

Silurian-Devonian coral associations across a sequence stratigraphic boundary in the Argentine Precordillera

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Silurian and Devonian corals occur abundantly in siliciclastic rocks of the Argentine Precordillera. They are distributed along a Silurian storm-dominated shallow-water platform, a transitional restricted nearshore environment, and a Devonian muddy platform setting. Four main associations of rugose and tabulate corals have been recorded: a Silurian association, a lowermost Devonian and two associations in Lower Devonian rocks. The Silurian shallow-water platform coral association shows abundant colonies of a tabulate pleurodictyform coral. The type and the domical form of corals indicate high-energy environments. The lowermost Devonian coral association shows the abundance of the tabulate coral *Argentinella argentina*, which could have formed patches in protected low-energy environments. The Lower Devonian coral associations correspond to a muddy platform environment. The first one includes rugose and hemispherical tabulate corals and the second is composed of tabulate corals assigned to *Parastriatopora sanjuanina*, and *Parastriatopora* sp. They are long stick-like, fasciculate forms, grouped in apparently life position. Rugose and tabulate corals in the Upper Silurian and Lower Devonian of Argentina constitute low-diversity associations of western Gondwana, developed in mid- to high-latitudes. The morphologies acquired by corals are related to water energy. Laminar or encrusting forms were more competitive in the Silurian shallow-water, high-energy environments. Slender branching forms with a high profile typically inhabited Devonian relatively deeper water or protected settings. The stratigraphic distribution observed partially followed the well-known pattern in which shallow-water faunas disappeared during regressive events and are replaced by new forms in the subsequent transgressive sequence. The turnover pattern detected across the Silurian-Devonian transitional interval is in agreement with that previously recognized on the basis of the accompanying fauna. Copyright © 2011 John Wiley & Sons, Ltd.

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1. INTRODUCTION

A variety of coral associations occur in the Silurian and Devonian siliciclastic rocks of the Argentine Precordillera. The corals are mainly associated with brachiopods and trilobites and they are distributed across the transition between the Silurian and Devonian systems. In recent years several taxonomic studies of the coral fauna have been carried out (Fernández Martínez *et al.*, 1999, 2002, 2007; Rodríguez *et al.*, 2002). The species of tabulate and rugose corals, identified up to now, occur in a lithofacies gradient from shallow shoreface facies to muddy siliciclastic platform deposits.

The coral associations described in this contribution come from the mainly Silurian to lower Devonian (Wenlock – earliest Lochkovian) Los Espejos Formation and the Devonian

(Lochkovian – Emsian) Talacasto Formation in the Cerro del Fuerte section near the Jáchal locality and the Los Algarrobos section in the Talacasto Range.

Corals are new sessile components of the faunal associations in the Silurian of the Argentine Precordillera, since Lower Ordovician and Middle – Upper Ordovician associations are dominated by sponges and bryozoans, respectively (Carrera, 1997, 2003). The siliciclastic Middle and Upper Ordovician units contain many bryozoan genera (Carrera, 2003; Carrera and Ernst, 2010 and references therein), but very few corals occur (Fernández Martínez *et al.*, 2004). On the contrary, and after the Ordovician extinction, no bryozoans have been recovered from the Silurian units and corals became important components of the attached suspension-feeding organisms among Silurian and Devonian communities.

Although at a global scale there was not an important diversity crisis at the Silurian/Devonian boundary, in the Precordillera basin of western Argentina a significant faunal

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turnover event has been recorded at that time. This event shows the transition from the Afro-South American Realm (the *Clarkeia* fauna) and the Malvinokaffric Realm (Sánchez *et al.*, 1991, 1993; Benedetto and Sánchez, 1996).

The main objective of this work is to report the distribution of coral associations along a lithofacies gradient and across a sequence stratigraphic boundary in the Silurian - Devonian transition in the Argentine Precordillera. A brief discussion on how the corals were affected by the environmental change and the palaeogeographical framework is also included.

2. GEOLOGICAL SETTING AND STRATIGRAPHY

In the studied area the upper interval of the Los Espejos Formation and the lower part of the Talacasto Formation crop out.

The (mainly) Silurian Los Espejos Formation corresponds to a siliciclastic storm-dominated platform with a shallowing-upward succession, from open-shelf muddy bioturbated facies associations to shallow platform and shoreface facies (Sánchez *et al.*, 1991; Astini and Piovano, 1992). The base of the Los Espejos Formation represents a transgressive event after an erosive unconformity. Two major shallowing-upward and hundreds of metres-thick cycles occur before the Silurian-Devonian interval (Astini and Piovano, 1992; Sánchez *et al.*, 1993).

The upper Silurian interval of the Los Espejos Formation (*ca.* the upper 100 m) is an alternation of fossiliferous bioturbated mudstones and interbedded hummocky cross-stratified sandstones and coquinas. The facies association consists of extensively bioturbated, highly fossiliferous, yellowish-green mudstones interbedded with fine-grained sandstones 5 to 20 cm thick. Some sandstone beds exhibit hummocky cross-stratification and are capped by wave-ripple lamination. A basal concentration of shells is almost invariably present. The fauna is present either as autochthonous associations in the mudstones or as para-autochthonous assemblages in the storm beds.

Overlying these uppermost tempestite (coquina) levels of the Los Espejos Formation a reddish mudstone interval, 12 m thick, locally crops out. This interval, interpreted within the uppermost (earliest Lochkovian) part of the Los Espejos Formation (Astini, 1996; Benedetto *et al.*, 1992), is absent in most of the localities in which the Silurian-Devonian transition occurs. Only in the Cerro del Fuerte section and the nearby La Chilca section has it been confidently recorded (Figure 1). This interval is located in between shallow-water platform to shore-face facies associations (Astini and Piovano, 1992; Benedetto *et al.*, 1992) and according to Sánchez *et al.* (1993), Astini and Maretto (1996) and Astini (1996) it represents a preserved regressive system

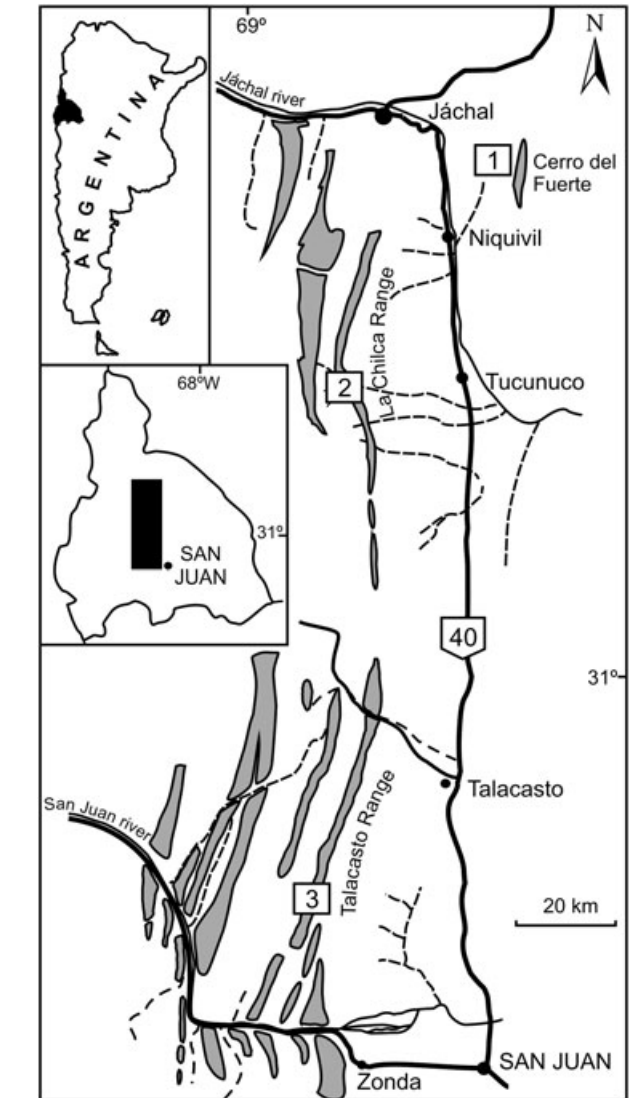
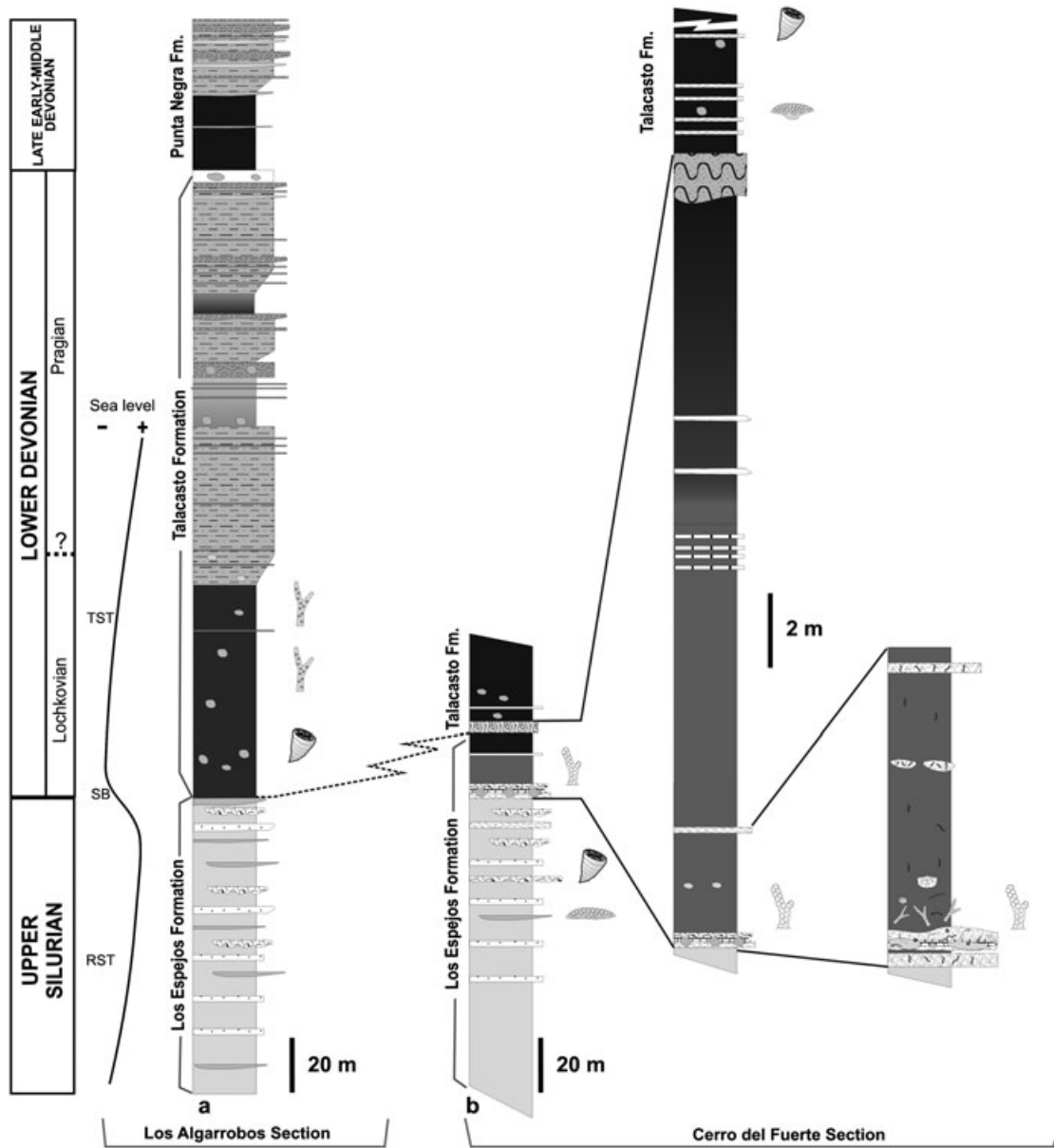


Figure 1. Location map of the studied area showing fossiliferous localities. 1, Cerro del Fuerte section. 2, La Chilca section. 3, Los Algarrobos section. Grey shaded area, representing Silurian and Devonian sedimentary outcrops.

tract developing shallow, marginal and restricted facies. The base of this reddish unit, consists of a thin (about 10 cm) profusely bioturbated sandstone bed of light brownish to slightly greenish colour, and immediately above, a ferruginous mudstone bed 20–40 cm thick. This mudstone bed contains abundant greenish grey fossiliferous marly nodules exhibiting a conspicuous three-dimensional framework of a dendritic ferruginous mineral. The nodules are mostly elongated, tending to be anastomosed, becoming overall bed-like in aspect (although isolated ones are also frequent). On top of this nodular mudstone there is a 12 m-thick interval of a monotonous succession of reddish extensively bioturbated mudstones. It exhibits a 10 cm-thick nodular silty bed nearly 2 metres above the base, and, near the

top, some thinner sandy tabular beds (see Figure 2). Corals are abundantly present in the first 70 cm of the reddish mudstone interval.

Overlying the reddish mudstone interval, there are nearly 2 metres of greyish mudstones with a couple of chocolate bioturbated siltstone layers. Conformably overlying, occurs



References

- | | | | |
|--------------------------|--|------------------------------------|------------------------|
| Shales and mudstones | Coarse-grained sandstones | Fine- to medium-grained sandstones | <i>Enterolasma</i> |
| Mudstones and siltstones | Fossiliferous marly nodular siltstones | Nodules | <i>Argentinella</i> |
| Reddish mudstones | Coquinas (tempestites) | Pleurodictyform coral | <i>Parastriatopora</i> |
| Wackes and siltstones | Convolute sandstone bed | <i>Favosites?</i> | |

Figure 2. Stratigraphic columns of the Silurian-Devonian studied units, showing occurrence of corals. **a:** the Los Algarrobos section, **b:** the Cerro del Fuerte section with the reddish mudstone interval (dark grey) showed in detail on the right.

an 8 metre-thick interval of green silty levels, which is succeeded by a *ca.* 2 m-thick bed of contoured and convoluted sandstone. At the Cerro del Fuerte section, the base of the Talacasto Formation is interpreted to lie immediately above the top of this convoluted sandstone bed (Figure 2).

The entire interval, between the uppermost coquina levels of the Los Espejos Formation and those immediately below the base of the Talacasto Formation, has been interpreted as deposited in a shallow-water platform to shore-face setting, and the genesis of the convoluted bed has been related to the effects of a seismic event (Astini, 1996).

The Talacasto Formation is widely exposed in the Central Argentine Precordillera in the San Juan Province, western Argentina. The lower interval (*ca.* 100 m at Cerro del Fuerte section) consists of a monotonous succession of black and green mudstones and shales with a few intercalated levels of siltstones and fine-grained sandstones (Figure 2). The Talacasto Formation has been referred to a muddy shelf depositional system developed during a highstand, which overlies the shelf system of the Los Espejos Formation (Astini, 1991).

Fossil remains are sparsely distributed and well preserved in the mudstones of the lower part of the Talacasto Formation. The fauna is mainly represented by brachiopods, trilobites, echinoderms and corals. Passing into the upper part of the formation, the frequency of sandstones beds increases and lenses and calcareous concretions occur conspicuously. In these levels tabulate corals are abundant and occasionally form aggregates preserved in life position.

Based on all geological and palaeontological data, Astini (1996), Astini and Maretto (1996) and Sánchez *et al.* (1993) identified a sequence stratigraphic boundary in the Silurian-Devonian transition. This interval is related with an important palaeogeographic and tectono-sedimentary change, which implies an abrupt increase in the rate of sedimentation at the beginning of the Devonian units (Astini, 1996). Hence the stratigraphic record of the Silurian-Devonian boundary in the Central Precordillera is poor due to a stratigraphic discontinuity spanning the boundary between the Los Espejos and Talacasto formations.

Age

The Los Espejos Formation and the base of the Talacasto Formation are faunally constrained to the Wenlockian to Lochkovian time interval (Herrera, 1993; Sánchez, *et al.*, 1993; Le Hérisse *et al.*, 1997).

The Los Espejos Formation overlies the Llandoverly La Chilca Formation. On the basis of palynomorphs and graptolite data, the basal interval has been dated by Rubinstein and Brussa (1999) as late Wenlockian, equivalent to the *Monograptus ludensis* Zone. The middle interval has yielded graptolites of the *Neodiversograptus nilssoni* Zone (Rickards *et al.*,

1996) and palynomorphs of the A4 Zone (Rubinstein and Brussa, 1999).

The base of the upper Silurian interval includes the palynomorph association A5 (Rubinstein and Brussa, 1999) related to the *Neodiversograptus nilssoni* - *Lobograptus scanicus* Zone indicative of a Gorstian age. The graptolite association comprises the species *Monograptus uncinatus notouncinatus*, *Saetograptus (Colonograptus?) roemeri* and *Saetograptus (Colonograptus?) argentinus*, which indicate an early Ludlovian age (Cuerda, 1969; Rickards *et al.*, 1996). These levels are equivalent to those studied by Albanesi *et al.* (2006) in the Talacasto area, where graptolites and conodonts are indicative of an early Ludlovian (Gorstian) age.

The last 50 metres of the upper Silurian interval do not record definite graptolite or palynomorph associations. Recently, Heredia *et al.* (2007) on the base of a conodont fauna, suggested an early Ludlovian age for the upper 50 metres of the Los Espejos Formation below the reddish mudstone interval. These conodonts were recovered from coquina beds which contain resedimented clasts, so the accurate age for the uppermost part of the formation is still in debate.

The overlying reddish mudstones include a brachiopod fauna indicative of the earliest Lochkovian (*Orthostrophia* association, Benedetto *et al.*, 1992; Sánchez *et al.*, 1993; Herrera, 1993; Racheboeuf and Herrera, 1994).

The base of the Talacasto Formation does not record the earliest Lochkovian levels (Le Hérisse *et al.*, 1997), but all the muddy lower part record early to late Lochkovian ages (Herrera, 1993; Racheboeuf and Herrera, 1994).

3. MATERIAL

The fossil specimens studied in this contribution come from previous and recently collected material in the Cerro del Fuerte section near Jáchal city, Los Algarrobos section and Talacasto Range, San Juan Province, Argentina. The analysis is based also on the material cited in the literature. New fossils studied in this contribution are housed at the Palaeontological collection of CIPAL-CICTERRA under the prefix CEGH-UNC.

4. CORAL ASSOCIATIONS

Four main associations of rugose and tabulate corals have been recorded from the Silurian and Devonian rocks: the Silurian association in the Los Espejos Formation, a transitional coral fauna in the reddish mudstone interval and two coral associations in the lower part of the Devonian Talacasto Formation. Distribution of corals among different intervals is variable. Some occur concentrated in a few

metres of strata, as for example in the reddish mudstone transitional interval, while others appeared sparsely distributed over tens of metres, as in the base of the Talacasto Formation.

In addition to the study of the stratigraphic distribution, the coral associations were investigated in relation to the ecological significance of their components. A general ecological characterization of the coral faunas is described here.

Water movement and type of substrate are two important constraints for coral distribution (Jackson, 1977; Pandolfi 1984; Elias 1984; Neuman 1988; Zhen, 1996; Scrutton, 1999). Coral growth rate is related to water turbulence and depositional rate. The growth form is theoretically the expression of different ratios or combinations of the growth rate in vertical or horizontal directions, varying from cylindrical or slender branching forms at one end, to the encrusting or laminar forms at the other. The compound forms of tabulate corals, in spite of some few differences of growth and developed on the substrate, show a similar scenario with fasciculate or slender branching forms with predominantly vertical growth, while laminar or encrusting forms show horizontal growth.

According to the palaeoecological review of Palaeozoic corals of Scrutton (1999), colonial corals could follow one of two fundamental strategies:

The peripheral growth, in which most offsets appeared around the colony margin and the colony tended to be flat-based with a high diameter. Such colonies were adapted to substrates with low sedimentation rate, across which they could spread rapidly. The result of this growth form is a wide, flat colony with almost exclusively upward-facing corallites. In some cases, peripheral strategies could accommodate faster sedimentation rates or high levels of suspended sediment, by leaving spaces between corallites as in fasciculate corals (cateniform halysitids).

In the medial growth strategy, offsets mainly appeared within the colony between pre-existing corallites, resulting in corallites fanning upward and outwards in longitudinal section. Such colonies had the potential for more rapid upward than lateral growth. This strategy was most effective on a substrate with faster sedimentation rates and produced colonies with relatively high height and often convex bases. Medial strategies produced domed, bulbous and ramose colony shapes.

In the case of solitary corals, most of them were free-living for much of their lives, often resting on their sides partially buried in a soft substrate producing characteristically horn-shaped coralla. An alternative solution to the stability problem is the adoption of a discoidal growth form, spreading the weight across the substrate and maintaining a low profile.

Both, colonial and solitary corals also initiated growth on sediment grains or skeletal debris. Many others could

successfully develop an extensive area of attachment when a suitable hard substrate was available.

4.1. The Silurian shallow-water platform coral association

Fragmentary moulds and calcareous skeletons of tabulate pleurodictyform corals have been found in the muddy fossiliferous intervals as well as in the storm-generated sandstone levels encompassing the Silurian uppermost 100 metres of the Los Espejos Formation. Coral specimens are relatively scarce in the highly diverse fossil associations present in the same levels, mainly dominated by the brachiopods *Harringtonina acutiplicata*, *Australina jachalensis* and different species of *Clarkeia* (see Table 1).

The sandstone beds represent high-energy deposits formed by the effect of storms in the nearshore zone, described as shoreface storm deposits (Sánchez *et al.*, 1991; Astini and Piovano, 1992). The storm shell beds contain nearly the same taxa found in the surrounding fossiliferous mudstones and they are considered as *in situ* reworked para-autochthonous coquinas.

There are two types of shell concentrations in the sandstone facies of the Los Espejos Formation: those associated with the base of the hummocky cross-stratification, which are composed of disarticulated and sometimes fragmented brachiopod valves (mainly *Clarkeia* and *Harringtonina*) or monospecific articulated brachiopod valves (mainly *Clarkeia*), and those related with highly fossiliferous lenses ranging in thickness from 5 to 30 cm enclosed in muddy intervals (Figure 3). Some of these levels are discontinuous sandstone or siltstone beds with flat tops and strongly concave upward bases, which resemble gutter cast deposits (Sánchez *et al.*, 1991). Fossil remains in these lenses are complete and articulated and the assemblages are highly

Table 1. Corals and the associated fossil fauna from the Silurian shallow-water platform association

Corals
• <i>Enterolasma</i> sp.
• Pleurodictyform indet.
Brachiopods
• <i>Harringtonina acutiplicata</i>
• <i>Coelospira expansa</i>
• <i>Australina jachalensis</i>
• <i>Clarkeia alta</i>
• <i>Clarkeia bodenbenderi</i>
Trilobites
• <i>Kazachstania gerardoi</i>
• <i>Paciphacops argentinus</i>
• <i>Dipleura kayseri</i>
Others
• Gastropods
• Ostracods
• Bivalves
• Crinoids

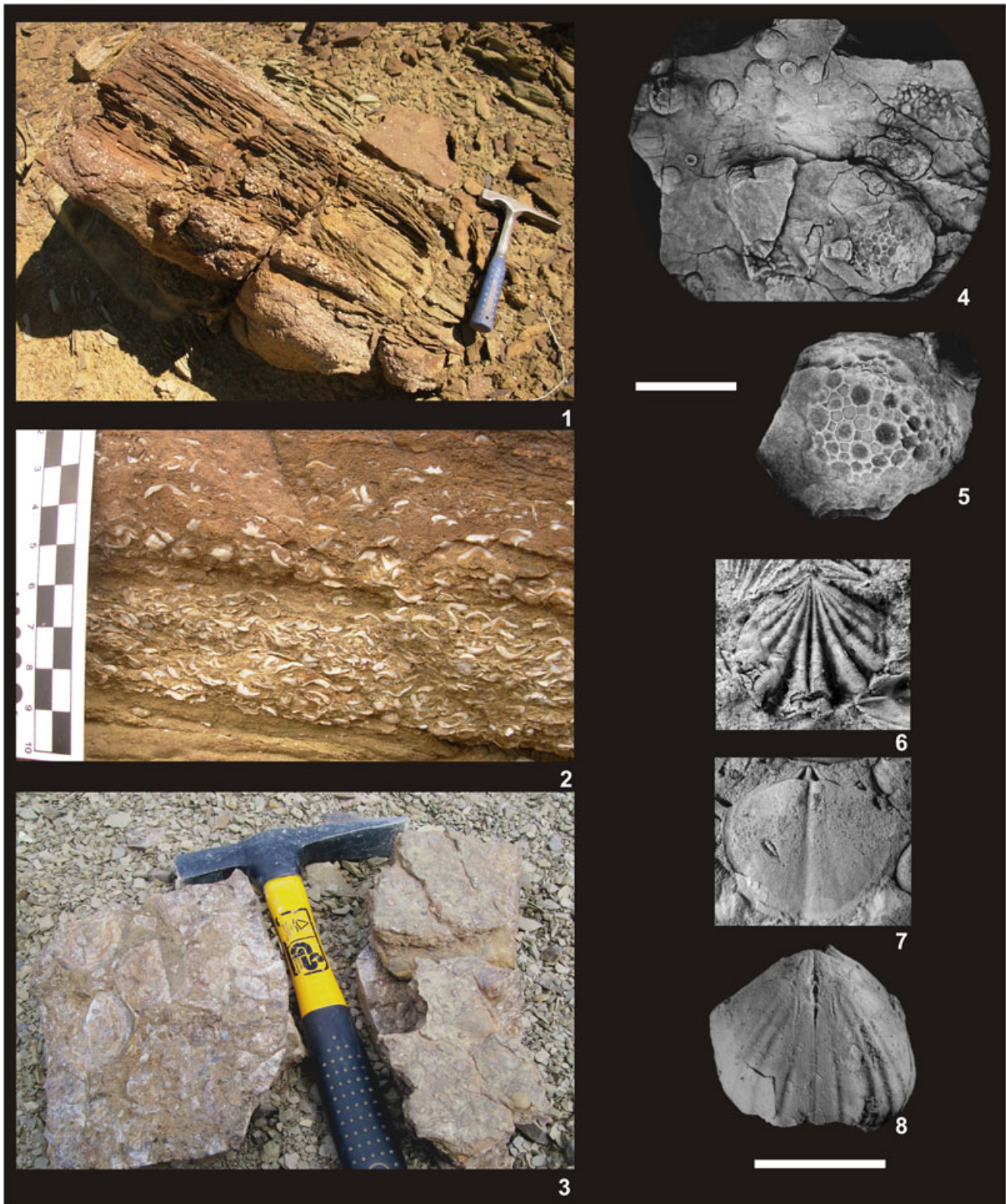


Figure 3. 1–2, Shell concentrations at the base of the hummocky cross-stratification beds in the upper part of the Los Espejos Formation. Scale: for 1 and 3 hammer is 30 cm. 3, Highly fossiliferous lenses enclosed in muddy intervals, upper part of the Los Espejos Formation. 4–5, Domical tabulate pleurodictyform corals of the Silurian shallow shelf association, scale bar 2 cm. 6–8, Associated brachiopod fauna collected in the upper interval of the Los Espejos Formation, scale bar 1 cm. 6, *Harringtonina acutiplicata*. 7, *Australina jachalensis*. 8, *Clarkeia alta*. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

diverse with brachiopods, echinoderms and trilobites as the main components.

Corals are completely subordinated in these associations to other attached suspension feeders such as crinoids. Two forms have been recovered: the most abundant is a domical tabulate coral, and less frequent is a small solitary rugose coral. Taxonomic identification of the coral specimens is difficult due to poor preservation. A preliminary analysis was carried out by Rodríguez *et al.* (2002) and the domical forms were tentatively assigned to the Family Pleurodictyidae and the rugose coral to *Enterolasma* sp.

The type and the domical form of corals indicate morphotypes of high-energy environments. They exhibit wide concave bases slightly irregular expanded to the substrate. These characteristics suggest that they were initially attached to sediment particles or skeletal fragments and later rested directly on the sea floor (Neuman, 1988; Zhen, 1996; Scrutton, 1999). Corallite expansions served to stabilize the colony in unstable or mobile substrates. We can ascribe this colony form to the peripheral growth strategy (Scrutton, 1999), adapted to substrates with low sedimentation rate, across which they could spread rapidly.

4.2. The reddish mudstone coral association

Corals are included in two different lithologies in the reddish mudstone interval. The first one is the marly nodular layer which shows very scarce corals probably assignable to small specimens of *Argentinella argentina* (Fernández Martínez *et al.*, 2002). Shelly remains in the carbonate-clay matrix of these nodules are frequent to abundant in some cases, conferring a distinctive diluted coquina-like aspect to the rock. Despite pervasive fragmentation, fossils remains tend to be oriented parallel to bedding planes, a noticeable taphonomic signature is the presence of articulated individuals either of groups with bivalved (i.e. brachiopods) or multielemental (i.e. trilobites) exoskeletons. These articulated specimens are frequently preserved in a number of orientations with interference among them, which gives a slightly chaotic internal arrangement to the nodules.

Brachiopods are dominant in the abundance of articulated remains, yet the majority of trilobites (mainly dalmanitids, phacopids and proetids), although subordinant in the number of individuals in the fossil association, are perfectly articulated and include a couple of phacopid specimens preserved in a tight enrollment.

Rather fragmentary shelly remains should be indicative of a background winnowing under settings of sedimentary bypass and stratigraphic condensation. However, this appears not to be the case considering the preservational implications of articulated individuals, particularly trilobites, which are sensitive taphonomic indicators. The articulated remains of trilobites, and especially the enrolled specimens, are

diagnostic elements for recognizing exceptional taphonomic circumstances of rapid burial and isolation from disruptive postmortem processes (Speyer, 1987). Hence, we interpret this nodular marlstone bed as originating by a moderately energetic, sudden obstruction-like burial episode.

A taxonomic list of the accompanying fauna including brachiopods, trilobites, gastropods and conularians is provided in Table 2 and a few examples are represented in Figure 3.

The second coral-bearing strata consists of the first 70 cm of the reddish mudstone, and shows abundant and very well preserved fragments of the tabulate coral *Argentinella argentina*. Hundreds of fragments of this species are found in this interval. The accompanying fauna is the same recorded from the marly nodules (Table 2), and it is mainly constituted by brachiopods from which the liberossile form *Leptaena* sp. is by far the most abundant (Figure 3).

The ramose colonies of *Argentinella* show branches from 1 to 3.5 cm in diameter and some preserve bases expanded to 5 cm thick (Figure 4.7–4.11). Ramose colonies with long, widely-spaced corallites indicate relatively low water energy. The very long segments of *Argentinella* suggest that they grew to a substantial height and their very loosely branching growth form with long, slender corallites indicates low- energy and high-sedimentation rate. This ramose form corresponds to the medial growth strategy (Scrutton, 1999) with the potential for more rapid upward than lateral growth.

The great abundance of these branching corals formed patches in protected low-energy environments more than crowded thickets. However, the aggregation and recruitment locally can produce a thicket-like structure. As only one

Table 2. Corals and the associated fossil fauna from the reddish mudstone association

Corals	• <i>Argentinella argentina</i>
Brachiopods	• <i>Leptaena</i> n.sp. A
	• <i>Australocoelia intermedia</i>
	• <i>Orthostrophia meridionalis</i>
	• <i>Isorthis megamyaria</i>
	• <i>Coelospira</i> n.sp. A
	• <i>Amosina pediculorum</i>
	• <i>Amosina</i> n.sp. A
Trilobites	• <i>Paciphacops</i> sp.
	• Odontopleurid indet.
	• Proetidae indet.
	• Dalmanitidae indet.
Others	• Crinoids
	• Conulariids
	• Ostracods
	• Gastropods



Figure 4. 1, Calcareous/ferruginous nodular mudstone bed. 2, Fossiliferous concretions with the collected fauna. 3, Reddish mudstones interval, the arrow indicates the occurrence of the *Argentinella argentina* fossiliferous levels. 4, *Australocoelia intermedia*. 5, Pygidium of Dalmanitid trilobite. 6, *Leptaena* n. sp. A. 7–11, *Argentinella argentina* from the reddish mudstone interval (CEGH-UNC 24801–24805). 7, Base of a colony with three radial expanded branches. 9, Elongated specimen with expanded base for attachment. 8, 10–11, Fragmented ramose colonies. Scale bars 2 cm. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

rugose coral is cited in these basal levels of the reddish mudstone interval (Rodríguez *et al.*, 2002), it appears to be completely outnumbered by *Argentinella*. It has been suggested that tabulate corals were more tolerant of terrestrial mud or sand influx (Zhen, 1996).

The particularity of this earliest Lochkovian fauna, especially the abundance of corals, is consistent with a marginal near-shore environment, restricted without wave action. This association shows marked differences from those of the Silurian part of the Los Espejos Formation and those from the overlying Talacasto Formation.

4.3. The Devonian muddy platform coral associations

In the lower part of the Talacasto Formation, we have distinguished two different intervals with coral associations: those that appear in the lowermost 30 metres of the Talacasto Formation included in the black and green mudstones and shales, well preserved in the Cerro del Fuerte section, and those that occur 70 metres from the base of the same unit, associated with mudstones, fine sandstones and calcareous nodules recorded in the Los Algarrobos section.

The first association includes isolated rugose and tabulate corals found associated with brachiopods, echinoderms and trilobites (Table 3).

Two types of corals were recorded: fragments and complete specimens of a rugose coral assignable to *Enterolasma* sp. (Rodríguez *et al.*, 2002) and a low conical tabulate colony related to the genus *Favosites?* which has only been recorded at the Cerro del Fuerte section (Figures 5.3 and 5.4). They are 4 to 6 cm in maximum diameter with flat to concave bases 2 to 3 cm in diameter. The morphology of

Favosites? could be developed as a result of a predominantly lateral growth for stabilizing the colony in predominantly unstable muddy substrates. The morphotype has a composite growth strategy, although the peripheral growth predominates. It is associated with low-energy environments and low- to moderate-sedimentation rate.

The second association corresponds to corals recently collected by the authors in the Los Algarrobos section (to the south, near the type section of the Talacasto Formation, in the Talacasto area, see Figure 1). The fossils were found in life position in siliciclastic mudstones in two different stratigraphic levels (Figures 5.1 and 5.2), corresponding to Astini's (1991) facies A: green to grey mudstones and highly bioturbated wackes, lacking primary sedimentary structures, often with well-preserved macrofossils. Hundreds of tabulate corals appear in the bioturbated mudstones and wackes and as well in lenticular carbonate nodules, associated with trilobites, brachiopods, crinoids and hyolithids among others.

Corals were easily differentiated into two morphotypes respectively assigned to the species *Parastriatopora sanjuanina* Fernández Martínez *et al.*, 1999 (Figures 5.5. **a**, **b** and **c**) and to *Parastriatopora* sp. (Figures 5.6. **a**, **b** and **c**). The size of the branches, size of the corallites (as observed in longitudinal section), and the number of corallites in cross-section, were considered diagnostic features as suggested by Lafuste *et al.* (1992) and later by García López and Fernández Martínez (1995). Branches of *P. sanjuanina* (Fernández Martínez *et al.*, 1999) have a small number of corallites in cross-section and the corallites arrive perpendicularly to the external surface of the wall in longitudinal section, which is characteristic of the species.

P. sanjuanina usually presents long stick-like fasciculate forms of 11.7 mm mean diameter, showing considerable variability (± 3.63 mm) in the size of branches. It occurs embedded in carbonate lenses with other faunal components (Figure 5.1), but also occurs in the mudstones associated with *Parastriatopora* sp.

Branching delicate forms are frequent among the *Parastriatopora* sp. specimens, and are 8.4 mm mean in diameter with a narrow range of variability (± 1.17 mm). This form commonly appears in life position, restricted to muddy substrates.

P. sanjuanina is a long stick-like, fasciculate form, rarely ramose. *Parastriatopora* sp. is a delicate branching form. In both cases their features suggest that they grew to a substantial height. Their medial growth strategy and slender corallites indicate low water energy and high sedimentation rate. These corals, like the *Argentinella* specimens, were able to establish themselves as thickets or clusters. However, only in the lenticular calcareous sandstone levels (Figure 5.1), can a certain degree of aggregation be seen. They are grouped together, in apparent life position, but forming a very loose

Table 3. Corals and the associated fossil fauna from the Devonian muddy platform association

Corals
• <i>Enterolasma</i>
• <i>Favosites?</i>
• <i>Parastriatopora sanjuanina</i>
• <i>Parastriatopora</i> sp.
Brachiopods
• <i>Sanjuanetes andina</i>
• <i>Athyris</i> sp.
• <i>Lingula</i> sp.
• <i>Meristella</i> sp.
• <i>Metaplasia baldisi</i>
• <i>Anoplia</i> sp.
Trilobites
• <i>Paciphacops</i> sp.
• <i>Parabouleia</i> sp.
• <i>Maurotarion</i> sp.
• Dalmanitidae indet.
Others
• Crinoids
• Hyolithids

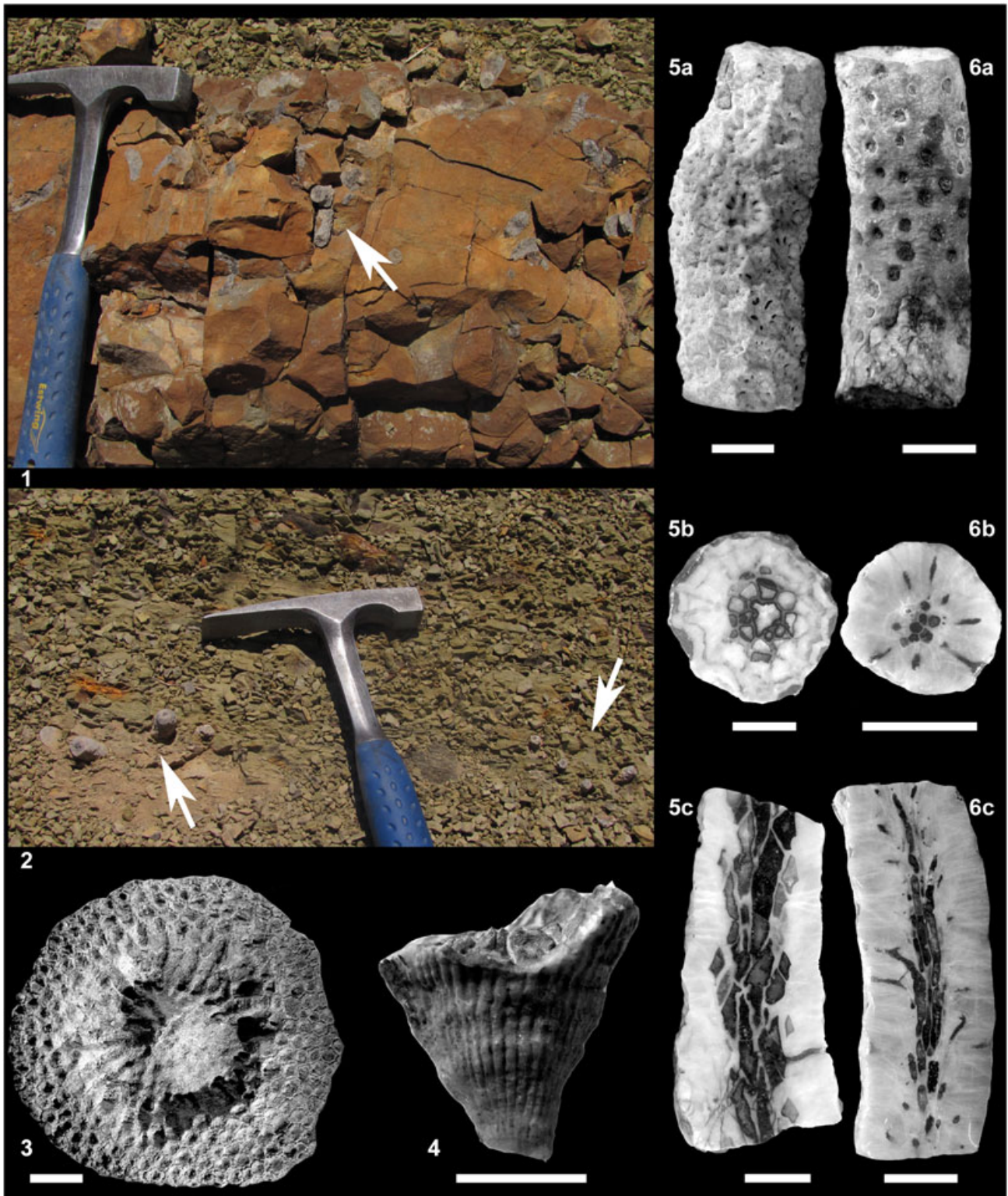


Figure 5. Early Devonian corals. 1, Calcareous sandstone lenses from the lower part of the Talacasto Formation including specimens of *Parastriatopora sanjuanina* (arrowed). 2, Mudstones from the lower beds of the Talacasto Formation including *Parastriatopora* sp. colonies in upright position (arrows indicating the branches of the coral). 3, *Favosites*? sp. from Cerro del Fuerte section (CEGH-UNC 24812). 4, Fragmented specimen of *Enterolasma* sp. from Cerro del Fuerte section (CEGH-UNC 20211). 5, *Parastriatopora sanjuanina* (CEGH-UNC 24810–24811), a: external view, b: transversal section and c: longitudinal section. 6, *Parastriatopora* sp. (CEGH-UNC 24807–24808) a: external view, b: transversal section and c: longitudinal section. All scales bars 5 mm, except 5.3 and 5.4, 1 cm. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

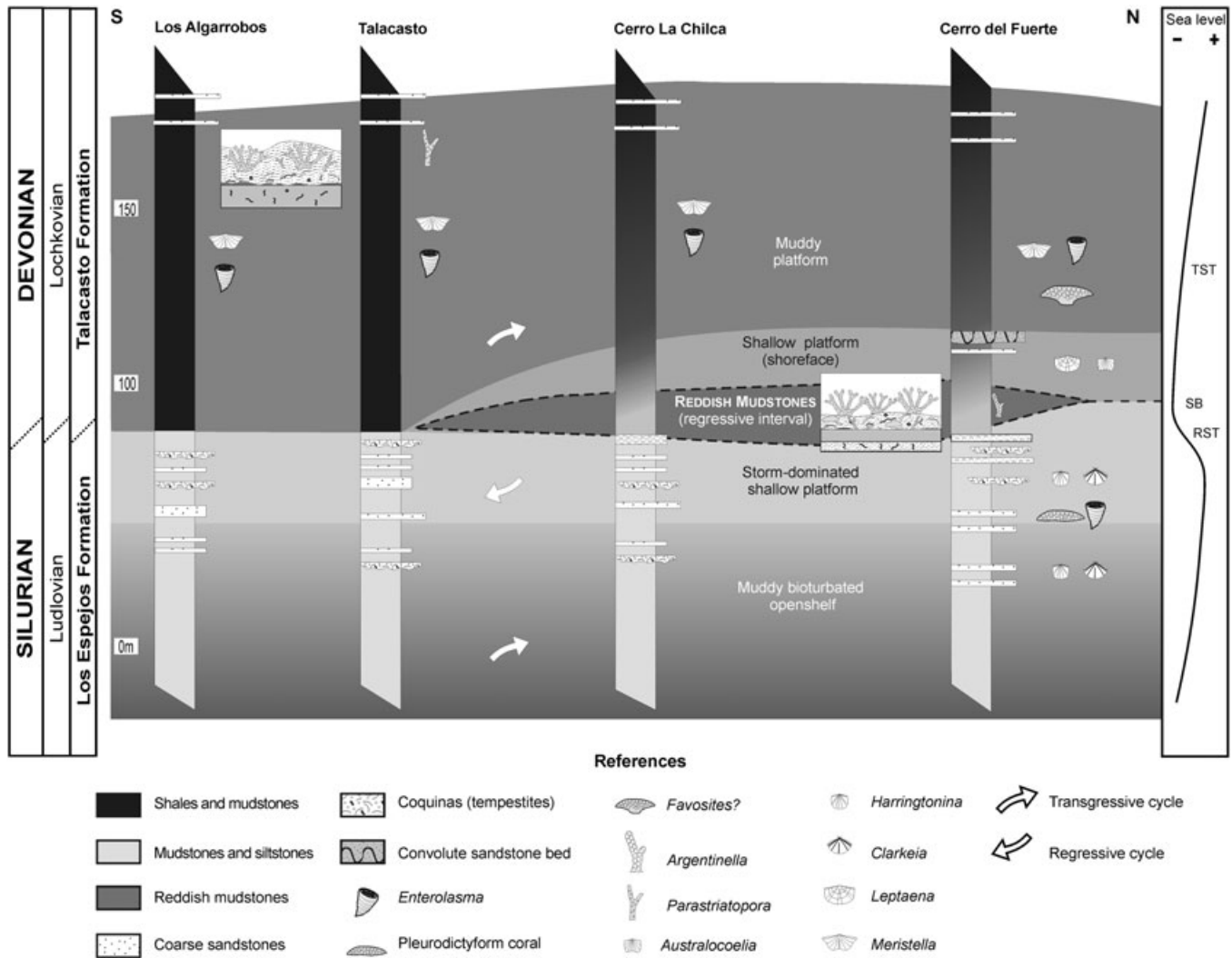


Figure 6. Stratigraphic scheme showing sea-level variations and a regressive-transgressive cycle. A reconstruction of the coral associations is shown in the reddish mudstones interval (Cerro del Fuerte section) and the Los Algarrobos section, respectively. SB: sequence boundary, RST: regressive system tract, TST: transgressive system tract.

pattern. They probably were initially attached to sedimentary grains or hard skeletal fragments and subsequently remained attached directly on the substrate through an expanded base.

5. DISCUSSION AND CONCLUSIONS

Rugose and tabulate corals in the Upper Silurian and Lower Devonian of Argentina show low-diversity associations, including a maximum of two genera, but are commonly represented by numerous specimens. As a whole, they constitute a low diversity western Gondwanan association.

One of the first Devonian palaeogeographic approaches on coral faunas was carried out by Oliver (1977). He proposed three main coral realms that partially coincide with the distribution of other macrofossils such as brachiopods

(Boucot, 1974). The Eastern Americas Realm consisted of the eastern half of North America and the northern part of South America, the Old World Realm including faunas from western North America and Europe, and the Malvinokaffric Realm developed in southern South America and Africa associated with cold climates and containing few corals (Oliver, 1977).

Based on brachiopod faunas of South America and South Africa, Benedetto and Sánchez (1996) defined the Silurian to lowermost Devonian Afro-South American Realm, differentiated from the typical Devonian Malvinokaffric associations. They stressed the marked differences between the brachiopods from the Silurian Los Espejos Formation and the Devonian Talacasto Formation.

Among the Argentinean coral genera, *Argentinella* is an endemic form. *Parastriatopora*, represented by at least two

endemic species, is a widespread genus recognized in almost all continents by the Early Devonian (except in North America). *Enterolasma* is also a widespread genus recorded in North America, Europe (Spain and Russia) and China. Although *Pleurodictyum* has been considered mainly a gondwanic genus (Fernández Martínez *et al.*, 2007), it is also known from Europe, North America and Asia. Meanwhile, *Favosites* is a classical Palaeozoic genus and shows a widespread distribution.

The other record of Devonian corals in South America is from Bolivia (Fernández Martínez *et al.*, 2007). These authors mentioned the presence of previously described genera now re-evaluated as: *Parastriatopora gigantea* (Knod), *Praemichelinia transitoria* (Knod), *Pleurodictyum* cf. *problematicum*, Knod; *Pleurodictyum* sp.; *Thamnoptychia* cf. *limbata* (Eaton) and the endemic genus *Amazonodictyum*, represented by *A. amazonicum* (Katzer). This association is different from the Argentinean corals, although they share some widespread genera.

Most of the studies concerning palaeoecological or palaeobiogeographical aspects of coral associations in the Palaeozoic are devoted to lower latitude reef-related species (Sando, 1980; Kato *et al.*, 1981; Zhen, 1996; Fernández Martínez *et al.*, 2010 and references therein). The western Gondwanan Silurian and Devonian corals developed in mid to high latitudes, although some temperate intervals or climatic amelioration can be observed, and this palaeogeographic location is the main factor responsible in their distribution and diversity pattern.

The sequence stratigraphic framework appears to be a subordinate factor controlling the distribution pattern of the coral associations. Corals distributed in relation to an environmental tracking along a sequence stratigraphic boundary from shallow-water platform associations, a regressive stage and a transgressive event in a muddy platform facies (Figure 6).

The morphologies acquired by corals are related to water energy. Laminal or domical forms occur in the shoreface to shallow platform environments in the Los Espejos association. Laminal or encrusting forms were more competitive in the shallow-water high-energy environments. Slender branching forms with a high profile typically inhabited relatively deeper water or protected settings. Long erect to ramose or dendroid forms are associated with muddy platforms, quiet water settings in the Talacasto Formation or protected environments in the reddish mudstone association.

The type of substrate is also an important factor. Moving, unstable siliciclastic substrates are physically destructive to corals, especially colonial forms (Jackson, 1977). Conversely, solitary forms with high recruitment rates were suggested to have a preferential advantage on soft, mobile, sand substrate (Copper, 1988). This is probably the cause of the coral segregation, with levels dominated by colonial ramose corals in more stable, muddy calcareous levels with

hard fragments for attachment, and unstable substrates with the occurrence of solitary corals. This is a possible explanation for the variable occurrence of rugose corals. *Enterolasma* is found in all the associations studied and was apparently best adapted to environmental shifting.

An important faunal turnover was detected across the studied interval, which is correlated with the Silurian-Devonian boundary (Sánchez *et al.*, 1991, 1993; Benedetto and Sánchez, 1996). According to these authors, the typical *Clarkeia* brachiopod fauna disappeared and was replaced by the *Orthostrophia* association (Benedetto *et al.*, 1992), which is only recorded in the reddish mudstones associations of the Cerro del Fuerte section. This association developed for a relatively short period of time and is different from the fauna recorded in the base of the Talacasto Formation.

The coral associations show basically a similar pattern. Those corals included in the shallow marine Silurian upper part of the Los Espejos Formation, such as the domical pleurodictyform, disappeared and the rugose *Enterolasma* continued to the base of the Talacasto Formation.

The reddish mudstone interval includes *Argentinella argentina*. This endemic form is recorded only in this regressive interval as an exclusive fauna developed in a restricted nearshore area. Sánchez *et al.* (1993) suggested a refuge area for this anomalous *Orthostrophia* brachiopod faunal association. The important replacement is evident in the brachiopod faunas, as stated above, with several Silurian species that disappeared, some new species that are exclusive of this interval, and a few that continue in the Devonian Talacasto Formation.

Argentinella differs from the pleurodictyform corals recovered in the underlying Los Espejos Formation (Rodríguez *et al.*, 2002), and it differs from the *Parastriatopora* association in the Talacasto Formation. The Family Parastriatosporidae first occurs in the reddish mudstone association, with the robust morphotype *Argentinella*. The family possibly diversified later in two different morphotypes, developed in the subsequent transgressive sequence: a more closely related form *Parastriatopora sanjuanina* (Fernández Martínez *et al.*, 1999), and the slender *Parastriatopora* sp.

The observed distribution partially followed the well-known pattern in which shallow-water faunas disappeared during regressive-transgressive events and their scarce descendants reappeared when the previous conditions were re-established. This seems to indicate that when the flooding events started, communities followed the coast line and remain in shallow-water areas as refuge settings. Alternatively, the pattern observed in the Argentine Precordillera indicates that during the regressive stages, biofacies migrated basinward, remaining in peripheral platform areas. The selective pressure produced high levels of extinction and in a few cases the development of autochthonous species. The refuge

areas are difficult to preserve in the geological record possibly as a consequence of the erosive truncation coincident with the surface boundary of the overlying depositional sequence.

Elias (1991) and Elias and Young (1998) related the evolution, dispersion and diversity of the Ordovician coral association of central western North America with water depth and the degree of restriction found in the basin. In maximum transgressive stages the corals mainly occurred in shallow-water areas and basin margins, while in regressive stages corals appeared restricted to cratonic interior basins. This can be applied to the sudden appearance of *Argentinella* in the reddish mudstone interval and its disappearance after this event.

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