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Author: Sebastián Richiano Marina Aguirre Ester Farinati Karen Davies Ignacio Castellanos Lucia. E. Gómez-Peral

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Enigmatic traces in infaunal bivalves from the late Quaternary of Argentina, Southwestern Atlantic. Bioerosion, bioclaustration or nothing? ✡

Sebastián Richiano [a,*], Marina Aguirre [b,c], Ester Farinati [d], Karen Davies [b], Ignacio Castellanos [b], Lucia. E. Gómez-Peral [b,e]

[a] Instituto Patagónico de Geología y Paleontología (CONICET–CENPAT), Boulevard Brown 2915, Puerto Madryn, Chubut, Argentina

[b] Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata; Edificio Institutos, Laboratorios y Cátedras, calle 64 N°3, 1900 La Plata, Argentina

[c] CONICET. Cátedra de Biogeografía (FCNYM–UNLP)

[d] Departamento de Geología, Universidad Nacional del Sur, San Juan 670, Bahía Blanca, Argentina

[e] Centro de Investigaciones Geológicas (CIG-CONICET), Diagonal 113 n°275, 1900 La Plata, Argentina

* Corresponding author. E–mail address: richiano@cenpat–conicet.gob.ar (S. Richiano).

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Abstract

Ichnological investigations were carried out on late Quaternary shells of the intertidal deep infaunal bivalve *Tagelus plebeius* (Lightfoot, 1786) found along the southwestern Atlantic, between Uruguay and the southernmost Buenos Aires Province in Argentina. Analyses reveal distinctive marks that are spread on the outer shell surface only. The marks are regular–unbranched–elongate, perpendicular to the outer shell growth lines, with deflections on the margins, never interconnected, without bifurcations, conforming bottom–up constructions. They occur in hundreds of specimens from many samples taken from

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sediments ranging in age from the late Pleistocene to the Recent. These marks have never been reported or described for this species and their origin and formation remain elusive. We describe these traces thoroughly and we propose an explanation for their preservation on about half the shells examined. Potential destructive boring structures (excavated from outside–in) or bioerosion activities by other macro- or micro-organisms are dismissed. These antimarginal asymmetric traces point instead to a process of constructive bioclaustrations (grown from the bottom–up) produced *in situ* during the life of the bivalve by unknown symbiont organisms. Additionally, the regular pattern observed for the marks exclude host growth as a consequence of abiotic/extrinsic causes. From a palaeoecological perspective, these structures suggest a biotic interaction that was hitherto undescribed neither for bivalves nor for the late Quaternary of the southwestern Atlantic.

Keywords:
Late Quaternary
Southwestern Atlantic
Biotic interactions
Bivalve
Bioclaustration

1. Introduction

Shells of the euryhaline stout “razor clam” *Tagelus plebeius* (Lightfoot, 1786) (Veneroida, Solecurtidae), a deep burrower bivalve typical of soft fine sediments and warm waters, are common and abundant in marginal marine environments (estuaries, coastal lagoons, tidal flats) along the southwestern Atlantic littoral (Carcelles, 1944; Barattini and Ureta, 1960; Castellanos, 1967, Scarabino et al., 1975; Capitoli et al., 1978; Bemvenutti et al., 1978; Ríos, 1994; Layerle and Scarabino, 1984; Elías, 1985; Bremec, 1987; Aguirre, 1994; Gutierrez and Iribarne, 1999, 2004). Moreover, along Brazil, Uruguay and Argentina, this species has abundant records in marine Quaternary deposits, especially for the Holocene (e.g., Sprechmann, 1978; Camacho, 1966; Forti, 1969; Closs and Forti, 1971; Farinati, 1985a, 1985b; Aguirre and Whatley, 1995a; Aguirre and Farinati, 2000; Ritter and Erthal, 2013; Fig. 1). Along the Bonaerensian coastal area in northern Argentina, excellently preserved complete specimens – often with jointed valves – in life position are frequently found within low-energy facies and, less frequently, in sand shell ridges where they normally occur as isolated

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valves. Considering mid–Holocene deposits (i.e., beach ridges assigned to the mid-Holocene Thermal Maximum), *T. plebeius* is dominant between the mouth of the Río de la Plata and Bahía San Blas (central Bahía Samborombón, Mar Chiquita, Quequén Salado, Quequén Grande, and Bahía Blanca surroundings; Fig. 1), whereas late Pleistocene records are scarcer and occur in few localities (e.g., central Bahía Samborombón; Farinati et al., 1992; Aguirre and Whatley, 1995a, 1995b).

An exhaustive analysis of extant and fossil shell materials of *T. plebeius* from the southwestern Atlantic coast, between Uruguay and southernmost Buenos Aires Province (Fig. 1); see below, Section 3), reveals distinctive thin elongated marks present exclusively on the external shell surface. They occur in hundreds of specimens from many samples of different ages (late Pleistocene, mid–Holocene, and Modern). Surprisingly, they have never been mentioned or described before, and their origin (physical, taphonomic, diagenetic, intrinsic, etc.) has yet to be explained. It is worth noting that these structures are shown in illustrations and photographic plates of catalogues and research papers within the extensive bibliographic sources from Argentina, Brazil, Uruguay, and USA, where *T. plebeius* has been recorded. However, for more than 70 years they have been completely overlooked (Carcelles, 1944). Considering the microscopic marks on *T. plebeius* collected from the Bonaerensian coastal area, we address the following issues: (*i*) establishing the distribution of such marks with respect to ecology and habitat; (*ii*) evaluating the possible origin of the marks (taphonomic *vs.* biogenic); and (*iii*) to propose a model of generation for these marks.

2. Shell features and ecology of *Tagelus plebeius* (Lightfoot, 1786)

2.1. Shell features

The shell of *Tagelus plebeius* (Veneroida, Solecurtidae), locally named “razor clam” (although true razor clams belong to the Solenidae, e.g., *Solen* and *Ensis*; Stanley, 1970; Emerson and Jacobson, 1976), is thin to very thin, moderately fragile, extremely elongated in outline, subquadrate with rounded ends, equivalve and inequilateral, with reduced ligament and teeth, two gapes (pedal and siphonal) and a deep pallial sinus. Overall these morphological features are directly linked to its deep infaunal life habit. The shell exhibits concentric growth lines on its outer surface and, when preserved, a dark brown periostracum. The mineralogy is aragonitic and the microstructure consists of a prismatic outer layer and an irregular crossed lamellar inner layer (Kennedy et al., 1969; Taylor et al., 1973; Carter, 1990; Do Campo, 1991). Shells are 10 to100 mm in length (Stanley, 1970; Holland and Dean,

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1977a, 1977b; Farinati et al., 1992; Aguirre and Whatley, 1995b; Aguirre and Farinati, 1999a).

2.2. Distribution

The Modern geographical range of *Tagelus plebeius* (Fig. 2(A)) includes mostly the western Atlantic (34°N–41°S): North America from Cape Cod (North Carolina) to Texas, Antilles, Suriname, Brazil, Uruguay, northern Argentina (along the Buenos Aires province, Río de La Plata margin to Bahía San Blas) (Stanley, 1970; Holland and Dean, 1977 a, 1977b; Andrews, 1981; Ríos, 1994; Aguirre and Whatley, 1995b; Iribarne and Botto, 1998). Although Modern records were mentioned for Patagonia (e.g., the Golfo San Matías; Scarabino, 1977; Forcelli, 2000), no living specimens were found south of the Río Negro river (41ºS). Doubtful Modern records were also mentioned from the Magellan Strait (but they most probably belong to *Ensis,* a true razor clam).

The fossil record of *T. plebeius* goes back to at least the late Miocene in Argentina (Paraná Fm. in Entre Ríos province, northern Argentina; Aguirre and Farinati, 1999b). Other species, close to *T. plebeius* and living in the Pacific (e.g., *T. californianus*, California and Mexico; *T. affinis,* Gulf of California to Panama; *T. peruvianus,* Costa Rica, central America; *T. dombeii*, Baja California to Chile) (Keen, 1971; Rojas et al., 1988; Coan and Valentich–Scott, 2012) and along western African coasts (*T. adamsonii*; Ardovini and Cossignani, 2004; Huber, 2010) could be posterior (subjective) synonyms (Aguirre and Whatley, 1995b), but this needs to be confirmed by further taxonomic revisions. A full list of references for the Modern records of *T. plebeius* is provided in Appendix A.

2.3. Habitat and life habits

A number of ecological studies performed in benthic communities from the Río de La Plata and other estuarine areas of Argentina (e.g., Scarabino et al., 1975; Elías, 1985; Iribarne and Botto, 1998) included *Tagelus plebeius* in their taxonomic lists. However, its habitat and life mode (Fig. 2(B)) were derived from experimental studies carried out in other areas within its geographic range, such as eastern North America (Stanley, 1970; Krantz, 1974; Holland and Dean, 1977a, 1977b) or southeastern Brazil (Bemvenutti et al., 1978). In addition, studies dealing with the orientation of shell beds of *T. plebeius* preserved in Mar Chiquita area were performed by Iribarne and Botto (1998) and Iribarne et al. (1998).

Tagelus plebeius is a slow deep burrower (low burrowing rate, BRI = 0.4) living predominantly as an intertidal macrobenthic species which prefers muddy sand substrates

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(silty sands to very fine sands, occasionally in medium to coarse sands) in the margins of bays and estuaries, at the mouth of river outlets and marginal marine ponds. In tidal flat areas, it lives between the mean low tide level and 90 cm above this level (Holland and Dean, 1977a, 1977b; Fig. 2(B)). It is able to make a relatively large burrow with a typical Y form (Stanley, 1970). In life position, it lies with the longitudinal axis vertical (perpendicular to the sediment–water interface), with the extended foot emerging downwards and the divergent siphons –exhalant and inhalant– extended upwards, in contact with the surface.

Tagelus plebeius reaches up to 30 cm in length and stretches according to the tidal daily regime: upwards to the sediment–water interface (low tides) or downwards (high tides). The foot is adapted to excavation in the substrate where it forms permanent burrows, thus lacking any active wide lateral mobility. *Tagelus plebeius* occupies the upper part of the burrow during low tide and the lower part when the tide is high (Holland and Dean 1977a, 1977b); it is a suspension feeder (Stanley, 1970). Its Modern geographical distribution shows that it lives preferably in shallow warm waters (tropical, subtropical, warm temperate). It is characterized by a short life span and a high mortality (Abrahão et al., 2010). Rapid mass mortality events, due to sudden catastrophic influx of sandy fluvial sediments, have been documented by Farinati et al. (1992) for Bahía Blanca in the southeastern Bonaerensian coastal area.

3. Material and methods

The sampling surveys carried out along the coastal area of Argentina, between the Río de La Plata margin and southern Patagonia, provided well-preserved shells of *Tagelus plebeius*. Samples of 5,000 cm^3 were obtained from beach ridges, marine terraces, tidal flats and coastal lagoonal facies from the Pleistocene and Holocene and from the Modern littoral of the Buenos Aires province, between the Río de La Plata margin and Bahía Blanca-Bahía San Blas. A total of 991 shells were examined for marks. Modern shells were sampled at adjacent marginal marine sites (Fig. 1: localities 1, 6, 7, 8, 9, 11, 23, 24, 25, 26, 28, 29 and 32). Overall, the area of collection includes 32 localities (13 Modern, 18 mid-Holocene, and 1 Pleistocene) between Río de la Plata and Bahía San Blas (Fig. 1; Tables 1, 2). The specimens belong mainly to mid–Holocene coastal deposits (Las Escobas Fm. and equivalent units; Fig. 3; 812 shells), from Modern estuarine settings (177 shells), and 2 shells come from late Pleistocene landforms (Pascua Fm.). No fossil or extant shell was found along Patagonia (but see mention by Scarabino, 1977 for San Antonio Oeste, Golfo San Matías).

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Additionally, Modern and subfossil shells from different areas along the SW Atlantic were examined from museum collections for comparative purpose, e.g., Museo de Ciencias Naturales “Bernardino Rivadavia” at Buenos Aires and Museo de La Plata (Argentina), and Natural History Museum (London). Other examined subfossil material belongs to the collections of the Museo de La Plata (MLP-PI: 3964, 6284, 5406, 72, 76, 6321, 3964, 1567, 1575, 10078, 8400, 1576, 5405, 1587, 6284; Buenos Aires Capital federal; Villa Elisa; Los Talas; Punta Indio; Miramar at Arroyo Las Brusquitas, Arroyo Malacara and Arroyo El Durazno; Bahía Blanca) and the Museo de Ciencias Naturales “Bernardino Rivadavia” (MACN-PI) at Buenos Aires (Camacho, 1966) and at Departamento de Geología at Universidad Nacional del Sur in Bahía Blanca (PI UNS: 2991, 2572, 2580, 2609, 3013, 1374, 2840, 1372, 1366, 2545, 3001, 2990, 3008, 3173; localities between Quequén Salado and Bahía San Blas surroundings). Other Modern specimens were examined from collections deposited at several museums or from oceanographical expeditions carried out along the Mar Argentino: Museo de Ciencias Naturales “Bernardino Rivadavia” (MACN, Malacology Section) at Buenos Aires, and Museo de Ciencias Naturales at La Plata (MLP-ZI) (Carcelles, 1944; Castellanos, 1967). Material from historical collections at the Natural History Museum (NHMUK) in London (Molluscan Section) was also examined. Taxonomic lists of molluscan collections from Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) in Mar del Plata, Argentina, were taken into account (Bastida et al., 1981, 1992, 2007 an other references therein). From MACN-ZI: 1843, 427, 8224, 5021; 29985, 15343, 29988, 9856-3; 14323, 10326, 10751, 10750, 111578; 19543-1, 10682, 14161, 13035, 23188, 10769, 417; 12036, 9668-34; 9210-11, 6619; 6620-7, 11130, 11121-1; 11131, 11129, 25211; 10620-9, 6620-9; 20206; 20206, 15332, 15363 (Brazil; Uruguay; Punta Médanos; Mar del Plata; Puerto Quequén/Quequén Grande, Necochea; Monte Hermoso; Bahía Blanca; Puerto Militar; Bahía San Blas; Buque “San Luis”). From MLP-ZI: 2533; 1864, 2309, 2326, 2316; 515; 2719 (Puerto Quequén, Quequén Salado/Balneario Oriente; Monte Hermosos; Arroyo Parejas, Bahía Blanca).

Whenever possible, fossil specimens from dated stratigraphic levels were considered. Radiocarbon dating from selected localities yielded age ranges between 1.340 and 7.600 ka B.P. and 1.430 and 7.720 ka B.P. for the northeastern and southeastern Bonaerensian coastal areas, respectively: 6,150 ± 190 to 6,764 ± 195 at Bahía Samborombón; 1,340 ± 50 to 3,850 ± 60 at Mar Chiquita surroundings; 7,720 ±100 at Quequén Salado; 3,120 ± 70 to 6,290 ± 90 at Bahía Blanca area (Fasano et al., 1982; Farinati, 1985b; Farinati et al., 1992, Farinati and Zavala, 1995; Aguirre, 1993a, 1993b; Aguirre and Whatley, 1995a, 1995b).

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All the material studied was air-dried and photographed using a digital camera Nikon D3100, a digital camera Nikon Coolpix S10 VR attached to a Nikon SMZ1000 binocular loop and SEM as is frequent in most ichnological studies. When necessary, the material was washed with an ultrasonic cleaner (Lilis 3.8). Specimens from 12 Holocene and 6 Modern localities were measured with a calliper to establish the average shell length (measured from the anterior shell margin to the posterior shell margin) and the occurrence and abundance of the traces observed over the shell surface were recorded. The mineralogical composition of the shells was analysed at Universidad Nacional del Sur (UNS, Bahía Blanca, Argentina) with a Rigaku D–Max IIIC X–ray diffractometer and with EDAX. Additionally, in order to characterize the traces, we observed thin sections with a polarization microscope Nikon Eclipse E–200 of the Centro de Investigaciones Geológicas (CIG, La Plata, Argentina). We took SEM photos in two institutions: at the UNS with an EVO 40 v.p. SEM using a Cambridge metallization in sputter coater PELCO 91000 with 5 kw gold; at Facultad de Ingeniería, La Plata University (Argentina), shells were observed in detail with a FEI Quanta 200 SEM and an EDAX Phoenix 40, accelerating voltage 20 kw, spot size from 3 to 4 µm, at different magnifications in order to explore the details of the traces. Experimental studies of living *T. plebeius* were not conducted because they would not reproduce specific environmental conditions of this species in nature, or the nature and origin of the traces within its ecological niche and through time.

4. Results

Out of the 991 shells of *Tagelus plebeius* studied here, 465 (47%) show superficial marks. Among 177 Modern shells, 82 have marks (46%), while in the mid–Holocene samples (812 shells), 381 (47%) exhibit these marks (Fig. 4). The marks consist of regular–unbranched–elongated cavities, perpendicular to the outer shell growth lines, with deflection on the margins. They are never interconnected and there are no bifurcations. The same pattern was observed in complete shells, as well as in isolated valves. It could be recognized in shells from all three ages (late Pleistocene, mid–Holocene, and Modern). Five key features characterize this pattern:

* In all samples, marks are concentrated on the outer shell surface only and in the central part of the shells (Figs. 4(B-H), 5(A-C)). In a few Modern shells recovered with their periostracum, the traces are clearly placed below it, and they could be seen from outside just by the translucency of the periostracum;

* The marks are developed between growth lines (always starting or finishing at one growth line) and their orientation is from the umbonal region towards the ventral margin, i.e., following the direction of shell growth;

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* When the marks appear in both valves of the same individual, they do not show the same pattern on both sides (Fig. 4(H));

* The marks show a straight and unbranched pattern, which is developed in the outside layer only (Fig. 4(C, D)). The margins of the marks are characterized by a deflection of the growth lines that generates a “V” model at the surface (Fig. 5(A-E)). This pattern is similar to the one illustrated by Tapanila and Ekdale (2007: fig. 19.1);

* The marks are between 1 and 10 mm long, 0.1 mm wide, and *ca*. 0.1–0.15 mm deep from the outer shell surface (Fig. 5(B-F)). A comparison of the shell dimensions relative to the occurrence of traces showed that there is no distinctive pattern or relationship between shells with or without marks and shell size (Fig. 4(I)). In Modern (6 localities; 144 shells) and mid–Holocene (12 localities; 684 shells) samples, the shells with marks range between 36 and 70 mm, while those without traces reach 30 to 72 mm long (Fig. 4(I)).

Regarding the composition of the shells, X–ray diffractometry conducted on *T. plebeius* from different ages and localities (two samples from the Holocene localities 11 and 15; one Modern sample from locality 20) reveals that the shells have the same typical pristine aragonitic composition (Appendix B). In the same way, SEM–Edax analyses confirm the original aragonitic composition of the study material (Fig. 5(G)).

5. Discussion

In 47% of the late Quaternary and Modern shells of *Tagelus plebeius* thin superficial marks were found. Such a proportion is not anecdotal. The origin of these marks can result from abiotic factors to intrinsic aspects of the bivalve (biotic factors) or to biotic interactions between the bivalve and other organism(s).

5.1. Identifying the origin: abiotic, intrinsic, or biotic interaction?

An abiotic origin, like *in situ* or *post-mortem* (taphonomic) shell abrasion can confidently be ruled out. The traces are perpendicular to the longitudinal shell axis. However, no lateral (umbo–ventral margin direction) movement of the valves occurs in the burrow, but only up and down (posterior–anterior direction, i.e., siphonal gape–pedal gape). Also, the muddy bottoms which characterize the typical habitat of *T. plebeius* do not usually favour abrasive processes on the shells. Corrosion and dissolution, which leave *Rodocanalis*–like structures on shells (Mayoral and Sequeiros, 1979), could be confounded with the studied traces. However, the latter exhibit no etchings or netlike of marks (Häntzschel, 1975). In summary, a destructive physical origin during the burrowing activity of *T. plebeius* inside its

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permanent burrows can be dismissed. A *post-mortem* origin within the taphonomically active zone would imply the occurrence of traces in both surfaces of articulated or disarticulated shells, whereas the traces have never been observed in the interior shell surface.

5.1.1. Biotic origin

Regarding a possible biotic origin, identifying the producer is neither easy nor unequivocal. Shell features allowing residence for other organisms (bioerosion, parasitism, or symbiotic interactions) could all be hypothesized. Micro- and macro-borers commonly leave traces on molluscan shells (Glaub, 1999, 2004; Edinger, 2002; Edinger and Risk, 2007; Glaub et al., 2007; Radtke et al., 2011). Microborings and microbial endoliths produced by bacteria, fungi, algae, and foraminifers leave very different microscopic traces (Radtke, 1993; Friedman et al., 1997; Glaub et al., 2007; Tapanila and Ekdale, 2007; Wisshak et al., 2008; Oliver and Taylor, 2011). These microborings are often produced by euendolithic microorganisms which can penetrate actively the shells by chemical dissolution to conform a network of tunnels (while other microorganisms can live in preexisting cavities like pores and fissures with no need to bioerode the shells; Golubic et al., 1981; Glaub et al., 2007). For example, traces of microscopic size (e.g., tunnels less than 100 µm in diameter) have been shown to be produced by cyanobacteria, algae (Chlorophyta, Rodophyta), and fungi. However, these potential tracemakers are disregarded here because, according to illustrations by Glaub et al. (2007), Radtke et al. (2011), and Cherchi et al. (2012), the traces consist of either interconnected tunnels, branching tubular cavities, bifurcations and arborescent patterns, or globose irregular structures that differ from the pattern of traces seen in *T. plebeius*.

Macroborers can also be dismissed. Among the most typical macroboring organisms that could leave comparable traces during bioerosion activities (e.g., Bromley, 2004; Taylor and Wilson, 2003; Wilson, 2007; Chattopadhyay et al., 2014, 2015, 2016), the following can be ruled out: porifers (not infaunal), bryozoans (not infaunal), annelids (not deep infaunal; however some polychaetes live within the sediment in intertidal habitats), gastropods (not infaunal), crustaceans (crabs from the area of study are not infaunal; but amphipods have been found inside intertidal sediments). Sipunculids and phoronids (sometimes infaunal) are also ruled out as they leave only subcircular traces different from the marks observed on *T. plebeius*. It could be expected that plant roots (e.g., *Spartina*) could scrape the shell surface within the substrate when buried, but they would not leave a regular pattern like the one described here (Fig. 4).

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Focussing on bioerosion activity observed on shells from the late Quaternary of Argentina, traces of Domichnia, Praedichnia and Fixichnia were reported by, among others, Farinati et al. (2006) and Richiano et al. (2012, 2015, 2017). They are preserved in bivalves and gastropods from Pleistocene, mid–Holocene and Modern settings (Richiano et al., 2012). Nevertheless, although at first glance the traces analysed were thought to represent destructive boring structures, excavated from outside–in, several features allowed us to dismiss such a potential origin: the exclusive location of the traces on the outer shell surface, the lack of shell destruction through penetration, and the regular pattern of the marks between growth lines. By contrast, regular–unbranched–elongate marks, perpendicular to the outer shell growth lines, and deflection of the growth lines adjacent to the marks (V–shape lines towards the ventral margin), like the ones observed here in *T. plebeius*, are all features which can typically distinguish boring (destructive) signatures from bioclaustration (constructive) structures, grown from bottom–up (Tapanila and Ekdale, 2007: fig. 19.1). Also, these features and the regular pattern of the marks make abiotic/extrinsic causes unlikely.

Lastly, among vertebrates, birds can produce traces on the outer shell surface of *T. plebeius*, as documented by Lomovasky et al. (2005; 2016) in the Mar Chiquita area. Nevertheless, birds break shell portions, generally the posterior siphonal gape area, leaving destroyed shell margins, producing totally different marks (Lomovasky et al., 2005; 2016).

5.1.2. Biotic interactions

Traces of symbiosis in molluscs are abundantly documented in the fossil record (Dreier and Hoppert, 2014). The lack of ribs on the external surface of *Tagelus plebeius*, probably linked to its deep infaunal life habit, with no need of protection against predators (Stanley, 1981; Savazzi, 1982, 1984; Checa and Jiménez–Jiménez, 2003), does not offer much chance of protection and symbiotic interactions with other infaunal groups. Potential producers of these marks could be searched for within the associated macro and meiofauna which typically live in muddy marginal marine settings, where *T. plebeius* occurs along the study area. Only a few meiofaunal organisms (like amphipods, polychaetes, and the gastropod *Littoridina australis*) were mentioned living in the sediment within its shell cavities (Gutiérrez and Iribarne, 1999). For example, in the intertidal and supratidal zones at Bahía Samborombón tidal flats, Mar Chiquita coastal lagoon, Bahía Blanca tidal flats, and Bahía San Blas estuarine area (Fig. 1), the following groups of organisms are the most common: crabs (*Chasmagnathus* sp., *Cyrtograpsus* sp., *Uca* sp.), amphipods, ostracods, worms (polychaetes, nematodes), as well as varied plants (*Salicornia* sp., *Juncus* sp.), bacteria and

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microbial mats (Boschi, 2000; Gutiérrez and Iribarne, 1999; Gutiérrez et al., 2003; Cuadrado and Pizani, 2007; Cuadrado et al., 2011). Among those, only some polychaetes have been registered occupying the inner shell of *T. plebeius* (Gutiérrez and Iribarne, 1999).

Parasite–host biotic interactions could also represent a possible candidate for the traces described here, but they are also ruled out for *T. plebeius*. For example, Modern bivalves can be infested by trematodes and polychaetes. The traces corresponding to polychaete infection consist of pits, completely enveloped igloo-like structures, U–shaped borings and mudblisters (Linehan, 2016) that are totally different from the marks seen in *T. plebeius*. Moreover, trematodes are documented on Modern bivalves of the Bonaerensian littoral, but they are generally located in the gonads and digestive system and, besides, there are no records of trematode parasitism in *T. plebeius* although they are well documented for other bivalves of the Mar Argentino (Bagnato et al., 2015). Lastly, when parasitism occurs, changes in shell size and asymmetry are common among a wide range of phenotypic effects on the host (Poulin and Thomas, 1999). For example, infected shells tend to be smaller than non-infested ones (Huntle, 2007). Here there is no pattern correlating shell size and trace patterns in *T. plebeius* (Fig. 4(I)).

To sum up, the data obtained point to the origin of these marks most probably as a result of a bioclaustration process (*Impedichnia* ethological category of trace fossils produced by symbiont organisms; Tapanila, 2005). These structures were originally named *embedment structures* by Bromley (1970) and later renamed *bioclaustration* by Palmer and Wilson (1988). Curiously, they have been well documented from different geographical areas and geological ages for various skeletal marine invertebrate groups (e.g., stromatolites, porifers, corals, bryozoans, brachiopods, crinoids), but not yet for bivalves (Tapanila and Ekdale, 2007; Cónsole–Gonella and Marquillas, 2014). Also, bioclaustration has never been described or cited for the area and time period analyzed in this study or for other coastal areas along the southwestern Atlantic.

5.2. Bioclaustration traces and proposal of a formation model

Bioclaustration is defined by marks produced when one organism, a settler symbiont, takes residence on the skeletal surface of another live organism, the host symbiont (e.g., Palmer and Wilson, 1988). Bioclaustration traces can only be formed by the interaction of two organisms that must necessarily be alive in the same place and at the same time. It generates direct evidence for a symbiotic relationship (Tapanila and Ekdale, 2007). The resulting trace fossil therefore records dual activities on the part of the embedded settler: interference with

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host growth and maintenance of a dwelling structure. In the present case study, the traces are developed below the periostracum showing that the symbiont is biologically claustrated or enclosed behind a periostracal wall. Recognition of bioclaustration in the fossil record requires the host organism to be skeletonized. In our case, the host symbiont is represented by the larger of two organisms involved in the symbiosis, *Tagelus plebeius*. The settler symbiont is the smallest and is probably a soft–bodied organism that remains unknown. Our model of successive formation of these traces implies a repetitive pattern through the life of an individual bivalve, as presented in Figs. 6, 7.

During the life of *Tagelus plebeius*, the symbionts (polychaetes?) are expected to enter inside the shell, between the periostracum and the outer shell layer, in the ventral margin area but only in the central portion of the shell, which is not exposed to friction (Fig. 6(A)). During the biotic interaction between *T. plebeius* and the unknown organism, one trace is generated in a direction parallel to the shell growth, but leaving no traces in the periostracum. It is well known that the periostracum has an important role in protecting the organism against epizoans and acts in the stabilization within mobile sediments, overall providing camouflage and defense (Checa and Domènech, 2009). In addition, the periostracum help to prevent the shell from dissolution in corrosive environments or to protect it from attacks by predators (Checa et al., 2014). Once the biotic interaction starts, the trace begins to grow perpendicular to the direction of the shell growth lines (antimarginal). It is possible that the interaction starts and finishes in different parts of the ventral margin and associated to diverse stages of the life of *T. plebeius*, resulting in a complex pattern of traces that always begins and ends in shell growth–lines margins (Fig. 6(B)). This could occur by multiple infestations of a same infester or by attempts by several infesters at different growth stages. An example of the pattern obtained in a single shell is represented in Fig. 7. It is worth highlighting that a different pattern could appear on the other valve of the same individual, as revealed by articulated shells (Fig. 4(H)).

Being a deep infaunal element from tidal flat facies, *T. plebeius* can be a major indicator for (palaeo)coastal deposits of Argentina if it occurs as complete shells, in life position, and/or with high relative abundance and good preservation. It is also one of the most valuable bivalve species for geochronological studies involving numerical dating (radiocarbon, aminoacid racemization; Fasano et al., 1982; Aguirre et al., 1995). The marks present in *T. plebeius* are produced *in situ* during the life of the bivalve, suggesting that their presence could also enlarge palaeoenvironmental inferences on the Quaternary deposits along the Argentinian coastal area where this bivalve is found. The relations of tracemakers to

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environmental factors (substrate, temperature, salinity, nutrients; Seilacher 1967; Vogel et al. 1995; Bromley 1996; Glaub and Bundschuh 1997; Richiano et al., 2015; 2017) imply that once the producer is confirmed, these traces could be used as additional evidence to support palaeoenvironmental reconstructions.

For more than 70 years, pictures of *T. plebeius* with these traces were published and never described or mentioned until now, showing a hidden biotic interaction below the surface and for the first time documented for bivalve shells. The identity of the trace maker remains unfortunately elusive, as in many other ichnological studies (Martinell et al., 1999).

6. Conclusions

The antimarginal orientation marks observed on Modern, subfossil and fossil specimens of *Tagelus plebeius* (Lightfoot, 1786) from the late Quaternary of Argentina are interpreted as *in situ* bioclaustration signatures made during the life of the bivalve. There is no difference between shells with or without marks relative to their minimum and maximum size. This aspect represents strong evidence against parasitism that would have led the affected individuals to be smaller than unaffected ones. From a palaeoecological perspective, these marks point towards the existence of biotic interactions between a host symbiont (*T. plebeius*) and a currently unknown settler symbiont. Within the shell of *T. plebeius* the settler symbiont produces a mark where it lives, as already described for several groups and geological ages by Tapanila and Ekdale (2007). As far as we know, the present work is the first mention of this kind of marks for bivalves and in the fossil record of the Quaternary from the southwestern Atlantic.

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Appendices A, B. Supplementary information

Supplementary information (including additional references [Appendix A] and X-Ray Diffraction Analysis detailed results [Appendix B]) associated with this article can be found, in the online version, at:

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Table and Figure captions

Table 1. Detailed information (Age, total number of shells and shells with traces) of the best-preserved shell material selected for the study of the enigmatic traces in the 32 localities analyzed in this work. M: Modern; H: Holocene; P: Pleistocene.

Table 2. Complete information for total samples, areas and ages of the material studied in this work. Age: Las Escobas Fm. = Holocene; Pascua Fm. = late Pleistocene and equivalents. BR = beach ridges; CL = coastal lagoon; TF = tidal flats; F = fragmented shells; WJ = whole jointed valves.

Figure 1. Study area. **A**. Coastal localities sampled (Modern littoral, and fossil Holocene and late Pleistocene fossiliferous landforms). Locality numbers as in Table 1. Note that other Holocene records of *Tagelus plebeius* (Lightf.) occur at Quequén Grande area (southern Bonaerensian sector), and Holocene and late Pleistocene records occur at Bahía San Blas surroundings (southernmost Buenos Aires Province); however, they did not provide sufficient excellently preserved shell materials. **B**. Detail of localities sampled in the Bahía Blanca city surroundings.

Figure 2. Distribution and ecological aspects of *Tagelus plebeius* (Lightf.). **A**. Fossil and extant occurrences along the western Atlantic Ocean. Mc: Miocene. **B**. life habit and habitat of *T. plebeius* (A) showing the most common associated marginal marine bivalve species: B, *Abra aequalis* (Say); C, *Macoma uruguayensis* (Smith); D, *Mactra isabelleana* d´Orb.; E, *Corbula patagonica* d´Orb.; L, *Raeta plicatella* (Lamk.). Other molluscan species commonly found in these settings are: F, *Nucula nucleus* (Linn.); G, *Natica isabelleana* d´Orb.; H, *Venericardia* sp.; I, *Pitar rostratus* (Koch); J, K, *Littoridina* sp. See Stanley (1970), Holland and Dean (1977a, 1977b), and Aguirre and Whatley (1995b) for detailed information.

Figure 3. Photographs showing the aspect of the coastal deposits sampled where *Tagelus plebeius* occur (position of localities as in Fig. 1; Table 1). **A-C**. Holocene deposits of Canal de las Escobas Fm. at central Bahía Samborombón (localities 3 and 4). **D**. Image of the sampled Punta Ancla deposits (Holocene; locality 13). **E, F**. Pictures showing the holocene

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Aguará deposits (locality 20). Yellow circles mark the *in situ* jointed valves of *T. plebeius*. Scale bars: 50 cm (A, D), 20 cm (E).

Figure 4. Shells of *Tagelus plebeius* and their traces. **A**. Histogram showing a comparison between the total number of shells of *T. plebeius vs*. shells with traces in the Modern and mid-Holocene study samples. **B**. Pleistocene shell from Puente de Pascua locality. **C, D**. Holocene shells from Cerro de la Gloria locality. **E**. Holocene shell from Isla Verde. **F**. Modern shell from Mar Chiquita. **G**. Modern shell from Balneario Oriente. **H**. Holocene shells from Punta Ancla;t he two jointed valves have different trace patterns. **I**. Range of dimensions (in mm) of *T. plebeius* with and without marks in the Holocene (black) and Modern (grey) samples. Location of localities as in Fig. 1; see also Table 1. Scale bars: 1 cm.

Figure 5. Detailed images of the traces. **A**. General aspect of the marks under a binocular microscope. The marks are developed between growth lines and from the umbonal region towards the ventral margin, i.e., following the direction of shell growth; shell from Cerro de la Gloria locality. **B**. Transversal thin section of a shell under a petrographical microscope showing that the marks (black arrows) are located only on the superficial side of the shells; sample from Monte Hermoso locality. **C-G**. SEM images of the marks (C from Arroyo Durazno, and D-G from Cerro de La Gloria locality); C: general view of the marks showing a straight and unbranched pattern; D: trace mark showing a near straight pattern (yellow arrow); E: detailed of the margins of marks showing the deflection of the growth lines in inverted “V” in an umbonal direction; F: detail of one of the marks; G: inner layers of the shell, EDS (upper right) shows the composition of calcium carbonate with low magnesium content. Scale bars: 500 µm (B), 300 µm (C),

Figure 6. Synthetic model of trace formation. **A**. Position of the traces in relation with the movement of *Tagelus plebeius* inside its burrow according to its mode of life (experimental studies by Stanley, 1970). **B**. Sequence of the generation of traces, formed from the ventral shell margin and in the central shell region (starting or finishing at a growth line), during the life of a bivalve. At each stage, there are several possibilities: (*i*) it is possible that a new biotic interaction starts with the same or with a new symbiont, in another position in the shell; (*ii*) the progress of an old biotic interaction continues; or (*iii*) the end of the interaction. The stages are marked by different antimarginal lines.

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Figure 7. Hypothetical development of the different stages of biotic interaction (from **B** to **G**), applying the model proposed in Fig. 6 to a real shell of *Tagelus plebeius* (**A**, **H**) of the late Quaternary from Argentina.

13	Punta Ancla	H	40	28
14	Ebytem	H	4	4
15	Ao. Napostá	H	113	38
16	Colonia Ferroviaria	H	71	18
17	Puente La Niña	H	43	12
18	White	H	26	7
19	Maldonado	H	6	1
20	Aguará	H	150	28
21	Cerri	H	14	1
22	Boya 24-25	H	30	18
23	Tres Brazas	M	14	6
24	Bahía del Medio	M	69	17
25	Isla Ariadna	M	12	7
26	Isla Conejo	M	6	2
27	Isla Verde	H	116	83
28	Balneario La Chiquita	M	1	1
29	Balneario San Antonio	M	6	4
30	Las Isletas	H	46	30
31	Los Pocitos	H	2	2
32	Bahía San Blas	M	2	2
			991	**465**

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Table 2.

	Latitude (S)	Longitude (W)	Geographical sector	Age	Facies	Number o
s	34º 53' 30"	57º 49' 30"	Berisso	Holocene	BR	56
La Elvira	35º 11' '	57º 26'	Punta Indio	Holocene	BR	145
San Felipe	35º 22' 30"	57º 19' 30"	Punta Indio	Holocene	BR	50
de Don Hidalgo	35º 26' 30"	57º 16' 30"	Punta Piedras	Holocene	BR	28

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El Ceibo	35º 39' 30"	57º 19' 30"	northern Bahía Samborombón	Holocene	BR	20
San José	35º 42' 30"	57º 22' 30"	northern Bahía Samborombón	Holocene	BR	48
Rincón de López	35º 46' 10-20"	57º 24'	central Bahía Samborombón	Holocene	BR	220
la Gloria	35º 58' 20"	57º 27'	central Bahía Samborombón	Holocene	BR	100
as Escobas	35º 58' 10"	57º 29' 15"	central Bahía Samborombón	Holocene	CL	150 (WH)
e Pascua	35º 55' 36.77"	57º 43' 14.13"	central Bahía Samborombón	Pleistocene	CL	2 (F)
Canal 1	36º 26' 30"	57º 21'	southern Bahía Samborombón	Holocene	BR	14
La Huella	36º 26' 40"	57º 21' 35"	southern Bahía Samborombón	Holocene	BR	124
Lavalle	36º 24' 50"	56º 55' 45"	southern Bahía Samborombón	Holocene	BR	1 (F)
La Salada Grande	36º 18'	57º 07' 42.91"	southern Bahía Samborombón	---	TF	---
eresita	36º 32' 36.82"	57º 41' 23.81"	oceanic coast	Holocene	BR	1 (F)
La Atlántida	37º 27' 10"	57º 15' 05"	Mar Chiquita coastal lagoon	Holocene	EF	4 (WJ)
Grande	37º 31' 40"	57º 19' 20"	Mar Chiquita coastal lagoon	Holocene	BR	10
a Inés	37º 31' 40"	57º 19' 45"	Mar Chiquita coastal lagoon	Holocene	BR	10
San Antonio	37º 36'	57º 23' 45"	Mar Chiquita coastal lagoon	Holocene	BR	10
Tarrhué	37º 33' 30"	57º 21' 05"	Mar Chiquita coastal lagoon	Holocene	BR	61
	37º 34' 20"	57º 22' 40"	Mar Chiquita coastal lagoon	Holocene	BR	20
a Mar Chiquita	37º 44' 05"	57º 26' 35"	Mar Chiquita coastal lagoon	Holocene	BR	460
Cobo	37º 46' 02"	57º 26' 04"	Mar Chiquita coastal lagoon	Holocene	BR	5
Los Cueros	37º 47' 08"	57º 27' 20"	Mar Chiquita coastal lagoon area	Holocene	TF	10
a Salado	38º 54' 54.94"	60º 31' 42.26"	river outlet at oceanic coast	Holocene	TF	24
	38º 56' 24.87"	61º 57' 46.33"	eastern Bahía Blanca area	Holocene	BR	2
ncla	38º 56' 24.87"	61º 57' 46.33"	eastern Bahía Blanca area	Holocene	BR	40
	38º 47' 03.70"	62º 16' 06.77"	eastern Bahía Blanca area	Holocene	BR	4
Napostá	38º 47' 03.70"	62º 16' 06.77"	eastern Bahía Blanca area	Holocene	TF	113
Ferroviaria	38º 47' 03.70"	62º 16' 06.77"	Bahía Blanca	Holocene	BR	71
La Niña	38º 47' 03.70"	62º 16' 06.77"	Bahía Blanca	Holocene	TF	43
	38º 47' 03.70"	62º 16' 06.77"	Bahía Blanca	Holocene	BR	26
ado	38º 43' 18.80"	62º 17' 05.36"	Bahía Blanca	Holocene	BR	6
	38º 41' 07.54"	62º 17' 14.91"	western Bahía Blanca area	Holocene	BR	150
	38º 43' 41.91"	62º 23' 54.15"	western Bahía Blanca area	Holocene	BR	14
-25	39º 08' 42.74"	61º 34' 20.79"	Bahía Blanca estuary	Holocene	E	30
de	39º 19.57' 94"	62º 01' 21.86"	southernmost Bonaerensian	Holocene	TF	116
an Blas and surrounding areas	40º 25' 44.12"	62º 41' 57.22"	southernmost Bonaerensian	Holocene	TF	2 (F)

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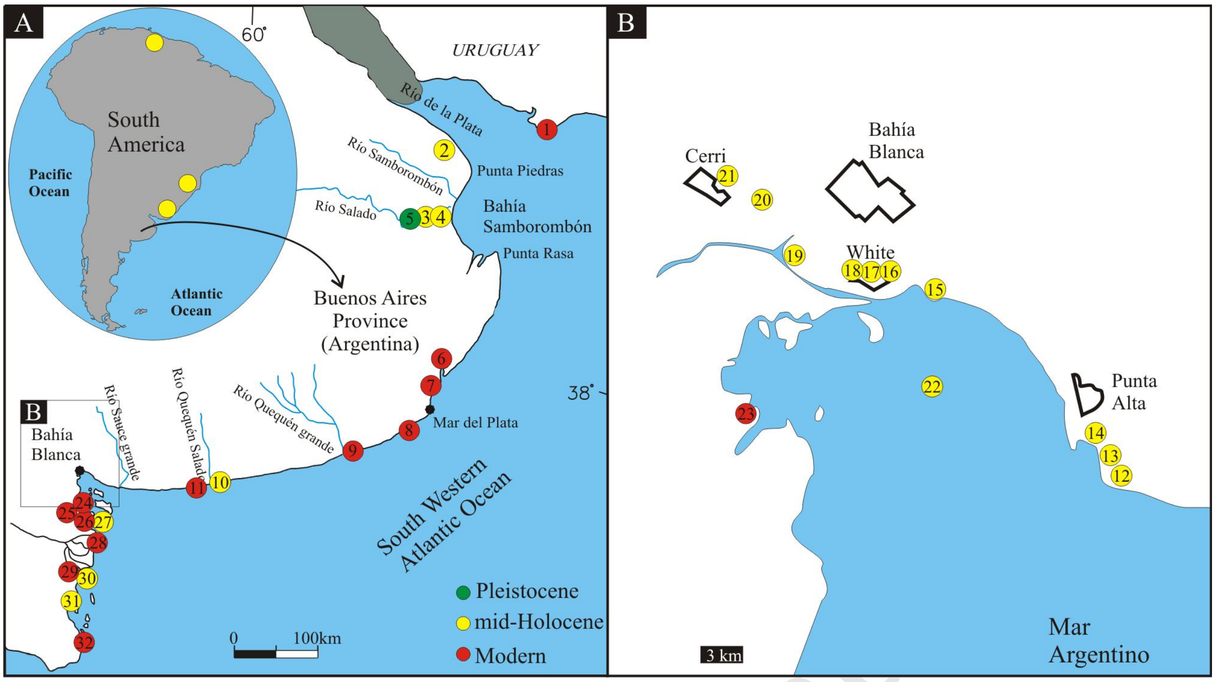

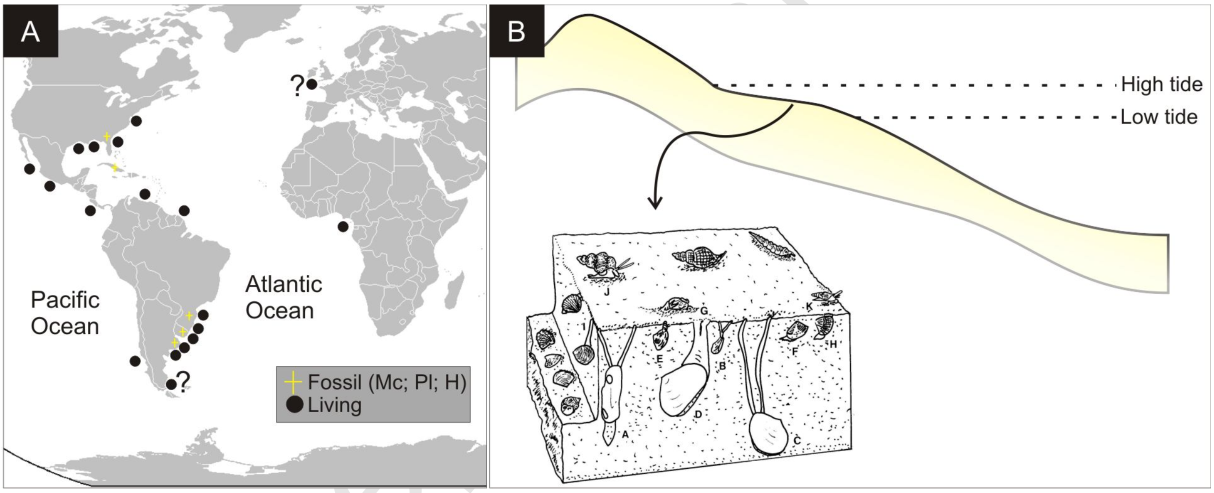

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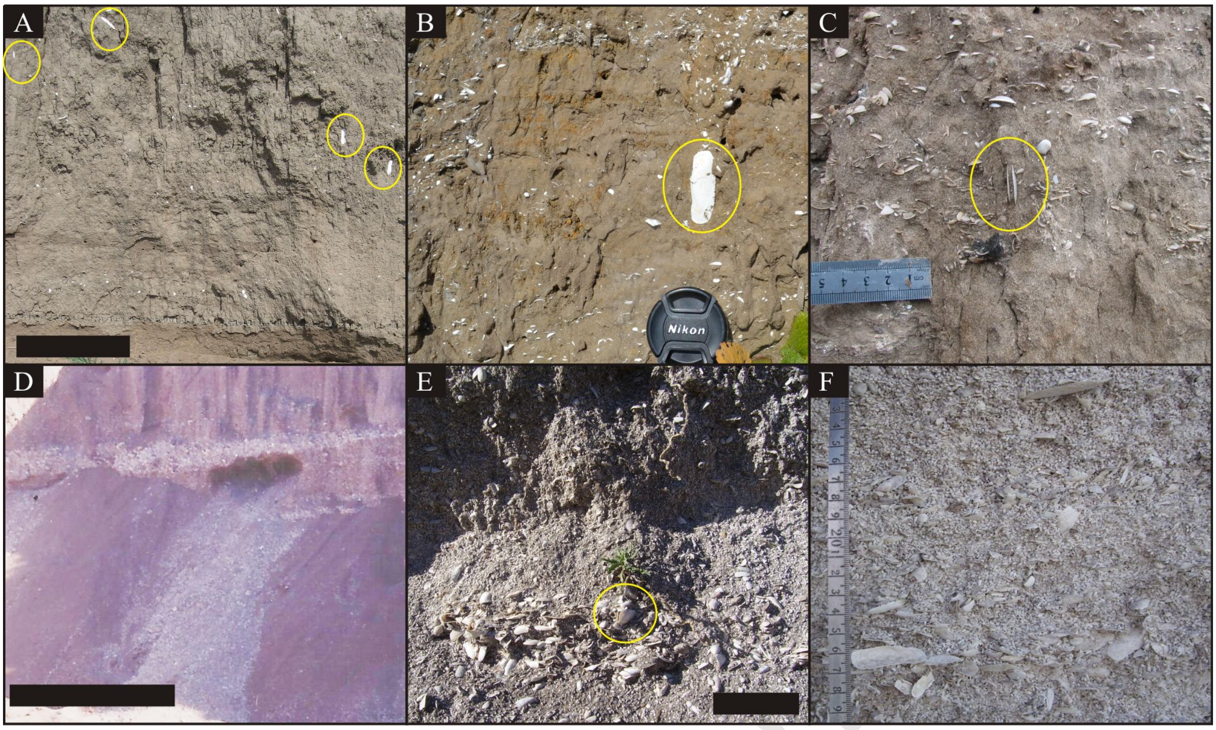

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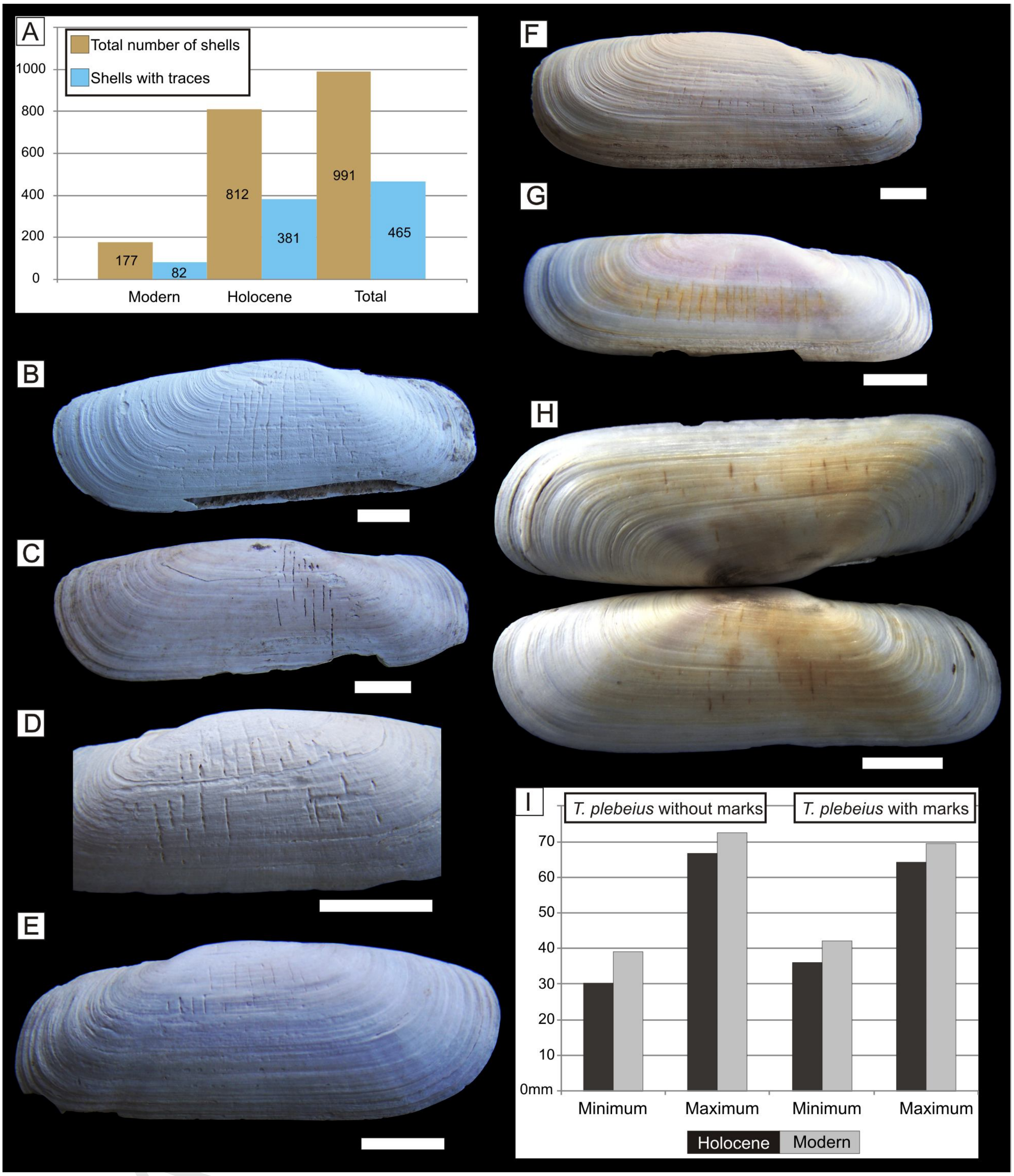

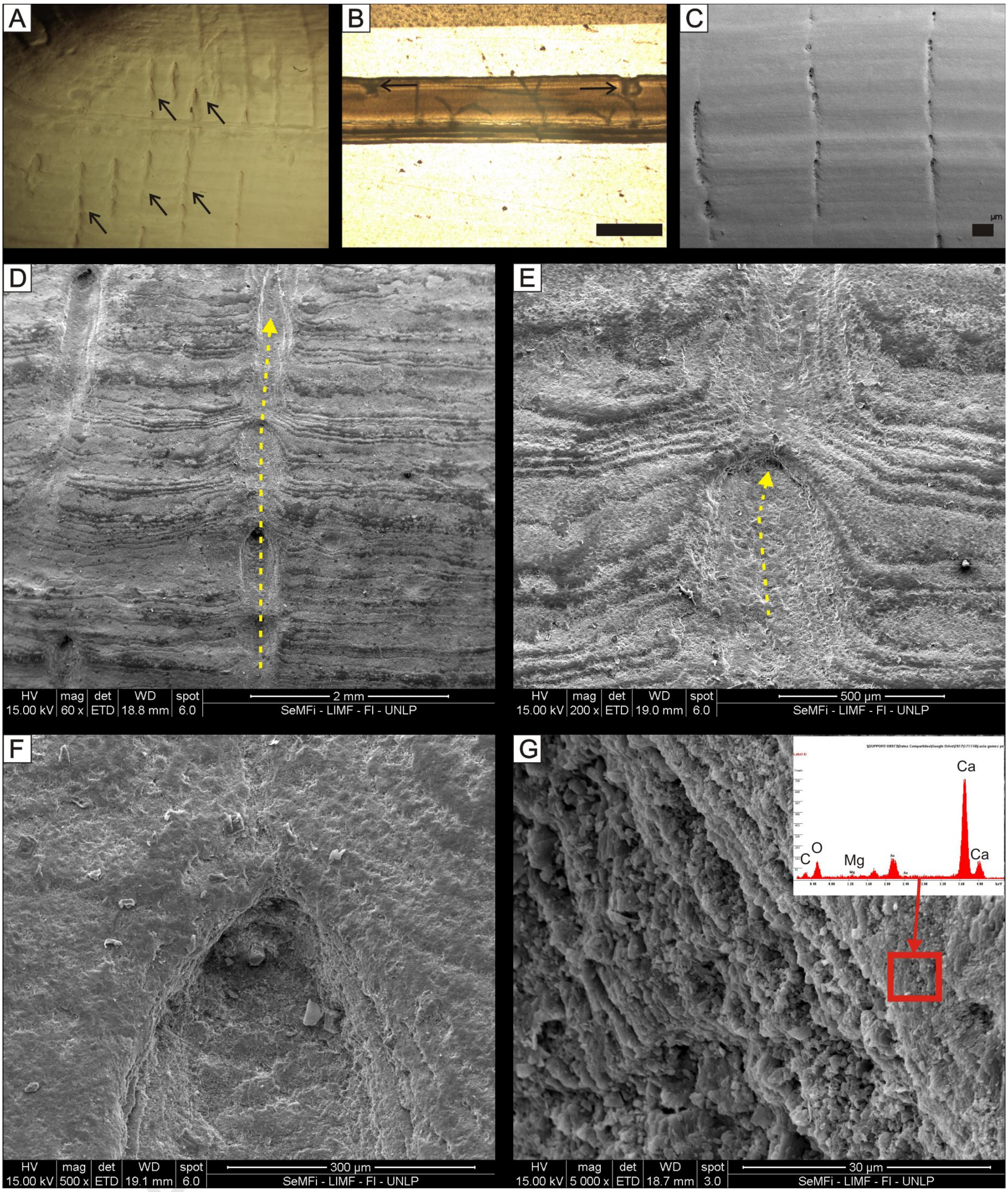
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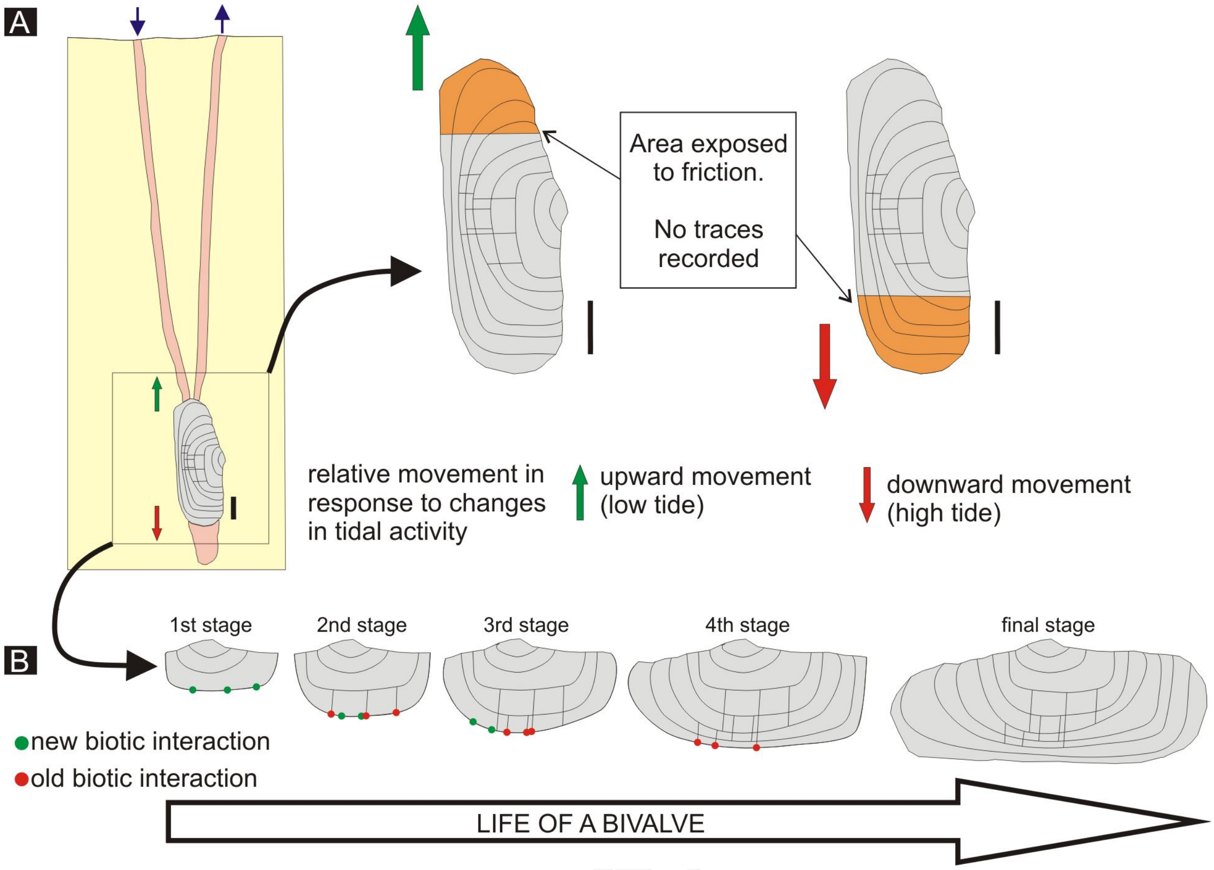

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