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Living on an island: characterization of the encrusting fauna of large pectinid bivalves from the Lower Cretaceous of the Neuquén Basin, west-central Argentina

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Exposed mollusc shells may act as benthic islands in soft bottoms, and the analysis of their encrusting faunas provides unique palaeoecological information. In the late Valanginian of the Agrio Formation (Neuquén Basin, west-central Argentina), the large pectinid *Prohinnites* acted as a benthic island on soft substrates. Inequivalved *Prohinnites* adults with small, smooth cementing scars on the right valve suggest that a free reclining life habit followed the epibyssate juvenile and cementing phases. The encrusting fauna on *Prohinnites* was studied taxonomically and palaeoecologically by means of a quantitative approach. Over 90% of 123 valves presented encrusters. Encrustation was equally common in both valves. Internal encrustation was rare. The left umbonal region was less encrusted probably due to sediment accumulation or early colonization by soft-bodied taxa. The fauna was composed of 14 encrusting taxa, including oysters, serpulids, sabellids and cyclostome bryozoans. Oysters exceeded 50% of the total abundance, but serpulids and bryozoans were more diverse. Serpulids and particularly oysters showed a gregarious life habit. Few interactions took place among encrusters and most were *post-mortem*, involving the overgrowth of already dead oysters. The oysters were early settlers that took advantage of their gregarious behaviour to rapidly cover available hard surfaces. However, they were unable to exclude bryozoans and polychaetes, which settled on the pectinid's valves regardless of the presence of oysters. The studied fauna corresponds to a climax community that was structured by larval abundance rather than by competitive interactions; oysters settled first and replenished themselves while polychaetes and bryozoans settled over or alongside them ☐ *Benthic island, encrustation, gregariousness, hard substrate fauna, Prohinnites.*

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Fossil hard substrate faunas provide exceptional opportunities for palaeoecological studies, as they preserve several key features that are typically lost during fossilization of soft-bottom dwellers, such as absolute abundance and spatial relationships among individuals (Liddell & Brett 1982; Lescinsky 1996; Taylor & Wilson 2003). These communities also provide valuable information on environmental parameters, such as the interplay between sedimentation rate and consistency of the substrate, water energy and depth. Recently, Brett *et al.* (2011) have defined the concept of 'sclerobiofacies' as associations of hard substrate communities that are characteristic of different marine environments. These biofacies can be used with caution to interpret environments from the past.

However, the study of hard substrate faunas presents some drawbacks; for example, to evaluate the faunal succession, it is vital to establish the order in which different organisms settled on the hard substrate, and *in vivo* interactions and *post-mortem* overgrowths can be somewhat difficult to discern. It must be kept in mind that in hard substrate faunas, occupation of space is intimately related to access to resources (Buss 1979) and thus intense competition for space may take place.

Colonial organisms tend to be more successful in these communities as they may spread in all directions, easily cover irregular surfaces, and are able to tolerate partial mortality of the colony (Taylor & Wilson 2003). This predominance of colonial organisms is particularly true for recent tropical settings (see Jackson 1977, 1979; Buss & Jackson 1979). *In vivo* interactions are sometimes preserved in spectacular detail among colonial hard substrate dwellers, by means of skeletal modifications along contact margins of the organisms involved (see Taylor & Wilson 2003, for several examples).

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Hard substrate islands on soft sea-bottoms are commonly provided by pebbles, cobbles, boulders and the mineralized skeletons of marine organisms. The concept of the benthic island, introduced by Kauffman (1978), refers to these isolated patches of hard substrate scattered on a soft sea-bottom. In the case of benthic islands provided by shells, it is necessary to distinguish between *in vivo* and *post-mortem* colonizers. *In vivo* colonizers are true epibionts (sensu Taylor & Wilson 2002) and were necessarily adapted to the life habit and general ecological requirements of their host or basibiont. *Post-mortem* settlers, on the contrary, may have colonized the shell in a very different situation than the original one. Differentiation of *in vivo* and *post-mortem* colonization of a fossil shell is often difficult (see Taylor & Wilson 2003) and hence in this work we will refer, *a priori*, to all organisms fixed to the host shell as encrusters.

Benthic islands are subject to periodic reorientation, which impacts on the encrusting community. The effects that this disturbance may have on encrusters have been addressed by many authors. Among these, Osman (1977) performed a detailed analysis on this subject, finding that those patches undergoing disturbance too frequently or too rarely will have a reduced diversity. In the first case, the community is constantly maintained in the early stages of colonization; the first settlers establish on the patch and are quickly overturned and killed, and the community cannot progress further. In the second case, if a community is left to progress without disturbance for too long, it will eventually become dominated by a few, competitively superior species. Hence, an intermediate frequency of disturbance allows the community to progress beyond the very first few colonizers, but not for so long that domination by one or few taxa is established (Osman 1977). This varies with substrate size and wave energy, which are also related to water depth, and hence, this scenario is a general rule for either small to large substrates at one depth or equal-sized substrates at increasing depths.

Numerous examples of hard substrate faunas have been described throughout the Phanerozoic (Taylor & Wilson 2003) and have been particularly common during the intervals of 'calcite seas' (Palmer 1982). After the Permian extinction, hard substrate faunas experienced a major change; a variety of sessile groups originated and/or expanded, such as serpulids, pedunculate cirripeds, foraminifers and scleractinian corals (Lescinsky 2003). Cyclostome bryozoans gained importance during the Mesozoic while cheilostomes greatly expanded during the Late Cretaceous (Boardman & Cheetham 1987). Bivalves (particularly oysters) and serpulids were the commonest Mesozoic macroencrusters; the first experienced a radiation of cementing forms as a consequence of an increased predation pressure (Harper 1993; Harper & Skelton 1993).

In particular, during the Cretaceous, encrusting faunas were composed mainly by serpulids, oysters, foraminifers, cyclostome and cheilostome bryozoans, sponges, and thecideidine and craniid brachiopods (Taylor & Wilson 2003). The Cretaceous was a time of calcite sea (Calcite II; see Hardie 1996; Stanley 2006), favouring the precipitation of calcite and thus the proliferation of well-calcified organisms as well as the formation of hardened horizons (Taylor & Wilson 2003).

Many of these encrusting taxa typically present a gregarious behaviour (see Pawlik 1992; Hadfield & Paul 2001) and are commonly found in clusters. Serpulids and oysters are (along with balanids) particularly well-known examples of gregarious settlers, favouring attachment on surfaces in which conspecifics (and even congenerics; see Tamburri *et al.* 2008) have already settled. Chemical cues released by adult and juvenile oysters, and serpulids are detected by larvae, inducing settlement (e.g. Toonen & Pawlik 1996; Tamburri *et al.* 2008). Despite aggregation results in increased competition as well as in some larvae being eaten or removed by conspecifics, advantages of gregariousness must outweigh disadvantages, as it is widespread among marine invertebrates (Pawlik 1992). Jackson (1983) considered that the occurrence of aggregated conspecifics, despite the intense intraspecific competition, would have an overall benefit given by the rapid colonization of a greater amount of the available surface, maintaining competitors at bay. According to Jackson (1983), benefits of a gregarious behaviour also include protection against predators and interspecific competition for space and resources, as well as stabilization of substrates. Further, clustered conspecifics can be considered to simulate a colonial habit by presenting a surface consisting mostly of feeding openings (Jackson 1977).

Numerous examples of hard substrate faunas (including rocky shores, hardgrounds, cobbles and shells) are known from the Cretaceous (e.g. Pugaczewska 1965; Bromley 1970; Kennedy & Klinger 1972; Bottjer 1982; Wilson 1986; Lescinsky *et al.* 1991; Lehmann & Wippich 1995; Dhondt & Dieni 1996; Villamil 1996; Stilwell 1997; Wilson & Taylor 2001; Záruba *et al.* 2002; Taylor & Wilson 2003; Žítt. *et al.* 2003; Jagt *et al.* 2007; Lukeneder 2008; Zamora *et al.* 2008; Taylor *et al.* 2009; Zágoršec *et al.* 2009; Sørensen & Surlyk 2010; Borszcz *et al.* 2013). Most known cases are, however, of Late Cretaceous age, and very few are from the Cretaceous of the South-

ern Hemisphere. This results in an underrepresentation of Early Cretaceous and southern hard substrate faunas.

The genus *Prohinnites* Gillet (Bivalvia, Pectinoidea), a large pectinid bivalve, was a commonly abundant component of shallow Early Cretaceous seas. Despite most of its records being Tethyan, the genus was quite widespread (Harper *et al.* 1996). Several species have been nominated, mostly from Europe, and all of them are known to have had a byssate juvenile and a cementing adult stage (Harper *et al.* 1996).

In the Lower Cretaceous of the Neuquén Basin, west-central Argentina, *Prohinnites* is locally abundant in the Pilmatué Member of the Agrio Formation. It is heavily encrusted, suggesting that it commonly acted as a benthic hard substrate island on soft sea-bottoms. Thus, it provides an opportunity to perform a detailed study on its encrusting fauna and its palaeoecological implications. Therefore, the main objectives of this work are to study the taxonomy of the encrusting fauna of *Prohinnites* from the Lower Cretaceous Agrio Formation of the Neuquén Basin, west-central Argentina; to statistically evaluate the diversity, abundance, interactions and distribution of encrusters on *Prohinnites*; and to analyse the dynamics of the encrusting fauna.

Geological setting

The Agrio Formation in the Picún Leufú depocentre, Neuquén Basin

The Neuquén Basin, located in west-central Argentina, extends through most of the Neuquén and Mendoza provinces along the Andean foothills, between 32° and 40° SL (Fig. 1A). During most of the Jurassic and Early Cretaceous, it was a back-arc basin with a gentle thermal subsidence regime. Oceanic waters from the Pacific Ocean flooded through the Andean volcanic arc, conforming a large marine epicontinental engulfment. During the Early Cretaceous this basin had a mid-latitudinal location close to its current position, approximately between 28° and 36°S, based on palaeomagnetic data (Somoza 2011). Thus, it was placed near the boundary between the tropical and subtropical belts.

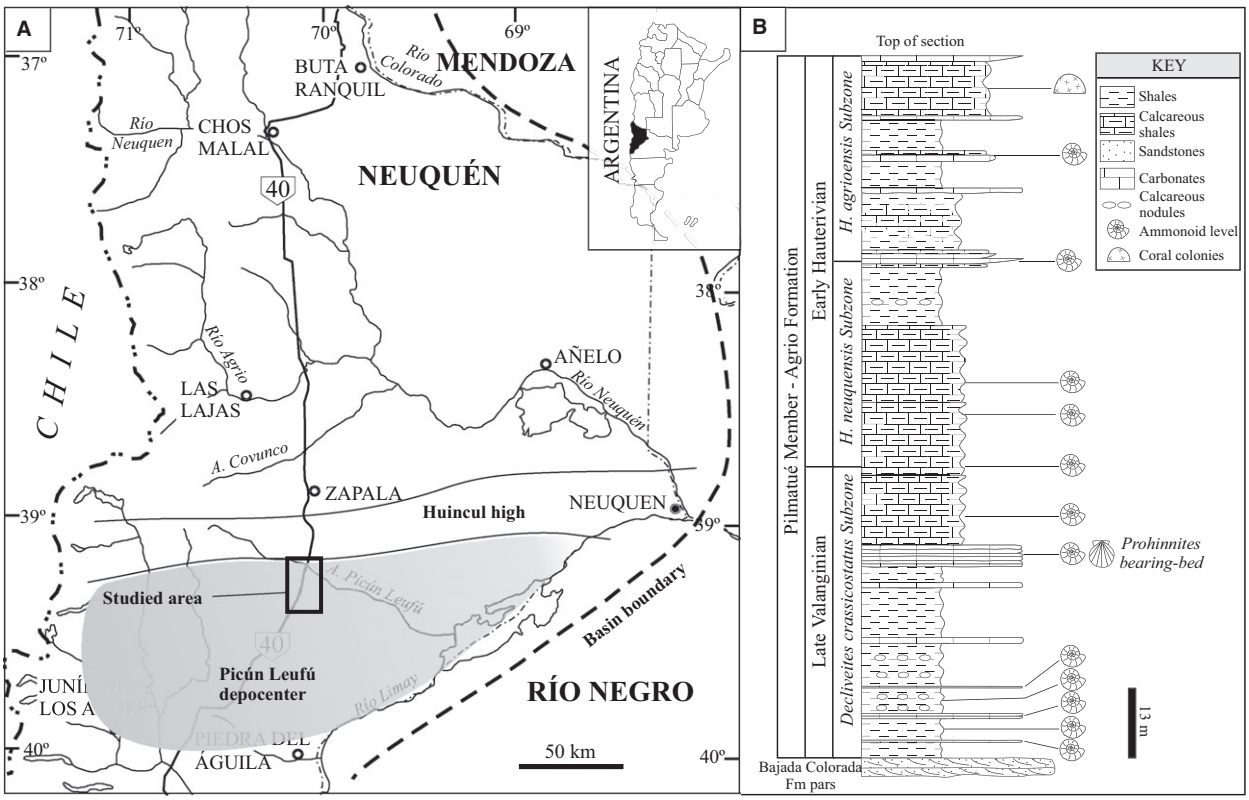


Fig. 1. A, map of west-central Argentina showing the boundaries of the Neuquén Basin and the Picún Leufú depocentre to the south during the Early Cretaceous. B, sedimentary log of the Agrio Formation at Cerro Birrete showing the *Prohinnites* bearing-bed, late Valanginian.

In this work, we have focused on the Picún Leufú depocentre, which developed in the southern region of the basin, between the Huincul High in the north and the Somún Curá Massif in the south (Fig. 1A). The Huincul High, an east-west oriented morphostructural feature, was recently proved to have been an ancient positive element developed since the Early Jurassic and prior to the main Andean contractional cycle that started in the Late Cretaceous (Naipauer *et al.* 2012). This topographic high was at times a true division between the northern and southern regions of the basin, especially during times of relative sea level falls. However, during transgressive episodes, marine waters surpassed it and both regions became partially connected. It is within this southern depocentre that the *Prohinnites* bearing-bed was recorded in the Pilmatué Member of the Agrio Formation. The presence of *Prohinnites* in this part of the basin (while it is absent from the central region) is coincident with a predominance of facies containing a greater carbonate content that were deposited under reduced clastic input from the continent in the Picún Leufú depocentre.

The Agrio Formation, defined by Weaver (1931), is a well-known stratigraphic unit containing an abundant and diverse marine fossil content, and it is also one of the main target units explored by oil companies in the basin. It was deposited from early Valanginian to earliest Barremian times according to a refined ammonoid zonation, which has been correlated to the European Standard Ammonoid Zonation and constrained by a U-Pb shrimp age (Aguirre-Urreta *et al.* 2007, 2008). The stratotype of the unit comprises three members, namely the lower Pilmatué Member, the middle Avilé Member and the upper Agua de la Mula Member (Weaver 1931; Leanza *et al.* 2005). In the studied localities, the unit overlies the Bajada Colorada Formation and underlies the La Amarga Formation (Fig. 1B). Both the Pilmatué and Agua de la Mula members are composed mainly of dark-grey shales and calcareous shales with intercalations of thin sandstone bodies and shell beds. They were interpreted as deposited in a shallow mixed clastic-carbonate ramp with occasional storm influence (Spalletti *et al.* 2001; Lazo *et al.* 2005). The Avilé Member is a thin, but laterally continuous continental sandstone deposited during a relative sea level fall in the mid Hauterivian (Veiga *et al.* 2011).

Prohinnites *bearing-bed in the Agrio Formation*

The *Prohinnites* bearing-bed was recorded in the lower third of the Pilmatué Member in the Picún Leufú depocentre (Fig. 1B). The associated ammonoids belong to the *Decliveites crassicostatus* Subzone of late Valagninian age (Aguirre-Urreta & Rawson 2010). The bearing-bed was easily correlated among the studied localities by means of associated ammonoids, but also because its benthic faunal composition, characterized by a high abundance of pleurotomariid gastropods and irregular echinoids, is rather unusual in the Agrio Formation (see Cataldo & Lazo 2012). This bed was recorded in the localities of Cerro Birrete, Cerro Negro Chico, Puesto Marucho, Marucho Oeste and Barda Marucho (Fig. 2). These localities are characterized by thinner sections of the Agrio Formation in comparison with the stratotype, absence of the middle Avilé Member and a greater proportion of carbonate content in comparison with other localities of the central region of the basin. These southern sections are composed mainly of limey shales alternating with coquinas, skeletal sandstones, packstones and grainstones. Microfacies indicate a range of environments from high-energy neritic shoals to tidal flats and channels deposited on a shallow homoclinal clastic-carbonate ramp (Di Paola 1990).

A bed-by-bed log of the Agrio Formation was performed at Cerro Birrete taking into account stratigraphical and sedimentological features such as geometry, thickness, lithology, contacts, sedimentary and biogenic structures, and macrofossil content (Fig. 1B). Focus was made on the *Prohinnites* bearing-bed to address its degree of time-averaging and lateral transport (see also Cataldo & Lazo 2012). The bed, a composite skeletal carbonate, is characterized by wedge-shaped amalgamated skeletal wackestones and packstones reaching a maximum thickness of 3.2 m. The basal contact is sharp to locally erosional. Single beds are elongated lenses tens of metres wide. They are loosely to densely packed and range in thickness from 0.2 to 0.8 m. They may show internal horizontal lamination, poorly defined cross-bedding or heterolithic bedding. The dominant fraction is composed of shell debris mixed with whole shells. The matrix is a clay–lime mixture. Bioturbation is very common only towards the top.

Bioclasts are concordant in cross-section (shells convex-down and convex-up). However, deep-burrowing infaunal bivalves are usually in life position. The macrofossil assemblage is rich, including 32 taxa of invertebrates represented by nautilids, ammonoids, gastropods, bivalves, echinoids, serpulids and corals (see appendix 1 in Cataldo & Lazo 2012). Suspension-feeders dominate the assemblage. This facies is intercalated between thick shale

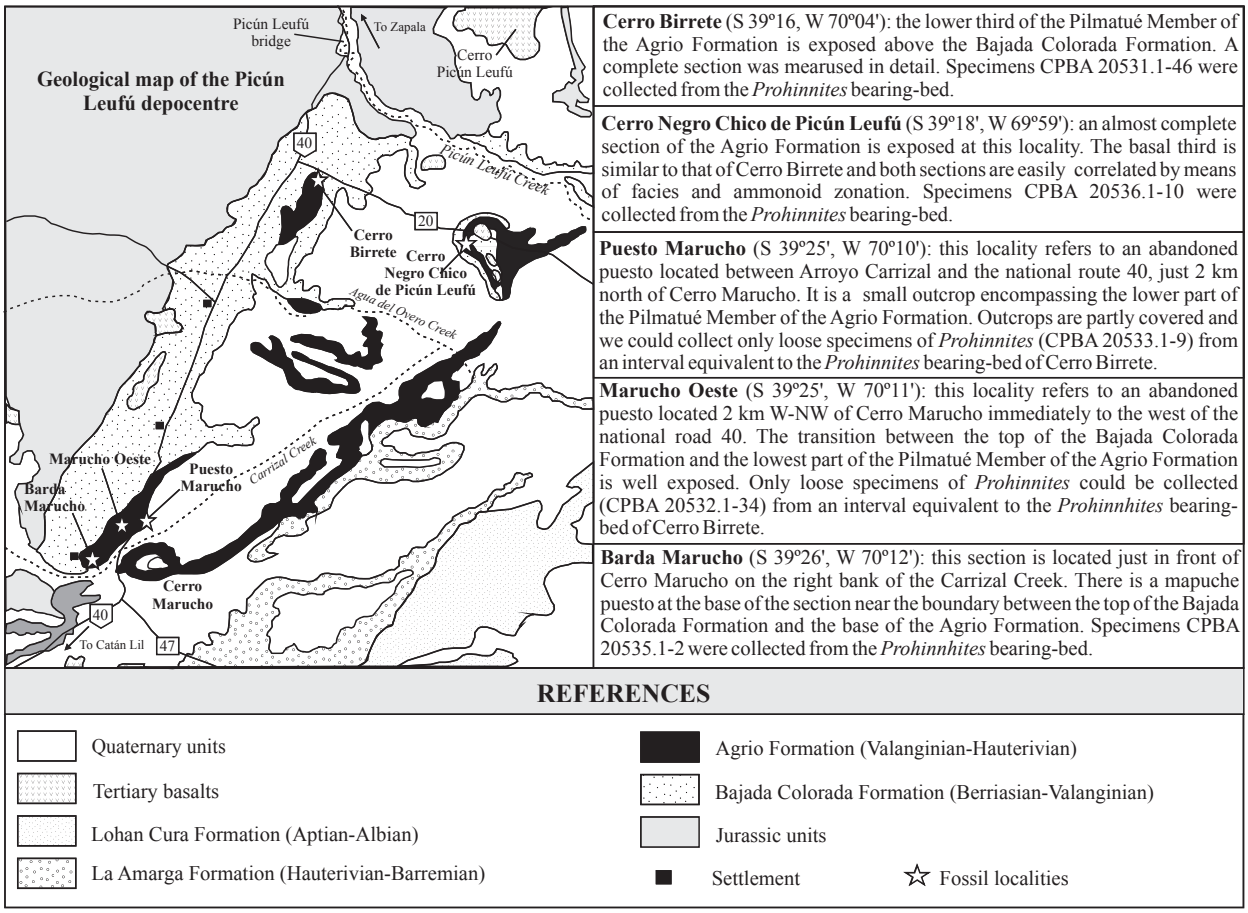


Fig. 2. Geological map of the Picún Leufú depocentre showing stratigraphical units and fossil localities. Based on Leanza & Hugo (1997).

beds and records the amalgamation of skeletal banks deposited under the influence of episodic high-energy waves, currents and tides. Wedge-shaped skeletal banks were defined as fringing banks of carbonate ramps (Read 1985); they are complex linear accumulations of shoals and bars that parallel the shoreline and are cut by interbar tidal channels. Bioclast concentration in these deposits is due mainly to physical processes, but deep infaunal organisms remain in life position, as seen in the *Prohinnites* bearing-bed. Whole shells have not been significantly transported and are thus deemed to be parautochtonous of a very shallow-marine setting. The fauna indicates a well-oxygenated bottom, soft substrate, normal marine conditions and warm-temperate waters. The record of macrobioerosion on the studied shells suggests a shallow sea-bottom placed entirely within the photic zone and likely colonized by benthic algae (Bromley 1992). The degree of time-averaging corresponds to the within-habitat time-averaged assemblages of Kidwell (1998) and likely spans rather <0.5 My taking into account the duration of the ammonoid zones in this basin (see also Cataldo & Lazo 2012).

Study materials and statistical methods

Materials and mapping

All studied materials are deposited in the repository of the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales (CPBA), Universidad de Buenos Aires, Buenos Aires, Argentina. Catalogue numbers refer to a set of specimens collected from a given section. Suffixes indicate the number of a particular specimen within a given catalogue number. All specimens are from the authors' collection except for the materials from Barda Marucho locality (see below), which were collected by M.B. Aguirre-Urreta and D. Rodríguez.

A total of 123 valves (including some articulated specimens) and valve fragments of *Prohinnites* were

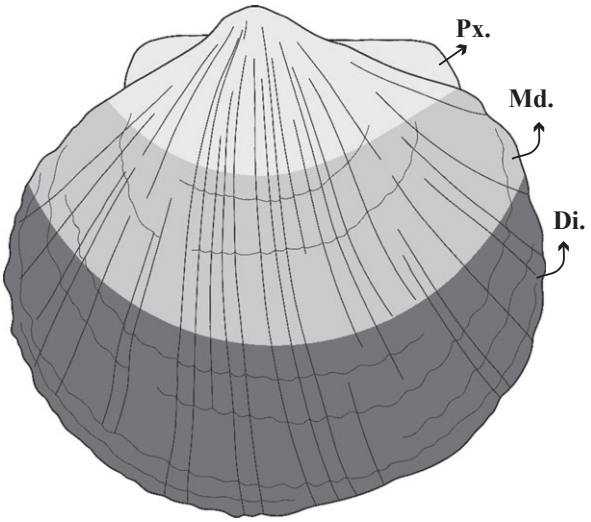
collected from Cerro Birrete (CPBA 20531.1-46), Barda Marucho (CPBA 20535.1-2), Marucho Oeste (CPBA 20532.1-34), Puesto Marucho (CPBA 20533.1-9) and Cerro Negro Chico de Picún Leufú (CPBA 20536.1-10). Specimens were cleaned by vigorous washing and brushing of the surfaces of the valves, and some of the most tenacious matrix was removed with a needle. Some specimens were also submerged in a 50% acetic acid–water solution to help remove the strongly attached carbonate matrix. Two specimens (CPBA 20531.16 and 20536.2), abundantly encrusted by bryozoans, were treated with an ultrasound bath after cleaning and then taken to an environmental scanning electronic microscope (ESEM) belonging to the Servicio de Microscopía Electrónica de Barrido Analítica of the Facultad de Ingeniería of the Universidad Nacional de La Plata (La Plata, Argentina).

We use, throughout text, the following terms: 'adult' refers to specimens in which the cementing stage of growth had been at least initiated at the time of death and usually refers to specimens with $10 < H < 15$ cm; 'small adult' refers to specimens with $10 < H < 11$ cm; and 'large adult' refers to specimens with $H > 11$ cm (H=height). The overall state of preservation of each valve was determined as follows: complete articulated valves; incomplete articulated valves (one or both of the valves lacking more than 25% of its surface); complete disarticulated valve; and valve fragment (lacking more than 25% of total valve surface).

Each specimen was observed and mapped in detail under a binocular microscope of up to 50X magnification, and valve drawings were used to annotate the position of each encruster, taking into account their size, location and relative orientation to the basibiont and surrounding encrusters. As all drawings were of the same size, this procedure also meant the standardization of the basibiont's size. All encrusters were classified to the lowest taxonomic rank possible. All photographed specimens were previously coated with ammonium chloride except for ESEM pictures.

Statistics

A series of statistical tests were performed on the total number of encrusters by valve and valve zone. Three concentric zones were defined and compared in left and right valves; a proximal third, a medial third and a distal third (Fig. 3). Thus, the number of specimens of each encrusting taxon was recorded by type of valve (left/right), surface (external/internal) and zone of attachment (proximal/medial/distal). Number of encrusters (count data) was more suitable than areal cover which focuses on the intensity of utilization of available space, while our objective, for this study, is to assess the distribution of encrusters across valve zones. In addition, areal cover does not directly reflect abundance of taxa, especially in the case of solitary organisms, and may underestimate the occurrence of small and solitary organisms (Lescinsky 1997), which are the most abundant in the present study case, with the exception of bryozoans and a single coral. Each separated bryozoan colony was counted as one individual.



Prohinnites sp.

Fig. 3. Zonation of the valves of *Prohinnites* sp. used for mapping of encrusters. Px., proximal zone; Md., medial zone, Di., distal zone; the three apply to both left and right valves.

General descriptive statistics were calculated, including the total number of encrusters, mean of encrusters per valve, percentage and total abundance of each encrusting taxon, total incidence of encrustation (defined as the percentage of all valves presenting at least one encruster), and incidence of internal and external encrustation separately. The individual incidence of each encrusting taxon was also recorded. Intensity of encrustation (total amount of encrusters per valve) was plotted to evaluate variability of encrustation across valves. The general orientation of encrusters with respect to the growing direction of the basibiont and occurrence of gregariousness in encrusting taxa were qualitatively assessed. Overgrowth relationships and their likelihood of representing true *in vivo* interactions among encrusters were accounted for, taking note of the encrusters involved, the number of occurrences of each type of interaction and their outcome (which encruster overgrew the other).

The number of right and left valves was calculated, taking into account all well-preserved specimens (the first three states of preservation defined above; valve fragments were in most cases unrecognizable as either right or left valves). A deviance analysis was made to compare the mean of encrusters between right and left valves; a similar application can be found in Everitt & Hothorn (2006). This analysis was repeated for each major group of encrusters separately (i.e. bryozoans, serpulids and oysters) to evaluate preference for a given valve in any of them. A chi-square analysis was made to compare the proportion of articulated specimens (states of preservation 1–2) with both valves encrusted against those with encrusters on just one valve.

To compare the distribution of encrusters across valve zones, a generalized linear mixed model was used (GLMM). Overviews of GLMMs and their applications in ecology can be found in Hedeker (2005) and Bolker *et al.* (2008); this technique allows independent comparison of valve zones as it incorporates the error associated with each valve, in addition to the residual error. Only specimens with articulated or disarticulated complete valves were included in this analysis. Those valves too heavily covered by tenacious carbonatic matrix, which precluded observation of most of the valve surface, were excluded; this resulted in many of the left valves of articulated specimens being left out of the GLMM analysis. Fragments of valves were included only when they were anterior or posterior halves of valves, and thus, all three valve zones were at least partially represented.

Finally, diversity indexes of Simpson Dominance and Pielow's Equitability (see Hammer & Harper 2006) were calculated for the whole encrusting fauna. Pielow's Equitability is independent of the number of species found in the community and easier to interpret than the Shannon–Wiener index, as it takes values between 0 and 1 (Hammer & Harper 2006). Simpson's Dominance gives greater importance to the more represented species and expresses the probability that two individuals picked at random belong to the same species (Hammer & Harper 2006). Values closer to 1 indicate strong dominance. Statistics were performed on R (v.2.15.1).

Morphological and palaeoecological features of Prohinnites

Gillet (1922) erected the genus *Prohinnites* for those species of Cretaceous age previously assigned to *Hinnites* Defrance, which she considered to be phylogenetically separated from the Cenozoic and extant lineage. Gillet (1924) noted that the similarity between *Hinnites* and *Prohinnites* was due to convergence related to a shared life habit. This opinion was later supported by other authors (see Harper & Skelton 1993). According to Hertlein (1969), *Prohinnites* is restricted to the Valanginan-Aptian interval and is known mainly from Europe, but records are also known from Argentina, Mexico, Trinidad, Tanzania, Morocco and Algeria (see Harper *et al.* 1996). All known occurrences are from shallow-marine facies associated with an abundant fossil content (Harper *et al.* 1996).

Prohinnites corresponds to large and thick pectinid bivalves of about 15 cm maximum height. The genus has a *Chlamys*-like byssate juvenile stage, with subcircular, almost flat, thin valves with delicate radial ribs, which is uncommonly well preserved in the umbo of adult right valves. The adult right valve (lower valve) is typically more convex than the flat to slightly convex left valve (upper valve). Both may be ornamented with radial ribs (with occasional hyotal spines) that can be very conspicuous, especially on the left valve. Auricles are little developed in adults. The adult shell presents an attachment mark on the right valve corresponding to a cementing stage, of variable size, but generally small, surrounding the byssate juvenile stage. Attachment marks are quite distinct, with hardly any remains of the original attachment surface. Xenomorphism is absent from both valves. Internally there is a large, subcentral adductor scar and an entire pallial line (Gillet 1924; Harper *et al.* 1996). According to Harper *et al.* (1996), *Prohinnites* individuals could have had life spans of tens of years, as is the case of the recent *Hinnites giganteus* (Gray 1825).

The studied specimens of *Prohinnites* (Fig. 4) are very similar to *Prohinnites ordoniesi* Imlay 1940 (corrected according to ICZN 2000; art. 11, 27) from the Lower Cretaceous of Mexico. However, our material is left in open nomenclature (as *Prohinnites* sp.) until a taxonomic revision of the genus is made. The studied specimens show considerable morphological variation, especially in the convexity of the right valve, the development of its ornamentation and the size of the attachment mark. In the *Prohinnites* bearing-bed, there are records of small, *Chlamys*-like pectinids belonging to *Mimachlamys robinaldina* (d'Orbigny 1847). Their external morphology is similar to the juveniles as observed in adult valves of *Prohinnites* sp., and they could be actual juveniles of it which had not yet reached adulthood at the time of death and burial.

Adult specimens of the studied material may show an oval outline, higher than longer (Fig. 4C) or a subcircular outline with a similar length and height, and flattened right valves (Fig. 4D, F); intermediate

morphologies can also be seen (Fig. 4E). These variations illustrate a great plasticity in the growth of *Prohinnites* sp. Adult specimens of *Prohinnites* sp. are seldom preserved attached to a substrate. In small adult specimens, valves are rather thin (<2 mm), and the cementation scar occupies a large portion of the right valve (50% or more; Figs 4B and 5A–C; Figs 4B and 5B are the same specimen). Large adult specimens present much thicker valves, sometimes reaching 2 cm of thickness (most commonly around 1 cm), and attachment marks are much smaller (about 20% of the valve's height; see Figs 4C–F and 5D). Some of the right valves present the commissure elevated from the substrate by means of a geniculation (Fig. 5D) or a marked shift of growth direction (Fig. 5E).

Large adult right valves commonly present little development of radial ribs in comparison with left valves and rather present strong concentric thickenings along growth lines (Fig. 4C–E). By contrast, in the small adult specimens, ornamentation on the idiomorphic portion of the right valve is very regular

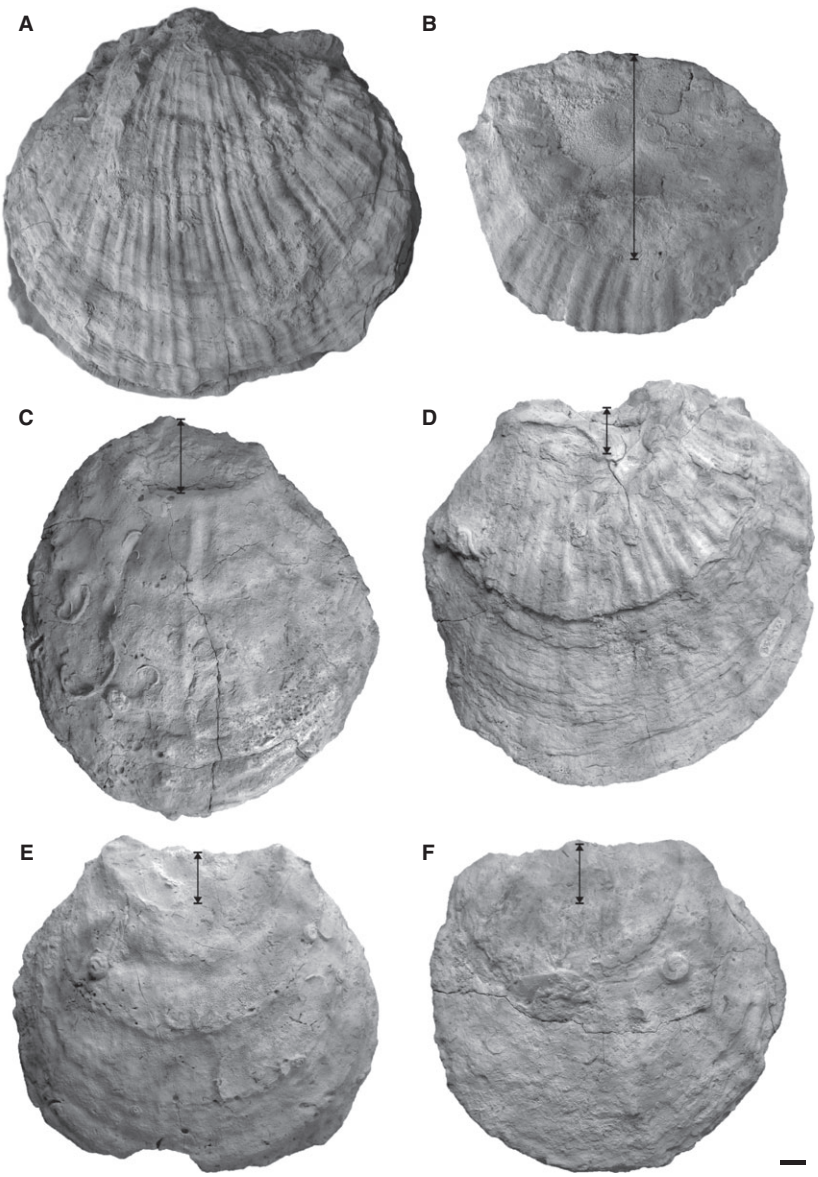


Fig. 4. Morphological features of *Prohinnites* sp. All specimens are large adults except for B, a small adult A, CPBA 20531.1, left valve displaying the regular and well-developed ornamentation. B, CPBA 20531.2, right valve of a small adult specimen with a very large cementation mark. C, CPBA 20531.3, right suboval valve higher than long, with small cementation mark. D, CPBA 20531.4, right valve almost equally longer than high, with strongly developed growth lines, and ribs well developed especially proximally. E, CPBA 20531.5, worn right valve with pronounced growth lines. F, CPBA 20531.6, almost smooth right valve. All from Cerro Birrete locality, early Valanginian of the Agrio Formation, Neuquén Basin, west-central Argentina. All arrowed bars delimit the cementation area in the right valve. Scale bars: 1 cm.

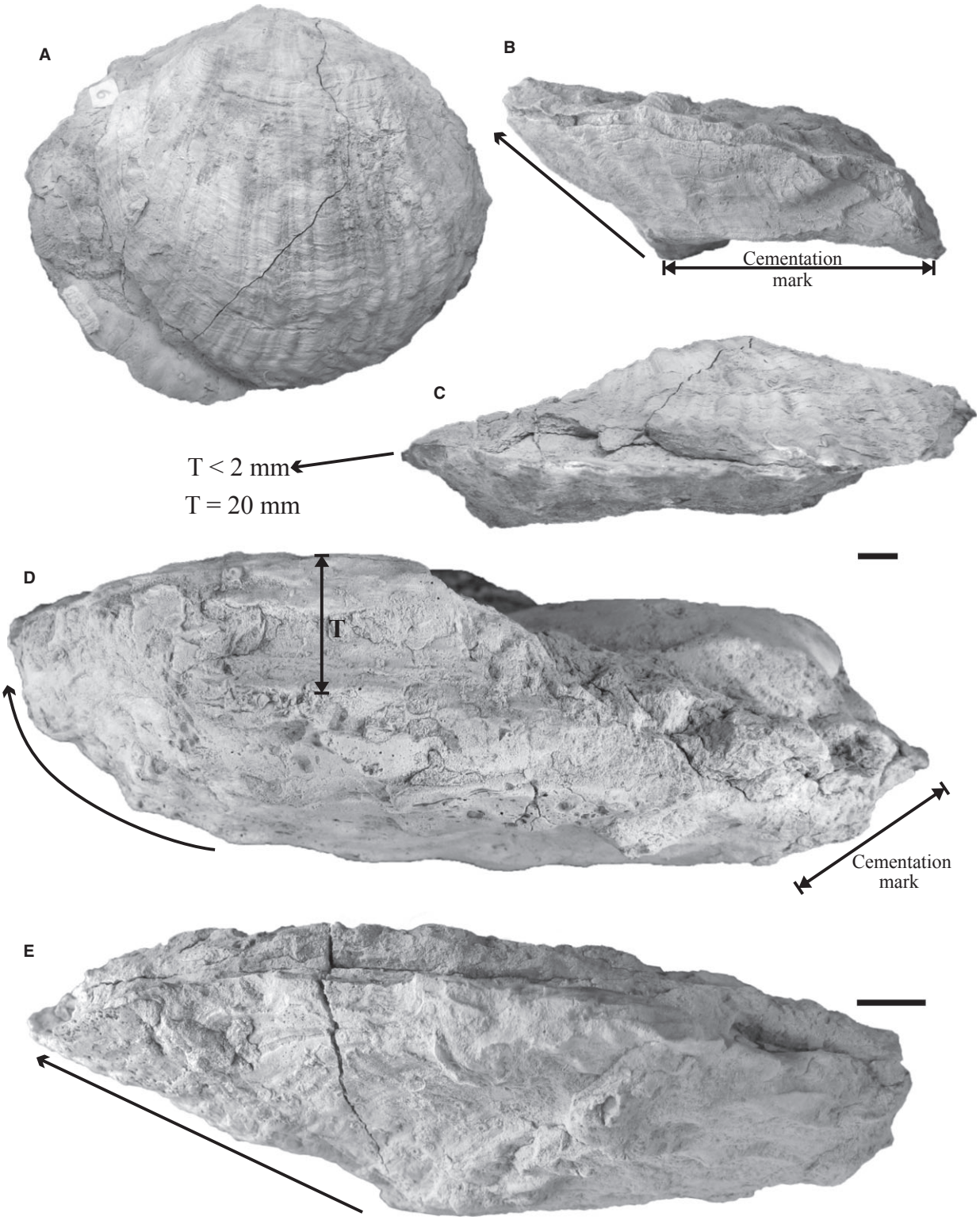


Fig. 5. Valve morphology variation in different growth stages in *Prohinnites* sp. A–C are small adults, D, E are large adults. A, C, CPBA 20531.7, articulated specimen with valves slightly displaced. A, left view, showing well-developed, delicate ribs. C, commissure view, showing thin valves less than 2 mm thick. B, CPBA 20531.2 (see Fig. 4B) in posterior view, showing that the cementation mark occupies more than 50% of the right valve height, and the straight idiomorphic portion that orients the commissure upwards. D, CPBA 20531.3 (see Fig. 4C) in posterior view, showing the great thickness of the valve, and how it presents a curved, convex shape that turns the commissure upwards. E, CPBA 20531.4 in posterior view (see Fig. 4D for a right view, in which the small cementation mark can be appreciated), showing a sharper change in the valve's curvature than seen in D, and more similar to the sharp upturn seen in the specimen pictured in B. All from Cerro Birrete, early Valanginian Agrio Formation, Neuquén Basin, west-central Argentina. T: thickness; Scale bars: 1 cm.

and displays ribs as seen in the left valve (Figs 4B and 5B are the same specimen).

Considering the changes in morphology with growth, and that *Prohinnites* sp. inhabited an environment in which available hard substrates consisted in smaller, more slender shells, it is suggested that it presented three distinct stages in its mode of life. Firstly, juveniles were epibyssate as is known for all species of both *Prohinnites* and *Hinnites*. Secondly, with maturity, a cemented stage followed, in which the right valve attached to an available hard substrate. The absence of xenomorphism, as well as the clean detachment from the substrate, evidenced by smooth cementation marks without remains of the attachment surface, suggests that cementation was rather weak. Thirdly, as the shells grew, likely they exceeded their substrate in size and eventually overgrew it and detached itself, becoming free-lying recliners on the soft seafloor. This is suggested by the small attachment mark in large adults, which would have provided insufficient surface and strength to counter the size and weight of the fully grown valves. In addition, at the third stage, the valves became very large and very thick, much like seen in free reclining bivalves (Seilacher 1984). The elevation of the commisure caused by the pronounced curvature of the right valve likely contributed to keep it away from the substrate and free from sediment.

Our proposal of an ulterior reclining life habit for *Prohinnites* sp. is similar to that proposed by Seilacher (1984, fig. 10, p. 230) for the Pliocene *Hinnites crispus* (Brocchi 1814). According to Seilacher (1984), the species presented an idiomorphic cementation area with radial ribs and thickened valves similar to the typical reclining oyster morphology (Seilacher 1984). Our materials are similar to *H. crispus* in presenting a small attachment scar and thick, convex right valves in large adult specimens.

Results

Taxonomic composition of the encrusting fauna

A total of 14 taxa (Fig. 6) were found encrusting 123 valves and valve fragments of *Prohinnites* sp. Oysters were the most abundant elements of the encrusting fauna, but only a single taxon was recognized; *Amphidonte (Ceratostreon)* sp. Polychaetes include both serpulids and sabellids; the first were represented by six taxa, while sabellids by one, *Glomerula* cf. *serpentina* (Goldfuss 1831). Cyclostome bryozoans were represented by five encrusting taxa and a single colonial coral specimen belonging to the species *Actinastrea colliculosa* (Trautschold 1886) was also found (see Fig. 6).

All encrusters had a cementing life habit, and with the exception of the coral colony, all of them were suspension-feeders. The overall taxonomic composition of the encrusting fauna is along the lines of typical Cretaceous hard substrate faunas (see Introduction). Habit and palaeoecological traits of encrusters agree well with the interpreted shallow, well-oxygenated, agitated marine environment and with a moderate to low turbidity setting. Most of the taxa (the oyster, sabellid, serpulids and several bryozoans) presented Tethyan affinities, which is also true for the basibiont (see 'Morphological and palaeoecological features of *Prohinnites*' above, Luci *et al.* 2013; Taylor *et al.* 2009), which indicates a temperate to warm water temperature. Oysters presented a strong tendency to gregariousness, although they may be found isolated as well. Serpulids and sabellids were also commonly aggregated, but neither did they reach the number of individuals per cluster, nor cover as much of the valve's surface as oysters.

Statistical results

Most of the available material corresponded to valve fragments (45.53%) and right valves were more abundant than left ones (Fig. 7A); articulated specimens were also quite common (34.15% of valves; 21 articulated specimens). Of the 123 studied specimens of *Prohinnites*, 114 presented encrusters, resulting in a total incidence of encrustation of 92.7%. Internal encrustation was rare, involving 17. 9% of encrusted shells, all of which presented external encrustation as well. A total of 2418 encrusters were observed, with a mean of 19.66 encrusters per valve (SD=17.34). Intensity of encrustation was, however, rather variable (Fig. 8); although most valves present up to 30-40 encrusters, the maximum number of encrusters observed in one valve is 82.

Oysters were the main component of the encrusting fauna (comprising 57.5% of the whole fauna), followed by the cyclostome bryozoans '*Berenicea*' (11.1%) and *Neuquenopora carrerai* (9%). Only 6 taxa exceeded a 5% of the total abundance (the aforementioned taxa and several polychaetes; see Table 1). When considering polychaetes and bryozoans as a whole, the first were, however, slightly more abundant than the bryozoans (Fig. 7B). The most abundant taxa were commonly found in a third of the valves, or more (see Table 1), indicating that they were rather widespread and not isolated occurrences.

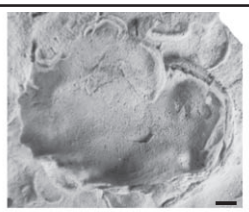
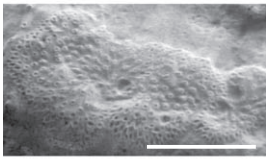
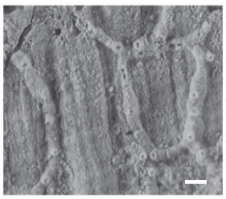
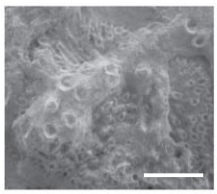
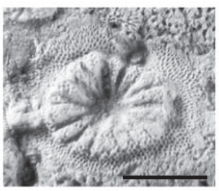
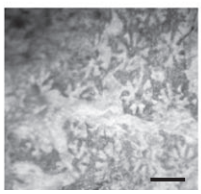
	Encrusting taxa	General Features	References
Oyster	 *Amphidonte (Ceratostreon)* sp.	Small (heigth <3 cm) exogyrid oysters with characteristic marginal chomata and crenulated margins. Most dissaticulated; only left valves remained attached to the basibiont. Commonly aggregated. Scale bar: 5 mm	Cooper 1997; Lazo 2007; Malchus 1990; Stenzel 1971
Bryozoans	 *'Berenicea'* sp.	Subcircular to flabelliform encrusting cyclostome. Tubular autozoecia, porous frontal wall. The genus has been declared invalid by Taylor and Sequeiros (1982) due to loss of the type material; it is now used for bereniciform colonies lacking gonozooids. Scale bar: 2 mm	Gregory 1896; Taylor & Sequeiros 1982; Taylor *et al.* 2009
	 *Microeciella* sp.	Morphology of the colony as in *'Berenicea'*, but presents small, bulbous gonozoecia, with frontal wall similar to that of the autozoecia but imperforated by them. Ooeciopores are small, circular to elongate in outline. Scale bar: 2 mm	Taylor & Sequeiros 1982
	 *?Proboscinopora* sp.	Uniserial encrusting cyclostomes, autozoecia with peristome, with single expanded zooecium conforming the gonozoecium. Scale bar: 1 mm	Pitt & Taylor 1990
	 *Oncousoecia* sp.	Oligoserial encrusting cyclostome, regularly branched. Tubular autozoecia with peristomes. Bulbous gonozooids. Lateral, unconspicuous kenozooids. Scale bar: 1 mm	Taylor & Zatoñ 2008
	 *Neuquenopora carrerai*	Thick, encrusting cyclostome with multiple generations of autozoecia along the margins. In late astogeny develops radial fascicles. Gonozoecium wider than long with pseudopores. Scale bar: 2 mm	Taylor *et al.* 2009
Coral	 *Actinastrea colliculosa*	Small, colonial scleractinian; specimen of 3 cm diameter. Small corallites, separated by 0.2-0.3 mm of coenosteum. Two cicles of septa, the greater ones form the collumella. Septa thickened towards the outer edge of the calix. Scale bar: 1 mm	Löser 2012

Fig. 6. Taxonomic composition of the encrusting fauna found on *Prohinnites* sp. from the late Valanginian of the Neuquén Basin, west-central Argentina.

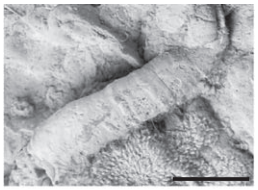
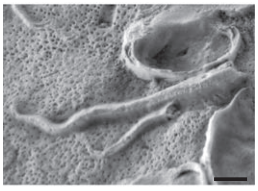
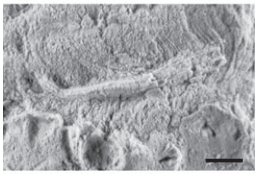
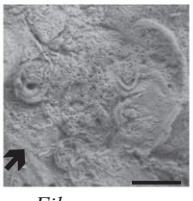
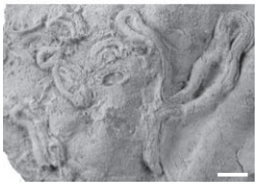
	Encrusting taxa	General Features	References
Serpulids	 *Parsimonia antiquata*	Uncoiled serpulid, smooth tube with occassional transversal thickenings. Transversal section cylindrical. Often broken at the ends. May be aggregated. Scale bar: 5 mm	Regenhardt 1961; J. de C. Sowerby 1829; Luci *et al.* 2013
Serpulids	 *Propomatoceros semicostatus*	Uncoiled serpulid, smooth tube with occassional transversal thickenings. Often broken at the ends. May be aggregated. Scale bar: 5 mm	Regenhardt 1961; Ware 1975; Ippolitov 2007; Luci *et al.* 2013
Serpulids	 *Mucroserpula mucroserpula*	Small, uncoiled but commonly curved sepulid tube with three upper keels, irregularly shaped. Pentagonal to oval transversal section. Base slightly expanded. Often broken at the ends. Scale bar: 2 mm	Regenhardt 1961; Ippolitov 2007; Luci *et al.* 2013
Serpulids	 *Placostegus* cf. *conchophilus*	Coiled serpulid tube with one upper keel, final whorl resting on top of the previous, planispiral coils. Apertural end always broken. Scale bar: 2 mm	Jäger 1983; Luci *et al.* 2013; Radwañska 2004
Serpulids	 *?Neomicrorbis* sp.	Coiled spirorbid tube, planispiral, with transversal ornamentation. Strongly worn. Often aggregated. In the picture a colony of '*Berenicea*' is arrowed. Scale bar: 2 mm	Jäger 1993, 2012; Luci *et al.* 2013
Serpulids	 *Filograna* sp.	Colonial serpulid, tubes more or less subparalell to each other, very small. In the picture a berenicean bryozoan colony is arrowed. Scale bar: 5 mm	Jäger 1983; Luci *et al.* 2013; Pernet 2001; ten Hove & Kupriyanova 2009
Sabellid	 *Glomerula* cf. *serpentina*	Thin (diameter < 1 mm), long sabellid tube of irregular coiling, forming meanders, sharp bends, loops and ofter overgrowing younger portions. Scale bar: 2 mm	Brünnich Nielsen 1931; Jäger 2004; Perkins 1991; Luci *et al.* 2013; Vinn *et al.* 2008

Fig. 6. (Continued)

Only 16 pairs of interactions were observed (Fig. 9), with a total of 37 cases (Table 2). Most of them involved the overgrowth of disarticulated oysters by polychaetes or bryozoans; hence, most interactions were likely *post-mortem*. Some of the overgrowth pairs could either have taken place *in vivo* or *post–mortem*, for example the overgrowth of part of a serpulid tube by bryozoans, which caused no prejudice to the polychaete (Fig. 9B). However, a single undisputed case of *in vivo* interaction was found between two bryozoan taxa, in which none was able to overgrow the other, resulting in a 'tie' with the margins of both colonies elevating from the substrate along the contact face (Fig. 9F).

Although means of right and left valves were quite different, with 22.07 encrusters per right valve ($N = 43$) and 16.4 encrusters per left valve ($N = 20$), the difference was not statistically significant

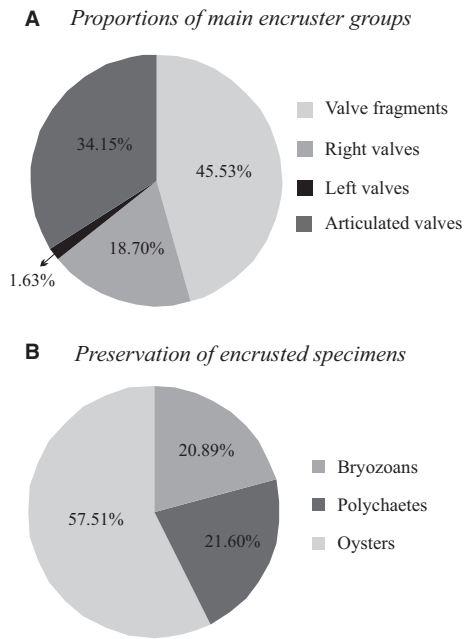


Fig. 7. Statistical results for 123 valves and valve fragments. A, pie chart showing state of preservation of the studied specimens of *Prohinnites* sp. B, pie chart showing proportions of large groups of encrusters (notice, though, that oysters comprise a single taxon, while polychaetes and bryozoans are represented by seven and five taxa, respectively). The single coral specimen is excluded from this graph due to an insignificant participation in the fauna.

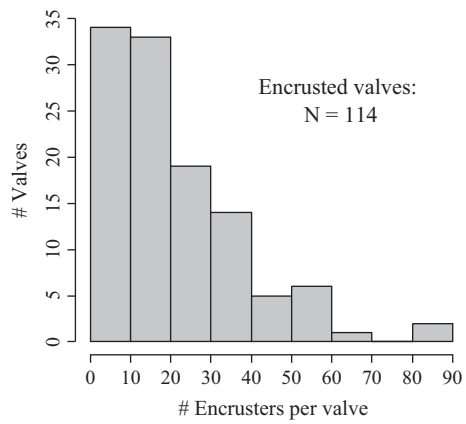


Fig. 8. Histogram depicting the variability of intensity of encrustation in *Prohinnites* sp. from the late Valanginian of the Neuquén Basin, west-central Argentina.

Table 1. Composition of the encrusting fauna, showing the absolute and relative abundance values of each encruster taxon, and the number and percentage of encrusted *Prohinnites* sp. valves presenting at least one individual of each.

Taxa	# Individuals	%	# Valves	% Valves
Amphidonte (Ceratostreon) sp.	1390	57.49	97	85.09
Filograna sp.	3	0.12	2	1.75
Parsimonia antiquata	144	5.96	53	46.49
Mucroserpula mucroserpula	3	0.12	2	1.75
Placostegus cf. *conchophilus*	48	1.99	27	23.68
Propomatoceros semicostatus	39	1.61	15	13.16
Glomerula serpentina	147	6.08	60	52.63
?Neomicrorbis sp.	138	5.71	11	9.65
'Berenicea'	269	11.12	71	62.28
Oncousoecia sp.	9	0.37	5	4.39
?Proboscinopora sp.	9	0.37	5	4.39
Microeciella sp.	1	0.04	1	0.88
Neuquenopora carrerai	217	8.97	55	48.25
Actinastrea collicullosa	1	0.04	1	0.88

Table 2. Pairs of interactions observed among encrusters on *Prohinnites* sp., showing the outcome or 'winner' of the interaction, which is the organism that overgrew the other (*a priori* it cannot be known whether the interaction took place as both encrusters lived or after the death of the overgrown one). The 'T' stands for tie, when none of the encrusters involved could overgrow the other.

Encruster Pairs (A-B)	Frequency	Winner A	Winner B
Actinastrea-Parsimonia	1	0	1
Amphidonte-Actinastrea	1	1	0
Amphidonte-Berenicea	12	0	12
Amphidonte-Glomerula	5	1	4
Amphidonte-Neuquenopora	3	0	3
Amphidonte-Oncousoecia	1	0	1
Amphidonte-Parsimonia	3	0	3
Amphidonte-Propomatoceros	1	0	1
Berenicea-Glomerula	1	0	1
Berenicea-Oncousoecia	1	0	1
Berenicea-Propomatoceros	1	1	0
Berenicea-Spirorbinae	3	2	1
Filograna-Glomerula	1	1	0
Neuquenopora-Berenicea	1	T	T
Neuquenopora-Glomerula	1	1	0
Placostegus-Berenicea	1	0	1

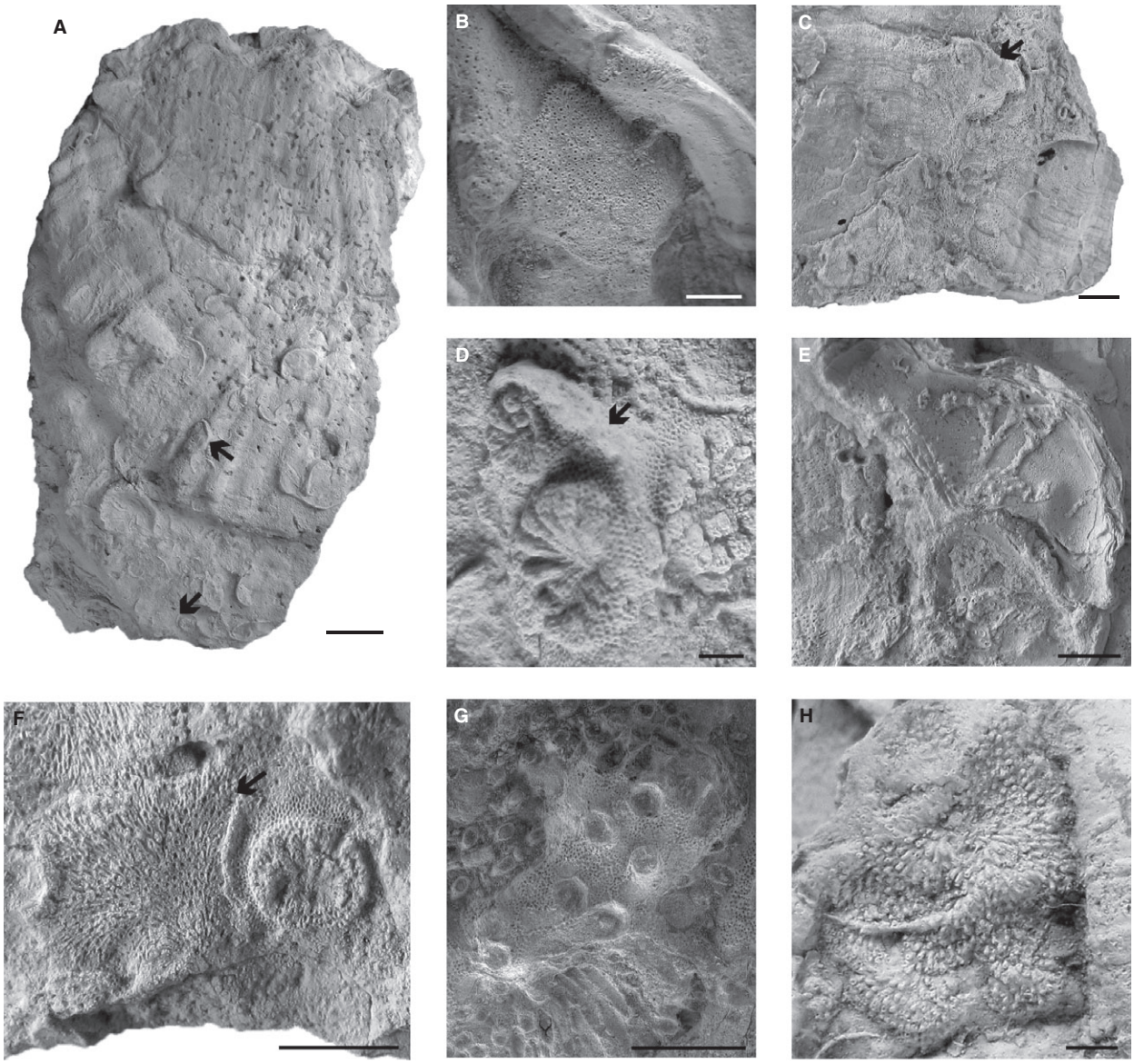


Fig. 9. Examples of encruster–encruster interactions in *Prohinnites* sp. from the Lower Valanginian of the Neuquén Basin, west-central Argentina. A, valve fragment (CPBA 20536.1) in which two interactions are arrowed. Details of each are shown in D, F. B, bryozoan colony ('*Berenicea*') overgrowing a serpulid tube (*Propomatoceros semicostatus*) on specimen CPBA 20531.13. C, worn '*Berenicea*' colony overgrowing the inner surface of an oyster's left valve (edge arrowed) in CPBA 20531.10. D, details of upper arrowed interaction in A, showing a colony of *Neuquenopora carrerai* growing upon an oyster's left valve (arrowed). E, colony of *Oncousoecia* sp. overgrowing an oyster's left valve. F, detail of lower arrowed interaction in A, showing a worn colony of '*Berenicea*' to the left, and a colony of *Neuquenopora carrerai* to the right. Along the contact (arrowed), both colonies grew upwards and away from the substrate. G, colony of *Oncousoecia* sp. overgrowing a '*Berenicea*' colony (CPBA 20536.2). H, '*Berenicea*' colony overgrowing the inner surface of the left valve of an oyster (CPBA 20531.9). All interactions but B, F, G were *post-mortem*; F was *in vivo*, and B, G could have been either. Scale bars: A, 1 cm; B, D, 2 mm; C, E, F, 5 mm; D, G, 1 mm.

($P = 0.149$). Articulated specimens were encrusted on both valves in all cases but one (in which only the right valve was encrusted), and hence, the proportion of articulated shells encrusted on both valves was significantly greater than that of articulated shells encrusted on one valve only ($P < 0.0001$). None of the taxa were more or less significantly recorded in any of the valves in particular.

For the GLMM, 33 valves were included, of which 27 were right valves and six were left ones. The proximal zone presented the lowest values of encrustation ($P = 0.0001$), while the medial and distal zones presented higher encrustation than the proximal one, but do not differ between each other. The same pattern is sustained when considering left and right valves separately. None of the taxa were more or less

significantly recorded in any of the valve zones. Taxonomic richness was of 14 taxa; Simpson's Dominance was 0.361, and Pielow's Equitability was 0.565.

Some of the encrusting taxa presented particular orientations and/or a tendency to occur aggregated. Oysters were variably oriented, but commonly clustered (within clusters their orientation remained variable; see Fig. 10A, F). Spirorbids presented no particular orientation, but were often aggregated (Fig. 10B). Uncoiled serpulids were often aligned to the dorsoventral axis of the valve, sometimes along the ribs, while sabellids were commonly found along thickened growth lines and lamellate edges of the valve (Fig. 10C–E). Both may also occur aggregated, although their clusters were smaller than those of oysters. Bryozoans were most common between ribs of the valves.

Discussion

The encrusting fauna of *Prohinnites* sp. was a diverse, abundant community that shows that the robust,

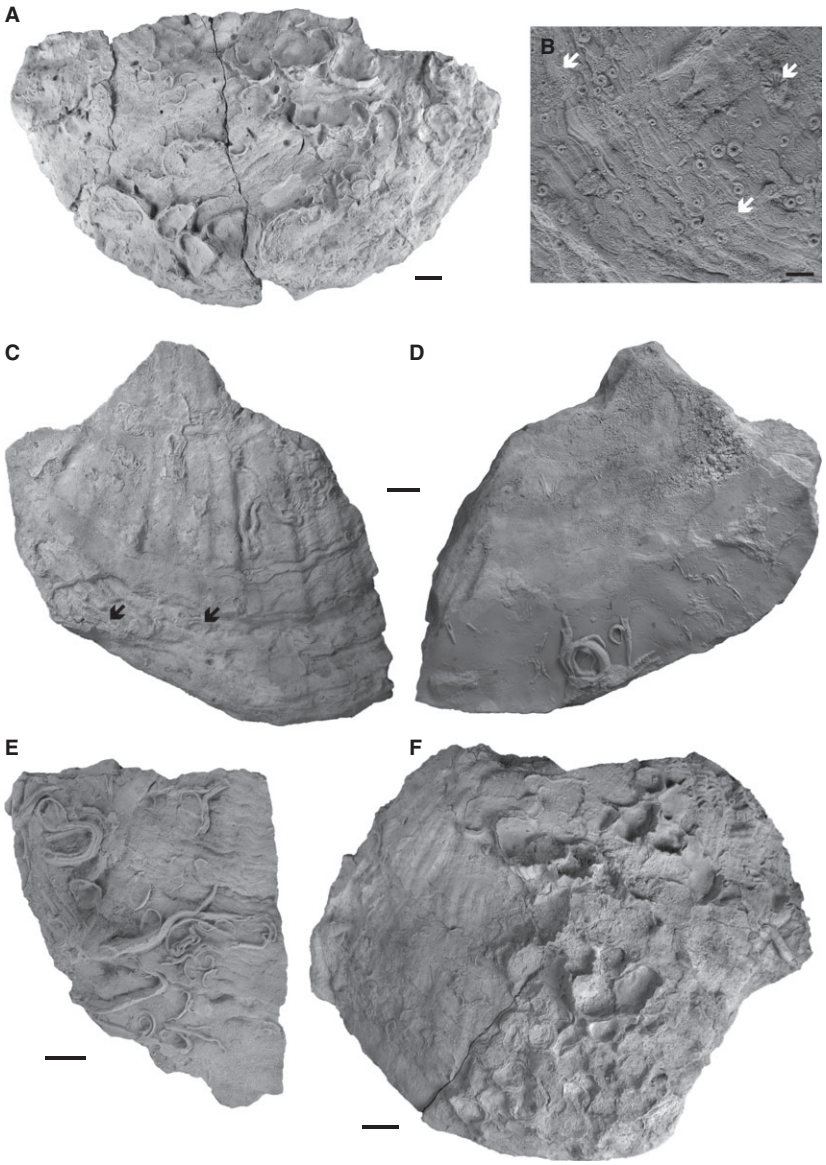


Fig. 10. Examples of gregariousness in the encrusting fauna of *Prohinnites* sp. A, valve fragment (CPBA 20536.3) heavily covered by oysters (over 60 individuals). B, close up on right valve of an articulated specimen of *Prohinnites* sp. (CPBA 20531.16) showing aggregated spirorbids. Arrows indicate some bryozoan colonies ('*Berenicea*' to the left and the lower right, and *Neuquenopora carrerai* to the upper right). C, valve fragment in outer view, with sabellids clustered to the right, and growing alongside the pectinid growth lines (arrowed; CPBA 20531.8). D, same valve fragment as in C in interior view, with a small cluster of serpulids near the margin. E, valve fragment (CPBA 20531.13) with a small serpulid cluster. F, undetermined valve (CPBA 20531.9) with a large oyster cluster (over 60 specimens). Scale bars: A, B, D, F, 1 cm; C, 5 mm; E, 3 mm.

ample valves of the pectinid were commonly favoured as sites of attachment by a variety of organisms. Several issues need to be discussed regarding the conformation of this encrusting community, the first and foremost of which is the time of occurrence of the encrustation.

Time of occurrence of encrustation: post-mortem *or* in vivo?

To address the timing of encrustation, it is important to consider that internal encrustation is an undisputable proof of *post-mortem* encrustation, given that organic tissues must have decomposed to expose the internal valve surfaces. The low incidence (and intensity) of internal encrustation is suggestive of a short time of exposition of the internal surface of the valves and a rapid burial of most specimens. It seems unlikely that internal surfaces were purposely avoided, as several studies have shown that rather than avoided, they are preferred by encrusters (e.g. Bottjer 1982; Bishop 1988; Lescinsky *et al.* 2002). Complete specimens with articulated valves are the ones most likely to have been buried very quickly after death, and although they were not preserved in life position, the finding of articulated specimens in a shallow-marine environment of high wave energy points to a reduced transport and quick burial, likely due to a high sedimentation rate (see Cataldo & Lazo 2012). Complete articulated specimens are then the best candidates to have preserved with greater fidelity the original *in vivo* encrustation patterns. The fact that both valves were almost always (and similarly) encrusted in these cases indicates that both the upper (left) and lower (right) valves were available for colonization during most of the life of the pectinid.

On the other hand, disarticulated valves and valve fragments were likely exposed for a longer time, given that disarticulation and fragmentation took place, with a few valves and fragments encrusted on the inner side. These specimens likely present further *post-mortem* encrustation in comparison with the articulated ones and it is difficult to determine, apart from the obvious internal encrustation cases, which encrusters settled while the pectinid was alive and which ones after its death. It is important to mention at this point that Lescinsky (1993) observed that valves of dead extant *Chlamys* Röding inhabiting soft bottoms suffered little post-mortem encrustation due to the quick burial of their valves. In contrast, those *Chlamys* dwelling in rocky bottoms were exposed for a more prolonged time and thus were more intensely encrusted (Lescinsky 1993). On the other hand, Schejter & Bremec (2007a) found that an extant *Zygochlamys* Ihering species inhabiting soft substrates was extensively encrusted in life, but less so after death, with a different, less diverse epibiont community. Overall, the *Prohinnites* specimens studied here represent variable times of exposure, ranging from a short period after they died, to a moderate time during which valves disarticulated and broke as they suffered reworking, while post-mortem encrustation took place. This is expected in within-habitat time-averaged assemblages as is the case of the studied *Prohinnites* bearing-bed.

Spatial distribution of encrusters on valves

In both the right and left valves, the proximal zone was the least encrusted, while the medial and distal zones were equally encrusted, and more heavily so than the first. While in the right valve this is probably because the proximal zone contains the attachment mark, which was unavailable for colonization, in the left valve the proximal zone would have remained exposed and could have been easily covered by encrusters. The reason why this zone was less encrusted than the others in the left valve could be explained by an early colonization of the shell by unpreserved encrusters, such as algae (*Prohinnites* inhabited shallow depths within the photic zone) or soft-bodied sponges, which prevented settlement of larvae. According to Lescinsky (1993), in extant *Chlamys,* most of the left valves is covered by soft-bodied organisms (mainly mutualistic sponges), which would hardly have been preserved in the fossil record. Mutualistic sponge cover is common in pectinids and can be found in both the upper and lower valves in some cases, but sponges may also coexist with pectinids without colonizing their valves (see Schejter & Bremec 2007a,b, and references there). Another possibility is that the left valve, facing upwards, was partially covered by sediment, especially in the umbonal region (as the distal part, and the commissure, should have been kept away from the substrate), precluding larval settlement in the proximal zone.

Left and right valves present non-significant differences in intensity of encrustation, but still the right valve is more intensely encrusted (about 25% more encrusted than the left valve). At this point, the great dispersion of the data (see Fig. 8; some valves present few encrusters, while others present several dozens of them) results in large error bars, which require very pronounced differences to result in statistical significance. The more intense utilization of the right valve could be indicating a general preference of encrusters for a sheltered, cryptic habit. However, all encrusters were found to be equally

common in both valves, and whether they preferred a cryptic habit or not, they were also clearly able to survive in the upper valve. Again, it is possible that the left valve was covered by sediment or by light-depending algae or other soft-bodied organisms of peripherical growth (sponges, tunicates), leaving less available space for colonization by less competitive, solitary organisms with hard skeletons.

The common and comparable encrustation of the medial and distal zones of both valves indicates that they were exposed during the pectinid's life. The distal zone may have been attractive to encrusters by providing a position close to the respiratory currents of the basibiont. The medial zone in the right valve was likely very close to the substrate, but enough space was left for colonization by small encrusters. This closeness to the substrate could also have represented an increased protection against predators.

If *Prohinnites* sp. adopted a reclining habit, as proposed here, it does not necessarily imply that the whole right valve came into contact with the substrate, given that statistical results showed that both the medial and distal areas of both valves are comparably encrusted. Due to the curvature of the right valve, its distal zone and at least a portion of the medial zone remained exposed during the reclining phase and thus continued to be available for encrustation. The proximal zone of the valves might have been slightly sunk towards the sea-bottom, thus precluding encrustation in this area in both the right and the left valves.

Dynamics of basibiont-encrusters and encruster-encruster interactions

The elevated incidence of encrustation and mean of encrusters per valve observed in the studied specimens is strongly suggestive of this bivalve acting as an attractive substrate for sessile, hard substrate organisms. In general, other molluscs in the Pilmatué Member are not nearly as intensely and commonly encrusted as *Prohinnites* sp. and domination by oysters is much more pronounced, while richness is lower (personal observations; other cases of study can be found in Luci & Cichowolski 2014; and in an older unit in Luci 2010). Given that the adult *Prohinnites* sp. was sessile epifaunal and robust-shelled, it provided a stable habitat for its encrusters, unlike the case of more mobile substrates as gastropods, and semiinfaunal, byssate or infaunal bivalves.

In the studied encrusting fauna, although oysters clearly predominate in abundance and are widespread on the valves of *Prohinnites* sp., other encrusting groups are more diverse (bryozoans, polychaetes) and include one or more taxa that are also common. In addition, although numerically less abundant than oysters, bryozoans and polychaetes are found in a large number of valves as well, indicating that they were able to colonize a considerable proportion of the available substrates (see number of valves presenting each encrusting taxon; Table 1). Polychaetes presented two common taxa, the serpulid *P. antiquata* and the sabellid *G.* cf. *serpentina*. Both were present in 40-50% of valves and were also quite abundant. The serpulid *P.* cf. *conchophilus* was less abundant, but also rather widespread on shells. The remaining serpulids were rare, both in abundance and number of colonized valves.

Bryozoans were important in the encrusting fauna considering both richness and abundance, but they rarely occupy large valve surfaces. The commonest taxon, '*Berenicea*' sp., is a small subcircular colony, rarely exceeding 1 cm in diameter (the same is the case of *Microeciella* sp. of which a single specimen was found). It was, however, rather widespread on *Prohinnites* sp., being found in over 60% of valves (Table 1). *Neuquenopora carrerai*, next in abundance and number of valves colonized, could seldom cover a considerable portion of the shell (approximately the half of a valve), but it only did so in very rare occasions. The remaining taxa are both very rarely found and consist in runner-type colonies presenting insignificant areal cover. Interactions involving bryozoans are almost always to the favour of the latter, which are found covering other encrusters, but they are mostly *post-mortem* cases.

Therefore, in the studied fauna, five taxa (*Amphidonte (Ceratostreon)* sp., *P. antiquata*, *G. serpentina*, '*Berenicea*' and *N. carrerai*) can be considered to have been common, while the nine remaining species were quite to very uncommon. This is reflected in the pairs of interactions, of which the most frequent ones involve two of the five commonest taxa (Table 2).

Overall, interactions among encrusters are rare when their total number is considered, and few of the possible pairs of interaction are represented. Many of the contacts observed between encrusters were clearly *post-mortem* and while others could have taken place *in vivo*, they resulted in little impact on the overgrown organism. The single example of *in vivo* interaction, between two bryozoans (Fig. 9F), indicates that *in vivo* interactions existed, but were rare and most likely unimportant, as the outcome was a 'tie'. Even *post-mortem* overgrowths are not abundant, considering that only 35 cases of them were observed. Overgrowth of disarticulated oyster valves indicates that at least two pulses of colonization took place, because polychaetes and bryozoans

(and rarely oysters) settled over already dead previous encrusters. This suggests as well that oysters were commonly early colonists on *Prohinnites* sp.

Given the rarity of interactions, the predominance of solitary organisms and the absence of clear patterns of *in vivo* overgrowth among encrusters, it is unlikely that competitive relationships were of great importance in the studied encrusting fauna. Moreover, predominance of oysters does not appear due to superior competitive skills, given that in most interspecific interactions oysters were already dead at the time they were covered by other organisms. In addition, in very few cases, oysters were the overgrowing organisms. If oysters are poor competitors for space in the study case, how could they, then, become the most conspicuous element of the encrusting fauna?

One factor of likely importance on the prevailing of *Amphidonte (Ceratostreon)* sp. is that this taxon is capable of surviving by itself on a soft bottom; that is, these oysters had the ability to detach themselves and lead an independent existence reclining on the left valve (Stanley 1970; Stenzel 1971). This could have ensured their survival regardless of the amount of hard substrate available for colonization, while all other encrusters in this fauna could not have survived without a hardened surface to settle on and grow upon. This would have provided oysters with an advantage over other encrusters, as their larvae would have been available even when hard substrates were absent or scarce.

In addition, these oysters present a strong gregarious behaviour (see Introduction) with clusters of tens of specimens (see Fig. 10A, F). The same oysters were occasionally capable of great proliferation in the Pilmatué Member, conforming bioherms of positive relief on the seafloor, with thousands of individuals cemented upon each other, suggesting that they were capable of reproducing at a great rate (see Lazo 2006). The gregarious behaviour allowed oysters to rapidly cover available substrates once a single (or a few) larvae had settled, which, coupled with a high reproductive input, resulted in the common formation of oyster clusters on the valves of *Prohinnites* sp.

The combined gregarious behaviour, survivability in soft substrates and capacity for great proliferation of oysters, rather than superior competitive skills in struggle for space, allowed them to become the main component of this encrusting fauna. Both the abundance of larvae of a species and the order of colonization are of great importance in determining the composition of an encrusting community (Osman 1977). In this study case, both of these factors were in favour of oysters; not only were they very abundant, but were likely the first colonizers, evidenced by the common overgrowth of disarticulated (dead) oysters by serpulids and bryozoans. Oysters are not considered to have been pioneers (understood as early colonists which modify and prepare the substrate for newcomers) in this case, but rather early settlers which were, however, not indispensable for the settlement of other encrusters. Not all encrusted valves present oysters (Table 1), indicating that polychaetes and/or bryozoans were capable of settling on *Prohinnites* sp. regardless of the presence/absence of oysters.

The great amount of oysters did not discourage the settlement of other encrusters, either as indicated by common and more diverse polychaetes and bryozoans, and reflected in the low value of the Simpson's Dominance index. Oysters could even have made the substrate more attractive to new settlers by creating a rougher surface (see Eckman 1990; Hoover & Purcell 2009). This does not mean that there was a single event of oyster settlement, after which polychaetes and bryozoans followed in succession and excluded them. Rather, after the first individuals established on *Prohinnites* sp., oysters likely replenished their stock as polychaetes and bryozoans established themselves as well; all of them were able to coexist on the same substrate.

Many other invertebrate shells were available within the environment and could have acted as hard substrates (see Cataldo & Lazo 2012), providing additional settlement places, as complete coverage of shells is very rare. Among these available shells, *Prohinnites* sp. was one of the most stable, likely maintaining a sessile epifaunal position. Is its encrusting community, then, in the initial stage of development or at its climax?

Osman (1977) defined three general models of development of an encrusting community; successional, seasonal and random. In the first, there is an established competitive hierarchy among intervening species and successive steps in colonization can be recognized, the earlier ones being necessary for the occurrence of the following ones. In seasonal developments, there is an annual sequence that repeats itself, causing changes in composition across seasons and ultimately leading to domination by one or a few species. In a random development, no particular trends guide the evolution of the system.

The community studied here is clearly not coincident with the successional model, as oysters, though most commonly being the first settlers due to the characteristics described above, are not necessary for the establishment of other encrusters. Species of bryozoans and polychaetes that settle later do not displace the oysters and establish none or little

competitive relationships between them. In addition, these same 'later settling' species are also found as encrusters in the absence of oysters, indicating that they were able to be the first colonizers when the occasion presented itself.

Our study case coincides with Osman's (1977) seasonal development model in that colonization was a function of larval abundance, and encrusters were able to colonize the valves of *Prohinnites* sp. regardless of the presence/absence of other encrusting species. The present study case differs, however, with Osman's (1977) seasonal model, in that there seems to have been only a moderate dominance and in that the composition of the community seems to have been stable rather than cyclical.

Therefore, the encrusting community of *Prohinnites* sp. had a development strongly related to larval abundance, which reflected itself on the composition of the encrusting fauna. No domination was established through direct interspecific competition through overgrowth, but rather the most abundant species had an initial advantage given by a high larval input and a strong gregarious behaviour. However, domination was not strong, likely because the ability of oysters to quickly colonize available space was compensated by poor competitive skills. Hence, the studied community was likely in its climax stage; although oysters maintained their first-hand advantage, they were unable to exclude polychaetes and bryozoans, which sooner or later established themselves on *Prohinnites* sp. either alongside oysters or independently of them. It seems that the studied fauna had rather unique dynamics, which differs from those observed in recent settings and probably reflects a particular set of climatic, environmental and biological factors that were present in the Neuquén Basin during the Early Cretaceous.

Conclusions

1 Many features of the studied materials of *Prohinnites* sp., especially the small, smooth cementation marks, thick shells and convex-shaped right valves in large adults, point to a third stage in their life habit, given by a free reclining mode of life after the cementing phase.
2 The shells of *Prohinnites* sp. acted as benthic islands on soft marine bottoms during the early Valanginian in the Neuquén Basin, sustaining an abundant and diverse encrusting fauna characterized by the predominance of gregarious oysters, as well as by serpulids, sabellids, cylcostome bryozoans and a single species of coral.
3 The proximal zone of both valves was avoided by encrusters due to the attachment mark in the right valve and sediment accumulation and/or soft-bodied early colonists in the left valve. The convexity of the right valve allowed encrustation to continue in its distal zone and at least in part of the medial zone after reclining.
4 Encrusting oysters are represented by a single taxon, and they are the most abundant encruster. However, polychaetes and bryozoans are represented by several taxa, some of which are very common and widespread in the valves of *Prohinnites* sp.
5 Competition for space was not important in the studied encrusting fauna, given that interactions were rare and in most cases involved the overgrowth of previously dead encrusters.
6 The oysters showed a gregarious behaviour that allowed them to rapidly and successfully colonize hard surfaces. It is suggested that oysters were not competitively superior, but rather very abundant, early gregarious settlers that could quickly colonize and rapidly cover a substantial part of the available substrate.
7 The encrusting fauna of *Prohinnites* sp. was structured by the early colonization of oysters (probably the commonest larvae in the pool), after which serpulids, sabellids and bryozoans followed. Although oysters were very common, their presence was not required for the settlement of polychaetes and bryozoans, as oysters were not present in all of the encrusted valves. In addition, oysters lacked the competitive ability to exclude polychaetes and bryozoans from the substrate.
8 This scenario has in common with Osman's (1977) seasonal mode of development of an encrusting community that colonization was a function of larval abundance, and encrusters settled regardless of the presence/absence of other encrusting species. However, it differs in that no cyclical pattern of colonization is evident and in that dominance is not strongly established.
9 The studied fauna represents a climax stage, in which oysters were commonest, maintaining their initial advantage by continued settlement, but with rather diverse polychaete and bryozoan components coexisting in *Prohinnites* sp., conforming a community in which interspecific competitive interactions were not of importance.

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