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Ichnology of fossil oysters (bivalvia, ostreidae) from the southern Brazilian coast

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ABSTRACT

Ichnological features over fossil oysters from southern Brazilian coast are described herein. In the deposits *Ostrea puelchana* d'Orbigny, 1841 is the dominant oyster, followed by *O. equestris* Say, 1834 and *Crassostrea virginica* Gmelin, 1791. Although these taxa are found along the entire coast, they exhibit some geographical variations regarding the presence of borings. The most conspicuous ichnogenera are *Caulostrepsis* and *Entobia*, with *Gastrochaenolites* being common in fossils from the central sector of the coast, and scarce in the southern one. *Maeandropolydora* and incrustations (made by fouling organisms, e.g. cirripeds and bryozoans) are scarce. Most of the borings are found on the external side of the valves which suggest a dominant bioerosion activity during the life span of the organisms.

Key words: Quaternary, Ostreidae, bioerosion, *Entobia*, *Caulostrepsis*, *Gastrochaenolites*.

RESUMO

ICNOLOGIA DOS OSTREÍDEOS FÓSSEIS (BIVALVIA OSTREOIDA) DO SUL DA COSTA BRASILEIRA. Feições de bioerosão identificadas em ostreídeos fósseis de acumulações da costa sul brasileira são descritas. Os depósitos são caracterizados pela presença dominante de Ostrea puelchana d'Orbigny, 1841, seguida por O. equestris Say, 1834 e Crassostrea virginica Gmelin, 1791. Embora esses táxons sejam encontrados ao longo de toda a costa, exibem variações geográficas com relação à presença de bioerosão. Os icnogêneros mais comuns são Caulostrepsis e Entobia e Gastrochaenolites caracteriza a atividade mais comum entre aqueles do setor central da costa, sendo mais raro no setor sul. Maeandropolydora e incrustações (p. ex. cirripédios e briozoários) são pouco numerosas. A maioria das perfurações é encontrada na superfície externa das valvas, sugerindo que grande parte dos processos bioerosivos tenha ocorrido enquanto os organismos ainda estavam vivos.

Palavras-chave: Quaternário, Ostreidae, bioerosão, *Entobia*, *Caulostrepsis*, *Gastrochaenolites*.

INTRODUCTION

Trace fossils are widespread features in the geological record and can be considered as 'fossilized behaviours', as they record the activities of the tracemakers (Gibert *et al.*, 2004). The assemblages containing specific trace fossils are characteristic of a given environment, because the organisms that produce such traces are adapted to specific environmental conditions (Frey, 1975). Not only sediments and rocks, but also dead remains of organisms consisting of hard parts such as shells and bones, can be altered by such biogenic activities.

Bioerosion is the result of alterations on hard substrates produced by organisms, either in the form of structures such as tunnels and borings or in the form of scrapings, rasping and gnawing (Warme, 1975). These alterations may be caused by predators (such as naticid gastropods), fouling (cirripeds, oysters) and boring (sponges, bryozoans, polychaetes) organisms. Tunnels, chambers and other structures built for protection and sheltering are produced by endoskeletozoans (*sensu* Taylor and Wilson, 2002) and are assigned to the Domichnia ethological class.

Shells of marine molluscs are subject of alteration by a wide array of organisms, not only after death, but also while the individuals are still alive. In soft-bottom areas, shells can provide the only hard substrate available for colonization by epi- and endoskeletozoans. Oyster larvae settle preferentially near or on other oysters, thus forming large bioherms known as 'oyster reefs'; because of this habit, plus its usually large and thick shell, oysters are useful as substrate for the settlement of several different types of communities of boring and encrusting organisms (Parras and Casadío, 2006).

The Coastal Plain of Rio Grande do Sul State (CPRS), in southern Brazil, is known by the presence of several accumulations of fossil remains, both marine and terrestrial, on the continental shelf (Figueiredo Jr., 1975; Lopes and Buchmann, 2010). This mixture of marine and terrestrial fossils on the continental shelf is a result of the Quaternary sea-level oscillations that affected the Brazilian coast (Tomazelli *et al*., 2000; Angulo *et al*., 2006). The fossils from these accumulations are transported to the beach by storm events during winter; in the southern portion of the CPRS these events create on the beach large concentrations (konzentratt-lagerstätte) known as "Concheiros". In a study about the taphonomy of the fossil molluscan from this place, Lopes and Buchmann (2008) included an analysis of the ichnological aspects of the shells. However, due to the low proportion of fossil oysters among the analyzed samples, this group was not properly addressed.

In order to evaluate in detail the ichnological aspects of fossil oysters from CPRS, several specimens that have been collected in the last two years, plus fossil specimens from the paleontological collection of Universidade Federal do Rio Grande (FURG) were analyzed. The results of this survey are presented herein.

LOCATION AND GEOLOGICAL SETTING

The CPRS is a 618 km-long geomorphological unit formed by sediments accumulated in the southern Brazilian coast (Figure 1A). After the split between South America and Africa in the Late Cretaceous, sediments eroded from Paleozoic and Mesozoic rocks accumulated in the continental margin, forming the Pelotas Basin, which has a maximum thickness of 10 km and had its uppermost portion influenced by eustatic oscillations correlated to the glacial-interglacial cycles between the Neogene and Quaternary. As a result of these oscillations, two major depositional systems were formed parallel to the coastline: the Alluvial Fans System and the Complex Multiple Barrier system (Villwock and Tomazelli, 1995).

The Complex Multiple Barrier System is subdivided into four major barrier-lagoon depositional systems and associated features (Figure 1B). Each of these systems was formed in response to a major sea-level transgression during Quaternary interglacial episodes. The exact ages of such deposits are still unknown, but are correlated to the interglacial maxima at 400 ky (Barrier-Lagoon System I), 325 ky, (Barrier-Lagoon System II), 123 ky (Barrier-Lagoon System III) and 6 ky (Barrier-Lagoon System IV). The sediments that constitute these systems are essentially terrigenous sicliciclastic, well-selected and mature, with small fractions of organic matter, biogenic carbonate and diagenetic clays, with some important concentrations of heavy minerals (Villwock and Tomazelli, 1995). During the Holocene marine transgression, around 6-7 ky, variations in the rates of sea-level rise resulted in the reworking and concentration of terrigenous clastic sediments of the shelf, and erosive terraces were formed in response to episodes of sea-level stabilization (Kowsmann and Costa, 1974; Martins *et al*., 1996).

In the southern portion of the coast, large concentrations of Pleistocene marine bioclasts composed mostly of rounded shell fragments are found (Buchmann *et al*., 2009). Figueiredo Jr. (1975) obtained ^{14}C ages between 16 ka and more than 38 ka for fossil marine shells collected from the continental shelf. These bioclasts can be classified as palimpsests, i.e., relict sediments (deposited during and/or right after the last glacial maximum) that are being reworked by dynamic processes of today and constitute some 70% of the sediments from continental shelves around the world (Emery, 1968; Pilkey and Frankenberg, 1964; Swift *et al*., 1971).

MATERIALS AND METHODS

The fossils described herein were all collected on the shoreline, in three main areas of the coast. Fossil oysters are found all along the coast of Rio Grande do Sul State, usually associated with recent and fossil shell remains accumulated on the beach by storm waves. 150 specimens were collected in the central sector of the coast, near Mostardas, while in the southern sector 80 remains were collected in the Verga lighthouse area and 119 in the Concheiros (Figure 1B). At each collecting site, a 1 km-long sector of the beach was surveyed for fossil remains accumulated by storm waves between the surf zone and the foredunes. In Mostardas, fossil oysters constitute some 80% of the bivalve remains found on the shoreline; in the Verga lighthouse area, oysters constitute some 20% of the bivalve remains, while in Concheiros they constitute less than 1% of the remains. These differences probably reflect the fact that in Concheiros the amount of fossil shells accumulated on the shoreline is larger than on the other areas, and the dominant fossil taxa in this area are *Amiantis purpuratus*

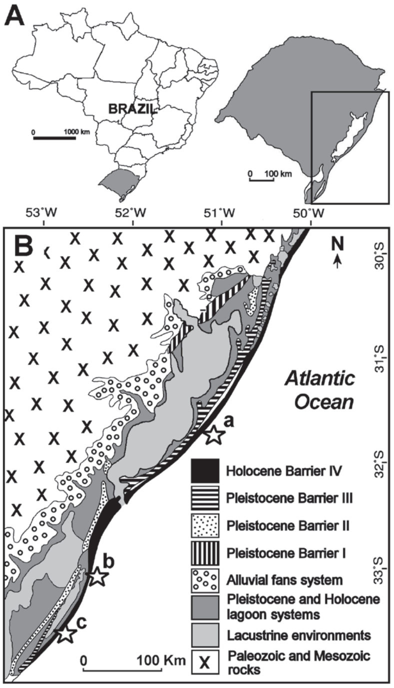

Figure 1. A. Location of the Coastal Plain of Rio Grande do Sul State (CPRS) in Southern Brazil; **B**. geomorphological subdivisions of the CPRS; the places were the samples were collected are indicated by stars: **a**. Mostardas; **b**. Verga; **c**. Concheiros.

Lamarck, 1818, *Pitar rostratus* Koch, 1844 and *Glycymeris longior* Sowerby, 1833 (Lopes and Buchmann, 2008). All molluscan taxa identified so far from fossil remains are essentially the same that still inhabit the southern Brazilian coastal area today (Rios, 1994). The fossil shells do not have periostracum and their colour patterns are much different than those found in recent specimens, ranging from reddish colour to dark gray. These differences may be possibly related to diagenesis under different conditions (oxidizing vs. reducing). The fossils also exhibit signs of recrystallization and are mechanically more resistant than recent specimens, although most are broken and abraded (Lopes and Buchmann, 2008).

The 349 oyster specimens were collected between 2009 and 2011 and are housed at the paleontological collection of FURG. Taxonomic identification was based on Rios (1994) and the description of fossil oysters from CPRS by Bianchi (1969). The specimens were identified and surveyed for macroscopic bioerosion on both internal and external sides of the valves. To this study the internal and external sides of the valves were divided in sectors, like expressed in Figure 2.

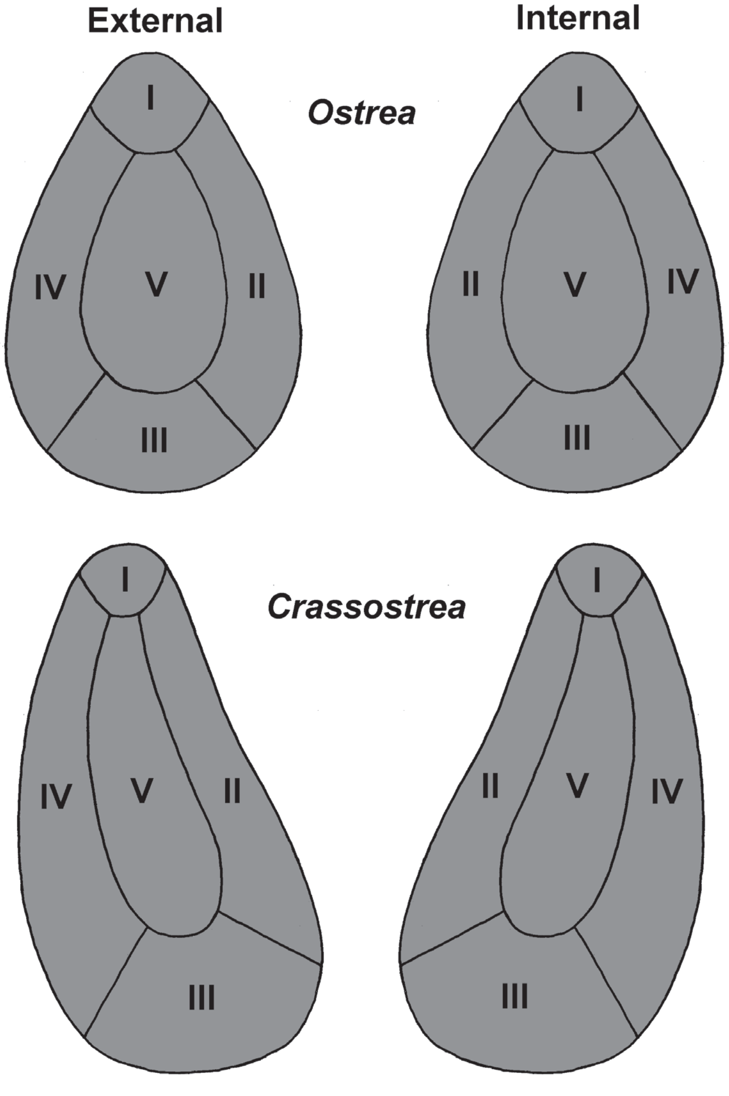

Figure 2. Schematic view of the divisions on internal and external sides of the valves (modified from Parras and Casadío, 2006).

RESULTS

The fossil oysters belong to the species *Ostrea puelchana* d'Orbigny, 1841, *Ostrea equestris* Say, 1834 and *Crassostrea virginica* Gmelin, 1791. The most abundant species in the three collecting sites is *O. puelchana* (59% of the total specimens), followed by *C. virginica* (8.8%) and *O. equestris* (7.7%). Most specimens of the genus *Crassostrea* (95%) were collected in Mostardas, and only one specimen of this genus was found in Verga and one in Concheiros. Specimens of *Ostrea* and *Crassostrea* unidentified at species level make 17.4% and 6.5%, respectively, of the total analyzed samples. Because of their greater thickness, oyster shells are mostly complete, although most exhibit signs of abrasion, which in many specimens obliterated diagnostic features, making difficult to identify the specimens at species level. Fossil oysters from Mostardas and Verga exhibit dark gray colour, while those from Concheiros exhibit colour ranging from light gray to white, and some even show traces of the original colour pattern.

All fossils consist of disarticulated valves, although three specimens from Mostardas are preserved with valves still closed, filled by coquinas. Of the total samples, 49.6% are right valves, 39.8% are left valves and 10.6% could not be identified (Figure 3A). The proportion of right/left valves is very similar among samples from Mostardas and Concheiros, while in the Verga sector right valves are more abundant. Both right and left valves are mostly bioeroded (Figure 3B). Of the 349 specimens analyzed, 73.6% exhibit bioerosion traces produced by endoskeletozoans, found mostly on the external surface of the valves (Figure 3C). Episkeletozoans are very scarce, with 15,3% valves colonized by other oysters, 2.5% by bryozoans and 1.1% by cirripeds.

Endoskeletozoans

The most conspicuous borings produced by endoskeletozoan organisms

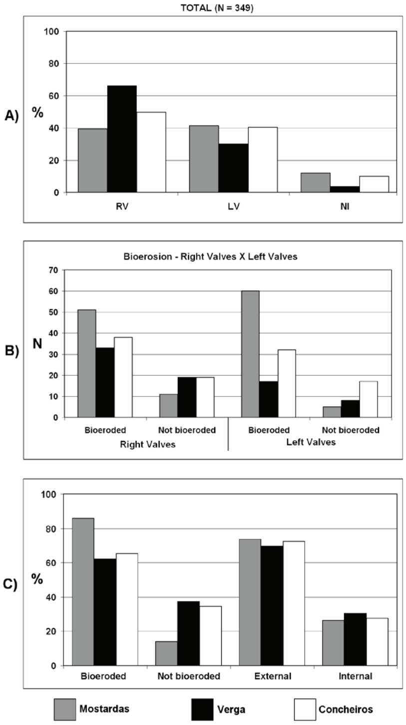

Figure 3. **A**. relative proportions, by collecting areas, between right (RV), left (LV) and unidentified (NI) valves; **B**. total number of right and left valves with and without bioerosion; **C**. proportion of specimens with or without bioerosion and proportion of bioerosion on the external and internal sides of the specimens.

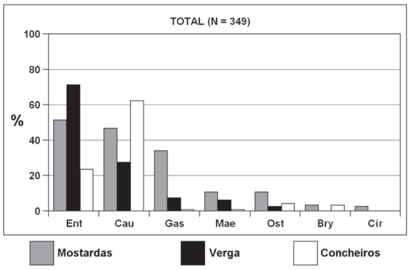

Figure 4. Relative proportions of *Entobia* (Ent), *Caulostrepsis* (Cau), *Gastrochaenolites* (Gas), *Maeandropolydora* (Mae), Bryozoa (Bry) and Cirripedia (Cir) in the collected sites.

are *Caulostrepsis* (47.5%) and *Entobia* (46.4%), followed by *Gastrochaenolites* (16.6%) and *Maeandropolydora* (6.3%). However, these values are different when the specimens from the three collecting areas are separately analyzed. *Gastrochaenolites* are found mostly in specimens from Mostardas, while in specimens from Verga the most conspicuous ichnogenus is *Entobia*. *Caulostrepsis* is the most abundant form among Concheiros specimens (Figure 4).

Caulostrepsis Clarke, 1908

Caulostrepsis is observed as U-shaped galleries excavated parallel to the surface of the shells, and is produced by polychaetes (Figure 5A). In thicker specimens, such as large valves of *Crassostrea*, a series of *Caulostrepsis* openings can be seen aligned along the lamellae that represent growth increments (Figure 5B), suggesting bierosion during the life span of the oyster. The openings are 8-shaped, indicating the ichnospecies *C. taeniola* (Pickerill *et al.*, 1998).

Caulostrepsis was found in 46.6% of the specimens from Mostardas, 27.5% from Verga and 62.2% from Concheiros. In 83.5% of the specimens this ichnogenus is found only externally, in 4.1% it is seen only on the internal surface and in 12.4% on both surfaces. Yet, 53.6% of the specimens exhibit only *Caulostrepsis*. Externally, the sectors of the shells that exhibit lowest and highest bioerosion by *Caulostrepsis* are I and IV, respectively; internally, the sectors II and I are the most and least bioeroded (Figure 6A). Of the total specimens that exhibit *Caulostrepsis*, 55.4% are right valves and 44.6% are left valves.

Entobia Bronn, 1838

Entobia consists of round chambers interconnected by cylindrical galleries bored beneath the surface of the shell by clionid sponges (Bromley and D'Allessandro, 1984). The galleries are bored parallel to the shell surface and may be either simple, with only two openings, or may form a network of interconnected chambers; diameter varies between 0.1 and 1.5 mm and in some cases, openings of different diameters can be observed in the same specimen (Figure 5C).

In several specimens most of the shell surface is covered by chamber openings and in specimens that were much subject to abrasion the external layers of the shell were removed, exposing the internal chamber network (Figures 5D-E). In some broken shells, the presence of high numbers of *Entobia* clearly contributed for the fragmentation of the specimen (Figure 5F).

This ichnogenus is present in 51.3% of the specimens from Mostardas, 71.2% from Verga and 23.5% from Concheiros. Also 23.5% of the total number of specimens exhibit only *Entobia*. Although there is no clear preference for colonization regarding the sector of the shell, *Entobia* is slightly more numerous in sectors IV and V (Figure 6B). Regarding external/internal colonization, such borings are more conspicuous externally (35.5%) than internally (10.5%), and also appears on both sides in 54% of the valves. Of the total specimens with *Entobia*, 52.6% are right valves and 47.4% are left valves.

Gastrochaenolites Leymerie, 1842

This ichnogenus is produced by mytilid bivalves (Kelly and Bromley, 1984). It was observed mostly on fossil oysters from Mostardas, being almost absent in specimens from Verga and Concheiros (Figure 4). Of the total specimens analyzed, 10.1% exhibit only *Gastrochaenolites*. It is visible mostly on the sectors IV and V (Figure 6C) of the shells and is exclusive of the external side of valves in 72.4% of the specimens. In 4.2% of the specimens it is seen only internally, and in 23.4% is observed in both external and internal surfaces. *Gastrochaenolites* is found mostly on left (52.5%) than on right (47.5%) valves. The chambers measure up to 20 mm in length and 8 mm in width and the morphology indicates the ichnospecies *G. torpedo* (Kelly and Bromley, 1984).

Gastrochaenolites occurs as ovoid chambers oblique, parallel (Figure 7A) or perpendicular in relation to the valve; in the last case is not clear whether the shell were excavated from the external or internal surface of the valve (Figure 7B). The size of the chambers ranges from 5 to 20 mm in length, and as much as seven chambers were observed in the same

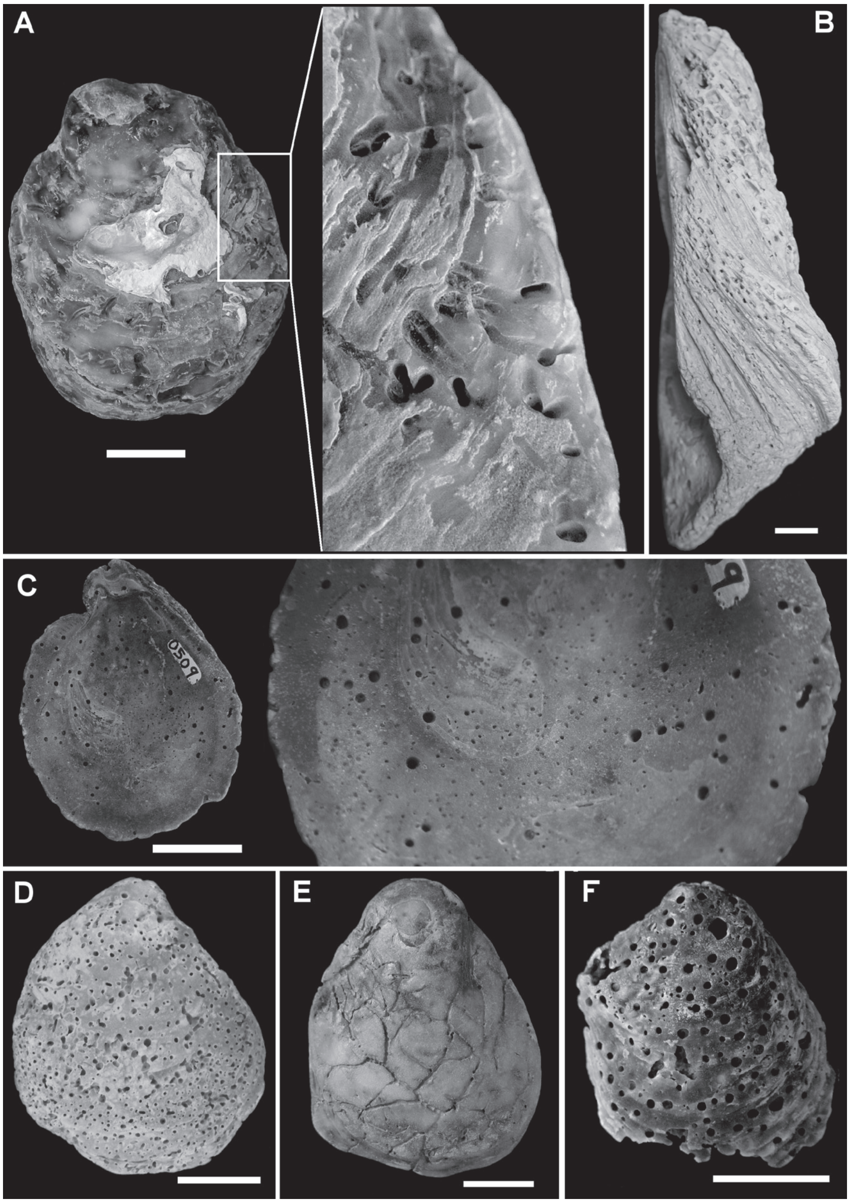

Figure 5. A. *Caulostrepsis* borings over the external side and anterior margin (detail) of a right valve of *Ostrea puelchana*; **B**. *Caulostrepsis* borings aligned with the growth lamellae on a left valve of *Crassostrea virginica* (lateral view); **C**. different sizes of *Entobia* borings on the internal side of *O. puelchana* left valve; **D**. external view of a highly bioeroded left valve of *O. puelchana*; **E**. internal network of *Entobia* galleries over an abraded left valve of *O. puelchana*; **F**. broken ventral margin of a left valve of *O. puelchana* due to *Entobia* activity. Scale bars = 20 mm.

specimen (Figure 7C). As for *Entobia*, in some specimens the presence of *Gastrochaenolites* resulted in the fragmentation of the oyster (Figure 7D).

***Maeandropolydora* Voigt, 1965**

This ichnogenus is the result of excavation by several families of polychaetes, mostly Spionidae (Bromley and D'Allessandro, 1983). It occurs as galleries excavated on the surface of the shell, measuring between 1 and 3 mm in diameter, and can be short and almost straight or long and meandering (Figures 8A- B). It is very scarce in comparison with the other ichnogenera and it appears mostly in specimens from Mostardas and Verga; 8.3% of the specimens exhibit only this ichno-trace and its presence on the sectors of the valves follow a similar pattern on both external and internal side of the valves, except for the internal sectors II and V which are the most and the least bioeroded, respectively (Figure 6D).

Episkeletozoans

The record of episkeletozoans among the analyzed specimens is very scarce, represented by oysters, bryozoans and cirripeds. A total of 23 oysters were found incrusting other oysters; mostly are small individuals of *O. equestris*, but some larger *O. puelchana* were also recorded (Figure 8C). 17 oysters were found on the external side of the valves and 6 on the internal side; some fossils exhibit oysters on both external and internal faces (Figure 8D).

Cirripeds were recorded only in 4 specimens from Mostardas. The cirripeds belong to the family Balanidae (cf. *Balanus* sp.) and occur only on the external surface (Figure 8E), isolated or forming clusters. Some cirripeds are recent, but those filled with lithified sediment are clearly fossils. The only bryozoans found so far belong to the Cheilostomata, which build thin calcium carbonate skeletons (Figure 8F). These skeletons have not been found in oysters from Verga; in specimens from Concheiros, they have been found only in the internal surface of four individuals. Bryozoans have been found in the external side of 4 specimens and in the internal side of 1 specimen from Mostardas.

DISCUSSION

The shells of *C. virginica* and *O. puelchana* are inequivalve, with the left valve larger and thicker than the right one, while *O. equestris* have both valves nearly equal (Bianchi, 1969). Thus, the higher proportion of right valves may result from differential transport, as this valve is thinner and smaller than the left one, is easily remobilized even by weak currents after death and decomposition of the soft parts. This difference may also reflect the fact that the oyster larvae

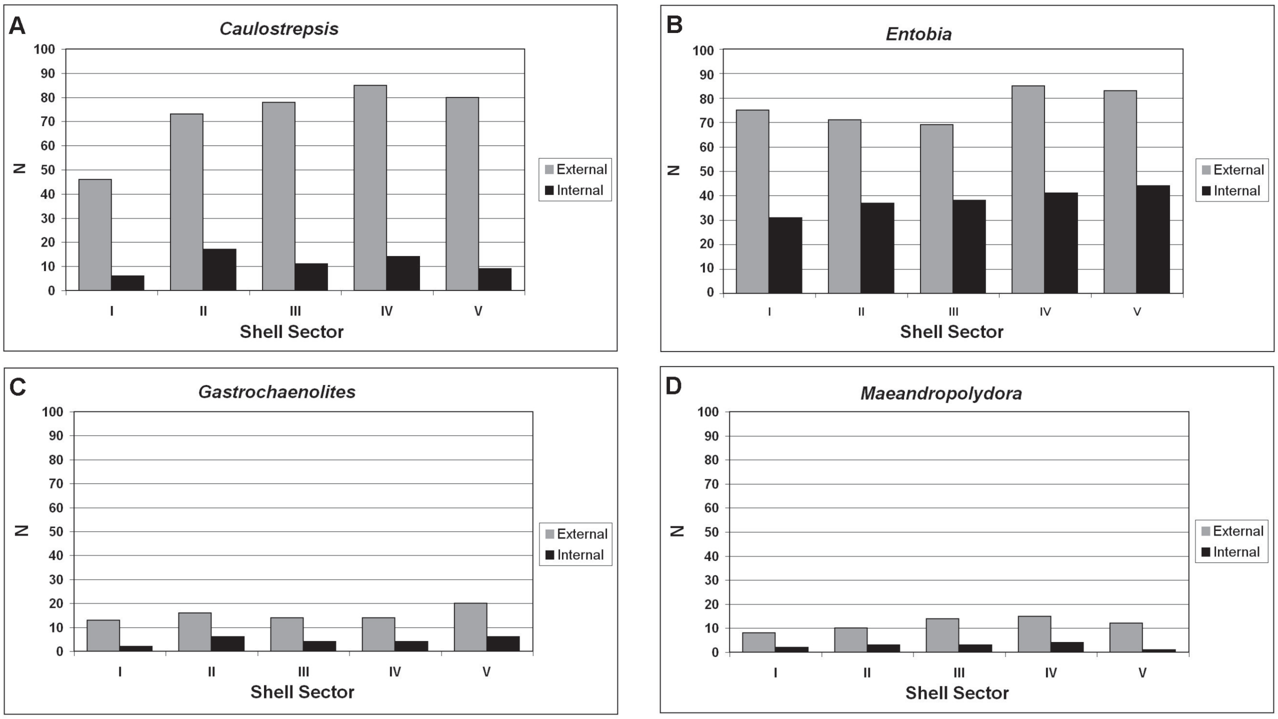

Figure 6. Relative proportions of borings found on the external and internal side of the 349 specimens, according to its presence on the different sectors of the valves (I-V) and genera: **A**. *Caulostrepsis*; **B**. *Entolobia;* **C**. *Gastrochaenolites*; **D**. *Maeandropolydora*.

attach themselves to the substrate by the left valve (Stenzel, 1971), making its removal by wave action in hard, stable substrates (rocks and oyster banks), almost impossible. The lower proportion of left valves from Verga, in comparison to Mostardas and Concheiros, may be related to the presence in that sector of rocky outcrops on the inner shelf, formed by beach rocks, that indicate lithified paleo-beachlines (Asp, 1999). These outcrops provide stable attachment surfaces for the oysters and difficult their removal.

Also due to the inferred left valve attachment to hard substrates, one should expect to find a very low number of this valve all along the coast. The herein observed pattern, however, suggests that in CPRS, probably most of them live unattached over the sandy or shelly bottoms. In Patagonia, most individuals of *O. puelchana* have this habit, with the right valve downwards, a position that provides more stability under strong water currents, mainly during early life stages (Pascual *et al.*, 2001). It seems likely that most oysters from the CPRS adopted a similar lifestyle, taking in account the scarcity of suitable hard substrates.

The large concentrations of fossil marine shells and other remains on the continental shelf (a stable environment below the depth affected by waves, up to 10-12 meters), would provide a quasi-stable substrate for oysters. However, settlement of oysters on other biogenic remains from these concentrations is scarce. One remarkable example is a fragment of a fossil echinoid *Encope emarginata* Leske, 1778 that was colonized by an oyster that outgrew the echinoid (Lopes, 2011). This association does indicate that the fossil echinoid remained in a stable position on the bottom for long periods of time before its removal to the beach.

Bioincrustation in fossils from the continental shelf of CPRS seems related to depth. Lopes and Buchmann (2010) reported that vertebrate remains found near the shoreline exhibit few episkeletozoans, contrary to those collected in deeper areas (between 20 and 40 m), that exhibit many colonizers and from distinct groups. Because all the available fossil specimens of oysters and other bivalves come from the near-shore, the pattern of bioerosion and bioincriustation in molluscan specimens from deeper areas of the shelf is not yet known, but it may be similar to that of vertebrate remains.

The higher frequency of *Entobia* in oyster shells from Mostardas, in comparison to those from Concheiros, is probably due to the relative absence of other bivalve remains in the former and the occurrence of large submarine concentrations of fossil shells in the latter. While in Mostardas the endoskeletozoans would colonize the most available hard substrate, namely oyster shells, in Concheiros those organisms have much more options of substrate in the proper fossil concentrations. The most abundant taxa in such concentrations are the bivalves *Glycymeris longior*, *Amiantis purpuratus* and *Pitar rostratus*, while oysters are comparatively scarce (Lopes and Buchmann, 2008); thus, the boring sponges would settle preferentially on the former.

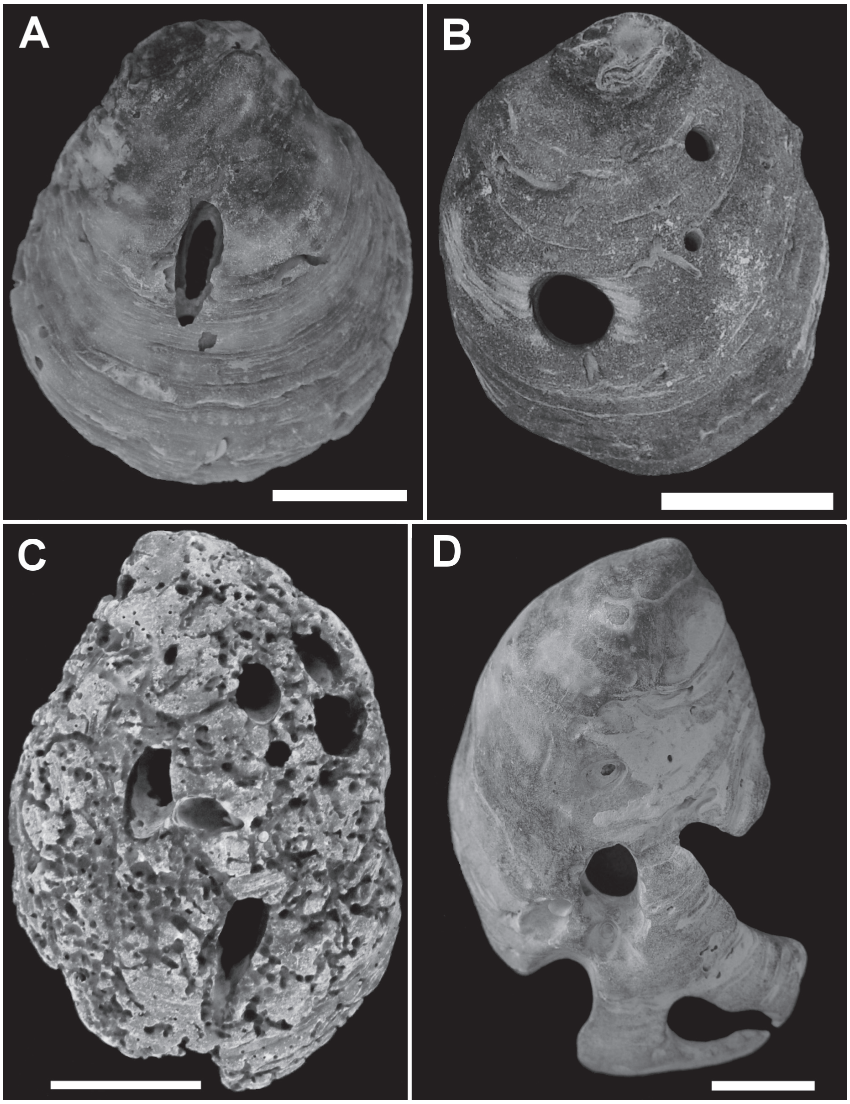

Figure 7. **A**. *Gastrochaenolites* borings parallel to the external surface of the valve; **B**. *Gastrochaenolites* borings perpendicular to the valve; **C**. left valve of *O. puelchana* showing six large *Gastrochaenolites* borings; **D**. fragmentation of the ventral margin of the valve due to the presence of *Gastrochaenolites* borings. Scale bars = 20 mm.

On the other hand, *Caulostrepsis* is more abundant among oysters from Concheiros, probably due to the larger size of the polychaetes that produce these borings, which would require larger shells for their settlement. Lopes and Buchmann (2008) found that this ichnogenus is scarce among the smaller bivalves found in Concheiros.

The scarcity of *Gastrochaenolites* among oysters from Verga and Concheiros suggests that in these areas the mytilids prefer to colonize the lithified paleo-beachlines instead of shells. Many blocks of beach rock removed from these rocky structures and collected along the beach are bored by mytilids. In the southern Brazilian coast, *Lithophaga patagonica* d'Orbigny, 1847 is likely the producer of such traces (Rios, 1994). Mauna *et al*. (2005) found a higher proportion of *Gastrochaenolites* borings on the left valve of recent and Miocene oysters from large concentrations found in Patagonia, including *O. puelchana*; all borings were observed on the external surface, indicating that were produced while the individuals were still alive. On the specimens analyzed here, the percentage of *Gastrochaenolites* on both valves is similar (52.5% in the left one, and 47.5% in the right one), and present both on the external and internal sides. This seems to indicate that were produced not only during the lifetime but also after death of the oysters.

All ichnogenera observed on the oyster shells also occur in other fossil molluscan taxa, except *Gastrochaenolites* that is very scarce among the smaller taxa (Lopes and Buchmann, 2008). This is probably related to the larger size of the oyster shells, which make it suitable for the settlement of larger mytilids. It is noteworthy that *Pennatichnus*, a bioerosion made by ctenostomate bryozoans was not found in the oysters, although it is common in other molluscan fossils from CPRS, and has been reported in Miocene oysters from Patagonia (Parras and Casadío, 2006).

Oichnus, produced by predatory gastropods (Bromley, 1981) is found in few bivalves from the continental shelf, but is totally absent in oysters, possibly due to their thicker shells. On the other hand, several smaller oysters from fossil accumulations found in Chuí Creek, a fossiliferous outcrop located some 10 km far from the present coastline, exhibit borings produced by such predators (Lopes, s.d.).

The higher proportion of borings on the external side of the valves suggests that most of the bioerosion was produced while the oysters were still alive. If the oysters assume a living position with the convex (external) side of the left valve upwards, as seen in Patagonia (Pascual *et al*., 2001), then they will remain stable under weak currents, and most of the bioerosion will be produced externally. The same could apply to disarticulated valves, but in this case the stable position would be a result of hydrodynamic regime. While the oysters were alive, bioerosion on the internal surface of the valves would be absent or restricted to the marginal area, due to the soft tissues that cover most of the internal surface. Oysters could also defend themselves from larger

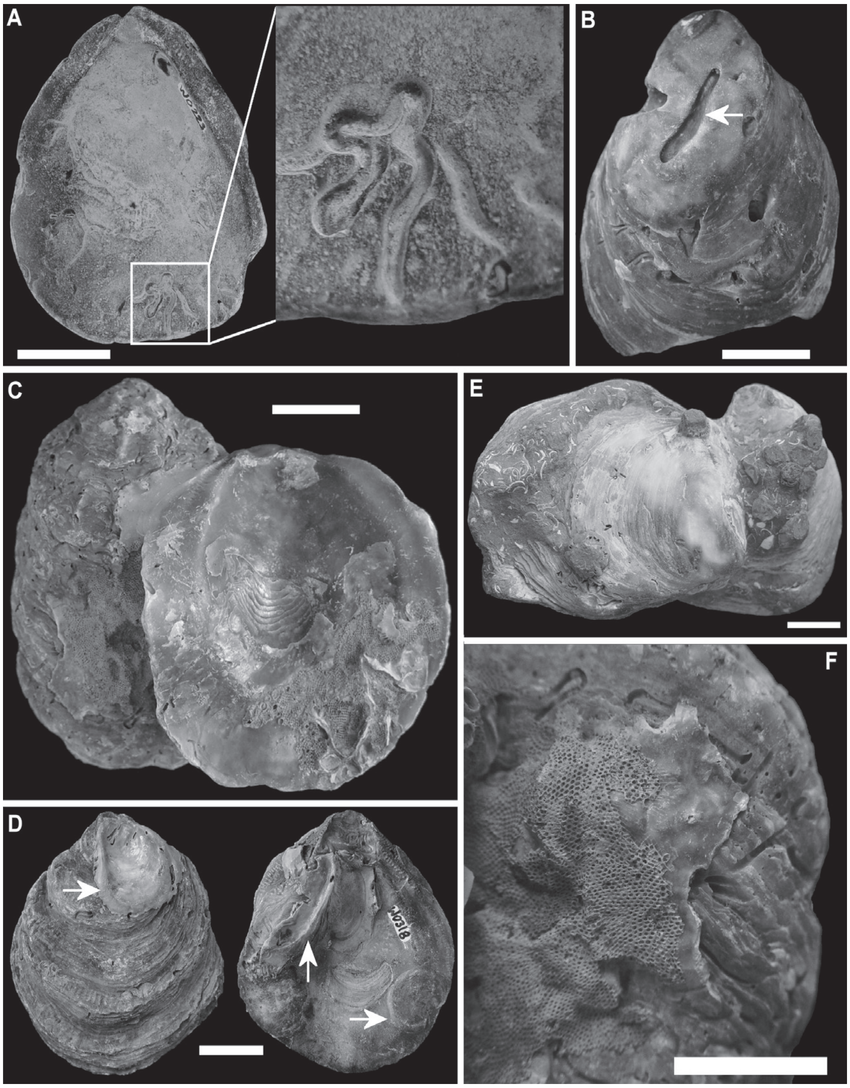

Figure 8. **A.** *Maeandropolydora* gallery on the internal surface of a right valve of *O. puelchana*; **B.** *Maeandropolydora* gallery on the external side of *O. puelchana*; **C.** left valve (at left in the photo) of *O. puelchana* attached to a right valve of other specimen; **D.** *O. puelchana* with encrusting ostreids (at arrows) on the external and internal sides; **E.** cirripeds over two attached individuals of *O. puelchana*; **F.** a bryozoan colony on the exernal surface of a valve. Scale bars = 20 mm.

bioeroders such as polychaetes closing their valves, but the decomposition of the soft parts and disarticulation of the valves after death would provide additional substrate for several organisms, which is indicated by the presence of borings and episkeletozoans on the internal side of the valves. The presence of bioincrustation by large oysters on both internal and external sides, indicate that the valves were subject to several cycles of reworking intercalated with relatively long periods of stability and exposure on the water-sediment interface.

Long periods of stability with low sedimentation rates would be required for the settlement and growth of the *Lithophaga* mytilids and also clionid sponges that produce *Entobia* (Lorenzo and Verde, 2004). In the CPRS, such conditions would occur during marine transgressions, when sea-level could reach some 2-3 m above the present level (Angulo *et al.*, 2006; Dillenburg and Hesp, 2009), eroding the coastline and leaving behind transgressive lag deposits formed by coarser material on the ravinement surface (e.g., shell remains). Under the following marine regression, the once deep and stable bottoms in which the oysters were preserved would be reworked and the remains buried by the next marine transgression.

The apparent absence of a preferential settlement area in the external side of the valves indicates that the endoskeletozoans would occupy any available surface, or, given that the fossil oysters were probably reworked and colonized several times, the borers would use any available surface that has not been previously occupied. The relative absence of episkeletozoans could be explained by the speed of water currents, which would be strong enough to preclude its settlement. Yet, the fossil remains collected along the beach come from shallow areas (up to 10-12 m in depth), which are constantly affected by waves. Given that vertebrate fossils from deeper areas exhibit many episkeletozoans (Lopes and Buchmann, 2010), it seems likely that oysters from these areas may be colonized as well. Endoskeletozoans would not have been much affected by these conditions, because once the process of boring had begun, these organisms would be protected on their cavities.

COMPARISON TO OTHER MOLLUSCAN TAXA

Lopes and Buchmann (2008) described the presence of bioerosion in fossil shells from the most abundant taxa found in Concheiros (*A. purpuratus*, *P. rostratus* and *G. longior*). A comparison between the bioerosion on these remains and that on oysters shows some interesting differences (Table 1). Most of the three taxa in the Concheiros materials are bioeroded by *Entobia*, while the oysters mainly exhibit *Caulostrepsis* and are characterized by the absence of the ichnogenera *Pennatichnus* and *Oichnus*. The absence of *Oichnus* is probably related to the thickness of the oyster shells in comparison to the

Table 1. Percentage of fossil bivalves from the CPRS exhibiting bioerosion by *Entobia* (Ent), *Caulostrepsis* (Cau), *Pennatichnus* (Pen), *Maeandropolydora* (Mae), *Gastrochaenolites* (Gas) and *Oichnus* (Oic).

	Ent	Cau	Pen	Mae	Gas	Oic
A. purpuratus	71	21	62.5	4	0	0
P. rostratus	90	25	35	0	5	0
G. longior	76	23	34	1.5	3	1.5
O. equestris	20	30	0	3	3	0
O. puelchana	33	47	0	6,5	10	0
C. virginica	39	39	0	13	30,5	0

other bivalves, which would difficult the perforation by the predatory gastropods that produce this ichnogenus (Bromley, 1981). On the other hand, the larger and thicker oyster shells are a suitable substrate for the settlement of larger endoskeletozoans such as polychaetes and mytilids, which would explain the relative larger proportion of *Caulostrepsis*, *Maeandropolydora* and *Gastrochaenolites* in oysters, when compared with the thinner shells of smaller bivalves. And the low proportion of bioerosion in *O. equestris* is probably related to its smaller and thinner shell, when compared with *O. puelchana* and *C. virginica*.

A. purpuratus, *P. rostratus* and *G. longior* are infaunal suspension-feeders that spend most of their lives buried in the sediment. So, their life habit does not seem to be a factor that controlled the ichnological differences between these taxa and the oysters. Besides, most of the bioerosion on the former (except for *Caulostrepsis*) is observed on the internal side of the valves, indicating post mortem attack by endoskeletozoans (Lopes and Buchmann, 2008).

CONCLUSIONS

Bioerosion is the dominant ichnological process found in fossil oysters from CPRS. The identified ichnogenera are *Caulostrepsis*, *Entobia*, *Maeandropolydora* and *Gastrochaenolites*. Most of the oysters are bioeroded, a process more common on the external surface of the valves. Such observation suggests that most of the settlement by endoskeleotozoans occurred while the oysters were still alive. Nevertheless, bioerosion is also found in the internal surface of the valves, and is most likely that have occurred after death and decomposition of the soft tissues.

The low proportion of *Entobia* among samples from Concheiros is probably due to the high abundance of other bivalve fossils in this area, which would be the most readily available substrate for settlement.

Bioincrustation is comparatively scarce, and the only endoskeletozoans observed are other oysters (*O. puelchana* and *O. equestris*), cirripeds (cf. *Balanus* sp.) and bryozoans (order Cheilostomata). The ichnological differences between the oysters and other bivalves are probably related to the greater thickness and size of the shells of the former, rather than to the life modes. The complex patterns of bioerosion and bioincrustation in the fossil oysters indicate several episodes of exhumation and burial, correlated to sea-level oscillations that affected Brazilian coast during the Late Quaternary.

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