudstones (Vallecillo and Bercowski, 1998). The *Levipustula* Fauna in this section is not well known. The brachiopod assemblage appears to be dominated by the genus *Kitakamithyris*, with *Kitakamithyris booralensis* (Campbell) and *Kitakamithyris* sp., accompanied by *Septosyringothyris* aff. *S. keideli* (Harrington) and *Orthotetoidea* indet. González and Taboada (1987) and González (2002) have also suggested the presence of the brachiopods *Spiriferellina octoplicata* (Sowerby), *Costuloplica leonciticensis* (Harrington), *Septosyringothyris keideli* (Harrington), *Kitakamithyris septata*? (Chronic), *Lingula* sp., and *Chonetacea* indet.; the bivalves *Oriocrassatella andina* González, *Myofossa calingastensis* González, *Leptodesma* (*Leiopteria*) sp., *Schizodus* sp., *Promytilus* sp., *Pyramus*? sp., and *Cypricardina*? sp.; the gastropods *Peruvispira reedi* Sabatini, *Peruvispira* cf. *kuttungensis* Campbell, *Murlonia* ssp., *Straparollus* (*Euomphalus*) sp., *Leptotygya* sp.; and the bryozoans *Fenestella* sp.

Leoncito Formation. Outcrops of the Leoncito Formation (Baldís, 1964) are located ~22 km southeast of Barreal village on the western flank of the Precordillera (Fig. 1B), along the southern margin of the Las Cabeceras river. This section is dominated by sandy facies and the diamictite beds appear to the top of the section, where a striated pavement has been also identified. This pavement is shaped on bioturbated fine-grained sandstones with plant fragments and the surface is covered by a massive diamictite (López-Gamundí and Martínez, 2000). In the Leoncito Formation section the *Levipustula* Fauna occurs in sandstone and mudstone horizons, located below the glacial diamictic beds in an interval ~11 m thick. The fauna associated with the sandstones appears concentrated in distinct lenses and is composed of the *Septosyringothyris keideli*–*Costuloplica leonciticensis* brachiopod assemblage, accompanied of “*Spiriferellina*” *octoplicata* Sowerby and very scarce *Beecheria* sp. and *Levipustula levis* Maxwell; bivalves (*Phestia* sp., *Schizodus* sp. and *Pleurophorella*? sp.), bryozoans (*Fenestella*? sp.); and gastropods (*Barrealispira*?

sp.). The fauna from the mudstone-dominated interval is quite different and composed of brachiopods (*Levipustula levis* and *Beecheria* sp.), bivalves (*Nuculopsis*? and bivalvia indet.), ostracods (probably some *Aurycirkbya*), gastropods, crinoids, and bryozoans (Cisterna and Sterren, 2008).

Although we have not conducted fieldwork in the Yalguaraz Formation outcrops, we are tempted to state that this unit contains some diagnostic elements of the *Levipustula* Fauna. The Yalguaraz Formation (Amos and Rolleri, 1965) is exposed on the west flank of the Cordillera del Tigre, close to the boundary between San Juan and Mendoza provinces (Fig. 1B). In the type section (Arroyo del Tigre Creek), this unit is characterized by a predominantly diamictic sequence with mudstones and sandstones increasing toward the upper part. An intertill striated pavement on the top of this section has been also suggested (Taboada, 1997). The marine fossil assemblage, present in mudstones and sandstones of the middle part of the section, is composed of brachiopods, gastropods, bryozoans and bivalves (Taboada and Carrizo, 1992; Taboada, 1997). From this assemblage, Taboada and Cisterna (1996) have described the brachiopods *Kitakamithyris immensa* (Campbell) and *Torynifer tigrensis* Taboada and Cisterna, which can be considered conspicuous elements of the *Levipustula* Fauna.

AGE AND FAUNAL AFFINITIES WITH OTHER BASINS

The *Levipustula* Fauna is known from eastern Australia where it is also characterized by a low-diversity, cold-water assemblage dominated by brachiopods referred to the *Levipustula levis* Zone (Campbell and McKellar, 1969; Jones et al., 1973). It has not been associated with a specific reference section within eastern Australian basins but Roberts et al. (1976) have provided a summary of its composition, stratigraphic occurrence, and relationships with other zones. The age of this zone was widely discussed by different authors (Campbell, 1961; McKellar, 1965; Lindsay, 1969; Jones et al., 1973; Roberts, 1976; Roberts et al., 1976, 1993) and finally assigned, on the basis of faunal considerations, to the Namurian–Westphalian interval (Roberts et al., 1976). However, sensitive high-resolution ion microprobe (SHRIMP) zircon dating of volcanic horizons in the glaciogenic sediments of the Seaham Formation (Southern New England Orogen) appears to confine the age of this zone to early Namurian (Roberts et al., 1995).

In Argentina the *Levipustula levis* Zone was defined by Amos and Rolleri (1965) in the Calingasta–Uspallata Basin. The La Capilla Formation has been proposed as the reference section of the *Levipustula levis* Zone, but a detailed study in the Hoyada Verde Formation suggests that the latter unit contains the most complete record of the *Levipustula* Fauna in the basin.

The age of the *Levipustula levis* Zone in Argentina was considered Namurian–Westphalian owing to its Australian affinity (González, 1981; Archangelsky et al., 1987; Archangelsky et al., 1996; Taboada, 1997). The lower limit of age for the *Levipustula*

levis Zone in Precordillera was discussed by Taboada (1997), who recognized a mudstone-rich interval in the lowermost Hoyada Verde Formation with *Barrealispira mesigosi* Taboada and Sabbatini, *Ptychomphalina striata* (Sowerby) and *Sphenotallus stubblefieldi* Schmidt and Teichmüller, associated with *Levipustula levis* Maxwell. Such an assemblage would indicate an early Namurian age. A recent biostratigraphic review of the Hoyada Verde Formation (Sterren and Cisterna, 2006) indicates that the fauna suggested by Taboada (1997) occurs within the diamictic section. There are no diagnostic elements to suggest the precise upper limit of this fauna but, for the moment, its biostratigraphic relationships would indicate a Westphalian age (González, 1981, 1990, 1993; Archangelsky et al., 1987).

Brachiopods of the *Levipustula levis* Zone in the Precordillera of Western Argentina appear to be the main tool for biostratigraphic correlation, and their Australian faunal affinities would be essentially based on the common species *Levipustula levis* Maxwell, *Kitakamithyris booralensis* (Campbell), and *Kitakamithyris immensa* (Campbell) (Taboada and Cisterna, 1996). Although there are previous systematic studies (Reed, 1927; Keidel and Harrington, 1938; Amos et al., 1963; Lech, 1989; Taboada and Cisterna, 1996), a taxonomic review of new collections of *Levipustula* Fauna brachiopods from Precordillera started by one the authors (G.A.C.) can shed further light on some of the current correlation problems. In this sense, the first problem related to the systematics of this fauna’s brachiopods is the original definition of *Levipustula levis* in Australia (Maxwell, 1951). This species was described from different units in eastern Australia, such as the Booral Formation in New South Wales (Campbell, 1961) and the Poperima Formation and Branch Creek Formation in Queensland (Maxwell, 1964). However, specimens from different localities assigned to *Levipustula levis* appear to have distinct species-diagnostic features.

Other South American basins where the *Levipustula* Fauna have also been identified are the Tepuel–Genoa Basin in southwestern Argentina and the Tarija Basin in Bolivia. In the Tepuel–Genoa basin, the *Levipustula levis* Zone was previously recognized in the Pampa de Tepuel and Las Salinas Formations (Amos et al., 1973). However, the brachiopods from the Tepuel–Genoa basin originally assigned to the *Levipustula levis* Maxwell by Amos (1960) were included in the synonymy of *Lanipustula patagoniensis* Simanaukas (1996) and *Verchojania inacayali* Taboada (2008). The genus *Lanipustula* proposed by Klets (1983) is very close to *Levipustula* Maxwell but it has been differentiated by the disposition of the cardinal ridges and the shape of the anterior adductor muscle scars (Simanaukas, 1996). Recent studies of the genera *Levipustula* and *Lanipustula* in Argentina suggest that the diagnostic features proposed for distinguishing these genera by Klets (1983) can be considered of intraspecific hierarchy (Taboada, 2006). Instead, other main differences, such as the abundance of external dorsal spines and variable rugae and/or lamination on both valves developed in *Lanipustula*, clearly separate it from *Levipustula* (A.C. Taboada, 2010, personal commun.).

A multivariate analysis of the *Levipustula levis* Zone in the Tepuel-Genoa Basin was conducted by Simanaukas and Sabattini (1997), who subdivided the zone into the late Carboniferous *Lanipustula* Zone, the Early Permian *Pyramus* faunule (Asselian), and the *Tuberculatella* Zone (Sakmarian). The *Lanipustula* Zone was referred to the lower part (“*Fenestella* and *Productus*” horizon) of the Pampa de Tepuel Formation (Freytes, 1971) and to the lower member of the Las Salinas Formation (González, 1972); Simanaukas and Sabattini (1997) suggested a Namurian–Stephanian age for this zone.

In the Tarija Basin the *Levipustula* Fauna is not well known but an invertebrate marine assemblage composed of *Levipustula levis* Maxwell, *Cypricardina?* *boliviana* Rocha-Campos, Carvalho and Amos, *Limipecten* cf. *L. burnettensis* Maxwell, *Stuchburia* sp., *Myonia* sp., and *Mourlonia balapucense* Rocha-Campos, Carvalho and Amos was described from the upper part of the Taiguatí Formation (Bolivia) by Rocha-Campos et al. (1977). The bivalves *Naiadites* cf. *N. modiolaris* (Sowerby) and *Wilkingia* cf. *W. elliptica* (Phillips) have been identified from the Taiguatí Formation as well (Trujillo Ikeda, 1989).

LEVIPUSTULA FAUNA IN THE HOYADA VERDE FORMATION

The typical *Levipustula* Fauna can be easily identified associated with mudstone facies, located above of the glacial diamictic sequence, in the upper part of the Hoyada Verde Formation. However, a detailed study along this section indicates that a scattered and very poorly diversified faunal assemblage can be recognized in the lower part of the section, interbedded with diamictic horizons. These faunas are herein proposed as the “Postglacial *Levipustula* Fauna” (Fig. 3, PG) and “Intraglacial *Levipustula* Fauna” (Fig. 3, IG), respectively, and their compositional, taphonomic, and paleoecological features are discussed.

The “Intraglacial *Levipustula* Fauna”

The outcrops that contain the “Intraglacial *Levipustula* Fauna” can be recognized in the exposed core of the Hoyada Verde anticline. Therefore, these mudstones with fauna have been usually referred to the lowermost part of the section (Mésigos, 1953; Taboada, 1997). Recent field work has allowed us to recognize the correct location of this fossiliferous interval and its stratigraphic relationships (Fig. 3).

The new fossil assemblage appears in the lower part of the Hoyada Verde Formation, interbedded with diamictic horizons, in a 20-m-thick interval made up of grayish, laminated mudstones characterized by the presence of glendonites and dropstones.

The “Intraglacial *Levipustula* Fauna” (Fig. 4) is characterized by a monotonous assemblage of marine invertebrates and stems of “*Dadoxylon*.” The fauna is dominated by brachiopods, bivalves, and annelids, accompanied by gastropods, ostracods,

and fragmentary bryozoans. The brachiopods recognized are *Levipustula levis?* Maxwell and *Levispustulini* indet., apparently the dominant species, and very scarce specimens of “*Spiriferellina*” *octoplicata* and *Spiriferidae* indet. The bivalves distinguished in this fauna are *Nuculopsis* sp., *Phestia* sp. aff. *P. bellistriata* (Stevens) and *Palaeolima retifera* (Shumard). A preliminary study of the fauna associated with the brachiopods and bivalves has allowed us to recognize the ostracods *Kirkbyidae* indet. (probably the genus *Aurykirkbya* Sohn), the annelids *Sphenotallus stubblefieldi* Schmidt and Teichmüller, and the gastropods *Barrealispira* sp., and the bryozoans *Fenestella?* sp.

The intraglacial fauna is scarce, poorly diversified, and very scattered within thick mudstone packages. The bioclasts show a random distribution, degree of fragmentation is low, and delicate details of the fine sculpture are preserved. In addition, individual shells are generally small, exhibiting a relatively wide range of valve sizes, from 0.3 to 2 cm. Shells of both brachiopods and bivalves are mostly disarticulated; however, specimens belonging to the bivalve family Nuculanidae (*Nuculopsis* sp., *Phestia* sp. aff. *P. bellistriata* (Stevens)), are exceptionally found with articulated valves.

The attributes described for these fossils suggest a fauna buried in situ. Features such as its low diversity and abundance indicate environmentally stressed conditions probably related to glacial environment. The presence of articulated bivalves might be related to minor reworking and transport, and conditions of sudden burial (Kidwell and Bosence, 1991; Aigner, 1985; Peterson, 1985) when the ligament was still active (Fürsich and Heinberg, 1983). In addition, low temperatures might have delayed the decomposition of the soft tissues that unite the valves (Kidwell and Baumiller, 1990).

The bivalves that characterize this interval, *Nuculopsis* and *Phestia*, are commonly found associated with stress conditions (Sterren, 2000; Simanaukas and Cisterna, 2000; Lebold and Kammer, 2006). The abundance of the eurytopic bivalve *Nuculopsis* is significant because the deposit-feeding nuculid bivalves are common component of fossil assemblages in oxygen-deficient basins (Kammer et al., 1986). The annelid *Sphenotallus stubblefieldi* is another conspicuous element in the “Intraglacial *Levipustula* Fauna.” The annelids are considered stress-tolerant taxa and their presence in glaciomarine sequences indicates a wide range of temperature, salinity, and oxygen tolerance (Collinson et al., 1994; Chakraborty and Bhattacharya, 2005).

The presence of glendonite concretions and dropstones in the stratigraphic interval that contains the “Intraglacial *Levipustula* Fauna” suggests extreme environmental conditions related to the glacial proximity. The glendonite, a carbonate pseudomorph that might indicate freezing water (González, 1980; Swainson and Hammond, 2001; McLachlan et al., 2001) has been also recorded in similar Carboniferous and Permian sequences of Argentine Patagonia (Tepuel-Genoa basin, González, 1980), as well as in South Africa and Australia (McLachlan et al., 2001; Thomas et al., 2007; López-Gamundí, this volume).

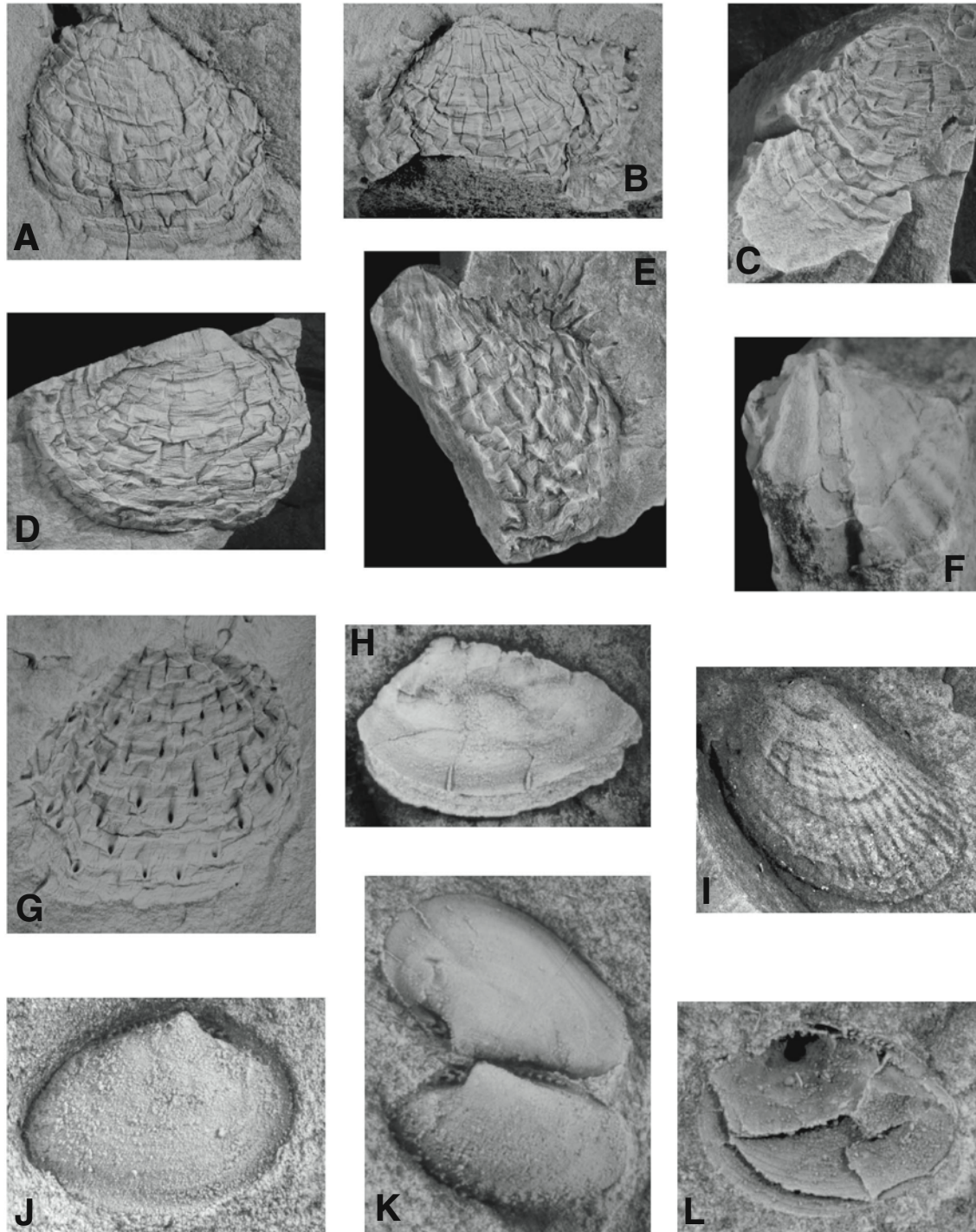


Figure 4. "Intraglacial *Levipustula* Fauna." (A–D, G) *Levipustula levis*? Maxwell. (A, G) internal and external mold of ventral valve, CEGH-UNC 22171 ($\times 3$); (B) internal mold of ventral valve, CEGH-UNC 22172 ($\times 2.5$); (C) external mold of ventral valve, CEGH-UNC 22173 ($\times 3$); (D) internal mold of ventral valve, CEGH-UNC 22175 ($\times 2.5$); (E) *Levipustululini* indet., internal mold of ventral valve, CEGH-UNC 22174 ($\times 2.5$); (F) "*Spiriferellina*" *octoplicata* (Sowerby) fragmentary ventral valve, CEGH-UNC 22176 ($\times 4$); (H) *Phestia* sp. aff. *P. bellistriata* (Stevens) outer view of left valve, CEGH-UNC 22160 ($\times 9$); (I) *Palaeolima retifera* (Shumard) outer view of right valve, CEGH-UNC 22161 ($\times 4$). (J–L) *Nuculopsis* sp. (J) internal mold of left valve, CEGH-UNC 22163 ($\times 10$); (K) internal mold of articulated valves, CEGH-UNC 22162 ($\times 14$); (L) interior of left valve, CEGH-UNC 22164 ($\times 11$). Fossils with the prefix CEGH-UNC are housed in the Centro de Investigaciones Paleobiológicas (Universidad Nacional de Córdoba) and those with the prefix IPI are housed in the Fundación Miguel Lillo (Instituto de Paleontología).

The “Postglacial *Levipustula* Fauna”

The first marine invertebrates of the “Postglacial *Levipustula* Fauna” have been identified ~20 m above of the uppermost diamictic horizon of the Hoyada Verde Formation (Fig. 3). The fossil assemblages associated with the postglacial shales are composed of bryozoans, brachiopods, and bivalves (Fig. 5), accompanied by less abundant gastropods and crinoids. This fauna is very abundant and highly diversified, and it exhibits compositional variations throughout the fossiliferous interval studied.

The fossil concentrations occur either as thin (1–5 cm) shell beds or nests. The bioclasts show poor sorting and a random distribution. In cross section, the shells are mainly concordant to slightly oblique to the bedding plane and display predominantly concave-upward orientations. Low degrees of abrasion and fragmentation have been observed in the shells. Similar proportions of dorsal/ventral valves in brachiopods and left/right valves in bivalves are recognized. Some articulated shells are present and delicate details of fine sculpture, such as spines in *Levipustula levis*, are also preserved. The taphonomic features described suggest biogenic fossil concentrations, produced by a gradual accumulation of successive benthic colonizations (Sterren, 2002).

Cisterna (1999) carried out a detailed paleoecologic analysis that includes the dominant groups (bryozoans, brachiopods and bivalves) of the postglacial fauna. From this paleoecologic study, Simanaukas et al. (2001) recognized three subfaunas (Fig. 6), based primarily on the changes observed in the brachiopods in the fossiliferous interval: the lower *Costuloplica leoncitisensis* subfauna, an intermediate *Kitakamithyris* sp. subfauna, and the upper, *Levipustula levis* subfauna.

From our most recent fieldwork we were able to confirm the presence of the three brachiopod associations previously identified by Simanaukas et al. (2001) in the postglacial interval (although the bryozoans and the brachiopod *Costuloplica leoncitisensis* appear to be conspicuous elements throughout the interval). The lower association (Fig. 6A) is characterized by the low number of species and low total biovolume. The communities of this association are dominated by bivalves of the genus *Streblochondria*, accompanied, in decreasing order, by bryozoans and *Costuloplica leoncitisensis*, organisms characterized as epifaunal and suspension feeding. This association would represent a gradual deepening of cold waters and a relatively low nutrient availability, which is evidenced by the low biovolume and the low species richness.

The intermediate association (Fig. 6B) is dominated by brachiopods or bryozoans and characterized by the highest species richness and the highest values of biovolume. The bivalves are less important in these communities but those of epibyssate habits (*Streblochondria sanjuanensis* Sterren, *Streblochondria stapperbecki* Reed, and *Palaeolima retifera* (Shumard)) show a relative increase. The brachiopod communities of this association are dominated by *Costuloplica leoncitisensis*, accompanied by *Kitakamithyris* sp., “*Spiriferellina*” *octoplicata*, *Beecheria* sp., and *Levipustula levis* as a subordinate element. This brachiopod association could correspond to the maximum flooding with a substra-

tum more stable in which the suspension-feeding and epifaunal organisms appear more diversified (epibyssate, libero-sessile, and pedunculate habits). The relatively more benign climatic conditions would have triggered an abundant food supply. Hence, the communities of this association have the highest faunal species richness and biovolume.

The fossiliferous interval that contains the upper brachiopod association is characterized by abundant sandstones linked to a shallowing-upward trend. This association is dominated by *Levipustula levis*, a small quasi-infaunal productid, and the ubiquitous *Costuloplica leoncitisensis* accompanied by the bivalve *Phestia* sp. aff. *P. bellistriata* (Fig. 6C). The values of species richness and biovolume are relatively low and the presence of the opportunistic organisms *Levipustula levis* and *Phestia* sp. aff. *P. bellistriata* could be related to fluctuating environmental conditions (i.e., an unstable substratum and higher sediment rate).

The communities of the three associations described above would have been developed in a stable marine environment, such as an open shelf with moderate bottom currents (Cisterna, 1999). Variations in these associations would have been controlled by substrate types and food supply fluctuations during the postglacial transgression.

DISCUSSION

A complex glacial history with advances and retreats of glaciers might have been the main control on the distribution of the *Levipustula* Fauna. Although this fauna is a conspicuous element in the Calingasta-Uspallata Basin, the glacial influence is more evident in the faunas present in the Hoyada Verde Formation. The identification of the “Intraglacial *Levipustula* Fauna” and the “Postglacial *Levipustula* Fauna” described in this paper constitutes a new element for understanding the particular relationship between the faunal assemblages and the climatic variations due to the Gondwanan glaciation.

The features discussed for the Intraglacial Fauna strongly suggest environmentally stressed conditions probably related to low (glacial) temperatures. Although low temperatures seem to be the dominant factor of stress for the faunas discussed herein, other variables such as oxygen and nutrient availability, salinity, substrate type, and water depth would have been affected by the glacial action.

The very abundant and highly diversified “Postglacial *Levipustula* fauna” can be considered to represent the record of climatic amelioration in more stable environmental conditions. This fauna exhibits compositional variations that reflect slight changes in the substrate stability and food supply, related to the moderate bottom currents. Some features of this fauna in the middle part of the postglacial interval, such as high diversity of the filter-feeder and epifaunal organisms, suggest the presence of maximum flooding conditions during the postglacial transgression. The major sandstone component of the uppermost part of the interval is related to a shallowing-upward trend. The low

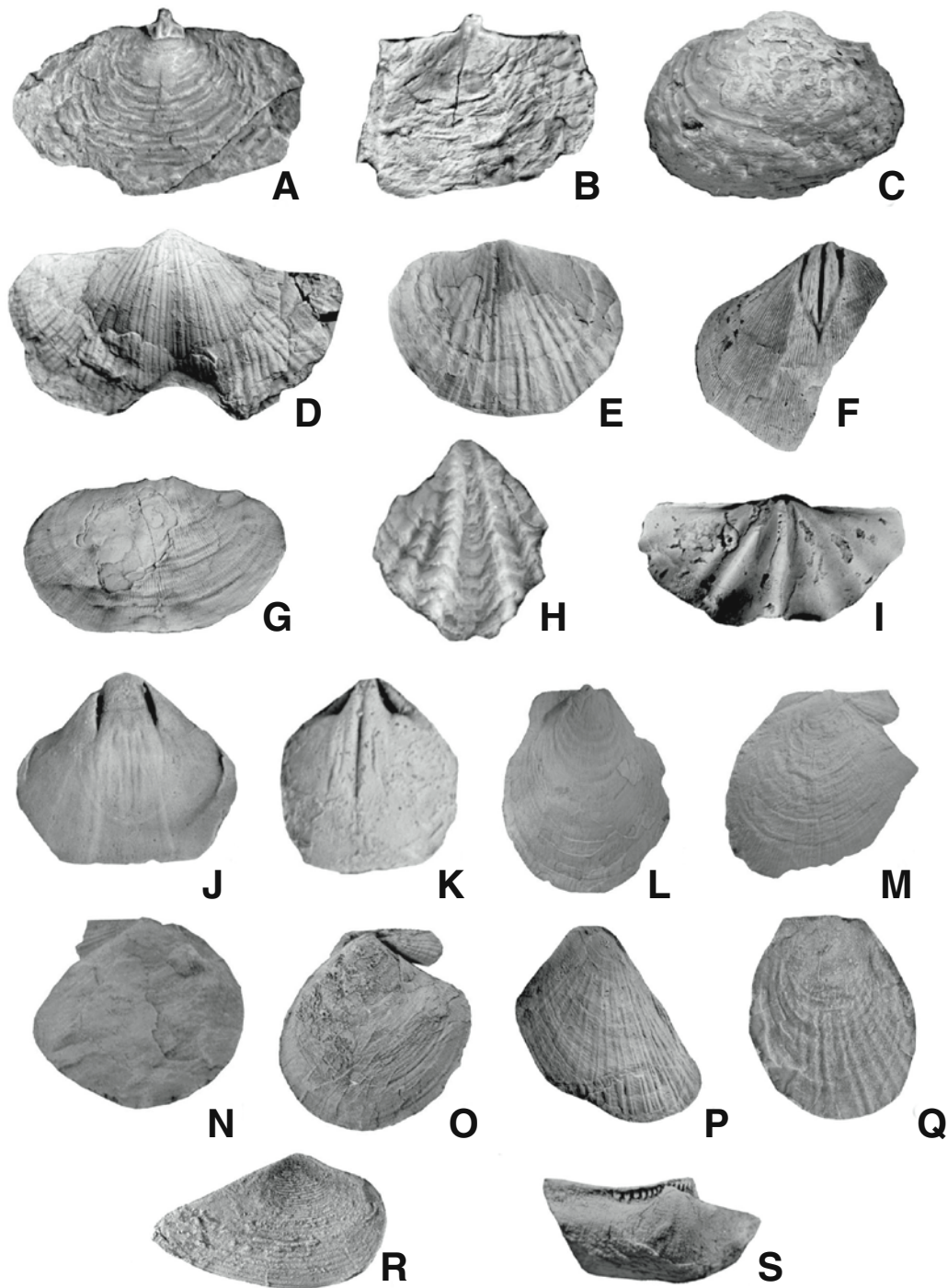


Figure 5. Postglacial “*Levipustula* Fauna.” (A–C) *Levipustula levis* Maxwell. (A) dorsal valve partially decorticated, IPI 3442 ($\times 2.5$); (B) internal mold of dorsal valve, IPI 4501 ($\times 3$); (C) ventral valve, IPI 3238 ($\times 2$). (D–E) *Costuloplicia leoncitensis* (Harrington); (D) ventral valve, IPI 3221 ($\times 1$); (E) dorsal valve partially decorticated, IPI 3223 ($\times 2.5$). (F–G) *Kitakamithyris* sp. (F) internal mold of ventral valve incomplete, IPI 4502 ($\times 1$); (G) internal mold of dorsal valve, IPI 4503 ($\times 1$). (H–I) “*Spiriferellina*” *octoplicata* (Sowerby); (H) ventral valve incomplete, IPI 3232 ($\times 3.5$); (I) internal mold of dorsal valve, IPI 3235 ($\times 2.3$). (J–K) *Beecheria* sp.; (J) internal mold of ventral valve, IPI 4504 ($\times 5$); (K) internal mold of dorsal valve, IPI 4505 ($\times 4$). (L–M) *Streblochondria sanjuanensis* Sterren; (L) paratype, composite mold of left valve, CEGH-UNC 19750 ($\times 1.5$); (M) holotype, composite mold of right valve, CEGH-UNC 19748 ($\times 1.5$). (N–O) *Streblochondria stappenbecki* (Reed); N, internal mold of left valve, CEGH-UNC 19757 ($\times 2.5$); (O) internal mold of right valve, CEGH-UNC 19755 ($\times 1.8$). (P–Q) *Palaeolima retifera* (Shumard); (P) outer view of right valve, CEGH-UNC 22168 ($\times 7$); (Q) outer view of right valve, CEGH-UNC 19773 ($\times 2.3$). (R–S) *Phestia* sp. aff. *P. bellistriata* (Stevens); (R) interior of left valve, CEGH-UNC 22165 ($\times 4$); (S) dorsal view of right valve showing denticulations, CEGH-UNC 19717 ($\times 6$).

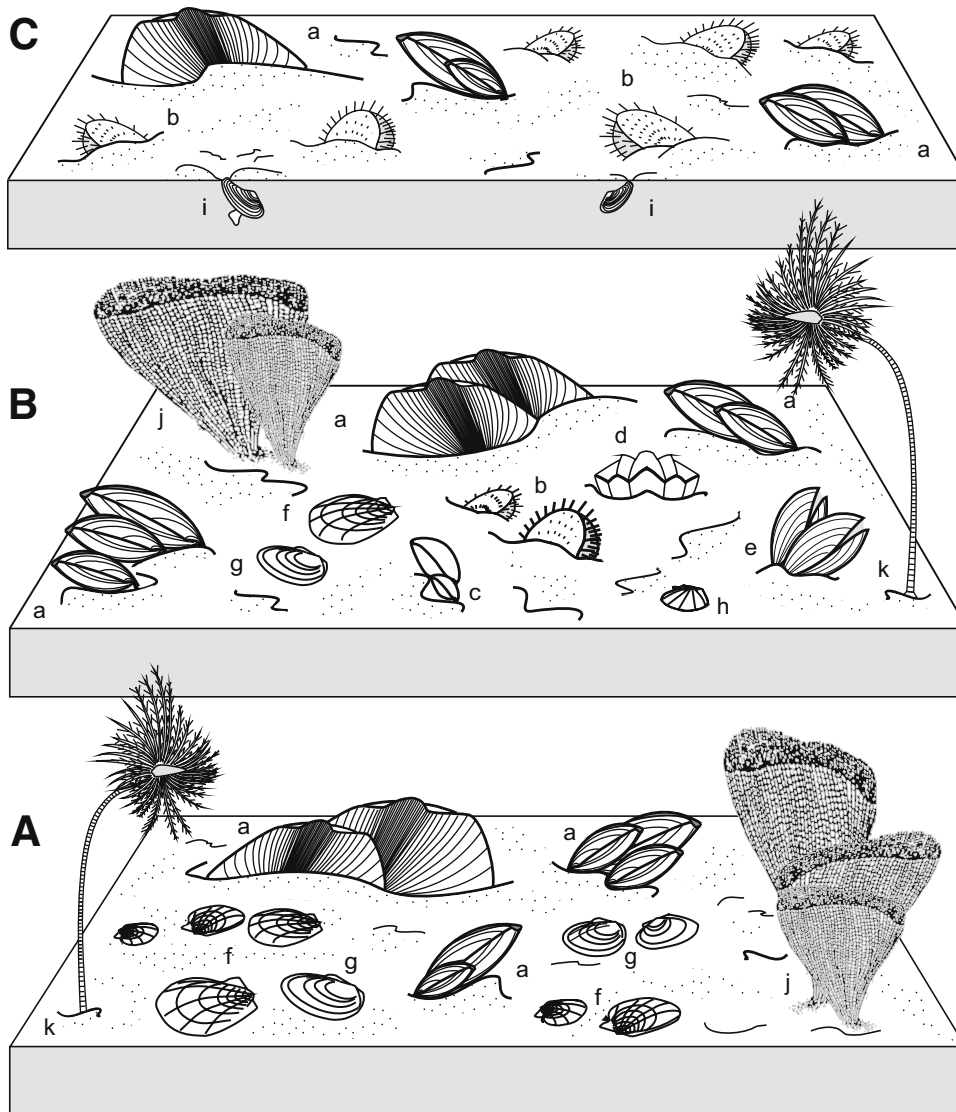


Figure 6. Hypothetical paleoecological reconstructions of the three brachiopod associations recognized in the post-glacial interval. (A) Lower association dominated by bivalves of the genus *Streblochondria*, accompanied by bryozoans and *Costuloplica leoncitisensis*. (B) Middle association dominated by brachiopod communities, characterized by the highest species richness and the highest values of biovolume. (C) Upper association dominated by *Levipustula levis* and *Costuloplica leoncitisensis*, accompanied by *Phestia* sp. aff. *P. bellistriata*. a—*Costuloplica leoncitisensis* (Harrington), b—*Levipustula levis* Maxwell, c—*Beecheria* sp., d—“*Spiriferellina*” *octoplicata* (Sowerby), e—*Kitakamithyris* sp., f—*Streblochondria sanjuanensis* Sterren, g—*Streblochondria stappenbecki* Reed, h—*Palaeolima retifera* (Shumard), i—*Phestia* sp. aff. *P. bellistriata*, j—*Fenestella* sp., k—*Crinoidea* indet.

diversity of the fauna in this part of the postglacial interval as well as the presence of the opportunistic organisms may represent a relatively unstable substratum.

The distinctive pattern of the faunal distribution in the Hoyada Verde Formation, as well as the persistence of some taxa after the glaciation, have been recognized and studied in modern ecosystems close to glaciers. Faunal variations in the postglacial phases, mainly related to differences in substrate types, water depth, and variations in clastic and organic content sediment rates, have suggested by Gordillo and Aitken (2001) for the modern ecosystems of the Arctic region. These important changes are reflected in the development of different associations, from the onset of the deglaciation to the postglacial phase. When the glacier retreats, large volumes of sediment discharged by the meltwater flows can suppress the vertical circulation and the nutrient generation in the surface water, limiting the marine primary production and the food supply in ice-proximal benthic habitats. These condi-

tions drastically change in the postglacial phase and the increase of the nutrients accounts for the diversification of the mollusk assemblages. This model can be useful for understanding why the “Postglacial *Levipustula* Fauna” is more diversified than the “Intraglacial *Levipustula* Fauna”; it also allows us to understand the other variations of the postglacial fauna in the different associations identified in this contribution.

Studies of the behavior of modern bivalve assemblages from circumpolar regions suggest that during a glacial event the ice can negatively affect much of the benthic marine fauna in continental shelves, but some species are able to survive using some form of refugium. Various strategies for the subfossil mollusks have therefore been proposed, such as displacing into deeper waters, moving into subpolar regions, or surviving in nonglaciated pockets in continental shelves (Crame, 1996). This type of behavior in glacial conditions could explain the recurrence of some bivalves along the Hoyada Verde section, such as the presence of *Phestia*

sp. aff. *P. bellistriata* and *Palaeolima retifera* in the Intra- and Postglacial Faunas.

The influence of the glaciation in the late Paleozoic marine biota has been also documented in other basins of western Argentina such as the western Paganzo Basin. Pazos (2000) recognized a glacial opportunistic ichnofaunal assemblage characterized by a low diversity and a high degree of burial, which could suggest stress conditions in a cold-water environment. Buatois et al. (2006, this volume) proposed that high sedimentation rates and fluctuations in the water salinity might have characterized the depositional conditions during the Gondwanan glaciation. These authors suggested in addition that the postglacial assemblages were developed during a transgressive event and the subsequent deltaic progradation, which set new conditions characterized by abundant supply of nutrients and oxygenation of the water column.

The conclusions from the present study conducted in the Hoyada Verde Formation can be extended to other areas of the Calingasta-Uspallata Basin. Although the Hoyada Verde section exhibits the best record of the glacial-postglacial transition and associated faunas, a fossil assemblage compositionally and taphonomically equivalent to the “Intraglacial *Levipustula* Fauna” has been recently recognized in the Leoncito Formation (Cisterna and Sterren, 2008). Ostracods are unusual in the Carboniferous sequences of the basins of western Argentina, and the presence of the genus *Aurysirkbya* Sohn in the “Intraglacial *Levipustula* Fauna” could have significant biostratigraphic implications. This ostracod genus has been described from equivalent stratigraphic sequences in the Tepuel-Genoa Basin in Argentine Patagonia. Díaz Saravia and Jones (1999) considered that the ostracod faunas described from this basin in the lower part of the Pampa de Tepuel Formation would be early Namurian (lower part of the *Levipustula levis* Zone). In this sense the new “Intraglacial *Levipustula* Fauna” identified in the Hoyada Verde Formation would have biostratigraphic and paleogeographic implications for intra- and even interbasinal correlations.

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