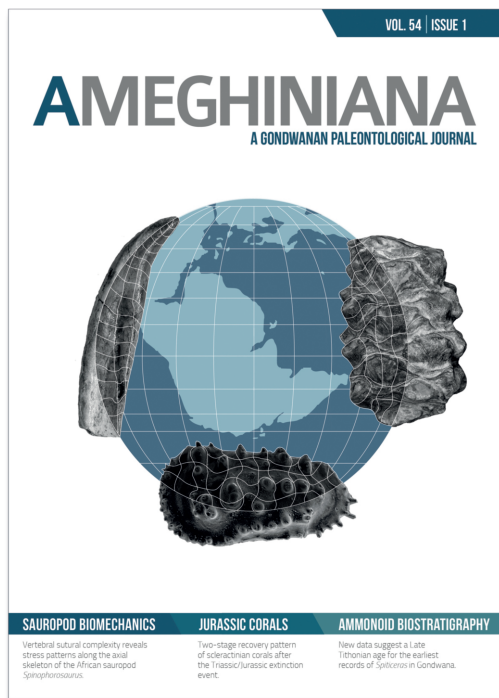




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Abstract. Information about barnacles as fossil components of hard substrate communities from middle latitudes in the Southern Hemisphere is scarce. Changes in these barnacle communities during episodes of extinction, such as that which occurred during the Cretaceous/Paleogene (K–Pg) boundary, are almost unknown. We describe encrusting and boring barnacles associated with Maastrichtian and Danian oysters, evaluate the involved taphonomic processes and report changes in their frequencies over time. A total of 1,174 valves belonging to nine oyster species, collected from the Jagüel and Roca formations of the Neuquén Basin, were analyzed. Presence/absence of barnacles or their bioerosional traces were recorded, frequencies of host incrustation and bioerosion were calculated and taphonomic and statistical analyses were performed. The encrusting barnacles identified on the oyster shells were assigned to *Verruca rocana* and, their traces, to the ichnospecies *Centrichnus concentricus* Bromley and Martinell. The boring barnacles are represented by traces assigned to the ichnogenus *Rogerella*. A preliminary taphonomic analysis indicated that late Maastrichtian and early Danian shells presented a fair-poor condition given by abrasion and fragmentation as taphonomic attributes while late Danian shells exhibited mostly good-fair or mixed condition for both attributes. *Verruca rocana* was not recorded during the late Maastrichtian but high frequencies of encrusted valves did become apparent after the K–Pg boundary. Boring barnacles represented by the trace *Rogerella* exhibited a decline in abundance during the early Danian but an increase during the late Danian. Both the encrusting and the boring barnacles associated with oysters presented an increase in their frequencies during the late Danian.

Key words. Cirripedia. Sclerobionts. Hard substrates. Oysters. Neuquén basin.

Resumen. CIRRIPEDIOS INCRUSTANTES Y PERFORANTES A TRAVÉS DEL LÍMITE CRETÁCICO/PALEÓGENO EN PATAGONIA NORTE (ARGENTINA). La información sobre cirripedios como componentes fósiles de las comunidades de substratos duros de latitudes medias en el Hemisferio Sur es escasa. Los cambios en estas comunidades durante episodios de extinción como el que ocurrió durante el límite Cretácico/Paleógeno (K–Pg), son casi desconocidos. En este trabajo describimos los cirripedios incrustantes y perforantes asociados a ostras maastrichtianas y danianas, evaluamos los procesos tafonómicos involucrados, y registramos los cambios en su frecuencia de ocurrencia en el tiempo. Se estudiaron 1.174 valvas pertenecientes a nueve especies de ostras, recolectadas de las formaciones Jagüel y Roca de la Cuenca Neuquina. Se registró la presencia/ ausencia de los cirripedios o de sus trazas bioerosivas, se calcularon las frecuencias de incrustación y bioerosión y se realizaron análisis tafonómicos y estadísticos. Los cirripedios incrustantes identificados fueron asignados a *Verruca rocana*, y sus trazas asignadas a la icnoespecie *Centrichnus concentricus* Bromley y Martinell. Los cirripedios perforantes, están representados por trazas asignadas al icnogénero *Rogerella*. Los análisis tafonómicos indicaron que durante el Maastrichtiano tardío y Daniano temprano, las ostras muestran una condición intermedia a pobre para la abrasión y la fragmentación, mientras que las ostras del Daniano tardío exhibieron una condición buena-regular o mixta para ambos atributos. *Verruca rocana* no muestra registros durante el Maastrichtiano tardío pero sí presenta alta frecuencia de incrustación de valvas luego del límite K–Pg. Los cirripedios perforantes presentaron una declinación en la abundancia durante el Daniano temprano y un aumento en el Daniano tardío. Ambos grupos presentaron un aumento en sus frecuencias durante el Daniano tardío.

Palabras clave. Cirripedia. Esclerobiontes. Substratos duros. Ostras. Cuenca Neuquina.

BARNACLES (Cirripedia) are a major group of crustaceans including exclusively sessile organisms (Glenner and Hasgaard, 2006) found currently in all marine environments and distributed from the tropics to the poles and from intertidal zones to abyssal depths (Farrapeira, 2010). The radiation of cirripedes is reflected in the variety of biogenic

and abiogenic substrates on which they are able to attach or bore (Pitombo, 2010). Also, the incidence of planktonic larval dispersal in some species combined with a permanent calcareous shell in adults represents an adaptive strategy for occupying and persisting in diverse and physiologically challenging environments (Van Syoc, 2009). Cirripedia

mainly consists of three well-defined superorders: Thoracica (encrusting or “true” barnacles), Acrothoracica (boring barnacles) and Rhizocephala (parasitic barnacles) (Glennier and Hasgaard, 2006; Pitombo, 2010). Thoracica and Acrothoracica make use of their feathery thoracopods (cirri) in order to suspension feed whereas rhizocephalans are parasites of other crustaceans and especially of decapods (Brusca and Brusca, 2005).

Although encrusting barnacles bear a fossil record dating back to the Cambrian (Foster and Buckeridge, 1987), verruciforms (*i.e.*, barnacles with asymmetric plates) present the earliest known representative genera from the Cenomanian–late Maastrichtian (*i.e.*, *Proverruca* Withers, 1914) and the early Santonian–late Campanian (*i.e.*, *Eoverruca* Withers, 1935) (Buckeridge *et al.*, 2008). During the Late Cretaceous, *Verruca* was restricted to Europe or Australasia; yet migration via an open seaway along the south Pacific West Antarctic margin of Gondwana may have also provided the route for *Verruca* to reach southern South America (Buckeridge, 2011). The genus *Verruca* is characterized by a stratigraphic record ranging from the Maastrichtian to Recent (Buckeridge *et al.*, 2008).

Boring barnacles are known from the Upper Devonian (Rodríguez and Gutschick, 1977) mainly in the form of borings or casts of borings (Newman, 1987) and are limited in distribution by hard substrates found largely in carbonate sedimentary rocks and on skeletons of marine invertebrates (Newman 1971; Kolbasov and Newman, 2005).

Fossil hard substrate assemblages mostly preserve the sessile components of the original communities, particularly sclerobionts (*sensu* Taylor and Wilson, 2002), which encrust or bore into the shells of living and dead organisms (Taylor and Wilson, 2003; Brett *et al.*, 2012) or mineralized skeletons in general. These shells are sometimes the only available substrates for sclerobiotic communities in soft bottom environments. In this sense, oysters as hard substrates provide a good opportunity for the study of changes in abundance and the observation of the distribution of boring and encrusting organisms.

Information about barnacles as fossil components of encrusting and boring communities associated with hard substrates from middle latitudes in the Southern Hemisphere is scarce. Additionally, changes in these communities during episodes of extinction such as those which occurred around

the Cretaceous/Paleogene (K–Pg) boundary are almost unknown. The main aim of this work is to describe the encrusting and boring barnacles associated with Maastrichtian and Danian oysters and report changes in their abundances over the critical K–Pg transition. Also, other sclerobionts on valves were identified in order to acquire knowledge on the assemblage composition and assess whether there is an assemblage distribution pattern marking the time interval considered here.

GEOLOGICAL AND PALEONTOLOGICAL SETTINGS

The Neuquén Basin (Fig. 1) covers approximately 120,000 km² of central-western Argentina (Howell *et al.*, 2005) and includes part of the provinces of Mendoza, Neuquén, Río Negro and La Pampa. The sedimentary infilling reaches a thickness of over 6,000 m and comprises marine and continental deposits spanning the Late Triassic–Paleocene (Casadío and Montagna, 2015).

During the Late Cretaceous, marine sedimentation occurred as a result of the flooding from the Atlantic which began during the Maastrichtian. The Atlantic Ocean then covered an estimated surface of 507,000 km² of presently emerged Patagonia (Malumián and Caramés, 1995).

In the northwest of the basin, the Malargüe Group records its greatest thicknesses outcropping in many localities situated at the foot of the Andes (Groeber, 1947; Dessanti, 1973, 1978; Legarreta *et al.*, 1989, 1993; Parras *et al.*, 1998). This group is composed from base to top of the Loncoche/Allen, Jagüel, Roca and Pircala/El Carrizo formations.

Along the past two decades, significant progress has been made regarding available knowledge on the stratigraphic, sedimentological and paleontological profiles of the Malargüe Group. Most of these advances occurred during the 1980s and are related to the rising interest in studying the events surrounding the K–Pg boundary. The Malargüe Group contains the K–Pg boundary in both marine and continental facies and is therefore considered to be key for understanding the changes occurring in ecosystems of the Southern Hemisphere mid-latitudes during the Maastrichtian–Danian interval (Parras and Casadío, 1999).

The sedimentary sequence studied herein consists of the marine Jagüel and Roca formations recognized in eight localities (Fig. 1, appendix of Supplementary Online Information). These units would represent the final Atlantic

transgressive-regressive phase of the sea that flooded the eastern sector of the Neuquén Basin during the Late Cretaceous and the early Paleogene (del Río *et al.*, 2011). The Jagüel Formation is composed of marine mudstones and claystones that represent an inner shelf (Casadío, 1998). The Roca Formation transitionally overlaps this unit and represents shallow marine environments deposited during a regressive phase comprising marl rocks and bioclastic limestones with abundant skeletal fragments (del Río *et al.*, 2011).

Among the bivalves recorded in the Jagüel and Roca formations, oysters are the most conspicuous constituent of the fossil assemblages. The calcitic composition of the valves enhanced oyster preservation probabilities in these deposits and favored the identification of the sclerobiotic communities associated with them.

Oyster accumulations from the K–Pg transition in the Neuquén Basin were studied by Casadío (1998). Taphonomic and facies data collected for this work are included in Table 1.

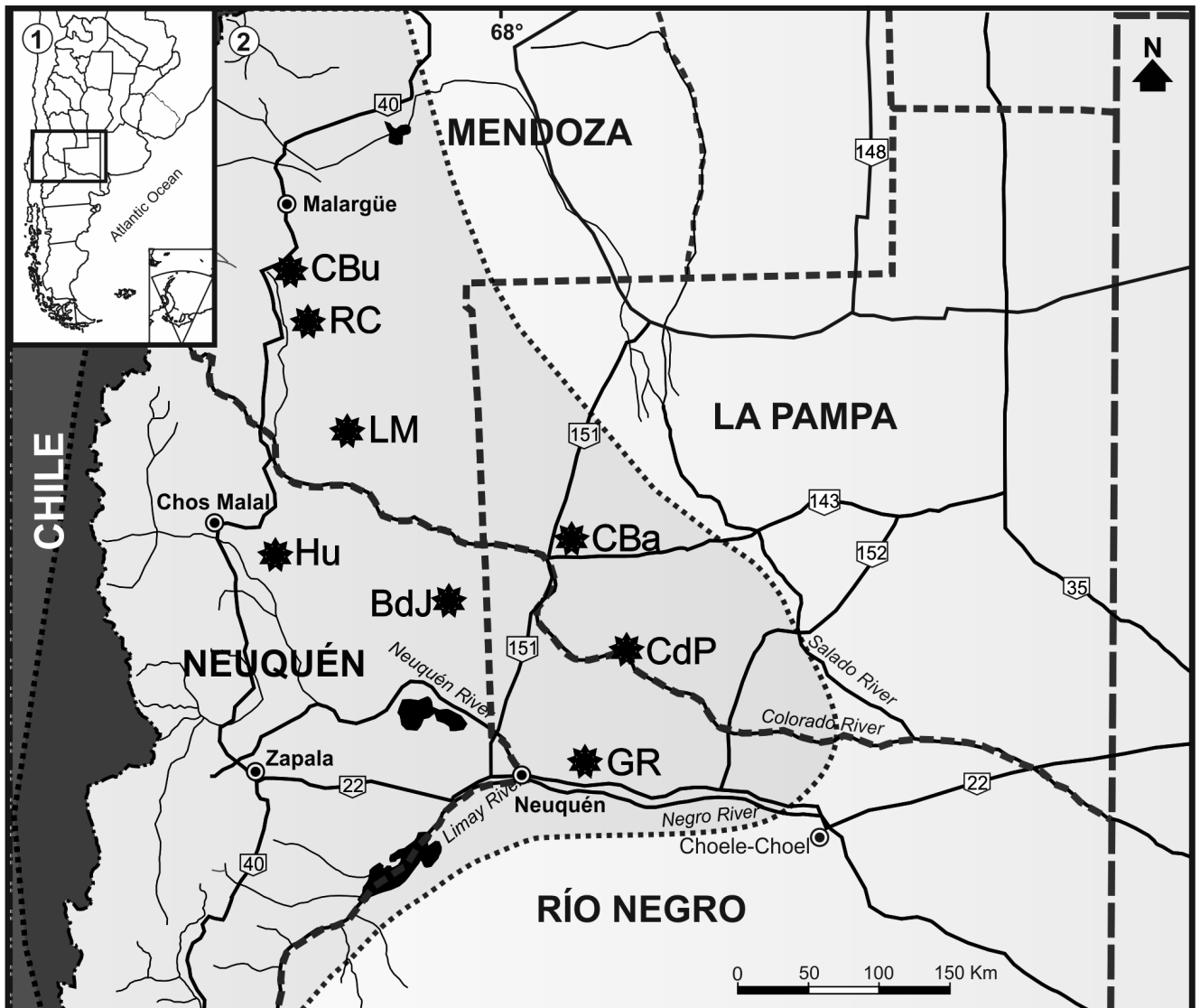


Figure 1.1. Map of Argentina; 2, map showing the study area. Black symbols indicate the localities from which oysters were collected; the dotted line indicates the Neuquén Basin boundaries. **BdJ**, Bajada del Jagüel; **CBu**, Cerro Butaló; **CBa**, Cerros Bayos; **CdP**, Casa de Piedra; **GR**, General Roca; **Hu**, Huantraico; **LM**, Liu Malal; **RC**, Ranquil-Có.

MATERIAL AND METHODS

Nine oyster species ranging in age from the late Maas-
trichtian to the late Danian were studied (Figs. 2–4; Tab. 1)
in order to analyze, using a binocular microscope, the abun-
dance and distribution of barnacles on them. A total of
1,174 valves were randomly collected from non-lithified de-
posits –in which, in some cases, the K–Pg boundary can be
recognized– from the Jagüel and Roca formations along

several localities in the Neuquén Basin (Fig. 1) (e.g., Bajada
del Jagüel, Cerros Bayos and Liu Malal; Fig. 1) (Concheyro
and Villa, 1996; Casadío *et al.*, 2005; del Río *et al.*, 2007;
2011; Brezina *et al.*, 2014). Also, other sclerobionts (e.g.,
boring and encrusting organisms) associated with these
oysters were observed and identified.

The analysis focused on encrusting and boring barna-
cles. Sclerobiont occurrence frequencies (*i.e.*, encrusting or

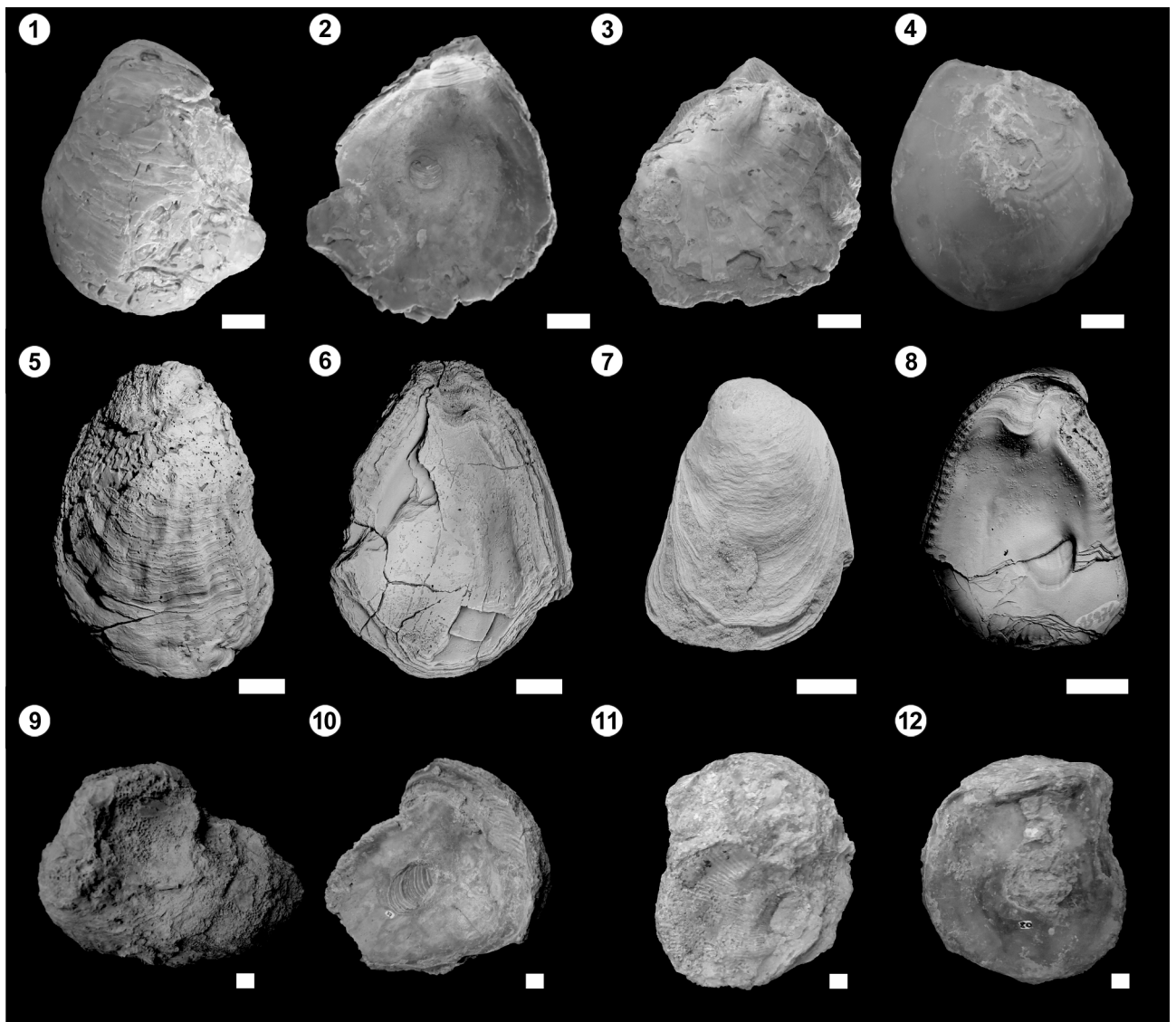


Figure 2. Late Maastrichtian oysters. 1–4, *Pycnodonte (Phygraea) vesicularis*, Jagüel Formation, Bajada del Jagüel, Neuquén; 1–2, Left valve, MPEF-PI 6130.4; 1, exterior; 2, interior. 3–4, Right valve, MPEF-PI 6130.5; 3, exterior; 4, interior. 5–8, *Turkostrea damborenae*, Roca Forma-
tion, Cerro Butaló, Mendoza; 5–6, Left valve, GHUNLPam 10625; 5, exterior; 6, interior; 7–8, Right valve, GHUNLPam 15976; 7, exterior;
8, interior. 9–12, *Amphidonte mendozana*, Roca Formation, Huantraico, Neuquén; 9–10, Left valve, MPEF-PI 6130.6; 9, exterior; 10, interior;
11–12, Right valve, MPEF-PI 6130.7; 11, exterior; 12, interior.

boring barnacles) were calculated as the number of host shells encrusted or bored on the total number of shells observed for each time interval. Goodness-of-fit tests and exact confidence intervals for binomial distribution were performed in order to assess the distribution of barnacles on oyster species from different time intervals. Then, in null hypothesis terms, the distribution of barnacles on oyster valves is random at a significance level $\alpha=0.05$ (Zar, 1999).

This methodology was followed in accordance with the analyses performed in several previous works (Mauna *et al.*, 2005; Parras and Casadío, 2006; Romero *et al.*, 2013; Brezina *et al.*, 2014).

The taphonomic analysis was focused on the 1,174 valves of the nine identified species of oysters with the aim of evaluating their accumulation history. Fragmentation and abrasion were described as taphonomic attributes by

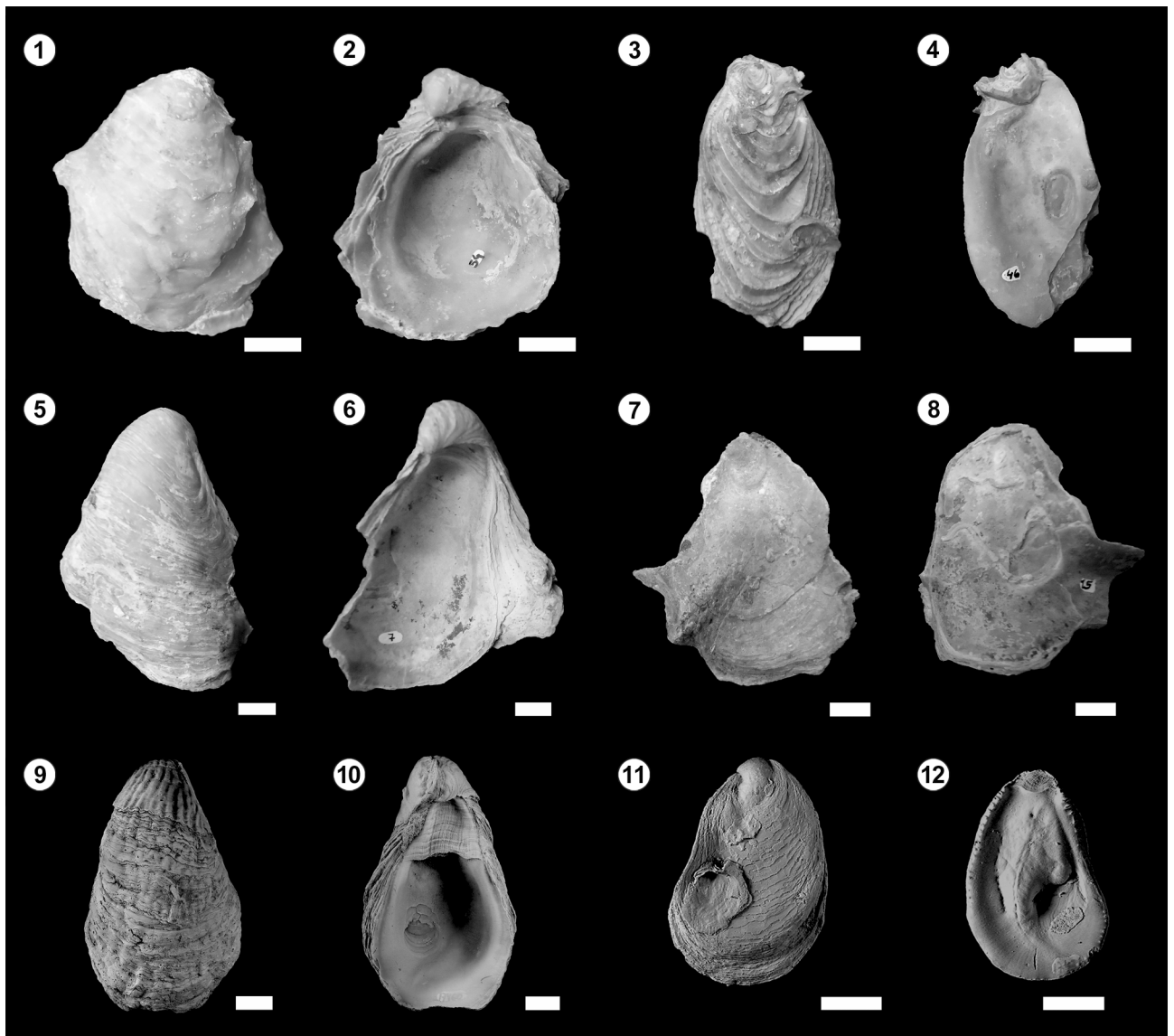


Figure 3. Early Danian oysters. 1–4, *Gryphaeostrea callophyla*. Roca Formation, General Roca, Río Negro; 1–2, Left valve, MPEF-PI 6130.8; 1, exterior; 2, interior; 3–4, Right valve, MPEF-PI 6130.9; 3, exterior; 4, interior. 5–8, *Pycnodonte (Phygraea) burckhardti*. Roca Formation, General Roca, Río Negro; 5–6, Left valve, MPEF-PI 6130.10; 5, exterior; 6, interior; 7–8, Right valve, MPEF-PI 6130.11; 7, exterior; 8, interior. 9–12, *Turkostrea argentina*. Roca Formation, Liu Malal, Mendoza. 9–10, Left valve, GHUNLPam 17460; 9, exterior; 10, interior; 11–12, Right valve, GHUNLPam 17431; 11, exterior; 12, interior.

drawing on semi-quantitative taphonomic grades (Flessa *et al.*, 1993) and were then presented in the form of ternary taphograms. Three taphonomic grades were employed: good (grade 0= best preservation), fair (grade 1= intermediate) and poor (grade 2= poorest) (Kowalewski *et al.*, 1994, 1995). Shell preservation was labeled as good when <5% of the surface of a sample was affected by each attribute; as intermediate, when such processes only marked between 5% and 50% of the sample; and, as poor, when >50% of the

surface proves affected. Taphonomic attribute analyses were adapted from Parsons and Brett (1991) and Kowalewski *et al.* (1994; 1995) to achieve a preliminary approach of transport and hydrodynamic regimes that could affect bioclasts according to Kowalewski *et al.* (1995).

Abbreviations. GHUNLPam, Cátedra de Geología Histórica de la Universidad Nacional de La Pampa, Santa Rosa, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

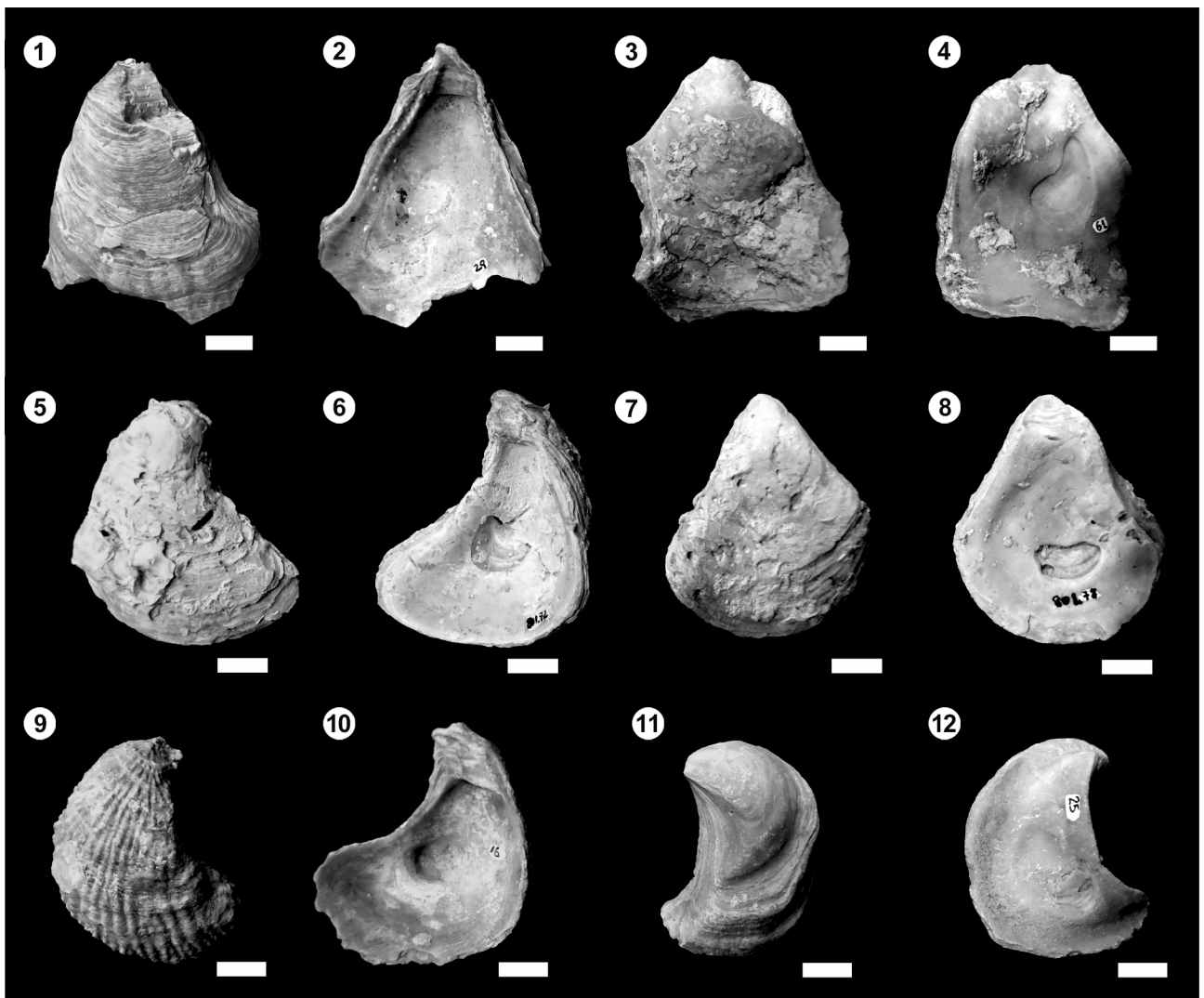


Figure 4. Late Danian oysters. 1–4, *Ostrea wilckensi*. Roca Formation, General Roca, Río Negro; 1–2, Left valve, MPEF-PI 6130.12; 1, exterior; 2, interior; 3–4, Right valve, MPCN 802.61; 3, exterior; 4, interior. 5–8, *Pycnodonte (Phygraea) sarmientoi*. Roca Formation, Casa de Piedra, La Pampa; 5–6, Left valve, MPEF-PI 6130.13; 5, exterior; 6, interior; 7–8, Right valve, MPEF-PI 6130.14; 7, exterior; 8, interior. 9–12, *Cubitostrea ameghinoi*. Roca Formation, Bajada del Jagüel, Neuquén; 9–10, Left valve, MPEF-PI 6130.15; 9, exterior; 10, interior; 11–12, Right valve, MPEF-PI 6130.16; 11, exterior; 12, interior.

TABLE 1 – Stratigraphic and taphonomic data of oyster accumulations.

	Fossil locality	Unit	Age	Taphonomic data of oyster accumulations	Facies data
Amphidonte mendozana (Ihering, 1907)	Huantraico (Neuquén)	Roca Fm.	late Maastrichtian	Valves grouped in nests or in parautochthonous accumulations. Dense packing, good size-selection, convex-up valves, low disarticulation and moderate fragmentation.	Valves are included in mudstones. Facies association indicates inner to middle-shelf environments.
Pycnodonte (Phygraea) vesicularis (Lamarck, 1806)	Bajada del Jagüel (Neuquén)	Jagüel Fm.	late Maastrichtian	Valves grouped in parautochthonous accumulations or in life position. Dispersed packing, poor size-selection, convex-up valves and moderate disarticulation and fragmentation.	Valves are included in mudstones. Facies association indicates inner to middle-shelf environments.
Turkostrea damboreneae Griffin, Casadio and Parras, 2005	Cerro Butaló (Mendoza) Ranquil C6 (Mendoza)	Roca Fm.	late Maastrichtian	Valves grouped in parautochthonous accumulations. Dispersed packing, good size-selection, chaotic orientation, high disarticulation and poor fragmentation.	Valves are included in mudstones. Facies association indicates inner to middle-shelf environments (Jagüel Formation) or shallow subtidal environments (Roca Formation).
Pycnodonte (Phygraea) burckhardtii (Böhm, 1903)	Cerros Bayos (La Pampa); General Roca (Río Negro)	Roca Fm. Jagüel Fm.	early Danian	Valves grouped in parautochthonous accumulations or in life position. Dispersed packing, poor size-selection, convex-up valve, low disarticulation and moderate fragmentation.	Valves are included in mudstones. Facies association indicates inner to middle-shelf environments.
Gryphaeostrea callophylla (Ihering, 1903)	Cerros Bayos (La Pampa); General Roca (Río Negro)	Roca Fm. Jagüel Fm.	early Danian	Valves grouped in parautochthonous accumulations. Dispersed packing, poor size-selection, convex-up valves, low disarticulation and moderate fragmentation.	Valves are included in mudstones. Facies association indicates inner to middle-shelf environments.
Turkostrea argentina Griffin, Casadio and Parras, 2005	Liu Malal (Mendoza)	Roca Fm.	early Danian	Valves grouped in parautochthonous accumulations. Dispersed packing, good size-selection, chaotic orientation, high disarticulation and poor fragmentation.	Valves are included in mudstones. Facies association indicates shallow subtidal environments.
Cubitostrea ameghinoi (Ihering, 1902)	Cerros Bayos (La Pampa); General Roca (Río Negro); Bajada del Jagüel (Neuquén)	Roca Fm.	late Danian	Valves grouped in parautochthonous accumulations. Dense packing, good size-selection, chaotic orientation, high disarticulation and moderate fragmentation.	Valves included in massive wackestones. Facies association indicates shallow subtidal environments.
Ostrea wilkensis Ihering 1907	Gral. Roca (Río Negro)	Roca Fm.	late Danian	Valves, grouped in nests or in parautochthonous accumulations. Dense packing, poor size-selection, associated in nests, low disarticulation and fragmentation.	Valves included in massive grainstones. Facies association indicates shallow subtidal environments.
Pycnodonte (Phygraea) sarmientoi Casadio, 1998	Casa de Piedra (La Pampa)	Roca Fm.	late Danian	Valves grouped in parautochthonous or allochthonous accumulations. Dense packing, poor size-selection, chaotic orientation, high disarticulation and fragmentation.	Valves included in massive packstones. Facies association indicates shallow subtidal environments.

RESULTS

Among the sclerobionts, the identified encrusters were bivalves (including oyster recruits and *Spondylus* sp.), polychaetes (serpulid tubeworms) and bryozoans (35 species of cyclostomes and cheilostomes). Bioerosional structures produced by boring activity upon the shells, such as sponges (*Entobia* isp.), polychaetes (*Maeandropolydora* isp. and *Caulostrepsis* isp.), bivalves (*Gastrochaenolites* isp.), ctenostome bryozoans (*Pennatichnus* isp.), phoronids (*Talpina* isp.), and algae and fungi; were also recorded on valves. The frequencies observed as regards their occurrence can be consulted in Supplementary Online Information.

The barnacles which were recognized on the oyster shells belong to Acrothoracica (i.e., boring barnacles) and Thoracica (i.e., encrusting barnacles). The encrusting barnacles were assigned to *Verruca rocana*. This species presents depressed and asymmetrical shells (Fig. 5.1–2) comprising four plates (carina, rostrum, fixed tergum and fixed scutum). Rostrum and carina are longitudinally ribbed, especially near the

base. The diameter of shells ranges between 1.5 and 3 mm.

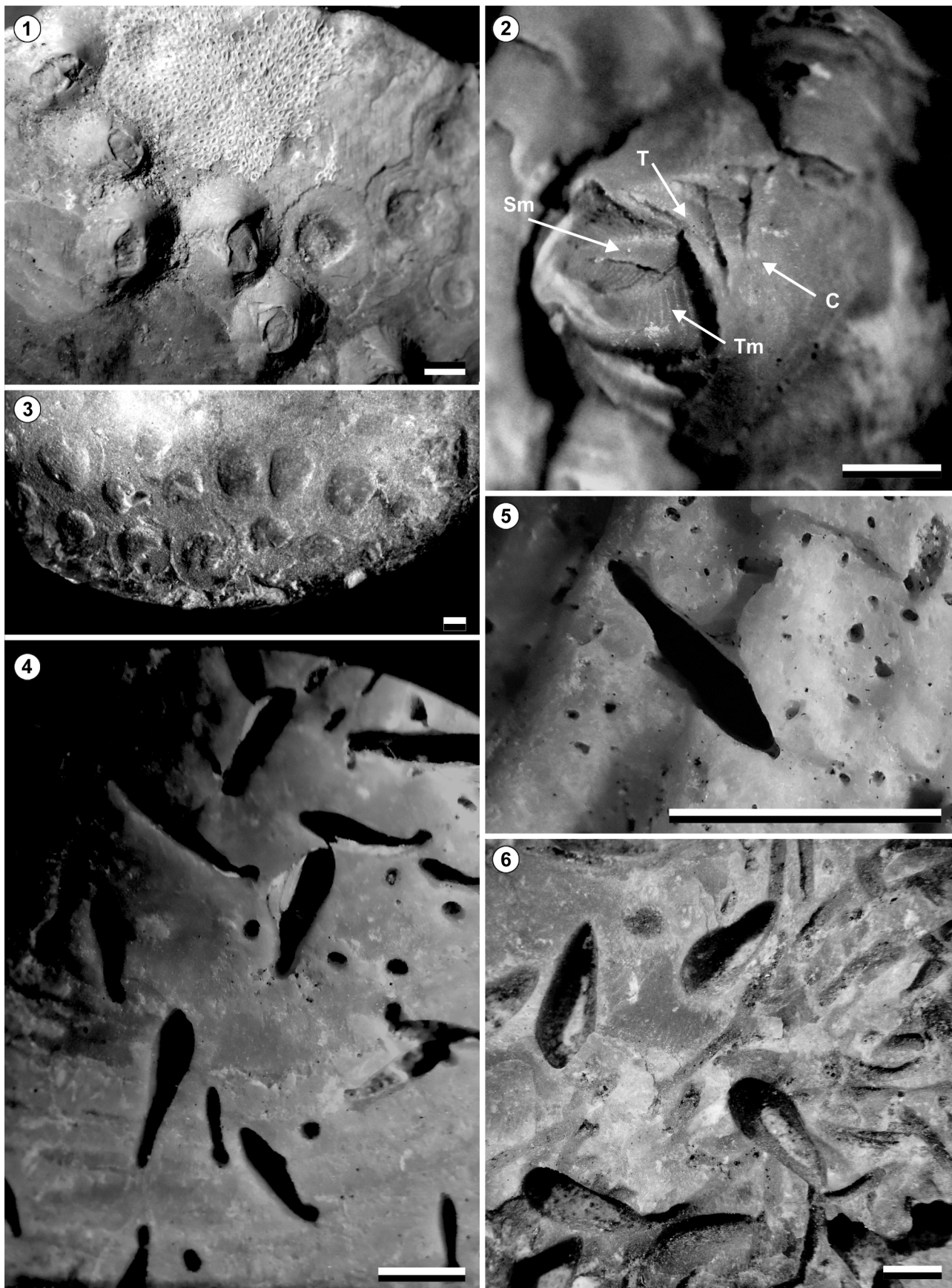
Also, the presence of verrucids was inferred by the identification of traces assigned to the ichnospecies *Centrichnus concentricus*. In the analyzed samples, *C. concentricus* is approximately circular and presents a central depression which is surrounded by a flat platform with edges marking a groove on the surface (Fig. 5.1, 5.3). The platform margin is crenulated and corresponds to the ornamentation of the verrucid plates.

The boring barnacles are represented by traces assigned to the ichnogenus *Rogerella*. *Rogerella* presents holes with an elliptical contour and an elongated distal portion as well as, sometimes, a slight curvature (Fig. 5.4–5) and a circular or conical proximal portion (Fig. 6.6). Length of the traces ranges between 1.2 and 2.5 mm. Erosion of the substrate can make them seem shallower than they actually are. The holes are arranged randomly and in a roughly equidistant, perpendicular or oblique to the substrate pattern. The traces can be found alone or in groups (Fig. 5.4).

TABLE 2 – Observed frequencies of barnacles on oyster valves according to the species, biozones (Papú et al., 1999) and ages.

	Biozones	Age	Number of valves (n)	Encrusting barnacles	Boring barnacles
P. (Ph.) vesicularis	CC25	late Maastrichtian	89	0	2
T. damboreneae	CC26	late Maastrichtian	137	0	29
A. mendozana	CC25–CC26	late Maastrichtian	82	0	0
G. callophylla	NP1	early Danian	178	0	0
P. (Ph.) burckhardtii	NP1	early Danian	179	1	0
T. argentina	NP1–NP2	early Danian	82	0	1
O. wilckensi	NP1–NP4	late Danian	84	45	1
P. (Ph.) sarmientoii	NP4	late Danian	94	31	21
C. ameghinoi	NP4	late Danian	249	19	34
Total			1.174	96	88

Figure 5. 1, *Verruca rocana*; several specimens with their traces (*Centrichnus*) on shells of *P. (Ph.) sarmientoii*, Danian, Roca Formation, Casa de Piedra, La Pampa, MPEF-PI 6130.1; 2, detail of a specimen showing the plates and operculum, attached to *C. ameghinoi*, Danian, Roca Formation, General Roca, Río Negro, MPEF-PI 6130.2. T, tergum; C, Carina; Tm, tergum movile; Sm, scutum movile. 3, *Centrichnus* isp. on the internal surface of *C. ameghinoi*, Danian, Roca Formation, General Roca, Río Negro, MPEF-PI 6130.3. 4, *Rogerella*, an overview of borings with elliptical contour and distal portion elongated; 5, detail of one boring with its slightly curved distal end on *C. ameghinoi*, Danian, Roca Formation, Cerros Bayos, La Pampa, GHUNLPam 25375; 6, drop-shaped borings with conical proximal portion on *T. damboreneae*, Maastrichtian, Roca Formation, Cerro Butaló, Mendoza, GHUNLPam 10492. Scale bars= 1 mm.



The observed frequencies of encrusting and boring barnacles on oyster species are shown in Table 2.

In general, late Maastrichtian shells are typically marked by a fair-poor condition as regards both taphonomic attributes (Fig. 6), with *Turkostrea damborenae* (Cerro Butaló) consisting of the poorest shells represented in the fragmentation taphogram. Furthermore, early Danian oysters also exhibited fair-poor preservation for both taphonomic attributes, except for a sample of *Gryphaeostrea callophyla* from the Cerros Bayos locality with a high proportion of shells in poor condition as a result of abrasion. Finally, late Danian oysters greatly vary. A good-fair condition for both attributes was recorded for *Cubitostrea ameghinoi* from Cerros Bayos, General Roca and Bajada de Jagüel while the taphonomic condition of the other samples representing *Ostrea wikensi* and *Pycnodonte (Phygraea) sarmiento* significantly varied.

Barnacles through the K–Pg boundary

Verruca rocana (i.e., encrusting barnacles) and their *C. concentricus* trace from the studied localities are characterized by the absence of records during the late Maastrichtian, a low frequency during the early Danian and a high frequency

during the late Danian (Fig. 7.1). On the other hand, the records of *Rogerella* (i.e., boring barnacles) exhibited significant differences in their frequency, reflecting an important decrease during the early Danian even though, during the late Danian, its abundance increased considerably (Fig. 7.1). Goodness-of-fit yielded significant differences in terms of both encrusting and boring barnacles on valves of different ages (i.e., late Maastrichtian, early Danian and late Danian) ($p < 0.0001$). Yet, the exact confidence intervals analysis evidenced that significant differences mark boring barnacles as regards the early and late Danian (Fig. 7.2) given that the expected frequency (EF) is lower than the observed frequency (OF) during the early Danian while the OF is higher than the EF during the late Danian.

Goodness-of-fit also confirmed significant differences in the distribution of both encrusting and boring barnacles on valves of different oyster species ($p < 0.001$). The exact confidence intervals analysis yielded that there are significant differences as regards boring barnacles on *P. (Ph.) vesicularis*, *T. damborenae*, *O. wilckensi* and *P. (Ph.) sarmiento*. For encrusting barnacles, significant differences are observed on *O. wilckensi* and *C. ameghinoi* (Figs. 7.4–6).

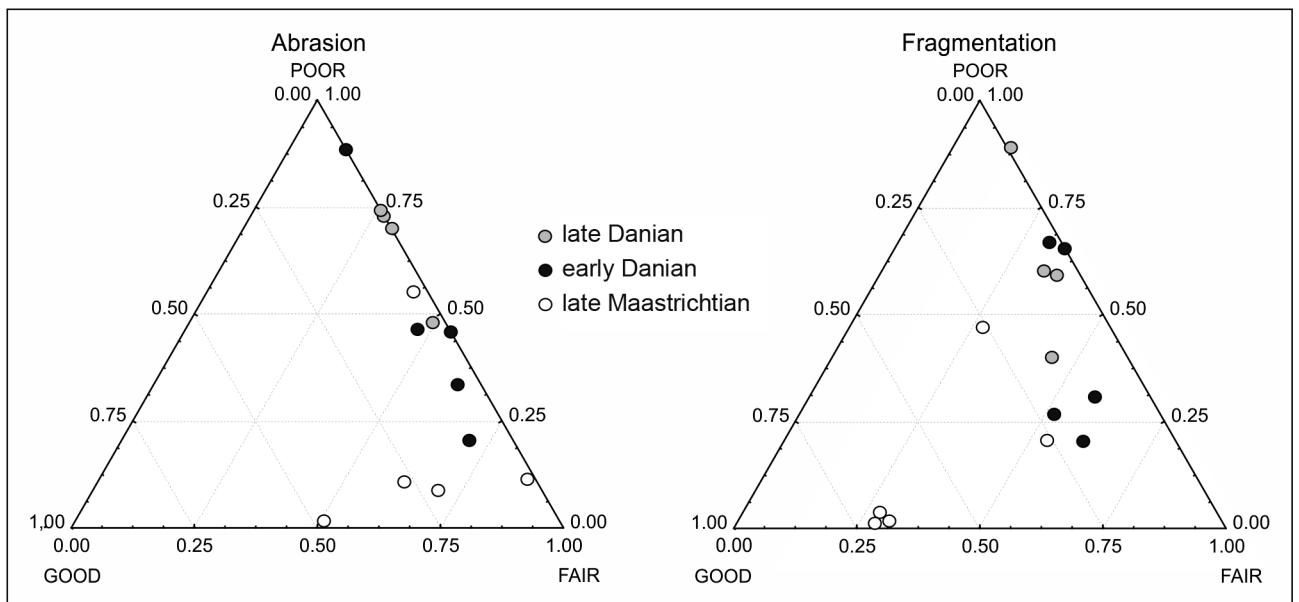


Figure 6. Ternary taphograms for nine oyster species presenting variations regarding abrasion and fragmentation. Some species are represented in more than one locality.

DISCUSSION

Buckeridge *et al.* (2008) considered that it is more common to find verrucids preserved as disarticulated wall plates than to get hold of articulated ones. In the analyzed samples, most encrusting barnacles are preserved in their articulated form. However, we recognized oysters with the trace *C. concentricus* in which an eroded platform was observed. Darwin (1854) stated this trace is produced by re-

cent specimens of *Verruca stroemia* (Müller, 1776) and found them to be comparable with fossil material. Additionally, Santos *et al.* (2005) described similar traces and assigned them to *Anellusichnus*, even though this ichnogenus is produced by balanomorphs and can present more crenulated edges in later stages. This feature was not observed in the studied specimens.

The recorded trace openings are marked by the form of

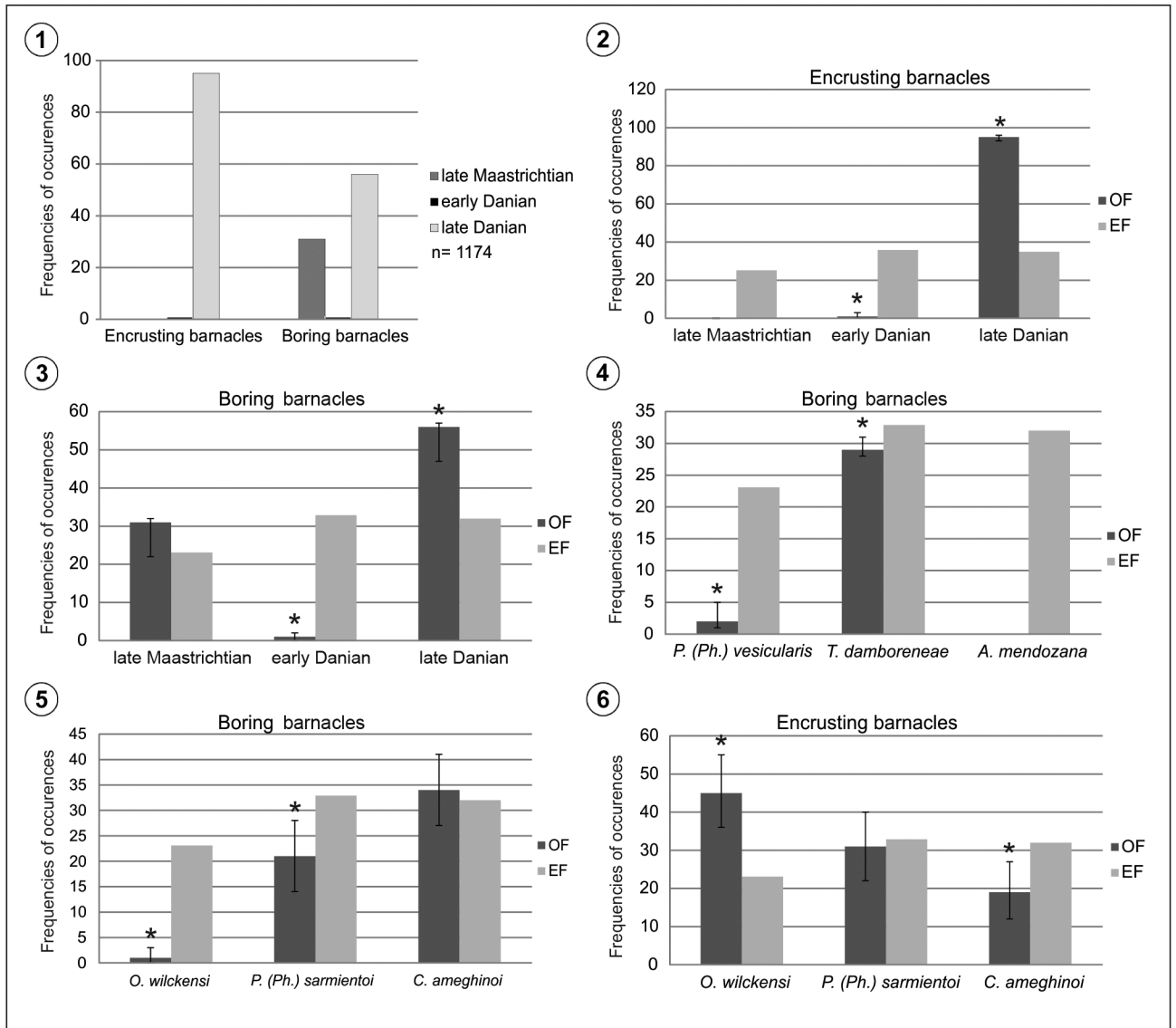


Figure 7. 1, Frequencies of occurrence of oyster shells from different ages encrusted or bored by barnacles. **2**, Differential distribution of barnacles through time. Note that there is a significant difference between expected frequency (EF) and observed frequency (OF) of barnacles during the late Danian. **3–6**, Differential distribution of barnacles on oyster species. Note that significant differences between expected frequencies (EF) and observed frequencies (OF) of barnacles are indicated with (*). Error bars represent confidence intervals.

a slot and the hole is narrower towards the bottom. Recent acrothoracican barnacles which belong to Lithoglyptidae, leave this trace. They penetrate the substrate during the larval stage (*Cypris* larvae), probably by chemical dissolution, and use chitinous bristles present on the outer side of their mantle to enlarge the chamber when adults (Abletz, 1993; Kolbasov and Newman, 2005). The boring protects the animal body as they lack shell plates (Abletz, 1993). According to Lambers and Boekschoten (1986), the recent species *Trypetesa nasseroides*, lives in gastropod shells inhabited by hermit crabs and bore by a combination of chemical and mechanical processes. These authors considered that the mode of life and the drilling processes of these organisms can be compared with fossil barnacles whose traces are assigned to *Rogerella*.

Late Maastrichtian and early Danian oyster shells exhibited a fair-poor condition for both abrasion and fragmentation while late Danian shells were mostly marked by a good-fair condition for the same attributes. These oyster species probably present differences in abrasion and fragmentation as a consequence of different preservational environments such as hydrodynamic regime, bioerosion, degree of subaerial exposure, differences in the size and architecture of the shells, or a certain combination of these parameters (Kowalewski *et al.*, 1995).

Shells of *T. damborenae* (Cerro Butaló) are included in accumulations associated with bars and tidal channels marked by poor preservation probably caused by short distances of transport and reworking. Nevertheless, fragmentation can also result from a combination of both physical and biological processes (Zuschin *et al.*, 2003). Such fact is coincident with the high bioerosion, represented mostly by sponges, boring barnacles, and phoronids, which is observed in this oyster.

G. callophyla (Cerros Bayos) shells are included in parautochthonous accumulations associated with offshore beds and probably experienced little transport. In this case, various factors, including microboring activity and dissolution, could have resulted in the loss of surface shell material (Schneider-Storz *et al.*, 2008). Also, shells revealed low frequencies of sclerobionts, with poorly preserved bryozoans on external shell surfaces and low bioerosion mostly represented by polychaetes on internal surfaces.

Additionally, in both ternary taphograms and following

the description of Kowalewski *et al.* (1995), the late Danian oysters *O. wilckensi* and *P. (Ph.) sarmientoi* presented mixed taphonomic grades. For both oyster species, a high degree of bioerosion and encrustation could indicate that there was no rapid burial or subaerial exposure (Kowalewski *et al.*, 1995). Moreover, *O. wilckensi* is preserved mostly in life position (*i.e.*, developing clusters or nests) and is characterized by a high frequency of articulation. Sclerobionts are preferentially distributed along external shell surfaces, thus indicating *in vivo* colonization. Mixed taphonomic grades also correlate well with the inferred depositional environments, where all oysters of Danian age were included in accumulations associated with bars and tidal channels characterized by a fluctuating hydrodynamic regime.

In this study, a preliminary examination of the taphonomic condition of Maastrichtian and Danian oysters was performed. Considering that the increase in frequency of occurrence of boring barnacles during the late Danian would be more closely related with taphonomic constraints than with evolutionary or paleoecology patterns, a larger sample would be necessary in order to arrive at more accurate interpretations of the studied environments in terms of the three times intervals. Additionally, according to Parsons and Brett (1991), given their higher sensitivity regarding taphonomic processes, skeletal fragments should be included in future taphonomic studies for they can provide useful information which may also prove different from that obtained by studying whole or broken shells.

Barnacles through the K–Pg boundary

The database regarding changes over time in sclerobiotic communities is limited and even more restricted on the subject of boring and encrusting barnacles. However, Brett *et al.* (2012) suggested that the records of Cretaceous to modern sclerobiotic communities apparently have not drastically changed as regards diversity and abundance since the re-emergence of encrustation in the Jurassic. These communities were dominated by the same sclerobionts which could be recognized during the Jurassic (*e.g.*, encrusting foraminifers, serpulid worms, cheilostome bryozoans, coralline algal encrusters, cementing bivalves as oysters, clionid borings and ctenostome etchings) (Brett *et al.*, 2012). Barnacles are an ancient group which at present remains very successful both in number of species and abundance

(Newman and Abbott, 1980). However, at least when considering northern patagonian records, some of them seemingly reflected a decrease in the frequency of occurrence in the fossil record across the K–Pg boundary.

In this sense and focusing on K–Pg events, even though the first records of *Verruca* are from the Santonian of Western Australia, it reached a wide geographic distribution by the late Campanian–Maastrichtian during which it was recorded in Europe, Western Australia (Buckeridge, 1983; Buckeridge *et al.* 2008) and South America. On the other hand, the earliest verrucid barnacles recorded after the K–Pg boundary were *V. punica* Buckeridge, Jagt, and Speijer, 2008, from the early Danian of Tunisia, and *V. rocana*, from the early Danian of Argentina. It is possible to consider that, during the early Danian, ecological factors could have affected populations of this species being underrepresented in the fossil record. Interactions between species are included among such factors (Paine 1969, 1984, 1994). Also, taphonomic conditions could disfavor the preservation of encrusting barnacles. Verrucid barnacles are commonly preserved in the form of isolated, disarticulated wall plates and only rarely as complete fossils (Buckeridge and Finger, 2001). The valves poorly preserved of Maastrichtian oysters tend to lack a good record of encrusting barnacles as the complete preservation of their plates is exceptional. Anyway, the fact that their traces are not recorded might suggest that the taxon was not abundant, that it was a rare species or that it was absent at such time. Additionally, superficial traces made by algae and fungi (Supplementary Online Information) and the lack of barnacle traces support the latter interpretation.

Biotic changes driven by live/ dead interactions defined as taphonomic feedback by Kidwell and Jablonski (1983) can be considered. Some marine invertebrates do not settle or look for refuge in clumps of dead oysters, probably because pore water underneath the oysters is anoxic (Kidwell, 1986). Moreover, early colonists could, by way of biochemical or other biotic interactions, inhibit later colonists (Kidwell and Jablonski, 1983). Barnacles respond to stimulatory and inhibitory external signals during the settling stage of their life cycle (Holmström *et al.*, 1992).

Possible negative effects on barnacles caused by the crisis during the K–Pg must also be taken into account. Buckeridge *et al.* (2008) considered that the genus *Verruca*

seemed to have persisted across the boundary without having been drastically affected and that such was also the case of other taxa (Macleod *et al.*, 1997; Jablonski 1998; Håkansson and Thomsen, 1999; Stilwell, 2003; Parma and Casadío, 2005). Yet, the possibility of being new to the region after the K–Pg boundary could also explain the low frequencies during the early Danian.

Borings made by acrothoracican cirripedes present a highly rich and extensive record (Seilacher, 1969). In this work and in view of the fact that the preliminary analysis with exact confidence intervals revealed that the OF was lower than the EF during the early Danian and that, then, the OF was higher than the EF during the late Danian, results suggest that encrusting and boring barnacles varied their frequencies at the K–Pg boundary (Figs. 7.2–3).

The preferential distribution of encrusting and boring barnacles on the species could be related to many biotic and abiotic factors such as, for example, life habits of these oysters as in clusters composed of mutually attached specimens or reclining mode of life (Stenzel 1971; Machalski, 1998), morphology and texture of the valves (Romero *et al.*, 2013 and references therein) or environmental conditions that favor the settlement of barnacle larvae on the valves (Fraschetti *et al.*, 2003; Hadfield, 2011). Encrusting barnacles presented a preferential distribution on two late Danian oysters (*i.e.*, *C. ameghinoi* and *O. wilckensi*). Although their mode of life and the morphology of the shells are not the same, the facies analysis indicates the same subtidal environment. On the other hand, boring barnacles exhibited a preferential distribution on Maastrichtian (*i.e.*, *P. (Ph.) vesicularis* and *T. damboreneae*) and late Danian species (*i.e.*, *O. wilckensi* and *P. (Ph.) sarmiento*). With the exception of *O. wilckensi*, these species are characterized by a solitary mode of life and a different morphology of shells although the facies association indicates the same shared inner to middle-shelf or subtidal environments. However, there is no clear pattern that may explain such differential distribution.

Barnacles are suspension feeders and their abundance could have been reasonably affected by the reduction of food supply. This hypothesis is supported by other studies that postulate that the collapse of primary production across the K–Pg boundary correlates with the high extinction rates in organisms dependent on primary producers (Zachos *et al.*, 1989; Veron, 2008; Jiang *et al.*, 2010; Van De

Schootbrugge and Gollner, 2013). Conversely, Sogot *et al.* (2013) questioned the extent to which this killing mechanism affected suspension feeders during the K–Pg mass extinction. If the collapse of primary producers hypothesis is considered to be valid, the scarce record of encrusting barnacles during the late Maastrichtian and early Danian could evidence that these organisms were underrepresented and that the crisis during the K–Pg interval severely affected them. This situation seems to have changed during the late Danian, as a significant increase of both encrusting and boring barnacles is recorded in the analyzed samples. This increase after the earliest Danian is observed in other sclerobionts associated with the same oysters (*e.g.*, encrusting bryozoans, polychaetes and bivalves) (Brezina, 2013) and can also be correlated with an increase in the number of species of corals, mollusks, echinoids and crabs from low latitudes, therefore reflecting higher seawater temperatures spreading southwards (Casadío *et al.*, 2005; Aguirre-Urreta *et al.*, 2008).

According to Erwin (2001), evolutionary opportunities which open up during mass extinctions bear disproportionate effects on species. He stated that mass extinctions appear to cause a collapse of the ecospace, which will be rebuilt during recovery times, but within which responses in organisms are variable, even between species and regions. Accordingly, the ecosystem dynamics during post-extinction times can be complex. Some benthic communities in other localities underwent considerable diversity reduction at the K–Pg boundary, experienced an initially retarded recovery of the early Danian community and then diversified quickly during the late Danian (Håkansson and Thomsem, 1999). These results are consistent with the case of bryozoan species from northern Patagonia, which are highly diverse during the late Danian (Brezina *et al.*, 2011).

CONCLUSIONS

During the early Danian, *Verruca rocana* could have been affected by ecological and environmental factors; yet, during the late Danian, its frequency of incrustation increased significantly.

Boring barnacles represented by the trace fossil *Rogerella* exhibited a decline in their frequencies at the K–Pg boundary while, during the late Danian, their abundance also increased considerably.

In a preliminary attempt to acquire knowledge regarding the taphonomic history of the shell accumulations, a differential preservation was observed. As a result of reworking and short distance transport in offshore beds, late Maastrichtian and early Danian assemblages exhibited a fair-poor condition as regards abrasion and fragmentation. On the other hand, late Danian assemblages were mostly characterized by good-fair condition or a mixture condition for both attributes. This reflects either rapid burial or sub-aerial exposure, or a hydrodynamic regime fluctuation in the depositional environment (*e.g.*, bars and tidal channels). Frequencies of barnacles proved higher during the late Danian and such results could be correlated. However, it would be necessary for the taphonomic analysis to focus on the barnacles in order to attain more accurate interpretations.

Although differences in distribution of encrusting and boring barnacles among the species of oysters were also recorded, there is no clear pattern that could explain these results.

An ecological explanation can also be considered. As observed in recent communities, biotic and abiotic conditions regulate the dynamics of populations. The hypothesis considering a collapse of primary production could provide an explanation as to why suspension feeders were affected during the K–Pg mass extinction. In this sense, the reduction of barnacles recorded in this study could reflect the decrease of food supply in the seas.

Although many factors could have affected the boring and encrusting pattern of sclerobiotic organisms, a change in barnacle abundance through the K–Pg boundary was documented. In northern Patagonia, encrusting and boring barnacles associated with oysters presented, during the late Danian, an increase in their frequencies coincident with the increase in abundance and diversity of other benthic communities of the southern hemisphere.

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