ENCRUSTING AND BORING BARNACLES THROUGH THE CRETACEOUS/PALEOGENE BOUNDARY IN NORTHERN PATAGONIA (ARGENTINA)

CIRRIPEDIOS INCRUSTANTES Y PERFORANTES A TRAVÉS DEL LÍMITE CRETÁCICO-PALEÓGENO EN PATAGONIA NORTE (ARGENTINA)

SOLEDAD SILVANA BREZINA, MARÍA VIRGINIA ROMERO AND SILVIO CASADÍO

Instituto de Investigación en Paleobiología y Geología, CONICET-Universidad Nacional de Río Negro, Av. Roca 1242, General Roca, 8332, Argentina

sbrezina@unrn.edu.ar, *mvromero@unrn.edu.ar*, *scasadio@unrn.edu.ar*

30 Pages, 7 Figures, 2 tables

Corresponding author: *sbrezina@unrn.edu.ar*

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 occurred during the Cretaceous/Paleogene (K-Pg) boundary are almost unknown. We describe encrusting and boring barnacles associated with Maastrichtian and Danian oysters, evaluate taphonomic processes involved, 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. Encrusting barnacles identified on the oyster shells were assigned to *Verruca rocana* Steinmann and their traces assigned to the ichnospecies *Centrichnus concentricus* Bromley and Martinell. Boring barnacles are represented by traces assigned to the ichnogenus *Rogerella* De Saint-Seine. A preliminary taphonomic analysis indicated that late Maastrichtian and early Danian shells showed fair-poor condition by abrasion and fragmentation as taphonomic attributes, while late Danian shells exhibited mostly good-fair or mixed condition for both attributes. *Verruca rocana* shows no records during late Maastrichtian but high frequencies of encrusted valves after the K-Pg boundary. Boring barnacles represented by the trace *Rogerella* exhibited a decline in abundance during early Danian but an increase at late Danian. Both encrusting and boring barnacles associated with oysters presented an increase in theirfrequencies during late Danian.
Keywords: 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 sustratos 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 frecuencias 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* Steinmann y sus trazas asignadas a la icnoespecie *Centrichnus concentricus* Bromley y Martinell. Los cirripedios perforantes, están representados por trazas asignadas al icnogénero *Rogerella* De Saint-Seine. 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, para 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 that consists exclusively of sessile organisms (Glenner and Hasgaard, 2006). They are found today in all marine environments, distributed from the tropics to the poles and from intertidal zones to abyssal depths (Farrapeira, 2010). The radiation of cirripeds is reflected by the variety of biogenic and abiogenic substrates on which they are able to attach or bore (Pitombo, 2010). Also, the existence of planktonic larval dispersal in some species combined with a permanent calcareous shell in adults provides an adaptive strategy to occupy and persist 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) (Glenner and Hasgaard, 2006; Pitombo, 2010). Thoracica and Acrothoracica use their feathery thoracopods (cirri) to suspension feed, whereas rhizocephalans are parasites of other crustaceans, especially decapods (Brusca and Brusca, 2005). Although encrusting barnacles have a fossil record dating back to the Cambrian (Foster and Buckeridge, 1987), verrucomorphs (*i.e.*, barnacles with assymmetric plates) have the earliest known representative genera from the Cenomanian–Late Maastrichtian (*i.e.*, *Proverruca* Withers, 1914) and from the Upper Santonian–Upper Campanian *(i.e.*, *Eoverruca* Withers, 1935) (Buckeridge *et al*., 2008). During the Late Cretaceous, *Verruca* was restricted to Europe or Australasia, but 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* have a~~n e~~stratigraphic range from Maastrichtian to recent (Buckeridge *et al.*, 2008).

Boring barnacles are known from the Upper Devonian (Rodriguez and Gutschick, 1977) mainly in the form of borings or cast of borings (Newman, 1987). They 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 preserve mostly 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 to study changes in abundance, and 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 Southern Hemisphere is scarce. In addition, changes in these communities during episodes of extinction like those occurred during 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 to report changes in their abundances over the critical K-Pg transition. Also, other sclerobionts on valves were identified to know the assemblage composition and asses if there is a pattern of distribution of them in the considerated time intervals.

GEOLOGICAL AND PALEONTOLOGICAL SETTINGS

The Neuquén Basin (Fig. 1) covers approximately 120,000 km^2 of central-western Argentina (Howell *et al.*, 2005), including part of the provinces of Mendoza, Neuquén, Río Negro and La Pampa. The sedimentary infilling reaches a thickness of over 6,000 m and includes marine and continental deposits spanning the Late Triassic–Paleocene (Casadío and Montagna, 2015).

During the Late Cretaceous, marine sedimentation occurred as a result of flooding from the Atlantic, which began during the Maastrichtian. The Atlantic Ocean then covered an estimated surface of 507,000 km^2 of presently emerged Patagonia (Malumián and Caramés, 1995).

In the northwest of the basin, the Malargüe Group records its greatest thicknesses outcropping at 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 by the Loncoche/Allen, Jagüel, Roca and Pircala/El Carrizo formations.

During the past two decades, significant progress in the stratigraphic, sedimentological and paleontological knowledge of the Malargüe Group was made. Most of these advances are related to the interest generated by the 1980s in studying the events around the K-Pg boundary. In this way, the Malargüe Group contains the K-Pg boundary in both marine and continental facies and is considerated as a key to understand the changes occurring in ecosystems of the Southern Hemisphere mid-latitudes during the Maastrichtian-Danian interval (Parras and Casadío, 1999).

The sedimentary sequence studied in this work, consists of 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).

142 Among the bivalves recorded in Jagüel and Roca formations, oysters are the most
143 conspicuous constituent of their fossil assemblages. The calcitic composition of valves
144 enhanced the chance of preservation of this oyster in these deposits, and also allowed
145 the identification of the sclerobiotic communities associated with them.
146 Oyster accumulations of the K-Pg transition from the Neuquén basin were studied by
147 Casadío (1998). Taphonomic and facies data collected for this work are included in
148 table 1.
149 **[Figure 1]**
150 **MATERIAL AND METHODS**
151 Nine oyster species ranging in age from late Maastrichtian to late Danian were studied
152 (Figs. 2-4; Tab. 1) to analyze the abundance and distribution of barnacles on them under
153 a binocular microscope. A total of 1,174 valves were collected randomly from the
154 Jagüel and Roca formations at several localities in the Neuquén Basin (Fig. 1) from
155 non-lithified deposits, in some of which the K-Pg boundary can be recognized (*e.g.*,
156 Bajada del Jagüel, Cerros Bayos and Liu Malal) (Concheyro and Villa, 1996; Casadío *et*
157 *al*., 2005; del Río *et al*., 2007; 2011; Brezina *et al*., 2014). Also other sclerobionts (*e.g.*,
158 boring and encrusting organisms) associated with these oysters were observed and
159 identified.
160 The analysis was focused on encrusting and boring barnaclesThe frequencies of
161 occurrences of sclerobionts (*i.e.* encrusting or boring barnacles) were calculated as the
162 number of host shells encrusted or bored of the total number of shells observed for each
163 time interval. Goodness of fit tests and exact confidence intervals for the binomial
164 distribution were performed in order to assess the distribution of barnacles on oysters
165 species from different time intervals. Then, the n-ull hypothesis was that the distribution
166 of barnacles on oyster valves is random at a significance level $\alpha = 0.05$ (Zar, 1999). This

167 methodology was followed according to the analysis performed in several previous
168 works (Mauna *et al.*, 2005; Parras and Casadío, 2006; Romero *et al.*, 2013; Brezina *et*
169 *al.*, 2014).
170 Taphonomic analysis was focused on the 1,174 valves of the nine species of oysters
171 identified to assess the accumulation history of them . Fragmentation and abrasion were
172 described as taphonomic attributes using semi-quantitative taphonomic grades (Flessa *et*
173 *al*., 1993) and presented using ternary taphograms. Three taphonomic grades were used:
174 good (grade 0 = best preservation), fair (grade 1 = intermediate) and poor (grade 2 =
175 poorest) (Kowalewski *et al*., 1994, 1995). Shell preservation was characterized as good
176 when <5% of a sample's surface was affected by each attribute, intermediate between 5
177 and 50%, and poor when >50% of the surface was affected. Taphonomic attribute
178 analyses were adapted from Parsons and Brett (1991) and Kowalewski *et al*. (1994;
179 1995) to have a preliminary approach of transport and hydrodynamic regimes that could
180 affect bioclasts according to Kowalewski *et al*. (1995).
181 ***Abbreviations***. **MNCN**, Museo Provincial de Ciencias Naturales, General Roca, Río
182 Negro; **GHUNLPam**, Cátedra de Geología Histórica de la Universidad Nacional de La
183 Pampa, Santa Rosa, Argentina; **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew,
184 Argentina.
185 **[Figure 2-4]**
186 **[Table 1]**
187 **RESULTS**
188 Among the sclerobionts, the identified encrusters were bivalves (including oyster
189 recruits and *Spondylus* sp.), polychaetes (serpulid tubeworms), and bryozoans (35
190 species of cyclostomes and cheilostomes). Bioerosional structures produced by boring
191 activity upon the shells were also recorded on valves as sponges (*Entobia* isp.),

192 polychaetes (*Maeandropolydora* isp. and *Caulostrepsis* isp.), bivalves
193 (*Gastrochaenolites* isp.), ctenostome bryozoans (*Pennatichnus* isp.), phoronids (*Talpina*
194 isp.), and algae and fungi. Their observed frequencies can be consulted in in
195 Supplementary Online Information.
196 The recognized barnacles on the oyster shells belong to Acrothoracica (*i.e.*, boring
197 barnacles) and Thoracica (*i.e.*, encrusting barnacles). The encrusting barnacles were
198 assigned to *Verruca rocana* Steinmann, 1921. This species has depressed and
199 asymmetrical shells (Fig. 5.1-2) comprising four plates (carina, rostrum, fixed tergum
200 and fixed scutum). Rostrum and carina are longitudinally ribbed, especially near the
201 base. The diameter of shells is between 1.5 and 3 mm.
202 Also, the presence of verrucids was inferred by the identification of traces assigned to
203 the ichnospecies *Centrichnus concentricus* Bromley and Martinell, 1991. In the
204 analyzed samples, *C. concentricus* is approximately circular, with a central depression
205 which is surrounded by a flat platform whose edges mark a groove in the surface (Fig.
206 5.1, 3). The platform margin is crenulated and corresponds to the ornament of the
207 verrucid plates.
208 The boring barnacles are represented by traces assigned to the ichnogenus *Rogerella* De
209 Saint-Seine, 1951. *Rogerella* showed holes with an elliptical contour and elongated
210 distal portion, sometimes with a slight curvature (Fig. 5.4-5), and a circular or conical
211 proximal portion (Fig. 6.6). Length of the traces ranges from 1.2 to 2.5 mm. Erosion of
212 the substrate can make them seem shallower than they actually are. The holes are
213 arranged randomly and roughly equidistant, perpendicular or oblique to the substrate.
214 The traces can be found alone or in groups (Fig. 5.4).
215 The observed frequencies of encrusting and boring barnacles on oyster species are
216 shown in Table 2.

[Figure 5]

[Table 2]

In general, late Maastrichtian shells are typically in fair-poor condition for both taphonomic attributes (Fig. 6), with *T. damboreneae* (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 *G. callophyla* from the Cerros Bayos locality with a high proportion of shells in poor condition as a result of abrasion. Finally, late Danian oysters vary greatly. A good-fair condition for both attributes was recorded for *C. ameghinoi* from Cerros Bayos, General Roca and Bajada de Jagüel, while the taphonomic condition of the other samples representing *O. wikensi* and *P. (Ph.) sarmentoi* varied greatly.

[Figure 6]

Barnacles through K-Pg boundary

V. rocana (*i.e.* encrusting barnacles) and their trace *C. concentricus* in the studied localities showed absence of records during the late Maastrichtian, low frequency during the early Danian, and high frequency during the late Danian (Fig. 7.1). On the other hand, the records of *Rogerella* (*i.e.* boring barnacles) showed significant differences in its frequency, reflecting an important decrease during early Danian, although, during the late Danian its abundance increased considerably (Fig. 7.1). Goodness of fit showed significant differences for both encrusting and boring barnacles on valves of different ages (*i.e.* late Maastrichtian, early Danian and late Danian) ($p<0.0001$). But the analysis with exact confidence intervals showed that the significant differences are for boring barnacles during early and late Danian (Fig. 7.2), considering that the expected frequency (EF) is lower than the observed frequency (OF) during early Danian and the OF is higher than the EF during late Danian.

Goodness of fit also showed significant differences in the distribution of both encrusting and boring barnacles on valves of different oyster species ($p<0.001$). The analysis with exact confidence intervals showed that there are significant differences for boring barnacles on *P. (Ph.) vesicularis*, *T. damboreneae*, *O. wilckensi* and *P. (Ph.) sarmientoi*. For encrusting barnacles, significant differences are on *O. wilckensi* and *C. ameghinoi* (Figs.7.4-6).

[Figure 7]

DISCUSSION

Buckeridge *et al*. (2008) considered that it is more common to find verrucids preserved as disarticulated wall plates than articulated ones. In the analyzed samples most of encrusting barnacles are preserved articulated. However, we recognized oysters with the trace *C. concentricus* in which an eroded platform was seen. Darwin (1854) mentioned this trace is produced by recent specimens of *Verruca stroemia* (Müller, 1776) and found them to be comparable to fossil material. In addition, Santos *et al*. (2005) described similar traces and assigned them to *Anellusichnus* Santos, Mayoral, and Muñiz, 2005, although this ichnogenus is produced by balanomorphs and can have more crenulated edges in later stages. This feature was not observed in the studied specimens. The recorded trace openings have the form of a slot, and the hole is narrower towards the bottom. Recent acrothoracican barnacles which belong to Lithoglyptidae Aurivillius, 1892, leave this trace. They penetrate the substrate during the larval stage (*Cypris* larvae), probably by chemical dissolution, and when they are adults, they use chitinous bristles present on the outer side of their mantle to enlarge the chamber (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* Turquier, 1967, lives in gastropods shells inhabitated by

hermit crabs, and they 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 fair-poor condition for both abrasion and fragmentation, while late Danian shells exhibited mostly good-fair condition for the same attributes. These oyster species probably are showing 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 some combination of these parameters (Kowalewski *et al*., 1995).

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

Gryphaeostrea 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 result 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 represented mostly by polychaetes on internal surfaces.

Additionally, in both ternary taphograms, the late Danian oysters *Ostrea wilckensi* and *Pycnodonte* (*Ph*.) *sarmientoi* presented mixed taphonomic grades following the

292 description of Kowalewski *et al.* (1995). For both oyster species, a high grade of
293 bioerosion and encrustation could indicate that there was no rapid burial or subaerial
294 exposure (Kowalewski *et al.*, 1995). Moreover, *O. wilckensi* is preserved mostly in life
295 position (*i.e.*, developing clusters or nests) and has a high frequency of articulation.
296 Sclerobionts are preferentially distributed on external shell surfaces indicating *in vivo*
297 colonization. Mixed taphonomic grades also correlate well with the inferred
298 depositional environments, where all oysters of Danian age were included in
299 accumulations associated with bars and tidal channels characterized by a fluctuating
300 hydrodynamic regime.
301 In this study, a preliminary examination of the taphonomic condition of Maastrichtian
302 and Danian oysters was performed. Considering that the increase in frequency of
303 occurrence of boring barnacles during the late Danian would be related to taphonomic
304 constraints more than evolutionary or paleoecology patterns, a larger sample would be
305 necessary for more accurate interpretations of the studied environments at the three
306 times intervals. Additionally, according to Parsons and Brett (1991), skeletal fragments
307 should be included in futures taphonomic studies as the fragments may be more
308 sensitive to taphonomic processes. They can provide useful and different information
309 than whole or broken shells.
310 ***Barnacles through K-Pg boundary***
311 There is a limited database about the changes over time in sclerobiotic communities,
312 and even less in boring and encrusting barnacles. However, Brett *et al.* (2012) suggested
313 that the records of Cretaceous to modern sclerobiotic communities apparently have not
314 changed drastically in diversity and abundance since the re-emergence of encrustation
315 in the Jurassic. These communities were dominated by the same sclerobionts as those in
316 the Jurassic (*e.g.*, encrusting foraminifers, serpulid worms, cheilostome bryozoans,

317 coralline algal encrusters, cementing bivalves as oysters, clionid borings and ctenostome
318 etchings) (Brett *et al.*, 2012). Barnacles are an ancient group that remains very
319 successful today, both in number of species and abundance (Newman and Abbott,
320 1980). However, it seems that across the K-Pg boundary, at least according to the
321 Northern Patagonian records, some of them reflected a decrease in the frequency of
322 occurrence in the fossil record.
323 In this sence, and focusing on K-Pg events, The first records of *Verruca* are from the
324 Santonian of Western Australia, but it reached a wide geographic distribution during the
325 late Campanian-Maastrichtian, being recorded in Europe, Western Australia
326 (Buckeridge, 1983; Buckeridge *et al*. 2008) and South America. On the other hand, the
327 earliest verrucid barnacles recorded after the K-Pg boundary were *V. punica*
328 Buckeridge, Jagt, and Speijer, 2008, from the early Danian of Tunisia, and *V. rocana*
329 from the early Danian of Argentina. Is possible to consider that during early Danian,
330 ecological factors could have affected populations of this specie being underrepresented
331 ~~and no registered~~ in the fossil record. These factors include the availability of resources
332 and also interactions between species (Paine 1969, 1984, 1994). Also taphonomic
333 conditions could disfavor the preservation of encusting barnacles. Verrucid barnacles
334 are commonly found preserved as isolated, disarticulated wall plates and rarely as
335 complete fossils (Buckeridge and Finger, 2001). The valves of Maastrichtian oysters
336 with poor preservation conditions tend to have not a good record of encrusting
337 barnacles, since the complete preservation of their plates is exceptional. Anyway, as
338 their traces are not recorded, this might suggest that either the taxon was not abundant,
339 it was a rare specie or it was not present at ~~these~~ time. Additionally, as there are
340 ~~registered~~ superficial traces made by algae and fungi (Supplementary Online
341 Information) and there are not barnacles traces, then they ~~possibly were~~ absent.

342 Taphonomic feedback ~~(~~*i.e.* biotic changes driven by live/dead interactions *sensu*
343 Kidwell and ~~Jablonsky~~ (1983) can be considered. Some marine invertebrates do not
344 settle or look for refuge in clumps of dead oysters, probably because pore waters
345 underneath the oysters are anoxic (Kidwell 1986). Moreover, early colonists could
346 inhibit later colonists by biochemical or other biotic interactions (Kidwell and
347 ~~Jablonsky,~~ 1983). Barnacles respond to stimulatory and inhibitory external signals
348 during the settling stage of their life cycle (Holmström *et al.*, 1992).
349 Possible negative effects on barnacles caused by the crisis during K-Pg also must be
350 taken into account. Buckeridge *et al.* (2008), consideredthe genus *Verruca* seems to
351 have persisted across the boundaryand have not been drastically affected~~-~~, as was the
352 case with other taxa (Macleod *et al.*, 1997; Jablonski 1998; Håkansson and Thomsen,
353 1999; Stilwell, 2003; Parma and Casadío, 2005). But the possibility of being new to the
354 region after the K-Pg boundary could also explain the low frequencies during early
355 Danian.
356 Borings made by acrothoracican cirripeds have a high richness and extensive ~~geologic~~
357 record (Seilacher, 1969). In this work, results suggest that at the K-Pg boundary
358 encrusting and boring barnacles varied their frequencies in view of the fact that the
359 preliminary analysis with exact confidence intervals showed that the OF was lower than
360 the EF during the early Danian and then, the OF was higher than the EF during late
361 Danian (Figs. 7.2-3)..
362 The preferential distribution of encrusting and boring barnacles on the species could be
363 related to many biotic and abiotic factors. For example, life habits of this oysters such as
364 clusters composed of mutually attached specimens or reclining mode of life (Stenzel
365 1971; Machalski, 1998), morphology and textures of the valves (Romero *et al.*, 2013
366 and references therein) or environmental conditions that favor the settlement of

367 barnacles larvae on the valves (Fraschetti *et al.*, 2003; Hadfield, 2011). Encrusting
368 barnacles showed preferential distribution on two late Danian oysters (*i.e. C. ameghinoi*
369 and *O. wilckensi*). Although their mode of life and morphology of shells are not the
370 same, the facies analysis indicates the same subtidal environment. On the other hand,
371 boring barnacles showed preferential distribution on Maastrichtian species (*i.e. P. (Ph.)*
372 *vesicularis* and *T. damboreneae*) and late Danian species (*i.e. O. wilckensi* and *P. (Ph.)*
373 *sarmientoi*). With exception of *O. wilckensi*, these species have solitary mode of life,
374 different morphology of shells, but the facies association indicates same inner to
375 middle-shelf or subtidal environments. However, there is no a clear pattern that explain
376 this differential distribution.
377 Barnacles are suspension feeders and their abundance could have been reasonably
378 affected by the reduction of food supply. This hypothesis is supported by other studies
379 that postulate that the collapse of primary production across the K-Pg boundary
380 correlates with the high extinction rates in organisms dependent on primary producers
381 (Zachos *et al.*, 1989; Veron, 2008; Jiang *et al.*, 2010; Van De Schootbrugge and
382 Gollner, 2013). Conversely, Sogot *et al*. (2013) questioned the extent to which this kill
383 mechanism affected suspension feeders during the K-Pg mass extinction. If the collapse
384 of primary producers hypothesis is consider valid, the scarce record of encrusting
385 barnacles during de late Maastrichtian and early Danian could show that these
386 organisms were underrepresented and that the crisis during the K-Pg interval severely
387 affected them. This situation seemed to have changed during the late Danian, as a
388 significant increase of both encrusting and boring barnacles is recorded in the analyzed
389 samples. This increase after the earliest Danian is observed in other sclerobionts
390 associated with the same oysters (*e.g.*, encrusting bryozoans, polychaetes and bivalves)
391 (Brezina, 2013), and can also be correlated with an increase in the number of species of

392 corals, mollusks, echinoids, and crabs from low latitudes, reflecting higher seawater
393 temperatures spreading southwards (Casadío *et al.*, 2005; Aguirre-Urreta *et al.*, 2008).
394 According to Erwin (2001), evolutionary opportunities open up during mass extinction
395 have disproportionate effects on species. He stated that mass extinctions appear to cause
396 a collapse of ecospace, which will be rebuilt during recovery times, but responses in
397 organisms are variable, even between species and regions. So the ecosystem dynamics
398 during post-extinction time could be complex. Some benthic communities at other
399 localities experienced considerable diversity reduction at the K-Pg boundary, showed a
400 recovery of the early Danian community, but initially retarded, and diversified quickly
401 during the late Danian (Håkansson and Thomsem, 1999). These results are coincident
402 with bryozoan species from northern Patagonia, which are highly diverse during the late
403 Danian (Brezina *et al.*, 2011).

404 **CONCLUSSIONS**

405 During early Danian *Verruca rocana*, could have been affected by ecological and
406 environmental factors~~, being underrepresented and no registered~~, but during the late
407 Danian its frequency of incrustation increased significantly.
408 Boring barnacles represented by the trace fossil *Rogerella* exhibited a decline in their
409 frequencies at the K-Pg boundary, and during the late Danian, their abundance also
410 increased considerably.
411 In an attempt to preliminarily know the taphonomic history of the shell accumulations,
412 a differential preservation was observed. Late Maastrichtian and early Danian
413 assemblages exhibited a fair-poor condition for abrasion and fragmentation, as a result
414 of reworking and short distance transport in offshore beds. On the other hand, late
415 Danian assemblages exhibited mostly good-fair condition or a mixture for both
416 attributes, reflecting rapid burial or subaerial exposure, or a hydrodynamic regime

fluctuation in the depositional environment (*e.g.*, bars and tidal channels). Frequencies of barnacles are higher during late Danian and these results could be correlated. However it would be necessary to focus a taphonomic analysis on the barnacles for more accurate interpretations.

Differences in distribution of encrusting and boring barnacles among the species of oysters also are recorded, although there is not a clear pattern that could explain this results.

An ecological explanation also can be considered. As it is observed in recent communities, biotic and abiotic conditions regulate the dynamics of populations. The hypothesis considering a collapse of primary production could explain 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 ~~been~~ affected the boring and encrusting pattern of sclerobiotic organisms, a change in barnacle abundance through the K-Pg boundary is documented. In northern Patagonia, encrusting and boring barnacles associated with oysters presented an increase in theirfrequencies during late Danian which is coincident with the increase in abundance and diversity of other benthic communities of the southern hemisphere.

ACKNOWLEDGEMENTS

This research was supported by a doctoral fellowship of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) to S.S. Brezina. We also thank N. Carmona, R. Feldmann and anonymous reviewers for constructive comments and suggestions, which improved the final version of this paper.

REFERENCES

441 Abletz, V.V. 1993. Trace fossils of Acrothoracica (Cirripedia) from the Eocene of the
442 Krivoy Rog Basin. *Paleontological Journal* 27: 73–80.
443 Aguirre-Urreta, M.B., Casadío, S., Cichowolski, M., Lazo, D.G. and Rodríguez, D.L.
444 2008. Afinidades paleobiogeográficas de los invertebrados cretácicos de la
445 Cuenca Neuquina. *Ameghiniana* 45: 591–611.
446 Aurivillius, C.W.S. 1892. *Neue Cirripeden aus dem Atlantishchen, Indischen und*
447 *Stillen Ocean.* Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar,
448 Stockholm, 3:123–134.
449 Böhm, J. 1903. *Uber Ostreen von General Roca am Río Negro.* Zeitschift der Deutsche
450 geologisches Gesellscaft, 55: 71–72.
451 Brett, C.E., Smrecak, T., Parsons Hubbard, K. and Walker, S. 2012. Marine
452 Sclerobiofacies: Encrusting and endolithic communities on shells through time
453 and space. In: J.A. Talent (Ed.), *Earth and life, global biodiversity, extinction*
454 *intervals and biogeographic perturbations through time.* Springer, 129–157.
455 Brezina, S. 2013. Estudio de las comunidades incrustantes y perforantes asociadas
456 ostras del límite Cretácico/Paleógeno, Patagonia norte. Tesis doctoral, Facultad
457 de Ciencias Exactas y Naturales, Universidad Nacional de Córdoba: 255 p.
458 Inédita.
459 Brezina, S., Taylor, P.D. and Casadío, S. 2011. The record of sclerobiotic communities
460 changes through the Cretaceous-Paleogene transition in Patagonia, Southern
461 Argentina. *Geological Society of America Annual Meeting* (Minneapolis),
462 *Abstracts with Programs* 43: 657.
463 Brezina, S.S., Romero M.V., Casadío, S. and Bremec, C. 2014. Boring polychaetes
464 associated with *Pycnodonte (Phygraea) vesicularis* (Lamarck) from the Upper
465 Cretaceous of Patagonia. A case of commensalism? *Ameghiniana* 52: 129–140.

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

Brusca, R.C. and Brusca, G.J. 2005. Invertebrados, 2º edición. In: McGraw-Hill-Interamericana (Eds.), Madrid, 1005 p.

Buckeridge, J.S., 1983. Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. *New Zealand Geological Survey Paleontological Bulletin* 50: 1–151.

Buckeridge, J.S. 2011. Taphonomy and systematics of a new late Cretaceous verrucid barnacle (Cirripedia, Thoracica) from Canterbury, New Zealand. *Palaeontology* 54: 365–372.

Buckeridge, J.S., and Finger, K.L. 2001. First record of a fossil verrucid barnacle in California— *Verruca digitali* sp. nov. (cirripedia: thoracica) from the late Miocene. *Journal of Crustacean Biology* 21: 443–449.

Buckeridge, J.S., Jagt, J.W.M. and Speijer, R.P. 2008. *Verruca punica*, a new species of verrucomorph barnacle (Crustacea, Cirripedia, Thoracica) from the lower Danian (Palaeocene) of Tunisia. *Zootaxa* 1844: 37–46.

Casadío, S. 1998. Las ostras del límite Cretácico-Paleógeno de la cuenca Neuquina (Argentina). Su importancia bioestratigráfica y paleobiogeográfica. *Ameghiniana* 35: 449–471.

Casadío, S. and Montagna, A.O. 2015. Estratigrafía de la cuenca Neuquina. In: J.J. Ponce, A.O. Montagna and N Carmona. *Geología de la cuenca Neuquina y sus sistemas petroleros. Una mirda integraora desde los afloramientos al subsuelo*. Fundación YPF and Universidad Nacional de Río Negro, Buenos Aires, p. 8–21.

Casadío, S., Griffin, M. and Parras, A. 2005. *Camptonectes* and *Plicatula* (Bivalvia, Pteriomorphia) from the Upper Maastrichtian of northern Patagonia: Palaeobiogeographic implications. *Cretaceous Research* 26: 507–524.

Concheyro, G.A. and Villa, G. 1996. Calcareous Nannofossils across the Maastrichtian-Danian of Liu Malal Section, Northern Patagonia, Argentina. *Paleopelagos* 6: 281–297.

Darwin, C.R. 1854. *A monograph on the sub-class Cirripedia, with figures of all the species. The Balanidae (or sessile cirripedes); the Verrucidae, etc., etc., etc.* Ray Society, London, 684 p.

del Río, C.J., Stilwell, J.D., Concheyro, A. and Martínez, S.A. 2007. Paleontology of the Danian Cerros Bayos section (La Pampa Province, Argentina). *Alcheringa* 31: 241–269.

del Río, C.J., Concheyro, A. and Martínez S.A. 2011. The Maastrichtian–Danian at General Roca (Patagonia, Argentina): A reappraisal of the chronostratigraphy and biostratigraphy of a type locality. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 259: 129–156.

Dessanti, R.N. 1973. Descripción geológica de la Hoja 29b Bardas Blancas (Provincia de Mendoza). *Boletín del Servicio Nacional Minero Geológico* 139: 1–70.

Dessanti, R.N. 1978. Descripción geológica de la Hoja 28b Malargüe, provincia de Mendoza. *Boletín del Servicio Nacional Minero* 149: 1–50.

Erwin, D.H. 2001. Lessons from the past: biotic recoveries from mass extinction. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5399–5403.

512 Farrapeira, C.M.R. 2010. Shallow water Cirripedia of the northeastern coast of Brazil:
513 The impact of life history and invasion on biogeography *Journal of*
514 *Experimental Marine Biology and Ecology* 392: 210–219.
515 Flessa, K.W., Cutler, A.H. and Meldahl, K.H. 1993. Time and taphonomy: quantitative
516 estimates of time-averaging and stratigraphic disorder in a shallow marine
517 habitat. *Paleobiology* 19: 266–286.
518 Foster, B.A. and Buckeridge, J.S. 1987. Barnacle Palaeontology, In: A.J. Southward
519 (Ed.), *Crustacean Issues 5: Barnacle Biology*. A.A. Balkema Publishers,
520 Rotterdam, p. 43–62.
521 Fraschetti, S., Giangrande, A., Terlizzi, A. y Boero, F. 2003. Pre- and post-settlement
522 events in benthic community dynamics. *Oceanologica Acta* 25: 285-295.
523 Glenner, H. and Hasgaard, M.B. 2006. Phylogeny and evolution of life history strategies
524 of the Parasitic Barnacles (Crustacea, Cirripedia, Rhizocephala). *Molecular*
525 *Phylogenetics and Evolution* 41: 528–538.
526 Griffin, M., Casadío, S. and Parras, A. 2005. Maastrichtian and Danian species of
527 Turkostreini (Ostreidae, Crassostreinae) from the Neuquén Basin, Argentina.
528 *Ameghiniana* 42: 257–276.
529 Groeber, P. 1947. Observaciones geológicas a lo largo del meridiano 70°. *Revista de la*
530 *Asociación Geológica Argentina*, 2: 409–433.
531 Hadfield, M.G. 2011. Biofilms and Marine Invertebrate Larvae: What bacteria produce
532 that larvae use to choose settlement sites. *Annual Review of Marine Science*
533 3:453–70.
534 Håkansson, E. and Thomsen, E. 1999. Benthic extinction and recovery patterns at the
535 K-T boundary in shallow water carbonates, Denmark. *Palaeogeography,*
536 *Palaeoclimatology, Palaeoecology* 154: 67–85.

537 Holström, C., Rittschof, D., and Kjelleberg, S. 1992. Inhibition of settlement by larvae
538 of *Balanus amphitrite* and *Ciona intestinalis* by a surface-colonizing marine
539 bacterium. A*pplied and Environmental Microbiology* 58: 2111–2115.
540 Howell, J.A., Schwarz, E., Spalletti, L.A. and Veiga, G.D. 2005. The Neuquén Basin:
541 an overview. In: Veiga, G.D., Spalletti, L.A., Howell, J.A. y Schwarz, E. (Eds.),
542 *The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin*
543 *dynamics*. Geological Society Special Publications, London 252: 1–14.
544 Ihering, H. Von. 1902. Historia de las ostras argentinas. *Anales del Museo Nacional de*
545 *Historia Natural, serie 2da* 7: 109–125.
546 Ihering, H.V. 1903. Les Mollusques des Terrains Crétaciques Supérieurs de l'Argentine
547 Orientale. *Anales del Museo Nacional de Buenos Aires, serie 3ra* 2: 193–229.
548 Ihering, H. Von. 1907. Les Mollusques fossils du Tertiaire et du Crétacé supérieur
549 del´Argentine. *Anales del Museo Nacional de Buenos Aires, serie 3ra* 7: 1–611.
550 Jablonski, D. 1998. Geographic Variation in the Molluscan Recovery from the End-
551 Cretaceous Extinction. *Science* 279: 1327–1330.
552 Jiang, S., Bralower, T.J., Patzkowsky, M.E., Kump, LR. and Schueth, J.D. 2010.
553 Geographic controls on nannoplankton extinction across the
554 Cretaceous/Palaeogene boundary. *Nature Geoscience* 3: 280–285.
555 Kidwell, S.M. 1986. Taphonomic feedback in Miocene assemblages; Testing the role of
556 dead hardparts in benthic communities. *Palaios*, 1: 239–255.
557 Kidwell, S.M., and Jablonski, D. 1983. Taphonomic Feedback: ecological consequences
558 of shell accumulation. In: M.J.S Tevesz and P.L. McCall (Eds.), *Biotic*
559 *interactions in Recent and fossil Benthic Communities*, Plenum Press, New
560 York, p. 195–248.

561 Kolbasov, G.A. and Newman, W.A. 2005. Revision of the Lithoglyptidae sensu
562 Tomlinson, 1969 and Lithoglyptes Aurivillius, 1892 (Cirripedia,
563 Acrothoracica,), including a new species from Bermuda. *Zootaxa* 1013: 35–64.
564 Kowalewski, M., Flessa, K.W. and Aggen, J.A. 1994. Taphofacies analysis of Recent
565 shelly cheniers (beach ridges), northestern Baja California, Mexico. *Facies* 31:
566 209–242.
567 Kowalewski, M., Flessa, K.W. and Hallman, D.P. 1995. Ternary taphograms: triangular
568 diagrams applied to taphonomic analysis. *Palaios* 10: 478–483.
569 Lamarck, J.P. 1806. Memoire sur les fossiles des environs de Paris. *Annales du Museum*
570 *d'Histoire naturelle de Paris* 8: 156–166.
571 Lambers, P. and Boekschoten, G.J. 1986. On fossil and recent borings produced by
572 acrothoracic cirripeds. *Geologie en Mijnbouw* 65: 257–268.
573 Legarreta, L., Kokogián, D.A. and Boggetti, D.A. 1989. Depositional sequences of the
574 Malargüe Group (Upper Cretaceous-lower Tertiary), Neuquén Basin, Argentina.
575 *Cretaceous Research* 10: 337-356.
576 Legarreta, L., Uliana, M.A., Larotonda, C.A. and Meconi, G.R. 1993. Approaches to
577 nonmarine sequence stratigraphy-theoretical models and examples from
578 Argentine basins. In: B. Schard and B. Doligez (Eds.), *Subsurface reservoir*
579 *characterization from outcrop observations*. Paris, p. 125-143.
580 Machalski, M. 1998. Oyster life positions and shell beds from the Upper Jurassic of
581 Poland. *Acta Palaeontologica Polonica* 43: 609–634.
582 Macleod, N., Rawson, P.F., Forey, P.L., Banner, F.T., Boundagher-Fadel, M.K., Bown,
583 P.R., Burnett, J.A., Chambers, P., Culver, S., Evans, S.E., Jeffery, C. Kaminski,
584 M.A., Lord, A.R., Milner, A.C., Morris, N., Owen, E., Rosen, B.R., Smith, A.B.,

585 Taylor, P.D., Urquhart, E. y Young, J.R. 1997. The Cretaceous–Tertiary biotic
586 transition. *Journal of the Geological Society* 154: 265–292.
587 Malumián, N. and Caramés, A. 1995. El Daniano marino de Patagonia (Argentina):
588 paleobiogeografía de los foraminíferos bentónicos. *Asociación Paleontológica*
589 *Argentina, Publicación Especial* 3: 83–105.
590 Mauna, C., S. Casadío, A. Parras, and M. Pascual. 2005. Frequency and distribution of
591 Lithophaga (Mytilidae) perforations in recent and fossil oysters: Taphonomic
592 and paleobiological implications. *Ameghiniana* 42: 395–405.
593 Müller, O.F. 1776. *Zoologica Danicae Prodromus seu Animalium Daniae et Norvegiae*
594 *indigenarum characters, nomine, et synonyma imprimis popularium.* Havniae.
595 XXXII, 274 p.
596 Newman, W.A. 1971. A deep-sea burrowing barnacle (Cirripedia: Acrothoracica) from
597 Bermuda. *Journal of Zoology* 165: 423–429.
598 Newman, W.A. 1987. Evolution of cirripedes and their major groups. In: A.J.
599 Southward (Ed.), *Barnacle Biology*. Crustacean Issues, Rotterdam, Balkema,
600 496 p.
601 Newman, W.A. and Abbott, D.P. 1980. Cirripedia. In: R.H. Morris, D.P. Abbott and
602 E.C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University
603 Press, Stanford, p. 504–535.
604 Paine, R.T., 1969. A note on trophic complexity and community stability. *The American*
605 *Naturalist* 103: 91-93.
606 Paine, R.T. 1984. Ecological determinism in the competition for space. *Ecology* 65:
607 1339-1348.
608 Paine, R.T. 1994. Marine rocky shores and community ecology: an experimentalist's
609 perspective. *Excellence in Ecology* 4: 1-152

610 Papú O.H., Prámparo M.B., Náñez. C. and Concheyro, A. 1999. Palinología y
611 micropaleontología de la formación Jagüel (Maastrichtiano-Daniano), perfil
612 Opaso, cuenca Neuquina, Argentina. Servicio Geológico Minero Argentino,
613 Anales 33: 17–31.
614 Parma S.G. and Casadío, S. 2005. Upper Cretaceous–Paleocene echinoids from
615 Northern Patagonia, Argentina. *Journal of Paleontology* 79: 1072–1087.
616 Parras, A. and Casadío, S. 1999. Paleogeografía del sector septentrional de la cuenca
617 Neuquina durante el intervalo Campaniano-Daniano. *7º Jornadas Pampeanas de*
618 *Ciencias Naturales, Actas*: 261–268.
619 Parras, A. and Casadío, S. 2006. The Oyster Crassostrea? hatchery (Ortmann, 1897), a
620 physical ecosystem engineer from the upper Oligocene–lower Miocene of
621 Patagonia, Southern Argentina. *Palaios* 21: 168–186.
622 Parras, A., Casadío, S. and Pires, M. 1998. Secuencias depositacionales del Grupo
623 Malargüe (límite Cretácico-Paleógeno), sur de la provincia de Mendoza,
624 Argentina. In: Casadío, S. (Ed.), *Paleógeno de América del Sur y de la*
625 *Península Antártica, Publicación Especial de la Asociación Paleontológica*
626 *Argentina* 5: 61–69.
627 Parsons, K.M. and Brett, C.E. 1991. Taphonomic processes and biases in modern
628 marine environments: an actualistic perspective of fossil assemblage
629 preservation. In: S.K Donovan (Ed.), *The processes of fossilization.* Columbia
630 University Press, New York, p. 22–65.
631 Pitombo, F.B. 2010. Cirripedia. In: V. Häusserman and G. Försterra (Eds.), *Marine*
632 *benthic fauna of Chilean Patagonia.* Fundación Huinay, Santiago, p. 599–622.

633 Rodriguez, J. and Gutschick, R.C. 1977. Barnacle borings in live and dead host from the
634 Lousiana limestone (Famennian) of Missouri. *Journal of Paleontology* 51: 718–
635 724.
636 Romero, M.V., Brezina, S.S., Hernández, D., Casadío, S., and Bremec, C. 2013.
637 Differential Settlement of Associated Species on Ostrea puelchana d'Orbigny,
638 1842 (Ostreidae) in Patagonia (Argentina). *American Malacological Bulletin*,
639 31: 311–320.
640 Saint-Seine, R. de. 1951. *Un Cirripede acrothoracique du Cretace: Rogerella*
641 *lecointrei, n.g., n.sp.* C.R. Séances de l'Académie des Sciences 233: 1015–1053.
642 Santos, A., Mayoral E. and Muñiz, F. 2005. Bioerosion scars of acorn barnacles from
643 the southwestern Iberian Peninsula, Upper Neogene. *Rivista Italiana di*
644 *Paleontologia e Stratigrafia* 111: 181–189.
645 Schneider-Storz, B., Nebelsick, J.H., Wehrmann, A. and Federolf, C.M.J. 2008.
646 Comparative taphonomy of three bivalve species from a mass shell
647 accumulation in the intertidal regime of North Sea tidal flats. *Facies* 54: 461–
648 478.
649 Seilacher, A. 1969. Paleoecology of Boring Barnacles. *American Zoologist* 9: 705–719.
650 Sogot, C.E., Harper, E.M and Taylor, P.D. 2013. Biogeographical and ecological
651 patterns in bryozoans across the Cretaceous-Palegene boundary: Implications for
652 the phytoplankton collapse hypothesis. *Geology* 41: 631–634.
653 Steinmann, G. 1921. *Anhang. Über eine Verruca von Roca*. In: O. Wilckens (Ed.),
654 *Beiträge zur Paläontologie von Patagonien, mit einem Beitrag von G.*
655 *Steinmann.* Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 1: 4–5.

Stenzel, H.B. 1971. Oysters. In: R.C. Moore and C. Teichert (Eds.), *Treatise on Invertebrate Paleontology (N) Mollusca 6, Bivalvia 3*, University of Kansas Printing Service, Lawrence, p. 953–1224.

Stilwell, J.D. 2003. Patterns of biodiversity and faunal rebound following the K–T boundary extinction event in Austral Palaeocene molluscan faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195: 319–356.

Taylor, P.D. and Wilson, M.A. 2002. A new terminology for marine organisms inhabiting hard substrates. *Palaios* 17: 522–525.

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

Turquier, Y., 1967. Le développement larvaire de Trypetesa nassarioides Turquier, Cirripéde Acrothoracique. *Archives de zoologie expérimentale et générale* 108: 33–47.

.

Van Syoc, R., 2009. Barnacles. In: I.S. Wehrtmann, and J. Cortés (Eds.), *Marine Biodiversity of Costa Rica, Central America.* Springer, New York, p. 283–289.

Van de Schootbrugge, B. and Gollner, S. 2013. Altered primary production during mass-extinction events. In: A.M. Bush, S.B. Pruss, and J.L. Payne (Eds.), *Ecosystem Paleobiology and Geobiology*, The Paleontological Society Papers, Denver, 19:1–27.

Veron, J.E.N. 2008. Mass extinctions and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs* 27:459–472.

Withers, T.H. 1914: A remarkable new cirripede from the Chalk of Surrey and Hertfordshire. *Proceedings of the Zoological Society of London* 84 945–953.

Withers, T.H. 1935: *Catalog of fossil Cirripedia in the Department of Geology of the British Museum. Cretaceous.* British Museum, London 2: 325–326.

Zachos, J.C., Arthur, M.A., and Dean, W.E. 1989. Geochemical Evidence for Suppression of Pelagic Marine Productivity at the Cretaceous/Tertiary Boundary. *Nature* 337: 61–64.

Zar, J.H. 1999. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, 663 p.

Zuschin, M., Stachowitsch, M. and Stanton, R.J. 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth-Science Reviews* 63: 33–82.

Figure captions

Figure 1. 1, map of Argentina. **2,** map showing the study area. Black symbols indicate the localities where oyster were collected, and the dotted line indicate the Neuquen 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.

Figure 2. Late Maastrichtian oysters. ***Pycnodonte (Phygraea) vesicularis***, Jagüel Formation, Bajada del Jagüel, Neuquén. **1-2**, Left valve (**MPCN-PI** 803.59). **1**, exterior; **2**, interior. **3-4**, Right valve (**MPCN-PI** 803.34). **3**, exterior; **4**, interior. ***Turkostrea damboreneae***. Roca Formation, Cerro Butaló, Mendoza. **5-6**, Left valve (**GHUNLPam 10625**). **5**, exterior; **6**, interior. **7-8**, Right valve (**GHUNLPam** 15976). **7**, exterior; **8**, interior. ***Amphidonte mendozana***. Roca Formation, Huantraico, Neuquén. **9-10**, Left valve (**MPCN-PI** 808.77). **9**, exterior; **10**, interior. **11-12**, Right valve (**MPCN-PI** 808.80). **11**, exterior; **12**, interior.

Figure 3. Early Danian oysters. ***Gryphaeostrea callophyla***. Roca Formation, General Roca, Río Negro. **1-2**, Left valve (**MPCN**-PI 805.54). **1**, exterior; **2**, interior. **3-4**, Right valve (**MPCN**-PI 805.46). **3**, exterior; **4**, interior. ***Pycnodonte (Phygraea) burckhardti***. Roca Formation, General Roca, Río Negro. **5-6**, Left valve (**MPCN**-PI 804.7). **5**, exterior; **6**, interior. **7-8**, Right valve (**MPCN**-PI 804.15). **7**, exterior; **8**, interior. ***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.

Figure 4. Late Danian oysters. ***Ostrea wilckensi***. Roca Formation, General Roca, Río Negro. **1-2**, Left valve (**MPCN**-PI 802.29). **1**, exterior; **2**, interior. **3-4**, Right valve (MPCN 802.61). **3**, exterior; **4**, interior. *Pycnodonte (Phygraea) sarmientoi*. Roca Formation, Casa de Piedra, La Pampa. **5-6**, Left valve (**MPCN**-PI 801.72). **5**, exterior; **6**, interior. **7-8**, Right valve (**MPCN**-PI 801.78). **7**, exterior; **8**, interior. ***Cubitostrea ameghinoi***. Roca Formation, Bajada del Jagüel, Neuquén. **9-10**, Left valve (**MPCN**-PI 806.16). **9**, exterior; **10**, interior. **11-12**, Right vlave (**MPCN**-PI 806.25). **11**, exterior; **12**, interior.

Figure 5. ***Verruca rocana*** Steinmann, 1921. **1**, several specimens with their traces (*Centrichnus* Bromley and Martinell, 1991) on shells of *P. (Ph.) sarmientoi*, 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. ***Rogerella*** De Saint-Seine, 1951**. 4**, an overview of borings with elliptical contour and distal portion elongated and **5**, detail of one boring with its slightly curved distal end on *C. ameghinoi*,

730 Danian, Roca Formation, Cerros Bayos, La Pampa, **GHUNLPam** 25375. **6**, drop-
731 shaped borings, with conical proximal portion on *T. damboreneae*, Maastrichtian, Roca
732 Formation, Cerro Butaló, Mendoza, **GHUNLPam** 10492. Scale bars= 1 mm.
733 **Figure 6.** Ternary taphograms for nine oyster species showing variations among them
734 for abrasion and fragmentation. Some species are represented in more than one locality.
735 **Figure 7. 1,** Frequencies of occurrence of oyster shells from different ages encrusted or
736 bored by barnacles. **2,** Differential distribution of barnacles through time. Note that
737 there is a significant difference between expected frequency (EF) and observed
738 frequency (OF) of barnacles during the late Danian. **3-6**, Differential distribution of
739 barnacles on oyster species. Note that significant differences between expected
740 frequencies (EF) and observed frequencies (OF) of barnacles are indicated by (*). Error
741 bars represent confidence intervals.

TABLE 1. ~~Species of oysters~~ studied and relevant information

~~Species of oysters~~	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 parautochtonous accumulations. Dense packing, good size-selection, convex-up valves, poor 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, Casadío and Parras, 2005	*Cerro Butaló (Mendoza) Ranquil Có (Mendoza)*	*Roca Fm.*	*late Maastrichtian*	Valves grouped in parautochthonous accumulations. Dispersed packing, good size-selection, chaotic orientation, good disarticulation and por fragmentation.	Valves are included in mudstones. Facies association indicates inner to middle-shelf environments (Jagüel Formation) or shallow subtidal environments (Roca Formation).
Pycnodonte (Phygraea) burckhardti (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, poor 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, poor disarticulation and moderate fragmentation.	Valves are included in mudstones. Facies association indicates inner to middle-shelf environments.
Turkostrea argentina Griffin, Casadío and	*Liu Malal (Mendoza)*	*Roca Fm.*	*early Danian*	Valves grouped in parautochthonous accumulations. Dispersed packing, good	Valves are included in mudstones. Facies association indicates shallow

Parras, 2005				size-selection, chaotic orientation, good disarticulation and poor fragmentation.	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, Good disarticulation and moderate fragmentation.	Valves included in massive wackstones. Facies association indicates shallow subtidal environments.
Ostrea wilckensi Ihering 1907	*Gral. Roca (Río Negro)*	*Roca Fm.*	*late Danian*	Valves, grouped in nests or in parautochtonous accumulations. Dense packing, poor size-selection, associated in nests, poor disarticulation and fragmentation.	Valves included in massive grainstones. Facies association indicates shallow subtidal environments.
Pycnodonte (Phygraea) sarmientoi Casadío, 1998	*Casa de Piedra (La Pampa)*	*Roca Fm.*	*late Danian*	Valves grouped in parautochthonous or allochthonous accumulations. Dense packing, poor size-selection, chaotic orientation, good disarticulation and fragmentation.	Valves included in massive packstones. Facies association indicates shallow subtidal environments.

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

Species of oysters	*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.) burckhardti	*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.) sarmientoi	*NP4*	*late Danian*	*94*	*31*	*21*
C. ameghinoi	*NP4*	*late Danian*	*249*	*19*	*34*
Total			*1.174*	*96*	*88*

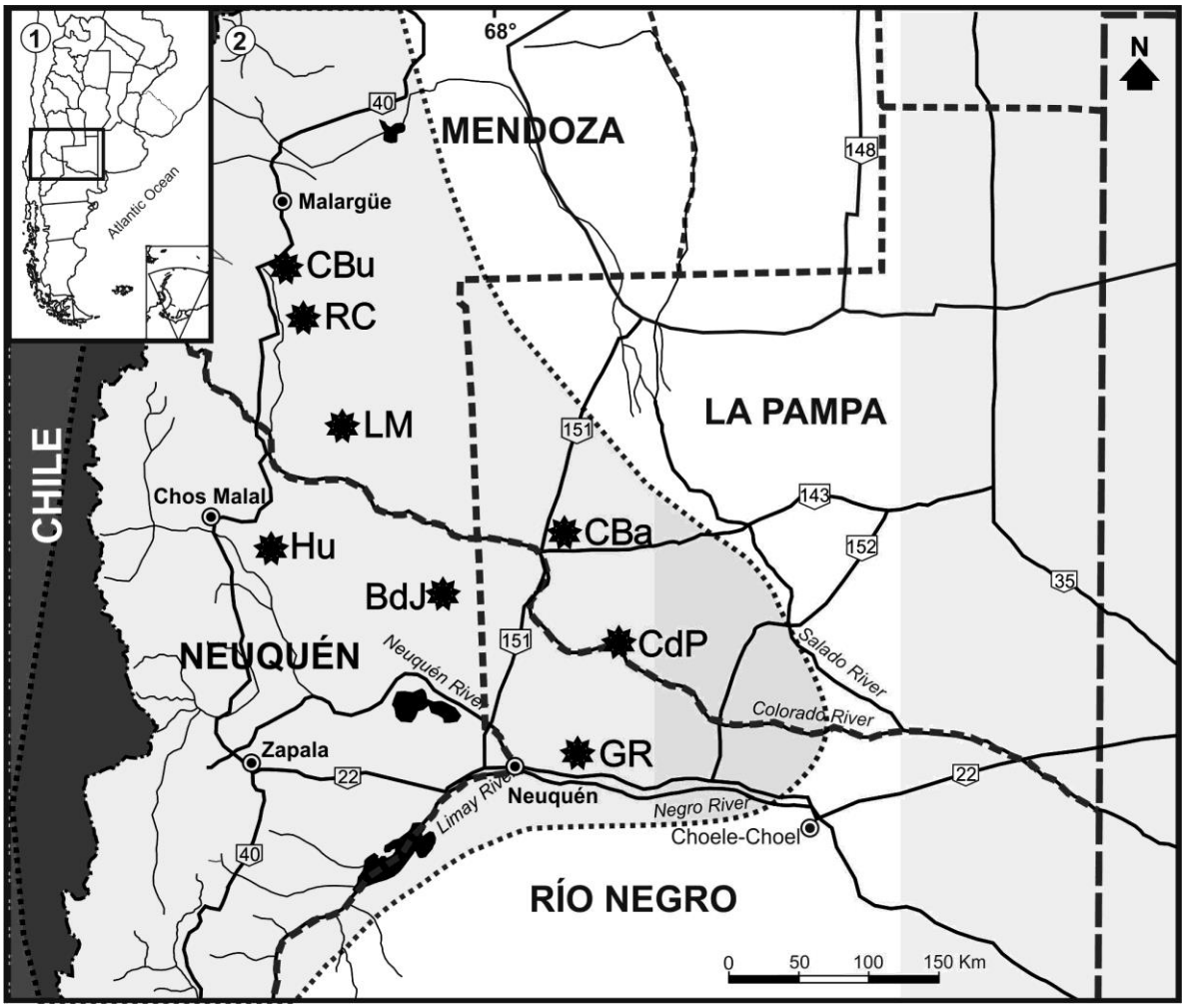
1
2
Atlantic Ocean
68°
N
40
MENDOZA
148
Malargüe
CBu
RC
LM
LA PAMPA
151
CHILE
Chos Malal
143
Hu
CBa
152
BdJ
35
NEUQUÉN
Neuquén River
151
CdP
Salado River
Colorado River
Zapala
22
GR
22
Neuquén
Limay River
Negro River
Choele-Choel
40
RÍO NEGRO
0 50 100 150 Km

Figure 1

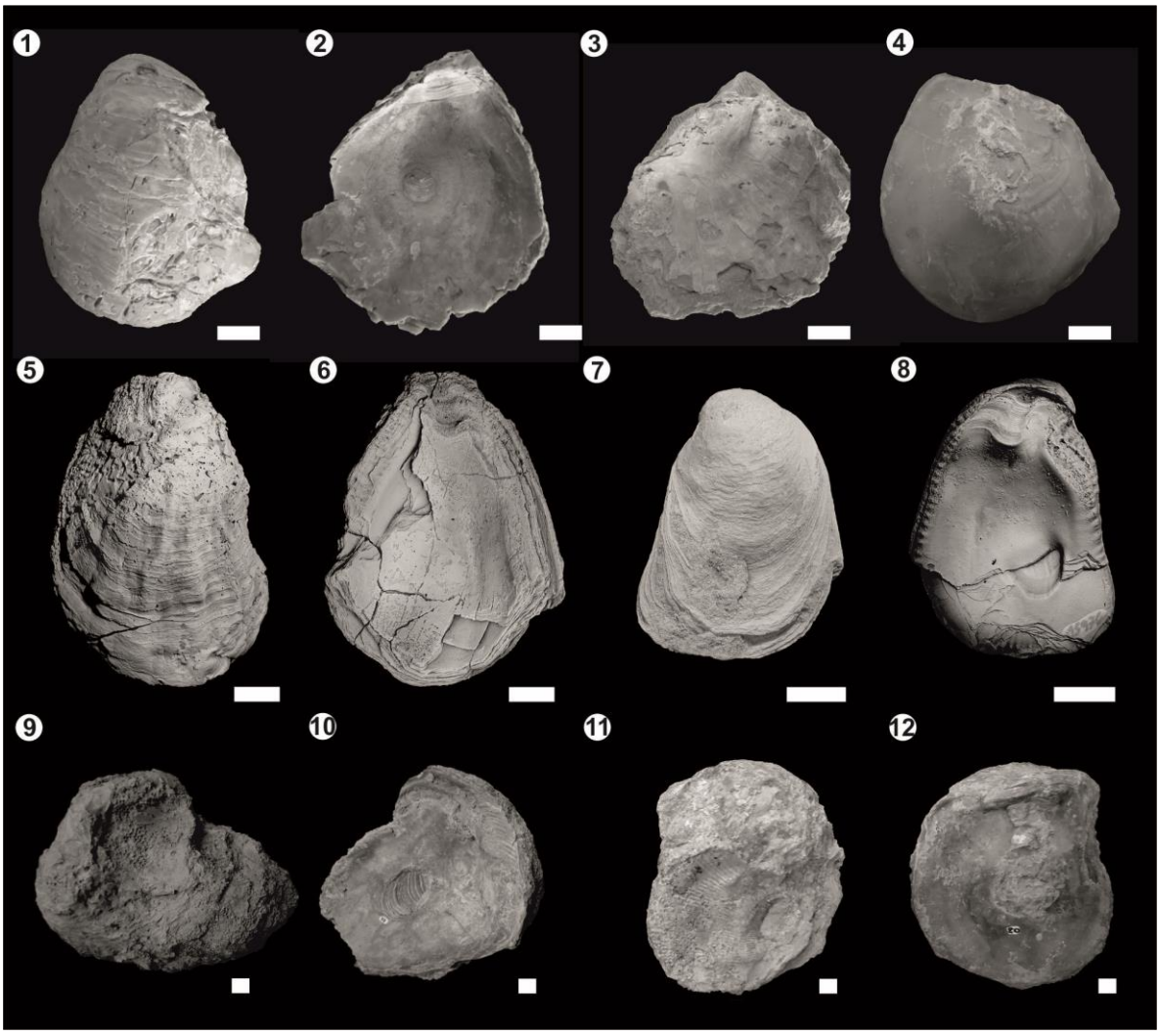

Figure 2

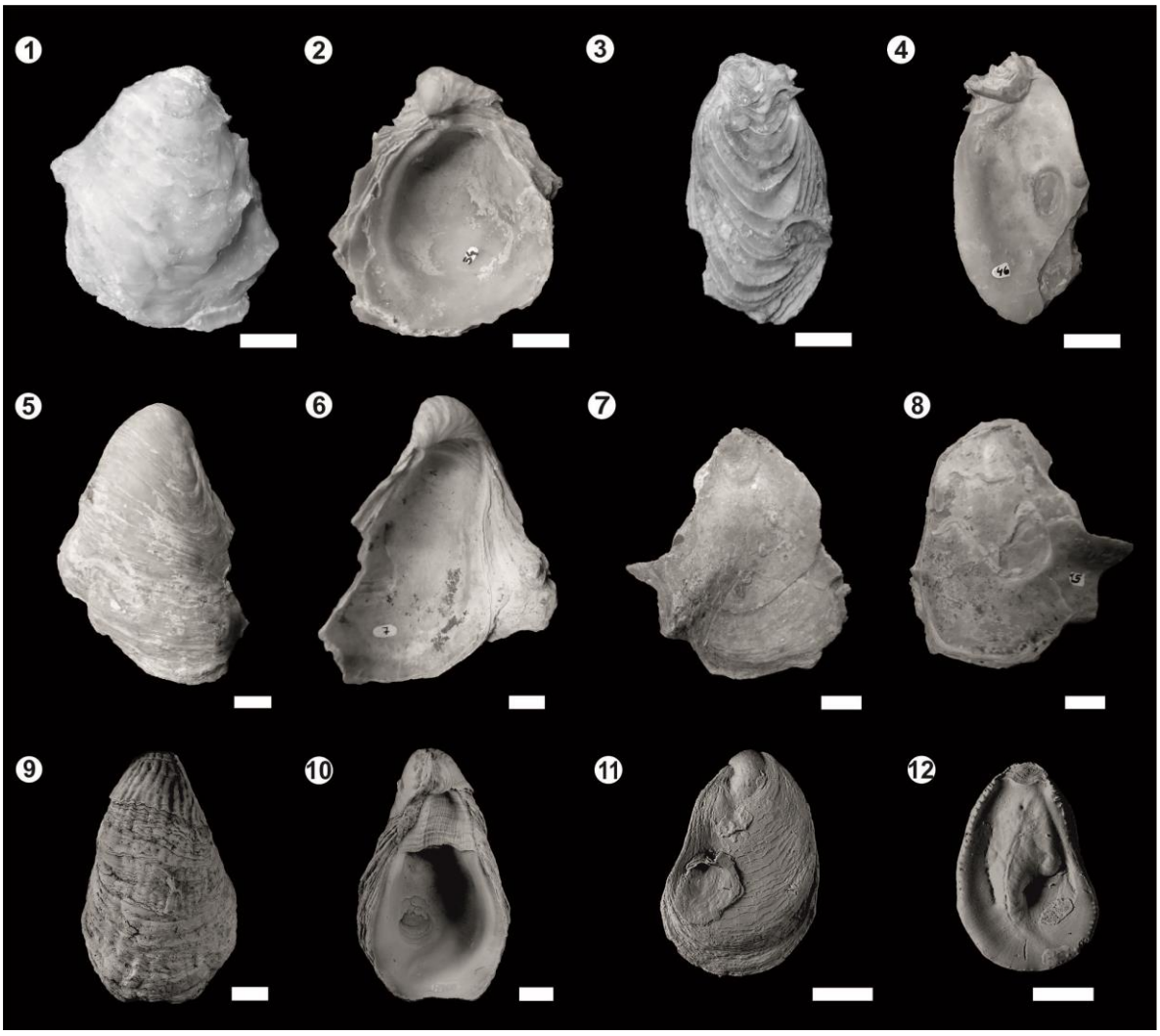

Figure 3

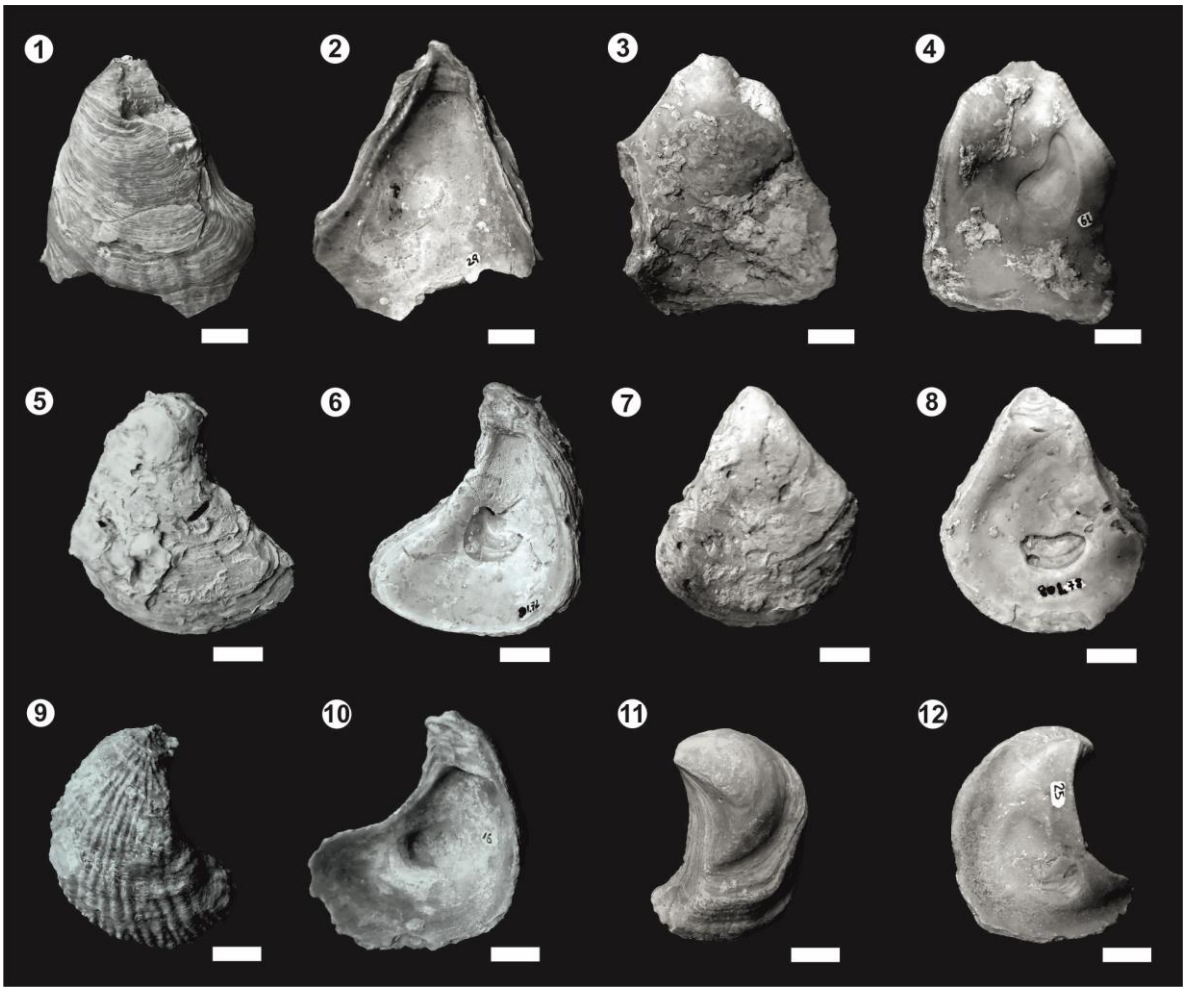

Figure 4

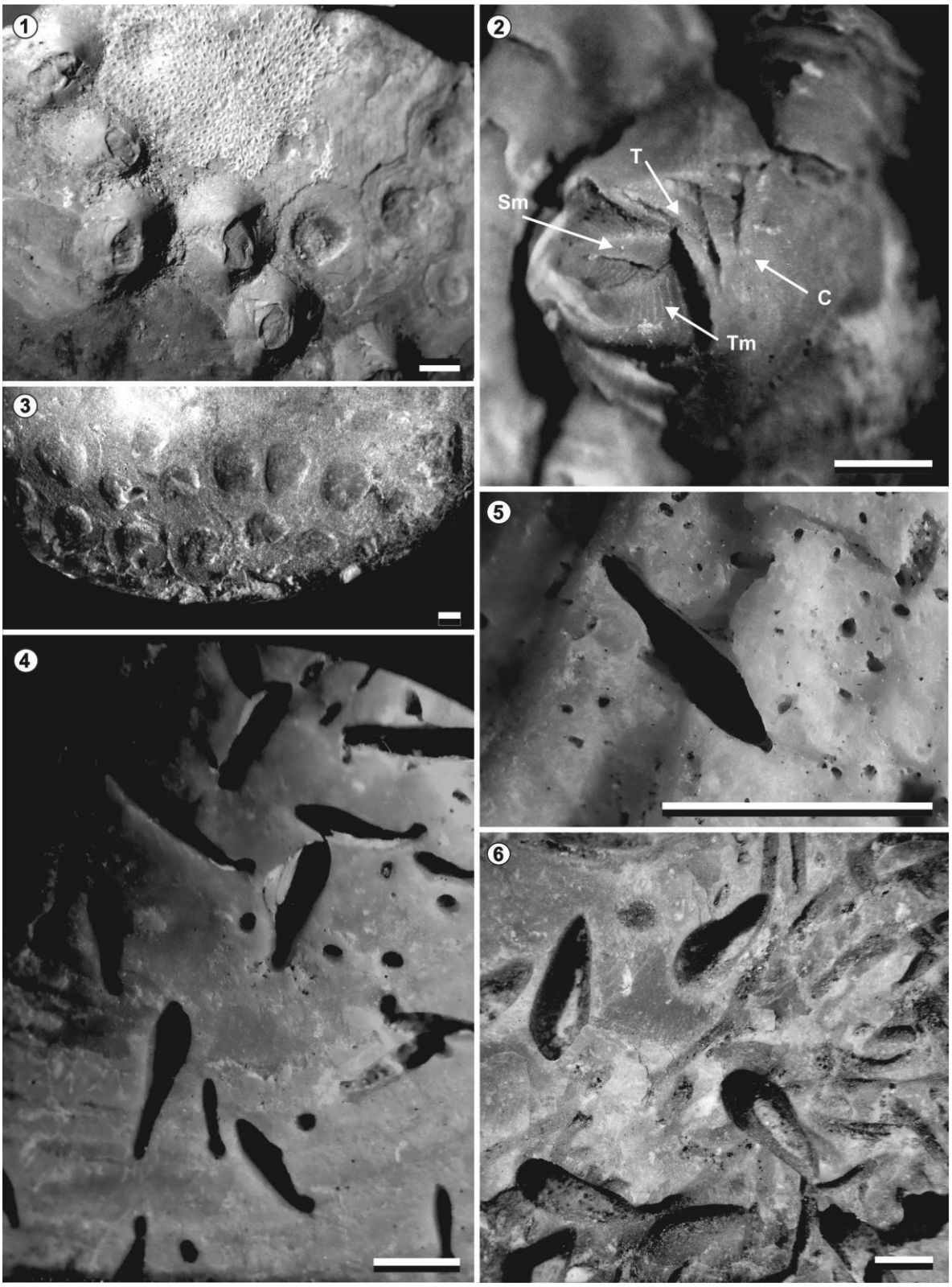

Figure 5

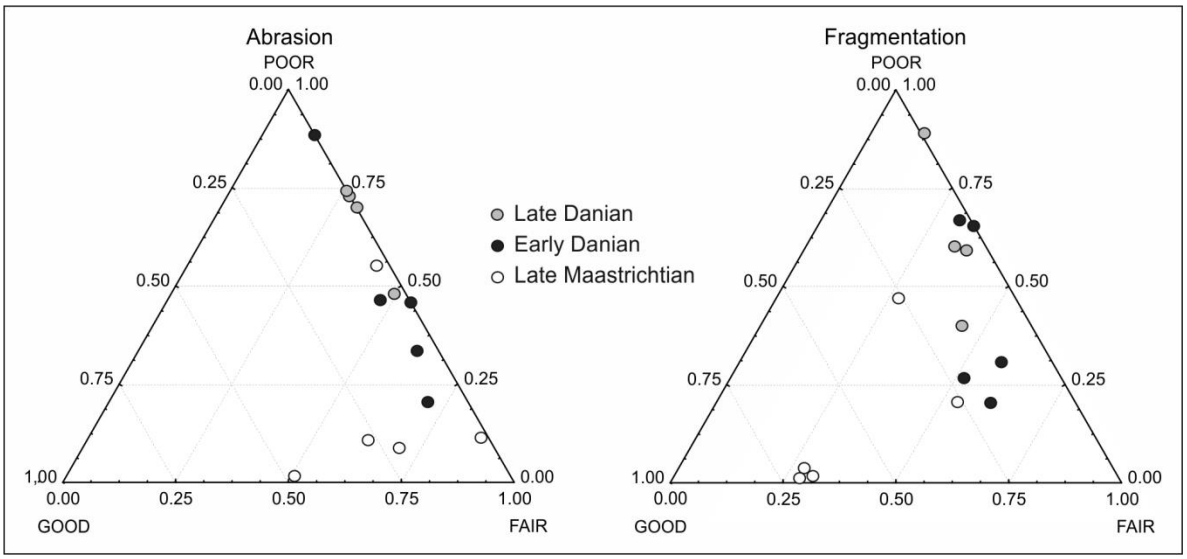
Abrasion
POOR
0.00 1.00
0.25
0.75
0.50
0.50
0.75
0.25
1,00
0.00
0.00 0.25 0.50 0.75 1.00
GOOD
FAIR
Late Danian
Early Danian
Late Maastrichtian
Fragmentation
POOR
0.00 1.00
0.25
0.75
0.50
0.50
0.75
0.25
1.00
0.00
0.00 0.25 0.50 0.75 1.00
GOOD
FAIR

Figure 6

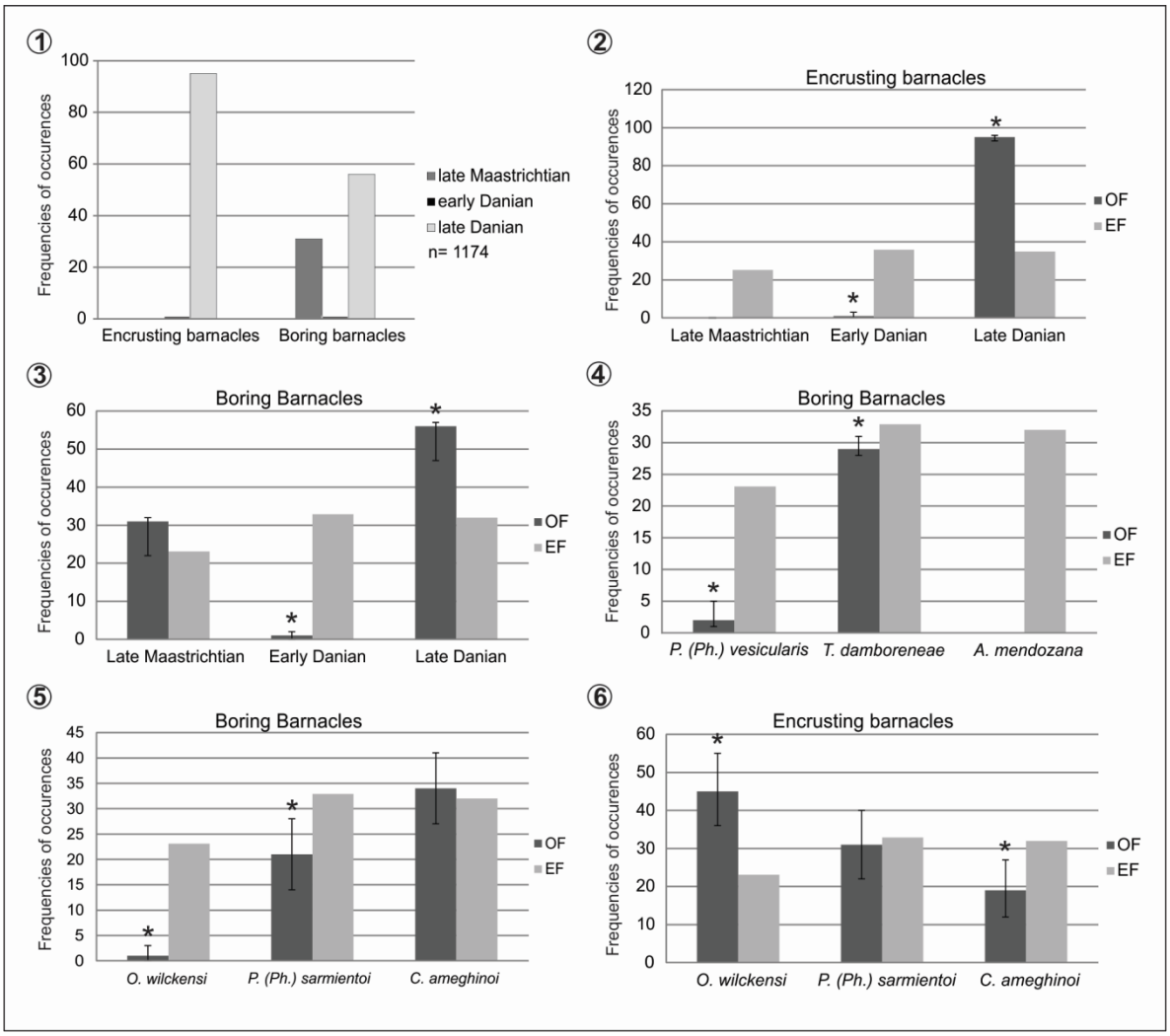
①
Frequencies of occurences
late Maastrichtian
early Danian
late Danian
n= 1174
Encrusting barnacles
Boring barnacles
②
Encrusting barnacles
Frequencies of occurences
OF
EF
Late Maastrichtian
Early Danian
Late Danian
③
Boring Barnacles
Frequencies of occurences
OF
EF
Late Maastrichtian
Early Danian
Late Danian
④
Boring Barnacles
Frequencies of occurences
OF
EF
P. (Ph.) vesicularis
T. damboreneae
A. mendozana
⑤
Boring Barnacles
Frequencies of occurences
OF
EF
O. wilckensi
P. (Ph.) sarmientoi
C. ameghinoi
⑥
Encrusting barnacles
Frequencies of occurences
OF
EF
O. wilckensi
P. (Ph.) sarmientoi
C. ameghinoi

Figure 7