Journal of South American Earth Sciences 56 (2014) 242–250

Contents lists available at ScienceDirect

Journal of South American Earth Sciences

journal homepage: www.elsevier.com/locate/jsames

Paleoenvironmental setting and description of an estuarine oyster reef in the Eocene of Patagonia, southern Argentina

Martín Rodríguez Raising [a], Silvio Casadío [b,*], Nadine Pearson [c], Gabriela Mángano [c], Luis Buatois [c], Miguel Griffin [d]

[a] XR-GEOMAP, R. Durand Av. N 397, Grand Bourg, Salta, Argentina
[b] Universidad Nacional de Río Negro, Av. Roca 1242, 8332 General Roca, Río Negro, Argentina
[c] University of Saskatchewan, Department of Geological Sciences, 114 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada
[d] Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

ARTICLE INFO

Article history:
Received 12 May 2014
Accepted 7 September 2014
Available online 18 September 2014

Keywords:
Crassostrea
Oyster reef
Middle Eocene
Río Turbio Formation
Patagonia
Argentina

ABSTRACT

A middle Eocene *Crassostrea* sp. reef near Río Turbio, southwestern Patagonia (Argentina), represents the earliest record of an oyster reef associated with estuarine facies in the southern hemisphere, and also one of the few known worldwide occurring in Paleogene rocks. The reef grew in an outer estuary environment subject to periodic changes in salinity and may have reached a maturing phase. The Río Turbio reef – by its dimensions, geometry, and substrate lithology– would have been located in a tidal channel convergence area. This reef provides new evidence suggesting that estuaries served as refuges for *Crassostrea* populations allowing them to disperse into fully marine environments many times throughout the Cenozoic.

1. Introduction

Oysters are among the most abundant bivalves to be found in shallow-marine and estuarine environments. They are filter-feeding organisms and they can deposit or self-silt eight times the volume of sediment that would have been deposited in the same time due to gravity alone. Lund (1957) calculated that a single layer of oysters could biodeposit sediment at a rate of about 6×104 g/m^2/yr. The results presented by Mitchell (2006) indicate that biodeposition loadings from intertidal oyster reefs can be significant. However tidal flow can disperse this material resulting in minimal enrichment of the sediments around the reefs. The outcome of this material deposited elsewhere in the lagoon and their impact on the benthic community remains unknown.

Oyster reefs affect the geomorphology and hydrologic regime of estuaries in three ways: (1) modifying current velocity, (2) passively changing sedimentation patterns, and (3) increasing sedimentation through biodeposition (Bahr and Lanier, 1981). Ample evidence supports interactive connections between oysters and hydrology (Kennedy, 1996a,b; Lenihan, 1999; McCormick-Ray, 2005), and also their impact on estuaries; thus, Newell (1988) stated that the extensive *Crassostrea* populations of Chesapeake Bay before 1870 had the potential –during the summer months– to filter the bay's entire water column in less than a week.

The incubatory oysters show no promyal passage in the exhalant chamber of their mantle cavity, a trait that renders them less efficient in selecting food particles. For this reason they do not tolerate high turbidity levels (Hopkins, 1979) and are restricted to nearshore oceanic waters; or to the outermost zones of estuaries, where salinity, temperature, and turbidity are not significantly different from those in the ocean. Conversely, non-incubatory species –belonging according to Stenzel (1971) in the genera *Crassostrea*, *Saccostrea*, and *Striostrea* – can live in the ocean but are more abundant in estuaries, as they are better adapted to frequent changes in salinity, temperature, and high levels of turbidity.

Most species of *Crassostrea* are able to withstand freshets in tidal rivers or estuaries by keeping their valves closed for long periods of time.

In the southeastern United States, the living *Crassostrea virginica* forms large reef systems in estuaries and lagoons with the associated marsh, mudflat and tidal drainage networks.

In the modern analogues of the southeastern United States the reefs observed are found restricted to the middle portion of the intertidal zone. In this area competition and predation are reduced due to longer periods of subaerial exposure allowing the oyster

* Corresponding author. Tel./fax: +54 298 4427399.
E-mail addresses: scasadio@unrn.edu.ar, silvio63ar@yahoo.com.ar (S. Casadío).

http://dx.doi.org/10.1016/j.jsames.2014.09.009
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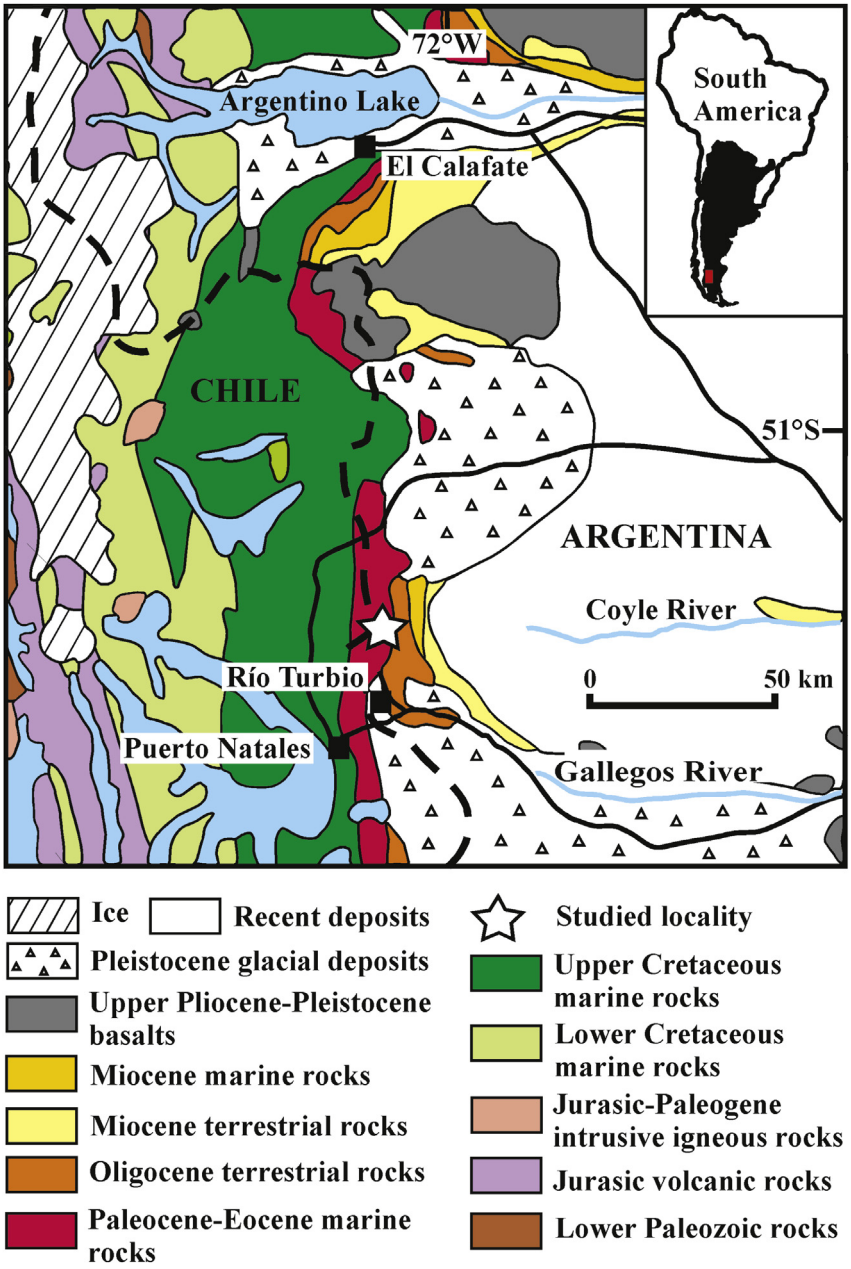

Fig. 1. Simplified geological map of the studied area and location of the *Crassostrea* reef.

populations to flourish (Bahr and Lanier, 1981). The lower intertidal and subtidal areas have an increase in both pelitic sedimentation and predation, which restricts the populations of oysters to only a few scattered individuals (Bahr and Lanier, 1981; Hopkins, 1979). Bahr and Lanier (1981) proposed that the aptitude of most species of *Crassostrea* to tolerate wider ranges of salinity, turbidity, temperature, and oxygenation was the main feature that favored its worldwide distribution and early colonization of brackish-marine environments.

Seilacher (1984) separated soft-botton oysters into heavyweight and lightweight types. The second type appeared later and was related to the acquisition of shell chambers and chalky deposits that were main innovations in the evolution of *Crassostrea*.

The earliest records of euryhaline oysters associated with marginal marine facies are from the Middle Jurassic of the British Isles (Hudson and Palmer, 1976). The earliest records specifically of *Crassostrea* reefs associated with estuarine facies are from the Ushimaro Formation (Middle Jurassic) of Japan (Komatsu et al., 2002) and from the upper Coniacian of New Mexico (Brown, 1988). Late Cretaceous to Neogene references including descriptions of oyster reefs in estuarine environments are few (Toshimitsu et al., 1990; Jiménez et al., 1991, Pufahl and James, 2006) and most of them doubtful (e.g., Martinius, 1991), as they are usually associated with marine facies and stenohaline organisms (e.g., corals and echinoids) characteristic of fully marine conditions.

In this paper we describe a *Crassostrea* sp. reef from the middle Eocene of southern Argentina (Fig. 1), located at approximately 50°S paleolatitude. This is the earliest record of an oyster reef associated with estuarine facies in the southern hemisphere, and also one of the few known worldwide occurring in Paleogene rocks. This reef provides us with information that not only increases our knowledge of the evolution of *Crassostrea* reefs and their

paleoenvironmental significance, but also offers new evidence suggesting that estuaries served as refuges for *Crassostrea* populations allowing them to disperse into fully marine environments many times throughout the Cenozoic (Kirby, 2000, 2001).

2. Geological setting

Although Eocene rocks and faunas have been documented in southern South America since the beginning of the Twentieth Century (Azcuy and Amigo, 1991; Malumián, 1993), interest in their study has been recently renewed (Camacho et al., 2000, 2001; Casadío et al., 2009; Pearson et al., 2012a,b; 2013, Guerstein et al., 2014). These rocks are widely distributed in the Austral or Magallanes Basin, and lie discontinuously exposed along the southwestern corner of Santa Cruz Province and along the Atlantic coast of Tierra del Fuego.

Eocene rocks encompass the Man Aike and Río Turbio formations exposed along the western margin of the Austral Basin. In the Lago Argentino area, Santa Cruz Province, the Man Aike Formation unconformably overlies the Upper Cretaceous rocks of the Calafate Formation (Casadío et al., 2009). According to Marenssi et al. (2002), south of the town of El Calafate the Man Aike Formation represents the infilling of an incised valley excavated during the middle Eocene phase of the Patagonian Cordillera uplift (Ramos, 2002; Kraemer et al., 2002), while sedimentation in subtidal environments began during a transgressive period during the late middle Eocene (Malumián, 2002). A glauconitic bed representing this transgressive event is widely distributed within the Austral Basin, and is found in the Río Turbio (Upper Member), Man Aike, "Glauconítico B", and Leticia formations.

In the southwestern corner of Santa Cruz Province, the Río Turbio Formation unconformably overlies the Paleocene rocks of the Cerro Dorotea Formation. The Río Turbio Formation includes two members. The Upper Member that contains the *Crassostrea* reef records sediment accumulation in tide-dominated, outer-estuarine and coastal-plain environments. Outer-estuarine associations comprise facies that were deposited in channel-thalweg, subtidal sandbar complex, oyster-reef and reef-margin environments. Coastal-plain facies associations include distributary channel, floodplain, salt-marsh, swamp, and swamp margin deposits (Pearson et al., 2012a,b).

The oyster reef studied herein is included in the Upper Member of the Río Turbio Formation (late middle Eocene to early upper Eocene) and is exposed along National Highway 40 at about 15 km North of the town of Río Turbio (51°29′45.6″ S – 72°14′59.8″ W). The exposed section is 148 m thick, and the base and top are covered (Fig. 2).

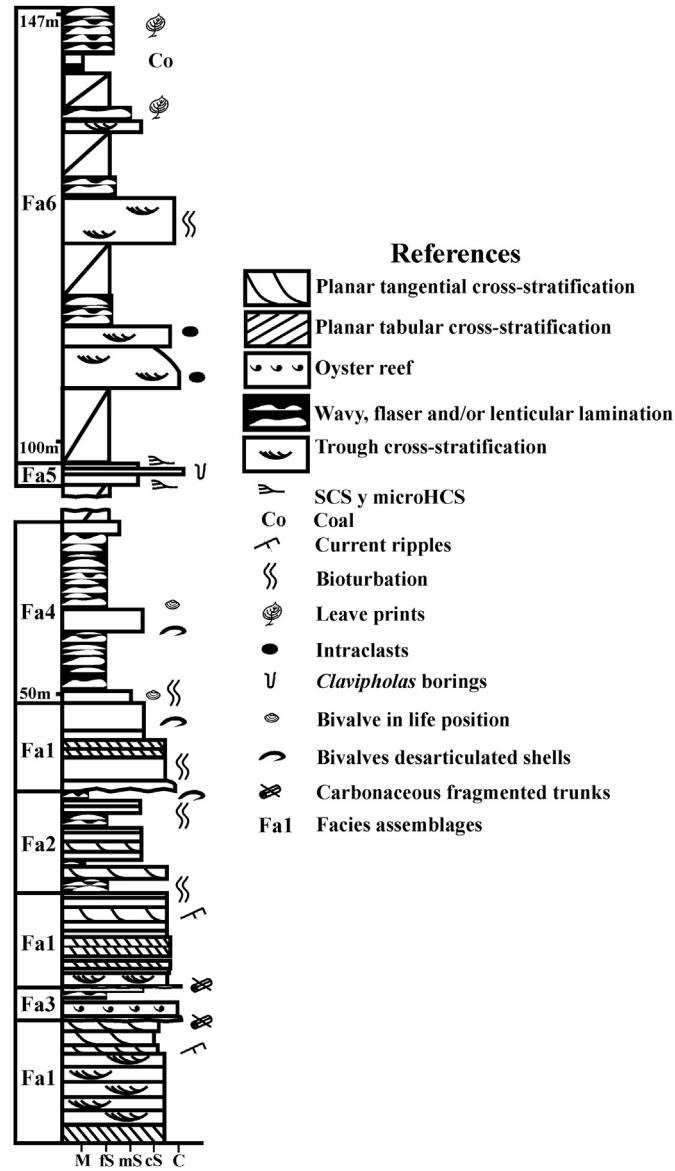

Fig. 2. Stratigraphic section of the Río Turbio Formation at the reef locality.

3. Sedimentology

Fourteen facies, grouped into six facies-associations, are recognized (Table 1) in the Upper Member of the Río Turbio Formation. The sedimentology and ichnologic content of each of these facies is discussed below, along with the implications in terms of depositional conditions and sedimentary environments. Information on the degree of bioturbation is based on schemes produced and refined by Taylor and Goldring (1993), Taylor et al. (2003), Bann et al. (2004), and MacEachern et al. (2005). Terminology for skeletal accumulations is based on Kidwell et al. (1986). Terminology for the scale of cross bedding is based on Ashley (1990).

3.1. Facies associations and sedimentary environments

The outer estuarine facies associations (Fig. 3A) include subtidal channel thalweg conglomerates (Facies A, Fig. 3B); subtidal channel sandstones (Facies B, Fig. 3C); tidal sandbar sandstone (Facies C); tidal sandbar heterolithic sandstone and mudstones (Facies D); flaser-to wavy-bedded sandstones of the protected areas within the tidal sandbar complex (Facies E); hyperpycnal, rhythmically laminated mudstone and sandstones (Facies F); sandstones associated with coquinas interpreted as oyster reefal accumulations (Facies G and H); massive bioturbated sandstones showing low sedimentation rate (Facies I); mixed to mud flat, pinstriped heterolithic sandstone, siltstone and mudstone (Facies J); ripple cross-stratified to parallel-laminated sandstone of the upper flow regime sand flats (Facies K); *Clavipholas pholladoides* coquina associated with a marine reworking surface (Facies L); tidal distributary channel sandstones (Facies M); and the carbonaceous shale and coal found in paralic swamps (Facies N).

The subtidal channel thalweg (FA1) and sandbar (FA2) deposits display low trace fossil diversity, including *Thalassinoides*, *Ophiomorpha*, *Planolites*, *Asterosoma* and *Arenicolites*. The bioturbation index is variable (BI 0-6; commonly 0–3) with the dwelling structures of suspension-feeders dominant and feeding structures

Table 1
Facies descriptions from the Upper Member of the Middle Eocene Río Turbio Formation.

Facies assemblages	Facies	Sedimentological description	Ichnological description	Depositional process	Sedimentary environment
FA1: Outer Estuary Subtidal Channels	A: Trough cross-stratified conglomerate	Bed thickness 0.13–1 m Clast-supported Polymictic Clasts: subrounded pebbles Matrix: fU to cU sand	*Thalassinoides, Ophiomorpha* BI: 0–2 *Skolithos* Ichnofacies	Migration of subaqueous, unidirectional dunes	Thalweg
	B: Trough cross-stratified pebbly sandstone	Bed thickness 0.1–5 m Clasts: granule to pebble Matrix: fU to cU sand Fragmented bioclasts	*Ophiomorpha, Planolites* BI: 0–1 increasing upward to 3–5 *Skolithos* Ichnofacies	Migration of subaqueous, unidirectional dunes	Channel fill
FA2: Outer Estuary Subtidal Sandbars	C: Intermediate-scale trough cross-stratified sandstone	Bed thickess 0.15–3.5 m vfU to cU sand Reactivation surfaces Rare pebbles	*Ophiomorpha, Planolites, Asterosoma*BI: 0–3 *Skolithos* Ichnofacies	Migration of subaqueous dunes, lateral accretion	Tidal sandbars, dune topsets, and foresets
	D: Heterolithic sandstone and mudstone/shale	Bed thickness 0.05–2.2 m fL to mU sand silt to clay Flaser, wavy and lenticular bedding	Firmground: *Thalassinoides, Psilonichnus* BI: 0–2 *Glossifungites* Ichnofacies Softground: *Planolites, Arenicolites, Asterosoma* BI: 0–1 Impoverished *Cruziana* Ichnofacies	Migration of subaqueous dunes, lateral accretion, fluid mud	Tidal sandbars, dune bottomsets
	E: Moderately burrowed, flaser- to wavy-bedded sandstone	Bed thickness ranges between 0.5 and 1.5 mthick. mL to vcU sand Rare granules and pebbles Flaser, and wavy bedding	Firmground: *Gastrochaenolites* BI: 1–2 *Glossifungites* Ichnofacies Softground: *Planolites, Palaeophycus, Asterosoma* BI: 1–6 Diminuitive traces Mixed *Skolithos-Cruziana* Ichnofacies	Migration of subaqueous dunes, lateral accretion, fluid mud	Protected areas associated with tidal sandbars
	F: Rhythmically laminated mudstone and sandstone	Bedset thickness 7–10 cm Wavy, flaser and lenticular bedding Inverse and normal graded	*Planolites, Thalassinoides, Skolithos, Arenicolites* BI: 0–1 Impoverished *Cruziana* Ichnofacies	River-flood generated turbidity currents Hyperpicnites	Position close to the coast associated with tidal sandbars
FA3: Outer Estuary Oyster Reef	G: *Crassostrea* shells and sandstone	Deposit thickness averages 1.75 m Matrix: fL to mL sand Shells in life position and found as articulate valves (subhorizontal) Low bioerosion and encrustation	*Ophiomorpha* BI: 0-1 *Skolithos* Ichnofacies	Tidal currents	Protected areas associated with tidal sandbars, oyster reef
	H: *Crassostrea* sp. coquina	Bed thickness is 25 cm Trough cross-stratified Matrix: fL to cU sand Shells oriented concordant to bedding Encrustation, abrasion, bioerosion, and dissolution low Packing is dense and size selection is poor	No trace fossils observed	Tractive currents, winnowing of finer particles and concentration of coarser particles and shells	Barren central zone in a mature oyster reef
FA4: Outer Estuary Low tidal flat	I: Massive bioturbated sandstone	Bed thickness is 2 m thick. vfU to mL sand with abundant glauconititic grains Bioclasts are found in life position or as articulated valves	BI: 5–6	Migration of subaqueous, unidirectional dunes	Relatively condensed interval
	J: Pinstriped heterolithic sandstone, siltstone and mudstone	Mudstones with fU to fL sandstone intercalations		Tidal currents, sediment fallout	Mixed to mud flats
FA5: Outer Estuary high tidal flats	J: Pinstriped heterolithic sandstone, siltstone and mudstone	Mudstones with fU to fL sandstone intercalations		Tidal currents, sediment fallout	Mixed to mud flats
	K: Ripple cross-stratified to parallel laminated sandstone	Bed thickness is 25 cm thick in ripple cross-stratified beds and 1 m in the parallel laminated beds. Uppermost	*Rosselia, Asterosoma, Thalassinoides* BI: 0–2 (parallel laminated beds) to 3–4 (ripple cross-stratified beds) *Skolithos* Ichnofacies	Fluctuating energy, upper flow regime tidal currents	Sand flats

(*continued on next page*)

Table 1 (*continued*)

Facies assemblages	Facies	Sedimentological description	Ichnological description	Depositional process	Sedimentary environment
	L: Coquina, *Clavipholas* shells	20 cm has articulated *Clavipholas* shells in life position Bed thickness is 15 cm Matrix: m (L or U?) sand Disarticulated valves oriented subhorizontally Packing is higher then 15% High degree of fragmentation Moderate levels of abrasion Low to moderate degrees of encrustation	*Entobia*, *Maeandropolydora*	Winnowing of finer particles and concentration of coarser particles and shells	Reworking surface
FA6: Outer Estuary Tidal marsh	J: Pinstriped heterolithic sandstone, siltstone and mudstone	Current and wave ripples in sandstones (fU to mU). Plant remains	No trace fossils observed	Tidal currents, sediment fallout	Mixed to mud flats
	M: Small-scale trough cross-stratified sandstone	mU to cL sandsotnes. Bed thickness 0.4–1.1 m. Pebbles at the bottom of the sets	*Rosselia*, *Asterosoma*, *Ophiomorpha* BI: 0–2 *Skolithos* Ichnofacies	Migration of subaqeous, unidirectional flow dunes	Tidal distributary channel
	N: Carbonaceous shale and coal	Shale with abundant plant remains (1.41 m) covered by a 0.4 m thick coal bed.	No trace fossil observed	Organic accumulation	Paralic swamp

of deposit-feeders subordinate. The ichnofaunal assemblage suggests deposition in an overall high-energy setting punctuated by periods of lower energy as indicated by the presence of Facies E.

The oyster reef deposits (FA3) are essentially unbioturbated, with rare *Ophiomorpha* present. The bioturbation index is very low (typically 0–1), as is the trace-fossil diversity. The traces consist of the dwelling structures produced by opportunistic suspension feeders constituting the *Skolithos* Ichnofacies. There is an abundance of oysters in life position within Facies G. The taphonomic features of the oyster valves—very low bioerosion, and lack of encrusting organisms—together with the presence of rare *Ophiomorpha* supports the hypothesis that the reef developed in an outer estuary environment subject to periodic changes in salinity.

The upper part of the section contain trough cross-stratifed sandstone (Facies M), heterolithic sandstone and mudstone/shale (Facies J) and carbonaceous shale and coal with low sulfur content that is an indicator of reduced marine influence during the coalification process (Facies N). All these features suggest mixed to mud flats crossed by tidal distributary channels ending in paralic swamp deposits (Facies N).

4. The *Crassostrea* reef

The lower 13 m of the studied section (FA1) include beds of medium-to coarse-grained sandstone, sometimes conglomeratic, showing trough cross-stratification (Fig. 3C). An irregular (erosive) contact separates them from the overlying 40 cm of conglomerate, which includes clasts of up to 2 cm diameter and a coarse-grained sandy matrix. This conglomerate grades upwards into a conglomeratic sandstone containing plant remains, scarce fragments of shells of *Crassostrea* sp. (Fig. 3B), and burrows of up to 5 cm diameter referable to *Thalassinoides* isp. The bed is mainly massive, although trough cross-stratification can be observed at the base.

Immediately overlying these beds and showing a sharp contact surface, lies the oyster reef (FA3). It shows lenticular geometry with an average thickness of 1.5 m and a lateral extension of about 300 m (Fig. 4). The bed includes oysters in life position, both isolated and arranged in cemented cluster of several specimens (Fig. 3E), and articulated shells deposited concordant to the bedding plane. At 0.5 m from the base is the greatest concentration of oysters in life position. The shells show very little bioerosion and no encrustation.

Covering the reef, there is a lenticular shell-bed 25 cm thick and constituted by valves of *Crassostrea* sp. (Facies H). Most of the specimens are disarticulated, concordant or in chaotic position, sometimes arranged in stacking pattern (Fig. 3D). They show poor size selection (size range from 5 cm to 15 cm) and the bed includes juvenile and adult specimens. Packing is dense and disarticulation and fragmentation are high; there is no preference for left or right valves, while abrasion, bioerosion, and encrustation are very low. The matrix is fine sandstone. Based upon these sedimentologic and taphonomic features we interpret that this shell-bed is a coquina ridge.

The thickness of the Río Turbio reef combined with the presence of a coquina ridge (Facies H) implies that the reef reached a stage coincident with phase four of the Bahr and Lanier (1981) model. These authors proposed four stages of development in a *Crassostrea* reef: 1) initial colonization, 2) clustering phase, 3) accretionary phase, and 4) a maturing and senescence. According to Bahr and Lanier (1981) the last stage of development in an intertidal *Crassostrea* reef is characterized by vertical accretion, as the majority of live oysters populate only the flanks of reefs. The mature reef typically has a barren central zone, or ridge in the case of long linear reefs, composed of dead shells and shell fragments. The barren central region was referred to as a "hogback" by Gunter (1979). This

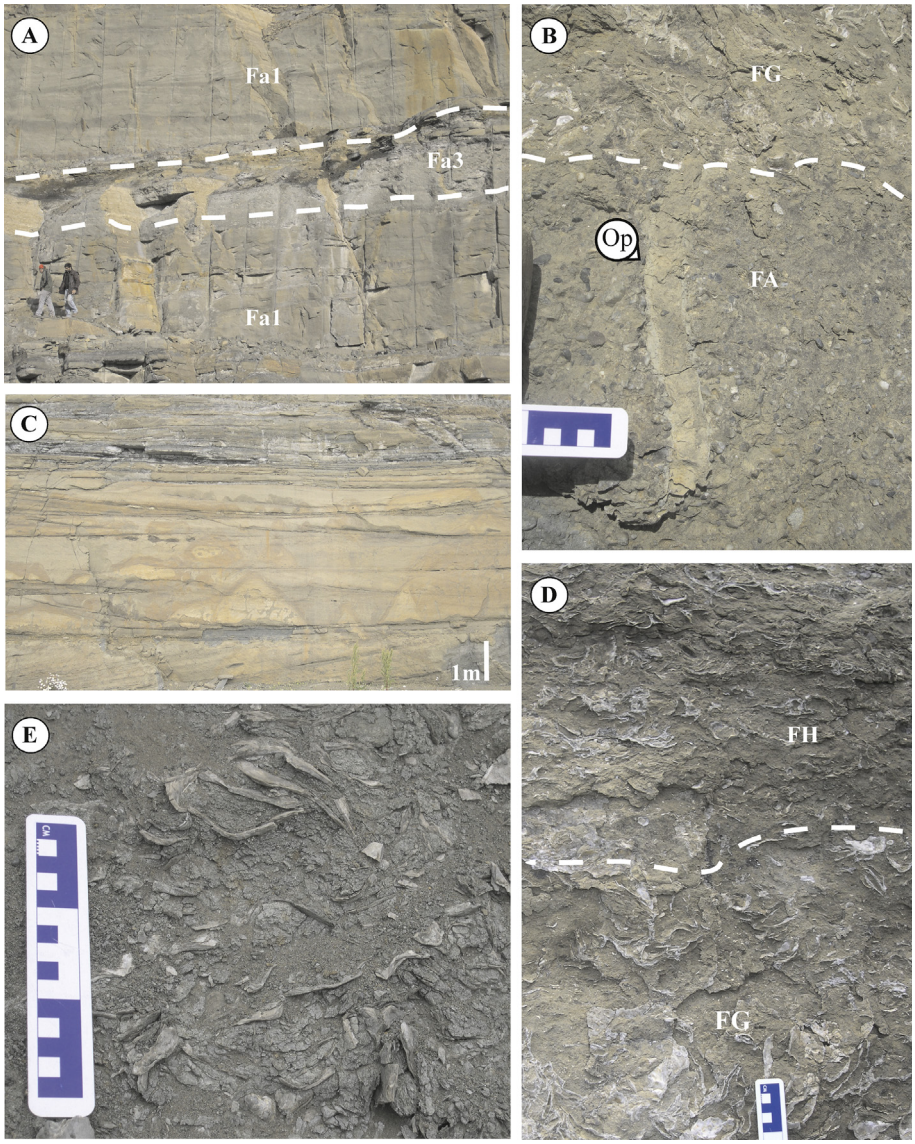

Fig. 3. The outer estuarine facies associations. A) Fa1 and Fa3 include subtidal channel thalweg conglomerates, subtidal channel sandstones and *Crassostrea* reef. B) Transition between trough cross-stratified conglomerate (FA) and *Crassostrea* reef (FG). Op = *Ophiomorpha* isp. C) Details of the subtidal channel sandstones (FB). D) Transition between FG (Facies with *Crassostrea* specimens in life position) and coquina ridge (Facies H). E) *Crassostrea* specimens in life position, both isolated and arranged in bunches.

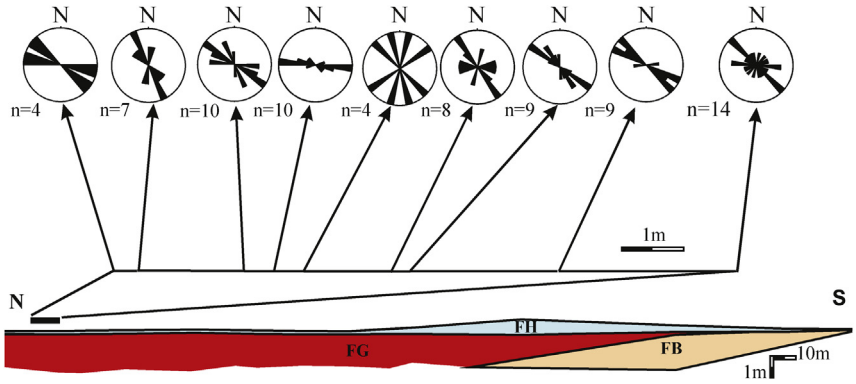

Fig. 4. Reconstruction of *Crassostrea* reef and lateral relationship of facies G (FG), facies B (FB) and facies H (FH). Commissure plane orientation of specimens found at the northern end of the Río Turbio reef.

ridge is more conspicuous at the southwestern end of the studied section.

Except for the thinner immature reefs, which presumably were still growing, the mature ones studied by Bahr and Lanier (1981) in Georgia (USA) were identical in height (1.5 m above mean low water).

In extant reefs of *Crassostrea* shells are oriented vertically, thus favoring mutual shading an important factor in keeping internal temperature within tolerable ranges (Bahr and Lanier, 1981). Many specimens are also oriented with their commissure plane aligned approximately parallel to current direction (Frey et al., 1987). Lawrence (1971) found that the anterior and posterior margins of the shell were positioned into the oncoming currents.

The measured orientations of the shells found at the northern end of the Río Turbio reef (Fig. 4) are interpreted as indicating a predominant paleocurrent direction towards the northwest. If we consider that the lateral growth of present day *Crassostrea* reefs is in a direction normal to tidal currents – so that the effectiveness of currents in transporting nutrients and removing fecal material is exploited (Grinnell, 1971) – then the largest axis of the Río Turbio reef lies in a northeastern direction. Considering the overall geometry of the reef deposits and the overlying and underlying facies we propose that the studied section is aligned normal to the large axis of the reef.

Bahr and Lanier (1981) demonstrated that *Crassostrea* reefs typically occur in three zones within a tidal channel system. The first zone is located along the concave outer banks of meander loops within the middle estuary. This area has the highest current velocity within the channel, and is characterized generally by firmer substrates that constitute a good spat settlement surface. Also, once the reef colony becomes established, these higher velocity currents circulate nutrients and remove waste more efficiently. The second zone is situated near the mouth of smaller tidal tributaries where marsh-derived nutrients are discharged into the main tidal channels. The distribution of oyster reefs in this zone is predictable and constant. Finally, the third zone is positioned at points of tidal channel confluence. Reefs in this zone are placed near the entrance of small tidal creeks that feed the larger subtidal channels. This location takes advantage of changes in energy produced by the channel convergence. During ebb tide the merging flow of the two tidal channels produces a zone of circular back-eddy formation. Turbulence associated with this process keeps the necessary nutrients for consumption in suspension and increases the probability for successful reef development. During ebb tide the tidal bar is an area subject to higher current velocity and little deposition (Bahr and Lanier, 1981). According to Bahr and Lanier's (1981) model, the Río Turbio reef – by its dimensions, geometry, and substrate lithology – would have been located in a channel-convergence area.

Laterally, 500 m north of the studied section there are deposits inferred to be equivalent to those containing the reef (Fig. 5A). The exact nature of the lateral relationship could not be established because the area separating the two exposures is covered. This section contains a coquina made up of valves of *Crassostrea* sp. (FH, Fig. 5B). The base shows continuous lenticular lamination with burrows referable to *Psilonichnus* isp. (Fig. 5C). Separated by an erosional contact overlie lenticular deposits (the base is a concave surface) comprising medium-to coarse-grained sandstones, partly conglomeratic, with up to 1.7 m thick lenses with valves of *Crassostrea* sp. Trough and planar cross-stratification were recorded. The valves show moderate to high fragmentation, packing ranges from 15% to 55%, moderate size selection, very low bioerosion, and low to very low encrustation. The general attitude is concave down, although numerous articulated valves were observed.

These deposits are interpreted as infillings of tidal channels across a tidal flat. Relating the two exposures allows a more detailed paleoenvironmental reconstruction. This includes in the outer estuary a low tidal flat crossed by tidal channels and at the junction of two of these channels grew the Río Turbio reef.

5. Discusion and conclusions

Analysis of the middle Río Turbio section shows that, as a consequence of migration and avulsion, subtidal channels eroded down into the underlying deposits of the subtidal sandbars (FA2). With stabilization of the channel system sedimentation commenced and there was deposition of the channel deposits (FA1) that include the conglomerates underlying the reef. There was a period in which these deposits after stabilization were colonized, which is supported by the presence of *Ophiomorpha* isp. This trace fossil is passively infilled by the fine-grained sand constituting the matrix of the reef. The *Ophiomorpha* shafts descend from the overlying reef deposits. Finally, once the energy within the channel system decreased conditions became favorable for the development of the *Crassostrea* reef (FG). By its dimensions, geometry, and substrate lithology the reef would have been located at the junction of two subtidal channels

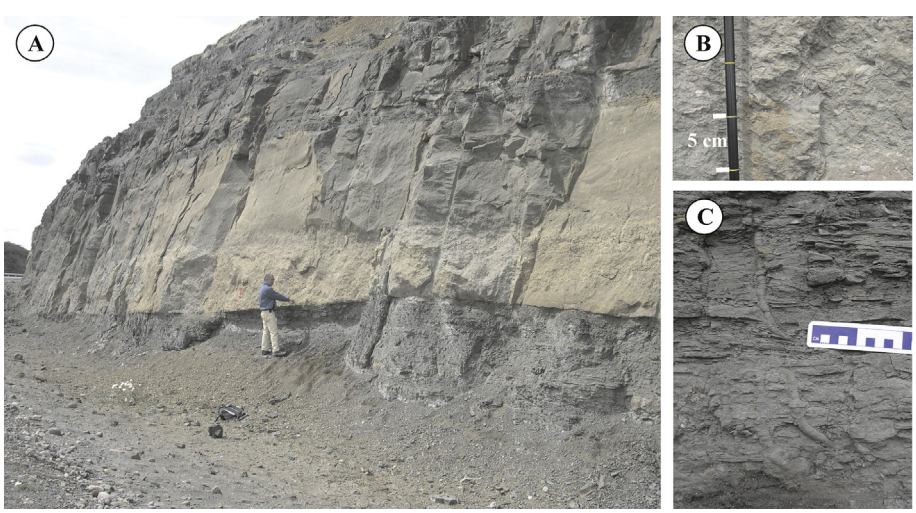

Fig. 5. Deposits inferred to be equivalent to those containing the reef. A) Medium-to coarse-grained sandstones, partly conglomeratic, with up to 1.7 m thick lens with valves of *Crassostrea* sp. B) Coquina made up of valves of *Crassostrea* sp. (FH). C) The base shows continuous lenticular lamination with burrows referable to *Psilonichnus* isp.

and may have reached phase 4 (maturity and senescence) of Bahr and Lanier (1981). The absence of encrusting and boring organisms on the valves of the oysters suggests that the reef grew in an environment subject to periodic changes in salinity. The dinocyst assemblages described by Guerstein et al. (2014) from the Upper Member of the Río Turbio Formation suggest shallow marine waters associated with coastal areas and high trophic levels, possibly related with freshwater input.

The Río Turbio reef is the earliest record of an oyster reef associated to estuarine facies in the southern hemisphere. It is also one of the few reefs of its kind known worldwide for this type of depositional environment occurring in Paleogene rocks. If –as pointed out by Camacho et al. (2000) – "*Ostrea*" *groeberi* Feruglio, 1937, a thick-shelled oyster found in the Río Turbio Formation and in rocks referable to the Man Aike Formation (exposed 150 km North from Río Turbio and equivalent to those containing the studied reef) belongs in *Crassostrea*, then thin shelled estuarine populations of *Crassostrea* and thick shelled marine populations would have coexisted during the middle Eocene of Patagonia.

The absence of records of thick-shelled species of *Crassostrea* between the Paleocene and the early Eocene (Malchus, 1990) suggests that the fully marine members of this genus may have become extinct during the Upper Cretaceous. If this hypothesis is correct then the marine thick-shelled species from the middle Eocene of North America and Patagonia would represent dispersals from previous estuarine populations.

Kirby (2001) suggested that the presence of populations of *Crassostrea* in shallow marine environments and in estuaries since the Cretaceous, points towards the fact that estuaries may have been refuges from where populations dispersed into normal marine environments several times during the Cenozoic. This ability of *Crassostrea* to colonize normal marine environments may have been possible because species of this genus show the ecophenotypic capability of producing chalky deposits when environmental conditions permit it, thus generating a rapid thickening of the shell. This innovation that began during the Mesozoic (Malchus, 1990, 1998) may be seen as an alternative strategy to avoid predators in marine environments (Kirby, 2001). In this sense, it is remarkable that the increase in abundance of thick-shelled species of *Crassostrea* from the mid-Cenozoic in Patagonia (Parras and Casadío, 2006) is coincident with the great increase in abundance of species of *Trophon*, a muricid gastropod that is one of the most conspicuous carnivores in the Atlantic shelf of the southern tip of South America from the Oligocene onwards (Griffin and Pastorino, 2005).

Acknowledgments

We thank the Agencia Nacional de Promoción Científica y Tecnológica, CONICET, Universidad Nacional de Río Negro, Universidad Nacional de La Pampa, and Natural Sciences and Engineering Research Council (NSERC) for grants to work in Patagonia.

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