SCLEROBIONTS ON PATAGONIAN OYSTERS FROM THE PUERTO MADRYN FORMATION (EARLY–LATE MIOCENE, ARGENTINA)

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Abstract. This work describes the composition and distribution of sclerobionts on the Miocene Patagonian oyster *Ostrea alvarezii* d'Orbigny and provides information about its paleoenvironment. The structure of sclerobiont assemblages and their preferential distribution on left/right valves (n=340) as well as their external/internal surfaces and areas was evaluated by means of multivariate analyses (nMDS, SIMPER), non-parametric tests for producing mean comparisons, and goodness of fit tests using coverage and abundance data. Sixteen ichnotaxa were recorded. Bivalves, polychaetes and bryozoans were the most representative encrusters. External surfaces, left valves and sediment-free areas were the most colonized. *O. alvarezii* beds are interpreted as within-habitat time-averaged assemblages. Oysters appear to have lived in small subtidal channels in a low energy tidal flat and closely related to the sediment-water interface, with the right valve resting on the substrate. Sclerobionts showed diverse behaviors, trophic levels and tiering. This suggests that sclerobiont assemblages on *O. alvarezii* had a complex structure with subdivision of resources, including a vertical colonization of valves by tracemakers at different levels of depth.

Key words. SW Atlantic Ocean. Tortonian. Patagonia. Boring and encrusting organisms. Oyster beds.

Resumen. ESCLEROBIONTES EN OSTRAS PATAGÓNICAS DE LA FORMACIÓN PUERTO MADRYN (MIOCENO TEMPRANO–TARDÍO, ARGENTINA). Este trabajo describe la composición y distribución de esclerobiontes registrados en la ostra patagónica del Mioceno *Ostrea alvarezii* d'Orbigny y provee información sobre el paleoambiente. La estructura de las asociaciones de esclerobiontes y su distribución preferencial sobre valvas izquierdas/derechas (n=340), sus superficies externas/internas y áreas fue evaluada mediante análisis multivariados (nMDS, SIMPER), pruebas no paramétricas para las comparaciones de medias y prueba de bondad de ajuste usando datos de cobertura y abundancia. Se registraron 16 icnotaxones. Los bivalvos, los poliquetos y los briozoos fueron los organismos incrustantes más representativos. Las superficies externas, las valvas izquierdas y las áreas libres de sedimento fueron las más colonizadas. Los depósitos de *O. alvarezii* se interpretan como asociaciones promediadas dentro del hábitat. Las ostras parecen haber vivido en pequeños canales submareales en una planicie de marea de baja energía y estrechamente relacionadas con la interfaz agua-sedimento, apoyando la valva derecha sobre el sustrato. Se registraron diversos comportamientos, niveles tróficos y escalonamiento de esclerobiontes. Esto sugiere que las asociaciones de esclerobiontes sobre *O. alvarezii* tenían una estructura compleja con subdivisión de recursos, incluyendo una colonización vertical de las valvas por organismos productores de trazas a diferentes niveles de profundidad.

Palabras clave. Océano Atlántico Sudoccidental. Tortoniano. Patagonia. Organismos incrustantes y perforantes. Depósitos de ostrasl.

OYSTERS have a good preservation potential and their epifaunal or partial infaunal habit favors the same condition for organisms that colonize their valves (Taylor and Wilson, 2003), which are hereinafter named sclerobionts (Taylor and Wilson, 2002). Sclerobionts can display different lifestyles. Encrusters can live engulfing the host-substrate or cemented like stickers on it and lacking significant vertical elevation, borers make perforations to dwell within or feed in the sub-strate, other sessile organisms are cemented or attached on the substrate by organic structures but grow away from it into the water column, and vagile organisms live or forage on the host-substrate (Taylor, 2016). After burial, sclerobionts have high taphonomic chances to retain their life positions and spatial relationships among them and with the host-substrate (Taylor and Wilson, 2003). Therefore, non-random distributions and orientations of sclerobionts on

host valves may often be preserved. These spatial distributions may occur in response to biotic interactions, physical or topological features of host valves, or search for a better use of resources by sclerobionts, such as food or shelter (Villamil *et al.*, 1998; Savazzi, 2001; Wisshak and Neumann, 2006; Tamburri *et al.*, 2008; Romero *et al.*, 2013; Yuan *et al.*, 2016). In addition, that hosts and their sclerobionts display similar exposure histories and suffer the same taphonomic biases, such as time averaging—the mixing of remains before final burial—and transport, can be expected (Rodland *et al.*, 2006). Accordingly, these spatial distributions have permitted an improved understanding of factors such as life position and burial rate of fossil oysters (Romero *et al.*, 2008; Ayoub-Hannaa and Fürsich, 2011; Harzhauser *et al.*, 2015) and the inference of specific interactions between sclerobionts, and between sclerobionts and host shells in fossil assemblages (Bien *et al.*, 1999; Taylor and Wilson, 2003; Zatón *et al.*, 2011; Brezina *et al.*, 2014; Liow *et al.*, 2016).

Oysters contained in Neogene successions of Northern Patagonia, southern Argentina, are well known as common components of benthic assemblages because of their exceptional preservation (del Río *et al.*, 2001; Parras and Casadío, 2005, 2006). *Ostrea alvarezii* d'Orbigny, 1842, is one of the most common oysters that inhabited on the sea floor in northern Patagonia and forms large shell beds in the Puerto Madryn Formation (Valdés Basin, northern Chubut Province, early–late Miocene). Valves are solid; the right valve is nearly flat and smooth, while the left one is convex, large, rough and with radial ribs. In different localities of the Puerto Madryn Formation, *O. alvarezii* occurs as two distinct ecophenotypes: clustered and reclined forms, both of which inhabited sandy bottoms. A complex assemblage of sclerobionts, which we describe in this paper, settled on *O. alvarezii*. Previously, only sponges (Romero *et al.*, 2008) and bivalves (Mauna *et al.*, 2005) had been recognized associated on this oyster.

Sclerobionts are useful tools to carry out paleoecological analyses. The study of the distribution and abundance of sclerobionts on *O. alvarezii* contributes to an understanding of depositional processes of oyster beds and their associated faunas through time. The paleoecological analysis of sclerobionts in shellbeds can provide time-weighted averages of ecological conditions in which they were de-posited, an approach avoiding the variability of short-term population dynamics (Rodland *et al.*, 2006, and references therein). Also, sclerobionts and taphonomic signatures preserved in shells provide unique clues to infer depositional environments (Brett *et al.*, 2011). Therefore, the detailed description of sclerobionts associated with *O. alvarezii* can be used as another proxy for paleoenvironmental reconstructions (Scasso and del Río, 1987; del Río *et al.*, 2001; Casadío *et al.*, 2005).

This work describes the composition and distribution of sclerobiont assemblages on the Miocene Patagonian oyster *O. alvarezii* and provides information regarding the environment in which the oysters and their sclerobiont assemblages developed.

GEOLOGICAL SETTING
Paleogeography

Patagonia, in southern Argentina, was flooded by shallow transgressions from the Atlantic during the Late Cretaceous to Cenozoic times (Malumián and Náñez, 2011).

Marine transgressions occurred mainly linked to subsidence of the Atlantic margin of Patagonia during the Paleogene–Neogene interval of South America (Casadío *et al.*, 2005). According to the $\delta^{18}O$ records from benthic foraminifers, a warm period peaked between 17 and 15 Ma, with a reduction in global ice volume and a slight increase in bottom sea temperature (Zachos *et al.*, 2001). This Miocene climatic optimum was the most widespread Cenozoic transgression, called the "Entrerriense or Paranense" *c.* 15 to 13 Ma, which flooded large areas of South America with shallow seas (Casadío *et al.*, 2005; Hernández *et al.*, 2005). Marine deposits are recognized in Bolivia, Uruguay and Paraguay as well as in different regions of eastern and northwestern Argentina that probably represent marginal marine environments (Sprechmann *et al.*, 2000; Casadío *et al.*, 2005). Hernández *et al.* (2005) considered that high sea level extended for up to *c.* 5 myrs and areas situated inside the continent experienced at least two episodic flooding events. In Northern Patagonia, a Tortonian flooding event (early–late Miocene) covered the Valdés Basin and is represented by the Puerto Madryn Formation (del Río *et al.*, 2013).
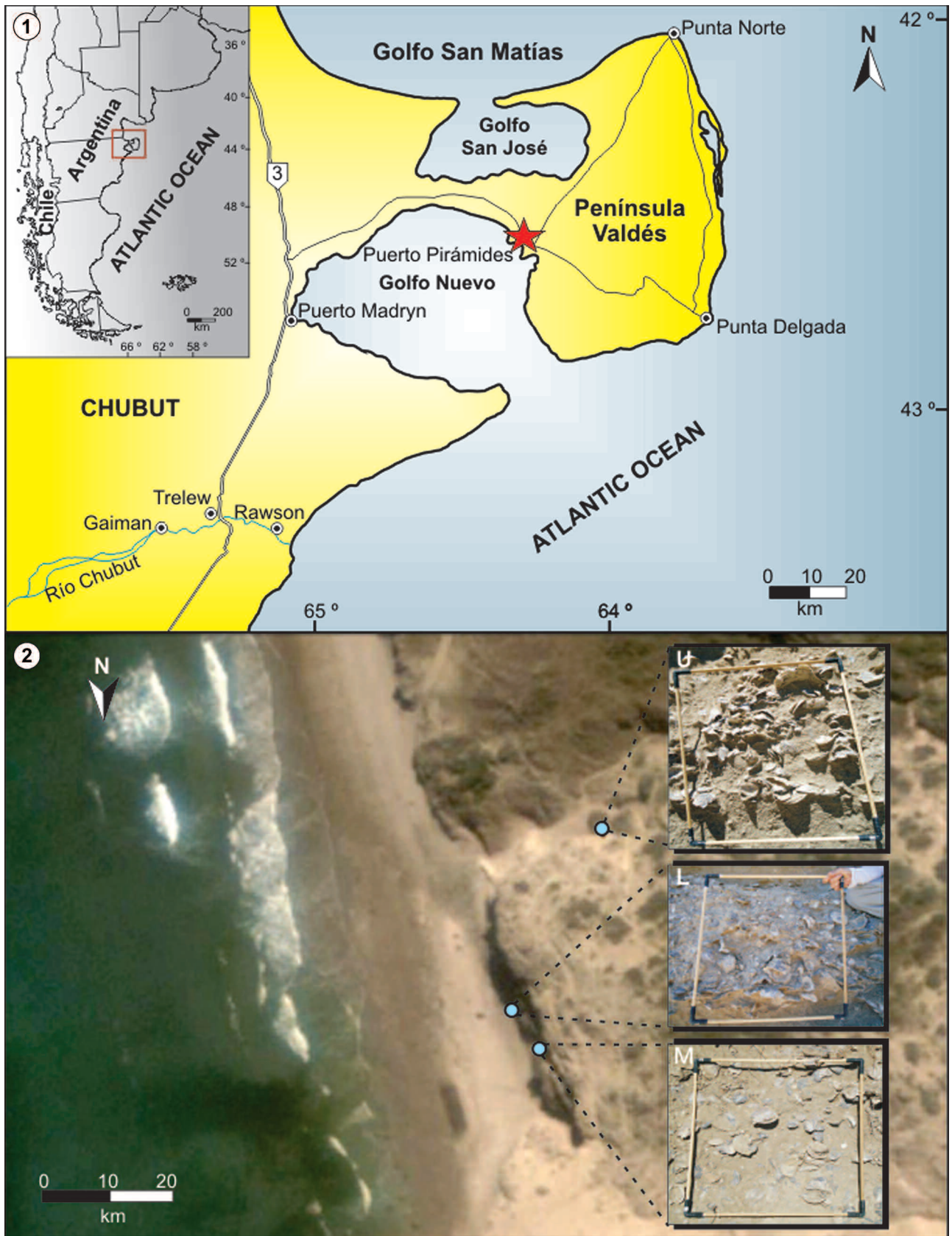
Figure 1. 1, Location map of the studied Puerto Pirámides section (red star). **2**, Satellite image showing the location of the upper (**U**), middle (**M**) and lower (**L**) level; source: BirdsEye Satellite Imagery © MDA Federal © Digital Globe 2016.
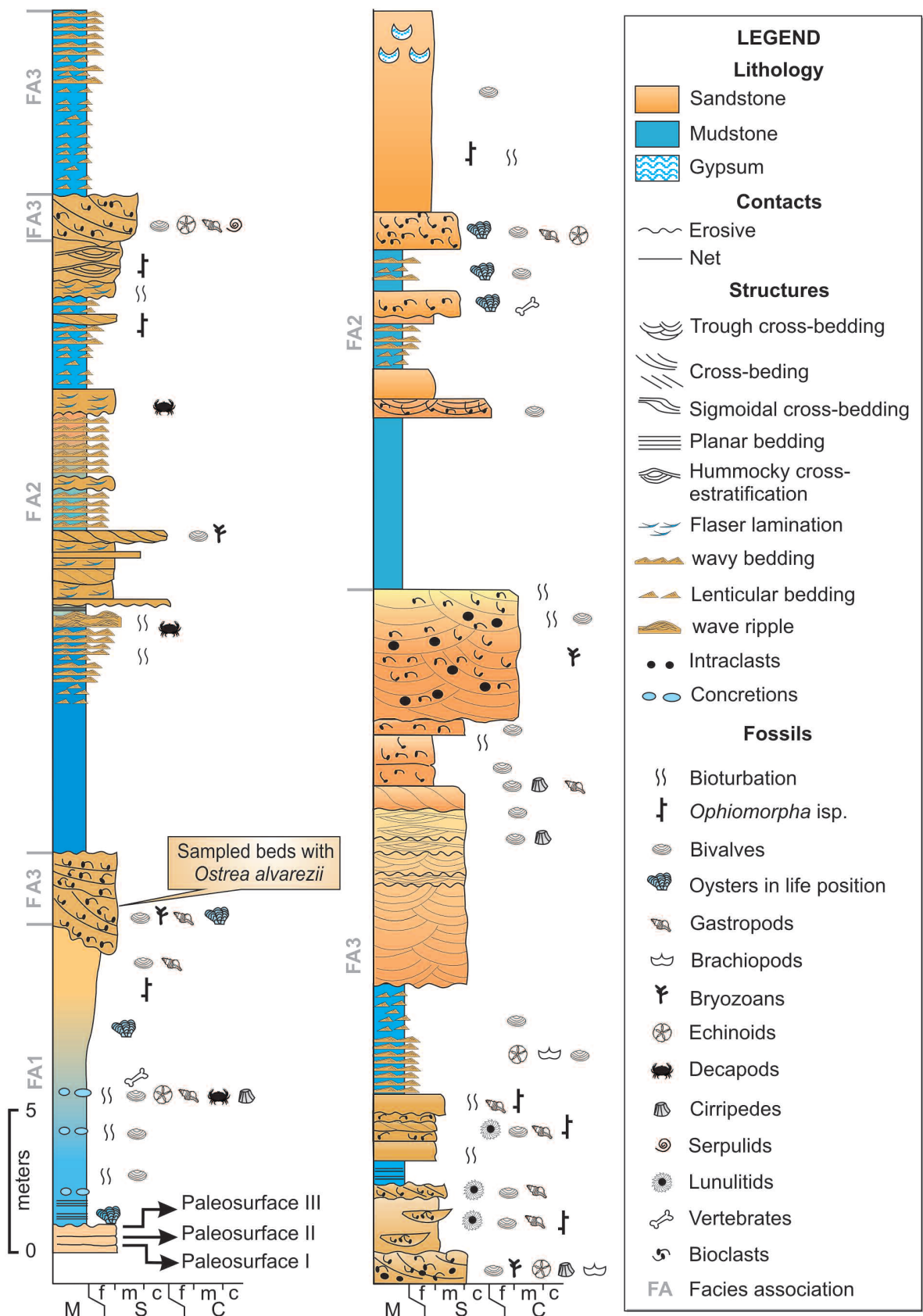
Figure 2. Stratigraphical and sedimentological log at the Puerto Pirámides section of the Puerto Madryn Formation. Modified from Casadío *et al.* (2005).

Puerto Madryn Formation

The Puerto Madryn Formation was formally described by Haller (1978). Scasso *et al.* (2001) proposed that the Puerto Madryn Formation was deposited, in accordance to the $^{87}Sr/^{86}Sr$ analysis from pectinid and oyster valves, during the middle Tortonian (10 ± 0.3 Ma). In contrast, Fuentes *et al.* (2016) suggested a late middle Miocene to early late Miocene age (Serravalian to Tortonian) based on dinoflagellate cysts.

The Puerto Madryn Formation overlies marine deposits of the Gaiman Formation (Late Oligocene) and it is overlain by marine terraces of the Caleta Valdés Formation as well as fluvio-glacial gravels named "Rodados Patagónicos" assigned to the Plio–Pleistocene (Haller *et al.*, 2000). It represents a regressive succession that occurred during the late Miocene and shows a transition from a shallow, storm influenced platform that evolved into a tide dominated estuarine environment at the top of the formation (Scasso and del Río, 1987). Scasso and del Río (1987), del Río *et al.* (2001) and Casadío *et al.* (2005) recognized three facies associations and concluded that the exposed section at Puerto Pirámides is the top of a depositional sequence that includes a transgressive systems tract (**TST**) and a highstand systems tract (**HST**).

MATERIALS AND METHODS

Study area

The studied section is located near Puerto Pirámides (Patagonia, Argentina, Fig. 1.1). The sequence is about 90 m thick and is composed of shelf and intertidal facies containing beds with diverse and abundant fossils that evolved into an estuarine and, finally, a continental environment. The oysters were collected at the base of the cliff, *c.* 10 m above present-day sea level, in fine to medium grained sandstones facies (**FA3**, Fig. 2). This facies association comprises deposits that are the result of infilling tidal channels and tidal sand waves (see Casadío *et al.*, 2005 for details).

Sampling

Oyster beds consist of three closely spaced shell-rich levels separated by shell-poor sands. 18 grids of 1 m^2 were employed at intervals of 1–4 m along three transects through the oyster bed. The transects covered the upper (42° 35'44.7"S; 64° 15' 22.7" W), middle (42° 35' 45.9" S;

64° 15' 23.5" W) and lower levels (42° 35' 45.7" S; 64° 15' 23.8" W) of the bed. Close-packing, size-sorting, proportion of left and right valves, orientation, disarticulation, fragmentation, encrustation, abrasion, bioerosion and concentration types were the taphonomic features that were recorded. The taphonomic analysis was restricted to those species which were considered "target" species, *i.e.* *O. alvarezii* (for examples, see Fürsich and Flessa, 1987; Kowalewski *et al.*, 1994; Kidwell *et al.*, 2001) due to the fact that shelly concentrations are dominated by this oyster, which makes up more or less monotypic shell beds. The paleoecological signatures of beds, such as taxonomic composition, life habits and size distribution frequency of the shells, were studied. The taphonomic and palecological features of skeletal concentrations were measured according to the methods described by Kidwell *et al.* (1986), Kidwell (1991) and Kidwell and Holland (1991). The nomenclature used by Machalski (1998) for oyster life positions was applied.

A total of 340 left and right valves of *O. alvarezii* were collected along transects through the beds. The samples used in this study are housed in the Departamento de Colecciones y Conservación of the Museo Paleontológico Egidio Feruglio, Chubut, Argentina, **MPEF-PI** 5001–5376. The oyster valves were carefully washed and brushed by hand to remove the sediment. Successive washes were performed using an ultrasound bath.

The internal and external surfaces of each right and left oyster valve were examined using a stereoscopic microscope to recognize solitary and colonial sclerobionts. Some sclerobionts were identified under a scanning electron microscope (**SEM**). The samples for the SEM analysis were obtained using a silicon carbide abrasive cutter to carefully cut small pieces of valves, which contained previously identified sclerobionts. In small valves, cutting was unnecessary. The samples were imaged at Laboratorio de Investigaciones de Metalurgia Física-Universidad Nacional de La Plata (**LIMF-UNLP**) using a Fei Quanta 200 SEM in low vacuum mode with an electron gun fitted with a tungsten filament cathode. A series of magnifications were selected for LFD and BSD images with magnifications ranging from 30x to 500x.

The presence/absence, the abundance (*i.e.*, number of individuals) and the coverage (*i.e.*, areal percent coverage)

of each taxon on host valves were recorded and their location was sketched on standardized maps of each valve (Fig. 3). Standardized maps define areas on each valve to test for differential colonization. These areas reflect dissimilar morphological features of valves that may influence the recruitment of different sclerobiont species and could be used to identify those areas in which sclerobionts may affect the development of the oyster. The left valve was divided into six areas: apex (10%), platform (5%), anterior margin (15%), ventral margin (25%), posterior margin (15%) and center (30%). There is no platform in the right valves, so the areas were: apex (10%), anterior margin (15%), ventral margin (30%), posterior margin (15%) and center (30%). The differential distribution on left/right valves, external/internal surfaces and morphologically different areas was evaluated following the methodology used in Romero *et al.* (2013).

Data analysis

The structure of sclerobiont assemblages on the oyster shells and their differential distribution on left vs. right valves and external vs. internal surfaces were evaluated with standard multivariate analyses used in benthic ecology (PRIMER 6.1.10, see Clarke 1993; Clarke and Warwick 2001) and non-parametric tests for mean comparisons (Zar, 1999). To fulfill this, similarity matrices based on the abundance and coverage of sclerobionts were calculated using the Bray-Curtis index. An ordination analysis named Multi-

dimensional Scaling (**nMDS**) was used to determine graphically the similarity between the left/right valves and the external/internal surfaces of sclerobiont assemblages. A Similarity Percentage (**SIMPER**) analysis was carried out to identify the sclerobionts responsible for the contribution to the average similarity (dissimilarity) within (between) left/right valves and external/internal surfaces.

SIMPER and nMDS analyses and the Wilcoxon paired-sample test were applied to establish comparisons between external and internal surfaces using abundance (fourth root transformed data, Bray-Curtis index) and coverage (percentage data, Bray-Curtis index). The Mann-Whitney test, nMDS and SIMPER were also applied to compare right and left valves using abundance (fourth root transformed data, Bray-Curtis index) and coverage (percentage data, Bray-Curtis index). Analyses for independent samples were used because left and right valves were found disarticulated and cannot be assumed to be parts of the same individual. The proportion of sclerobionts present and the McNemar test were employed to identify whether right or left valves and external or internal surfaces were more frequently colonized.

A goodness of fit test and exact confidence intervals for the binomial distribution were performed in order to assess a possible preference of sclerobionts for different areas of the valves. Following the recommendations described by Zar (1999), it would have been wise to have expected frequencies of at least five in order to assess a statistically remarkable robust test. Otherwise, data combination is suggested. Then, the expected frequencies in some valve areas with values under five were combined. Yates's correction for continuity was applied in those cases, with only one degree of freedom and relatively small samples (Zar, 1999). The null hypothesis was that the distribution of sclerobionts on valves is random at the significance level α= 0.05.

RESULTS
Taphonomy and paleoecology of oyster bed

The *Ostrea alvarezii* beds had a lenticular geometry with an erosive base and sandy matrix. These accumulations were found 10 m from the base of the section and reached between one and five meters in thickness. They are mixed biogenic-sedimentological concentrations. Left valves were more frequent than right valves. Three levels were recognized:
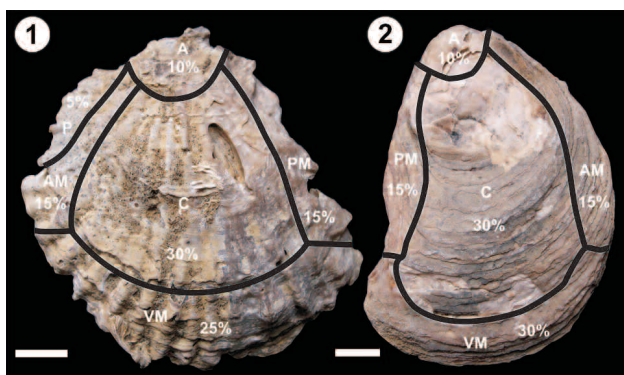

Figure 3. Zonation maps of *O. alvarezii* valves (external surface). **1,** right valve, MPEF-PI 5197. **2,** left valve, MPEF-PI 5019. **A,** apex, **AM,** anterior margin, **C,** center, **P,** platform, **PM,** posterior margin, **VM,** ventral margin. Percentage coverage is indicated in each area. Scale bars= 1 cm.

Lower level (mean thickness of 0.45 m, Fig. 1.2): bioclasts showed dense-loose packing, bimodal size-sorting, high disarticulation and low fragmentation and encrustation. Valves exhibited moderate to low abrasion and high bioerosion. Concordant orientation of bioclasts was common (61% of oyster valves were convex-up, and 22% of valves were convex-down); only 17% of the valves were oblique to bedding. Articulated specimens of *O. alvarezii* (1–3 individuals) were observed resting on their right valves or as mud-stickers obliquely orientated toward the bedding. Some clusters of a minimum of two or three specimens were also found. Occasional occurrences of disarticulated valves of *O. patagonica* and pectinids were recorded. Most taxa had filter-feeding and epifaunal habits.

Middle level (mean thickness of 0.95 m, Fig. 1.2): bioclasts showed loose-dispersed packing, bimodal size-sorting, high disarticulation and low fragmentation and encrustation. Valves exhibited moderate to low abrasion and high bioerosion. Concordant orientation of bioclasts was frequent (55% of oyster valves were convex-up, and 27% of valves were convex-down); only 18% of the valves showed oblique orientation. Two articulated specimens of *O. alvarezii* were found resting on the right valves and one specimen was oriented obliquely to bedding. The clumps of two or three articulated specimens of *O. alvarezii* were also observed obliquely orientated toward the bedding with the umbones downwards. Other disarticulated valves, such as pectinids, *O. patagonica* and brachiopods, were recorded but uncommon. Most taxa had filter feeding and epifaunal habits.

Upper level (mean thickness of 0.67 m, Fig. 1.2): bioclasts showed dense to loose packing, bimodal size-sorting, high disarticulation and low fragmentation and encrustation. Valves exhibited moderate to low abrasion and high to moderate bioerosion. The preferred orientation of most bioclasts was concordant (78% of the oyster valves were convex-up, and 11% of the valves were convex-down in cross-section) while no more than 11% of them had an oblique orientation. A low proportion of articulated specimens of *O. alvarezii* (up to 5 individuals) was observed in both ecophenotypic forms: recliners resting on their right valves or mud-stickers obliquely orientated toward the bedding with the umbones downwards, and some clusters of two or three specimens (*i.e.*, cemented valves of con-

specifics) were also found. Occasional disarticulated valves of *Ostrea patagonica* and pectinids were recorded. Most taxa had filter feeding and epifaunal habits.

Sclerobiont richness

A total of sixteen ichnotaxa were found on *O. alvarezii* (Fig. 4). Ichnotaxa were classified in nine trace producers in order to recognize different functional groups (Tab. 1). Encrusters on *O. alvarezii* valves (Fig. 5) were polychaetes belonging to Sabellida, basal plates from cirripeds, oysters and other recruits and bivalve adults. Bryozoans were the most diverse. A total of 22 taxa belonging to Class Gymnolaemata, Order Cheilostomata, and three taxa assigned to Class Stenolaemata, Order Cyclostomata, were identified.

Structure of sclerobiont assemblages

MDS plots based on coverage and abundance data indicated a weak grouping of samples when internal/external surfaces (Fig. 6.1–2) and left/right valves (Fig. 6.3–4) were considered. SIMPER results showed high percentages of average dissimilarity in both cases and the sclerobionts that most contributed to these differences were mainly the same, both when considering coverage (fungal and algal microborers, boring sponges, boring bivalves, encrusting bryozoans, worm-like organisms—*i.e.*, vermiform borings—, encrusting polychaetes, predatory gastropods and oysters) and abundance data (boring bivalves, worm-like organisms, predatory gastropods and oysters) (Tab. 2). A non-parametric analysis to compare sclerobionts on internal/external surfaces (Wilcoxon test, Tab. 3, in Supplementary Online Information) showed significant differences in their coverage (except for encrusting bryozoans and polychaetes) and abundance (except for oysters). External surfaces were more colonized than internal surfaces (Fig. 7, in Supplementary Online Information). In the case of sclerobionts on left/right valves, a Mann-Whitney test (Tab. 4, in Supplementary Online Information) showed significant differences in their coverage (except for fungal and algal microborers) and abundance (except for predatory gastropods). Left valves were, in general, more colonized than right valves (Fig. 8, in Supplementary Online Information). Significant differences in the presence of sclerobionts were found between the internal/external surfaces of the valves (McNemar test, Tab. 5, in Supplementary Online Information) and
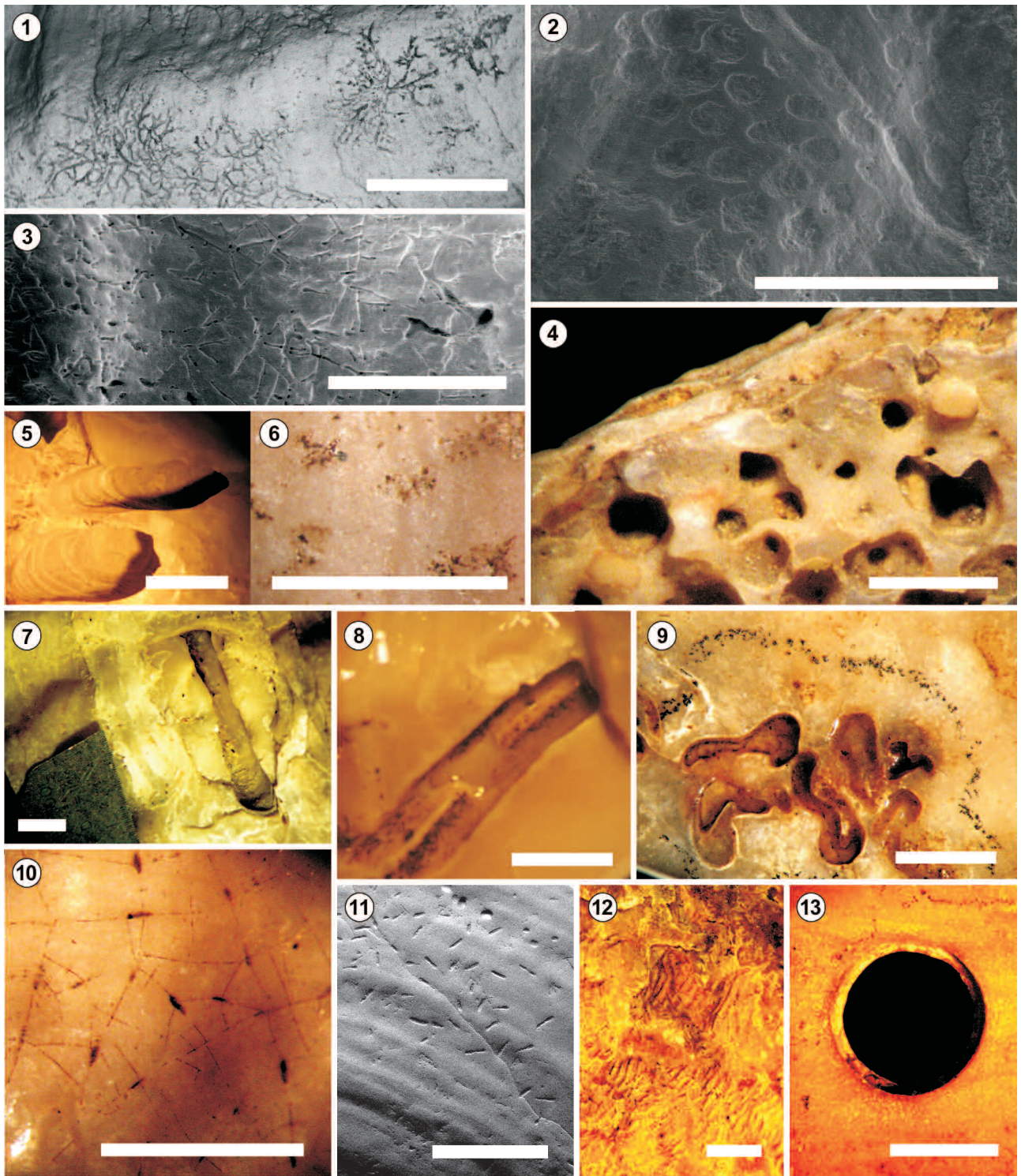
Figure 4. Most frequent ichnotaxa on *O. alvarezii*. **1,** *Clionolithes* Clarke, 1908, MPEF-PI 5064; **2,** *Finichnus* Taylor, Wilson and Bromley 2013, MPEF-PI 5064; **3**, morphotype C Mayoral, 1988a, MPEF-PI 5026; **4,** *Entobia* Bronn, 1837, MPEF-PI 5085; **5,** *Gastrochaenolites torpedo* Kelly and Bromley, 1984, MPEF-PI 5039; **6,** *Semidendrina* Bromley, Wisshak, Glaub, and Botquelen, 2007, MPEF-PI 5026; **7,** *Trypanites* Mägdefrau, 1932, MPEF-PI 5205; **8,** *Caulostrepsis* Clarke, 1908, MPEF-PI 5153; **9,** *Maeandropolydora* Voigt, 1965, MPEF-PI 5177; **10,** *Pinaceocladichnus* Mayoral, 1988b, MPEF-PI 5308; **11,** *Pennatichnus* Mayoral, 1988b, MPEF-PI 5338; **12,** *Radulichnus* Voigt, 1977, MPEF-PI 5003; **13,** *Oichnus simplex* Bromley, 1981, MPEF-PI 5206. Scale bars= 2 cm.

TABLE 1. Ichnotaxa identified in this study and grouped in trace producers and ethological categories.

Ichnotaxa	Trace producers	Ethological category
Entobia *Bronn, 1837*	*Boring sponges attributed to Clionidae Rafinesque, 1815*	*Domichnia*
Gastrochaenolites *torpedo Kelly and Bromley, 1984*	*Boring bivalves*	*Domichnia*
Pinaceocladichnus*? Mayoral, 1988b;* Pennatichnus*? Mayoral, 1988b*	*Boring bryozoans attributed to Orden Ctenostomatida (e.g., Spathipora? Fischer, 1866)*	*Domichnia*
Finichnus *Taylor, Wilson and Bromley 2013*	*Encrusting bryozoans*	*Domichnia*
Caulostrepsis *Clarke, 1908,* Maeandropolydora *Voigt, 1965;* Trypanites *Mägdefrau, 1932;* Talpina *von Hagenov, 1840; sipunculid traces Rice, 1969*	*Worm-like animals: boring polychaetes like* Polydora *Bosc, 1802, sipunculids and phoronids*	*Domichnia*
Clionolithes *Clarke, 1908; morphotype C Mayoral, 1988a*	*Fungal and algal microborers*	*Domichnia*
Semidendrina *Bromley, Wisshak, Glaub, and Botquelen, 2007*	*Boring foraminifers*	*Domichnia*
Radulichnus *Voigt, 1977*	*Grazers like gastropods and chitons*	*Pascichnia*
Oichnus simplex *Bromley, 1981,* Oichnus paraboloides *Bromley, 1981*	*Predatory gastropods: succsessful and failed attemps.* O. simplex *were more common than* O. paraboloides	*Praedichnia*

between the right/left valves (Mann-Whitney test, Tab. 6, in Supplementary Online Information). The analysis of the presence of sclerobionts showed a higher number of colonized external surfaces than internal ones (Fig. 9, in Supplementary Online Information), while more left than right valves were bored and encrusted (Fig. 10, in Supplementary Online Information).

The differential distribution of sclerobionts on different areas of the left and right valves is shown in Figures 11, 12 and 13. From nine trace producers that were identified, only six had sufficiently high frequencies for this analysis. The most colonized areas were the platform, the center and the posterior margin of the left valves as well as the apex, the anterior margin and the center of the right valves.

In the left valves, the platform was more colonized than the others areas by boring sponges, encrusting bryozoans and fungal and algal microborers on the external surfaces (Fig. 11), and by boring sponges, encrusting bryozoans, boring bivalves and oyster recruits on the internal surfaces (Fig. 12). Boring bivalves, oyster recruits, worm-like or-

ganisms and predatory gastropods showed a differential distribution at the center of the external surfaces (Fig. 11). Predatory gastropod borings were mostly incomplete. Only boring bivalves showed a differential distribution on the posterior margin of the internal surfaces (Fig. 12). The rest of the areas also showed observed frequencies of sclerobionts lower than expected (see asterisks in figures). Finally, the attachment areas of the oysters to substrates or other organisms during the larval stage, as well as in the living oysters, were registered mainly at the apex of the external surfaces (Fig. 11).

In the right valves, the apex was more colonized than the other areas of the external surfaces by fungal and algal microborers, boring sponges and boring bivalves; the latter also preferentially bored into the anterior margin. Predatory gastropod drill holes showed a differential distribution at the centre. The rest of the areas also showed observed frequencies of sclerobionts lower than expected (see asterisks in Fig. 13). Observed frequencies on the internal surfaces of right valves were low.
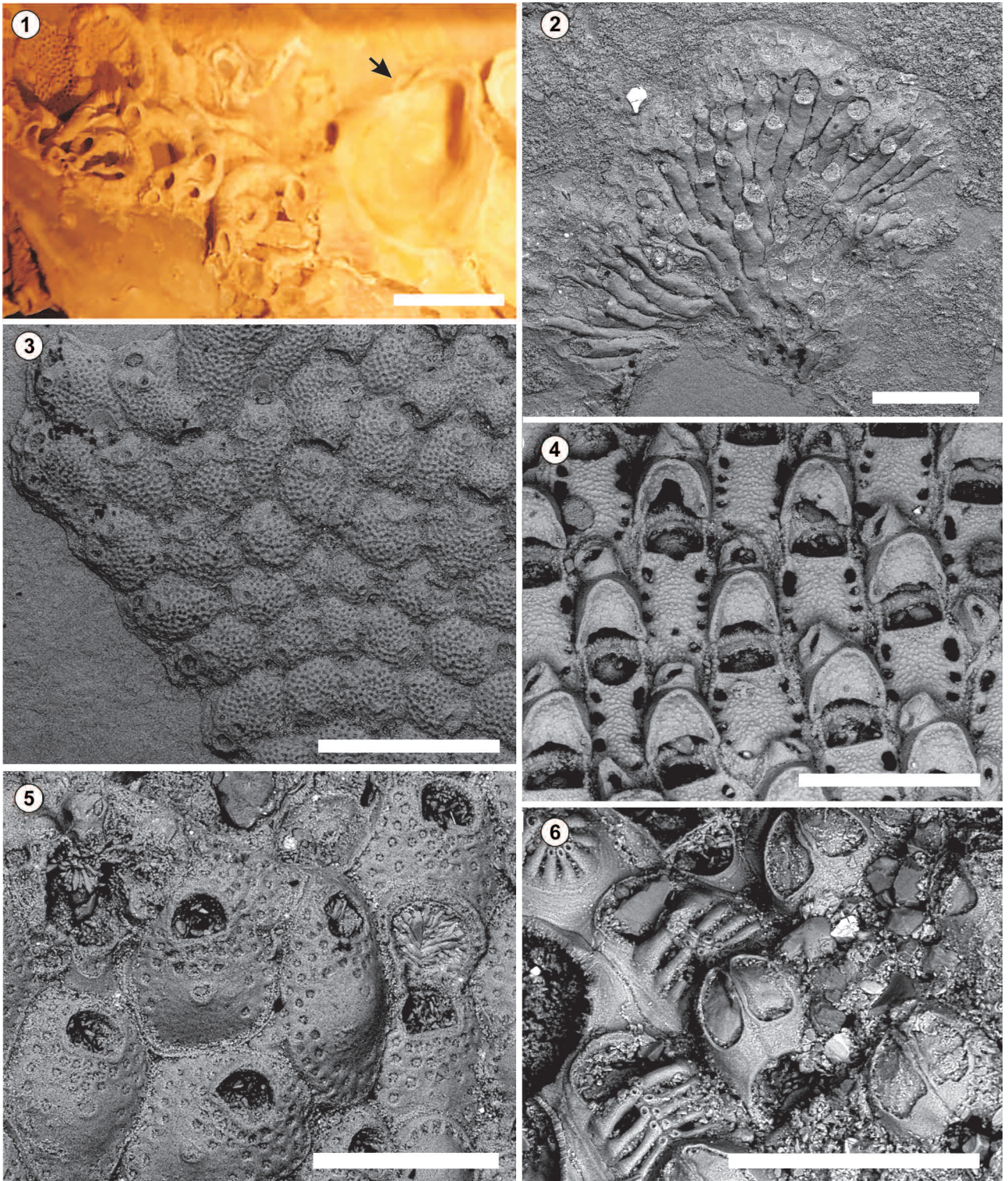
Figure 5. Encrusters on *O. alvarezii* valves. **1,** Encrusting polychaetes (Sabellida) and oyster recruits indicated by a black arrow, MPEF-PI 5035; **2,** *Plagioecia* Canu, 1918, MPEF-PI 5198; **3,** *Microporella* Hincks, 1877, MPEF-PI 5212; **4,** *Micropora* Gray, 1848, MPEF-PI 5368; **5,** *Fenestrulina* Jullien, 1888, MPEF-PI 5198; **6,** *Figularia* Jullien, 1886, MPEF-PI 5252.
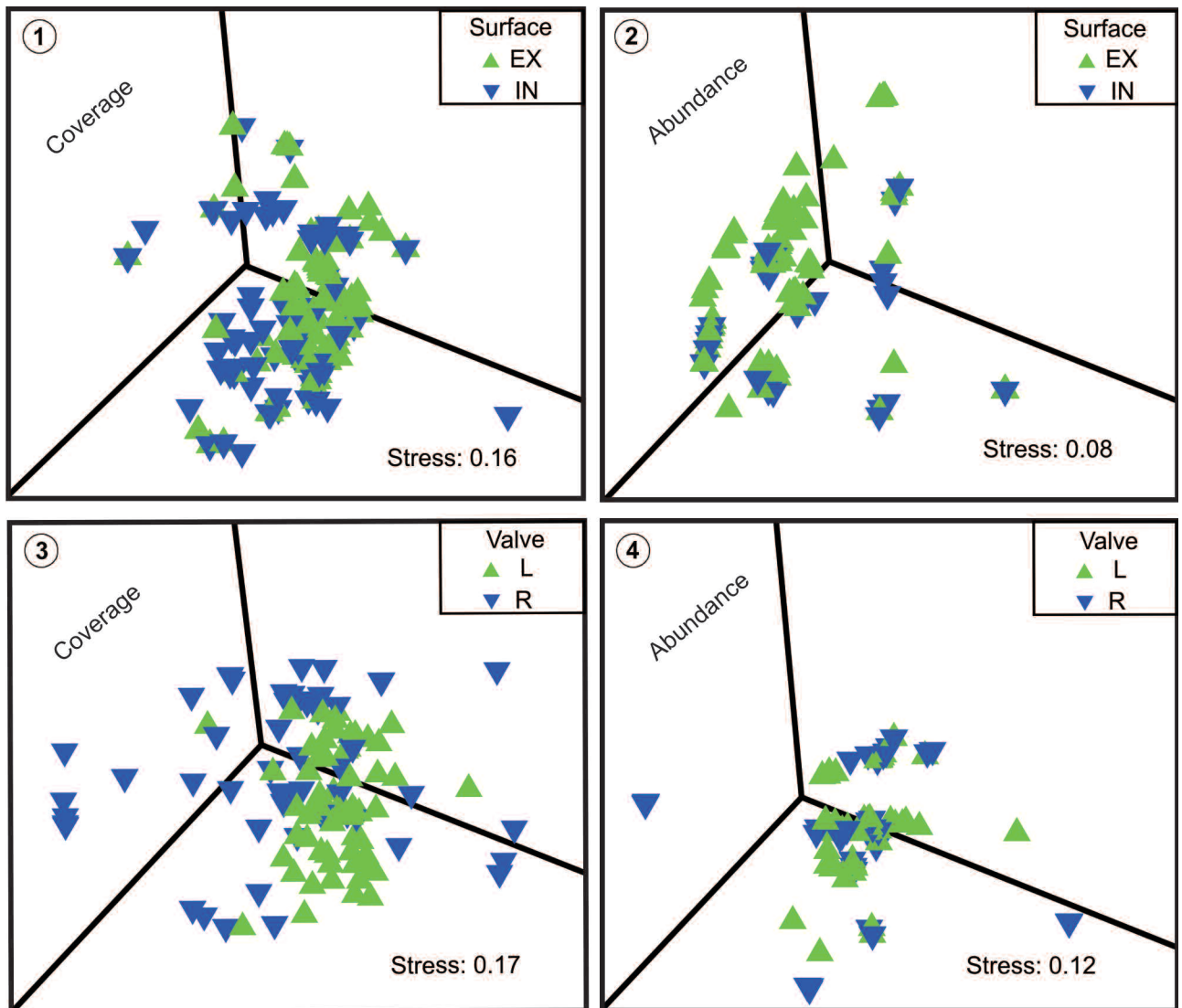
Figure 6. nMDS ordinations for external (**EX**) vs. internal (**IN**) surfaces and left (**L**) vs. right (**R**) valves of *O. alvarezii.* **1, 3,** coverage of sclerobionts. **2, 4,** abundance of sclerobionts.

TABLE 2. SIMPER results. Contribution percentages between kind of surfaces (external/internal) and valves (left/right). Contributions percentages of each taxa higher than 3% were considered. DP=dissimilarity percentage

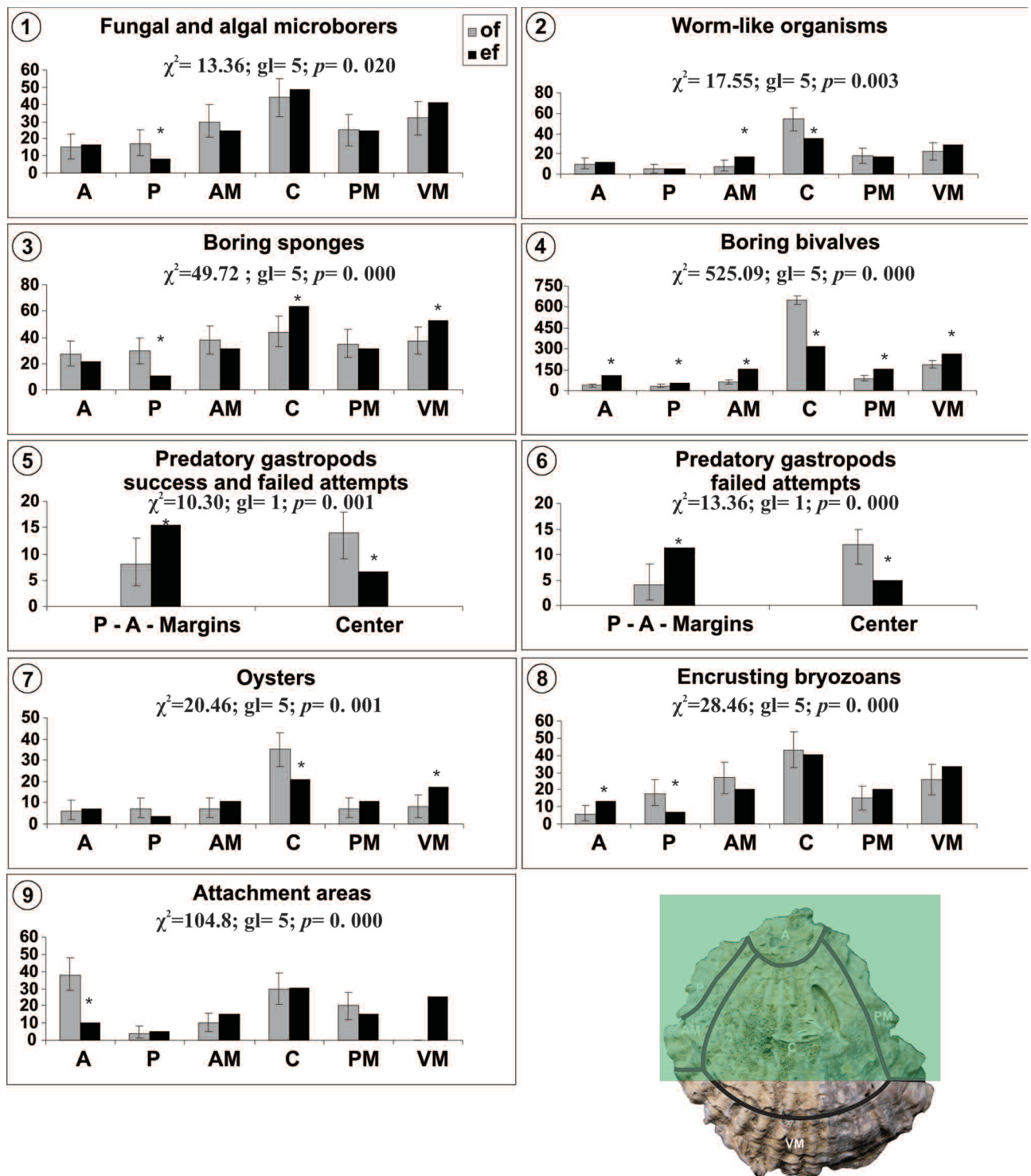| Sclerobionts	External vs. Internal surfaces		Left vs. Right valves	
	Coverage *DP = 77.11*	*Abundance* *DP = 84.07*	*Coverage* *DP = 69.28*	*Abundance* *DP = 72.50*
Fungal and algal microborers	*21.6*	*-*	*19.18*	*-*
Boring sponges	*19.71*	*-*	*23.35*	*-*
Boring bivalves	*16.6*	*50.09*	*12.11*	*43.76*
Encrusting bryozoans	*12.86*	*-*	*13.08*	*-*
Worm-like animals	*11.55*	*24.74*	*14.2*	*28.78*
Encrusting polychaetes	*5.88*	*-*	*6.27*	*-*
Predatory gastropods	*5.52*	*10.98*	*-*	*11.35*
Oysters	*-*	*10.81*	*6.38*	*11.04*

Figure 11. Goodness of fit test and exact confidence intervals for the binomial distribution for the external surfaces of *O. alvarezii* left valves. Graphics represent those sclerobionts whose distribution was not random. Asterisks indicate significant differences between expected (**ef**) and observed (**of**) frequencies. The most frequently colonized areas are indicated by a green rectangle in the oyster figure.
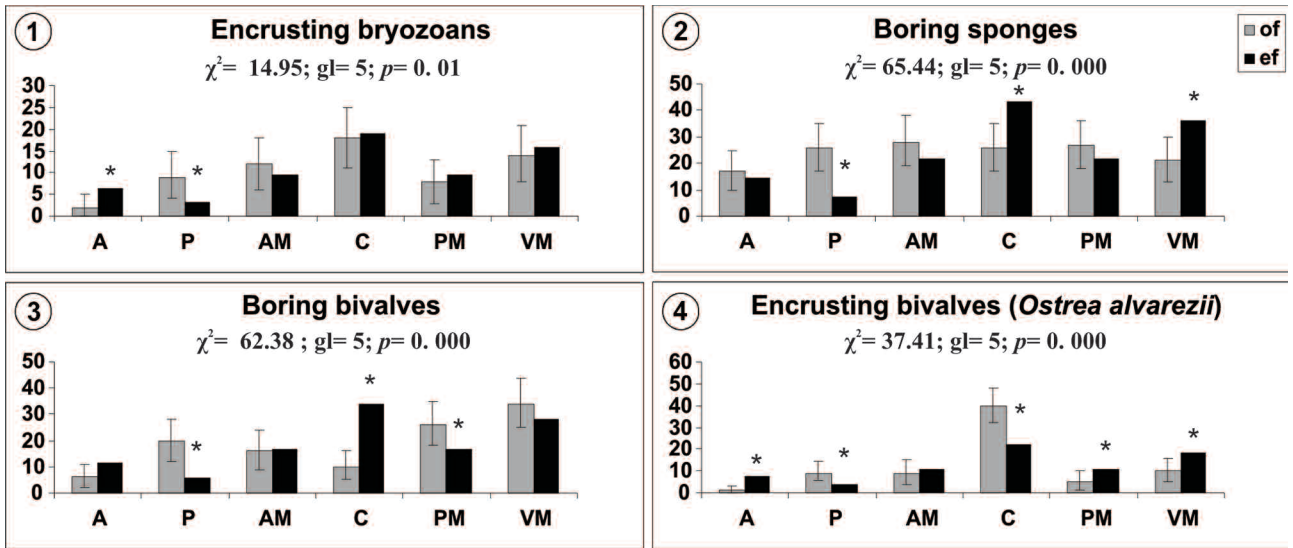
Figure 12. Goodness of fit test and exact confidence intervals for the binomial distribution for the internal surfaces of *O. alvarezii* left valves. Graphics represent those sclerobionts whose distribution was not random. Asterisks indicate significant differences between expected (**ef**) and observed (**of**) frequencies.
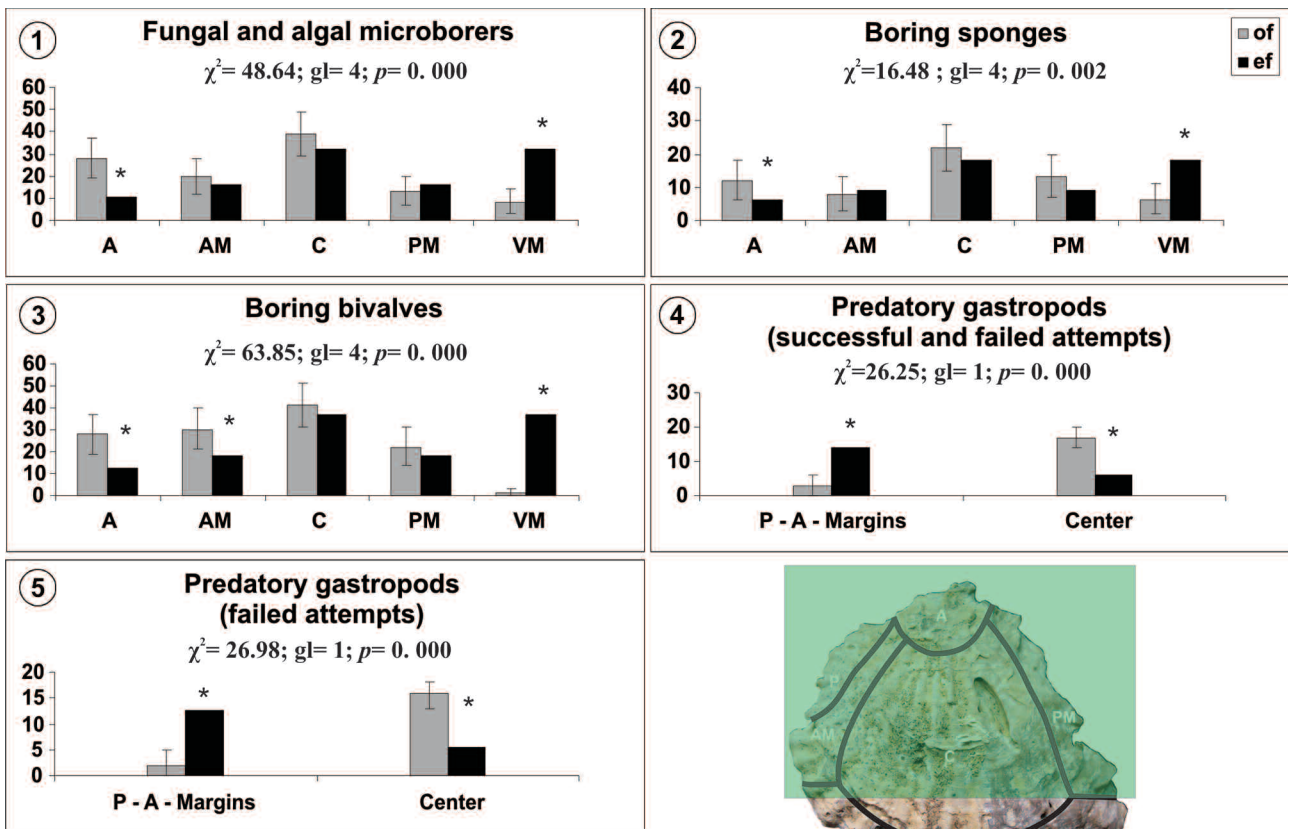

Figure 13. Goodness of fit test and exact confidence intervals for the binomial distribution for the external surfaces of *O. alvarezii* right valves. Graphics represent those sclerobionts whose distribution was not random. Asterisks indicate significant differences between expected (**ef**) and observed (**of**) frequencies. The most frequently colonized areas are indicated by a green rectangle in the oyster figure.

DISCUSSION

Paleoenvironment

The similar taphonomic, paleoecological and physical features found at three levels within the oyster beds suggest a complex history of a *post mortem* concentration of valves subjected to discrete events. *Ostrea alvarezii* beds were developed in a tide-dominated, shallow-marine clastic environment with a low sedimentation rate.

Using taphonomic features and sclerobionts, a moderate degree of taphonomic-reworking and hydraulic transport of valves within-habitat can be inferred by high disarticulation, low fragmentation and moderate to low abrasion along with a slightly uneven proportion of right/left valves. It is known that skeletons disarticulate quite rapidly after death in banks (Lowenstam, 1950 in Riding, 2002); oyster shells disarticulate in about two years (Christmas *et al.*, 1997). Therefore, the high frequency of disarticulation of *O. alvarezii* can be interpreted as the result of normal postmortem decay. A slightly uneven proportion of left and right oyster valves was found in the *O. alvarezii* beds, suggesting a community buried *in situ* or transported only a short distance (Seeling and Bengtson, 1999). In this study, *O. alvarezii* beds are proposed to be parautochthonous accumulations that concentrate several generations of individuals in the same environment (Kidwell *et al.*, 1986) and are therefore interpreted as within-habitat time-averaged assemblages (Kidwell and Bosence, 1991). Diverse studies in modern environments propose that the damage and most of the lateral movement of hardparts result from processes operating within the original life habitat of the source population (Kidwell and Flessa, 1996). Oysters appear to have lived in small subtidal channels and, maybe, in a low energy tidal flat, and could have been transported and concentrated on the channel floor throughout different events. It seems that *O. alvarezii* lived, like the recent oyster *Ostrea puelchana* d'Orbigny, 1842, in subtidal habitats in the Golfo San Matías (see Romero *et al.*, 2013).

Sclerobionts are affected by depth, turbulence and sedimentation rates in marine environments (Brett *et al.*, 2012). Also, bioerosion increases with productivity and decreases with high rates of sedimentation (Lescinsky *et al.*, 2002). The presence of well-developed bioerosional structures on *O. alvarezii* suggests that the rate of sedimentation was low or null for a period of time; only small quantities of sediment

are required to destroy an endolithic community, although some organisms are more tolerant than others (Bromley, 1994). Most of the organisms associated on *O. alvarezii* were suspension feeders, like bryozoans. These organisms develop preferentially in clear and oxygenated waters and exhibit a high vulnerability to turbidity and sedimentation (Smith, 1995). Some borers, such as bivalves, can live under a few millimeters of sediment while others, such as sponges, are much more sensitive to suffocation; in this sense, *Entobia* isp. displays a preference for environments with low rates of sedimentation (Bromley, 1994). On the other hand, the rate of bioerosion and the diversity of fossil traces decreases with increasing depth (Brett *et al.*, 2011). Fossil traces can provide useful information to estimate the intensity of light and are also good indicators of depth (Buatois and Mángano, 2011). Therefore, deposition within the photic zone can be inferred from the presence of the microperforations of algae and *Radulichnus* isp., representing the activity of gastropods and chitons grazing on a substrate, while shallow marine waters can be inferred from *Gastrochaenolites* isp. and *Entobia* isp. on *O. alvarezii*. Sclerobionts on *O. alvarezii* resemble the communities described in the modern euphotic and shallow environment of Lee Stocking Island, Bahamas, and the siliciclastic shelf settings of the Golfo de México (Brett *et al.*, 2011).

Both taphonomic feedback (Kidwell, 1991),—the colonization of transported and/or reworked valves by sclerobionts,—and taphonomic features, such as the degree of fragmentation, abrasion, bioerosion and encrustation, have been extensively employed as indicators of time of exposure of bioclasts on the seafloor (Kidwell and Bosense, 1991). These cannot be ignored when understanding the richness of the bryozoans and bioeroders recorded on *O. alvarezii*. The low fragmentation and abrasion together with the high degree of bioerosion in this concentration indicate the existence of well oxygenated waters with little clastic material in suspension and, perhaps, also a moderate exposure time for bioclasts on the interface water-sediment. However, we consider that the "fresh shell syndrome" (Brett *et al.*, 2011) could better explain the richness of colonizers on *O. alvarezii*. These authors documented that the surfaces of fresh shells are more attractive for the settlement of larvae than those of shells aged on the seafloor. The authors postulated that most sclerobionts colonize shells

within a time span shorter than one year and that the recruitment of new sclerobionts decreases with time. We consider that the high degree of bioerosion and encrustation on *O. alvarezii* can be the product of the colonization on fresh valves through a few years, according to the results provided by Brett *et al.* (2011) and, not undoubtedly, to taphonomic feedback.

Distribution patterns of sclerobionts and life position of oysters

Sclerobionts showed differential distributions on the external and internal surfaces of the shells. In general, the same types of sclerobionts were present on both surfaces. However, the number of colonized external surfaces was higher than the one of internal surfaces, therefore suggesting that colonization occurred *in vivo* and then *post mortem* too. Once disarticulated, the valves were exposed at the water-sediment interface. The difference between them could be explained by considering a more prolonged exposure of the external surfaces as valves adopted a more stable convex-upward position on beds according to the taphonomic signals registered in these deposits (McKinney, 1996). The higher number of rugose left valves colonized by sclerobionts, in relation to the smooth right ones, is explained by a rugophilic behavior (Bien *et al.*, 1999) and the active selection of structurally complex substrates by larvae of benthic invertebrates (Warner, 1997; Hoover and Purcell, 2009). The same difference between valves was observed by Mauna *et al.* (2005), who considered boring bivalves on *O. puelchana* and *O. alvarezii*. A differential distribution of sclerobionts on areas of the valves was also recognized. On the left valves, sclerobionts that were differentially distributed settled on the platform, center and/or posterior margin. These areas are sediment-free zones on the external surfaces of living oysters (personal observations), a feature that could have been an ecological constraint for the selection of primary settlement substrate by larvae (Moore, 1977). The edges of the internal surfaces seem to have been frequently colonized *in vivo* when devoid of fragile lamellae, as observed in *O. puelchana* (Romero *et al.*, 2013). On the external surfaces of the right valves, the apex and anterior margin seem to have been sediment-free areas suitable for colonization by sclerobionts. Also, traces of predatory gastropods, mostly of failed attempts, were

recorded in the center and were perhaps produced *in vivo* as gastropods are vagile organisms that can be buried in the sediment. The differential distribution of sclerobionts in response to shell topography has been observed on bivalves and brachiopods by other authors studying living hosts (*e.g.*, Rodland *et al.*, 2004, 2014).

The diversity and relative abundance of the encrusting and boring taxa are consistent with those described for other hard substrate fossil assemblages from Neogene shallow marine environments (Domènech *et al.*, 2001; Taylor and Wilson 2003). The diversity and differential distribution of sclerobionts on *O. alvarezii* are comparable with those observed by Parras and Casadío (2006) in sedimentological accumulations of *Crassostrea*? *hatcheri* (Ortmann, 1897) (Oligocene–Miocene, Centinela and San Julián Formation) and also resemble those of the epibiotic assemblages settled on *O. puelchana* from the Golfo San Matías (see Romero *et al.*, 2013).

The differential distribution of sclerobionts between valves can be used to infer the life position of *O. alvarezii*, which was close to the sediment-water interface with the right valve resting on the substrate. A similar approach has been used by other authors to infer the lifestyles of Cretaceous, Miocene and recent oysters (Bien *et al.*, 1999; Mauna *et al.*, 2005; Brezina *et al.*, 2014).

Sclerobiont assemblages: behaviors, trophic levels and tiers

From an ethological perspective, the 16 ichnotaxa that were registered represent three main types of behaviors—dwelling, grazing and predation—and can therefore be grouped into three ethological categories (Tab. 1). Ausich and Bottjer (1982) defined the term tiering as the vertical distribution of organisms in space above and below the sediment surface due to the partitioning of resources. Bromley and Asgaard (1993) employed this term to describe the vertical partitioning of endolithic communities on hard substrates. This concept can be applied to biogenic hard substrates and, in this context, it can be concluded that there was a well-developed tiering on the shells of *O. alvarezii*, *i.e.*, shallowest to deepest tier sclerobionts were represented on oyster valves occupying different levels beneath the external surfaces of the valves. Likewise, the concepts of tiering and ichnoguilds were taken from the ecological literature and adapted to describe certain pat-

terns found in ichnologic studies. Ichnoguilds refer to biogenic structures with shared features like use of space (*i.e.,* tier), trophic group, behavior and morphology (Bromley, 1996). The sclerobionts recorded in this work represented different trophic groups such as suspension feeders, selective deposit feeders, filter feeders, predators and grazers. Furthermore, the shells of *O. alvarezii* studied herein exhibit a set of different ichnoguilds reflecting diverse behaviors, trophic levels and tiers. This suggests that sclerobiont assemblages had a complex structure with a subdivision of resources and relationships between organisms. These results are consistent with the one expressed for communities of hard substrates by Ausich and Bottjer (2001). Infaunal communities from the Neogene ecosystems of Patagonia displayed vertical niche partitioning and a notable use of ecospace (Carmona *et al.*, 2012). In the same way, sclerobiont assemblages on *O. alvarezii* exhibited a remarkable use of the valves represented by different tiers and ichnoguilds.

CONCLUSIONS

Ostrea alvarezii beds are interpreted as within-habitat, time-averaged assemblages. Oysters appear to have lived in small subtidal channels in a low energy tidal flat resembling the subtidal habitats of the recent oyster *Ostrea puelchana* from the Golfo San Matías. Sclerobiont assemblages on *O. alvarezii* had a complex structure with subdivision of resources, including a vertical colonization of valves by tracemakers at different depths in the valves.

The sclerobionts on *O. alvarezii* can be considered a proxy to refine the paleoenvironmental reconstructions performed so far and to identify the life position of the oysters. Even if the critical question for paleontologists is how the lateral and vertical movement of shelly deposits limits the fidelity of species composition, research on sclerobiont assemblages which maintain their life position and spatial relationships with the host-substrate deepens the paleoenvironmental knowledge of spatial and temporal mixing.

ACKNOWLEDGMENTS

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