Ichnos: An International Journal for Plant and Animal Traces

Byssal Attachment Etchings: A New Bioerosion Trace on Recent Oysters

M. V. Romero [a] [b] [c] , S. S. Brezina [d] , C. Bremec [a] [b] [c] & S. Casadío [a] [d]

[a] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) , Buenos Aires , Argentina

[b] Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) , Mar del Plata , Argentina

[c] Instituto de Investigaciones Marinas y Costeras (UNMdP-CONICET) , Mar del Plata , Argentina

[d] Instituto de Investigación en Paleobiología y Geología , Universidad Nacional de Río Negro (UNRN) , Gral. Roca , Argentina
Published online: 18 Nov 2013.

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained
in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no
representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the
Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and
are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and
should be independently verified with primary sources of information. Taylor and Francis shall not be liable for
any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever
or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of
the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic
reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any
form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://
www.tandfonline.com/page/terms-and-conditions

Taylor & Francis
Taylor & Francis Group

Byssal Attachment Etchings: A New Bioerosion Trace on Recent Oysters

M. V. Romero,[1,2,3] S. S. Brezina,[4] C. Bremec,[1,2,3] and S. Casadío[1,4]

[1]*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina*
[2]*Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina*
[3]*Instituto de Investigaciones Marinas y Costeras (UNMdP-CONICET), Mar del Plata, Argentina*
[4]*Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro (UNRN),*
Gral. Roca, Argentina

Byssate bivalves can be attached to hard substrates by byssal threads. Dissolution of the substrate to which they are attached may leave superficial bioerosion traces. This study reports the scars produced by byssus of *Mytilus edulis* and *Aulacomya atra* recorded in shells of *Ostrea puelchana*. Oyster valves were cut and gold-sputtered prior to scanning electron microscope observation. Each byssal thread leaves a characteristic scar on shells substrate. They etch an irregular trace on the substrate which may reach a diameter of several centimeters. These etching-traces comprise shallow round/oval holes of variable number and placement. A bundle of pits corresponding to fibers that compose the thread core was identified in the interior of each hole. We suggest that this trace could be included in the ethological class Fixichnia. The description of this trace would allow adjusting the composition of fossil assemblages and therefore paleoenvironmental interpretations in those cases in which mytilid shells have not been preserved. The recognition of this trace along with other ones of tracemakers with reotaxis or positive phototaxis could be useful in inferring the life habit of fossil biogenic substrates and in reconstructing their taphonomic history.

Keywords   Oysters, Fixichnia, Byssal Etchings, SW Atlantic Ocean, Argentina

INTRODUCTION

Numerous styles of attachment have evolved in hard substrates communities and were described in detail by Bromley and Heinberg (2006). Several nonencrusting organisms can attach to hard substrates in the same way as encrusters but using organic compounds secreted by specific structures (Taylor and Wilson, 2003). These organisms may show permanent or temporary attachment to the substrate and different strategies for fixation, including adherence by means of soft-parts anatomical structures (e.g., echinoderm podia, gastropod foot) and chemical adhesives (e.g., gastropod pedal glue, bivalve byssus), all of them producing shallow trace fossils (Bromley and Heinberg, 2006). Attachment etchings are trace-fossil cavities produced by the shallow excavation of a holdfast form into a hard substrate (Tapanila and Ekdale, 2007). Palmer and Plewes (1993) inferred that the dissolution of underlying substrate (e.g., shells) where sessile organisms are attached may be a common event.

Since the Precambrian, mucins were involved in the development of different activities and functions that allowed the successful radiation in Bivalvia; initial pedal attachment structures were no more than adhesive mucins that were the evolutionary analogs of byssi (Prezant, 1990). Yonge (1962) proposed that byssal attachment evolved by neoteny from byssate larval stages of burrowing bivalves. This probably occurred in endobyssate forms (e.g., *Modiolus*-like forms), which living partly or entirely buried in sediment were the ancestors of major epibyssate bivalves and may be associated to growing colonization of epifaunal environments; nevertheless, evolutionary transition from infaunal to epifaunal life habits in Bivalvia was possibly polyphyletic (Stanley, 1972).

In Mytilidae, the byssus is confirmed by a root attached to the byssal retractor muscle, a stem that extends from the root and byssal threads. The stem is embedded in the byssal retractor muscle near the base of the foot (Silverman and Roberto, 2007). Elastic structures known as byssal threads are developed from the stem and they measure between 0.1 and 0.15 mm in diameter and 2 to 4 cm long (Coyne et al., 1997). Each byssal thread has a collagen inner core surrounded by a hardened proteinaceous cortex (Silverman and Roberto, 2007) that expands into an adhesive plaque adhering to the substratum (Wiegemann, 2005); its size depends on the individual size and the age of the byssus (Crisp et al., 1985, in Silverman and Roberto, 2007).

The thread is divided in a proximal and a distal portion, which show different morphological, mechanical, and compositional properties (Harrington and Waite, 2008; Harrington et al., 2009). The former is closer to the organism and is more elastic and commonly less tough than the distal portion (Waite et al., 1998; Wiegemann, 2005). The distal portion is composed of densely packed straight fibers between 7 and 9 nm in diameter (Waite et al., 1998). Prior to the attachment of a new thread, the mussel foot removes attached microfouling and surrounding particles abrading the surface (Wiegemann, 2005). Byssal threads are secreted sequentially in many directions, allowing mechanical stability to resist the water movement (Waite, 2002).

There are no descriptions of marks attributable to anchoring bivalve byssi. Different patterns of attachment etchings have been described, such as circular marks assignable to organic structures. Examples are circular arrangements of microscopic pits generated by the pedicle of articulate brachiopods or ring-shaped imprints produced by anomid bivalves cemented to a lithic or shelly substrate (Donovan and Pickerill, 1999). Nevertheless, bivalves as tracemakers in shells and other calcium carbonate substrates on the sea-bed have been widely studied by palaeontologists and most of these studies are referred to dwelling traces (Kelly and Bromley, 1984; Wilson and Palmer, 1988; Kleemann, 1996; Ekdale and Bromley, 2001; Zonneveld, 2001; Bassi et al., 2011). However, other bivalve ethological traces are less frequent in the paleontological literature (Buatois and Mangano, 2011).

Superficial etching scars is one of the six main groups of bioerosion structures proposed by Ekdale et al. (1984) based on morphology and ethology. Anchoring etchings were not contemplated by Seilacher (1953) in his ethological classification of trace fossils. Gibert et al. (2004) proposed a new ethological class named Fixichnia to include these superficial structures produced by epifaunal organisms to anchor or fix themselves to the substrate using soft or skeletal body parts. Ichnotaxa such as *Centrichnus* Bromley and Martinell (1991), *Podichnus* (Bromley and Surlyk, 1973), *Renichnus* (Mayoral, 1987a), *Leptichnus* (Taylor et al., 1999), and *Stellichnus* (Mayoral, 1987b) have been considered Fixichnia and their corresponding tracemakers have been identified.

This study reports the etchings produced by the byssus of *Mytilus edulis* Linnaeus, 1758 and *Aulacomya atra* (Molina, 1782), both byssate bivalves were attached to shells of *Ostrea puelchana* (d'Orbigny, 1842) (Fig. 1). The preferential settlement of the byssus and the byssal etchings on different areas of the left and right valves was assessed.

MATERIALS AND METHODS

Study Area

O. puelchana specimens were collected in San Matías Gulf (SMG, 40° 42' - 42° 41' S; 63° 45' - 65° 09' W). SMG is a semi-enclosed area of the Argentinean shelf. It shows particular oceanographic features (Guerrero and Piola, 1997); maximum depths are nearly 200 m in the central area (Parker et al., 1997) and the regime is macrotidal (Servicio de Hidrografía Naval, 2010). The average salinity is high (33.84) and the average annual temperature is $13.25 \pm 0.20°C$ with strong thermal stratification mainly in summer (Rivas, 1990). The bottom is sandy with high contents of silt and clay (Parker et al., 1997). Oyster banks grow on sand or sand-gravel substrates over 10 m deep (Escofet et al., 1978).

Sampling

A total of 142 oysters were collected in February 2009 in two natural banks located at northwest of SMG, called *El Buque* (EB, 40° 50' S; 65° 10' W) and *Zona de Colectores* (ZC, 40° 56' S; 65° 06' W), at a depth of 12 and 18 m, respectively, at low tide. Samples were taken randomly within the most densely packed zone of each bank. To avoid loss of macrofauna associated to the valve, each oyster was stored individually in a plastic bag. The valves were fixed in 5% seawater formalin and 15 days later they were stored in 70% alcohol. Mytilidae specimens were assigned to *Mytilus edulis* and *Aulacomya atra*. The marks produced by their byssal attachment on the external surfaces of the valves were recognized under binocular microscope. Samples for scanning electron microscope (SEM) analysis were obtained using a Silicon Carbide abrasive cutter by carefully cutting small pieces of valves which contained previously identified traces. After gold sputtering, the samples were visualized at the LIMF-*Universidad Nacional de La Plata* using a Fei Quanta 200 SEM in low vacuum mode. A series of magnifications were selected with images having a scale ranging from 1 mm to 500 μm.

Areas were defined within each valve to test preferential settlement of byssate bivalves. Zonification maps of both valves were performed. This map reflects dissimilar morphological features of the valves that may influence the settlement of bivalve larvae. The left valve exterior 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 into which they were divided are apex (10%), anterior margin (15%), ventral margin (30%), posterior margin (15%), and center (30%). Percentages were calculated in relation with the total valve area (100%) following Romero et al. (in press).

The coverage percentage of byssal threads and plaques and/or etchings was recorded in the zonification maps of each valve. The Wilcoxon paired-sample test (Zar, 1999) was used to compare the coverage percentage of byssal threads and plaques and/or etchings between external surfaces of both oyster valves. A goodness of fit test was performed in order to assess possible preferential location of byssus and their byssal etchings on different areas within left and right valves. The expected frequencies were calculated using a correction coefficient to take into account the different surface assigned to each area. This coefficient is different for each area and it corresponds to
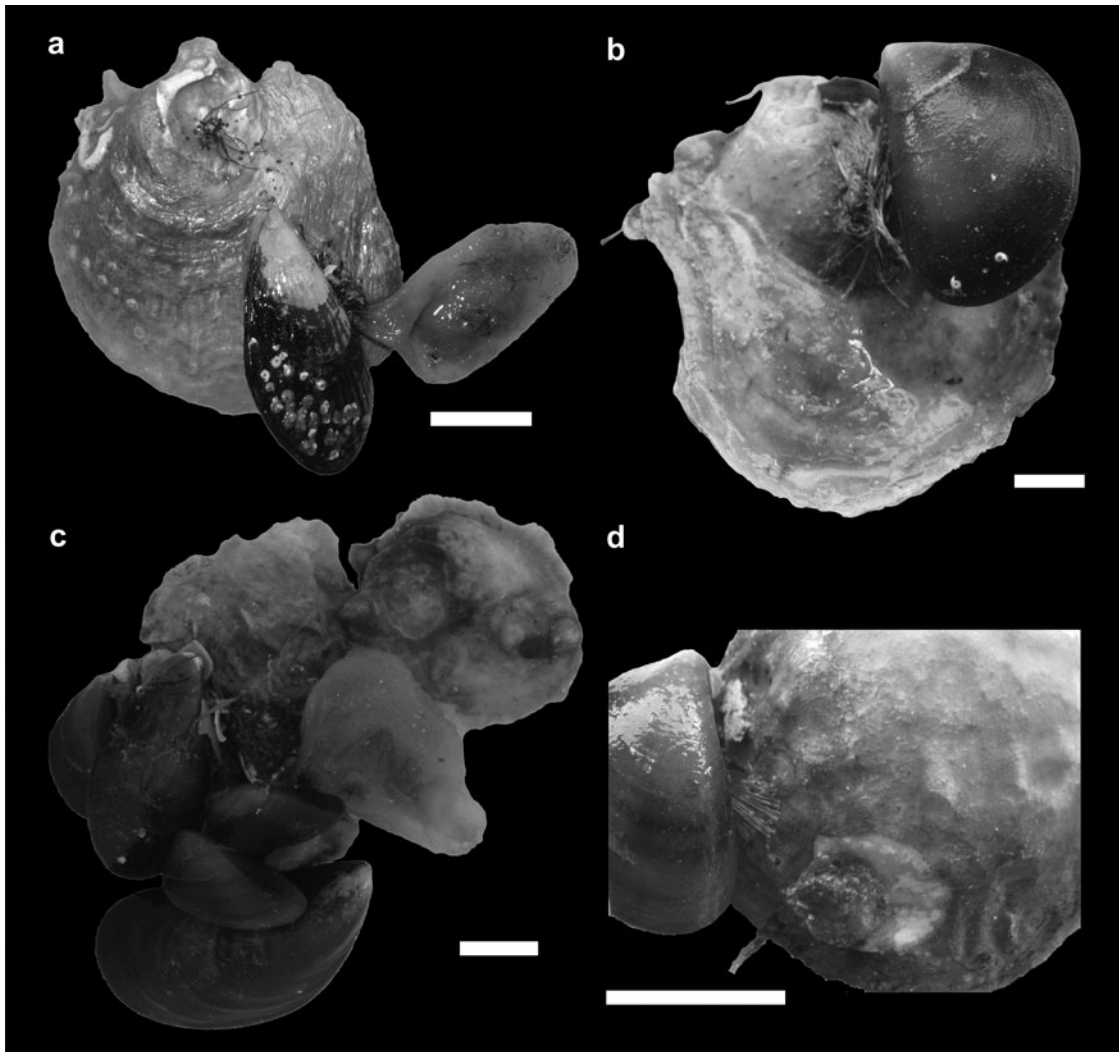
FIG. 1. Byssate bivalves and byssus attached to shells of *Ostrea puelchana* d'Orbigny 1842. **(A)** *Aulacomya atra* (Molina, 1782); **(B)** *Mytilus edulis* Linnaeus, 1758; **(C)** bunch of mytilids covering oyster valves; and **(D)** detail of mussel byssus fixed on oyster valve. Scale bars = 2 cm. (See Color Plate I.)

the proportion between the percentage assigned to one area and the percentage of the total valve area (e.g., correction coefficient for apex = 10/100). When more than 20% of the expected frequencies were less than five, valve areas were grouped to avoid this test becomes inaccurate. Yates's correction for continuity was applied in those cases in which there is only one degree of freedom, and relatively small samples (Zar, 1999). The null hypothesis was the random distribution of byssus and their etchings on valves at significance level $\alpha = 0.05$.

BYSSAL ETCHINGS

Each byssal thread (Figs. 2A and B) leaves a characteristic mark on shelly substrates, which is recognizable when the adhesive plaques are removed. They etched a whole irregular trace on the substrate which may reach a diameter of several centimeters. The trace can occupy an area between 1 and

5 cm^2 on oyster valves (shell height between 50 and 110 mm). This arrangement is produced by the radial extension of the threads from the small foot of the mussel. Some of the holes are found more closed one to another (e.g., 0.01 mm) and others neighboring holes are more distant between them (e.g. up to 1.5 mm) (Figs. 2C–F). These marks are shallow etching bioerosion traces that comprise round/oval holes in variable number and disposition. Each hole varied between 0.25 and 0.5 mm in diameter and normally less than 0.3 mm in depth (Fig. 2). The holes do not show a differential pattern in form or size in any direction and all of them are excavated to approximately the same depth; all enter the substrate perpendicularly. A dense bundle of pits corresponding to fibers that comprise the thread core is identified within each hole (Fig. 2D). In some cases, pits are partial or totally absent and in consequence the holes are smooth (Fig. 2E).
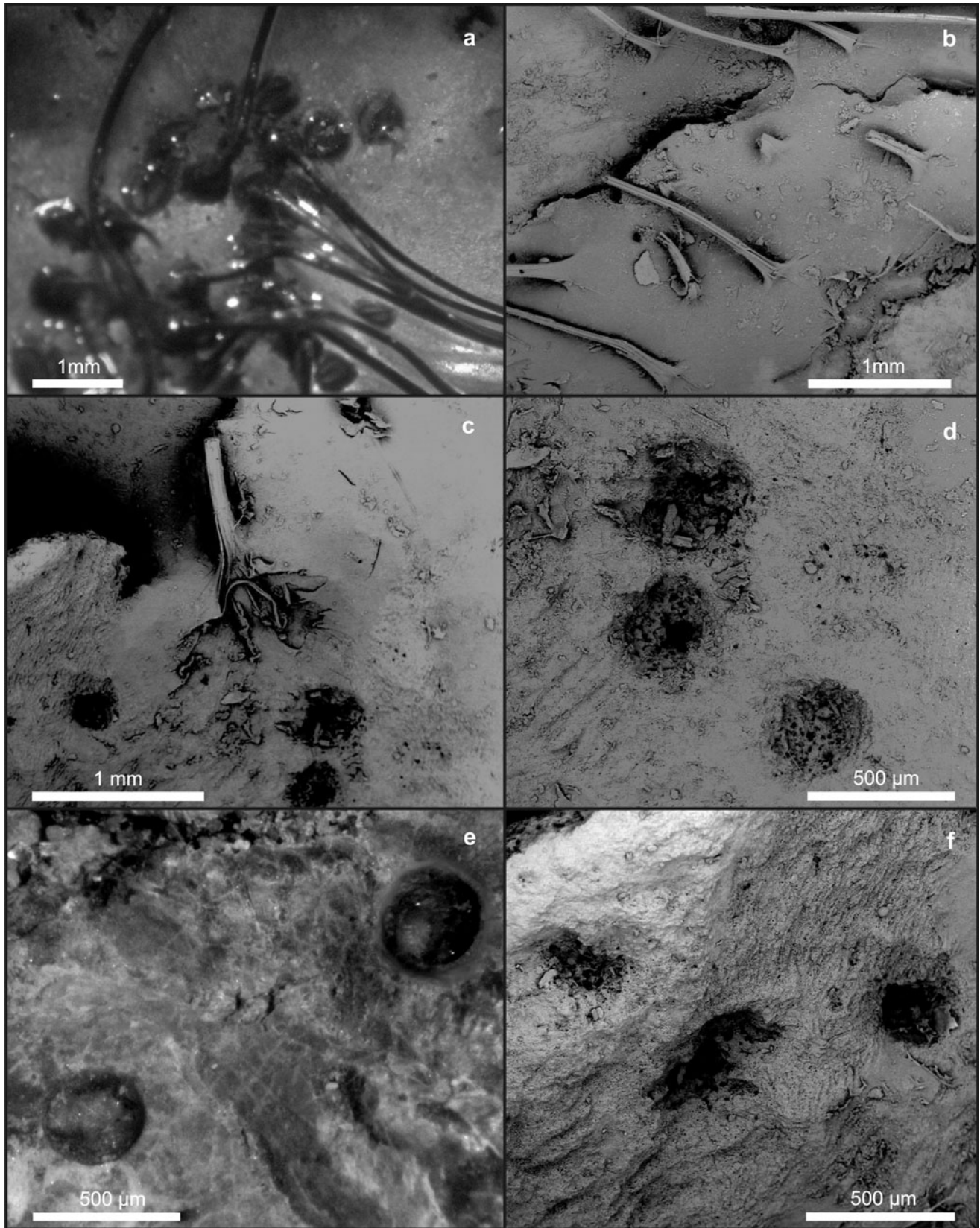
FIG. 2.   Byssus and byssal etchings on *O. puelchana* valves. **(A)** View of proteinaceous cortex of byssal threads and adhesive plaques using stereoscopic microscope. **(B)** SEM image showing byssal threads and adhesive plaques. **(C)** A byssal thread initially detaching from the oyster valve and three round/oval byssal etchings**. (D)** Dense bundle of pits corresponding to fibers that compose the thread core within each byssal etchings. **(E, F)** Pattern of variation of size and shape in byssal etchings.

Twenty-eight percent of oysters examined presented mytilids/byssi attached, and in 18% only the byssate bivalve trace was registered. The Wilcoxon paired-sample test indicated significant differences between left and right valves based on coverage of byssal threads and plaques and/or etchings. This trace was recorded in both valves, although left valves were more colonized by mytilids ($Z = 2.214$; $p = 0.027$) and their etchings occupied a greater area than on the right valves ($Z = 2.17$; $p = 0.030$). The Wilcoxon test was significant at level $p < 0.05$.

Differential location of byssus and byssal etchings on different areas within left and right valves was not detected ($p > 0.05$ for both cases and right and left valves).

The bioerosive trace described in this contribution presents distinctive characteristics and it represents a new ethological superficial structure produced by byssate bivalve. This trace would be assigned into the class Fixichnia within the recent ethological classification in use. This class includes superficial (epigenic) traces produced by sessile epiliths that anchor or fix themselves to the substrate using soft or skeletal body parts (Gibert et al., 2004).

Podichnus is a biogenic structure that evidences the fixation of brachiopods by the pedicles (Bromley and Surlyk, 1973). The byssal etchings are easily differentiated from *Podichnus* because they show a chaotic pattern in different directions and are more widely scattered than the borings produced by brachiopod pedicles, which shows a circular pattern of small holes that increase in size and become more skewed toward the outer edge of the trace (Taylor and Wilson, 2003). The byssal etchings unequivocally did not identify a single tracemaker, while in *Podichnus* each brachiopod "footprint" identifies just one individual (Bromley and Surlyk, 1973).

Centrichnus is attributed to cementation of anomiid bivalves as well as the attachment of verrucid cirripedes to a hard substrate (Bromley and Martinell, 1991).The difference between *Centrichnus* and byssate bivalves traces lies primarily in that the former is characterized by a series of concentric rings or arcs that demonstrate the accretionary growth of skeletal hard part of the tracemaker. *Centrichnus eccentricus* represents the byssal cementation of anomiid bivalves in which the right valve is completely and permanently attached to the substrate by a calcified byssus (Bromley and Martinell, 1991). This mode of attachment leaves a more compact and oval trace, drop shaped, curved about a center reminding of the tracemaker's valve shape. The newest growth increment towards the ventral margin of the lower valve is marked by a concentric etching groove in the substrate. *Centrichnus concentricus* presents a hole or central depression but with an oval and crenulate perimeter and a surrounding platform that usually reflects the plate-ornament of the verrucid barnacle and the concentric growth-lines (Bromley and Martinell, 1991). Moreover, *Centrichnus* is larger than the trace characterized here (i.e., maximum observed diameter = 8.5 mm in *C. concentricus* and 10 mm in *C. eccentricus*), and each trace would correspond with only one individual.

Leptichnus (Taylor et al., 1999) shows a similar pattern of several and shallow pits (i.e., by detachment of encrusted sheets of cheilostomate zooids), but each scar is eliptical and keeps an uniseriate pattern with regular distance between excavated pits with a more symmetric arrangement compared with byssate bivalve traces. *Renichnus* is assigned to vermetid gastropods (Mayoral, 1987a). This trace is easily distinguished from the byssal marks because they are deeper, with crescent or kidney shaped depressions, and in its more advanced stage it describes the shape of the gastropod.

Finally, *Stellichnus* (Mayoral, 1987b) is a star-shaped system of shallow grooves radiating from a central area. This morphology is reminiscent of ctenostomate bryozoans belonging to *Vinellidae*. Although this trace shows perforations in the center and at the sides of the grooves, they are smaller than the byssal scars (i.e., diameter between 5 and 45 μ). Moreover, *Stellichnus* shows a more regular arrangement than the byssus trace.

CONCLUSIONS

This article describes a new ethological superficial etchings produced by byssate bivalves classified as Fixichnia. The record of this endolithic bioerosion trace produced by a bivalve byssus may allow adjusting the composition of fossil assemblages and therefore paleoecological environmental interpretations, especially in those cases in which mytilid shells have not been preserved. In addition, the recognition of this trace, along with other ones whose tracemakers display reotaxis or positive phototaxis, could be useful to infer the life habit of fossil substrates and reconstruct their taphonomic history.

The shells of *O. puelchana* record a set of bioerosive traces which represent several ichnoguilds that reflect different behavior, trophic levels and depths in which were placed on the substrate (i.e., tiers). Along with byssal etchings, traces from shallowest to intermediate deeper tiers (see Bromley and Asgaard, 1993) have been frequently recorded (i.e., *Leptichnus* isp., *Radulichnus* isp., *Entobia* isp., *Gastrochaenolites* isp., and *Semidendrina* isp.). In all these cases, etchings are sufficiently deep to pass through the oyster periostracum and leave preservable traces when this layer is lost by physical and biological erosion.

According to Bromley and Asgaard (1993), *Radulichnus inopinatus* (Voigt, 1977) and *Gnathichnus pentax* (Bromley, 1975; absent in this study) are considered to be traces that make up the most superficial ichnoguilds, while *Renichnus arcuatus* (Mayoral, 1987a) and *Centrichnus eccentricus* (Bromley and Martinell, 1991) are almost as superficial as the former, constituting a different ichnoguild. Probably, these ichnospecies and byssal etchings represent an ecologic unit according to the depth at which they occur and because the tracemakers are sessile mollusks that produced superficial traces by attachment to the substrate. However, during the oyster colonization by different taxa this trace may be generated by detachment of the byssal plaques anytime. Although these traces compose a

shallow tier it does not imply that they originate at the beginning of a sequence of colonization, suggesting that the general tiering scheme proposed by Bromley and Asgaard (1993) does not necessarily carry temporal meanings in the colonization sequence which in some cases is very complex to identify.

Most of Paleozoic epifaunal bivalves were byssate; only a few groups (e.g., Japanese Permian forms) are known to have attached by cementation (Stanley, 1972). Furthermore, this bioerosion trace should be commonly found in fossil record.

Naming this new trace is controversial. The International Code of Zoological Nomenclature (ICZN, 1999) suggests that it is not advisable to assign names on the basis of unfossilized material. However, according to Nielsen et al. (2003) a new bioerosive trace must be named regardless of the age of the material in which it is registered, allowing the discovery of behaviors of living organisms and facilitate communication between biologists and geologists to work in this field. We followed this approach to include a trace described from recent material into an informal ethological classification based on fossil material.

ACKNOWLEDGMENTS

REFERENCES

Bassi, D., Humblet, M., and Iryu, Y. 2011. Recent ichnocoenosis in deep water macroids, Ryukyu islands, Japan. *Palaios*, 26: 232–238.

Bromley, R. G. 1975. Comparative analysis of fossil and recent echinoid bioerosion. *Palaeontology*, 18: 725–739.

Bromley, R. G. and Asgaard, U. 1993. Endolithic community replacement on a Pliocene rocky coast. *Ichnos*, 2: 93–116.

Bromley, R. G. and Heinberg, C. 2006. Attachment strategies of organisms on hard substrates: A palaeontological view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232: 429–453.

Bromley, R. G. and Martinell, J. 1991. *Centrichnus*, new ichnogenus for centrically patterned attachment scars on skeletal substrates. *Bulletin of the Geological Society of Denmark*, 38: 243–252.

Bromley, R. G. and Surlyk, F. 1973. Borings produced by brachiopod pedicles, fossil and Recent. *Lethaia*, 6: 349–365.

Buatois, L. A. and Mangano, M. G. 2011. *Ichnology: Organism-substrate Interactions in Space and Time*. Oxford, Cambridge University Press, 358 p.

Coyne, K. J., Qin, X., and Waite, J. H. 1997. Extensible collagen in mussel byssus: A natural block copolymer. *Science*, 277: 1830–1832.

Crisp, D. J., Walker, G., Young, G. A., and Yule, A. B. 1985. Adhesion and substrate choice in mussels and barnacles. *Journal of Colloid and Interface Science*, 104: 40–50.

Donovan, S. K. and Pickerill, R. K. 1999. Fossils explained 26: Trace fossils 4-borings. *Geology Today*, 15: 197–200.

d'Orbigny, A. 1842. Voyage dans l'Amerique Meridionale (Le Brésil, La République Orientale de L'Uruguay, La République Argentine, La Patagonie, La République du Chili, La République de Bolivie, La République du Pérou, exécuté pendant les anné 1826–1833. *In* Bertrand, C.P. (ed.), Chez Ve Levrault, Tome 3, 4th part, *Paléontologie*, Paris, 188 p.

Ekdale, A. A., Bromley, R. G., and Pemberton, S. G. 1984. Ichnology, the use of trace fossils in sedimentology and stratigraphy. Society of Economic Paleontologists and Mineralogists, Short Course 15, 317 p.

Ekdale, A. A. and Bromley, R. G. 2001. Bioerosional innovation for living in carbonate hardgrounds in the Early Ordovician of Sweden. *Lethaia*, 34: 1–12.

Escofet, A., Orensanz, J. M., Olivier, S. R., and Scarabino, V. 1978. Biocenología bentónica del Golfo de San Matías (Rio Negro, Argentina): Metodologia, experiencias, y resultados del estudio ecológico de un gran espacio geográfico de America Latina. *Anales del Centro de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México*, 5: 59–81.

Gibert, J. M., Domènech, R., and Martinell, J. 2004. An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of a new class, fixichnia. *Lethaia*, 37: 429–437.

Guerrero, R. and Piola, A. R. 1997. Masas de agua en la plataforma continental. *In* Boschi, E.E. (ed.), El Mar Argentino y sus recursos pesqueros Tomo 1. INIDEP, Mar del Plata, 222 p.

Harrington, M. J., Gupta, H. S., Fratzl, P., and Waite, J. H. 2009. Collagen insulated from tensile damage by domains that unfold reversibly: In situ X-ray investigation of mechanical yield and damage repair in the mussel byssus. *Journal of Structural Biology*, 167: 47–54.

Harrington, M. J. and Waite, J. H. 2008. Short-order tendons: liquid crystal mesophases, metal-complexation and protein gradients in the externalized collagens of mussel byssal threads. *In* Scheibel, T. (ed.), Fibrous Proteins (30–45). Landes Bioscience, Austin, Texas.

Kelly, S. R. A. and Bromley, R. G. 1984. Ichnological nomenclature of clavate borings. *Palaeontology*, 27: 793–807.

Kleemann, K. H. 1996. Biocorrosion by bivalves. *Marine Ecology*, 17: 145–158.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Holmiae, Impensis Direct. *Laurentii Salvii*, 824 p.

Mayoral, E. 1987a. Acción bioerosiva de Mollusca (Gastropoda, Bivalvia) en el Plioceno inferior de la Cuenca del Bajo Guadalquivir. *Revista Española de Paleontología*, 2: 49–58.

———. 1987b. *Stellichnus* nov. ichnogen., huellas de incrustación atribuidas a *Paravinella* nov. gen. (Bryozoa, Ctenostomata) de la formación Arenas de Huelva (Plioceno inferior) en la Cuenca del Bajo Guadalquivir (España). *Revista Española de Paleontología*, 2: 33–40.

Molina, I. J. 1782. Saggio sulla Storia Naturale del Chili. Bologna, Stamperia du S. Tommaso d'Aquino, 306 p.

Nielsen, K. S. S., Nielsen, J. K., and Bromley, R. G. 2003. Palaeoecological and ichnological significance of microborings in quaternary Foraminifera. *Palaeontologia Electronica*, 6 (2): 1–13.

Palmer, T. and Plewes, C. 1993. Borings and bioerosion in fossils. *Geology Today*, 9: 138–142.

Parker, G., Paterlini, M. C., and Violante, R. A. 1997. El fondo marino. *In* Boschi, E.E. (ed.), El Mar Argentino y sus recursos pesqueros Tomo 1. INIDEP, Mar del Plata, 222 p.

Prezant, R. S. 1990. Form, function and phylogeny of bivalve mucins. *In* Morton, B. (ed.), The Bivalvia: Proceedings of a Memorial Symposium in Honor of Sir Charles Maurice Yonge (1899–1986) at the 9th International Malacological Congress, 1986. Edinburgh, Scotland, 83: 95.

Rivas, A. L. 1990. Heat balance and annual variation of mean temperature in the North Patagonian gulfs. *Oceanologica Acta*, 13: 265–272.

Romero, M. V., Brezina, S. S., Hernández D., Casadío, S., and Bremec, C. 2013. Differential settlement of associated species on *Ostrea puelchana* d'Orbigny, 1842 (Ostreidae) in Patagonia (Argentina). *American Malacological Bulletin*, 31: 1–11.

Seilacher, A. 1953. Studien zur Palichnologie, I. Über die Methoden der Palichnologie. Neues Jahrbuch für Geologie und Paläentologie. *Abhandlungen*, 98: 87–124.

Servicio de Hidrografía Naval. 2010. Tabla de Marea 5, Armada Argentina, 176 p.

Silverman, H. G. and Roberto, F. F. 2007. Understanding marine mussel adhesion. *Marine Biotechnology*, 9: 661–681.

Stanley, S. M. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology*, 46: 165–212.

Tapanila, L. and Ekdale, A. A. 2007. Early history of symbiosis in living substrates: Trace-fossil evidence from the marine record. *In* Miller III, W. (ed.), Trace Fossils: Concepts, Problems, Prospects. Elsevier, Amsterdam, 637 p.

Taylor, P. D., Wilson, M. A., and Bromley, R. G. 1999. *Leptichnus*, a new ichnogenus for etchings made by cheilostome bryozoans into calcareous substrates. *Palaeontology*, 42: 595–604.

Taylor, P. D. and Wilson, M. A. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, 62: 1–103.

Voigt, E. 1977. On grazing traces produced by the radula of fossil and recent gastropods and chitons. *In* Crimes, T.P. and Harper, J.C. (eds.), Trace Fossils 2, Geological Journal, Special issue 9: 335–346.

Waite, J. H. 2002. Adhesion a la moule. *Integrative and Comparative Biology*, 42: 1172–1180.

Waite, J. H., Qin, X., and Coyne, K. J. 1998. The pecutiar collagens of mussel byssus. *Matrix Biology*, 17: 93–106.

Wiegemann, M. 2005. Adhesion in blue mussels (*Mytilus edulis*) and barnacles (genus *Balanus*): Mechanisms and technical applications. *Aquatic Sciences*, 67: 166–176.

Wilson, M. A. and Palmer, T. J. 1988. Nomenclature of a bivalve boring from the Upper Ordovician of the midwestern United States. *Journal of Paleontology*, 62: 306–308.

Yonge, C. M. 1962. On the primitive significance of the byssus in the Bivalvia and its effects in evolution. *Journal of the Marine Biological Association of the United Kingdom*, 42: 112–125.

Zar, J. H. 1999. *Biostatistical Analysis*. Prentice-Hall, Englewodo Cliffs, New Jersey.

Zonneveld, J. P. 2001. Middle Triassic biostromes from the Liard Formation, British Columbia, Canada: Oldest examples from the Mesozoic of NW Pangea. *Sedimentary Geology*, 145: 317–341.