



***Crassostrea patagonica* (d'Orbigny, 1842) shell concentrations from the late Miocene of Río Negro province, NE Patagonia, Argentina**

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ABSTRACT

The Río Negro Formation (late Miocene-early Pliocene) mainly consists of continental deposits, but it contains a middle member of marine origin. It represents a transgressive-regressive sequence that can be seen at several outcrops along the N Patagonian coast. The taphonomical approach to the El Espigón marine deposits permits the identification of four main layers containing different kinds of skeletal accumulation, which mainly consist of oyster shells [*Crassostrea patagonica* (d'Orbigny, 1842)]. These concentrations display three different morphologies (pouches, pavements and bouquets) with a different taphonomic signature. These deposits were formed in shallow marine environments influenced by wave activity that produced valve concentrations of different entities. They contain several shell beds that represent event, composite, hiatal to lag skeletal concentrations. Traces of bioturbation in the sediment (*Thalassinoides*, *Teichichnus*) and bioerosion on the shells (*Entobia*, *Gastrochaenolites*, *Caulostrepsis*), and encrusters (cirripeds, bryozoans), are also

RESUMEN

La Formación Río Negro (Mioceno superior-Plioceno inferior) consiste principalmente en depósitos continentales, pero contiene un Miembro Medio de origen marino. Este miembro representa una secuencia transgresiva-regresiva observable en diversos afloramientos a lo largo de la costa N patagónica. El análisis tafonómico a los depósitos marinos de El Espigón permite la identificación de cuatro capas principales que contienen distintos tipos de acumulaciones esqueléticas, principalmente formadas por conchas de ostras [*Crassostrea patagonica* (d'Orbigny, 1842)]. Estas acumulaciones muestran tres morfologías distintas (bolsadas, pavimentos y ramilletes) con señales tafonómicas diferenciadas. Los depósitos se formaron en ambientes marinos someros afectados por oleaje, dando lugar a la formación de acumulaciones de conchas con entidades distintas. Los depósitos contienen capas de conchas que representan concentraciones de evento, compuestas, y de hiato a residuales. Son también abundantes en el afloramiento las trazas de bioturbación (*Thalassinoides*, *Teichichnus*),

abundant in the outcrop and constitute common components of these Miocene materials. Layers 1 and 2 of the sequence were deposited in shoreface/foreshore environments at the beginning of a highstand systems tract, while layers 3 and 4 were deposited at the end, or at the beginning of a forced regression, in foreshore environments. A final erosional episode cut the top of layer 4, which truncated the abundant bioturbation developed there.

Keywords: Taphonomy, shellbeds, ichnology, bioerosion, bioturbation, Neogene.

de bioerosión en las conchas (*Entobia*, *Gastrochaenolites*, *Caulostrepsis*) y los incrustantes (cirrípodos, briozoos), y representan componentes comunes de estos materiales miocenos. Las capas 1 y 2 de la secuencia se depositaron en ambientes de anteplaya/playa baja al principio del cortejo de nivel alto (*highstand systems tract*), mientras que las capas 3 y 4 lo hicieron hacia el final, o al inicio de una regresión forzada, en ambientes de playa baja. Un episodio erosivo final cortó la parte superior de la capa 4, truncando la abundante bioturbación allí desarrollada.

Palabras clave: Tafonomía, capas de conchas, icnología, bioerosión, bioturbación, Neógeno.

1. INTRODUCTION

The interest in the study of the taphonomic attributes of shell concentrations in palaeoenvironmental analyses and in sequence stratigraphy is widely recognized and numerous articles have been published on this issue, both theoretical and applied, over a long period of time (e.g., Kidwell, 1986, 1991 a, b, c; Brandt, 1989; Fürsich & Oschmann, 1993; Brett, 1995; Abbott, 1997, 2000; Kondo *et al.*, 1998; Fürsich & Pandey, 1999, 2003; Holland, 2001; Botquelen *et al.*, 2004; Cantalamessaa *et al.*, 2005; Parras & Casadío, 2005, 2006; Pufahl & James, 2006; Damborenea & Lanés, 2007; Kietzmann & Palma, 2009; Ragaini & Di Celma, 2009; Yamashita *et al.*, 2011; Sharafi *et al.*, 2012). Among shells, oysters represent an especially interesting tool for taphonomic inferences and palaeoenvironmental reconstructions because of their abundance and high preservation potential, and also their role as bioherm builders (Parras & Casadío, 2005; Pufahl & James, 2006).

The excellent fossil record of the marine Phanerozoic deposits in Argentina has allowed for many palaeontological studies with a clear taphonomic component and palaeoenvironmental analysis. These studies demonstrate the utility of shell concentrations to obtain valuable data for both sequence stratigraphy and basin analysis. In this regard, it is worth mentioning papers such as del Río *et al.* (2001) on the late Miocene marine shell beds of the Puerto Madryn Formation in the Valdés Península and Puerto Madryn area (Patagonia); Parras & Casadío (2005) on Oligocene oyster-dominated concentrations from the San Julián Formation (Patagonia); or Damborenea & Lanés (2007) on Early Jurassic shell beds from marginal marine environments of Mendoza. All these studies are based on large three-dimensional skeletal concentrations, mainly composed by oysters and other bivalves.

However, it is not only these spectacular layers that provide information. Minor three-dimensional as well as

bi-dimensional shell accumulations also have potential, which has not been fully exploited. In this context, Videt (2007) draws attention to all these types of oyster concentrations and demonstrates its usefulness to highlight discontinuities within sedimentary successions.

Thus, the cliffs of the Río Negro Fm exposed along the Atlantic shore of Northeastern Patagonia are characterized by several thin shell concentrations dominated by *Crassostrea patagonica* (d'Orbigny, 1842) offering a good opportunity for taphonomic and palaeoenvironmental studies. Based on previous work (Zavala & Freije, 2000; Farinati & Zavala, 2005; Domènech & Farinati, 2007), the present study focuses on the taphonomic analysis of these oyster concentrations in one of the accessible outcrops of the Río Negro Fm, and on their interpretation in the context of the sequence stratigraphic framework established in the area (Zavala & Freije, 2000; Carmona *et al.*, 2013).

2. GEOGRAPHIC AND GEOLOGIC SETTING

The Argentinian marine Miocene is characterized by extensive exposures on the Atlantic coast, which bear an abundant record of fossil invertebrates (molluscs, corals, cirripeds, bryozoans, echinids, etc.), and traces of organic activity (both bioturbation and bioerosion). Among those exposures, the Puerto Madryn Fm strata that outcrop in Valdés Península and the area surrounding the city of Puerto Madryn, have been especially analyzed (del Río, 1988, 1992, 1994; del Río & Martínez, 1998; del Río *et al.*, 2001; Mauna *et al.*, 2005). This formation is Late Miocene in age (Scasso *et al.*, 2001) and it covers a complete transgressive-regressive cycle.

The working area chosen for the present study is located in the NE of Argentinian Patagonia, in the province of Río Negro. The particular area studied is the North shore

of the San Matías Gulf, south of Viedma city (Fig. 1). The landscape is a barren steppe which is marked by major marine cliffs where it meets the Atlantic Ocean. These cliffs contain excellent marine and continental outcrops belonging to the late Miocene-early Pliocene interval, assigned to the Río Negro Fm (Andreis, 1965), and are coeval with the Puerto Madryn Fm strata (Zavala & Freije, 2000). The marine sediments are characterized by an abundant, although little diversified, invertebrate fossil fauna that allows for interesting taphonomic and palaeoenvironmental inferences.



Figure 1. Geographical situation of El Espigón outcrop, Río Negro Province, Patagonia, Argentina.

3. STRATIGRAPHICAL SETTING OF THE RIO NEGRO FORMATION

3.1. General features of the Formation

The study of the Río Negro Fm cliffs reaches back more than 170 years to when d'Orbigny (1842) carried out the first observations in the Carmen de Patagones area (Buenos Aires province). Thereafter, he was followed by other authors like Roth (1898), Wichmann (1918), Frenguelli (1950), Feruglio (1950), Andreis (1965), De Ferraris (1966), Farinati *et al.* (1981), Angulo & Casamiquela (1982), Zavala & Freije (2000), Farinati & Zavala (2002, 2005), Domènech & Farinati (2007), Farinati *et al.* (2010), Carmona *et al.* (2012, 2013), among others.

The coastal outcrops of the Río Negro Fm are composed mostly of blue-gray mudstones and sandstones that appear as almost horizontal strata between Bahía Rosas and

Balneario El Cóndor (Fig. 1), with a great lateral continuity for over 100 km and a thickness exceeding 50 m.

This formation was initially interpreted as a unit of fluvial origin (Andreis, 1965). However, it is currently interpreted as a mostly aeolian unit (Zavala *et al.*, 2000; Zavala & Freije, 2000) that contains a marine intercalation in its middle part and along some 60 km (Farinati *et al.*, 1981; Angulo & Casamiquela, 1982; Carmona *et al.*, 2013). Thus, Zavala *et al.* (2000) and Zavala & Freije (2000) described a lower and an upper aeolian member, with an unconformably lying inserted middle marine member. The lower member consists of medium to coarse-grained sandstones and mudstones deposited in an aeolian environment. The upper member is composed of sandstones also deposited in an aeolian setting, at the base, followed by palaeosols and tuff levels at the top. The middle member is described in detail in the next section.

All members were described as bounded by sharp erosional discontinuities (Zavala *et al.*, 2000). Nevertheless, Carmona *et al.* (2012) describe gradational transitions between them in some protected areas where microbially induced sedimentary structures appear. The development of those microbial mats in tidal flat settings contributed to the preservation of vertebrate trace fossils, including a particular abundance of mammal and bird footprints in the levels immediately below and above the marine member (Casamiquela, 1974; Aramayo, 1987, 2007; Aramayo *et al.*, 2004; Melchor *et al.*, 2012; Carmona *et al.*, 2013).

3.2. The middle marine member of the Formation

The marine unit of the Río Negro Fm cliffs (middle member) is composed of gray mudstones and fine-grained bioclastic sandstones deposited in a shallow offshore to beach marine environment, affected by wave action in a partially confined setting. This marine member presents a maximum thickness of up to 10 m and a large-scale lenticular geometry. Following Farinati & Zavala (2005), offshore facies consist of massive bioturbated mudstones (*Cruziana* Ichnofacies, represented by *Chondrites*) where abundant oyster concentrations have been recognized. They grade, towards marginal sectors, to lower shoreface facies composed of mudstones and fine-grained, bioturbated sandstones (*Cruziana* Ichnofacies, represented by *Thalassinoides*, *Planolites* and *Chondrites*). Finally, foreshore and upper shoreface facies of the marginal sectors are composed of fine sandstones rich in invertebrate skeletons (*Oculina*, *Balanus*, *Ostrea*, *Pododesmus*, *Chlamys*), bioerosion on the shells (*Entobia*, *Caulostrepsis*, *Gastrochaenolites*) and bioturbation (*Skolithos* Ichnofacies, represented by *Ophiomorpha* and *Skolithos*). Carmona *et al.* (2013) revisited this formation from the ichnological point of view, describing a *Cruziana* Ichnofacies at the base

of the marine member (with *Ophiomorpha*, *Teichichnus*, *Siphonichnus*, *Asterosoma*), a *Glossifungites* Ichnofacies in the middle section (with *Ophiomorpha*, *Asterosoma*, *Teichichnus*, *Siphonichnus*), a *Skolithos* Ichnofacies in the upper part (with *Ophiomorpha* and *Maiakarichnus*), and a *Cruziana* (or *Psilonichnus*)-*Skolithos* Ichnofacies at the top of the member (with *Ophiomorpha* or *Arenicolites*).

According to the sequence stratigraphic analysis, these deposits are part of a depositional sequence recording a complete marine transgressive-regressive cycle whose main control would have been glacioeustatism (Zavala & Freije, 2000, 2001). Zavala & Freije (2000) analyzed 5 sections containing the middle member (Escalera, La Lobería, Playa Bonita, El Espigón and El Faro) along the entire exposure area of the formation. They identified a basal transgressive system tract (TST) followed by a highstand system tract (HST) and some higher levels corresponding to a forced regression (FR) due to a relatively rapid sea-level decline (Fig. 2). Nevertheless, Carmona *et al.* (2012, 2013) interpret the top of the member as tidal flat deposits, with vertebrate traces, suggesting a not so sharp but a progressive transition to the aeolian deposits of the upper member.

Domènech & Farinati (2007) recognised two distinct major oyster shell concentrations in this marine middle member: level 1, located in the upper section of the transgressive tract, composed of moderately bioturbated, massive mudstones in which monospecific pockets of *C. patagonica* (cited there as *Ostrea patagonica*) were recognized; and level 2, located in the HST, where *C. patagonica* shells were also dominant, in this case arranged in pavements. Previously, Farinati & Zavala (2002) studied the bioerosion present in oysters from the pavements of this marine member, based on material collected in La Lobería, Playa Bonita and El Espigón outcrops.

According to its position in the sequence and to K-Ar dating of equivalent marine deposits in the area (9.41 My, Zinsmeister *et al.*, 1981) and dating of $^{87}\text{Sr}/^{86}\text{Sr}$ on bivalves of the Puerto Madryn Fm (10 ± 0.3 My, Scasso *et al.*, 2001), the marine member of Río Negro Fm was assigned to the late Miocene (Tortonian) (Zavala & Freije, 2000). Moreover, the vertebrate findings at high levels in the upper member (Aramayo, 1987) indicated a Montehermosean Mammal Age (early Pliocene), which would support the dating of the middle member.

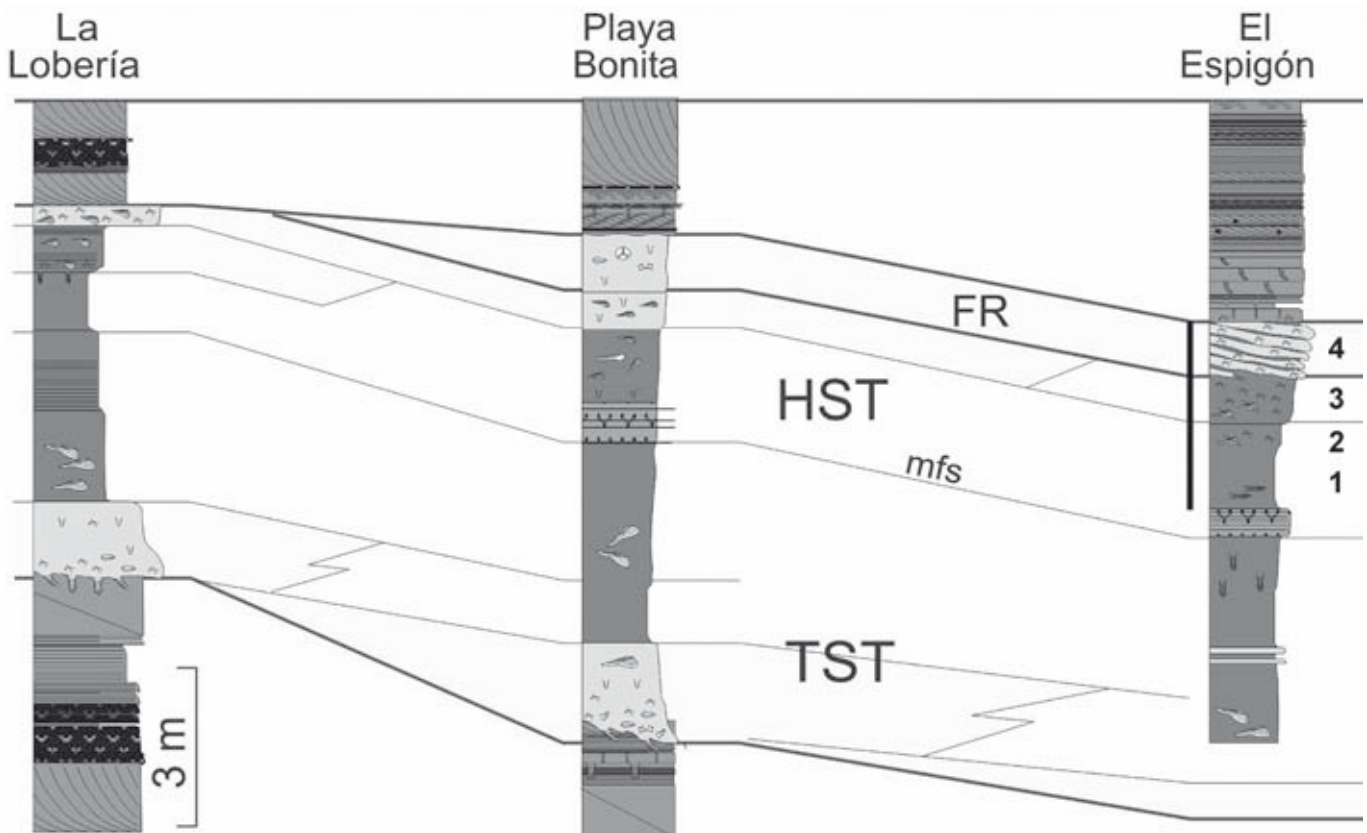


Figure 2. Stratigraphical correlation of the Río Negro Formation middle (marine) member among the main outcrops of the area. TST: transgressive systems tract; HST: highstand systems tract; FR: forced regression; mfs: maximum flooding surface. Vertical bar indicates the studied section in El Espigón outcrop and numbers correspond to the described layers (modified from Farinati & Zavala, 2002).

4. MATERIAL AND METHODS

Though the marine section of the Río Negro Fm is accessible at several locations on the NE coast of Patagonia, the present study has focused on the El Espigón site (Farinati & Zavala, 2005) (Fig. 1). The three most complete sections of the cliff (La Lobería, Playa Bonita and El Espigón) were described by Zavala & Freije (2000), and more recently enhanced by the description of bioturbation and microbially induced sedimentary structures (Carmona *et al.*, 2012, 2013). Farinati & Zavala (2005) carried out the study of their fossil invertebrate content. In this latter paper, the authors paid special attention to the Playa Bonita sequence, considered as the most complete outcrop, though they provided some complementary information from other sections. Currently, significant rockfalls occurring along the cliff make access to most of the Playa Bonita section impossible. As a result of this difficulty we decided to focus this research project on a detailed analysis of El Espigón, the easternmost outcrop, considered by Zavala & Freije (2000) as the outcrop which provides a record of the deepest sediments.

El Espigón site corresponds to a section of the cliff that allows the observation of Miocene strata along around 150 m of coast. The maximum outcropping thickness is 50 m, of which the lowest 6 m corresponds to the upper part of the middle member of the Río Negro Fm (Figs 2, 3).

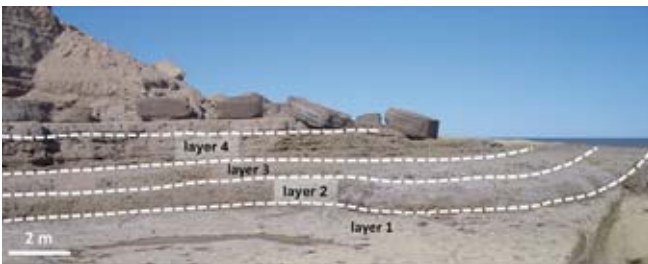


Figure 3. General overview of El Espigón outcrop, showing the four described main shelly layers.

The fieldwork consisted in measuring three stratigraphic sections in a W-E direction, with the three sections being spaced approximately 35 m apart (Fig. 4). On the basis of the lithological features, taxonomic characteristics and taphonomic attributes of fossils, four main layers observable in every section and along the outcrop were identified. A surface of 2 m² (2 x 1 m) was randomly delimited on each section, and countings were carried out of: articulated *vs.* disarticulated valves, bored *vs.* unbored valves, encrusted *vs.* non-encrusted valves and the location of the encrusters on the internal or external side of the valves. Qualitative observations on fragmentation and degree of abrasion were also made.

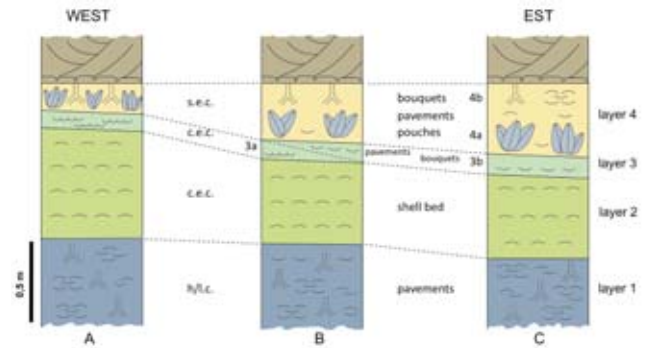


Figure 4. Schematics of the three sections at El Espigón outcrop (A, B and C), stressing the four levels described and the different kinds of oyster concentrations. h/l.c.: hiatal to lag concentration; c.e.c.: composite event concentration; s.e.c.: simple event concentration.

The numerous specimens of *C. patagonica* constituted the main malacological material used for the study, and shells were analyzed both in the field and the laboratory. The only exception to this dominance corresponds to layer 2, where *P. camacho* is the dominant species. As a result of this observation special attention has also been paid to this second species, both in the taphonomic description and the data analysis.

In this locality, the shell thickness of *C. patagonica* reaches nearly 3 cm, and up to 180 mm of umbonopallial diameter (i.e., the distance between the umbo and the posterior ventral edge). In addition to the evidence provided by the oysters, the accompanying fauna (other bivalves, cirripeds, corals, etc.), evidence of bioerosion by endoskeletozoans (*sensu* Taylor & Wilson, 2002), and the encrustation by episkeletozoans, and bioturbation were also considered.

Finally, several types of shell concentrations have been genetically and morphologically characterized through their taphonomic attributes and sedimentological data.

5. PALAEOBIOLOGICAL DATA ON *CRASSOSTREA PATAGONICA*

Crassostrea patagonica is a fossil oyster species that inhabited the NE Argentinian coast during the late Miocene. It is a large, heavy and thick-shelled oyster with left valves that may reach 30 cm in umbonopallial diameter, 20 cm of anteroposterior diameter and up to 5 cm of shell thickness. Right valves are somewhat smaller and nearly flat (Mauna *et al.*, 2005).

Generally speaking, oysters are epibenthic bivalves that have the ability to adapt to varied environments and substrates. Recent oysters inhabit shallow waters, from

the intertidal area down to 30 m depth. They develop better under slightly brackish water conditions in restricted marine environments, and between temperate and warm temperatures. Oysters can cement themselves to hard substrates to form banks, or alternatively occupy soft sedimentary bottoms as secondary soft-bottom dwellers (Seilacher, 1984). In the Argentinian Miocene strata, *C. patagonica* appears under two different modes of life related to soft bottoms: forming clusters (bunched or clustered forms) and reclined (recliner boulder-shaped or gryphaeate forms) (del Río *et al.*, 2001; Mauna *et al.*, 2005). Both habits represent a free lifestyle on sandy or muddy soft seafloor.

Crassostrea patagonica clusters are formed by several individuals arranged in almost vertical positions and cemented to each other. Del Río *et al.* (2001) found a minimum of 3 specimens for these clumps in the late Miocene Puerto Madryn Fm, while Mauna *et al.* (2005) mention clusters of up to 30 individuals in the same formation. Moreover, these authors describe beds formed by clustered forms that reach more than 5 m in thickness and occupy several hundred square meters. Reclined forms correspond to isolated specimens in which the left (more convex) valve rested on the seafloor. Oysters with both kind of forms inhabited soft sandy or muddy bottoms in the shoreface to offshore environments, although their shells/valves are not always in place, but transported and accumulated away from their living area (del Río *et al.*, 2001; Mauna *et al.*, 2005).

Because of its epibenthic habit in quite shallow waters and the dimensions of its shells, *C. patagonica* represents a very suitable substrate for endo- and episkelotobionts. Farinati & Zavala (2002) describe the presence of *Entobia* isp., *Maeandropolydora* isp. and *Gastrochaenolites torpedo* Kelly and Bromley in several valves of *C. patagonica* from the Río Negro Fm. For the latter ichnospecies, *Lithophaga patagonica* (d'Orbigny) was suggested as the most probable producer. Domènech & Farinati (2007) found the same ichnotaxa, and also *Caulostrepsis* isp. in specimens from the same places. Mauna *et al.* (2005) studied the presence of *Lithophaga* borings in extant (*Ostrea puelchana* d'Orbigny) and Miocene (*C. patagonica* -mentioned as *O. patagonica*- and *Ostrea alvarezii* d'Orbigny) oysters from the San Matías Gulf area (N to the Valdés Peninsula). Right and left valves of *C. patagonica* appeared bored in 98% of cases, while only 35% (mainly left valves) appeared bored in *O. puelchana* and *O. alvarezii*. This difference can be explained because of their distinct life habits: *C. patagonica* lived according to their clustered habit, while the current *O. puelchana* lay down as a reclining form, like *O. alvarezii* did in the Miocene.

Farinati *et al.* (2010) attempted to explain why shells of *C. patagonica* collected at Playa Bonita outcrop attained such high values of size and thickness, with the maximum length and thickness being 15 cm and 4

cm respectively. These authors concluded that species longevity, high growth rate induced by the abundant availability of nutrients, pressure due to bioeroders, and a special shell microstructure contributed to their large sizes. In fact, *C. patagonica* populations in the area were under chronic stress as a result of bioerosion, a situation that modern oysters have overcome by becoming adapted to environments which are less favourable to potential bioeroders (estuaries, lagoons).

Finally, it is worth noting that this species was originally ascribed to the genus *Ostrea* by d'Orbigny, and later authors maintained this attribution. Griffin & Nielsen (2008) reviewed the type material and included the species in the genus *Crassostrea* on the basis of shell morphology.

6. SEDIMENTOLOGIC AND TAPHONOMIC DESCRIPTION OF THE LAYERS

As indicated above, four main layers have been identified in the marine level of El Espigón outcrop, each with its own sedimentary and fossiliferous characteristics (Figs 3, 4).

6.1. Layer 1

This layer is composed of massive light grey mudstones, approximately 50 cm in thickness. It is characterized by the presence of *C. patagonica* accumulations and bioturbation (Fig. 4). However, the dominance of these elements is not uniform throughout the layer, and varies greatly along the outcrop.

Oysters are usually loosely packed, clearly matrix-supported, and they are accompanied by some small *Chlamys* spp. and cirripeds (*Balanus laevis* Bruguière). This latter encrusts the valves, sometimes in high numbers (between 70 and 100 individuals on a single shell), but they also appear in free groups. Equally remarkable is the presence of bioerosion affecting the oyster shells in this layer. Nearly 60% of shells show traces (Fig. 5), attributed to the activity of sponges (*Entobia* isp.), annelids (*Caulostrepsis taeniola* Clarke) and bivalves (large specimens of *G. torpedo*). Oysters are largely disarticulated (90%) and valves appear concordant to the bedding planes, though sporadically some shells are complete and show a sub-vertical position.

Near the top of the layer there are some small (about 25-30 cm in maximum diameter), irregularly contoured clumps of oyster valves, with a chaotic shell distribution in their interior (Fig. 6a). Clumps are laterally replaced by shell pavements, some of which are slightly oblique to the bedding planes (about 5°W of dip), and all the individual shell pavements cut across each other (Fig. 6b).

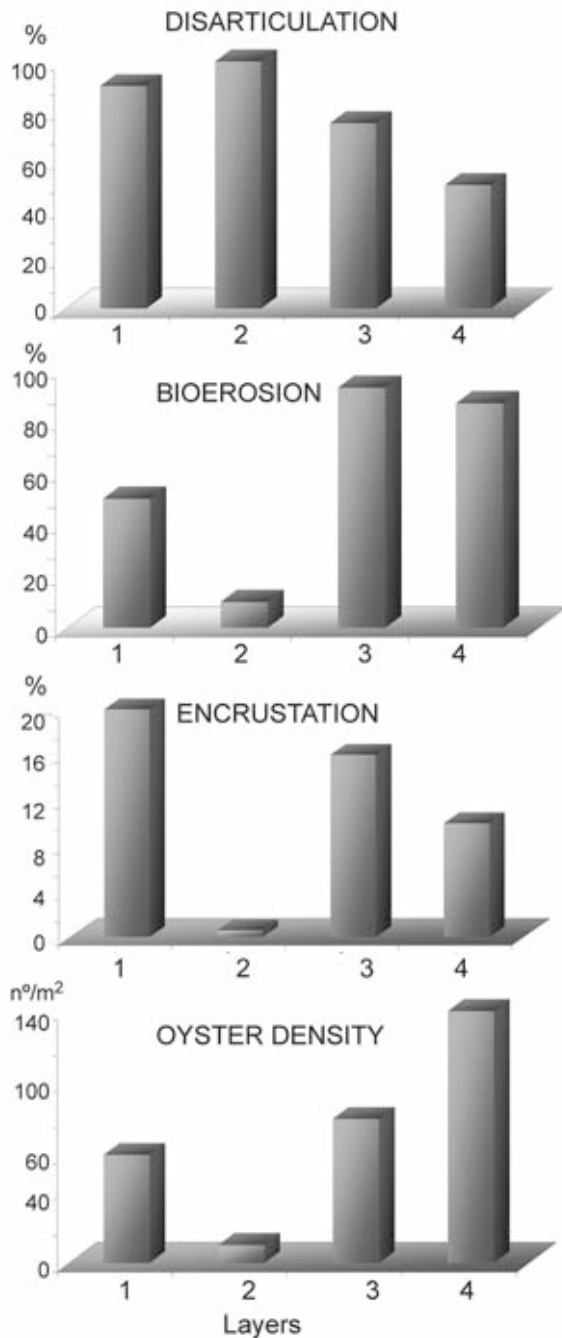


Figure 5. Histograms representing the main taphonomic attributes (percentage of disarticulated, bioeroded and encrusted oyster valves, and oyster density in a randomly chosen 1 m² area) quantified in each of the four layers of El Espigón outcrop. See the text for more details.

The countings in a selected area, located at the top of the layer, yielded 60 valves of *C. patagonica*, disarticulated in 90% of cases (Fig. 5). The percentages of right/left valves are unavailable because of the difficulty in assigning them correctly. Bioerosion is present in 50% of the valves,

with some of them highly affected by boring bivalves. Figure 6c, for example, corresponds to an impressive oyster “guest house” in this layer, with 22 perpendicular and oblique *G. torpedo*, which reach up to 30 mm in length. The proportion of encrusted valves is relatively low (20%; Fig. 5). Nevertheless, encrusted shells are often completely covered by episkeletozoans (*B. laevis*), which occupy both the inner and the outer sides of the valves.

At the western end of the outcrop the layer maintains a 50 cm thickness. At its base, oysters mostly show a concordant disposition and are fragmented, but there is a similar number of left and right valves. Some shells are open but still hinged and with a concave-up attitude (“butterflied preservation”) (Brett & Baird, 1986; Schatz, 2004) (Fig. 6d). A small, discontinuous layer, formed by cirripeds (*B. laevis*) of considerable size (up to 2 cm in height) is present within the layer (Fig. 6e). Laterally, the base of the layer displays a network of *Thalassinoides* and *Teichichnus* among which oyster shells can be seen (Fig. 6f).

6.2. Layer 2

The second layer is composed of very fine-grained sandstones of about 50 cm in thickness (Fig. 4). Its main fossiliferous component is the bivalve *Pododesmus camachoi* del Río and Martínez, accompanied by randomly scattered oysters (Fig. 7a), *Chlamys tehuelchus* d’Orbigny, and *Chlamys actinodes* Sowerby. All the valves are loosely packed within the layer, in a clearly matrix supported arrangement. Moreover, some thin (5-10 cm), irregular levels with abundant skeletal remains appear at the top of the layer. They show a discontinuous distribution and are detected in the central and eastern parts of the outcrop.

The dominant taxon in the area selected for counting in this layer is the bivalve *P. camachoi*, which represents 87.6% of the recorded valves (120). The remainder are *C. patagonica* (10), and *Ch. tehuelchus* (7). Almost 100% of the valves of *P. camachoi* are upper (left) valves, and appear loosely packed, concordant, and convex-upwards (Fig. 7b). Pectinids appear equally disarticulated and also display a concordant arrangement, but without a dominant orientation of the convexity, and with a similar number of left and right shells. Figure 5 reflects this high percentage of oyster disarticulation, reaching 100% of shells. Seven of the accounted *Crassostrea* valves show encrusted episkeletozoans (*B. laevis*), three contain *G. torpedo* and eight, *Entobia* isp. Bioerosion affects both inner and outer sides of the valves, although *G. torpedo* usually appears in the outer side, near the umbonal area, that is, in the thickest shell portion (Fig. 7a). Two specimens of the irregular echinoid *Monophoraster darwini* (Desor) have also been identified.



Figure 6. Layer 1. **a)** *C. patagonica* pouches with a chaotic inner fabric. **b)** Slightly oblique to the bedding planes pavements cutting each other because of erosion/deposition processes. **c)** *C. patagonica* with a high concentration of *G. torpedo* at the outer side of the valve. **d)** *C. patagonica* with convex-up butterfly preserved valves. **e)** Free valves of *C. patagonica* incrustated on both sides by *B. laevis*. **f)** Network of bioturbation traces (*Thalassinoides* isp. and *Planolites* isp.) with valves of *C. patagonica* trapped in it.

6.3. Layer 3

This layer is the most variable along the outcrop, as demonstrated by the sections (Fig. 4). Its easternmost part consists of about 10 cm of bioclastic sandstones with

loosely packed, scattered oysters whose surface shows abundant bioerosion. The Western part of the outcrop, however, is formed by three base-asymptotic, cross stratified, overlying pavements with a slight 5°E dip. They are dominated by densely packed, heterometric, mostly



Figure 7. Layer 2. **a)** *P. camachoi* valves together with a *C. patagonica* valve with abundant lithophagous borings (*G. torpedo*). **b)** Distribution of *P. camachoi* valves showing their mainly convex up disposition.

disarticulated oysters, some completely bored and others pristine, accompanied by some pectinids and some cirripeds. Valves are distributed concordantly (Fig. 8a), convex or concave-up (Fig. 8b), or oblique. Some complete shells appear in subvertical positions (Fig. 8c) forming scarce bouquets. Dominant endoskeletozoan borings are *Entobia* isp. and *G. torpedo* (Fig. 8d). The matrix of these pavements is made up of heterometric shell fragments of a maximum size not exceeding 0.5 cm. The central zone of the layer presents a more complex structure, which can be divided into sublayers 3a and 3b. The 3a sublayer forms the base and consists of an approximately 5 cm thick pavement which consists of disarticulated valves of *C. patagonica*, equivalent to the pavements observed in the western part of the outcrop. The overlying 3b sublayer (Fig. 9a) is composed of bioclastic sandstone with loosely packed, disarticulated valves of *C. patagonica* equivalent to the facies observed in the easternmost section of the layer (Fig. 9b).

The area selected for counting is situated in the 3a sublayer and corresponds to one of the oyster pavements (Fig. 5). Seventy specimens of *C. patagonica* were

counted, 10 of which were complete shells and 60 were disarticulated valves. It was difficult to distinguish between right and left valves in the outcrop. The umbonopallial diameter of shells ranges from 3 to 15 cm. Encrusting cirripeds (*B. laevis*) appear on 16% of the valves, and nearly 95% of the shells are bored on their outer side. All of them show *Entobia* traces (Fig. 8d) except eight which contain *G. torpedo*. Two valves display sponge borings on their inner surface. Borings occupy a large proportion of all the shell surfaces, and a small number of valves show both abundant *G. torpedo* and *Entobia* isp. The only *C. patagonica* shells which contain abundant *Entobia* isp. and *G. torpedo* on their outsides are those found in a subvertical life position (Fig. 8c).

6.4. Layer 4

Layer 4 is 50 cm thick on average and it also consists of two sublayers with variable characteristics (Figs 4, 10a). Overall, the layer tapers towards the western part of the outcrop. Where it is well developed, there is a lower layer (4a) consisting of a set of 5-6 cross stratified pavements, with an apparent inclination of about 5°E, roughly parallel to each other both at the base and the top. These pavements consist of accumulations of loosely packed valves and some complete specimens of *C. patagonica* within a sandy bioclastic matrix, similar to, though thinner than those of layer 3. However, the upper pavement contains numerous complete specimens of *C. patagonica* in a subvertical position, forming clusters composed of several individuals of large size (between 15 and 18 cm in umbonopallial diameter) (Figs 10b-10c). These clusters are separated from each other, sharing the space with disarticulated valves (50%; Fig. 11a). Oyster shells are dark coloured and show good preservation. Fragmentation is low, as well as abrasion, and there are no signs of valve dissolution. The fabric is matrix-supported and the clusters are embedded in bioclastic sediment where the maximum diameter of the skeletal fragments do not exceed 0.5 cm (Fig. 11b). The complete specimens maintain their valves fully articulated and the same external sediment infills the interior. Oysters in general show clear evidence of bioerosion (*Entobia* isp., *C. taeniola* and *G. torpedo*) (Figs 11c-11d), and some encrusting (serpulids, corals, cirripeds and bryozoans) (Figs 11e-11i). Bioerosion affects 99% of the valves. Sublayer 4b is found above 4a. The boundary between these two sublayers is fairly sharp. Sublayer 4b consists of one average 25 cm thick bioclastic sandstone. It exhibits intense bioturbation, represented primarily by *Thalassinoides* and *Ophiomorpha* (Fig. 10d). For more information, Carmona *et al.* (2013) provide further details on these traces. Bioturbation has a vertical development and it is sharply truncated at the top. This is, however, a general outline since the extent of these sublayers

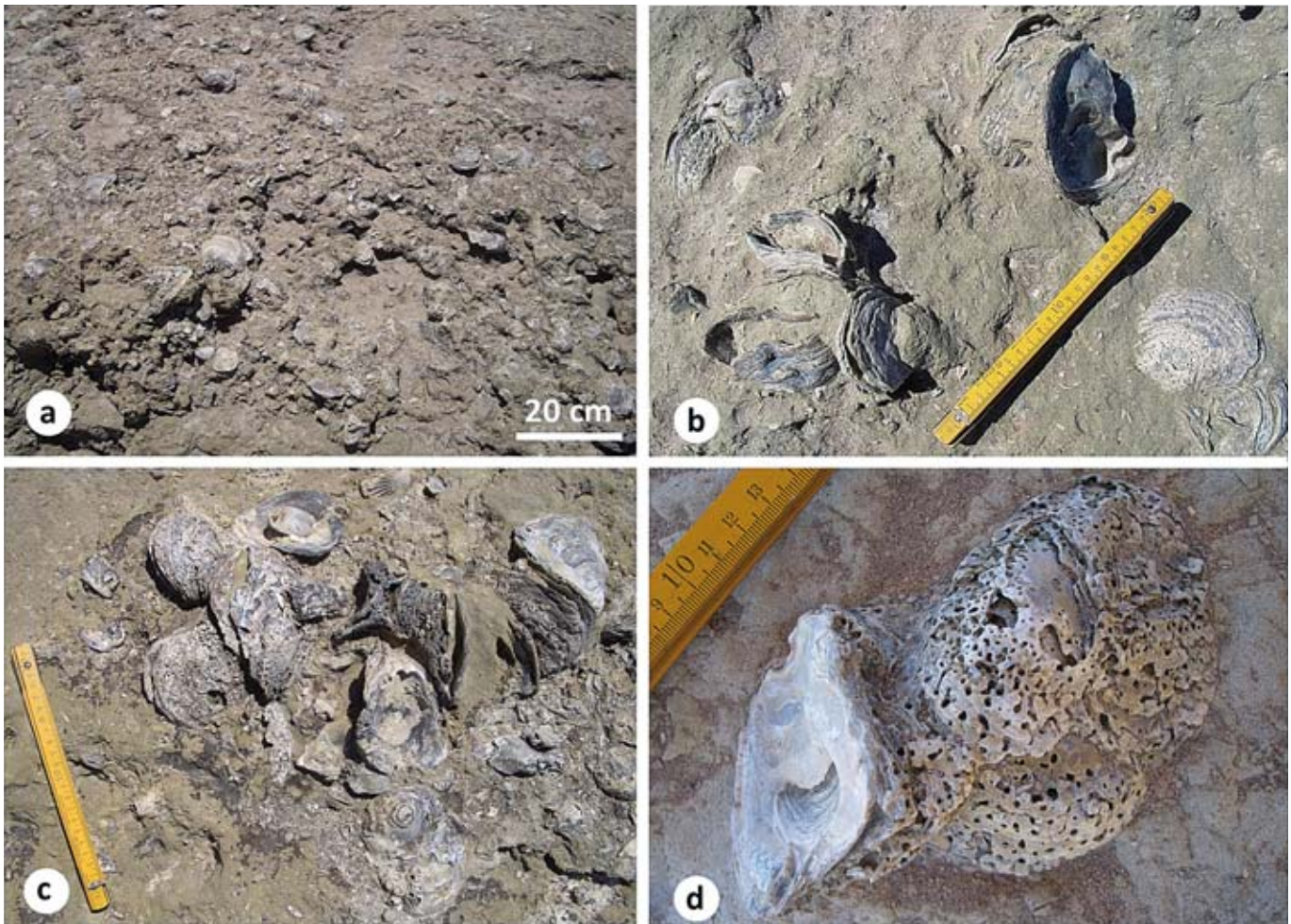


Figure 8. Layer 3a. **a)** Valves of *C. patagonica* concordant to the bedding plane. **b)** Some free valves of *C. patagonica* both upwards and downwards convexes. **c)** *C. patagonica* bouquet with abundant *Entobia* isp. and some *G. torpedo*. **d)** *C. patagonica* with abundant *Entobia* isp. and some *G. torpedo*.

displays a high degree of lateral variability within the outcrop. For example, there is a transition from areas with well-developed oyster clusters that occupy almost all the layer, with little to very abundant bioturbation with limited vertical development, to areas with no oysters and full occupancy by *Thalassinoides*, with intermediate situations between these extremes being displayed. The bioclastic underlying level, on which oysters are sustained, is constant throughout the outcrop. Towards the top, the bioclastic fraction varies in abundance and continuity, depending on the outcrop area considered. Sporadically, some small, badly defined pouches can be observed in it. However, the predominance of oyster clusters in almost the entire layer should be noted.

Disarticulation in this layer is relatively low (Fig. 5). On the surface demarcated for counting 140 valves appeared, consisting of 70 whole individuals (35 oysters with two valves) and 70 disarticulated valves, of which 14.2% are right valves. Disarticulated valves show a concordant, concave-up disposition. The umbonopallial diameter of

these oysters ranges between 7 and 15 cm. Among them, the incidence of encrustation is low, and only 10% of the valves present episkeletozoans (cirripeds and corals). Bivalve borings were not common, with only 4 specimens displaying *G. torpedo*. Instead, the boring activity of sponges is quite pronounced: 83% of the loose valves present *Entobia* isp. in their inner side, and 90% on their outer side.

7. RESULTS AND PALAEOENVIRONMENTAL INTERPRETATION

7.1. General taphonomic and ichnologic (bioerosion) observations

The preservation of skeletal remains in the study area seems to be clearly influenced by the mineralogical composition



Figure 9. Layer 3b (pavements). **a)** General overview of the layer. **b)** Detail of a pavement made by disarticulated *C. patagonica* valves.

and/or habitat of taxa. Although this aspect is not considered to be an important objective of this study, it is still worthy of comment. At El Espigón fossils belonging to endobenthic molluscs, which have mainly aragonitic shells, or to other endobenthic taxa, were not observed. However, in nearby outcrops (e.g., Playa Bonita), the presence of endobenthic bivalves preserved as molds in sedimentologically equivalent levels is common (Farinati & Zavala, 2005).

Almost all the invertebrates identified at El Espigón had an epibenthic life habit and dominant calcite skeleton. The only exceptions to the primary skeletal composition are *P. camachoi*, an anomiid bivalve, and the scleractinian *Oculina singleyi* (Fig. 11h). In the first case, the original aragonitic skeletons are preserved in layer 2, whereas in the second, fossilization occurred as diagenetic calcite. The clypeasteroid echinoid *Monophoraster darwini*, whose skeletal mineralogy is calcite, was part of the more superficial endofauna. Therefore, it has to be stated that fossildiagenetic agents played an important role in the preservation of skeletal remains in this outcrop, perhaps from the very early stages. Thus, possible invertebrates

with aragonitic skeletons living in this zone were not preserved. This would have facilitated the dominance of calcitic forms in the layers.

Moreover, the paucispecific composition of skeletal concentrations, dominated by *C. patagonica*, is to be stressed. Only the second layer is quite diversified, with the abundant presence of *P. camachoi*, several species of pectinids and some echinoids. In most cases, oysters appear in pouches or pavements, with clear evidence of biostratinomic processes, mainly transport evidenced by disarticulated and sorted valves and exposure prior to burial (borings and encrustation on the inner side of the valves).

Throughout the sequence, many of the valves of *C. patagonica* with *Entobia* are in fact intensely bored. It is especially notable in the clusters of layer 4. Moreover, the valves with *G. torpedo* do not usually present *Entobia* or, in any case, this trace is in its early stages.

7.2. Categorisation of the oyster shell concentrations

Oyster concentrations represent a useful tool for palaeontologic and stratigraphic analyses because of their abundance and high fossilization potential. Domènech & Farinati (2007) indicated the presence at El Espigón site of a biogenic oyster accumulation that corresponds to layer 4 described herein. The more detailed study of the outcrop allows for the categorisation of three different types of oyster dominated concentrations, which are characterized by the deposit geometry (Fig. 4) and their taphonomic attributes (Table 1):

7.2.1. Type I: Pouches

At the top of layer 1, some small *C. patagonica* pouches of irregular contour (about 25-30 cm in maximum diameter) appear with a chaotic distribution of valves within them (Figs 4, 6a). There is a smaller number of pouches, less defined than those in layer 1, which are also sporadically present at the top of layer 4. The term “pouches” is here preferred instead of “clump” (proposed by Kidwell *et al.*, 1986) to clearly differentiate them from the bouquets (type III, see below), also present in the sequence.

7.2.2. Type II: Pavements

There are pavements found particularly in layer 3, but also within layer 1 and at the base of 4, (Figs 4, 6b, 8a, 9a-9b) which are formed almost exclusively by *C. patagonica*. Valves have a high rate of disarticulation (75% at layer 3) and they are arranged in a mostly concordant and convex-up manner. Density of specimens is locally high (40 valves/m² on the surface measured in layer 3).

Table 1. Main taphonomical and sedimentological features of the concentrations studied.

layer	grain size	concentration types	disarticulation	bioerosion	incrustation	relative oyster density	genetic classification	environment
4		I,II,III (<i>Crassostrea</i>)	high / low	very high	low	high	simple event	shoreface/foreshore
3		II,III (<i>Crassostrea</i>)	very high	very high	medium	medium	composite	shoreface/foreshore
2		IV (<i>Pododesmus</i>)	very high	low	low	low	composite	shoreface
1		I,II (<i>Crassostrea</i>)	very high	medium	low	medium	hiatal to lag	shoreface

M FS MS CS

Likewise, pavements on layer 3 show the highest degree of bioerosion by endoskeletozoans (93% of the valves) and a relatively low encrustation rate (16.25%; Fig. 5). Every pavement of layer 1 has a one-valve thickness and is matrix supported, while those at levels 3 and 4 are thicker, with 2-3 valves overlapping in many areas, although they are too thin to be considered true beds (*sensu* Kidwell *et al.*, 1986).

7.2.3. Type III: Bouquets

This type corresponds to the oyster clusters of layer 4 (Figs 4, 10b, 11e-11f). Its main characteristic is the presence of groups of several cemented individuals in a sub-vertical position, forming sets in life position, around which some disarticulated valves appear. Because this form of life, density of specimens is the highest in the outcrop (70 specimens/m² on the counting surface), and rate of disarticulation is the lowest (50%). The life position of the bouquets clearly indicates the autochthonous character of the oysters and the absence of transport. Very scarce bouquets are also present in layer 3a.

7.3. Categorisation of the *Pododesmus camachoi* del Río & Martínez Chiappara concentration (type IV)

Layer 2 is dominated by *P. camachoi*, a sessile anomiid that had to live attached to a hard substrate through the byssus. This species was erected by del Río & Martínez (1998) from specimens collected in La Lobería outcrop, a location which is very close to El Espigón site. Formerly, it has been identified as *P. papyraceus* Philippi (Farinati &

Zavala, 2005). As stressed in the introduction, this species does not represent the main aim of the present research, but its local relevance within the section does merit special consideration. This is because the level contains a distinct, final category of shell concentration.

In the layer, valves of *P. camachoi* are 100% disarticulated, concordant, unfragmented, convex-up oriented, and loosely packed (matrix supported). They are left (upper) valves (100% in the measured area), indicating a clear selection by light currents. The virtual absence of right valves in the layer and the orientation of the left ones suggest an effective sorting due to their different sizes, morphologies, and life position. Right valves (lighter, small and fragile, but fixed) may have remained attached to substrate and left valves (heavier, but convex and free) could have been transported to this locality, requiring a minimally continuous current action. The concordant and convex-up disposition of the valves indicates a reworking process and reorientation by flows in a regime of high friction with the sea-bottom (Kidwell, 1991a). Biostratinomic processes, therefore, are the primary control of the taphonomic signals in the layer and *P. camachoi* should be considered a parautochthonous component of the layer. Although rather dispersed, this skeletal association can be described as a shell bed (Fig. 4), which will constitute the fourth type of shell concentration in the outcrop.

7.4. (Palaeo)environmental conditions of deposition

Oyster pavements in layer 1 (type II) consist of single relict levels of mainly disarticulated and loosely packed valves,

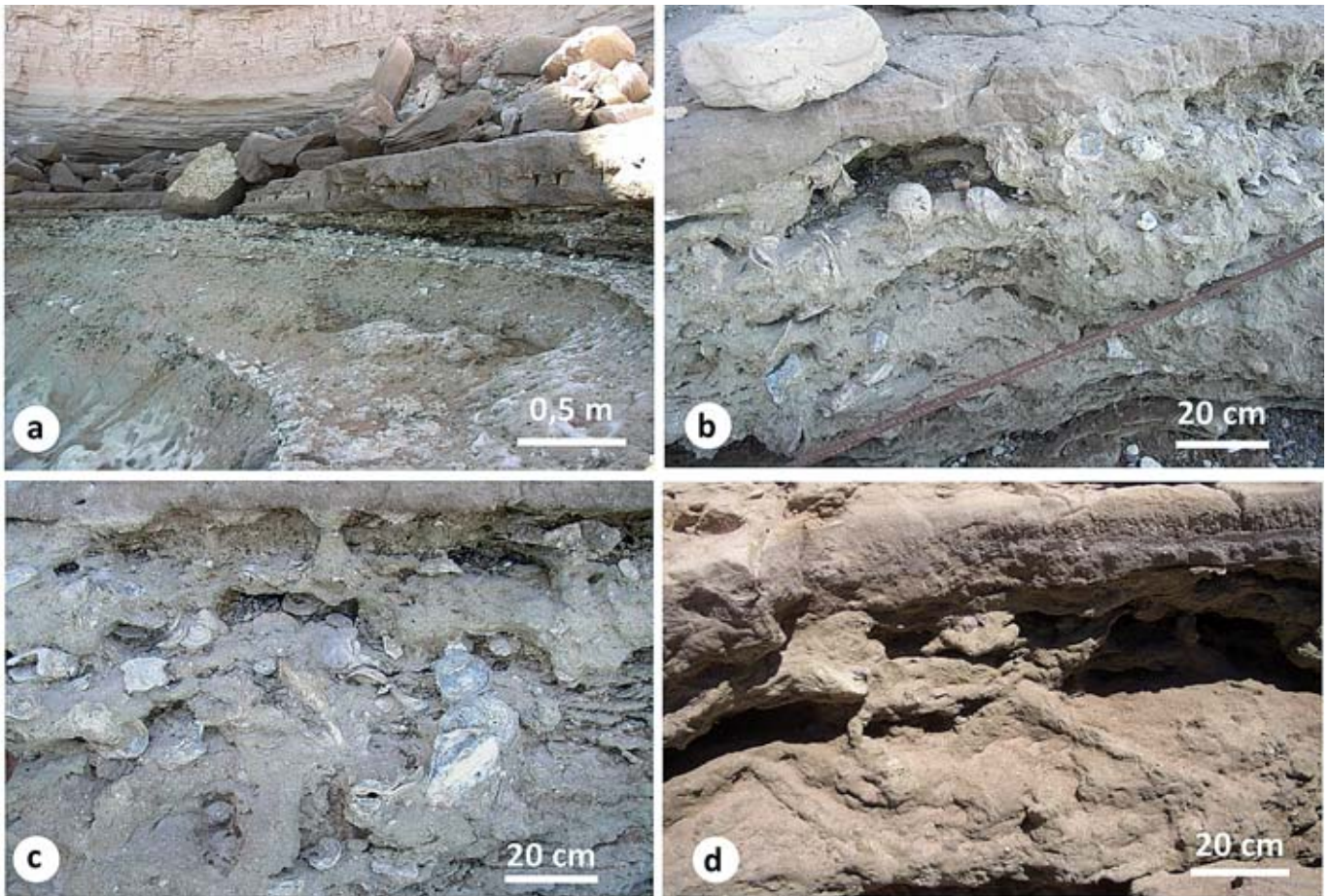


Figure 10. Layer 4 (I). **a)** General overview and erosive contact with the continental layers of the upper member. **b)** *C. patagonica* shells, many of them in life position forming bouquets. **c)** Detail of the oyster clusters at the base of the layer, together with some free valves in the matrix, which are replaced by *Thalassinoides* isp. towards the top. **d)** Detail of a *Thalassinoides* isp. network.

with a medium percentage of bioerosion or encrustation, although very intense in some particular specimens. Almost all the complete shells and free valves belong to oysters with a reclined habit. Pavements are usually the result of episodic transport in the foreshore/shoreface area (Kidwell *et al.*, 1986). During these episodes there would be some erosion of the marine bottom and deposition of mostly concordant and convex-up valves. The coexistence of bored and pristine valves denotes mixing from different episodes, and also a low local rate of net sedimentation allowing time-averaging. Different apparent dips of pavements in layer 1 (Fig. 6b) respond to alternating erosive and depositional episodes. Pavements change laterally to pouches (Fig. 6a) that could correspond to small depressions in the seafloor, where shells appear in a chaotic arrangement as a result of currents. A biogenic origin can be ruled out because of both the size and the thickness of the oyster valves. Sporadically, some oysters appear in a clustered habit, evidencing a life position; the loose valves could also correspond to this group, affected by transport.

In the Eastern part of the outcrop, it is also worth noting the presence of bioturbation (*Thalassinoides* and *Teichichus*) at the base of layer 1, showing oyster shells apparently concentrated in internal areas of the traces network (Fig. 6f). This arrangement can be interpreted as a result of the high activity carried out by endobenthic fauna during an episode of sedimentation decrease. Bioturbation affected previously buried shells and accumulated them within the *Thalassinoides* framework.

The loose pavements dominated by oysters in layer 1 could be tentatively referred as hiatal to lag concentrations, as they do not exactly correspond to either major surfaces of truncation, nor do they contain material from older deposits (Kidwell, 1991a). They must be associated with brief periods of erosion and short transportation.

The shell bed in layer 2, dominated by *P. camachoi*, shows a higher complexity and can be defined as a composite event concentration. The stratigraphic context indicates that these layers were deposited in shoreface/foreshore environments at the beginning of the HST (Farinati

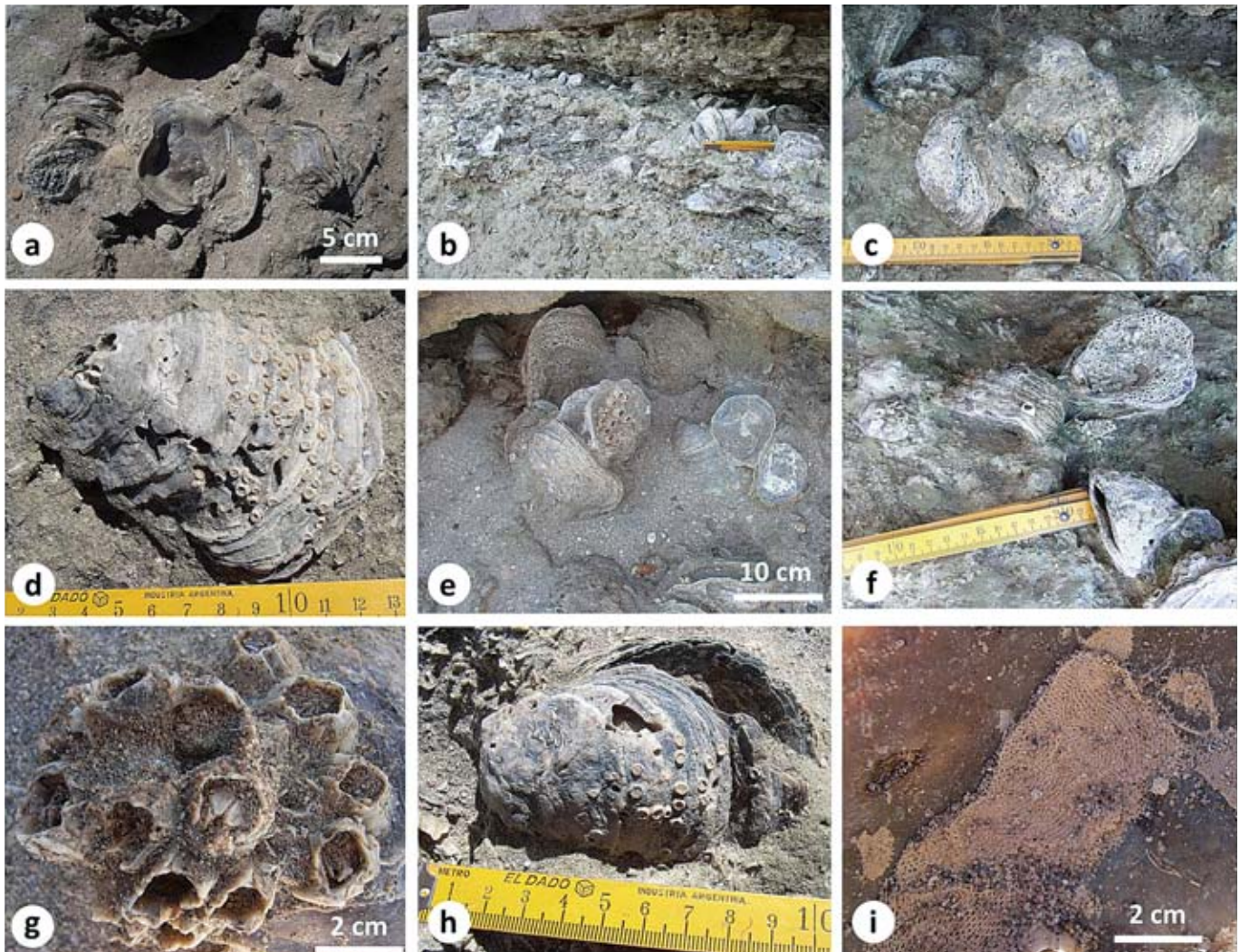


Figure 11. Layer 4 (II). **a)** *C. patagonica* in life position next to several disarticulated valves. **b)** General overview that demonstrates the way in which oysters grew from a bioclastic level formed by bioclasts. Bioturbation is visible at the top of the layer. **c)** *C. patagonica* bouquet with abundant *Entobia* in the valves. **d)** *Oculina singleyi* on *C. patagonica* with *G. torpedo*. **e)** Oysters bouquet next to some free valves; some specimens are pristine and others have attached *Balanus laevis*. **f)** Oysters bouquet with abundant encrustation by *B. laevis*. **g)** Detail of a *B. laevis* grouping encrusted on the outer side of an oyster shell. **h)** *Oculina singleyi* fixed on the outer side of a *C. patagonica* upper valve. **i)** Bryozoans colony and *B. laevis* encrusted on the inner side of a right *C. patagonica* valve.

& Zavala, 2002; Carmona *et al.*, 2013), which is consistent with the conditions inferred from taphonomic data.

The third layer is formed largely by oyster pavements (type II), but shows great lateral variability (Fig. 9b). This lack of uniformity is typical of coastal areas, with a clear wave and tidal activity. A low rate of sedimentation is interpreted due to the high rate of bioerosion and the relatively high rate of encrustation, as these processes need a relatively long residence time for the shells on the seafloor. These dipping oyster pavements represent foreshore frontal sheets and are more than the result of the addition of successive simple sedimentary episodes

and thus, they may be qualified as composite event concentrations (Kidwell, 1991a).

Layer 4 is characterized by both oyster bouquets (type III) and bioturbation. The detrital bed, in turn, is almost in continuity with the pavements of the lower layer. The development of these oyster bouquets would be an example of taphonomic feedback (Kidwell & Jablonski, 1983; Kidwell, 1991b), where bioclasts, derived largely from oyster shells, serve as a hard substrate for fixation. Bioerosion of the shells indicates stable conditions for a certain period of time, with a low rate of sedimentation. A single sedimentary event, however, buried the ensemble

with almost all shells in life position (census assemblage, Kidwell & Bosence, 1991). The result is a simple event biogenic concentration (Kidwell, 1991a) in the absence of time-averaging. Subsequently, the sediment that covered the oysters was affected by bioturbation, as reflected by the presence of *Thalassinoides* and *Ophiomorpha* networks. Layers 3 and 4 were deposited in a shallower environment than layers 1 and 2, and can be correlated with the upper shoreface/foreshore conditions established during the regression described in the depositional sequence (Zavala & Freije, 2000), as well as local sedimentation controlled by the algal mats that developed in protected areas of the palaeocoast (Carmona *et al.*, 2012, 2013).

The upper boundary of the layer, however, abruptly cuts the traces, therefore demonstrating a significant erosional episode. This period may relate to subaerial exposure at the end of the regressive episode, with a 20–25 cm thick mudstone layer displaying desiccation structures.

8. DISCUSSION

The taphonomic features of the various shellbeds studied in the outcrop greatly support the classical stratigraphical interpretation (Zavala & Freije, 2001) of the depositional sequence corresponding to the marine member of the Río Negro Fm. Nevertheless, these authors interpret the upper section as the result of a forced regression with an abrupt transition to the eolian member. The presence of oyster bouquets developed over a detrital bioclastic bed in this upper section may contradict an erosive episode. Carmona *et al.* (2012) describe a discontinuous level at the top of the HST, deposited under tidal flat conditions, where microbially induced sedimentary structures appear. These algal mats indicate that the transition to the subaerial conditions was not as sharp as previously considered, at least in some protected areas along the palaeocoast. This was probably the case for the sequence represented at El Espigón outcrop, which locally permitted the development of small shelly buildings. The final preservation of the bouquets was made possible by a sudden irruption of sediment, subsequently affected by bioturbation.

Similar oyster bed sequences have been studied in Phanerozoic sequences (Abbott, 1997; Fürsich & Pandey, 1999; Pufahl & James, 2006; Videt, 2007), and the Patagonian Cenozoic (del Río *et al.*, 2001; Parras & Casadío, 2005, 2006; Domènech & Farinati, 2007; Farinati *et al.*, 2010). Results presented in the current work are the equivalent of these previous studies in terms of palaeoenvironmental and sequential interpretations. Nevertheless, it is worth noting that the analysed sequence only represents the HST of the total transgressive-regressive cycle. The different concentration structures

would only represent local or sporadic environmental conditions within a wide shoreface-foreshore domain. The uppermost concentration (level 4), related to the ending of the HST, would represent an atypical situation perhaps favoured by the presence of local algal-mats, or directly for their growth in a protected location that also promoted the development of microbial structures.

9. CONCLUSIONS

El Espigón outcrop allows for the examination of most of the marine middle member of the transgressive-regressive sequence of the Río Negro Formation (late Miocene-early Pliocene), North Patagonia. Four main layers have been identified, which contain different kinds of shell accumulations, mainly oysters. Bioturbation (*Thalassinoides*, *Ophiomorpha*, *Teichichnus*, *Siphonichnus*, *Asterosoma*, *Maiakarichnus*) and bioerosion traces (*Entobia*, *Caulostrepsis*, *Maeandropolydora*, *Gastrochaenolites*) are common in the outcrop, as well as encrusters (cirripeds, bryozoans and corals). These deposits were formed in shallow marine environments during the HST of the regressive sequence, affected by waves that gave rise to valve concentrations of different entities. *C. patagonica* is the almost exclusive species within these accumulations, which have been characterized by their geometry and their taphonomic attributes (Table 1). Thus, three different concentration morphologies have been identified for oysters: pouches, pavements and bouquets. In addition, a *Pododesmus camachoi* layer can be considered as a shell bed, having a taphonomic signature similar to that of the pavements. The most visible at the outcrop scale are the bouquet concentrations, but pavement concentrations are the most abundant. In layer 1, pouches and pavements are defined as hiatal to lag concentrations; in layer 3, every pavement is a simple event concentration, although the ensemble shows a more complex history (composite concentration), and in layer 4, the bouquets correspond to a simple event biogenic concentration (census assemblage) without time averaging, and oysters are preserved mostly in life position. Concerning other fossil groups, *P. camachoi* shell bed in layer 2 could be also defined as a composite concentration.

Apart from oysters and anomniids, the main accompanying macrofauna is *Chlamys tehuelchus*, *Ch. actinodes*, *Oculina singleyi*, *Balanus laevis* and *Monophoraster darwini*. Layers 1 and 2 were deposited in shoreface/foreshore environments at the beginning of the HST, while layers 3 and 4 did were deposited at the end, or the very beginning of the regression, in clearer foreshore environments. The existence of algal mats in the top of the marine member indicates a not so abrupt change of environmental conditions and can explain the presence of oyster bouquets in life position in layer 4.

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