PALAIOS

Emphasizing the impact of life on Earth's history

PALAIOS, 2018, v. 33, 237–255
Research Article
DOI: http://dx.doi.org/10.2110/palo.2017.096

TAPHONOMY AND PALEOECOLOGY OF LOWER CRETACEOUS OYSTER MASS OCCURRENCES FROM WEST-CENTRAL ARGENTINA AND EVOLUTIONARY PALEOECOLOGY OF GREGARIOUSNESS IN OYSTERS

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ABSTRACT: **Lower Cretaceous (lower Hauterivian) oyster mass occurrences (OMOs) dominated by the gryphaeid small oyster *Ceratostreon* from the Neuquén Basin (west-central Argentina) are analyzed in terms of taphonomy and paleoecology in order to characterize their origin, reconstruct the oyster-dominated paleocommunity, and assess their paleoenvironmental implications. A laterally extensive oyster-bearing sedimentary interval with high oyster abundance was analyzed at three localities situated along a 75 km N-S transect. Three different types of OMOs were differentiated: biogenic bioherms with dominance of encrusting life habits, biogenic autobiostromes with dominance of soft bottom recliners, and mixed sedimentologic-biogenic parabiostromes with signs of reworking. The development of these different types of OMOs indicates a high nutrient input that favored high oyster proliferation, whereas the different life habits adopted by the oysters indicate a difference in sedimentation rate throughout the studied level: reclining oysters indicate a higher sedimentation rate than cementing ones. This Lower Cretaceous study case is framed in a general context of global shift of OMOs from a Tethyan distribution during the Jurassic to a mainly eastern Pacific distribution in the Cretaceous, occupying both coastal and deep continental shelf. Also, there is a taxonomic shift from primarily gryphaeid OMOs during the Jurassic and Lower Cretaceous to primarily ostreid OMOs during the Upper Cretaceous. Cenozoic OMOs are found in marginal marine environments and are exclusively built by ostreids. An increase in predation pressure from the mid-Mesozoic onwards could have pushed OMOs to marginal marine environments where predators cannot thrive and force a taxonomic shift towards brachyhaline taxa.**

INTRODUCTION

Oysters are one of the most important bivalve groups of Recent marine benthic communities and have been since their origin in the Early Triassic (Stenzel 1971; Hautmann et al. 2017). The success of this group lies not only in high reproduction rates but also in its ability to colonize both hard and soft substrates (Seilacher et al. 1985; Machalski 1998; Kidwell and Brenchley 1994; Anderson et al. 2004), a combination that often results in the formation of oyster mass occurrences (OMOs). Particularly, when the cementing life habit dominates and the balance between recruitment of oysters and mortality rate (shell input) surpasses carbonate loss (by physical, chemical or biological erosion) these concentrations may attain vertical relief (Powell et al. 2006; Powell et al. 2012; Waldbusser et al. 2011) being viewed by many authors as true reefs (see Bahr and Lanier 1981; Anderson et al. 2004; Manley et al. 2010; Seavey et al. 2011; Garvis et al. 2015 for Recent examples, and Delecat et al. 2001; Parras and Casadío 2006; Pufahl and James 2006 for fossil examples). Studies performed on Recent OMOs have demonstrated the important ecological role they play on marine bottoms, providing habitats for other organisms and affecting turbidity and nutrient recycling by their filter feeding (Gutiérrez et al. 2003; Newell et al. 2005). Some reef-building oysters have therefore been considered ecosystem engineers (Parras and Casadío 2006; Gutiérrez et al. 2011), which highlights the impact that these OMOs may have on their surroundings and arises the query on their fossil counterparts.

The gregarious life strategy underlying biogenic OMOs did not arise until the Late Triassic, some 30 million years after the first appearance of the group. At that time, oysters appeared as framebuilders along with other bivalves (Fürsich and Hautmann 2005), and then formed virtually monospecific OMOs later (Gaździcki 1974). Earlier oyster records from the Early and Middle Triassic of up to five individuals encrusting close together on ammonoid or bivalve shell fragments are not considered here, because it cannot be assigned as a gregarious behavior held over a period of time as it is in the case of OMOs, but rather marks the initial stages of settlement (Toonen and Pawlik 2001; Hautmann and Hagdorn 2013; Hautmann et al. 2017).

Gregariousness is the settlement of larvae in response to the presence of adults, juveniles or recent conspecific recruits (Hadfield and Paul 2001). The fossil record holds many examples, not only of oysters, but of different marine invertebrates (ten Hove and van den Hurk 1993; Brett et al. 2008; Nomura and Maeda 2008). Gregariousness is generated by short dispersal and positive intraspecific density dependence (i.e., juveniles benefit from their adults to which they attach; Buss 1981; Levin 2006), and is a facultative rather than an obligatory behavior. The biogenic OMOs developed by the aggregation of hundreds of thousands of specimens represent spectacular cases of gregariousness, where environmental conditions have a dual role: inhibiting the establishment of other organisms competing with or preying on oysters on one hand and favoring the explosive abundance of oysters on the other hand (Anderson et al. 2004).

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Particularly, in the Lower Cretaceous of the Neuquén Basin, Argentina, oysters are abundant throughout the marine sedimentary rocks of the Agrio Formation, both as soft-bottom recliners and hard substrate encrusters, providing many examples of OMOs of variable geometry and dimensions (Lazo 2007). Similar OMOs have been recorded from the Lower Cretaceous of Colombia and Mexico, but only those from Mexico have been studied in detail (Guzmán 1985; Hernández-Ocaña et al. 2015). Here, we focus on a particular oyster-bearing sedimentary interval in the upper third of the Pilmatué Member of the Agrio Formation where oysters peak in abundance and a variety of concentrations are recorded at several localities.

During the Jurassic and Cretaceous, reefs underwent an important expansion globally (Höfling and Scott 2002; Leinfelder et al. 2002). Special attention has been given to sponges, corals and rudist reefs, but the role of oysters as reef builders has been largely ignored. Jurassic examples of OMOs are found exclusively in the Northern Hemisphere, primarily in European successions at Tethys' margins, with minor occurrences in Asia, comprising many species from at least two different families (Fürsich 1981; Fürsich and Oschmann 1986; Fürsich and Werner 1986; Leinfelder 1986; Hoffmann and Krobicki 1989; Poulton 1989; Andrews and Walton 1990; Delecat et al. 2001; Komatsu et al. 2002; Olivier et al. 2004; Palma et al. 2007; Zatoń and Machalski 2014; Fürsich et al. 2016). During the Early Cretaceous, OMOs distribution shifted from the Tethyan margins to the north and south-eastern Pacific margins, appearing for the first time in the southern hemisphere (Flatt 1976; Damborenea et al. 1979; Guzmán 1985; Leckie 1989; Palma and Lanés 2001; Schwarz and Howell 2005; Lazo 2007; Kietzmann et al. 2014; Hernández-Ocaña et al. 2015; this paper). Afterwards, during the Late Cretaceous, OMOs maintained their presence on the Pacific margins and reappeared on the Tethys Ocean, but they were no longer as frequent in European succession as they were during the Jurassic, appearing instead on Jordan, India and Egypt (Stephenson 1956; Chinzei 1986; Hattin 1986; Eliuk 1989; Toshimitsu et al. 1990; Pucket 1994; Shaaban et al. 1995; Abed and Sadaqah 1998; Fürsich and Pandey 1999; Videt 2003; Powell and Moh'd 2011).

This major distribution shifts can indicate major geographic shifts in ecological or environmental conditions that forced OMOs to retreat from the Northern Hemisphere, and that could help to understand the ecology of these paleocommunities.

Therefore, the objectives of the present contribution are twofold: (1) to analyze in detail Lower Cretaceous OMOs from the Agrio Formation using a combined taphonomic-paleoecological approach, and (2) frame this case study within the global OMOs context, describing and interpreting their evolutionary paleoecology throughout the Jurassic-Cretaceous transition. Regarding the first objective, our aims are to (1) clarify the origin of the OMOs from Agrio Formation; and (2) reconstruct the geographical variation in paleoenvironment along a N-S transect in the Hauterivian of the Neuquén Basin.

GEOLOGICAL SETTING OF THE AGRIO FORMATION

The Neuquén Basin is located in the Andes foothills between 32° and 40° S (Fig. 1A, 1B). The basin covers an area of over 120,000 km^2 and is represented by a narrow N-S fold-and-thrust belt mainly in the Mendoza province. In the Neuquén province the basin expands to the east to form the Neuquén Embayment (Howell et al. 2005).

During Early Jurassic to Early Cretaceous times the basin was a back-arc depocenter developed under active convergence of the western margin of South America. A well-developed volcanic arc was coeval with deposition under a rather constant thermal subsidence regime (Ramos and Folguera 2005). Paleoceanographic marine connection was towards the Pacific Ocean in the west, while the bulk of the siliciclastic supply was from the southeast corner of the basin (Legarreta and Uliana 1991).

The basin was located at the boundary between the tropical and subtropical regions during the Early Cretaceous, between 28°–36°S based on paleomagnetic data from South America (e.g., Somoza 2011), and thus it is of interest to search for the development and extension of carbonate facies and reef belts.

Lower Cretaceous marine deposits are included in the Mendoza and Bajada del Agrio groups. The Mendoza Group was deposited during the Kimmerigdian–Barremian interval, and includes, from older to younger, the Tordillo, Vaca Muerta, Mulichinco, Chachao, and Agrio formations (Leanza et al. 2005). OMOs, of variable geometry and sizes, are common in the Vaca Muerta, Mulichinco, Chachao, and Agrio formations, suggesting that oysters played an important ecological role in the Early Cretaceous seas of the Neuquén Basin. However, OMOs are usually discrete in thickness and lateral extension and alternate with highly diverse benthic assemblages pointing to cyclic environmental conditions.

The Agrio Formation, defined by Weaver (1931) in the Río Agrio section (Neuquén Province), is divided into three members: the Lower or Pilmatué Member, the Middle or Avilé Member and the Upper or Agua de la Mula Member (Leanza et al. 2005). Both the Pilmatué and Agua de la Mula members are characterized by thick, dark shale successions, typical of a marine ramp environment, with intercalated thin shell beds and sandstones (Spalletti et al. 2011). The Avilé Member corresponds to continental facies, composed mainly of eolian sandstones, which have been interpreted as an abrupt but short interruption of the marine sedimentation in the basin (Veiga et al. 2011). The studied OMOs occur in the upper third of the Pilmatué Member, associated with ammonoids belonging to the *Olcostephanus* (*O.*) *laticosta* Subzone of early Hauterivian age (Aguirre-Urreta and Rawson 2001). This subzone has been precisely correlated with the *Olcostephanus* (*Jeanotticeras*) *jeannoti* Subzone, from the West Mediterranean Province (Reboulet et al. 2014). A combined detailed ammonoid and nannofossil biostratigraphic zonation has been developed in the last decade for the Tithonian–Barremian interval in the Neuquén Basin, which has been correlated with the Western Tethyan Zonation (see Aguirre-Urreta et al. 2005 and Vennari et al. 2014). Recently, this zonation has been calibrated with a high precision CA-ID TIMS U-Pb age of 130.39 ± 0.16 Ma for the Pilmatué Member of the Agrio Formation (Aguirre-Urreta et al. 2017).

The Agrio Formation as a whole has been interpreted as a storm-dominated shallow marine environment, with mixed siliciclastic-carbonate sedimentation (Brinkmann 1994; Spalletti et al. 2001). It essentially represents a homoclinal ramp depositional system rather than a shelf, as it has high-energy facies passing into shales and lacks significant sediment gravity flow deposits or slumping structures in the deep-water facies. In the study area, the unit overlies the continental to marginal marine Mulichinco Formation (Schwarz et al. 2011) by means of an important second-order transgressive surface of regional extent (Spalletti et al. 2011). Macroinvertebrates are represented by a diverse marine benthic fauna and ammonites are preserved in calcareous nodules or variably concentrated within the shales. Intercalations of shell beds, siltstones and sandstones contain reworked marine benthic fossils, nautiloids, and ammonites. Mixed quality of preservation and different orientations of fossils characterize these deposits.

The base of the Pilmatué Member of the Agrio Formation belongs to a regional transgressive episode that flooded the entire basin from the Pacific Ocean and covered most of Mendoza and Neuquén provinces. This rapid flooding episode was followed by a prolonged period of high relative sea level. Thus, the Pilmatué Member corresponds to a second-order transgressive and highstand systems tract. Along with the underlying Mulichinco Formation, which is a second-order lowstand systems tract, forms a complete second-order depositional sequence (Schwarz et al. 2011).

Lithofacies in the Pilmatué Member are characteristically arranged in shallowing-upward successions, which reflect a supply-dominated regime

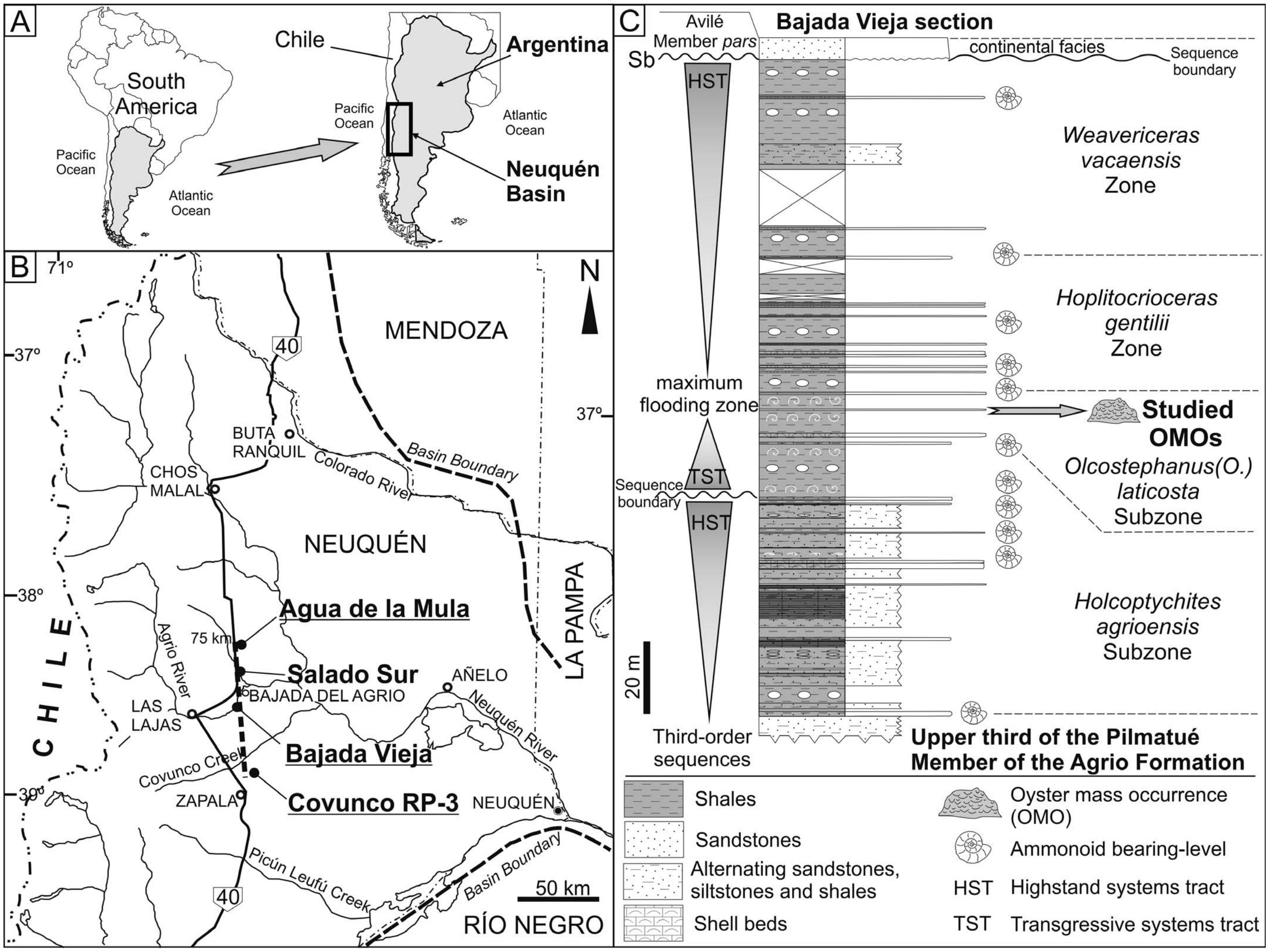

FIG. 1.—Schematic map of the study area and stratigraphic position of the studies oyster mass accumulations (OMOs). **A**) Regional map and map of Argentina showing the location of the study area. **B**) Map of the Neuquén province showing the location of the fossil localities, situated along a N-S 75 km transect. OMOs in the Salado Sur locality were recorded in previous works (Lazo 2007). Only qualitative observations were made there. **C**) Lithological column of the lower Hauterivian Upper third of the Pilmatué Member of the Agrio Formation at Bajada Vieja section showing the position of the studied OMO's along with the ammonoid biostratigraphy based on Aguirre-Urreta and Rawson (2001). Third order depositional sequences are also shown (modified from Lazo 2007).

where rate and type of sediment supply exceeds the rate of accommodation-space creation and sediment dispersal. Sediments are preserved as regressive deposits, including third- and fourth-order transgressive-regressive (T-R) cycles (see Lazo 2007, fig. 1C; Spalletti et al. 2011).

SEDIMENTOLOGICAL CONTEXT OF THE STUDIED OMOs

The OMOs were recorded from a sedimentary interval that can be laterally correlated, by associated olcostephanid ammonoids, but also by the high oyster abundance recorded, that is temporally restricted to one ammonoid zone (Fig. 1C). In this interval, the composition of benthic assemblages is greatly reduced in comparison to the general diversity and richness observed throughout the Pilmatué Member (Aguirre-Urreta et al. 2011). Only regular echinoid spines, small gastropods (*Exelissa* sp.) and scarce fragments of bivalves (astartids, pectinids, mytilids, and arcoids) were recorded within the OMO-bearing interval. This composition is in contrast to the underlying and overlying levels, where oysters are only occasionally found and a more diverse benthic fauna reappears (Fig. 2).

The localities Agua de la Mula (in the north), Bajada Vieja (central location) and Covunco-RP3 (in the south) were selected because of their excellent OMO exposures (Fig. 1B). They cover a 75 km-long N-S transect, Agua de la Mula occupying a more distal position on the marine ramp than Covunco-RP3, which is closest to the continental runoff coming from the southeast margin of the basin (Fig. 1B). At the Salado Sur section, placed geographically between Agua de la Mula and Bajada Vieja, additional qualitative observations were made on the OMO-bearing interval (Fig. 1B).

Detailed sedimentological sections of the OMO-bearing interval were measured at Agua de la Mula and Bajada Vieja, while qualitative taphonomic and paleoecological observations were additionally made at Covunco-RP3.The measured sections encompass the complete *Olcostephanus* (*O.*) *laticosta* ammonoid Subzone, from its first occurrence to the first occurrence of the index ammonoid of the subsequent *Hoplitocrioceras gentilii* Zone.

The OMOs at Agua de la Mula and Bajada Vieja sections are primarily immersed in dark-gray laminated shales, which are the most common and thickest lithofacies in the Agrio Formation, ranging from 2 to 60 m in

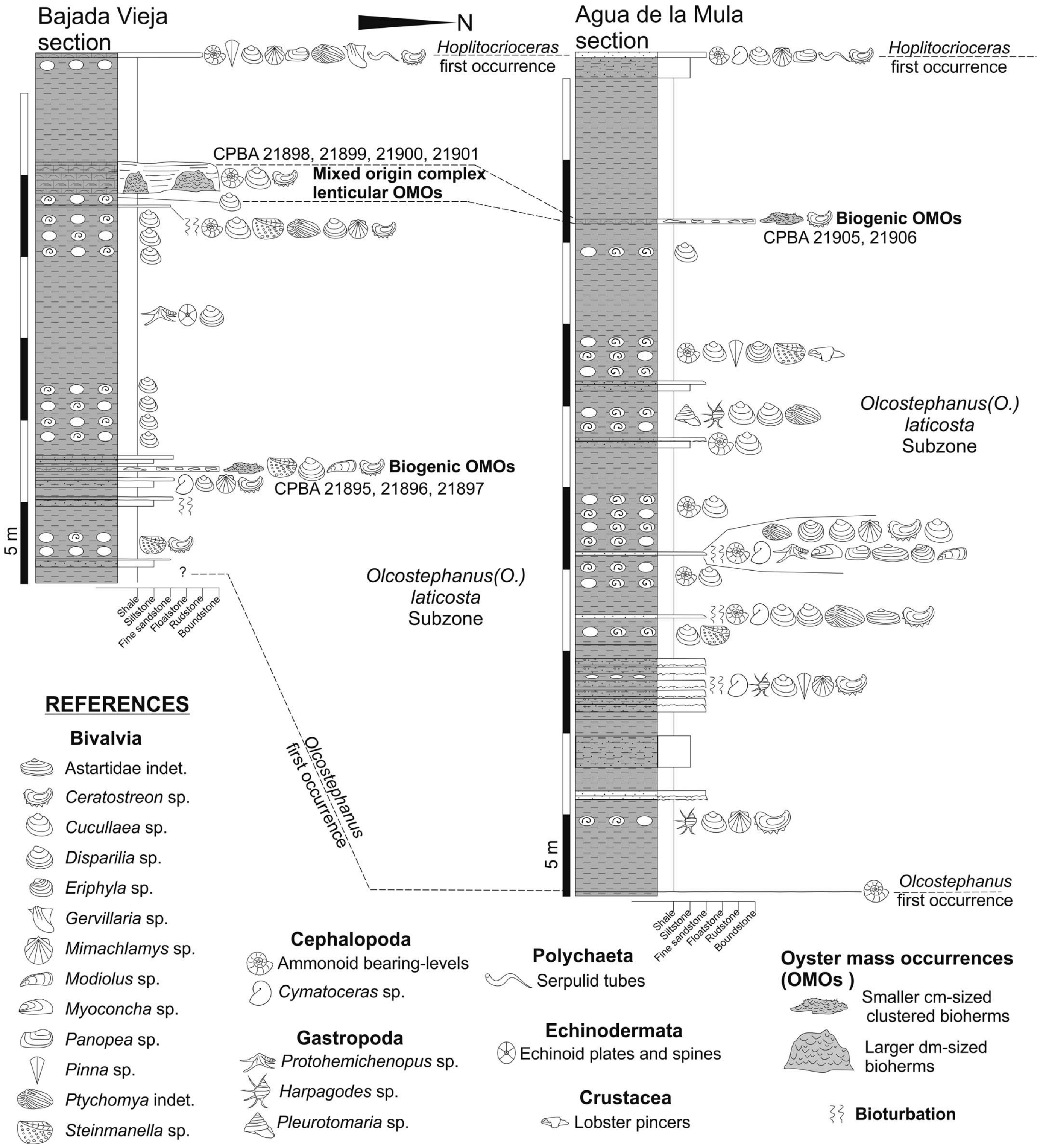

FIG. 2.—Sections of the proximal outer ramp deposits belonging to the *Olcostephanus* (*O.*) *laticosta* Subzone of the Pilmatué Member of Agrio Formation, encompassing the studied OMOs measured at Bajada Vieja and Agua de la Mula sections. Note differences in thickness and in the recorded OMOs.

thickness (Figs. 1C, 2). Within the Agrio Formation, dark-gray shales lithofacies with high organic matter content occur at the base of most shallowing-upward cycles and may alternate with thin shell beds, siltstones, or fine-grained sandstones. Levels of cm-sized precompactional calcareous nodules are usually present, which have been associated to pauses in sedimentation and dysaerobic pore-water conditions in sediment, because the anoxic decomposition of organic carbon produces bicarbonate ion which reacts with calcium from pore water, generating authigenic carbonates (Allison 1988; Sellés-Martínez 1996; Marshall and Pirrie 2013). In Agua de la Mula and Bajada Vieja, the shales underlying the

OMOs are massive to laminated, contain calcareous nodular levels and infaunal and epifaunal bivalves and ammonites (Fig. 2), whereas overlying shales are massive to laminated, with no distinct fauna. In these sections, the abundance and thickness of shale and the occasional intercalations of distal storms beds (see Burchette and Wright 1992; Lazo et al. 2005) indicate that they can be interpreted as fair-weather suspension fallout deposits of the mid to proximal-outer ramp.

In terms of sequence stratigraphy the OMOs occur approximately near the maximum flooding interval of the last third-order transgressive-regressive cycle of the Pilmatué Member (Fig. 1C).

At Covunco RP-3, OMOs are embedded in yellowish gray argillaceous marls forming a tabular bed up to 6 m thick and of at least 1 km in lateral extension. Bioturbation occurs throughout, although it is difficult to identify individual traces or producers due to weathering. The sedimentological context differs from other sections. The environment can be interpreted as a slightly shallower, more protected and oxygenated marine bay where marl settled under quiet water conditions, and which was repeatedly colonized by abundant, solitary oysters. This inference is supported by palynological studies performed in this particular area of the basin that indicate that the environment ranged from marine to coastal and even terrestrial (Peralta and Volkheimer 1997, 2000).

MATERIAL

The OMOs are composed by one small oyster taxon (maximum height: ~ 31 mm) with a keeled, variably ribbed, convex left valve and a slightly concave to flat right valve (Fig. 3). Internally, commissural chomata can be recognized along the margins of both valves (Fig. 3C). This combination of morphological characters places this oyster within the genus *Ceratostreon* Bayle 1878 (Order Ostreoida, Family Gryphaeidae, Subfamily Exogyrinae). *Ceratostreon* is a pandemic genus, with a stratigraphic range restricted to the Cretaceous. Lower Cretaceous records include Argentina, France, Germany, U.S.A., Poland, Spain, Mexico, Colombia, and Venezuela (Goldfuss 1833; Koch and Dunker 1837; d'Orbigny 1842; Matheron 1842; Roemer 1852; Cragin 1893; Stoyanow 1949; Alencáster 1956; Pugaczewska 1975; Calzada Badía and Botero Arango 1979), whereas Upper Cretaceous records are restricted to the U.S.A (Cragin 1893). Although some Lower Cretaceous records are from Chile, further information is required to support them (Rubilar 2008). Germany holds a single Cretaceous record, but with no further precision (Goldfuss 1833). Records from Argentina are restricted to the Mendoza Group in the Neuquén Basin (Vaca Muerta, Mulichinco, Chachao, and Agrio formations; Damborenea et al. 1979; Doyle et al. 2005; Schwarz and Howell 2005; Lazo 2007, among others). These oysters had an encrusting life habit (i.e., cemented to hard substrate) throughout lifetime (e.g., encrusting other oysters or other hard substrates such as mollusk shells), or overgrowing its attachment substrate, they acquire a reclining life habit (i.e., free-lying on soft substrate).

The material has been deposited in the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales (acronym CPBA), Universidad de Buenos Aires, Buenos Aires, Argentina. A total of 248 specimens from two oyster beds (see Fig. 2 for the exact stratigraphic position) at Bajada Vieja (right valves: CPBA 21895.1–11 and 21898.1–33; left valves: CPBA 21896.1–94 and 21899.1–51; articulated valves: CPBA 21897.1–46 and 21900.1–13), 289 from Covunco-RP3 (right valves: CPBA 21902.1–177; left valves: CPBA 21903.1–63; articulated valves: CPBA 21904.1–49), and 17 from Agua de la Mula (CPBA21905.1–17). Polished cross-sections of bioherms (CPBA 21901.3–5 and CPBA 21906.1) were made in order to analyze the biofabric, including close-packing, orientation, disarticulation, and sedimentary infill of shells.

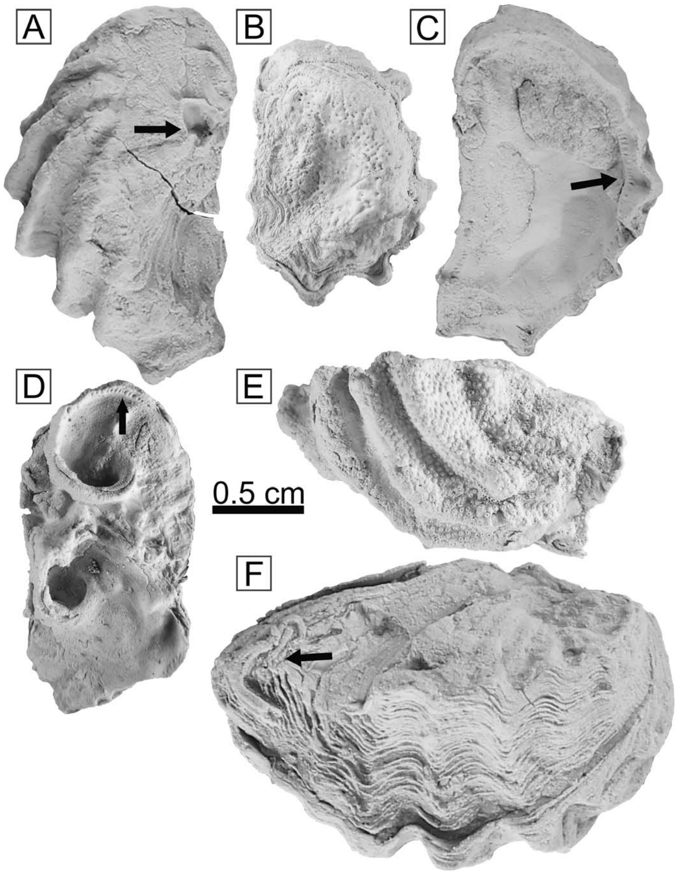

FIG. 3.—Oyster *Ceratostreon* sp. **A**) Lateral view of left valve; CPBA 21896.1. Black arrow indicates attachment area. **B**) Right lateral view of articulated specimen with *Entobia* isp. trace; CPBA 21904.3. **C**) Internal view of left valve; CPBA 21896.3. Black arrow indicates the commissural chomata. **D**) Lateral view of right valve with external attached oyster juveniles. Black arrow indicates the juvenile's chomata; CPBA 21902.1. **E**) Anterior view of left valve profusely covered by *'Berenicea'* sp.; CPBA 21904.2. **F**) Anterior view of articulated specimen; CPBA 21897.4. Black arrow indicates encrusting serpulids on right valve. Catalogue numbers refer to differently preserved specimens from different localities (i.e., left or right valve, articulated specimens and fragments of bioherms). Suffixes within a given catalogue number indicates the number of a particular specimen.

METHODS

Several terms have been used when describing oyster-rich deposits, referring to highly disparate oyster concentrations, both in dimension and geometry (e.g., "bank" in Flatt (1976); "bioherm" in Leckie 1989; "reef" in Pucket (1994), Toshimitsu et al. (1990) and Garvis et al. (2015); "patch reefs" in Delecat et al. (2001); "buildup" in Hoffman and Krobicki (1989) and Pufahl and James (2006). In this paper, the term "oyster mass occurrence" (OMO) is used in broad sense, referring to large concentrations of oysters, regardless of close-packing of shells, geometry, thickness, and genesis (Fig. 4). The classification established by Cumings and Shrock (1928) and Cumings (1932) and later reviewed by Kershaw (1994) was followed. Therefore, the term bioherm refers to "a dome-like, lens-like or other circumscribed mass built exclusively or mainly by sedentary organisms and enclosed in normal rock of different lithological character" (Cumings and Shrock 1928, p. 599). In contrast, the term biostrome refers to "distinctly bedded structures that do not swell into lens-like or reef-like form but (. . .) consist mainly of the remains of organisms" (Cumings 1932, p. 334). The latter term was broadened by Kershaw (1994) to include auto-, para-, autopara- and allobiostromes, for concentrations ranging from a fully

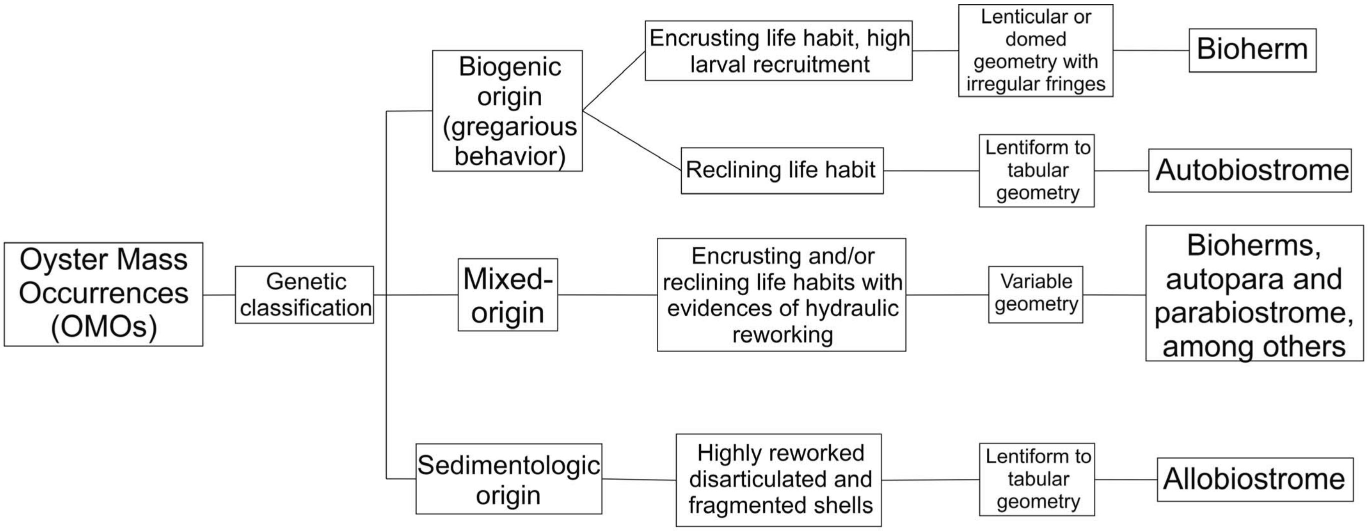

FIG. 4.—Diagram showing the proposed nomenclature of OMOs according to origin and geometry (modified from Cumings and Shrock 1928; Cumings 1932; Kidwell et al. 1986; Kershaw 1994).

biogenic origin to a fully sedimentologic and allochthonous one. Considering these definitions, bioherms point to an intrinsic biogenic origin whereas the different subtypes of biostromes range from intrinsic biogenic to a sedimentologic origin as defined by Kidwell et al. (1986) (Fig. 4).

Taphonomic Analysis.—OMOs were analyzed taking into account several sedimentological, stratigraphic, taphonomic, and paleontological features (Table 1) following the criteria established by Kidwell et al. (1986), Kidwell and Bosence (1991) and Kidwell and Holland (1991).

Table 1.—*Sedimentological, stratigraphic, taphonomic, and paleontological features of each taphofacies.*

	Bioherms	Parabiostromes	Autobiostrome
Sedimentological features			
Close-Packing of shells	Dense	Dense	Loose
Size Sorting	Poorly sorted	Poorly sorted	Poorly sorted
Type of matrix	Dark gray shales	Dark gray shales	Yellowish gray argillaceous marls
Physical sedimentary structures	Absent	Parallel lamination	Absent
Stratigraphic features			
Thickness (m)	0.1–0.85	0.04–0.2	6
Lateral extension (m)	0.25–1.3	0.15–2.5	> 1000
Geometry	Lenticular	Lentiform	Tabular
Basal contact	Sharp planar to irregular (slightly bioturbated laterally)	Sharp planar	Transitional
Top contact	Sharp domed	Sharp planar	Transitional
Taphonomic features			
Disarticulation	Low to moderate	High	High
Fragmentation	Low to moderate	High	Moderate
Abrasion	Null	Null	Null
Sedimentary infilling	Same as the host rock or absent with posterior coating of calcite cement	-	Same as the host rock
Encrustation	High	Low	Low
Orientation	Concordant to oblique, convex up and down; life position	Concordant	Concordant to oblique, convex up and down.
Paleontological features			
Richness	7	7	7
Life habit	Encrusting	-	Reclining
Age range	Adults and juveniles	-	Adults and juveniles
Taxonomic composition	Oyster dominated plus polychaeta (*Parsimonia antiquata* (Sowerby 1829) and *Propomatoceros* sp.) and bryoozoan ('*Berenicea*' sp.) encrusters, echinoids and gastropods (*Exelissa* sp.). Ichnological evidence of clionid sponges (*Entobia* isp.)	Abundant fragmented oyster shells, rare astartid, pectinid, mytilid, arcoid, serpulid tubes and echinoid spines fragments.	Oyster dominated plus polychaeta (*P. antiquata* and *Propomatoceros* sp.) and bryoozoan ('*Berenicea*' sp.) encrusters, echinoids and rare *Cucullaea* Lamarck 1801. Ichnological evidence of clionid sponges (*Entobia* isp.)

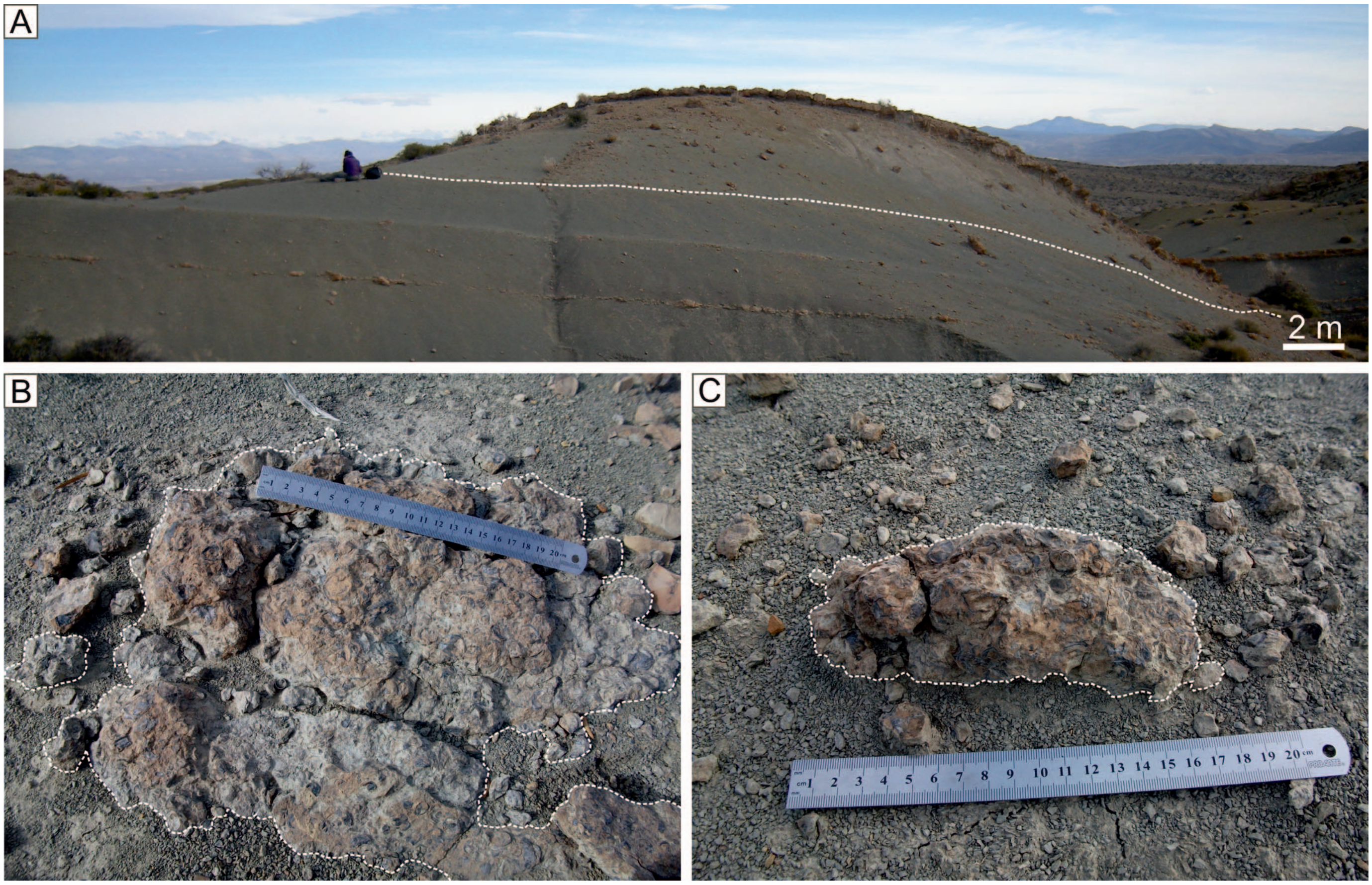

FIG. 5.—OMOs at Agua de la Mula. **A**) General view. Dotted line indicates the base of the OMO bearing level. **B**, **C**) Cross-section of two biogenic OMOs belonging to the bioherm taphofacies. Note the surrounding matrix composed of dark-gray shales.

OMOs from Agua de la Mula consist of small, scattered cm-sized bioherms and 10 were selected for study (Fig. 5). In Bajada Vieja the observations were made mainly on an internally complex lenticular OMO up to 2 m of maximum thickness and 35 m lateral extension (Fig. 6A, 6B), but also on its laterally adjacent smaller oyster bioherms (Fig. 6F). A total of 12 survey stations were investigated along strike including the complex lenticular OMO and lateral smaller, decimeter-width ones. OMOs from underlying levels were sampled for taxonomic purposes (Fig. 2). In Covunco-RP3 observations were made on a tabular, 6-m thick and over 1-km wide OMO (Fig. 7A). Data were gathered at five different survey stations, separated ~ 100 m from each other.

Sedimentological features were evaluated qualitatively and included the degree of packing of shells, size sorting, type of matrix, and physical sedimentary structures (such as planar or cross-stratification/lamination).

Taphonomic alterations were described semi-quantitatively at each survey station according to three categories; low ($\leq$ 33%), moderate (between 33–66%) or high ($\geq$ 66%). Fragmentation, disarticulation, and shell abrasion were thus considered as low, moderate, or high when $\leq$ 33%, 33%–66% and $\geq$ 66% of the valves observed in a given station were fragmented, disarticulated, or abraded respectively.

Encrustation was considered to be high when oysters formed rigid frameworks, and low when encrustation (either oyster on oyster, or involving other encrusters on oysters) was present but no framework was built. Cross-sectional orientation was observed at Agua de la Mula and Bajada Vieja, and in plan-view in Covunco-RP3 due to outcrop condition. In cross-sections, orientation was determined as “life position” when articulated specimens were found preserved and in concordant position or, when they were forming bioherms. Disarticulated valves were determined as convex-up or down. The orientation of valves was determined as concordant, oblique or vertical to bedding. The sedimentary infilling was evaluated both in the field and in the laboratory through the examination of polished slabs of bioherms.

Paleontologic features included the following: life habit, ontogenic age range, taxonomic richness, and taxonomic composition. Life habit was determined as encrusting when oysters were found attached (i.e., cemented) to any hard substrate or, if detached, when the length of the attachment area extended through half of the oyster’s total height or more. This is supported by previous studies that indicate that *Ceratostreon* attached by almost the whole surface of their left valves (Luci 2010). When the length of the attachment involved less than half the surface of the left valve, the oyster was considered a soft-bottom recliner (i.e., free lying). Age range was determined according to height: valves $\leq$ 10 mm in height represent juveniles and valves $>$ 10 mm represent adults, taking into account that these oysters very rarely exceed 3 cm in height (see Studied Materials). Taxonomic richness of the associated fauna was measured at the generic level.

Analysis of the Encrusting and Boring Fauna.—In order to further characterize the paleoecological context of biogenic OMOs, the encrusting and boring community of oysters was analyzed externally and internally on disarticulated right and left oyster valves and externally on articulated ones. This was performed only on biogenic OMOs (bioherms and autobiostromes) because, unlike parabiostromes, they maintain a biologic signal.

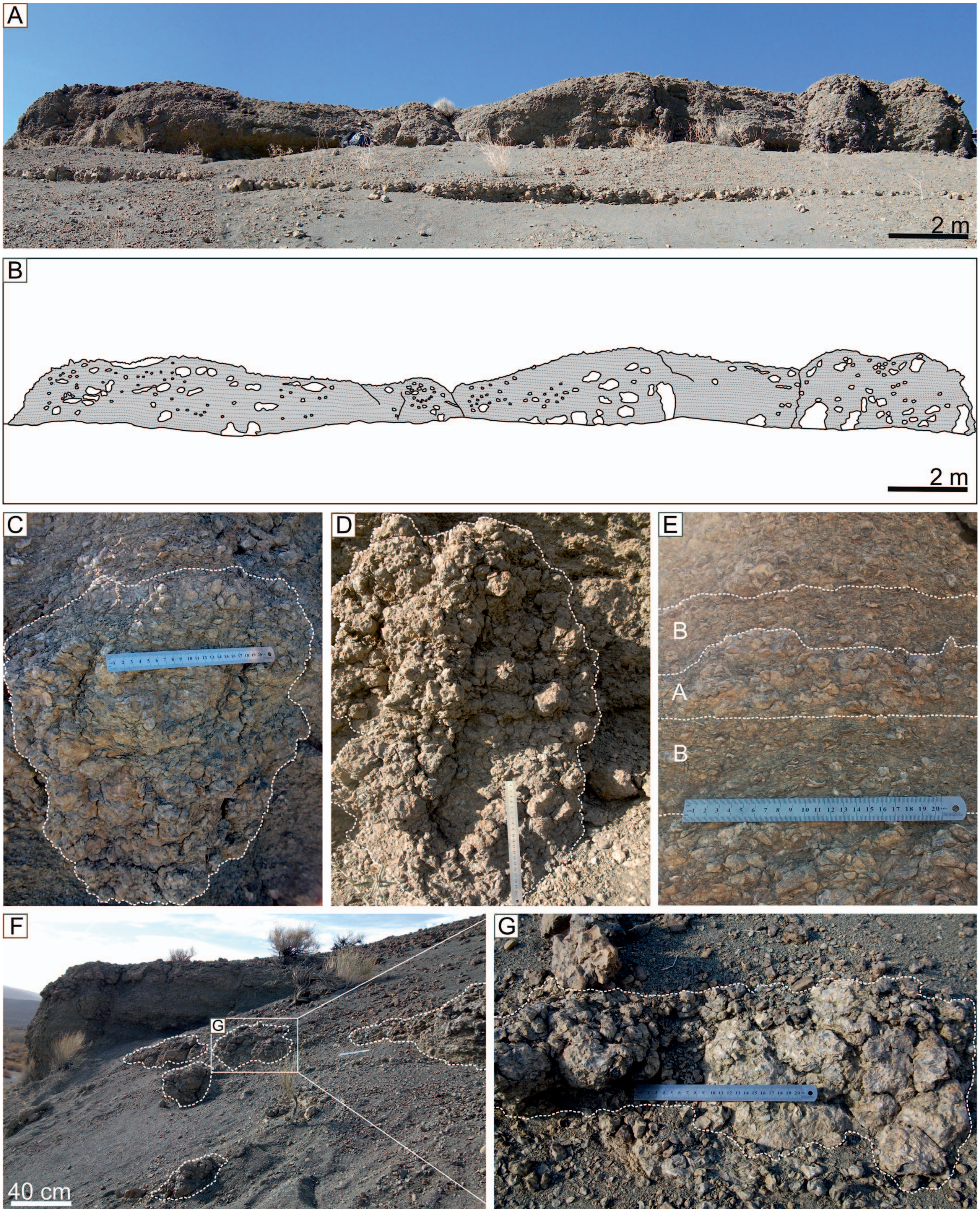

FIG. 6.—OMOs at Bajada Vieja. **A**) General view of the 35 m-thick, mixed-origin, complex, lenticular OMO. **B**) Schematic drawing of the mixed-origin, complex lenticular OMO showing the alternation of bioherm and parabiostrome taphofacies. **C**) Cross-section of a bioherm (dotted line) found within the mixed-origin, complex, lenticular

FIG. 7.—OMO at Covunco-RP3. **A**) Part of the biogenic, 1 km-wide OMO corresponding to the autobiostrome taphofacies. **B**) Detail of the autobiostromal OMO. Note the small clusters (white arrows) and the high proportion of solitary reclining individuals (orange arrows). **C**) Detail of the autobiostromal OMO. Note the high degree of disarticulation and the convex-up and -down orientations of shells.

Firstly, the proportion of valves bearing a given encruster or borer taxon over the total of valves presenting at least a single colonizing taxon was calculated. Given the different life habits adopted (encrusting in bioherms and reclining in autobiostromes), only juvenile oysters and not adults were counted as encrusters to standardize and compare results. Due to the obligatory cementation oysters attain as juveniles, by excluding adults we can separate the effect of the differential life habits. The sponge boring *Entobia* isp. was recorded as presence/absence per valve. Secondly, either a Fisher or Chi-square test (as required by the samples) was performed to compare the amount of encrusted and/or bioeroded valves among biogenic OMOs. This was performed separately for disarticulated left and right valves, both internally and externally and for articulated valves, externally. Finally, an analysis of deviance (see a similar application of this method in Everitt and Hothorn 2006) was carried out in order to compare the mean number of encrusters per shell (total amount of encrusters divided by the total amount of valves per OMO) between bioherms and autobiostromes. Both the internal and external surfaces of right and left disarticulated valves and external surfaces of articulated valves were tested. The statistical analyses were performed with R software (v.3.1.3). A total of 97 specimens were analyzed from bioherms (Bajada Vieja locality) and 289 from autobiostroms (Covunco-RP3 locality). Agua de la Mula was excluded from comparisons because isolated oysters were difficult to sample from the small-sized more consolidated bioherms present.

Some methodological considerations should be made. Oysters included in bioherms are more difficult to inspect and the majority are inaccessible, except for polished cross-sections. In contrast, oysters with reclining life habits can be inspected three-dimensionally. Other issues arise when considering some paleoecological and taphonomic restrains. On the paleoecological side, the adoption of an encrusting life habit in combination with a gregarious behavior generates a smaller surface available for other encrusters or bioeroders to colonize. On the taphonomic side, bioherms are less susceptible to reworking, especially by bioturbation, so oysters are less prone to be removed, overturned and fully encrusted and bioeroded. These methodological issues are inescapable but they will be taken into consideration when analyzing the results.

←

OMO. Note its vaulted morphology and zigzagging lateral flanks. **D**) Cross-section of a bioherm (dotted line) found at the base of the mixed-origin complex lenticular OMO. Note its irregular flanks and remarkable height. **E**) Detail of cross-section showing the alternation of taphofacies A (A, bioherms) and taphofacies B (B, parabiostromes) within the mixed-origin complex lenticular OMO. Within the parabiostrome taphofacies (B), note the parallel lamination formed by the alternation of shell pavements and millimeter thick dark-gray shales. **F**) Lateral view of the mixed-origin complex lenticular OMO. Note the occurrence of taphofacies A (bioherms) within the dark-gray shale matrix. **G**) Cross-section of a biogenic OMO of the bioherm taphofacies. Note the surrounding dark-gray shale matrix.

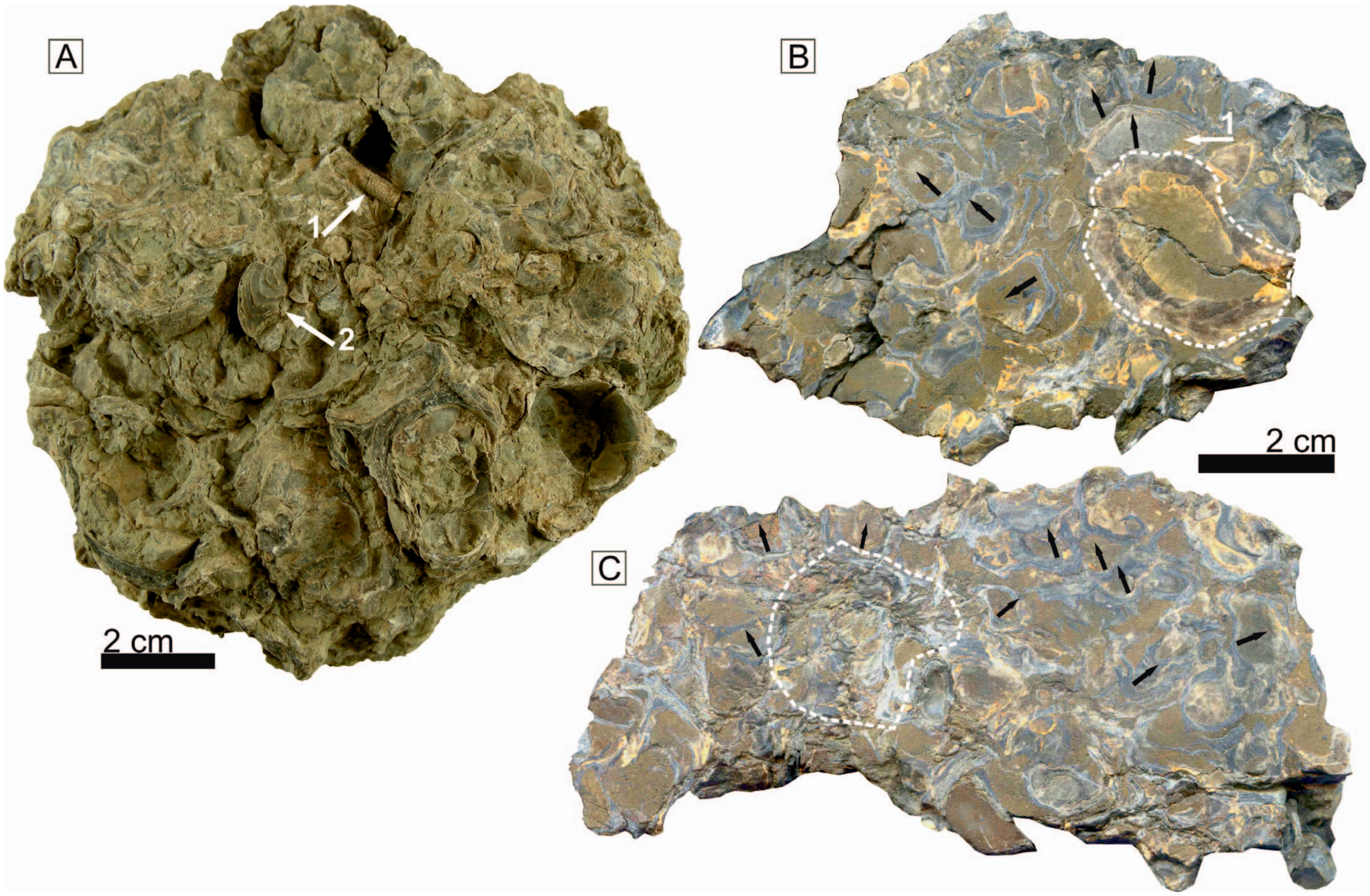

FIG. 8.—Oyster bioherms at Bajada Vieja. **A**) General view of a fragment of bioherm; CPBA 21901.1. Note the regular echinoid spine (arrow 1) and the right valve fragment (arrow 2) filling interstices between encrusting oysters. **B**) Polished cross-section of a bioherm fragment; CPBA 21901.5. Note the nucleus consisting of an articulated unidentified bivalve (dotted line) and granular carbonate infilling in one of the encrusting oysters (white arrow 1). **C**) Polished cross-section of a bioherm fragment; CPBA 21901.4. Note the nucleus consisting of a small aggregate of oysters (dotted line). Black arrows show the orientation of the concavity of left or articulated valves.

TAPHONOMIC ANALYSIS RESULTS

Taphofacies A: Bioherms

Description.—Bioherms are densely packed, poorly sorted biogenic OMOs and range in size from small, dm-scale, lenticular bioherms to large, meter-scale irregular bioherms, embedded in dark-gray shales or in close association with taphofacies B (parabiostromes) (Table 1). Larger bioherms (up to 1.3 m wide and 85 cm thick) are exclusively embedded in taphofacies B and show vaulted tops and irregular zigzagging flanks which grade laterally into shell debris (Fig. 6C, 6D). Smaller bioherms (up to 80 cm wide and 15 cm thick) are embedded in dark-gray shales and have lenticular geometries (Figs. 5B, 5C, 6F, 6G). Basal contacts are sharp and in some cases slightly bioturbated laterally. Fragmentation and disarticulation are low to moderate. No signs of abrasion are present. Oysters comprise both juveniles and adults. The superficial layers of the bioherms consist mostly of disarticulated oysters, whereas the internal layers bear a greater proportion of articulated specimens (Fig. 8). Encrustation is high given the encrusting life habit of the oysters, encrusting each other. Entrapped fine-grained carbonate matrix is common within the bioherms, filling interstitial spaces between oysters and including small dispersed gastropods (*Exelissa* sp.), isolated regular echinoid spines and fragments of oysters (Fig. 8A). Both articulated valves and single left valves are likewise filled with the same dark-gray shales as the host rock (Fig. 8B, 8C), but the internal cavity is filled by granular calcite in some articulated specimens (Fig. 8B.1). Orientation in cross-section is concordant or oblique to bedding; articulated specimens are in life position and disarticulated left valves are oriented convex-down. Only some disarticulated valves within the bioherms are oriented convex-up. An inner nucleus is observed in some of the bioherms, composed by a few oyster specimens or other bivalves. These were recognized internally in the polished cross-sections following the orientation of articulated, cemented valves (Fig. 8C). The right/left valves ratio was 0.74, indicating that the proportion of left valves was higher in this taphofacies. Oysters were attached with almost their whole length mainly to other oysters, although some were attached to the regular echinoid spines immersed in the bioherms.

Occurrence.—Bajada Vieja and Agua de la Mula localities (Figs. 5, 6). In Bajada Vieja, two bioherm morphologies can be distinguished: larger, irregular bioherms, found in association with taphofacies B, forming a complex lenticular OMO (Fig. 6C–6E) and smaller, lenticular bioherms, embedded in dark-gray shales (Fig. 6F, 6G). These smaller bioherms are found laterally to the complex lenticular OMO, where taphofacies B grades to dark-gray shale matrix. In Agua de la Mula, only the smaller, lenticular bioherms occur, although there they are fewer in number and more dispersed than in Bajada Vieja.

Interpretation.—Bioherms are interpreted as resulting from gregarious settling behavior under low sedimentation rates and can be classified as intrinsic biogenic *sensu* Kidwell et al. (1986). The growth of bioherms was facilitated by successive attachment of oysters through time (persistent recruitment). The external layers of bioherms represent the later stages of their growth. Geometry and size of bioherms depended on the type of the surrounding substrate. Small lenticular bioherms developed on soft substrate (dark-gray shale at Agua de la Mula) showing restricted vertical growth. In contrast, larger and thicker bioherms formed only in association with parabiostromes (taphofacies B, at Bajada Vieja). This indicates that the poor support given by the surrounding soft substrate might have limited the vertical growth of the bioherms at Agua de la Mula. The biological activity of the oysters (i.e.filter feeding) could have favored the settlement of sediment (Tomašových et al. 2006), whereas the formation of semi-open shelter cavities between oyster shells could have facilitated early cementation, providing extra support and enhancing preservation potential of shelly framework (Riding 2002). The presence of gastropods and regular echinoid spines might indicate browsing activity within the bioherms.

Polished cross-sections show that an initial bioherm core can be usually identified, formed either by a small oyster clump or fragments of other larger bivalve shells. Oyster larvae would encrust these initial cores, increasing their size and forming successive layers of the bioherm, providing larger hard surfaces for further encrustation. This process would generate a somewhat radial growth of the bioherm, resulting in a vaulted geometry. Also, the presence of granular calcite infilling in some articulated valves indicates that they might have been buried quickly, or overgrown by other oysters, remaining articulated and empty for posterior calcite cement development. This taphofacies comprises biogenic OMOs, both in Agua de la Mula and Bajada Vieja. Additionally, it forms a mixed-origin, complex, lenticular OMO in Bajada Vieja, where bioherms are interbedded and embedded in taphofacies B.

Taphofacies B: Parabiostromes

Description.—Oyster parabiostromes consist of densely packed, poorly sorted shell pavements alternating with millimeter thick dark-gray shale layers forming lentiform beds up to 2.5 m of lateral extension (Fig. 6E, Table 1). Thickness is very variable, ranging from 4 to 20 cm. Basal and top contacts are sharp. This taphofacies is embedding taphofacies A (bioherms). The degree of taphonomic alteration is high, especially fragmentation and disarticulation. Shell fragments (ranging from 0.5–2 cm) in cross-section are oriented concordant to bedding, both convex up and down, forming layers with parallel lamination (Fig. 6E, taphofacies B). Encrustation is low and abrasion is absent. No sedimentary infilling is recorded given that no articulated valves were found. Oysters dominate in abundance but fragments of astartid, pectinid, mytilid, and arcoid bivalves, as well as fragmented serpulid tubes and regular echinoid spines are present (Table 1). The right/left valves ratio was 5.4 which indicate that this taphofacies is enriched in right valves.

Occurrence.—This taphofacies is only found in Bajada Vieja, in close association to Taphofacies A (Fig. 6B, 6E). Remarkably, the combination of both taphofacies results in a 35-m wide and 2-m thick complex, lenticular OMO which stands out in an otherwise monotonous shale interval.

Interpretation.—Taphofacies B corresponds to skeletal concentrations formed through sediment reworking of hard parts and can be classified as sedimentologic in origin *sensu* Kidwell et al. (1986) alternating with low-energy fall-out deposits. Shell fragments attained hydrodynamically stable orientations during higher energy periods (episodic storms) that alternated with lower energy periods during which suspension fallout of shales took place (Allen 1984). Fragments of bivalves, regular echinoids spines and serpulids are probably parautochtonous. The higher proportion of right valves could have been caused by the disarticulation of oysters initially forming in the surficial layers of the bioherms, with the left valves remaining attached to the hard substrate and the right ones being deposited nearby.

Taphofacies C: Autobiostromes

Description.—This taphofacies is characterized by a predominance of loosely packed, poorly sorted reclining oyster specimens embedded in yellowish gray argillaceous marl, forming a nearly 1-km long, 6-m thick tabular bed with transitional upper and lower contacts (Fig. 7B, 7C, Table 1). Although some small oyster clusters are present (up to 5 cm wide), these are composed of very few individuals. Fragmentation is moderate, whereas disarticulation is high. Abrasion is absent and encrustation, low. Both articulated valves and single left valves are filled with the same yellowish gray argillaceous marl as the host rock. Some individuals are preserved in life position and disarticulated valves are found concordant or slightly oblique to bedding, both convex-up and -down. Oyster individuals comprise both juveniles and adults. Besides the oysters, rare individuals of *Cucullaea* sp. occur. The right/left valves ratio was 2.81, indicating that this taphofacies is enriched in right valves. Although attachment areas were mostly indiscernible, the cases where they were noticeable indicate that oysters attached mainly to other oysters and rarely to undetermined bivalve fragments.

Occurrence.—The taphofacies is found exclusively in Covunco-RP3 (Fig. 7). Although oysters were unable to form bioherms, they occurred in great abundance.

Interpretation.—The main characteristics of this taphofacies point to a biogenic origin, where the reclining solitary life habit predominated over the encrusting one. There was a high proliferation of oysters, similar to the case of Bajada Vieja, but without the development of gregarious bioherms by self-recruitment and encrustation. The initial attachment of the larvae occurred on fine-grained shell debris, acquiring later a reclining life habit on soft muddy bottoms. Although disarticulation is high and fragmentation moderate, there are no signs of sediment reworking. Hence, these relatively high taphonomic indices might be accounted for either high bioturbation or some degree of sediment reworking by storm events that was obliterated by subsequent bioturbation. This taphofacies constitutes a biogenic OMO (Fig. 4).

Analysis of the Encrusting and Boring Fauna

Bioherms and autobiostromes are characterized by similar encrusting and boring taxa, though in different proportions. A total of four encrusting taxa are recorded: juvenile oysters, cyclostome bryozoans ('*Berenicea*' sp., Fig. 3E) and serpulids (*Parsimonia antiquata* (Sowerby 1829) and *Propomatoceros* sp., Fig. 3D). In addition, the ichnotaxon *Entobia* isp. is also common (Fig. 3B). Although on both OMOs juvenile oysters are dominant (64 and 48% of the sclerobiont fauna, respectively), the abundance of juvenile oysters relative to all sclerobionts is significantly higher within bioherms (64%) than in autobiostromes (48%). In bioherms, juvenile oysters are followed in abundance by *Entobia* isp. (22%), serpulids, and bryozoans (7% each). Within autobiostromes, bryozoans are more abundant (23%) than within bioherms, sharing the second place after oysters with *Entobia* isp., which holds the same proportion as that observed in Bajada Vieja (22%). Serpulids are least abundant (7%) (Table 2).

In bioherms, internal encrustation and/or bioerosion in disarticulated left and right valves is almost nil (1.2% of analyzed valves were encrusted and/or bioeroded internally), whereas external colonization is considerably higher (21.4%). Within parabiostromes, 17.7% of the interior of disarticulated left and right valves are encrustated and/or bioeroded in contrast to 57.65% of the exterior surfaces. The proportion of internal

TABLE 2.—*Encrustation and bioerosion of oysters at Bajada Vieja and Covunco-RP3.*

		Taphofacies A: Bioherms	Taphofacies C: Autobiostromes
% colonized shells		23.71%	64.36%
Mean scler./shell	Right valve	0.24	1.36
	Left Valve	0.25	1.21
	Articulated valves	0.54	1.08
Maximum number of sclerobionts		2	7
Richness		5	5
Sclerobionts proportion	*Ceratostreon* sp.	18(64%)	183(48%)
	'*Berenicea*' sp.	6(22%)	89(23%)
	Entobia isp.	2(7%)	84(22%)
	Serpulids	2(7%)	26(7%)

encrustation and/or bioerosion is higher within the autobiostromes than in bioherms ($p < 0.05$ for both cases). External encrustation and/or bioerosion of disarticulated right and left valves is also higher in the autobiostromes ($p < 0.05$). This was not the case with the articulated valves, in which encrustation and/or bioerosion does not differ between bioherms and autobiostromes ($p > 0.05$). The lack of differences can be related to rapid burial of live specimens because oysters are edentulous and thus are easily disarticulated. The mean number of encrusting and boring specimens per valve is higher in the autobiostromes for both disarticulated and articulated valves (Table 2). The Analysis of Deviance indicates that the differences between the means of encrustation and/or bioerosion in autobiostromes and bioherms are significant.

DISCUSSION

Paleoecological and Paleoenvironmental Framework of the OMOs

Among the physical parameters that could be controlling the genesis of the different types of studied OMOs, nutrient supply, salinity, water energy, oxygen, turbidity, substrate, rate of sedimentation, depth, light, and temperature are considered the most important (Fürsich 1995). In the present case, oxygen, light, and temperature are interpreted to have been similar for the three studied localities. Water temperature was probably similar among the studied localities and thus was not a source of variation. Water temperature in the basin ranged between 15° to 25°C (warm-temperate waters), although 25°C is favored for the Agrio Formation given the record of coral assemblages, oolitic carbonates and thick-shelled bivalves (Lazo et al. 2005). The OMOs developed under fully oxygenated conditions above the sediment-water interface and rapidly decreasing oxygen concentration within the sediment (dysaerobic *sensu* Savrda and Bottjer 1991), given the limited bioturbation with low diversity, high organic matter content, and abundance and presence of syndepositional calcareous nodules (Allison 1988; Marshall and Pirrie 2013). In Convunco-RP3 the whitish color of the sedimentary matrix, persistent bioturbation, and absence of calcareous nodules point to a more oxygenated substrate. All localities represent settings within the euphotic zone.

For Covunco-RP3 a relatively shallower setting is envisaged due to its closer position to the southern margin of the basin. Bajada Vieja and Agua de la Mula are both located further from the southern margin indicating a slightly deeper environment. However, considering the ramp configuration of the basin and that both localities are closely located, difference in water depth between them should not have been significant. In addition, all three localities are situated at similar distance from the eastern basin margin suggesting there is no significant water depth difference towards the eastern direction. Therefore, differences in salinity, nutrient supply, water energy, turbidity, and rate of sedimentation may account for the formation of different types of OMOs in the studied region.

The most commonly cited environmental parameter for the formation of OMOs in Recent times is the presence of brackish waters, at least temporarily (Wells 1961; Hudson 1963) because it inhibits the settlement of competitors and prevents the attack from predators that cannot tolerate lowered salinity (Troost 2010; Johnson and Smee 2014). However, extant gryphaeids do not form OMOs and are considered strictly euhaline and stenohaline, although some can tolerate hyperhaline conditions (Stenzel 1971; Titschak et al. 2010). Previous paleoecological studies based on oxygen isotopes indicated that at certain times throughout its deposition, the Agrio Formation experienced deviations from normal marine conditions (Lazo et al. 2008). Salinity fluctuations were important enough to range from brachyhaline to hyperhaline throughout time (Lazo et al. 2008; Fig. 4). For the *Olcostephanus* (*O.*) *laticosta* ammonoid subzone, where the studied localities are temporally situated, the paleosalinity is within the euhaline range, although it shows a decreasing trend, from 36–35‰ to 33–32‰. Considering these mean salinity values and that freshwater input from the continent was mainly from the southeast of the basin, close to the studied localities (Eppinger and Rosenfeld 1996; Sagasti 2005), salinity fluctuations in the area could have been a factor that favored oyster spat settlement and OMOs development. The presence of echinoid spines shows that stable salinity conditions occurred at least temporarily, during which regular echinoids were able to colonize the OMOs (see Fürsich 1981).

As an alternative to variable salinity, the association of reduced sedimentation at times of maximum flooding, coupled with high nutrient supply, could have also positively influenced the OMOs' spatial extent and growth (Dame et al. 1989; Dattilo et al. 2012), especially considering that the continental runoff was close to the studied localities, but especially close to Covunco-RP3 (Eppinger and Rosenfeld 1996; Sagasti 2005). This is supported by palynomorph assemblages of the studied area (south of Covunco Creek, Fig. 1) which indicate a high continental influence (Peralta and Volkheimer 1997, 2000). The dark gray color of shales occurring throughout the studied section is indicative of high nutrient input sourced by continental runoff. The different life habits adopted by the oysters rather indicate differences in sedimentation rates along a basin transect (see below). Studies performed on extant OMOs indicate that oysters have great nutrient processing capacity, which allows them to proliferate under high nutrient input (Dame 1989; Newell et al. 2007).

Regarding Bajada Vieja and Agua de la Mula, there is a clear pattern from south to north of the study region that includes a decreasing overall oyster abundance, decreasing size of oyster bioherms and increasing spacing between bioherms along strike (Fig. 9). This decreasing trend towards the north is also supported by observations made in the Salado Sur section (Lazo 2007), placed between Agua de la Mula and Bajada Vieja sections (Fig. 1). There, OMOs are smaller than the ones recorded in Bajada Vieja (2 to 3 m of lateral extension, 1 m in thickness), but larger than the ones recorded in Agua de la Mula. Considering the southwestern freshwater input, a high nutrient input could explain the greater oyster proliferation in the studied sedimentary interval in comparison to the under- and overlying beds of the Agrio Formation. The great abundance of oysters in autobiostromes in Covunco-RP3 for a stretch of nearly 1 km is consistent with this interpretation (Fig. 9).

Not only abundance, but life habits varied also among localities, with oysters occurring primarily as encrusters in Agua de la Mula and Bajada Vieja, forming bioherms at both localities and also parabiostromes in the latter. In contrast, they were found predominantly as solitary recliners in Covunco-RP3, forming autobiostromes. This can be the result of the interplay between biological shell production and sedimentation rate in each locality (Dattilo et al. 2012; Brady 2016) both of which regulate substrate consistency. In Covunco-RP3, the reclining life habit adopted can indicate a higher sedimentation rate than in Bajada Vieja and Agua de la

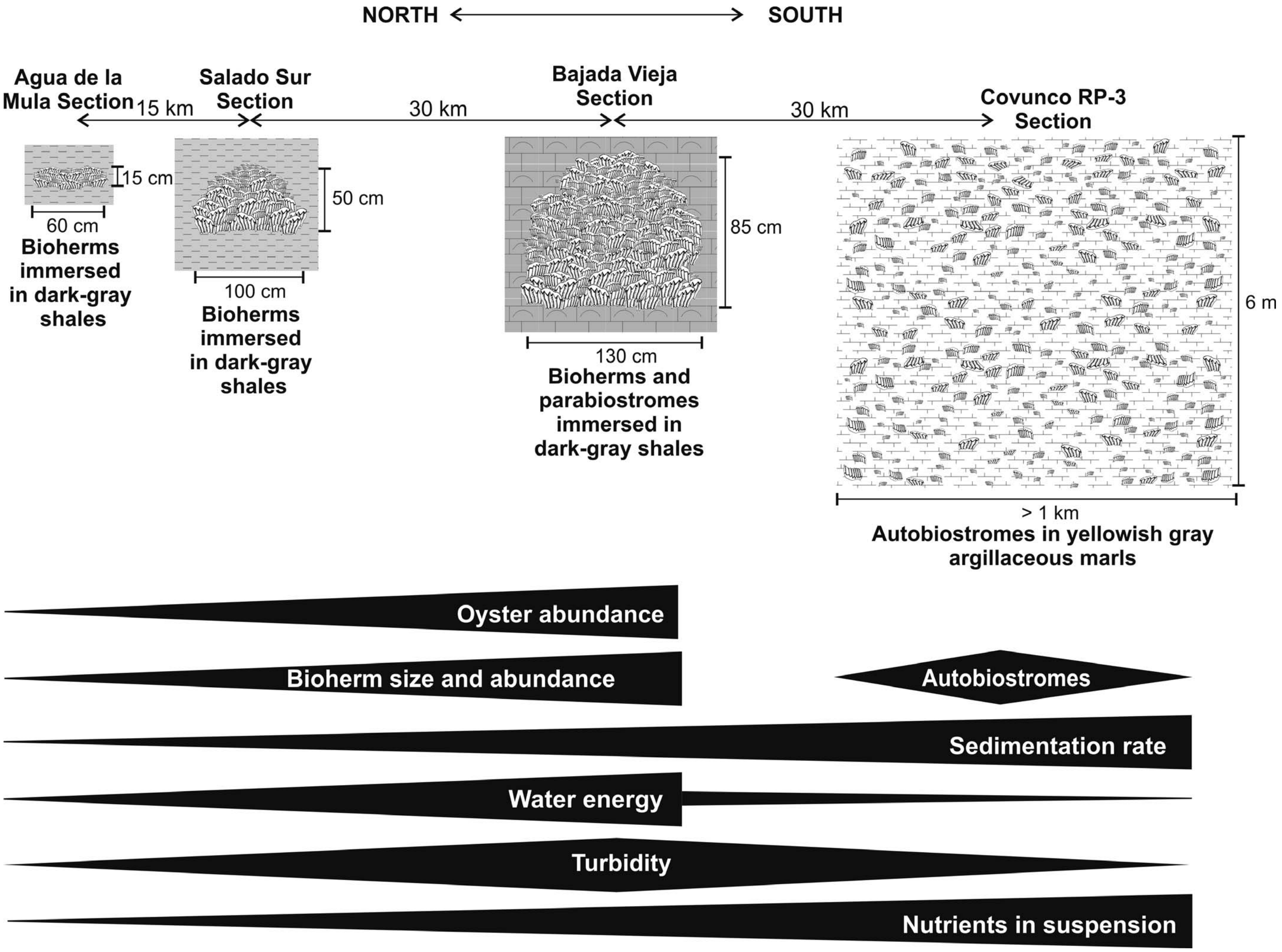

FIG. 9.—Schematic diagram of OMOs at Agua de la Mula, Salado Sur, Bajada Vieja, and Covunco-RP3 sections and proposed controlling environmental parameters. OMOs not to scale.

Mula, which would have inhibited the formation of bioherms given the limited hard substrate available for colonization and constant burial of oyster shells (Seilacher et al. 1985) maintaining a soft and unconsolidated substrate. Additionally, the high disarticulation and medium fragmentation can be indicative of high bioturbation (Fürsich and Pandey 1999). Alternatively, in Bajada Vieja and Agua de la Mula, a rather low sedimentation rate probably facilitated a positive taphonomic feedback, in which small oyster clusters eventually coalesced generating progressively larger and thus, more stable hard substrate (Kidwell and Jablonski 1983). As a consequence the cementing life habit prevailed and thus favored the formation of bioherms, generating vertically complex accretion (Powell et al. 2012). Also, in Bajada Vieja, the partial fragmentation of bioherms probably provided extra hard substrates for larvae attachment and the accumulation of taphofacies B (parabiostromes) could have provided extra support for the vertical growth of the bioherms (which was not observed in Agua de la Mula, where bioherms were thinner and there was no accumulation of parabiostromes). A trend of decreasing water energy is then interpreted from Bajada Vieja towards the north (Agua de la Mula) and south (Covunco-RP3) (Fig. 9), proven by the parabiostromal taphofacies present in Bajada Vieja, absent from the other studied localities. In Covunco-RP3 the moderate to high values of taphonomic indices are interpreted as the result of bioturbation rather than water energy, since there is no evidence of sediment reworking by currents or storms.

The different levels of water energy and sedimentation rate at each locality may have had an impact on water turbidity. The higher water energy at Bajada Vieja might have produced higher turbidity and higher levels of suspended particles, whereas in Agua de la Mula and Covunco-RP3, the lower water energy would imply less re-suspension of sediment and nutrients and clearer waters (Fig. 9). However, given oysters filter-feeding activity and biodeposit capacities (i.e., the production of feces and pseudofeces, Zurburg et al. 1994; Tomašových et al. 2006), turbidity would have had a minor impact on the proliferation of oysters.

Communities of encrusters and borers were taxonomically identical, although taxa occurred in different proportions between OMOs. *Ceratostreon* sp. is the main encruster in both OMOs, although with greater incidence in bioherms. It is followed by '*Berenicea*' sp., which appears with similar proportions in both OMOs, *Entobia* isp., which presents greater incidence in autobiostromes and serpulids, which appear with similar proportions in both OMOs. The greater intensity of encrustation and bioerosion on adult oysters in autobiostromes may seem contradictory with a higher sedimentation rate (Fig. 9). However, as stated in Methods, the reclining life habit and the overturning of shells caused by bioturbation would have created greater number of exposed surfaces giving more opportunities for encrusters and borers. Sediment trapping and baffling by bioherms could also negatively affect the colonization rate of encrusters and borers.

To summarize, two different paleoenvironmental settings seem to have prevailed in different parts of the basin, being primarily affected by nutrient input, sedimentation rates, and water energy. High nutrient input would have created a beneficial environment for the oysters to proliferate and form different types of OMOs. At Covunco-RP3, a high sedimentation rate combined with low water energy suggests a calm environment, characterized by reclining oyster concentrations, which were subject to reworking by bioturbation. Also, the argillaceous yellow marls where this OMO developed could indicate a shallower and protected environment. Towards the north, at Bajada Vieja, Salado Sur, and Agua de la Mula, lower sedimentation rates and moderate to high water energy suggest a more agitated environment, where oysters developed bioherms given the high availability of shells as hard substrate. Particularly, at Bajada Vieja, higher water energy becomes a relevant environmental factor given the development of parabiostromes.

Evolutionary Paleoecology of Mesozoic OMOs

During the Jurassic and Cretaceous, reefs experienced an important expansion globally (Höfling and Scott 2002; Leinfelder et al. 2002). Special attention has been given to sponges, corals and rudist reefs, but the role of gregarious oysters as reef builders has been largely ignored. Throughout the Mesozoic bivalves replaced brachiopods in the colonization of marine bottoms generating thicker and more numerous shell beds through time (Kidwell and Brenchley 1994). In this scenario, oysters become a relevant factor in benthic assemblages thanks to their high fecundity, growth rates and their potential to generate OMOs.

The Jurassic-Cretaceous time interval records frequent occurrences of OMOs since the Early Jurassic (Pliensbachian age, see Online Supplemental file for a summary of the reviewed OMOs). Scarce oyster concentrations were documented from the Late Triassic (Gaździcki 1974; Fürsich and Hautmann 2005). In that case oysters were a secondary frame builder, along with other bivalves (prospondylids, plicatulids, and pectinoids) rather than the main frame builder, so they will not be considered as OMOs. Only biogenic and mixed-origin OMOs will be discussed here, given that these are the only cases that preserve a biological signature. See Hattin (1986), Fürsich and Oschmann (1986), Eliuk (1989), Shaaban et al. (1995) and Palma et al. (2007) for sedimentologic examples of OMOs.

Since the Early Jurassic (examples from Spain and Germany, Fürsich and Hautmann 2005 and F.T. Fürsich personal communication 2017), OMOs have experienced important changes in their global distribution and habitat preferences. During that period, OMOs were recorded almost exclusively in European marine successions, especially in the northern margin of the Tethys Ocean, between 30° and 60°N (records from Portugal (Fürsich 1981; Fürsich and Werner 1986; Leinfelder 1986), Poland (Seilacher et al. 1985; Hoffmann and Krobicki 1989; Machalski 1998; Zatoń and Machalski 2013), Canada (Poulton 1989), Scotland (Andrews and Walton 1990), Germany (Delecat et al. 2001), and France (Olivier et al. 2004) with some non-European Tethyan records (Japan, Komatsu et al. 2002; Iran, Fürsich et al. 2016). They were mainly formed by taxa from the family Gryphaeidae and, secondarily, from the family Ostreidae (14 and three OMOs from the reviewed bibliography, respectively). They were associated with shallow environments with high continental influence such as deltas or lagoons or with deeper areas of the continental shelf with no continental influence (mid to outer ramp).

The Jurassic period was marked by a significant tectonic reconfiguration, characterized by the opening of a tropical oceanic corridor, which created a global east-west current system and a general sea level rise (Leinfelder et al. 2002). During this period, scleractinian corals, siliceous sponges, and microbialites were the major reef builders, occupying both shallow platform settings within open shelf environments and deeper platforms, below storm wave-base (Scott 1988). The result was a worldwide reef proliferation towards the Late Jurassic, when these major reef builders broadened their distribution. They appeared with high abundance throughout the globe, with occurrences in low and high latitudes and with presence both in the northern and southern Tethys and the eastern Pacific margin (Leinfelder et al. 2002). This indicates that these major reefs builders shared their main area of distribution with OMOs, but exceeded them greatly (Fig.10A).

This superposition of geographic locations indicates that OMOs were able to occupy the same platforms as the major reef builders of the Jurassic period, covering the marine platform but also shallower, marginal marine environments with higher sediment input and nutrient supply.

The Cretaceous period is characterized by an important change in major reef builders, with the displacement of corals by rudists. Initially, during the Early Cretaceous, corals, stromatoporoids, siliceous sponges, and rudists were the main actors within the reef systems, coexisting by occupying separate habitats: corals and sponges occupied calm environments, below the fair-weather wave-base, whereas rudists occupied shallower areas, within the zone of normal wave action (Scott 1984; Höffling and Scott 2002).

Environmentally, it was a period with general high sea level, with major flooding of continents and circumglobal equatorial circulation (Simo et al. 1993; Miller et al. 2005). In this context, global reef distribution was highly dispersed, appearing abundantly on the northern and southern Tethys margins, the proto Caribbean Sea and sporadically in the Pacific Ocean. Reefs appeared both on the southern and northern hemispheres, although more abundantly in the latter (Höfling and Scott 2002).

Meanwhile, OMOs experienced a major geographic shift, occurring exclusively in the Eastern Pacific Ocean, between 60°S and 60°N latitude (OMOs recorded from USA (Flatt 1976), Colombia (Guzmán 1985), Canada (Leckie 1989), Argentina (Damborenea et al. 1979; Palma and Lanés 2001; Schwarz et al. 2005; Lazo 2007; Kietzmann et al. 2014; this paper) and Mexico (Hernández-Ocaña et al. 2015). They occupied coastal, shallow- and deep-shelf marine environments. Oysters forming them were mainly from the family Gryphaeidae and secondarily from the family Ostreidae (7 and 2 OMOs from the reviewed bibliography, respectively). This restricted geographic distribution is in contrast with the broad distribution of major reefs of the time. This could indicate that the success of rudists, sponges, and corals reefs forced OMOs to retreat from the Tethys Ocean, establishing in less occupied platforms.

The present case study takes place within this scenario and deals with one of the oldest OMOs recorded in the southern hemisphere, along with those recorded in the Vaca Muerta, Mulichinco, and Chachao formations (Valanginian) in the same basin (Damborenea et al. 1979; Palma and Lanés 2001; Schwarz and Howell 2005; Kietzmann et al. 2014).

Particularly, the bioherms found in Bajada Vieja and Agua de la Mula are very similar to those described by Hernández-Ocaña (2015) from the San Juan Raya Formation in México. There, high abundance of oysters is also attributed to a physically controlled environment where episodic events of storms allowed the formation of bioherms and ostreoliths. The accessory fauna is more typical of tropical conditions, with the presence of rudists in direct competition with oysters. However, in this scenario rudists were not able to build a rigid framework, appearing mainly as solitary individuals.

The autobiostromes studied in Covunco-RP3 resemble those described by Guzmán (1985) from Rosablanca Formation in Colombia. There, the adoption of a solitary reclining life habit is also associated with low-energy, relatively stable, soft marine bottoms with episodic high siliciclastic input, but in this case associated with a relative fall in sea level.

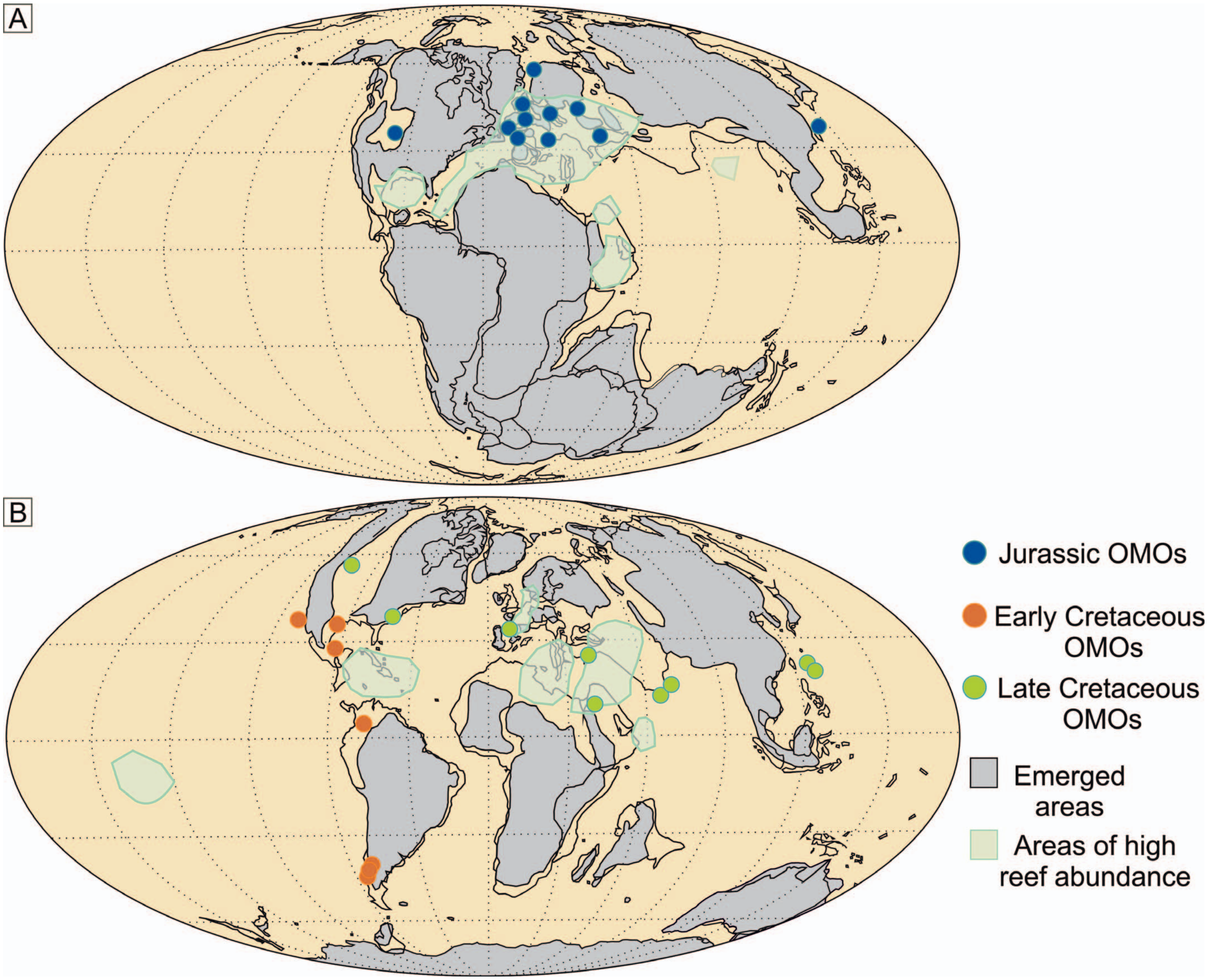

FIG. 10.—Global paleogeographic distribution of OMOs during the Jurassic–Cretaceous. **A**) Paleogeographic distribution during the Jurassic period. **B**) Paleogeographic distribution during Cretaceous period. Jurassic and Cretaceous OMOs records are based on an updated compilation of the literature (see Online Supplemental file). Reef abundance areas refer to high abundance of coral, sponge and/or rudist reefs and are based on Leinfelder et al. (2002), Scott (1988), Höffling and Scott (2002) and Johnson et al. (2002). Maps modified from Smith et al. (1994).

These cases display a similar strategy as adopted by the oysters in the Agrio Formation (i.e., encrusting or reclining life habits) facing environmental disturbances associated with variable sedimentation rates.

Lastly, during the Late Cretaceous, reefs were characterized by the dominance of rudists and the demise of corals, which were no longer reef builders by the late Albian. Their distribution was broad, with high abundance in the Tethys Ocean and some occurrences in the Western Interior Sea (Johnson et al. 2002).

At that time, OMOs maintained their position in the eastern Pacific margin but also reappeared scarcely in the Tethys Ocean: records from USA (Stephenson 1956; Puckett 1994); Japan (Chinzei 1986; Toshimitsu et al. 1990); Canada (Eliuk 1989); France (Videt 2003); Jordan (Abed and Sadaqah 1998; Powell and Moh'd 2011); India (Fürsich and Pandey 1999); and Iran (F.T. Fürsich personal communication 2017) (Fig.10B). In this period, the family Ostreidae becomes more relevant, taking the lead in the formation of OMOs over the family Gryphaeidae (six and two OMOs from the reviewed bibliography, respectively). OMOs occupied coastal, shallow- and deep-shelf marine environments. Although OMOs and rudists reefs global distribution coincide, it is noticeable that when OMOs occur, rudists appear as recliners (Videt 2003) and when rudists reefs occur, oysters appear as accessory fauna (Johnson et al. 2002), indicating that both buildups did not coexist.

During the Jurassic and Cretaceous, OMOs were built by either griphaeids or ostreids. They were recorded from various environments: from fully marine offshore to coastal, shallow marginal marine including bays and lagoons. This differs strongly from the OMOs environmental distribution during the Cenozoic, when they occupied primarily marginal marine environments, associated with high sediment input and strong salinity deviations, including estuaries and delta influenced bays sometimes associated with marshes (Lawrence 1971; Laurain 1980; Bahr and Lanier 1981; Leanza and Hugo 1985; Geyer and Herbig 1988; Littlewood and Donovan 1988; Demarcq and Demarcq 1992; Rivas et al. 1999; Videt 2003; Parras and Casadío 2006; Pufahl and James 2006; Garvis et al. 2015). Cenozoic OMOs are built exclusively by taxa from the family Ostreidae, some of which are capable to withstand salinities that deviate from normal marine (Kirby 2000). In the present times, the few extant species from the family Gryphaeidae are strictly euhaline and stenohaline and do not form buildups where individuals encrust one another (Stenzel 1971).

Therefore, these differences in OMOs environmental distribution and taxonomic composition may be accounted for by an increase in predation pressure from the mid-Cretaceous onwards. The increasing predation would push the OMOs towards more marginal marine environments where predators are incapable of thriving due to physical stress, forcing also the shift from primarily gripheids OMOs during the Early Cretaceous, to exclusively ostreids OMOs during the Cenozoic (Vermeij 1977, 2011; Aberhan 1994; Johnson and Smee 2014).

This is supported by current studies of invasive ostreids such as *Crassostrea gigas* (Thunberg 1793), which have been able to occupy fully marine environments and form mass aggregations in the Wadden Sea partly because it has no natural predators in that region ("enemy release hypothesis"; Troost 2010).

This could be the case for the studied examples, where a combination of environmental parameters allowed the proliferation of oysters and a low predation pressure allowed the establishment of gryphaeid OMOs in the marine ramp, which is not possible on present-day marine shelves. The geographic and stratigraphic distribution of fossil biogenic OMOs therefore records paleoenvironmental conditions and evolutionary changes.

CONCLUSIONS

OMOs first appeared during the Late Triassic and have been an important component of the fossil record since the Early Jurassic. They can be classified according to their origin as biogenic, sedimentologic or mixed biogenic-sedimentologic origin. Three different OMOs were recognized in this study case: two types of biogenic OMOs (bioherms and autobiostromes) and a mixed-origin one (bioherms embedded in parabiostromes).

The study and comparison of these OMOs allowed the distinction of different processes acting at different scales within the basin. At a larger scale, the massive oyster abundance could be associated to high nutrient input due to continental runoff. At a smaller scale, the different life habits adopted locally could be related to differential sedimentation rates. Reclining life habit was associated with a higher sedimentation rate and a rather calm environment, which prevented oyster from forming bioherms, whereas the encrusting life habit was associated with a lower sedimentation rate and higher water energy. Additionally, the different geometries of bioherms allowed the inference of different taphonomic processes acting at the time of their development, such as taphonomic feedback.

During the Mesozoic, OMOs occupied a broad geographical distribution, coinciding at first with Jurassic reefal facies. During the Cretaceous, they deviated from the reef distributions of the time and appeared exclusively in medium to low latitudes. At that time, OMOs occurred over a wide range of marine environments, from shallow coastal to offshore, and were formed by taxa from the families Gryphaeidae and Ostreidae. This is remarkably different from their current environmental distribution, which is restricted to marginal marine environments, with extreme conditions and their taxonomic composition, including only taxa from the family Ostreidae. This could be related to a low predation pressure during the Jurassic and Cretaceous periods that allowed gryphaeid OMOs to develop deeper into the marine shelf. The increased predation pressure from the Cretaceous onwards drove them to occupy marginal marine environments where predators are not able to thrive and forcing a taxonomic shift towards the family Ostreidae.

The present case study may be used as a base for further studies of Cretaceous OMOs recorded in the Eastern Pacific, especially beyond the tropics and Tethys margins, where typical Cretaceous carbonate reef builders such as corals and rudists are constrained by decreasing water temperature.

ACKNOWLEDGMENTS

We thank M.B. Aguirre-Urreta for providing the geographic information regarding locality Covunco-RP3 and I.M. Soto and P. Milla Carmona for help during the field work. We would also like to thank F.T. Fürsich, A. Tomašových, M. Zuschin and an anonymous reviewer for careful revisions and helpful comments. This paper was supported by grant UBACyT 20020130100106BA awarded to M.B. Aguirre-Urreta and grant CONICET PIP 11220120100542 awarded to Victor A. Ramos and grant PICT 2015-1381 awarded to Darío G. Lazo. This is the contribution N° R-224 of the Instituto de Estudios Andinos "Don Pablo Groeber".

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

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Received 15 November 2017; accepted 4 April 2018.